Conservation of raptors and vultures in Botswana: with a focus on lappet-faced vultures *Torgos tracheliotos*

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Declaration

This thesis reports original research that I conducted under the auspices of the FitzPatrick Institute, University of Cape Town. I declare that all of the work in this thesis, save for that which is properly acknowledged, is my own both in conception and execution. The work was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and with the approval of the Animal Ethics Committee. This work has not been submitted in any form for a degree at another university.

This thesis has been submitted to the Turnitin Module and I confirm that any issues resulting from the report have been discussed and resolved with my supervisor.

Signed by candidate

Signed: Rebecca A. Garbett Date: 13th July 2018

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Thesis abstract

Many raptor species are in steep decline across Africa. Botswana is regionally important for many of these species, including vultures, yet information on most raptors in this area is lacking. Along with the rest of the region, Botswana has seen a rise in poisoning incidences which have decimated vulture populations and threaten other scavenging raptor species. As a result, seven out of the nine sub-Saharan species of vulture are now at risk of extinction. The lappet-faced vulture *Torgos tracheliotos* exists at very low densities in comparison with most other African vultures and in 2015 was up-listed to 'Endangered' by the IUCN because of its recent rapid decline. Although it is one of the most commonly seen vultures in Botswana and is widespread across the continent, very little is currently known about its ecology. This thesis aims to provide information on how raptors and particularly vultures are faring in Botswana, the possible threats that they face in the region and how we can use ecological information to alleviate these threats and better protect these species.

I repeated transect surveys of raptors in northern Botswana from 20 years ago to investigate changes in abundance of species that were included in the original surveys. I used data for 29 raptor species to compare abundance between the two surveys and found that 14 species (48%) had experienced significant declines of between 37% and 97%, and that overall, 18 species had declined by >50%; three of which were vulture species. When I compared the overall trend between the two surveys, I found a 40% decline in total abundance of all raptors. Only three species (all eagles) showed significant increases in abundance, but these were small (6-15%). I then went on to explore changes in abundance inside and outside of protected areas. In contrast to what I expected, I found that only two species showed significantly different trends (both eagles) inside vs outside of protected areas. The bateleur eagle *Terathopius ecaudatus* declined less inside protected areas than outside of them, whereas the brown snake eagle *Circaetus cinereus* showed large increases outside of protected areas but remained stable within them. These findings suggest that Botswana raptor populations are declining in-line with global raptor populations and that vultures may be equally at risk in Botswana as in other parts of Africa. Declines were indiscriminate and spanned broad species groups, all with different life histories and ecological traits. Protected areas do not appear to be buffering declines for most raptor species, which suggests that drivers of decline may be numerous and acting in equal measure inside and outside of these areas.

The demise of some global raptor species has been associated with toxicity caused by the ingestion of heavy metals in food sources. Lead (Pb) toxicity in particular, can be a pertinent threat to scavenging raptors which feed on carcasses that may contain leftover Pb ammunition fragments from hunting. Elevated Pb levels caused by the ingestion of Pb fragments from hunting ammunition are of considerable concern to many species of scavenging birds around the world. The importance of Pb for scavenging raptors in Africa however remains under-studied, even though recreational hunting is rife across the continent. Furthermore, leftovers from hunted animals (gut piles) on hunting farms could represent an important but dangerous food source for African vultures. I therefore explored the association between blood Pb levels (BLLs) of the critically endangered African white-backed vulture *Gyps africanus* and hunting activity in Botswana. From 566 individuals tested, around 33% had elevated BLLs above levels considered as background exposure. Higher BLLs were associated with samples taken inside of the hunting season and from within hunting areas. Additionally, there was a significant interaction between hunting season and areas, with Pb levels declining more steeply between hunting and non-hunting seasons within hunting areas than outside them. Thus, the results are consistent with the suggestion that elevated BLLs in African white-backed vultures are associated with recreational hunting. Pb is known to be highly toxic to scavenging birds, thus it is recommended that Pb ammunition in Botswana is phased out as quickly as possible to help protect this rapidly declining group of birds.

In order to address the protection of declining species, we need fundamental knowledge on their movement behaviours and how they utilise their environment. To assess how widely vultures in Botswana range and how they use protected areas, I used GPS tracking data from 14 adult lappet-faced vultures captured and GPS-tagged at different geographic locations in Botswana during 2012-2017. I compared the ranging behaviours of breeding and non-breeding birds across the breeding and non-breeding seasons and found that breeding birds had vastly smaller ranges than non-breeding birds, particularly within the breeding season. Outside of the breeding season, these differences remained but were less contrasting. Despite these large differences in ranging behaviour, the use of protected areas between breeders and non-breeders did not differ, either during the breeding season or in the subsequent non-breeding season. However, selection of protected and non-protected areas did differ between seasons (inside and outside of breeding season) for both breeders and non-breeders. This study suggests that conservation approaches may need to differ to protect different sectors of a population, and likely need to be adapted for seasonal differences as well, therefore, requiring both a ‘full-cycle’ and ‘full spectrum’ approach.

Because vultures range so widely, they are difficult to protect. Using the lappet-faced vulture GPS data, I explored whether Vulture Safe Zones (VSZs) that have been used to recover Asian vultures, could be viable for African vultures. To do this, I identified areas of highest use by counting numbers of GPS fixes of each individual bird in each 1-degree grid-square (DGS) in Botswana and then used the proportion of use for each bird in each DGS to identify the five top scoring DGSs which would form the VSZ (an area of c. 50,000 km^2). This was performed for three different groups within the population: 1) all birds, 2) breeders and 3) non-breeders. On evaluating the differences between the protection of GPS fixes offered by VSZs for each of the three groups, the best protection was offered by VSZs targeting breeding birds, which offered around 80% cumulative protection of their movements in Botswana, as well as a substantial level of protection per individual. VSZs targeted at protecting the remaining two bird groups: ‘non-breeders’ and ‘all birds’, offered around 35% less cumulative protection of GPS fixes than VSZs targeting breeders. Furthermore, individual protection was substantially less for both groups. Thus, VSZs aimed at protecting GPS fixes of breeders were much more effective and could be a viable conservation tool for breeding adult lappet-faced vultures (or similarly wide-ranging) species in Africa.

The findings of this study show that raptors in Botswana are in dire need of conservation attention. The large decline of almost all surveyed raptors in northern Botswana suggests that these species are mirroring the plummeting trend of global raptor populations. Consequently, the biggest challenge that we face is how to address these broad-scale declines. The large decline of three endangered and critically endangered vulture species is of real concern given their already precarious state in Africa, and GPS data from lappet-faced vultures in Botswana shows that they are highly exposed to wide-ranging threats. Pb from hunting may pose an additional threat to vultures and other scavenging raptors in Africa, and could well be contributing to declines. This may be relatively easily addressed through legislations banning Pb ammunition. Such conservation measures must be actioned across the region in order to protect vultures across their range, particularly in terms of mitigating exposure to poisoning (with both illegal pesticides and Pb). Furthermore, conservation approaches need to consider different sectors of a population and how movement of individuals can change according to season. Protected areas may offer limited capacity for raptor conservation and therefore additional strategies need to be given attention. VSZs may be an effective conservation tool for tackling wide-scale threats and may work well in conjunction with protected areas. Whatever conservation approaches are considered, need to be underpinned by clear objectives, and be well-designed for long-term sustainability. Long-term monitoring of raptors throughout the region is crucial in order to identify broad-scale trends and enable effective conservation action.

Acknowledgements

Probably the most difficult section of my thesis is attempting to thank all of those that have been so integral to making it all possible and to summarise in few words the incredible road I have travelled over the past five years. I am forever grateful for the people that kept driving me forward when I lacked the strength to do it myself and for those that opened the windows of opportunity and took me into their fold - “Life is like riding a bicycle, to keep your balance you must keep moving forward!”

After a somewhat serendipitous beginning back in 2013, I was welcomed into the ‘vulture’ squad e.g., the Botswana vulture research project, based in Maun, Botswana. In hindsight, I wonder if I may have undergone an initiation unbeknown to me, one that involved vulture vomit, unworldly stenches from carcasses melting in the Kalahari sun and mollifying gaggles of large and feisty (but incredibly cool) birds. Five years on there is a sense of the familiar in the pungency of these awesome creatures (just as well because it hangs around for while!), and I am completely won-over by their quirky and endearing character. What a pleasure and a privilege it has been!

A heartfelt thanks to Dr. Glyn Maude, the oil for the ever turning cogs of ‘operation PhD’ and on a broader scale the driving force behind the Botswana vulture research project. Glyn conceived the idea of KRC’s sister NGO – Raptors Botswana and it’s been a real privilege to be part of its first few years of operation and part of such a dynamic team. Here’s to the team, whom I have much to thank for: Pete Hancock, James Bradley, Bahiti, Mmoloki, Rapps, Moses and a special thanks to David Thandi, who sadly passed away during the period of this study but is missed and fondly remembered - that smile! Big thanks to the vagrant international team recruits, my co-supervisor (from another mother…land) Dr. Rich Reading for your advice, energy, friendship, quick responses and ace writing skills, and to team vet Dave Kenny for your guidance (and humour) on many topics. Thank you to Chris Maude and Rapps for your hands and eyes during vulture captures and road counts. Vulture captures required many willing hands, patience and zero sense of smell, so to all those from near and far who joined in, a big thank you to you all!

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I was heavily reliant on the good will of landowners and concession managers to conduct vulture captures on their property. Luckily I needn’t have worried! Big thanks to Chris Kitchen, Henk Vorster, Santawani and Khwai Community Trust, Ant Johnson, Willie de Graaff, Val Gruener, Bill Sieberhagen, Ralph Bousfield of Uncharted Africa (and in particular those at Camp Kalahari) and last but by no means least, those that will be remembered for their help and conservation passion- Chris Woolcott and Jason Bridger. To all who went above and beyond, with the provision of willing hands, tasty bait and somewhere to rest our heads for the night, I am forever grateful.

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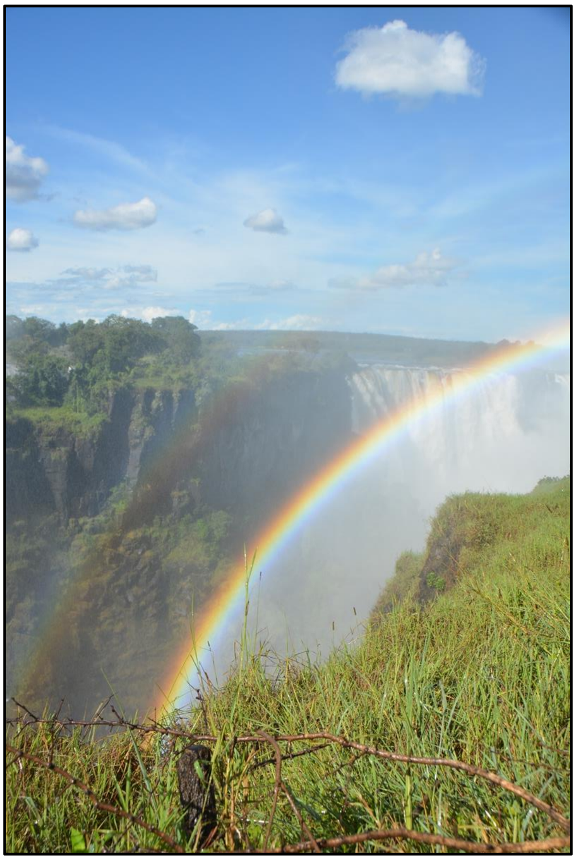
The biggest threat that African vultures currently face is intentional poisoning by poachers. Over the last five years we have recorded numerous cases in Botswana which would have gone un-noticed had it not been for those that reported them. Many were reported by local plane charter companies and safari operators, that consequently ‘made a plan’ to fly us into or over these remote areas. Thus, thanks go to Tico McNutt, Hal Bowker, Wilderness Air and Kwando Safaris; also to the Botswana Defence Force (BDF) and the Department of Wildlife and National Parks (DWNP) for their contribution and advice during these events. The concern and cooperation of the local community in our plight to conserve vultures has been overwhelming.

I can’t say that I have ever really understood why you should save the most important people for last but without breaking trend my most heartfelt thanks goes out to my beloved family and friends who have been unfaltering in their love, support and encouragement in my somewhat unconventional life; the last five years of which have been no exception. I am extremely blessed to have such solid support that has carried me through every challenge I have been faced with to date. For this, I owe my everything to my Mum and Dad, my sisters, Nay and Phil, my brother’s from another mother - Ed and Ian, and to the only kids that I never tire of, my nieces Izzie, Maddie, Annie and their long suffering brother Otis. This one’s for you kiddos! To my UK friends whom I have been absent from for so long but are still my closest sidekicks: Sarah, Katie, Bec, Tanya, Zoe, Ailsa, Jaime and Jane to name a few! You guys have never faltered in your encouragement of my irrational ideas! In Botswana, I have those that have walked the ‘developing country life’ road beside me and that can relate to my many ups and downs, in particular Ads, Sarah, Zoe (and Jase) and Verena whom I always knew would be grateful participants in wine drinking, chocolate or cake eating, stupid humour, and generally much needed moments of distraction. Finally to JP, my partner in crime and keeper of all things past, present and future. You’ve been my roadie, my ear to chew, my field assistant, my mechanic, my cheerleader, my pat on the back and slap in the face (where necessary) and my shrink. I owe much of this achievement to you. Thank you for tolerating, supporting, loving and fighting back.

In memory of David Thandi “Vulture Whisperer”



"Falling for you"

My soul burns as my feet touch the sand
Senses like static currents
My heart swells with relief
My breath speaks the sweet sound of Africa

Chapter 1: Introduction

“The Magic of the Makgadkgadi”

The loss of global biodiversity

The beginning of extinctions of much of the world's biota coincided with the first arrival of humans on earth (Burney and Flannery 2005). In 2015 the global human population reached 7.3 billion and is expected to rise to 9.7 billion by 2050 (United Nations 2015). Human activity is now the dominant driver of change to the Earth system. Consequently, unprecedented human pressures threaten to cause catastrophic irreversible environmental change (Rockström et al. 2009). As a result, many consider that the planet has now entered a new geological Epoch labelled "the Anthropocene" (Lewis and Maslin 2015). Changes in land use, depletion of natural resources, pollution and climate change are all factors driving rapid species losses (Sutherland et al. 2011), to such an extent that species extinction rates are predicted to increase another 10-fold over the next century (Pimm et al. 1995; Ricketts et al. 2005). Three times more species than those already recorded as extinct in the 1500's are at risk of imminent extinction (Ricketts et al. 2005). Furthermore, it is estimated that as much as 50% of Earth's biodiversity will be lost over the next century as a direct result of human expansion (Soulé, 1991). Africa has some of the highest population growth rates in the world (United Nations 2015), which is putting unprecedented pressure on biodiversity across the continent (Kruger et al., 2015; Moleón et al., 2014; Rondinini et al., 2006; Carrete et al., 2007). The detection of responses by animals and plants to these rapidly increasing human pressures are only possible through monitoring; however, in many areas that contain important biodiversity, such monitoring is almost entirely lacking.

Wildlife monitoring

With growing human pressures on wildlife resources and continued decline of global biodiversity, monitoring is becoming increasingly important to assess the magnitude and rates of loss that are occurring (Alonso et al., 2011; Magurran et al., 2010). For wildlife populations around the world, long-term monitoring has been a vital component in conservation biology (Chamberlain et al. 2000; Field et al. 2005; Ogutu, J. O. et al. 2011), particularly for identifying bird population trends (Bart et al. 2007; Underhill and Brooks 2014) and correlates associated with declines (Caughley 1994; Amar et al. 2011).

Monitoring is central to the establishment of effective conservation strategies and policy (Stem et al. 2005; Brashares and Sam 2005) and is often a pre-requisite of active management (Nichols and Williams 2006). Information from both baseline and repeat monitoring can help to address urgent conservation challenges (Alonso et al., 2011) by using methods aimed at investigating the drivers of population declines (Thiollay 2007; Woinarski et al. 2010; Amar et al. 2015) and assessing species abundance.

Sampling surveys are most frequently used for assessing animal abundance, whereby animals are counted, either on the ground or by air, in a systematic manner (Seber 1986). Transect surveys are most used for yielding information on numerous species over large geographical areas (Chiarello 2000; Nichols and Williams 2006). Moreover, for their ability to detect precipitous events (Wintle et al. 2010). Repeat surveys are important for detecting abundance changes within a population over time (Plumptre 2000; Johnson et al. 2005). In some cases however, the monitoring of certain indicator or 'umbrella' species (Caro 2003) that can reflect wider species trends (Shrader and McCoy 1993; Moore et al. 2003) can be a more efficient use of scarce resources (Wintle et al. 2010). Both broad-scale and targeted monitoring are considered useful for informing effective conservation planning (Roberge and Angelstam 2004). However, the costs associated with different monitoring methods can influence their use, with large-scale transect surveys being particularly expensive (Ogutu et al. 2006). Careful consideration of monitoring methods to meet their objectives is necessary to ensure the optimal allocation of resources available for species conservation (Nichols and Williams 2006; Lindenmayer et al. 2007) .

For declining populations, monitoring is crucial in order to constantly update management strategies in-line with global change (Gibbs et al. 1999). The rapidly deteriorating conservation status of global raptor populations has led to an increased need for monitoring efforts around the globe (Sánchez-Zapata et al. 2003; Berry et al. 2010). Because raptors can act as useful bio-indicators (Rodriguez-Estrella et al. 1998; Sergio et al. 2006), knowledge on their population trends can provide information on wider trends (Rodriguez-Estrella et al. 1998). Transect surveys in Africa have covered large areas and have elicited information on many species (Cuthbert et al. 2006; Thiollay 2007; Virani et al. 2011). Some of the first studies in Africa to identify severe and wide spread raptor declines used repeat road transect surveys (Thiollay 2007). The recent widespread decline of African vultures was identified through information from road transect surveys in different geographical areas. By the time some of the repeat surveys were conducted, declines exceeding 90% had occurred for some species (Thiollay 2007; Ogada et al. 2015), suggesting that more frequent monitoring efforts were needed in order to detect declines earlier. Vulture declines in Asia went completely undetected for around a decade due to lack of adequate monitoring, and as a result three species almost completely disappeared from the wild (Pain et al. 2003; Gilbert et al. 2007). In order to prevent this happening in other wildlife populations, the broad-scale implementation of sustainable and well-designed monitoring methods is necessary (Plumptre and Cox 2006). Such monitoring is already widespread in more developed parts of the world (e.g., Europe and North America). However, in many developing countries, where biodiversity are often highest but declining most, there is little systematic monitoring (Amano and Sutherland 2013). The African continent is renowned for its unique and abundant biodiversity (Toit 1999; Brooks et al. 2006), and conversely, for its dwindling wildlife populations as a result of increasing human pressures (Woodroffe and Ginsberg 1999; Thuiller et al. 2006; Rondinini et al. 2006; Caro and Scholte 2007). The African continent is a prime example of the consequences of inadequate monitoring, in that many wildlife declines have occurred largely undetected (Blake and Hedges 2004; Thiollay 2006a; Caro 2008), but still, in many parts of Africa, knowledge on wildlife population trends is almost non-existent. This represents a dangerous scenario for African wildlife, as increasing global threats continue to push many species closer to extinction (Cardillo et al. 2004).

A vulture crisis?

Despite the lack of systematic monitoring across the globe, we know that vertebrate scavengers have had some of the biggest declines (Mateo-Tomás et al. 2015; Buechley and Sekercioğlu 2016). Avian scavengers in particular are experiencing the largest declines (Butchart et al. 2004; Virani et al. 2011), and the conservation status of those within the scavenger and carnivore feeding guilds has declined most over the last decade (Buechley and Sekercioğlu 2016). Large declines of obligatory scavenging *Gyps* vultures in Asia have been recorded (Prakash et al. 2003; Gilbert et al. 2007), primarily caused by ingestion of the veterinary drug – diclofenac from cattle carcasses (Oaks et al. 2004; Swan et al. 2006; Taggart et al. 2007). This drug has now been banned for use in animals and this action together with direct conservation management has led to the tentative recovery of these species (Cuthbert et al. 2011; Chaudhry et al. 2012). However, over this time, a new crisis has emerged with African Vultures. Although little systematic monitoring of vulture populations occurs in Africa, what monitoring has occurred, shows that African vultures are heading towards extinction (Ogada et al. 2015). In 2015, six of the eleven African vulture species had their conservation status up-listed to 'Endangered' or 'Critically Endangered' by the International Union for the Conservation of Nature (IUCN) (IUCN 2017). The main driver of decline for African vultures is illegal poisoning with agricultural pesticides, whereby pesticides are placed onto carcasses that are then placed out for animals to feed on. For vultures, this is as a result of intentional (or sentinel) killing by poachers that kill vultures because they signal their illegal activity (Murn and Botha 2017), or unintentional killing by farmers that place poisoned carcasses out to kill predators that have killed their livestock (Santangeli et al. 2016). Poisoning with pesticides has been responsible for 61% of vulture mortality recorded in 26 African countries (Ogada et al. 2015). Increasing vulture mortality associated with intentional poisoning has been linked to the rapid increase of ivory poaching in Africa (Ogada et al. 2016). Currently, the pesticides used for poisoning vultures are unregulated and widely available across the continent (Ogada 2014).

Poisoning of raptors and vultures

Illegal poisoning with pesticides also threatens other scavenging raptor species (Watson 1987; Herholdt et al. 1996; Ogada 2012). An additional form of poisoning - lead (Pb) poisoning, has been shown to have major negative impacts on raptor populations around the world (Redig et al. 1980; Kramer and Redig 1997; Rideout et al. 2012) yet it remains under-investigated in Africa. This type of poisoning for raptors has been largely linked to Pb ammunition from hunting left over in carcasses that is ingested by scavenging raptors when they feed (Legagneux et al. 2014; Gil-Sánchez et al. 2018). Studies have shown that Pb ammunition can fragment throughout an entire carcass, making it easy for animals that feed on them to ingest (Hunt et al. 2009; Grund et al. 2010). Recreational hunting is of great economic importance in Africa and is wide-spread across the continent (Lindsey et al. 2007). In addition, other hunting activity such as subsistence hunting, poaching, wildlife culling and killing as a result of human-wildlife conflict also occurs (Carpaneto and Fusari 2000; de Merode et al. 2004; Kalahari Conservation Society 2009; McManus et al. 2015). As the only living obligate vertebrate scavengers purely reliant on carcasses for food (Dermody et al. 2011), African vultures are particularly susceptible to ingesting Pb from this source. Hunting farms however, likely pose the biggest risk because they often dispose of unused carcasses and viscera ('gut piles') by leaving them in the open for vultures to eat (Hunt et al. 2006; Legagneux et al. 2014). As a result, vultures can become reliant upon 'gut piles' as an additional food source (Deygout et al. 2009; Kane et al. 2015). Thus, these 'gut piles' from hunting are often termed ‘vulture restaurants’ (Margalida et al. 2010). The amount of Pb in ‘gut piles’ can be substantial enough to potentially kill hundreds of vultures and other scavenging raptor species (Pattee et al. 1981; Knott et al. 2010; Stokke et al. 2017). Some African countries have imposed hunting bans to preserve declining wildlife populations (Akama 2007; Mbaiwa 2018). However, vultures range widely across international borders (Lambertucci et al., 2014; Chapter 4) and are therefore exposed to hunting across the region. Thus, national hunting bans may have little benefit for vultures in terms of controlling Pb exposure. Whilst Pb poisoning may not be the driving force behind the decline of vultures, its impacts are under-studied. If African vultures are at risk of Pb poisoning from hunting, it should be relatively straightforward to address through legislations (e.g., a ban on Pb ammunition – like has occurred in other countries and regions), which is in contrast to the intractable issues surrounding illegal poisoning. Because of its detriment to both humans and wildlife, there is said to be no tolerable level of Pb exposure (Pattee et al., 2006; Pain et al., 2010; Center for Disease Control and Prevention, 2012), thus stressing the importance of eliminating it altogether from our ecosystems. A ban on Pb ammunition would be a positive step towards achieving this in Africa.

Importance of vertebrate scavengers and raptors

Vertebrate scavengers play a vital role within ecosystems (DeVault et al. 2003; Huijbers et al. 2016). It is suggested that they provide three distinct ecosystem services: 1) maintaining stability within food webs, 2) facilitation of nutrient flow throughout and beyond ecosystems, and 3) environmental sanitation through the removal of harmful pathogens from carrion (Inger et al., 2016; Moleón et al., 2014). Vertebrate scavengers help shape species communities and regulate trophic competition within ecosystems (Wilson and Wolkovich 2011; Sebastián-González et al. 2013; Huijbers et al. 2016). For instance, the presence of vultures and top predators e.g., raptors, can control populations of other scavengers and prey species (Mateo-Tomás et al. 2015). Furthermore, vultures help facilitate and regulate patterns of other scavengers at carcasses (Blázquez et al. 2009). In the absence of vultures, severe disruptions of other scavenging communities can occur and have widespread negative impacts on ecosystems (Pain et al. 2003; Ogada et al. 2012b). In Asia, both undesirable facultative scavengers (e.g., feral dogs) and human cases of rabies increased following the vulture population crash, resulting in huge human health costs (Markandya et al. 2008; Ogada et al. 2012a). Other raptor species act as apex predators in food webs, and their presence can be associated with increased biodiversity (Sergio et al. 2005). In a similar way to vultures, predatory raptors maintain the integrity of ecosystems through regulation of trophic structure (Berger et al. 2001; Ripple and Beschta 2006; Johnson et al. 2007; Wilson and Wolkovich 2011). The loss of apex predators can cause trophic cascades and overall deterioration of ecosystem function (Estes et al. 2011; Levi et al. 2012; Huijbers et al. 2015). An example of this is the catastrophic effects of cougar *Puma concolor* decline in the USA, when consequent increases in prey species led to drastic changes in vegetation and ground composition, resulting in the decline of many other species in the area (Ripple and Beschta 2006). The deterioration of ecosystems is confounded by increasing effects of global climate change (Malcolm et al. 2006; Root and Schneider 2006). Predatory raptors may play an important role in buffering the ecological effects of climate change by maintaining trophic stability in the face of changing seasonal weather conditions that may disrupt community structures (Sala 2006). The functional replacement of carrion disposal by vultures, could markedly increase carbon (CO_2) emissions, and thus vultures can play a role in CO_2 regulation (Morales-Reyes et al. 2015). Ultimately, vertebrate scavengers play an intrinsic role in our natural world and their demise has broad-scale effects on both humans and wildlife (O'Bryan et al. 2018).

There are numerous challenges associated with protecting scavenging raptors, mainly because most species range widely, meaning that focal conservation areas can be limited in their capacity to protect them. The global protected area network is our most powerful tool for biodiversity conservation; however it may be of little value for protecting wide-ranging species, due to the limited time that they spend within these areas. Other focal conservation areas such as Important Bird Areas (IBAs) have been formed to aid the protection of wide-ranging and threatened species (Runge et al. 2015). However, because many of the threats facing wide-ranging raptors, in particular vultures, occur outside of protected areas, other conservation strategies address the direct mitigation of threats outside of protected areas. For example, using more 'raptor friendly' powerline structures to reduce mortality from powerline collisions (Jenkins et al. 2010), and establishing 'vulture restaurants' to protect against poisoning by providing a safe food source (Moreno-Opo et al. 2015). Much emphasis has been placed on improving education and awareness of the importance of vultures and raptors, with the aim of changing attitudes and behaviours that are currently hindering their conservation (Al Fazari and McGrady 2016; Baral and Gautam 2007; Baral et al. 2017). Furthermore, establishing legislation and developing enforcement capacity in order to halt population declines, has been a primary focus, such as banning pesticides being used in vulture poisoning and enforcing stricter penalties for wildlife poisoning (Ogada 2014). In some areas, targeted conservation has been used to recover vulture populations that have collapsed as a result of negative impacts of anthropogenic activity (poisoning through veterinary drugs in carrion) (Gilbert et al. 2007). These target areas (Vulture Safe Zones) use 'vulture restaurants' as their central concept to protect important breeding populations from poisoning, thereby helping populations to recover from large losses through reproduction (Chaudhary et al. 2010; Murn et al. 2015). Despite the success of targeted conservation in some areas, protected areas still persist as the cornerstone of global biodiversity conservation and thus strategies need to consider how these areas can be built upon or incorporated within future management plans.

The global protected area network is aimed at maintaining habitat integrity and species diversity (Butchart et al. 2012; Saout et al. 2013). Protected areas currently cover 13% of Earth's land surface and 3% of marine environments (Watson et al. 2014); however 85% of all threatened species are still not adequately protected (Di Minin and Toivonen, 2015). In 2010, parties to the Convention on of Biological Diversity (CBD) showed their recognition of the failure of global protected areas to adequately protect biodiversity, by adopting a new strategic plan (Venter et al. 2014). The resulting Aichi target 11 of the CBD which promotes the rapid expansion of terrestrial protected areas (an increase of 4% by 2020) (Venter et al. 2014), could potentially triple the proportion of terrestrial vertebrate species that would feature within protected areas (Di Minin and Toivonen, 2015). However, for wide-ranging species, protected areas have to be large or well-connected in order to protect much of their range (Rodrigues et al. 2004; Di Minin et al. 2013). Currently, the proportion of global protected areas larger than 10,000 km^2 is only 0.2%. Although Africa holds around 20% of these larger areas (Deguignet et al. 2014), many are still much smaller than the ranges of wide-ranging species such as vultures (Blom et al. 2004; Burgess et al. 2007; Di Minin et al. 2013), which can have home ranges as large as 300,000 km^2 (Phipps et al. 2013b; Buechley et al. 2018) and can utilize areas even larger than this (Phipps et al. 2013a). Furthermore, many protected areas do not offer 'full life-cycle' protection e.g., protection across breeding and non-breeding seasons (Runge et al. 2015; Schuster et al. 2018) or 'full spectrum' protection e.g., protection of all individuals in a population that may have different ecological requirements (Gutowsky et al. 2015). This is most difficult to achieve for wide-ranging birds that can spend time in different geographical locations across their full life-cycle, thus creating large gaps in their protection (Burgess et al. 2005; Gillingham et al. 2015). These gaps in protection can be particularly important for populations when they apply to breeding ranges, particularly within the breeding season (Morrison et al. 2013; Runge et al. 2014). Thus, there is still considerable work to be done to achieve better protection for wide-ranging species.

In an attempt to fill gaps in the protected area network, additional 'finer grain' conservation strategies such as Key Biodiversity Areas (KBAs) are being used to complement larger-scale conservation initiatives (Eken et al. 2004). KBAs aim to set a universal standard for this type of 'site-scale' conservation using criteria addressing species vulnerability and irreplaceability (Eken et al. 2004). The most well-known application of KBAs is likely the global network of Important Bird Areas (IBAs), which over the past 20 years, has benefited numerous threatened species (Eken et al. 2004; Runge et al. 2015). Areas like this may be an effective way to target species that fall within gaps of the protected area network. However, even these areas, either as a standalone strategy or as an addition to existing protection networks, may be inadequate for some wide-ranging species (Runge et al. 2015). For example, wide-ranging Bonelli's eagles *Aquila fasciata* in Spain are still largely unprotected by IBAs and the European Union's Special Protected Areas (López-López et al. 2007). A key element in the discussions pertaining to improving conservation areas is the expansion of knowledge on species' space use and distribution, and the crucial need for scientific data to support management decisions (Margules et al. 2002; Fjeldså 2007; Cook et al. 2010; Venter et al. 2014; Di Minin and Toivonen 2015). It is anticipated that if future protected area expansion continues as it has historically, the protection of threatened species will only marginally increase (Venter et al. 2014). The prioritisation of key conservation areas will likely be most effective in halting declines of global biodiversity (Margules et al. 2002; Bruner et al. 2004; Butchart et al. 2015).

Animal movement ecology

One of the most effective ways in which science can contribute to better species protection is by increasing our understanding of free-living species (Wikramanayake et al. 1998; Jetz et al. 2008). Historically, biotelemetry has often been used to do this because of its ability to remotely capture ecological information (Ropert-Coudert and Wilson 2005; Maxwell et al. 2011). For endangered species in particular, it has been used as a way to inform on threats associated with population declines (Cooke 2008). Much of the basic knowledge required to make threat assessments and informed conservation decisions can be elicited through biotelemetry (Cooke 2008). For cryptic or wide-ranging species this may be the only way of obtaining robust data for conservation planning (Wilson et al. 2008). For birds in particular, satellite tracking has revolutionized the study of movement ecology (Sokolov 2011). Information emerging from tracking studies of birds has highlighted the inefficiencies of current conservation strategies and has acted as a platform for improved conservation management (Guixé and Arroyo 2011; Young et al. 2015; López-López et al. 2016). For migratory birds in particular, biotelemetry studies are enabling strategies which address 'full-cycle' protection of important seasonal ranges (such as breeding grounds), and that can also protect important sectors of a population (such as breeding birds) (Meyburg et al. 2004, 2012; Sheehy et al. 2011; Gutowsky et al. 2015; Buechley et al. 2018). However, suggested strategies aimed at achieving 'full-cycle' protection can differ. For example, some suggest investing in areas with highest population density dependence across seasons (breeding and non-breeding) (Sheehy et al. 2010), whereas others suggest protecting areas where species are most spatiotemporally abundant (Schuster et al. 2018). Achieving 'full cycle' protection can be further confounded by distinct differences between individuals within a population, for example, breeders and non-breeders. These two groups can often appear to act as separate populations, using different home ranges and utilizing different resources (Tanferna et al. 2013; Zurell et al. 2018). Thus, there is likely not an exclusive approach to better protect wide-ranging and complex species; however, understanding their movement ecology is a vital component of identifying suitable management approaches.

Study species

African (non-vulture) raptors

The majority of species in this study fall within the taxonomic order *Accipitriformes* which encompasses most diurnal birds of prey (otherwise known as raptors), with the exception of falcons and kestrels *Falconiformes*. Raptor species belong to two important and highly threatened functional guilds: carnivores and scavengers, and thus this genus accounts for 67% of all extinction –prone avian scavengers (Buechley and Sekercioğlu 2016). Two eagle species, the tawny *Aquila rapax* and bateleur eagle *Terathopius ecaudatus*, are among the most threatened eagles in southern Africa due to now being mostly confined to protected areas or areas with low human density (Loftie-eaton 2014). As largely scavenging species, these two eagle species are also highly susceptible to feeding on poisoned carcasses (Anderson 2000), which has largely contributed to the demise of the bateleur eagle in some parts of Africa (Watson 1987; Simmons and Brown 1997). With many raptor species being largely generalist feeders, they are found in most ecosystems (Herremans 1998; Buij et al. 2013). For the majority of raptors, mammalian prey is the staple diet, (Charley et al. 2014; Barnett et al. 2015; Dunne 2017), although some dietary specialists, such as snake eagles *Circaetus spp.* and African fish eagles *Haliaeetus vocifer* feed only on reptiles (snake eagle) or fish (fish eagle) (Lack 1946). The peregrine falcon *Falco peregrinus* and a few other highly specialized raptor species have a diet dominated by avian prey (Barton and Houston 1993). Although raptors are relatively well-studied in terms of life history and traits of different species, monitoring of their populations is lacking, particularly in developing regions such as Africa.

Despite the lack of systematic monitoring in Africa, it is clear that raptors are declining throughout much of the continent (Thiollay 2006b; Virani et al. 2011). In West Africa, 30 species of raptor declined significantly over a period of 30 years, with some large eagles, Palearctic migrants and vultures declining most steeply (Thiollay 2007). Even common species such as the black kite *Milvus migrans*, have declined by around 70%. Many large eagle and vulture species may now only have viable populations within protected areas in that region (Thiollay 2007). In East Africa, information is sparser, but repeat surveys have also identified declines of some vulture and large eagle species (e.g., tawny eagle) (Virani et al. 2011). In southern Africa, repeated atlas data from the two Southern African Bird Atlas Projects (SABAP 1 & 2) show that some of the largest declines have occurred for raptor species such as the white-headed vulture *Trigonoceps occipitalis*, black-shouldered kite *Elanus caeruleus*, rock kestrel *Falco rupicolus* and bateleur eagle *Terathopius ecaudatus* (Underhill and Brooks 2014). Despite these findings, the majority of resident African raptors are currently classified by the International Union for Conservation of Nature (IUCN) as species of ‘least concern’ (IUCN 2017; Amar et al. 2018). Some (non-vulture) exceptions are the bateleur eagle (near threatened), martial eagle (vulnerable) and the secretarybird (vulnerable) (IUCN 2017). Worryingly, atlas data and nest surveys in South Africa identified recent declines for all of these species (Hofmeyr et al. 2014; Underhill and Brooks 2014; Amar et al. 2015). For migratory species in Africa, the pallid harrier is classified as ‘near threatened’ and the steppe eagle as ‘endangered’ (IUCN 2017).

African vultures

Vultures also form part of the Accipitridae family but are quite ecologically distinct from other species in this family, in that are wholly reliant on carrion for food. As the only living obligate vertebrate scavengers on earth (Dermody et al. 2011), vultures act as ecosystem sanitisers by disposing of rotting carcasses (Ogada et al. 2012). Because of this unique feeding strategy, they are the most threatened avian functional guild on earth (Buechley and Sekercioğlu 2016). Botswana is home to five species of African vulture, and in this thesis I conduct research on four of them (excluding the cape vulture *Gyps coprotheres*). However, my main focus is on African white-backed vultures (AWBV) *Gyps africanus* (lead poisoning) and lappet-faced vultures (LFV) *Torgos tracheliotos* (movement ecology). The LFV occurs in Africa at one of the lowest densities of any African vulture (second to the white-headed vulture *Trigonoceps occipitalis*). Ninety-five percent of the global population occurs on the continent (population size: c. 8,000), with the remainder being found in the Middle East (population size c. 500) (BirdLife International 2017a). The LFV is non-territorial and a largely solitary species which inhabits semi-arid and arid areas (Mundy et al. 1992). Nests are often in the top branches of acacia trees that are sparsely distributed in remote areas (Bridgeford and Bridgeford 2003), and may be re-used over consecutive years (Mundy et al. 1992). Their breeding phase spans almost the entire year if the post-fledgling dependency stage is included (Pennycuick 1976) and both males and females participate in nesting duties. Due to this extensive period of breeding activity, it is thought that they may only breed biennially (Pennycuick 1976; Mundy et al. 1992). The AWBV only occurs in Africa but has an estimated population almost 34 times larger than the LFV (c. 270,000) (BirdLife International 2017b). The ecology of both species is largely similar (breeding ecology and seasons are the same) with the most marked difference being the far more gregarious nature of the AWBV. Often hundreds will congregate at a single carcass and they also breed in loose colonies (Murn et al. 2002; Monadjem and Garcelon 2005).

In 2015 the LFV had its conservation status elevated to 'Endangered' and the AWBV to 'Critically Endangered' by the IUCN, due to their large and rapid decline throughout Africa (Thiollay 2006b; Ogada et al. 2015; IUCN 2017). Much of their respective ranges cover all of southern Africa (African Raptor Databank 2017a,b), (Figure 1 & 2), thus it is an important region for vultures. This region also contains important vulture breeding areas (Mundy et al. 1992; Bridgeford and Bridgeford 2003; Monadjem et al. 2013; Murn and Botha 2016).

Botswana lies centrally within southern Africa. It has a semi-arid climate (Ringrose et al. 2003) and around 40% of land designated for wildlife conservation (Mbaiwa 2005), (Figure 3). Botswana may be particularly important for African vultures that mostly prefer arid environments. For both the LFV and AWBV, Botswana is the only country in the region where their ranges overlap the entire country, followed closely by neighbouring Namibia (African Raptor Databank 2017a, b), (Figure 1 & 2). Thus, Botswana is a vitally important area for vulture conservation.

Tracking data on ranging behaviours of AWBVs confirmed that they range widely across international borders (Phipps et al., 2013). In contrast, LFVs were initially believed to hold small resident ranges (Shimelis et al. 2005; Spiegel et al. 2013a). However, a tracking study in Namibia showed long-ranging movements of a few individual LFVs (Spiegel et al., 2013, 2015), and tracking studies on this species in Saudi Arabia show similar findings (Shobrak, 2014). Nonetheless, few studies have attempted to understand the movement ecology of LFVs, thus little is known about their conservation requirements. The wide-ranging behaviour of vultures makes them highly susceptible to multiple threats, particularly illegal poisoning with pesticides (Ogada et al., 2012; Phipps et al., 2013; Carrete et al., 2007). In southern Africa (Namibia), a single poisoning incident killed around 600 AWBVs, and this is likely a very modest estimate (IUCN 2013; Ogada et al. 2016). The severe decline of AWBVs and LFVs across Africa is therefore unsurprisingly attributed to increasing incidences of poisoning across their range (Ogada et al. 2015). Botswana appears to be a hotspot for intentional poisoning of vultures (African Raptor Databank 2017c; Leepile 2018). Therefore understanding additional threats that may be contributing to vulture declines in this area is crucial.

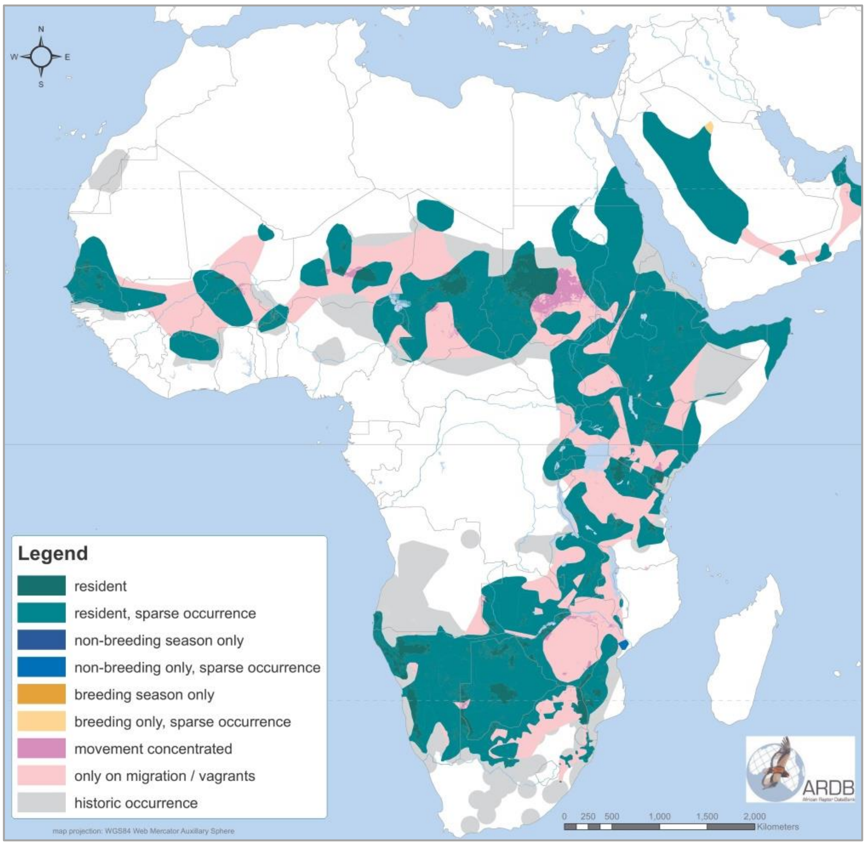


Figure 1. Lappet-faced vulture *Torgos tracheliotos* African range map (African Raptor Databank, 2017)

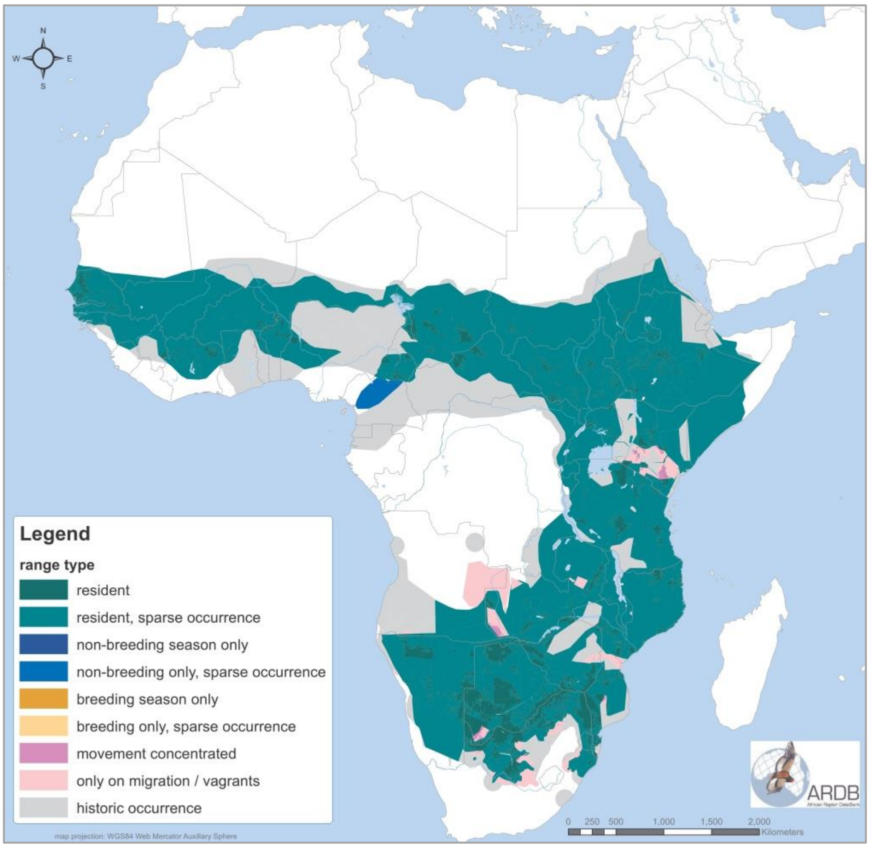


Figure 2. African white-backed vulture *Gyps africanus* range map (African Raptor Databank, 2017)

Study Area

Southern Africa is the southern-most part of Africa and is often now defined by the geographical coverage of member states of the Southern African Development Community (SADAC), which comprises of: Angola, Botswana, Democratic Republic of Congo (DRC), Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Zambia and Zimbabwe. SADAC is an inter-governmental organization whose aim is to promote balanced economic growth and socio-economic development throughout the SADAC countries (Moyo et al. 1993). The SADAC region has a combined Gross Domestic Product (GDP) over double that of the aggregate GDP of sub-Saharan Africa, with production from agriculture and mining contributing more than 50% of this (Chishakwe 2010). The United Nations Human Development Programme (UNDP) classifies economic growth and development of countries within the SADAC region using the Human Development Index (HDI). The economic status of SADAC countries ranges from low to high, thus economic development and stability is highly variable throughout the region.

Southern Africa is a largely semi-arid tropical region containing a broad diversity of terrestrial ecosystems such as: tropical and subtropical grasslands, savannahs and shrublands, Mediterranean forest, woodland and scrub, and deserts and xeric shrublands (Olson and Dinerstein 2002; Rutherford et al. 2006). Southern Africa is among the most drought-vulnerable regions in the world and is highly characterised by variable rainfall (Leichenko and O'Brien 2002). Temperatures in the region have increased over the last few decades, consistent with global climate change, as has the frequency and intensity of 'El Nino' events such as flooding and fires (Kruger 1999; Van der Werf et al. 2004; Lovett et al. 2005). Future climate change predictions show this region becoming hotter and drier, with increasing contrasts in temperature between seasons (wet and dry) (Collier et al. 2008; Chishakwe 2010).

Botswana lies centrally in southern Africa and is bordered by Angola and Zambia in the north, Namibia in the west, Zimbabwe in the east and South Africa in the south (Figure 3). The country is classified as a lower-middle income country, ranking 11th highest out of the 13 SADAC countries, in terms of HDI (Chishakwe 2010; Crawford 2016). The main contributor to Botswana's economic growth and current GDP is the mining industry, with diamonds accounting for the majority of wealth. Although the agricultural industry represents a significant source of national employment, it generates relatively little GDP compared to other economic sectors (Sarraf and Jiwanji 2001; Crawford 2016). Botswana covers an area of around 580,000 km^2 and has a semi-arid climate. Rainfall occurs in the Austral summer between November and April (the wet season) and ranges from an average of 250 mm in the south-west to an average of 650 mm in the north and north-east (Barnes 2001). Daily maximum temperatures range from an average of 22°C in winter (dry season) to 33°C in summer (wet season), with average minimum temperatures ranging from 5°C (winter) to 19°C (summer) (Winterbach et al. 2014). Botswana is vulnerable to the impacts of climate change and national temperatures have already risen by around 2°C over the last 50 years, with further increases expected (Crawford 2016). Annual patterns of rainfall are also predicted to become increasingly variable with future impacts of climate change (Batisani and Yarnal 2010).

Botswana is considered to hold some of the most pristine wilderness areas in Africa (Mbaiwa et al. 2007; Saarinen et al. 2014). It has almost 20% of land mass designated for protected areas and a further 20% for Wildlife Management Areas (WMAs) (Mbaiwa 2005), (Figure 3). The majority of the country is Kalahari Desert (an area of semi-arid savannah and scrub-woodland), (Ringrose et al., 2003), of which c. 53,000 km^2 is encompassed within the Central Kalahari Game Reserve (CKGR), the second largest game reserve in the world (Sapignoli and Hitchcock 2015). The country's other officially protected areas are: Khutse Game Reserve (c. 2,700 km^2), Moremi Game Reserve (c. 2,800 km^2), Chobe National Park (c. 10,800 km^2), the Makgadikgadi and Nxai Pan National Park (c. 6,000 km^2), and the Kgalagadi Transfrontier Park (inc. Mabuasehube GR) (c. 26,000 km^2) (Mordi 1989). The north of Botswana encompasses all or part of all officially protected areas besides the Kgalagadi Transfrontier Park, as well as RAMSAR site – the Okavango Delta (Figure 3). Predominant land use outside of protected areas and WMAs is communal and commercial agriculture, and on a much lesser scale, game ranching (Mordi 1989; Perkins 1996; Mbaiwa 2005).

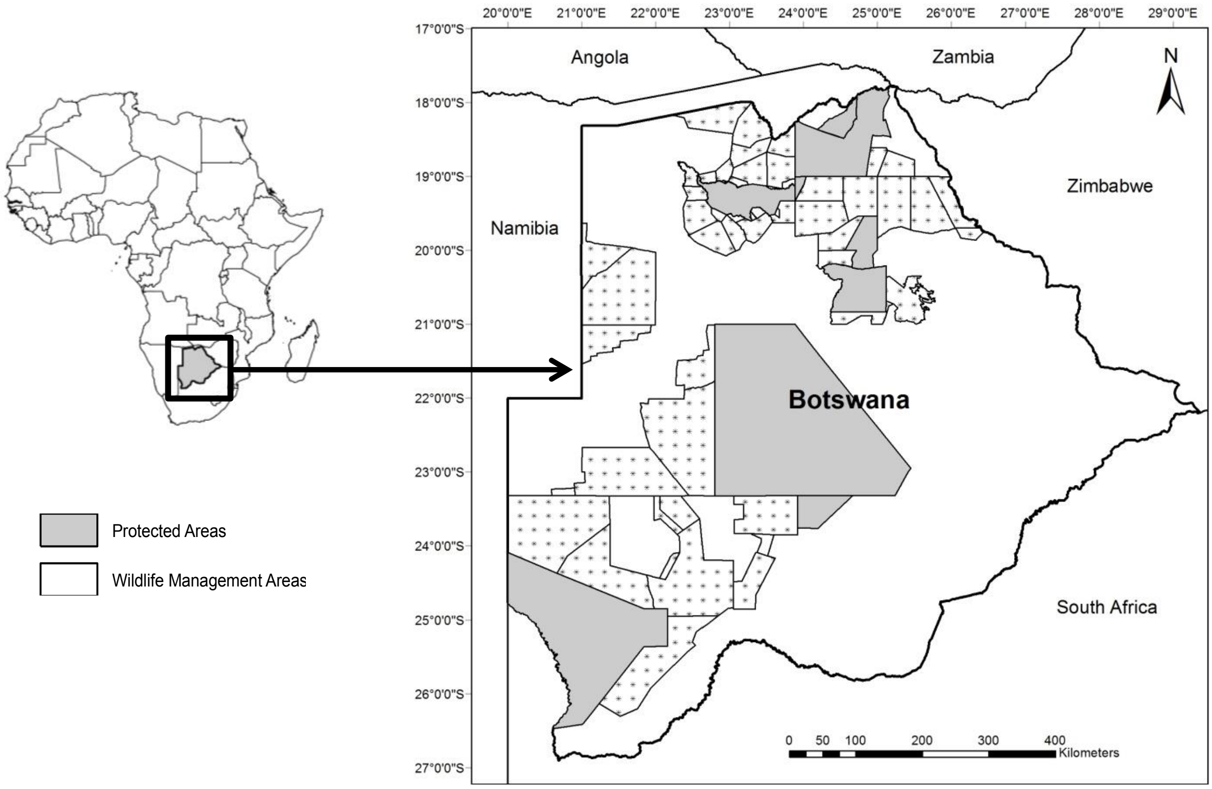


Figure 3. Maps showing the location of Botswana within southern Africa and the main study area - northern Botswana (area north of latitude -22°). Nationally protected areas and Wildlife Management Areas (WMAs) are illustrated. These areas cover around 40% of land in Botswana.

Although some of Botswana's wildlife populations are in decline (Chase et al. 2015), biodiversity remains relatively high, and due to year-round water availability, is more concentrated in the north of the country (Thouless 1998; Statistics Botswana 2015). Compared to other African countries, wildlife in Botswana is relatively sheltered from human activity, due to low human population density (2.3 million), (Statistics Botswana 2011), However, because livestock rearing (mainly cattle) occurs on the majority of land outside of protected areas, wildlife often competes for habitat with livestock, even within conservation areas (Mordi 1989; Wallgren et al. 2009). As a consequence of intensive agriculture, fragile arid rangelands have become severely degraded and are becoming increasingly unsuitable for sustaining wildlife (Darkoh 1999; Darkoh and Mbaiwa 2002).

The steep decline of the country's wildlife species prompted a ban on hunting on government owned land that was enforced in January 2014 (Chase 2011; Mbaiwa 2018), with the aim of the ban being to allow wildlife populations to recover. Prior to the ban, the revenue generated by recreational hunting in Botswana surpassed most of the other 13 countries within the

SADAC community. Over half of this revenue was generated by elephant hunting (Lindsey et al. 2007). Twenty-three percent of Botswana’s land mass was designated for hunting (most of which was within WMAs), much of which was in the north of the country where wildlife was most abundant (Barnett and Patterson 2006). As well as being an important economic activity, recreational hunting formed an integral part of sustaining rural communities through the Community-Based Natural Resource Management Programme (CBNRM) (Arntzen et al. 2003). The CBNRM programme aimed to empower and create incentives for rural communities to manage natural resources (Phuthego and Chanda 2004). Recreational hunting was incorporated into this framework by creating incentives for rural communities to conserve wildlife e.g., through local employment, provision of food (hunted meat) and by generating income through tourism (Kalahari Conservation Society 2009). Subsequently, after the ban was enforced, rural communities lost important income and experienced reduced food security (Mbaiwa 2003, 2018). Increased poaching in northern Botswana is also said to be as a result of the hunting ban and the consequent devaluation of wildlife by rural communities (Mbaiwa 2018). Non-consumptive tourism (photographic safaris) now occurs in many former hunting areas but may only generate a fraction of the revenue that was generated for rural communities by recreational hunting (Mbaiwa 2018). Hunting still occurs however, on privately owned concessions, although these only cover around 5% of the country’s land mass (Barnett and Patterson 2006). Despite this, recreational hunting is still a huge industry throughout the region (Di Minin et al. 2016; Angula et al. 2018).

Thesis aims

Despite the alarming declines that have been identified for raptors across parts of the continent, there are still major gaps in our knowledge of raptor population trends in several areas that are particularly important for many species. Currently, it is impossible to form effective conservation strategies without this fundamental knowledge. The aims of this thesis are to therefore 1) inform on raptor population trends in Botswana so that any priority species of concern can be identified, 2) further investigate threats that could be contributing to declines so that they can be addressed, 3) uncover new information on habitat and space use of a highly endangered raptor species, and lastly 4) to use this information to help inform conservation management.

Thesis overview

This thesis consists of a series of four data chapters that have been written as stand-alone papers to facilitate publication. As a result, there is some repetitive information within the introduction and methods section of different chapters.

Findings from this research conducted between 2012 and 2017 are presented in data chapters 2 - 5. A schematic diagram showing the flow of information between chapters is shown in Figure 4 on the following page.

Chapter 2 investigates population trends of raptors in northern Botswana that have occurred over the last 20 years to determine whether vultures are the main declining group in Botswana, or whether declines of other raptors species have also occurred. Within this chapter, I also explore changes in abundance in relation to protected areas to ascertain whether raptors are faring better inside protected areas than outside of them. These findings provide currently unknown information on population trends of raptors in Botswana and on the importance of protected areas for these species. They will also be useful for addressing Aichi Target 12 (By 2020 the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained) of the Convention on Biological Diversity (CBD). A version of this chapter has been published in Biological Conservation (Garbett et al. 2018a).

Chapter 3 explores a currently under-investigated threat to scavenging raptors in Africa, particularly vultures, using biological data collected from different geographic locations in Botswana. This chapter aims to determine whether elevated blood Pb levels found in African white-backed vultures are associated with hunting activity in Botswana. This species was used for this investigation in order to obtain a large enough sample size (this species is the most abundant vulture species). I aim to test the hypothesis that elevated blood Pb levels in vultures are most likely caused by the ingestion of Pb fragments from spent hunter ammunition in carcasses. If correct, this would represent an additional threat that may be contributing to declines of African vulture populations. If Pb is a problem for vultures, then this threat might also be important for other scavenging wildlife species, as well as for humans that consume meat from animals shot with lead bullets. A version of this chapter has been published in Science of the Total Environment (Garbett et al. 2018b).

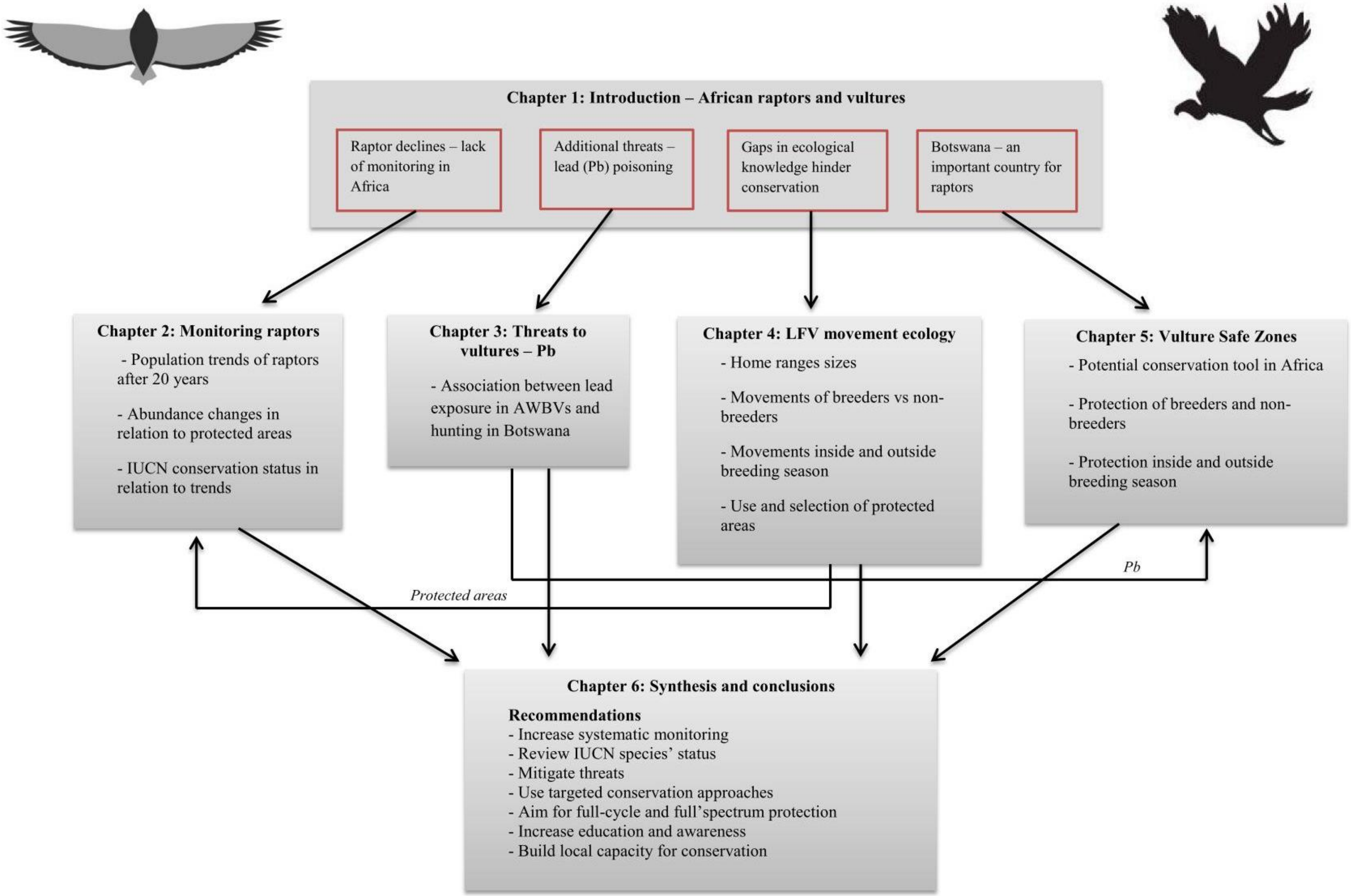


Figure 4. Schematic diagram showing the flow of information between chapters 1-6.

Chapter 4 examines the ranging behaviours and use of protected areas by adult lappet-faced vultures using data collected from individuals that were captured and GPS-tagged at different locations across Botswana. This chapter aims to fill knowledge gaps on lappet-faced vulture movement ecology, in particular, to explore differences between space and habitat use of breeding and non-breeding individuals both inside and outside of the breeding season, with special reference to protected area use. Information from this chapter will help determine firstly, where lappet-faced vultures range and their range sizes; and secondly, whether space use and range size differs between breeders and non-breeders inside and outside of the breeding season, and thirdly; whether use or selection of protected areas differs by breeding status and breeding season. These findings provide information on whether conservation approaches need to differ for different sectors of a population, and additionally, whether they need to be further adapted in accordance with seasonality. Findings will also inform against Aichi Target 12 (see above).

Chapter 5 builds upon the information provided by chapter 4 and uses the GPS tag data to assess whether Vulture Safe Zones (VSZs), as used for targeting vulture conservation action in Asia, could be a viable conservation approach for lappet-faced vultures in Botswana. The GPS tag data were used to calculate the proportion of each individual's use for all 1-degree grid-squares within Botswana. This chapter then uses these data to examine whether VSZs are firstly, appropriate for use with such a wide-ranging species (i.e., the proportion of fixes that a manageable number and size of VSZs would protect), and secondly, whether they would offer equal levels of protection for different sectors of a population (breeding and non-breeding birds). These findings will be important for determining whether VSZs could be effective for helping to protect and thus help stop the decline of lappet-faced vultures. The study aims to act as a framework that can be applied to other tracking data from other species of vultures to explore the efficacy of such an approach. Findings from this chapter will also contribute to achieving Aichi Target 12 (see above), but could also help inform against Target 11 in relation to increasing terrestrial protected areas or other effective area-based conservation measures integrated into wider landscapes by 2020.

Chapter 6 (discussion chapter) discusses the findings of chapters 2-5 in a wider context and links the key findings to conservation practice. In doing so, this study aims to provide vital information that is needed to fill some of the knowledge gaps that are currently hindering adequate conservation measures of vultures and raptors within the region, and sets out recommendations for some of the key future research and conservation actions that should be implemented in order to safeguard the conservation of these important species in Botswana and the wider region.

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Chapter 2:

Raptor population trends in northern Botswana: a re-survey of road transects after 20 years

"It's a Tawny thing"

Abstract

Across Africa, many raptor species, especially vultures, are in steep decline. Botswana is regionally important for numerous raptor species including vultures, but recent population trends of raptors within this country are totally unknown. In 2015-2016 I repeated road transects for raptors across northern Botswana that were first conducted in 1991-1995. In total, I re-surveyed 20,712 km of transects from the original study. From these data I explored changes in abundance of 29 species. Fourteen species (48%) showed significant declines. Of these, 11 species declined by >50% and three species declined by 37-50%. Non-significant declines of >70% were shown for four species, of 30-65% for six species and of <10% for a further two species. In contrast, only three species, all large eagles – tawny eagle *Aquila rapax*, brown snake eagle *Circaetus cinereus* and black-chested snake eagle *Circaetus pectoralis*, showed significant but small increases of between 6-15%. For most species, population trends were similar both inside and outside of protected areas, with only two species showing significantly different trends. Declines of bateleur eagle *Terathopius ecaudatus* were lower inside protected areas, whereas brown snake eagles showed stable populations inside protected areas but large increases outside of protected areas. These re-surveys suggest extremely worrying trends for multiple raptor species in Botswana, and highlights the benefit of repeating historical surveys to understand population trends in countries that lack systematic monitoring of wildlife populations.

Introduction

Africa has some of the highest human population growth rates in the world (United Nations, 2015) resulting in unprecedented pressure on wildlife resources (Blom et al., 2004; Moinde-Fockler et al., 2006; Woodroffe and Ginsberg, 1999). However, wildlife monitoring in Africa is less established than in more developed regions, although wildlife trends appear to be following patterns of global declines (Blom et al., 2004; Caro and Scholte, 2007; Ogutu et al., 2011). Global wildlife population declines are principally driven by anthropogenic threats associated with increasing human populations and development (Balmford et al., 2001; Darkoh, 2003; McManus et al., 2015; Ogada, 2014; Remis, 2009; Thuiller et al., 2006) and therefore African wildlife is increasingly at risk from growing human encroachment.

Bird species across the world are declining (BirdLife International, 2013), with scavengers and carnivores showing some of the greatest declines (Buechley and Sekercioğlu, 2016; Ogada et al., 2012). Within Africa, these patterns have also been apparent, with large declines in many raptor species (Amar et al., 2015; Ogada et al., 2015; Virani et al., 2011). African vultures in particular, appear to have suffered disproportionally large declines in recent decades, with many now describing the situation as an African vulture crisis (Krüger et al., 2014; Ogada et al., 2015) akin to that seen in Asia over the last 20 years (Green et al., 2004; Prakash et al., 2003). These declines have been reflected in the elevated threat status of many African vulture species by the International Union for the Conservation of Nature (IUCN) (IUCN, 2017; Ogada et al., 2015). However, our understanding of vultures' continental status suffers from knowledge gaps on population trends across many areas of the continent, including within many southern African countries outside of South Africa (Anderson, 2007; Monadjem et al., 2004).

Our current knowledge of raptor population trends in southern Africa comes from repeat atlas surveys (Amar et al., 2015; Hofmeyr et al., 2014) or repeat nesting surveys (Amar et al., 2015; Borello and Borello, 2002; Bridgeford and Bridgeford, 2003; Krüger et al., 2014). However, across Africa, road transects provide the main source of historical information for the greatest number of raptor species covering the largest areas (Ogada and Keesing, 2010; Thiollay, 2007a, 2006a; Virani et al., 2011). These types of surveys are particularly suitable for raptors, which often occur at low densities (Buij et al., 2013; Keys et al., 2012; Virani et al., 2011).

Within Africa, the protected area network is a primary strategy for species conservation (Burgess et al., 2007; Chape et al., 2005). Although not immune to threats (López-López et al., 2007; Pérez-García et al., 2011; Thiollay, 2006b), protected areas may buffer raptor populations from some of the key drivers of declines (Amar et al., 2015; Herremans and Herremans-Tonnoeyr, 2000; Thiollay, 2007a). Because of this, protected areas may be particularly important for raptors (Buij et al., 2013; Herremans, 1998; Ogada et al., 2015; Thiollay and Meyburg, 1988), especially as refuges for rare and threatened species (Sinclair et al., 2002; Turner et al., 2006). For example, the critically endangered' white-headed vulture *Trigonoceps occipitalis* exists almost exclusively within protected areas (Murn et al., 2016). For species like this, along with species that rely on protected areas for breeding habitat, protected areas are likely crucial for their survival. However, they may have limited value for wide ranging species that spend much of their time outside of protected areas (Arroyo et al., 2002; Greyling, 2008; Lambertucci et al., 2014; Phipps et al., 2013; Van Eeden et al., 2017).

Botswana's low human population (2.3 million) and large proportion of protected areas (20%) and Wildlife Management Areas (WMAs) (20%) (Central Statistics Office, 2012; Kootsositse et al., 2009) make it an important country for African raptor populations (Herremans and Herremans-Tonnoeyr, 2000). The country supports a number of raptors species listed by the IUCN as threatened; including the Vulnerable martial eagle *Polemaetus bellicosus* and secretarybird *Sagittarius serpentarius*, and migrant species such as the steppe eagle *Aquila nipalensis* (Endangered). It also holds important populations of five species of vultures, all of which are either endangered or critically endangered (IUCN, 2017).

No systematic monitoring of raptors currently occurs in Botswana, but historical raptor road transects carried out in 1990-1995 by Herremans and Herremans-Tonnoeyr (2000) provide a unique baseline survey to explore changes in the abundance of raptors in this region over the last 20 years. In this study I repeat a proportion of Herremans and Herremans-Tonnoeyr (2000) (herein after referred to as Herremans') transects in northern Botswana during 2015-2016. I also explore whether changes in abundance differ inside or outside of protected areas, as has been found elsewhere (Thiollay, 2007b).

Methods

Study Area

Botswana covers an area of c. 580,000 km^2 (FAO, 2017) (Figure 1). The country has amongst the lowest densities of people globally at around 2.3 million (World Population Review, 2017). Forty percent of the country is designated for the conservation of wildlife through protected areas (20%) and Wildlife Management Areas (WMAs) (20%) (Mbaiwa, 2005). Around half of the country is communal land, with agriculture (mostly free ranging livestock rearing) being the most predominant land use outside of protected areas (Central Statistics Office, 2013). Rainfall occurs in the Austral summer between November and April (the wet season) and ranges from an average of 250 mm in the south-west to 650 mm in the north and north-east (Barnes, 2001). During the wet season temperatures are high (18-45°C). Rain ceases between May and October (the dry season) and temperatures are much lower between May and August (-5-25°C). My repeat surveys were conducted in the north of Botswana (north of latitude -22°) which is an area of around 240,000 km^2 (Figure 1). It encompasses the majority of land mass designated as protected areas and six of the twelve nationally designated Important Bird Areas (Kootsositse et al., 2009). Around 25% of the national human population lives in northern Botswana (Statistics Botswana, 2011). The north of the country also holds around 30% of the country's traditionally farmed livestock populations and a much higher concentration of wildlife than the south (Statistics Botswana, 2015a, 2015b).

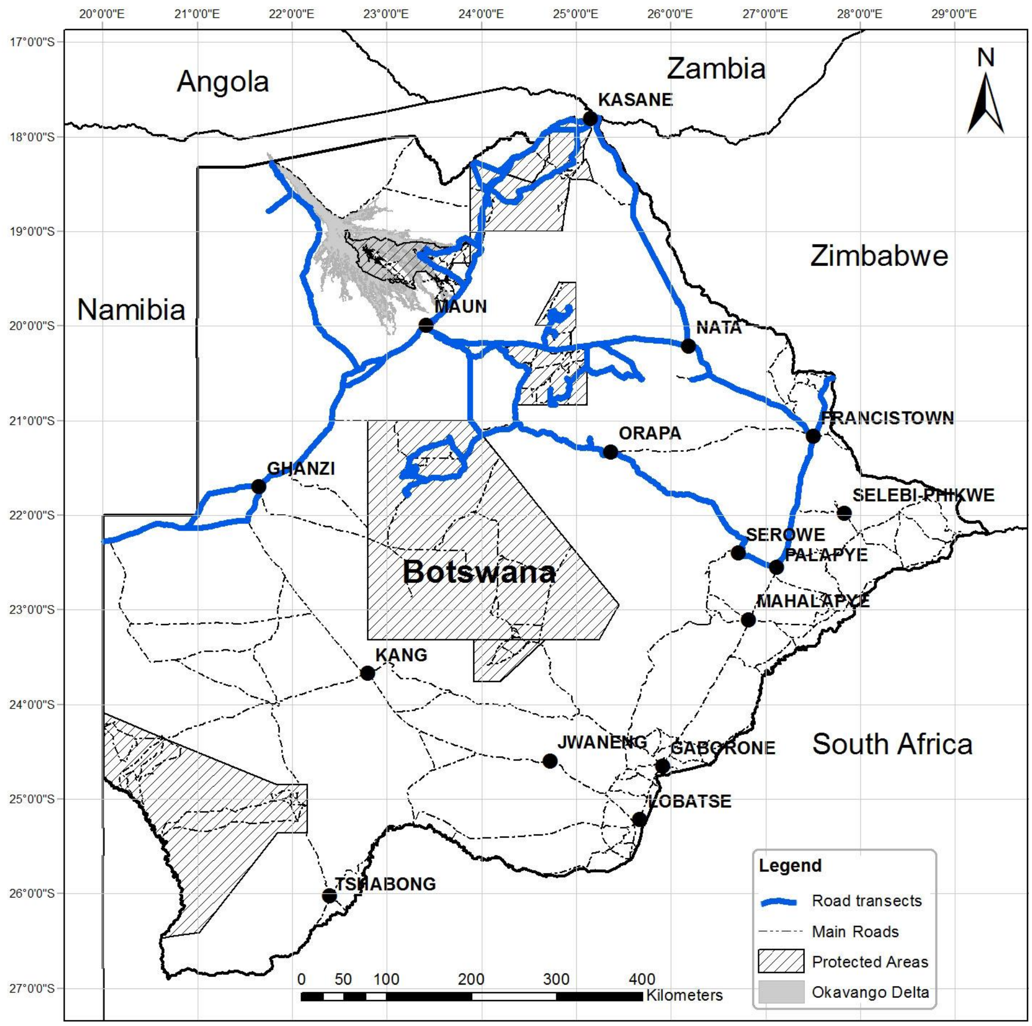

Figure 1. Map of study area – Botswana and bordering countries, showing main towns and paved roads. In bold are the 20,712 km driven over 96 separate road transects, which were then subdivided into 243 transects that were attributed to different Degree Grid Squares (DGSs). The grid reference overlay shows 1-degree grid squares (decimal degrees) that were used as reference points for data recording and analyses in the original surveys and the repeat surveys. DGSs and route descriptions were used to repeat original survey routes. A DGS was distinguished as the degree square lying SE of the meeting point of the south and easterly coordinates (e.g., S18° E24°).

Road Transects

I repeated Herremans' (2000) raptor road transects in northern Botswana (Figure 1) in 2015-2016. I aimed to repeat these surveys using the same approach as the original surveys in all respects. I used the original data to help facilitate repetition of the surveys to match them as closely as possible both in time and in space. The original surveys covered the whole of Botswana and comprised a total of 55,577 km of transects. However, due to logistical and time constraints, I resurveyed only those transects in the north of the country. The northern transect included the 1-degree grid-squares (DGSs) north of latitude -22°; with the exception of 4 DGSs (latitude of -23°) that were included in the study because some of the main transects briefly passed through them. The original survey in northern Botswana covered 28,864 km of transects. It encompassed both the wet (16 October-15 April) and dry (16 April-15 October) seasons, and I attempted to match the re-surveys of specific transects with the months when the original transects were completed. To repeat the transects I followed Herremans' (2000) route descriptions and the DGSs associated with them.

A driver and additional observer (in the passenger seat) drove the transects and recorded all diurnal raptors sighted, including perched or flying birds. I used the same vehicle (Toyota Hilux 4x4 double cab) throughout the study, which was very similar to that used in the early surveys (Nissan one-tonner). I recorded the GPS location and species observed for each sighting. I conducted transects during daylight hours between 0630 and 1830 following Herremans' (2000) study, and in keeping with their surveys I began transects later in the winter to allow for thermaling and therefore improved visibility of larger raptors when using thermals rather than when perched. All GPS tracks were saved to ensure future repeatability. The principle driver/observer remained the same for all transects, but seven secondary observers were used. As with Herremans' (2000) study I recorded all raptors seen with the naked eye, only stopping and using binoculars (8x42) and a digital camera with a 500 mm optical zoom to help with species identification.

Individual transect routes varied from 65 km to 585 km (Table 1). Each transect route followed that of the original study; however, distances varied slightly due to changes in road networks over time and due to interpretation of original transect route descriptions (no GPS coordinates were available 20 years ago during the original surveys). I did not repeat a transect route during the same day, but several routes were repeated on different days as in the original surveys. Average speed driven was 42 km/h but differed depending on terrain. I followed the speeds used during the original surveys of 20 km/h for sand/gravel roads and 59 km/h for paved roads.

Raptors counted along transects were sub-divided by the DGS (c. 100 km x 100 km) through which they passed (Figure 1), as did the Herremans' (2000) surveys. I recorded data from transects conducted on different dates in the same DGSs separately. To differentiate between transects inside and outside of protected areas (PAs), individual sub-transects (because some full transects passed through protected and non-protected areas) were allocated protected or non-protected status. Classification of PA and Non-PA transects for both the original and current surveys were based upon the current distribution of official government protected areas only. Protected area (national parks) boundaries have remained the same since the original study.

Table 1. Summary of distances (km) and numbers of transects (separated by 1-Degree Grid Square; DGS) driven in early (Herremans' surveys) and late surveys (my surveys) in protected and non-protected areas and numbers of raptors observed in protected and non-protected areas in both surveys.

	Early **surveys 1991-1995**				Late **surveys 2015-2016**			
	Total km driven	No. of transects driven by DGS	Av. no. of km driven per transect	No. of raptors observed	Total km driven	No. of transects driven by DGS	Av. no. of km driven per transect	No. of raptors observed
Protected areas	6,502 km	83	78 km	3,913	4,982 km	45	110 km	1,328
Non-protected areas	22,362 km	330	67 km	6,707	15,730 km	198	79 km	3,137
Total	28,864 km	413	-	10,620	20,712 km	243	-	4,465

Statistical Analyses

I categorised data into two time periods, 'Early' (Herremans' (2000) survey: 1991-1995) and 'Late' (my repeat survey: 2015-2016). I expressed species abundance for each period as the number of birds per 100 km with 95% confidence intervals, and only species for which ≥10 individuals were counted in the early surveys were examined.

I performed all statistical analyses in R version 3.3.0 (R Core Team, 2016) and used a Generalised Linear Mixed Model (GLMM) to test whether the abundance of each species had changed between the two survey periods. Models examined the count of each species along each DGS transect survey as the response variable, with the period (Early or Late) as the explanatory variable. I controlled for variable lengths of each transect within the DGS by including the log of the transect length (in km) as an offset. I logged the offset term because models were fitted with a log-link function. The specific DGS through which a transect passed was fitted as a random term in the model to account for the lack of independence of transects that traversed the same DGS. To test for differences in overall raptor abundance between the early and late surveys, the total count of all species was fitted as the response variable and period (Early or Late) as the explanatory variable.

Because count data often have a Poisson or Negative Binomial distribution and can be zero-inflated (Linden and Mantyniemi, 2011), I explored the best fitting distribution for each species and analysis, initially exploring six distributions: a zero-inflated or non-zero-inflated Poisson, Negative Binomial, or Negative Binomial with NB2 parameterization (variance $= \mu(1 + \mu/k)$). I ran all models within the 'glmmADMB' package (Fournier et. al, 2012) and used Akaike's Information Criterion (AIC) within the 'bblme' package (Bolker, 2016) to rank the models to select the model with the most appropriate distribution. I used the top model for each species in the analysis for each species (Appendix 1). I examined significance for the 'Period' term in each analysis using the 'car' package (Fox and Weisberg, 2011). I estimated means and 95% confidence intervals (CI) using the Predict Function for each period from the model outputs.

I ran an additional analysis using the same model framework to explore whether abundance change for each species differed inside or outside of protected areas. For this analysis I added PA status as the fixed effect (PA or Non PA) and its interaction with Period (Early or Late) to examine the significance of the interaction term.

To explore whether the probability of a species declining significantly differed according to their IUCN conservation status, I explored whether a species had declined significantly as a binary (yes, no) response variable and fitted the conservation status of the species as a two category explanatory variable (1 = least concern, 2= red listed, i.e., either Near-threatened, Vulnerable, Endangered or Critically Endangered), only two categories were used in this analysis due to the limited number of species in the different categories. Models were fitted using a Generalised Linear Model (GLM) with a binomial distribution in the 'lme4' package (Bates et al., 2015).

Results

Changes in abundance between 1991-1995 and 2015-2016

The total number of raptors declined significantly (40%) between the early and late surveys (X^2 = 23.5, df = 1, p <0.0005).

I collected sufficient data to examine abundance changes between the two surveys for 29 raptor species; 14 (48%) showed significant declines, two showed near significant declines (P < 0.1) and three (10%) showed significant increases (Table 2). The remaining 10 species showed no significant changes (Table 2, Appendix 3.a-e).

Two of the four vulture species examined showed large significant declines, lappet-faced vultures *Torgos tracheliotos*: 61%; white-headed vultures *Trigonoceps occipitalis*: 78% (Table 2, Appendix 3.b & 3.d). For hooded vultures *Necrosyrtes* monachus declines were large (79%) but not significant (Appendix 3.d). African white-backed vultures *Gyps africanus* showed smaller non-significant declines of 33% (Table 2, Appendix 3.a).

Three species of eagles showed significant, if relatively small increases: (tawny eagle *Aquila rapax*: 6%; brown snake eagle *Circaetus cinereus*: 15%; black-chested snake eagle *Circaetus pectoralis*: 12% (Table 2, Appendix 3.b & 3.c). These were the only species in the study to show significant increases. Three other species of eagle, along with the secretary bird (78%) showed large, significant declines: bateleur eagle *Terathopius ecaudatus*: 53%; African fish eagle *Haliaeetus vocifer*: 63%; and African hawk eagle *Aquila spilogaster*: 87%) (Table 2, Appendix 3.a, b & e).

Two small species of raptor showed significant declines in abundance: black-shouldered kite *Elanus axillaris*: 73% and shikra *Accipiter badius*: 87%) (Appendix 3.b & 3.c). The sample size for lizard buzzards *Kaupifalco monogrammicus* was too small for any statistical comparison; but was almost completely absent (n=1) in the later surveys compared to the earlier surveys (n=10).

Three of the four resident falcon species showed significant declines (greater kestrel *Falco rupicoloide*: 37%; lanner falcon *Falco biarmicus*: 50%; red-necked falcon *Falco chicquera*: -

88%), with the later demonstrating the greatest decline of all resident species (Table 2, Appendix 3.b & 3.c). Dickinson's kestrel's *Falco dickinsoni* also declined (72%), but this was non-significant (p = 0.056) (Table 2, Appendix 3.e).

I explored changes for two intra-African migrants. Wahlberg's eagle *Hieraaetus wahlbergi* showed a non-significant decline (62%) (p = 0.063); whereas I found no significant change in abundance for yellow-billed kite *Milvus aegyptius*, (Table 2, Appendix 3.a & 3.c).

Three of the four Palaearctic migrant species declined significantly (steppe eagles *Aquila nipalensis*: 81%; steppe buzzards *Buteo vulpinus*: 46%; lesser kestrels *Falco naumanni*: 96%. Lesser kestrels displayed the greatest decline for all species (Table 2, Appendix 3.b & 3.d). Lesser spotted eagles *Clanga pomarina*, showed a non-significant decline, but with very few counted in the late surveys (n = 3), (Table 2, Appendix 3.d).

Although I could not examine the changes statistically due to the small sample sizes, I observed no Montagu's harriers *Circus pygargus* or pallid harriers *Circus macrourus* during the later surveys, contrasting with the earlier surveys (n = 24 and 11 respectively).

Table 2. Estimated mean number of individuals per/100 km with 95% confidence intervals (shown in brackets) for each of the 29 species for which abundance could be compared between the early and late surveys in northern Botswana. Estimates per/100km are shown for both survey periods (early/late). Estimates come from a GLMM model fitted with either a zero-inflated or non-zero-inflated negative binomial or poisson distribution (Appendix 2). Percentage of decline/increase was calculated using species sample sizes from raw data from early and late surveys. Sample size for each species in each of the early and late surveys, as well as significance of abundance change between the two surveys is shown. The IUCN Red List conservation status of each species is included. Species are grouped by size, with migrant species grouped separately. Species with significant changes in abundance are shown in bold.

	IUCN Status	% of decline/increase	**1991-1995** Birds/100km	*n*	**2015-2016** Birds/100km	*n*	χ^2	*df*	*p*
Vultures									
White-headed vulture	**CR**	**-78%**	**0.06 (0.01,0.23)**	**60**	**0.02 (0.004,0.12)**	**13**	**5.28**	**1**	**0.0215**
Lappet-faced vulture	**EN**	**-61%**	**0.65 (0.46,0.91)**	**195**	**0.34 (0.19,0.61)**	**75**	**8.46**	**1**	**0.0036**
African white-backed vulture	CR	-33%	7.29 (5.11,10.40)	2606	6.94 (4.59,10.48)	1741	0.17	1	0.6733
Hooded vulture	CR	-79%	0.05 (0.009,0.26)	157	0.02 (0.002,0.12)	32	2.6	1	0.1031
Large raptors									
Bateleur eagle	**NT**	**-53%**	**2.02 (1.35,3.01)**	**888**	**1.28 (0.79,2.06)**	**410**	**15.31**	**1**	**0.0002**
Tawny eagle	**LC**	**+6%**	**0.66 (0.48,0.92)**	**226**	**0.93 (0.63,1.36)**	**241**	**6.89**	**1**	**0.0086**
African fish eagle	**LC**	**-63%**	**0.25 (0.08,0.72)**	**292**	**0.12 (0.03,0.42)**	**108**	**12.40**	**1**	**0.0004**
Brown snake eagle	**LC**	**+15%**	**0.32 (0.21,0.48)**	**120**	**0.50 (0.32,0.80)**	**138**	**9.120**	**1**	**0.0025**
Black-chested snake eagle	**LC**	**+12%**	**0.19 (0.14,0.26)**	**58**	**0.30 (0.19,0.45)**	**65**	**5.76**	**1**	**0.0163**
African hawk eagle	**LC**	**-87%**	**0.04 (0.01,0.13)**	**40**	**0.01 (0.001,0.05)**	**5**	**7.61**	**1**	**0.0057**
Secretary bird	**VU**	**-78%**	**0.07 (0.02,0.24)**	**59**	**0.02 (0.004,0.09)**	**13**	**9.71**	**1**	**0.0018**
Martial eagle	VU	-52%	0.14 (0.08,0.22)	46	0.09 (0.04,0.19)	22	2.19	1	0.1383
Small-medium resident raptors									
Black-shouldered kite	**LC**	**-73%**	**0.38 (0.21,0.68)**	**100**	**0.10 (0.04,0.26)**	**27**	**13.62**	**1**	**0.0002**
Shikra	**LC**	**-87%**	**0.29 (0.19,0.45)**	**99**	**0.04 (0.02,0.11)**	**12**	**29.66**	**1**	**0.0005**

Table 2 continued.

	IUCN Status	% of decline/increase	**1991-1995** Birds/100km	*n*	**2015-2016** Birds/100km	*n*	χ^2	*df*	*p*
Small-medium resident raptors									
Pale chanting goshawk	LC	-4%	0.43 (0.21,0.86)	219	0.46 (0.21,0.97)	209	0.15	1	0.6968
Dark chanting goshawk	LC	-42%	0.15 (0.09,0.25)	52	0.11 (0.05,0.23)	30	1.28	1	0.2571
Gabar goshawk	LC	-1%	0.15 (0.07,0.30)	64	0.15 (0.06,0.35)	63	0.01	1	0.9152
African harrier hawk	LC	-36%	0.05 (0.02,0.11)	22	0.04 (0.01,0.12)	14	0.17	1	0.6771
African marsh harrier	LC	-30%	0.01 (0.002,0.03)	10	0.01 (0.002,0.09)	7	0.29	1	0.588
Falcons									
Lanner falcon	**LC**	**-50%**	**0.20 (0.11,0.35)**	**63**	**0.10 (0.04,0.24)**	**31**	**5.22**	**1**	**0.0222**
Greater kestrel	**LC**	**-37%**	**0.68 (0.31,1.46)**	**327**	**0.42 (0.18,0.98)**	**204**	**8.39**	**1**	**0.0037**
Red-necked falcon	**LC**	**-88%**	**0.08 (0.03,0.16)**	**17**	**0.009 (0.001,0.07)**	**2**	**6.22**	**1**	**0.0125**
Dickinson’s kestrel	**LC**	-72%	0.003 (0.001,0.05)	22	0.001 (0.0008,0.06)	6	3.49	1	**0.0615**
Migrants									
Steppe eagle	**EN**	**-81%**	**0.24 (0.11,0.52)**	**52**	**0.04 (0.01,0.15)**	**10**	**12.15**	**1**	**0.0004**
Steppe buzzard	**LC**	**-46%**	**0.68 (0.50,0.92)**	**153**	**0.38 (0.21,0.68)**	**82**	**5.24**	**1**	**0.0220**
Lesser kestrel	**LC**	**-96%**	**0.11 (0.03,0.22)**	**105**	**0.01 (0.001,0.12)**	**4**	**33.22**	**1**	**0.0013**
Yellow-billed kite	LC	-28%	4.37 (2.32,8.20)	4019	3.13 (1.16,8.44)	766	2.53	1	0.1112
Wahlbergs eagle	LC	-62%	0.15 (0.08,0.27)	64	0.08 (0.03,0.20)	24	3.44	1	0.0632
Lesser spotted eagle	LC	-97%	0.10 (0.01,0.29)	135	0.01 (0.0001,0.14)	3	1.76	1	0.1835

LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered.

Species that were currently listed as ‘extinction prone’ on the Red List were no more likely to have declined significantly than those listed as Least Concern ($X^2 = 0.90_{(39.2)}$, $p = 0.34$), (Figure 2).

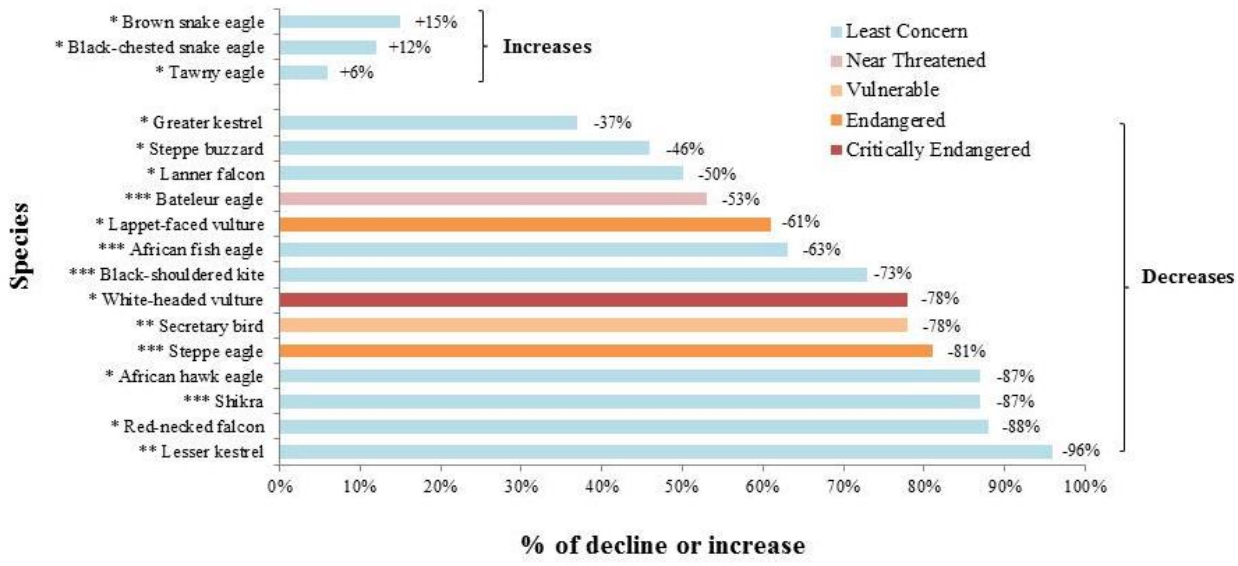

Figure 2. Percentages of significant declines and increases in relation to IUCN conservation status of all raptor species that showed significant changes in abundance between the early and late surveys in northern Botswana. * = $p \leq 0.05$, ** = $p \leq 0.001$, *** = $p \leq 0.0005$.

Changes in abundances inside and outside of protected areas

Abundance of all raptors combined, inside or outside of protected areas, differed significantly between the early and late surveys ($X^2 = 5.1$, df = 1, $p = 0.02$). The total abundance of all raptors was lower in the late surveys both inside and outside of protected areas. The overall decline between early and late surveys was much larger inside protected areas (57%) ($X^2 = 19.1$, df = 1, $p < 0.0005$) than outside of these areas (25%) ($X^2 = 8.1$, df = 1, $p = 0.004$), and both were significant.

Table 3. Comparison of mean number of birds/100 km with 95% confidence intervals (shown in brackets) from early and late surveys, inside and outside of protected areas in northern Botswana. Estimates come from the GLMM output that was fitted with a zero-inflated and non-zero-inflated negative binomial distribution (Appendix 2) and with the interaction period (early or late surveys)*PA (protected area status) as the explanatory variable. Species sample sizes from the respective surveys are shown and species that had significantly different abundance inside vs outside of protected areas between the early and late surveys are shown in bold.

	1991-1995		**1991-1995**		**2015-2016**		**2015-2016**				
	Birds/100km Protected	*n*	Birds/100km Unprotected	*n*	Birds/100km Protected	*n*	Birds/100km Unprotected	*n*	X^2	df	*p*
Bateleur eagle	**2.73** (1.71, 4.37)	397	**1.96** (1.08, 3.55)	491	**2.37** (1.32, 4.21)	201	**0.94** (0.37, 2.40)	209	6.98	1	**0.08**
Brown snake eagle	**0.36** (0.06, 0.33)	57	**0.29** (0.05, 0.57)	63	**0.35** (0.14, 2.23)	34	**0.58** (0.006, 0.72)	104	5.61	1	**0.01**

From the 29 species I examined, only two showed significantly different trends inside or outside of protected areas (PAs) (Table 3). Bateleur eagles showed large and significant declines outside of PAs (70%) ($X^2 = 17.3$, df = 1, p <0.0005), but had lower, non-significant declines inside PAs (35%) (p = 0.28). In contrast, brown snake eagles showed very small, non-significant (p = 0.55) declines inside PAs (6%) and significant large increases outside of PAs (52%) ($X^2 = 13.1$, df = 1, p = 0.0002), (Table 3).

Discussion

Changes in abundance of raptors and their status in Africa

My repeat surveys revealed that 14 out of 29 raptor species (48%) declined significantly over the last 20 years in northern Botswana. The abundance of many of these species displayed substantial declines, with eleven species showing significant declines of over 50% and three species showing significant declines of between 37% and 50%. There were many species which also showed large but non-significant declines, four of which declined by over 70% and six declined by between 30% and 65%. The remaining two species surveyed showed small non-significant declines of less than 10%. These declining species spanned a wide range of groups, from vultures and large eagles to smaller raptors and falcons. I recorded declines for both resident and migrant species, including both intra-African and Palaearctic migrants. It therefore appears likely that declines are driven by factors that affect a wide range of species with different life history and behavioural traits.

My study suggests that along with many other parts of Africa, Botswana's raptor populations are declining. Vultures in particular are in dramatic decline across Africa (Buechley and Sekercioğlu, 2016; Ogada et al., 2015; Thiollay, 2007a; Virani et al., 2011), and the abundance of two of the four species of vulture in this study (white-headed and lappet-faced vulture), showed large and significant declines (78% and 61%). These levels of decline were similar to those recorded for these species elsewhere in Africa (summarised in Ogada et al., 2015). Hooded vulture in my study also showed apparent declines (79%), which whilst non-significant, were in keeping with the levels of decline seen for this species in other parts of Africa (Ogada et al., 2015). For white-backed vultures, non-significant declines of 33% were observed, although the gregarious nature of this species when foraging makes it challenging to detect significant changes unless sample sizes are large, breeding populations are monitored, or declines are substantial (Linden and Mantyniemi, 2011; Murn and Botha, 2016; Royle, 2004). Nonetheless, these potential declines could have severe conservation implications for this critically endangered species. The same applies to declines of lesser-spotted eagles, yellow-billed kites and Dickinson's kestrels, which although were all non-significant, were extremely large (over 70%). Severe declines and complete disappearances of Palaearctic migrants in my surveys mirrors the situation in West Africa (Thiollay, 2007a). The large decline of some smaller raptors contrasted with Thiollay's (2007a) surveys, which found their declines to be more moderate in comparison with larger species. However, results from the more recent Southern African Bird Atlas Projects (SABAP) indicate that both large and smaller raptors are experiencing severe regional declines (Underhill and Brooks, 2014). Although Wild Bird Indices recently obtained from surveys in Botswana do not directly relate to raptor population trends, the findings showed more positive trends than those from my surveys, with around half of wild bird species showing significant increases in abundance between 2010 and 2015 (Wotton et al., 2017). This may suggest that raptors in Botswana are suffering disproportionately more than other bird species.

The only species to register increases were all resident eagles: the brown snake eagle, black-chested snake eagle and tawny eagle. These increases are in general contrast to other studies examining their trends in other regions of Africa. For example, Thiollay (2006a) found significant declines for all three species, with brown snake eagle and tawny eagle showing some of the largest declines of all raptor species in West Africa. Preliminary findings from comparisons between SABAP 1 and 2 suggest that tawny eagles are declining throughout the region, but that distributions of brown and black-chested snake eagles' could be shifting (Underhill and Brooks, 2014). In cases where seasonal fluctuation in eagle populations have occurred, regional shifts across their range might potentially be mis-interpreted as population increases (Herholdt, 2006). This might not explain the apparent increases recorded in this study however, since transects were repeated during the same months; although these fluctuations might be exacerbated by differences in prevailing environmental conditions at the time of surveying. Rainfall during my repeat surveys was considerably higher (av.172 mm p/year) than during the earlier surveys (av.76 mm p/year). Increased annual rainfall has been associated with increased eagle populations and further variations in inter-annual rainfall can also drive raptor population fluctuations (Wichmann et al., 2003). Thus, environmental differences between surveys may still explain the apparent increase in these three eagle species.

Raptors and protected areas

Levels of decline for most species were similar inside and outside of protected areas. Only two species showed changes in abundance that differed significantly inside vs outside of protected areas. These results contrast with several other studies that have found population declines are often buffered inside protected areas. For example, Thiollay (2006a) found that declines of most species across large regions of West Africa were far more severe outside of protected areas. I found this to be the case for only one species, the bateleur eagle, that declined by 70% outside of protected areas as appose to only 35% inside protected areas. Other trend data for this species is generally lacking, but the SABAP surveys identified bateleur eagles as being amongst the most rapidly declining species in South Africa (Underhill and Brooks, 2014). As with many other scavenging raptor species, bateleur eagles are at high risk of mortality from poisoning (Botha et al., 2015; Ogada, 2014) and are particularly sensitive to anthropogenic activity (Herholdt et al., 1996; Virani et al., 2011). The increase in poison use by poachers targeting vultures could be negatively affecting this species both inside and outside of protected areas (Ogada et al., 2016). For brown snake eagles, patterns of abundance change inside and outside of protected areas were different to the bateleur eagle. Brown snake eagles showed large increases outside of protected areas, but stable populations inside of protected areas. It therefore appears that this species may be reacting to changes outside of protected areas. The different feeding strategies of bateleur and brown snake eagles could explain their different patterns of change. Feeding strategies are known to influence species abundance inside and outside of protected areas (Greve et al., 2011). For example, food opportunities for brown snake eagles may have increased outside of protected areas but decreased for bateleur eagles in the same areas. Higher rainfall during my surveys could have influenced prey availability for both species. Wotton et al., (2017) reported abundance increases of wild birds in Botswana inside and outside of protected areas, but increases outside protected areas were twice as high as those found inside of them. Although, no direct comparisons can be made with this study in terms of raptor abundance trends, it does suggest that land outside of protected areas may be more important for national bird populations. However, raptors have vastly different ecological requirements to other avian species and thus their conservation is largely independent.

Conservation status of raptors

Raptor populations are suffering globally. However, despite most of the species analysed in this study being listed as least concern in the IUCN's Red List, nearly 40% of them showed significant declines and their global threat status was not reflected in abundance trends of species within Botswana. The large decline of numerous species of least concern illustrates the urgent need to re-visit conservation classification of raptors that currently sit within this category. However, the continued large declines of several species already recognised as endangered or critically endangered such as lappet-faced and white-headed vultures are extremely concerning in a global context, given their already suppressed global populations. Even though declines of the critically endangered hooded and white-backed vulture were not significant, their overall declines, including declines of 79% for hooded vultures are alarming. My results therefore reinforce the dire conservation status of African raptors and the urgent necessity for swift conservation action (Amar et al., 2018).

Key threats and the decline of raptors

Livestock numbers in Botswana appear to have increased significantly since the early surveys (Botswana Dept. of Wildlife and National Parks, 2015). Overgrazing can be detrimental to raptor populations (Amar et al., 2011; Anadón et al., 2010; Darkoh, 2003) and can have negative impacts on the structural diversity of important habitats (Kairis et al., 2015; Pei et al., 2008). The impacts of agriculturally transformed habitats can vary according to species. For example, some species may benefit from increased food abundance (Balbontín et al., 2008; Olea and Mateo-Tomás, 2009) and improved reproductive performance (Murgatroyd et al., 2016) in agricultural landscapes, whereas others may struggle to adapt to severely transformed natural habitats (Arroyo et al., 2002; Herremans, 1998). Nonetheless, intensely grazed landscapes are largely associated with overall loss of biodiversity caused by poor quality habitats (Darkoh, 2003; Diniz-Filho et al., 2009) and are likely an increasing threat for most raptor species (Herremans, 1998). Alongside increasing livestock numbers in Botswana, encroachment of livestock into PAs and in particular WMAs has also been apparent (Botswana Dept. of Wildlife and National Parks, 2015). Consequently, important habitat within areas designated for wildlife conservation could be deteriorating and causing observable population declines. Observed decreases in species richness and diversity within WMAs associated with influxes of cattle further supports this (Wallgren et al., 2009). However, domestic livestock also provides an important food source for scavenging raptors (Murn and Anderson, 2008; Olea and Mateo-Tomás, 2009), and thus increasing populations may result in increased food availability for some of the species I surveyed. The decline of scavenging raptors in my surveys however, suggests that any such potential benefit is being outweighed by other negative factors (e.g., poisoning).

Evidence suggests that climate change has or will influence distributions and migration patterns of birds (Gordo et al., 2005; Huntley et al., 2006; Visser et al., 2009; Jones and Cresswell, 2010). Changes in range sizes, timing of arrival at breeding or wintering grounds and avoidance of areas with decreasing productivity are some of the factors that can lead to species shifts (Balbontín et al., 2008; Erasmus et al., 2002), and could have caused some of the observed declines in my study. For migratory birds in particular climate change can have profound effects (Hurlbert and Liang, 2012; Jones and Cresswell, 2010) and this may explain why pallid and Montagu's harriers were completely absent in my repeat surveys, and others (lesser kestrel) showed very large declines. In contrast, Wild Bird Indices from Botswana showed an increasing trend of some Afro-Palearctic migrant bird species over a five year period (2010-2015), but no specific abundance trends of raptors were reported in this study to use as a comparison (Wotton et al., 2017). Different ecological characteristics of individual species may explain interspecific variation in responses to climate change. The impacts of climate change may, in theory, act equally within and outside of protected areas, and thus if climate change is one of the factors influencing the trends in this study, this might explain why trends for most species were similar between these areas. Evidence for the capacity of protected areas to buffer the effects of climate change however is conflicting (Gillingham et al., 2015; Virkkala et al., 2014). The impacts of climate change on African raptor populations has received relatively little attention thus far (Phipps et al., 2017; Wichmann et al., 2005, 2003), but is an area that does warrant further investigation.

The most prevalent threat to scavenging raptors in Africa and for vultures in particular is illegal poisoning (whereby people lace carcasses with poison) (Murn and Botha, 2017; Ogada et al., 2016, 2015). Poisoning incidents have killed thousands of vultures in Botswana and surrounding regions in recent years (BirdLife International, 2017; Murn and Botha, 2017; Roxburgh and McDougall, 2012; Santangeli et al., 2016). Large scavenging raptors such as vultures and eagles that rely heavily or wholly on carrion for food can be wiped out in large numbers through poisoning, which may be evident in the declines that we observed for these species groups. Poisoning by poachers is an increasing danger to scavenging raptors, threatening individuals inside protected areas (Murn and Botha, 2017; Ogada et al., 2015; Ogada, 2014; Virani et al., 2011). In Botswana, poaching appears to be increasing, as does other targeted and non-targeted poisoning of vultures (Statistics Botswana, 2015b). Given the scale of the losses of white-backed vultures from recent mass poisoning events (Murn and Botha, 2017), I had expected this species to have declined. However, a relatively small (33%) and non-significant decline from my road counts suggested that populations may be faring better in Botswana than in other areas of Africa (Ogada et al., 2015). However, a recent repeat of surveys of breeding birds in the area, suggest that this is not the case for the resident breeding population, where large declines of over 50% have been recorded (Leepile, 2018). Thus, my survey results may have underestimated the scale of localised decline for a species which ranges across international boundaries (Lambertucci et al., 2014), and for which my counts may include many transient individuals. For lappet-faced and white-headed vultures however, population sizes are far smaller than white-backed vultures (IUCN, 2017) and their declines are most likely due to unsustainable adult mortality through poisoning (Ogada et al., 2016). The recent revelation of substantial Pb exposure in Botswanan African white-backed vultures shows that hunting with Pb ammunition could have severe repercussions for vulture populations (Garbett et al., 2018). Vultures that ingest Pb ammunition fragments leftover in carcasses can either die or exhibit severe sub-lethal affects which can hinder reproduction and reduce overall fitness, consequently decreasing chances of survival (Gil-Sánchez et al., 2018; Vallverdú-Coll et al., 2016). This is yet another threat that could result in unsustainable population losses if not addressed.

Study limitations

Because my surveys were conducted during a limited number of years, any changes in abundance could simply have reflected responses to differing weather conditions at the time of the two surveys, rather than representing a longer term trend. For example, rainfall was higher during my surveys than during the earlier surveys. Road types (tar vs sand/gravel) influence driving speeds and can therefore affect the comparability of surveys, and although the speeds driven on each road type in the early and late surveys were the same, an increase in the proportion of tar roads, may have had some influence on detectability. To check that this issue didn't unduly affect my results, it would have been desirable to make comparisons between counts by road type; however, such data did not exist for the original surveys. However, if road type and thus driving speeds had differed substantially between the two surveys, I might have predicted that declines would have been detected for all species equally, which was not the case.

My re-surveys were limited to the northern surveys of Herremans' (2000). A repeat of the southern road transects from this original survey would be an obvious follow on from this work which would allow national trends for Botswana to be established for these species. In the future the ability to compare the abundance of raptor species across regions will be facilitated if transect survey techniques across Africa are standardized, and this is something that I would strongly advocate.

Conclusions

My results add to the growing evidence for declines in biodiversity across Africa. Although the situation in northern Botswana does not appear as extreme as the declines detected in some other areas of Africa (e.g., West Africa; Thiollay, 2006a), the level of declines observed in a country with such a large proportion of protected land, remains of great concern. My study shows that drivers of decline are apparently indiscriminate, inexplicit and are likely acting jointly, making defining appropriate conservation measures challenging. Furthermore, it highlights the necessity for historical data to enable repeat surveys and the quantification of changes in animal populations. Such changes might otherwise go undetected due to lack of systematic monitoring of wildlife in many developing countries (Amano and Sutherland, 2013). With this in mind, I hope to aid the repeat of the southern road transects, which may help provide more clarity on the processes driving changes in raptor populations in the country. I further encourage the sourcing and cataloguing of original historical datasets to facilitate surveys across the continent, and to ensure their availability for other similar studies.

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Appendices

Appendix 1.

List of Species Acronyms

YBK	Yellow-billed kite
BLSHKI	Black-shouldered kite
PCGH	Pale chanting goshawk
DCGH	Dark chanting goshawk
GAGH	Gabar goshawk
SHIKRA	Shikra
AFHAHA	African harrier-hawk
SEC	Secretary bird
GRKES	Greater kestrel
LESKES	Lesser kestrel
DIKES	Dickinson’s kestrel
RNFAL	Red-necked falcon
LAFAL	Lanner falcon
STBUZ	Steppe buzzard
AMHA	African marsh harrier
BE	Bateleur eagle
BCSNEA	Black-chested snake eagle
BRSNEA	Brown-chested snake eagle
TAEA	Tawny eagle
MAEA	Martial eagle
WAEA	Wahlberg’s eagle
LSEA	Lesser spotted eagle
STEA	Steppe eagle
AFHAEA	African hawk-eagle
FIEA	African fish eagle
WBV	African white-backed vulture
LFV	Lappet-faced vulture
WHV	White-headed vulture
HV	Hooded vulture

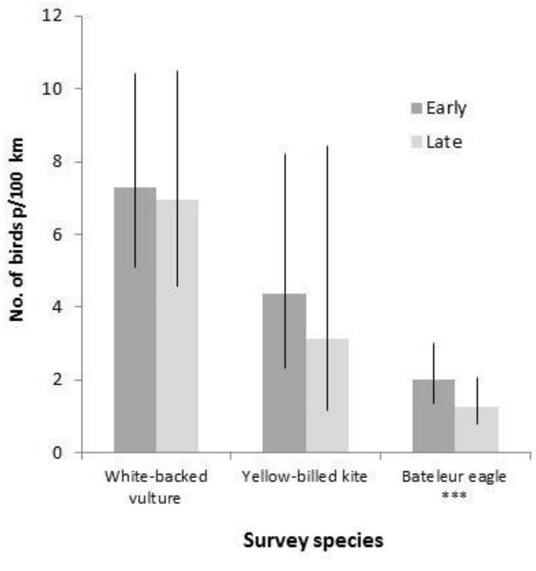
Appendix 2. Summary of results for best fitting model distributions (ΔAICc <2) for comparisons of raptor survey data from early (1991-1995) and late (2015-2015) road surveys in northern Botswana. (-) = non-convergent model. Heading abbreviations: ZFPOISS, non-zero inflated poisson glmmADMB, ZTPOISS, zero-inflated poisson glmmADMB, ZTNB, zero-inflated negative binomial glmmADMB with default "NB2" parameterization (variance = $\mu(1 + \mu/k)$, ZTNB1, zero-inflated negative binomial glmmADMB with default "NB1" (variance = $\phi\mu$), ZFNB, non-zero-inflated negative binomial glmmADMB with default "NB2" parameterization (variance = $\mu(1 + \mu/k)$, ZFNB1, non-zero-inflated negative binomial glmmADMB with default "NB1" (variance = $\phi\mu$). PE = models with period as the explanatory variable, italics are *PE*PA* = models with period*PA as the explanatory variable. Numbers in **bold** indicate top fitting distributions (i.e., those with ΔAICc <2). For species acronyms see Appendix 1.

	MODEL DISTRIBUTIONS					
MODEL	*ZFPOISS*	*ZTPOISS*	*ZTNB*	*ZTNB1*	*ZFNB*	*ZFNB1*
Allbirds~PE	3975.1	3068.7	**0.00**	92.2	23.9	170.7
*Allbirds~PE*PA*	*3957.2*	*3096.6*	***0.00***	*102.7*	*24.8*	*181.3*
YBK~PE	2081.00	765.90	**0.00**	69.00	10.70	136.30
*YBK~PE*PA*	-	*741.10*	***0.00***	*69.00*	*2.70*	*135.70*
BLSHKI~PE	144.90	28.00	2.00	-	**0.00**	20.00
*BLSHKI~PE*PA*	*137.50*	*25.20*	*2.00*	-	***0.00***	*17.20*
PCGH~PE	124.30	92.50	2.00	20.30	**0.00**	18.30
*PCGH~PE*PA*	*117.70*	*80.00*	*2.70*	*20.20*	***0.70***	*18.20*
DCGH~PE	5.90	-	-	-	3.40	**0.00**
*DCGH~PE*PA*	*6.00*	-	-	*2.00*	*4.20*	***0.00***
GAGH~PE	62.00	28.00	2.00	-	**0.00**	22.70
*GAGH~PE*PA*	*70.00*	*116.60*	-	-	***0.00***	*35.40*
SHIKRA~PE	11.70	-	2.00	-	**0.00**	1.20
*SHIKRA~PE*PA*	*11.10*	-	*2.10*	-	***0.10***	***0.90***
AFHAHA~PE	4.70	-	-	-	**0.20**	**0.20**
*AFHAHA~PE*PA*	*7.10*	***0.00***	-	-	*2.00*	*2.80*
SEC~PE	43.40	-	-	-	9.70	**0.00**
*SEC~PE*PA*	*44.60*	*76.50*	-	-	*8.10*	***0.00***
GRKES~PE	285.90	182.60	14.70	2.00	22.00	**0.00**
*GRKES~PE*PA*	*273.70*	*174.00*	*16.40*	*2.00*	*23.40*	***0.00***
LESKES~PE	105.10	-	2.00	-	**0.00**	9.90
*LESKES ~PE*PA*	*106.00*	*20.60*	-	-	***0.00***	*10.80*
DIKES~PE	7.00	**0.50**	-	-	**0.00**	-
*DIKES~PE*PA*	*5.90*	-	*60.70*	-	***0.00***	*3.30*
RNFAL~PE	16.20	5.50	2.00	-	**0.00**	-
*RNFAL~PE*PA*	*15.70*	*5.10*	-	-	***0.00***	-
LAFAL~PE	63.00	10.10	2.70	-	**0.70**	**0.00**
*LAFAL~PE*PA*	*63.30*	*9.80*	*2.00*	-	***0.00***	***1.00***
STBUZ~PE	246.80	42.90	2.00	4.00	**0.00**	16.50
*STBUZ~PE*PA*	*243.20*	-	***1.50***	*2.80*	***0.00***	*14.40*
AMHA~PE	2.60	**0.10**	-	-	**0.60**	**0.00**
*AMHA~PE*PA*	*2.50*	-	*2.90*	-	***0.90***	***0.00***
BE~PE	597.60	356.70	27.40	**0.00**	25.40	**1.50**
*BE~PE*PA*	*569.70*	*362.00*	*30.50*	*1.50*	*28.50*	***0.00***
BCSNEA~PE	**0.00**	-	2.20	-	-	-
*BCSNEA~PE*PA*	***0.00***	-	*2.40*	-	-	-
BRSNEA~PE	24.00	15.10	15.10	-	13.10	**0.00**
*BRSNEA~PE*PA*	*27.20*	*19.30*	*15.70*	-	*11.50*	***0.00***
TAEA~PE	156.80	86.40	22.70	**0.50**	18.10	**0.00**
*TAEA~PE*PA*	*155.60*	*86.70*	*20.10*	*0.40*	*18.10*	***0.00***
MAEA~PE	**1.00**	-	2.00	3.40	**0.00**	**1.40**
*MAEA~PE*PA*	***0.70***	*129.90*	*2.00*	-	***0.00***	-

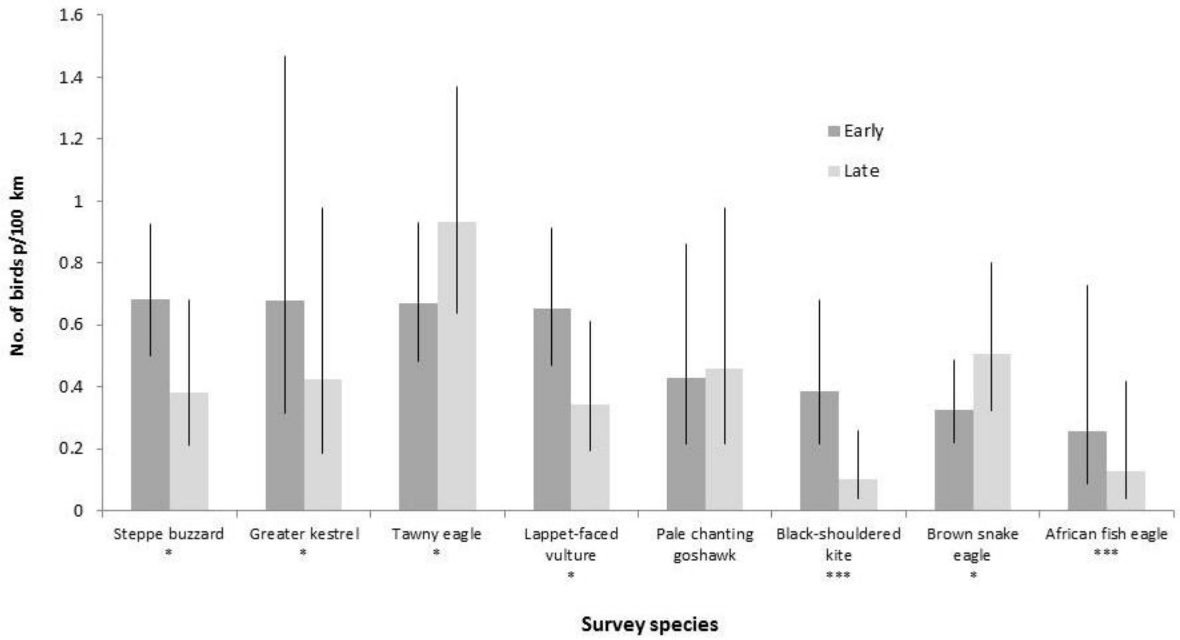
Appendix 2 continued.

MODEL	*ZFPOISS*	*ZTPOISS*	*ZTNB*	*ZTNB1*	*ZFNB*	*ZFNB1*
	MODEL DISTRIBUTIONS					
WAEA~PE	72.80	4.60	-	-	**1.50**	**0.00**
*WAEA~PE*PA*	*73.30*	*4.70*	-	-	***1.10***	***0.00***
LSEA~PE	62.50	116.50	2.00	6.60	**0.00**	5.00
*LSEA~PE*PA*	-	*6.00*	-	-	-	***0.00***
STEA~PE	70.30	5.50	-	-	**0.00**	3.60
*STEA~PE*PA*	*67.60*	***1.20***	-	-	***0.00***	*3.60*
AFHAEA~PE	20.70	7.70	6.20	-	4.20	**0.00**
*AFHAEA~PE*PA*	*19.60*	*6.50*	*5.00*	-	*3.00*	***0.00***
FIEA~PE	340.80	86.00	14.10	**0.00**	13.00	26.00
*FIEA~PE*PA*	*344.50*	*87.40*	*11.30*	***0.00***	*9.80*	*26.20*
WBV~PE	2953.40	1510.80	80.80	**1.40**	44.70	**0.00**
*WBV~PE*PA*	*2922.90*	*1502.70*	*48.90*	***1.30***	*47.00*	***0.00***
LFV~PE	262.30	53.40	19.30	2.00	14.40	**0.00**
*LFV~PE*PA*	*257.50*	-	*19.00*	*2.00*	*14.50*	***0.00***
WHV~PE	110.90	48.70	12.80	2.00	10.80	**0.00**
*WHV~PE*PA*	*109.20*	*46.30*	*12.50*	*2.00*	*10.50*	***0.00***
HV~PE	11.20	161.90	-	-	-	**0.00**
*HV~PE*PA*	*244.20*	*73.80*	-	-	-	***0.00***

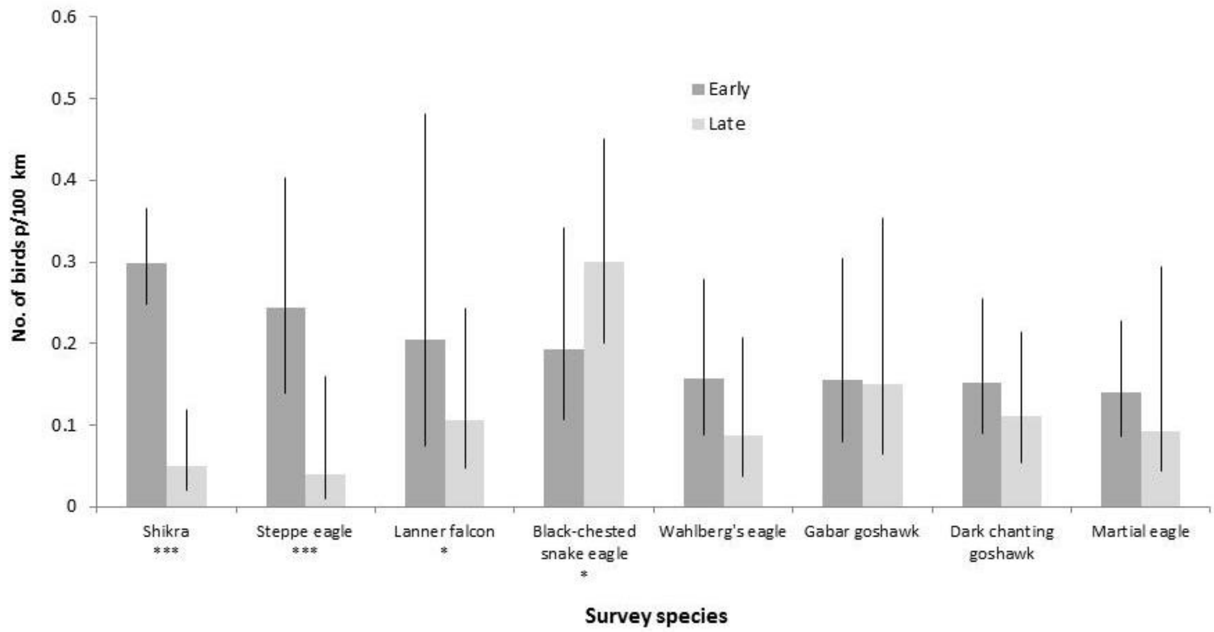
Appendix 3.a



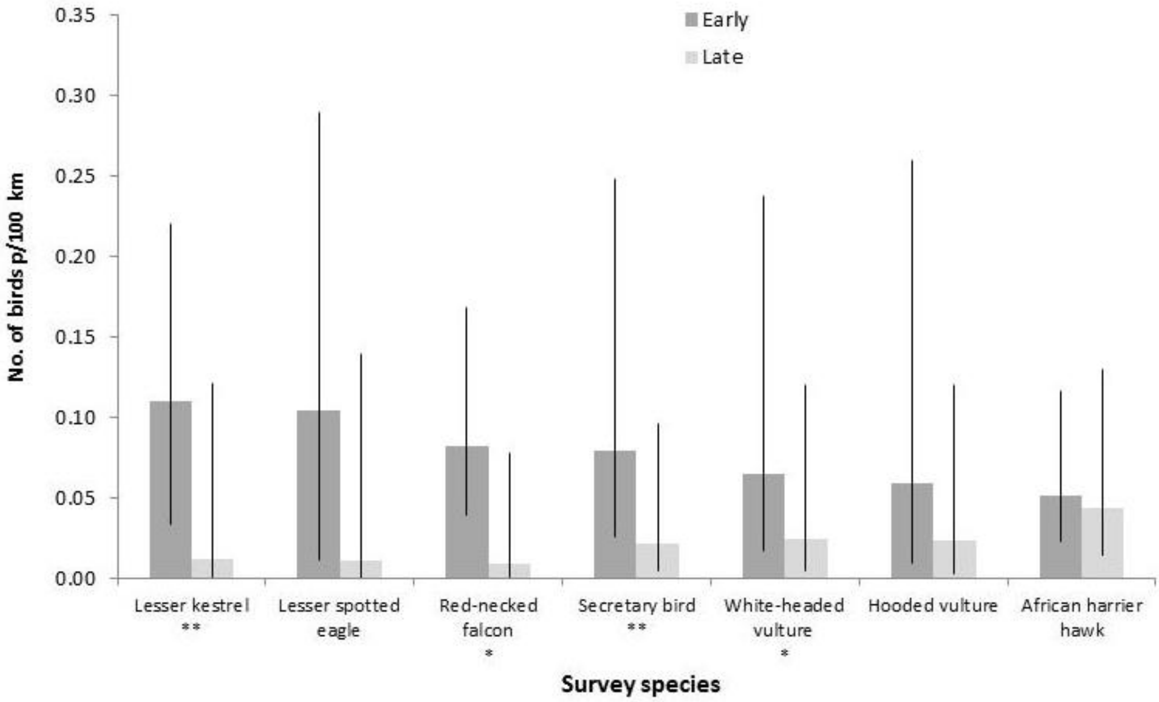
Appendix 3.b



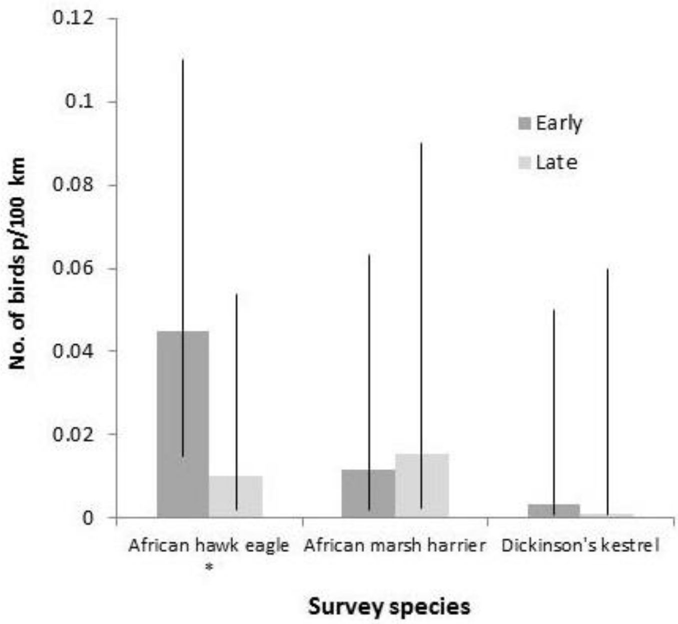
Appendix 3.c



Appendix 3.d



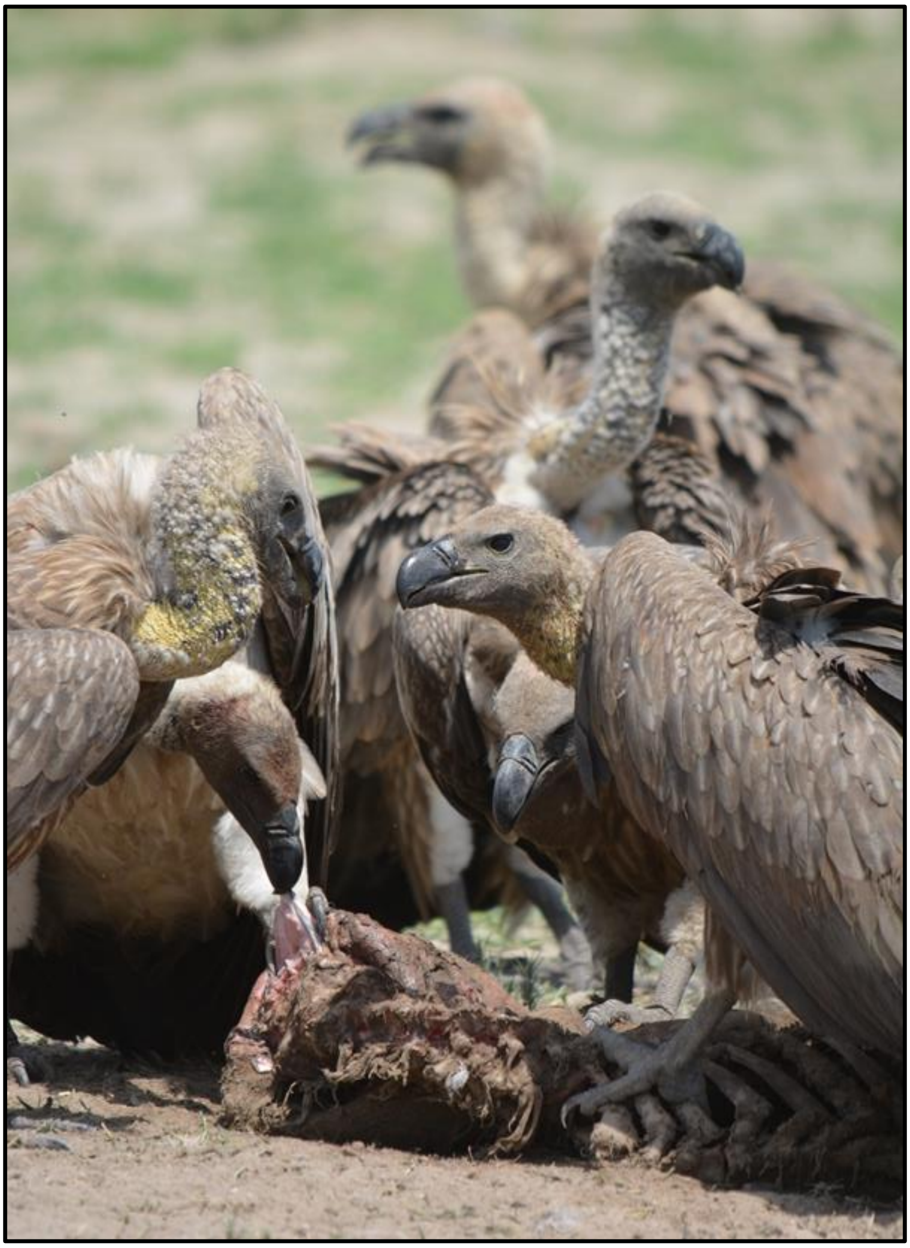
Appendix 3.e



Appendix 3 (a-e). The mean (with 95% confidence intervals) number of birds per 100 km counted in northern Botswana in early (1991-1995) and late (2015-2016) road surveys. The 29 raptor species for which we could make statistical comparisons, are grouped in the figures by their abundance. Figures show both significant and non-significant results: * = p ≤0.05, ** = p ≤0.001, *** = p ≤0.0005.

Chapter 3:

Association between hunting and elevated blood lead levels in the critically endangered African white-backed vulture *Gyps africanus*



"A feast for all"

Abstract

Lead (Pb) toxicity caused by the ingestion of Pb ammunition fragments in carcasses and offal is a threat to scavenging birds across the globe. African vultures are in critical decline, but research on whether Pb exposure is contributing to declines is lacking. In Africa, recreational hunting represents an important economic activity; however, Pb in leftover hunted carcasses and gut piles represents a dangerous food source for vultures. It is therefore important to establish whether recreational hunting is associated with Pb exposure in African vultures. I explored this issue for the critically endangered African white-backed vulture *Gyps africanus* in Botswana by examining their blood Pb levels inside and outside of the hunting season, and inside and outside of private hunting areas. From 566 birds captured and tested, 30% of birds showed elevated Pb levels (10 to <45 µg/dl) and 2% showed subclinical exposure (≥45 µg/dl). Higher blood Pb levels were associated with samples taken inside of the hunting season and from within hunting areas. Additionally, there was a significant interaction between hunting season and areas, with Pb levels declining more steeply between hunting and non-hunting seasons within hunting areas than outside them. Thus, my results were consistent with the suggestion that elevated Pb levels in this critically endangered African vulture are associated with recreational hunting. Pb is known to be highly toxic to scavenging birds and I therefore recommend that Pb ammunition in Botswana is phased out as soon as possible to help protect this rapidly declining group of birds.

Introduction

Environmental pollution as a result of human activity represents a considerable threat to wildlife (Sample and Suter, 1994; Campagna et al., 2011). Human produced Pb in particular, is now the most widely occurring toxic heavy metal worldwide (Cheng and Hu, 2010). The damaging effects of Pb have been a major cause of concern since the early 1970s (Graney et al., 1995). Although considerable amounts of Pb pollution originate from mining, paint and leaded fuel (Needleman, 2000; Mahram et al., 2007; Mathee et al., 2007), spent Pb ammunition from hunting is increasingly being recognised as a major contributor (Pain et al., 2010; Arnemo et al., 2016).

Pb from spent ammunition has caused mortality or severe sub-lethal effects in many bird species, particularly gamebirds and waterfowl (Dong-Ha and Doo-Pyo, 2011; Kim and Oh, 2013) and may have population level effects (Green and Pain 2016). As a consequence, legislation to reduce the risks to waterbirds has been implemented in several countries, for example through bans of Pb ammunition over water bodies (Avery and Watson, 2009). Scavenging birds are another group of birds that have been identified as being particularly at risk (Pain et al., 2009); for example, the California condor *Gymogyps californianus* almost became extinct through direct ingestion of Pb from hunted carcasses (Rideout et al., 2012). Scavenging raptors in other areas face similar pressures (Ecke et al., 2017; Komosa et al., 2008; Rodriguez-Ramos et al., 2008).

As the only obligate avian vertebrate scavengers, vultures belong to the world's most threatened avian functional guild (Buechley and Sekercioğlu, 2016). Over the last two decades, vulture populations have declined massively across Asia due to the veterinary drug diclofenac (Prakash et al., 2012), and more recently, African vultures have shown catastrophic declines (Thiollay, 2006; Virani et al., 2011), with many species now up-listed to Endangered or Critically Endangered (Ogada et al., 2015).

The most important drivers of vulture declines are currently considered to be illegal poisoning, killing for use in traditional medicine and collisions with electrical infrastructure (Ogada et al., 2015). However the impact of Pb exposure on African vulture populations has received considerably less attention than elsewhere. South Africa currently holds the most knowledge on Pb exposure in wild-ranging vultures, with sparse data from Namibia (Van Wyk et al., 2001; Krüger, 2014; Naidoo et al., 2017). In Botswana, Kenny et al., (2015) found around 30% of African white-backed vultures had elevated Pb levels. Despite these studies, our knowledge on this issue remains limited, with little research conducted to attribute sources of Pb contamination, or on the population consequences for elevated Pb levels (Van Wyk et al., 2001; Kenny et al., 2015; Naidoo et al., 2017). Current information suggests that in some African vulture populations Pb levels are often dramatically elevated, and that sources other than Pb from ammunition are unlikely to be the explanation (Naidoo et al., 2017). Thus, fragments of Pb from recreational hunting are the more likely source of contamination for vultures (Gangoso et al., 2009; Hernandez and Margalida, 2009).

The recreational hunting industry in southern Africa attracts almost 90% of all recreational hunters that visit the continent and is of considerable economic importance in many areas (Lindsey et al., 2007b; Van Der Merwe et al., 2014). In 2007, Botswana generated the highest proportion of GDP from trophy (recreational) hunting of all southern African countries (Lindsey et al., 2007b). However, since a nationwide hunting ban on government and tribal land was enforced in January 2014 (Mbaiwa, 2015), hunting activity in Botswana has decreased, but still occurs on privately owned game farms. South Africa however, which borders Botswana, continues to be the largest hunting nation in Africa (contributing 80% of the total revenue from hunting on the continent). Namibia and Zimbabwe, also still have strong hunting economies (Lindsey et al., 2007a). Thus, Pb ammunition is still widely used throughout the region despite a localised hunting ban in Botswana.

When an animal is shot with a Pb-based bullet, the bullet fragments can scatter widely throughout the carcass (Hunt et al., 2006; Knott et al., 2010), particularly when an animal is shot anywhere below the neck (Stewart and Veverka, 2011). It is common practice for hunting farms to dispose of unused carcasses and viscera (‘gut piles’) by leaving them in the open for vultures to eat (Hunt et al., 2006; Legagneux et al., 2014). Because of this abundant and reliable food that hunting farms supply, vultures may become heavily reliant on these resources (Deygout et al., 2009; Kane et al., 2015), making them highly susceptible to Pb poisoning. The bioavailability of Pb in carcasses was demonstrated by Hunt et al. (2009), which showed an almost immediate elevation of blood Pb levels (BLLs) in animals that fed on meat containing Pb.

Because vultures are long-lived, they are predisposed to bioaccumulate heavy metals such as Pb. This is exacerbated by their unique ability to solubilize and absorb Pb, which is eventually deposited in bone (Behmke et al., 2015). BLLs are most frequently used to assess acute exposure and the severity of exposure. Although the half-life of BLLs is around 14 days (Pain et al., 2009), BLLs can remain elevated for as long as 45 days after ingestion (Samuel and Bowers, 2000). The parameters for assessing Pb exposure levels however, remain under debate because of interspecific variation of Pb tolerance. For example, some Egyptian *Neophron percnopterus* and griffon *Gyps fulvus* vultures have been shown to be particularly tolerant to Pb exposure (Gangoso et al., 2009; Espín et al., 2014), whereas condor species *Cathartidae* appear more susceptible to mortality from Pb exposure (Finkelstein et al., 2012; Pikula et al., 2013).

In this study, I explore Pb levels in the critically endangered African white-backed vulture (AWBV) *Gyps africanus* (Birdlife International, 2016) from across Botswana. I explored BLLs within and outside of the hunting season, as well as inside and outside of hunting areas. My motivation was firstly, to quantify the extent of elevated BLLs and secondly, to explore the likely source of Pb. I hypothesised that vultures would show elevated Pb levels due to consumption of carcasses contaminated with spent Pb ammunition. I predict that if Pb ammunition used in hunting was the route for elevated Pb levels, then elevated Pb would be associated with hunting season, and, depending on the scale of vulture movements, I might also predict that Pb levels would be higher in hunting areas than non-hunting areas, particularly during the hunting season. Furthermore, in January 2014, a national hunting ban came into force on government land in Botswana, I therefore also explore whether AWBV BLLs were reduced following the implementation of this ban, which occurred mid-way through my data collection.

Methods

Capture

I captured AWBVs at 15 locations in Botswana, both within hunting and non-hunting areas (Figure 1). Hunting sites were located on recreational hunting farms or farms where some form of hunting (e.g.,, culling or consumptive) occurred. Non-hunting sites were located in protected areas, or on farms (usually livestock) or in community concessions where no hunting or shooting of any kind occurred. The status of all sites (hunting or non-hunting) remained the same through the study. I captured vultures throughout the year between 2012 and 2015, both inside and outside of the hunting season. Hunting season ran from April to November and outside of hunting season, December to March. A government ban on hunting was introduced in January 2014 and applied to all government owned land in Botswana (around 95% of total land mass). Therefore, captures conducted in 2012 and 2013 were pre-hunting ban and captures in 2014 and 2015 were post hunting ban.

I trapped vultures using bait (ungulate carcass, either donkey/goats or game animals) and a gas-propelled canon net system (WCS NetBlaster™, Wildlife Control Supplies, East Granby, CT 06026, USA) with a portable nitrogen tank to charge the canon and a 13 x 17.3 m braided nylon net with a 5.1 cm^2 mesh and 21.8 kg breaking strain. I removed the heads of baits shot with Pb ammunition (in the head), to remove any Pb fragments, but mostly attempted to use bait that had not been shot. Cannon nets have been used for decades to successfully capture similar species and are one of the best traps available for capturing gregarious species either collectively or selectively (Bloom et el. 2007).

Blood Sampling and Analyses

I chose the method of BLL sampling because it has an almost immediate detection rate after ingestion of Pb (within 24 hours) (Hoffman et al., 1981) and a half-life of 14 days (Fry et al., 2009; Pain et al., 2009), meaning that it gives a very recent representation of Pb exposure for an individual. This was crucial for testing the spatial and temporal patterns of Pb exposure at the appropriate scales for my predictions. It also permitted safe and high-volume sampling of live birds. I obtained blood from captured birds via venepuncture with a 1ml syringe and 25 G needle from the ventral ulnaris vein. For better visualisation of the vein I moistened the area with water, plucked some of the feathers, and sterilised with alcohol swabs prior to venepuncture. Extracted blood was transferred into ethylenediaminetetraacetic acid (EDTA) tubes (1.3-mL fill, Sarsted, Inc., Newton, NC) for subsequent analysis.

I mixed 50 µl of the whole blood from the EDTA tube (via a capillary tube) with hydrochloric acid treatment reagent; this reagent lyses the red blood cells freeing the Pb for detection. A single drop of this blood-reagent mixture was pipetted on a sensor strip containing gold colloids on a test electrode. The sensor strip was then inserted into a portable LeadCare® I clinical analyser in 2012 and the LeadCare® II clinical analyser from 2013 - 2015 (LeadCare® I & II, Magellan Diagnostics, North Billerica, Massachusetts 01862, U.S.A., http://www.Leadcare2.com). This portable device quantifies BLLs using Anodic Stripping Voltammetry (ASV). The analyser applies an electrical potential that causes the Pb atoms to accumulate at the gold colloids on the test electrode (sensor strip). The potential is then rapidly changed and the Pb removed from the gold, producing an electrical current. After three minutes, the analyser measures the amount of Pb on the sensor and displays the result in micrograms per decilitre (µg/dl). A calibration was undertaken for each new test kit (containing 48 disposable sensors, reagent tubes, pipettes and capillary tubes with plungers), as well as a quality control test using two controls (high and low) to ensure acceptable levels of test parameters. Lastly, every tenth sample was re-tested to examine robustness of results. Using the LeadCare® system enabled me to analyse the blood samples at the capture sites directly after sampling. All analyses were done within 12 hours of sample collection.

Aging and ringing

Following capture, I aged individuals by the colour variations of their plumage and assigned them to adult, sub-adult or juvenile categories. Adults were characterised by a uniform, pale beige colour of the underbody and underwing contour feathers and no covering on the head; sub-adults had dark beige and white streaked underbodies and underwing contours; and juveniles had very dark brown and white streaky (mostly dark brown) underbodies and underwing contours, with downy white hair on the head and neck (Mundy et.al., 1992; Duriez et al., 2011). All captured birds were fitted with metal rings and thus could be identified if re-captured. Only three birds were re-captured in subsequent capture events, all at the same sites at which they were first captured. Data from these re-captures were not included in the analyses.

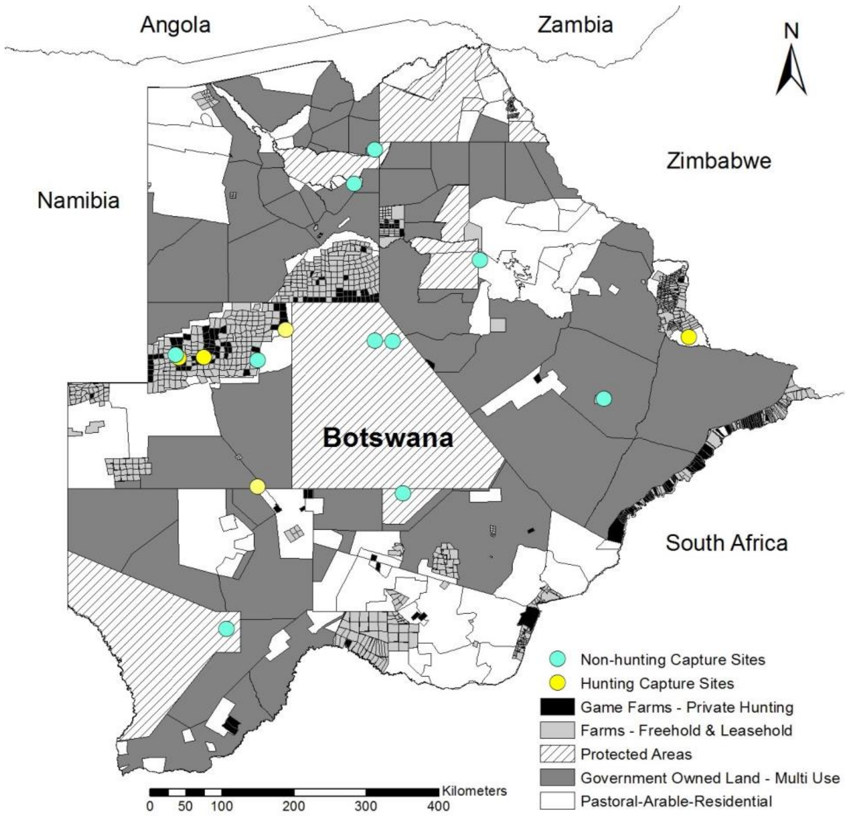


Figure 1. Distribution of sample locations in Botswana where all (*n* = 566) vulture blood samples were collected and tested. At some locations capture sites were moved a short distance if captures were unsuccessful after a given few days. Whether a capture site was in or out of a hunting area is illustrated. Government owned land (multi-use) where recreational (commercial) trophy hunting and citizen hunting could be conducted prior to

the ban at the beginning of 2014 (blood sampling took place before the ban 2012-2013, n = 218) is shown. Game farms are where recreational hunting can still occur on privately owned (freehold) land (DWNP, 2004) post government ban (blood sampling took place after the ban 2014-2015, n = 314). Pb ammunition is still used in non-shaded areas and in some shaded areas for alternative purposes, such as pest and predator control, killing of livestock or game for management, military training, and anti-poaching patrols. None of the sites status (hunting or non-hunting) changed over the course of my sampling period.

Statistical Analysis

The LeadCare I and II did not report exact blood Pb levels at the upper and lower range of concentrations; instead for samples registering at these extreme ends of the range they report values <3.3 μg/dl as "Low" and values >65 μg/dl as "High". Thus, for additional summary statistics (i.e.,, calculation of the population mean) I assigned a value of 1.6 ± μg/dl (i.e.,, midpoint between zero and 3.3) for levels determined as "Low" and a value of 66 μg/dl (i.e.,, the minimum for that sample) for levels reported as "High". In this way, I could make cross population comparisons with other published results, but my average estimations will be conservative and will most likely be an underestimation. For my main analyses of BLLs, I defined three categories of Pb exposure according to Finkelstein et al. (2012) and Kenny at al. (2015): <10 µg/dl = background exposure; 10 and <45 µg/dl = elevated exposure, and ≥45 µg/dl = subclinical exposure. I used these categories as an index of Pb exposure (Pb index score) in my subsequent analysis, scoring them as 0 (<10 µg/dl), 1 (10 and <45 µg/dl), and 2 (≥45 µg/dl), respectively. This approach was necessary because of the distribution of these data, caused by the clumping of values at these low and high points.

I performed all statistical analyses in R version 3.3.0 (R Core Team, 2016). A Multinomial Generalised Linear Mixed Effect Model (GLMM) was used to test whether blood Pb index scores (0, 1, 2) differed between various factors. The capture site was fitted as a random term in the models to account for the lack of independence of samples from the same capture site. I compared blood Pb index scores between the following factors 1) ages of birds (juveniles, sub-adults, adults), 2) hunting season (inside or outside), and 3) hunting areas (inside or outside) (Appendix 1).

Additionally, a fourth model examined the interaction between hunting season and hunting area; this analysis aimed to specifically explore whether declines in blood Pb between the hunting season and the non-hunting season were greater inside hunting areas than outside hunting areas (Appendix 1). A fifth model examined whether blood Pb index scores differed before and after the hunting ban (Figure 7), (Appendix 1). For this model, hunting season and hunting area, as well as their interaction, were included as explanatory variables to control for their influence on Pb index scores (Appendix 1). I ran sixth and seventh models on two subsets of data, including only the non-hunting season (sixth model) and only the hunting season (seventh model), to explore for the significance of differences between hunting areas, and within and outside of the hunting season respectively (Figure 6), (Appendix 1). I ran two final models (eighth and ninth) to examine whether the proportion of birds in each age class (nominal three level factor) differed significantly between hunting areas and between hunting seasons (Appendix 1). Models were implemented with Bayesian Markov chain Monte Carlo methods using the 'MCMCglmm' package (Hadfield 2010). I constrained the prior variance of the fixed effects to 1 (V = 1, fix = 1) and specified a weakly informative prior variance (V) and degrees of freedom (n) for random effects (V = 1, n = 0) for all Markov chain Monte Carlo (MCMC) GLMMs (Wilson et al. 2010; Hadfield, 2010). I ran models for 320,000 iterations with a burn-in (the number of initial MCMC iterations discarded) of 110,000 and a thinning interval of 220 to obtain an effective sample size of around 960 iterations. I estimated means and 95% credible intervals (CI) using the Predict function from the model outputs also using the 'MCMCglmm' package (Hadfield 2010).

Results

From 33 captures at 15 capture locations I caught and sampled BLLs from 566 AWBV, of which 554 were aged. Five capture sites were located within hunting areas and ten were within non-hunting areas. Nineteen capture events occurred during the hunting season and 14 events occurred outside of the hunting season (Table 1). For AWBVs, 197 (35%) blood samples came from hunting areas and 369 (65%) came from non-hunting areas; and 305 (54%) came from within the hunting season and 261 (46%) from the non-hunting season (Table 1) (Appendix 3). Thirty-three vultures of other species were also sampled but no formal analyses of Pb levels were undertaken due to these small sample sizes (Appendix 4).

Blood Pb Levels of white-backed vultures

The age ratio of juveniles (J): sub-adults (SA): and adults (A) of 554 AWBVs captured and aged was 0.63 (J):0.16 (SA):0.21 (A), and did not differ significantly inside or outside of the hunting season (χ^2 = 4.19, df = 2, p = 0.1) nor inside or outside of hunting areas (χ^2 = 2.85, df

= 2, p = 0.2) (Appendix 2). The mean BLL of all birds was 10.7 µg/dl, (Table 2), and overall 32% of birds had BLLs above back ground levels (Figure 2). I found no differences in BLLs between the three age classes ($\chi^2 = 3.01$, df = 2, p = 0.8), (Figure 3, Table 1).

Table 1. Information on each of the 15 capture sites, showing hunting area status i.e., hunting (yes) or non-hunting (no) and the numbers and ages of African white-backed vultures (AWBV) *Gyps africanus* caught in each area inside the hunting season (April – November) and outside of the hunting season (December – March) in Botswana. A total of 554 AWBVs were captured, sampled and aged. A further 12 AWBV were captured and sampled but not aged.

		Inside Hunting Season				**Outside Hunting Season**			
Capture Site	Hunt Area	WBV Total	Juv	Sub	Adult	WBV Total	Juv	Sub	Adult
Bokomoso	Yes	18b,31a	22a	4b,2a	2b,7a	22b	17b	1b	3b
Grasslands	No	34a	23a	5a	6a	56b,73a	41b,38a	8b,22a	7b,12a
CKGR (2 sites)	No	17b	10b	2b	5b	41a	31a	-	10a
Khwai	No	15a	9a	6a	1a	-	-	-	-
Santawani	No	-	-	-	-	18a	11a	-	7a
Kanana	Yes	33a	12a	12a	9a	1a	-	-	1a
Makgadikgadi	No	25b,11a	19b,6a	4b,1a	2b,4a	-	-	-	-
Thakadu	No	39a	25a	3a	11a	-	-	-	-
KTP	No	17b	14b	-	3b	-	-	-	-
Kalahari Rest	Yes	21b,19a	7b,11a	9b,4a	5b,5a	-	-	-	-
Khutse	No	1b	1b	-	-	-	-	-	-
Khama Rhino	No	-	-	-	-	23a	12a	-	11a
Tautona	Yes	-	-	-	-	40b	33b	1b	6b
Lesegolame	Yes	-	-	-	-	11a	5a	3a	3a
Totals		99b,182a	51b,108a	19b,33a	17b,43a	118b,167a	91b,97a	10b,25a	16b,44a

b = before the hunting ban (2012-2013), a = after the hunting ban (2014-2015)

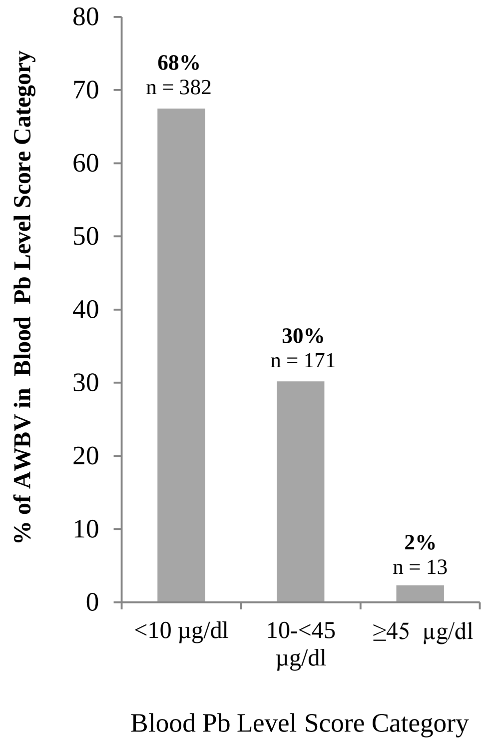


Figure 2. Percentage and samples size of 566 African white-backed vulture *Gyps africanus* captured and sampled in Botswana that were within each blood Pb index score category used for analyses of blood Pb levels.

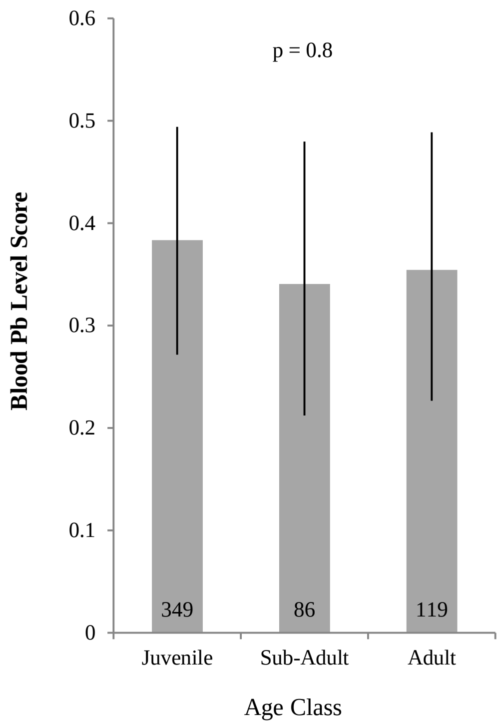


Figure 3. Mean blood Pb level index score (µg/dl) (with 95% credible intervals) for each of the three age classes of 544 African white-backed vulture *Gyps africanus* captured and sampled in Botswana, showing blood Pb levels for: Juveniles, Sub-Adults and Adults, and indicating no significant difference between blood Pb levels within each age class. Values inside bars = sample size.

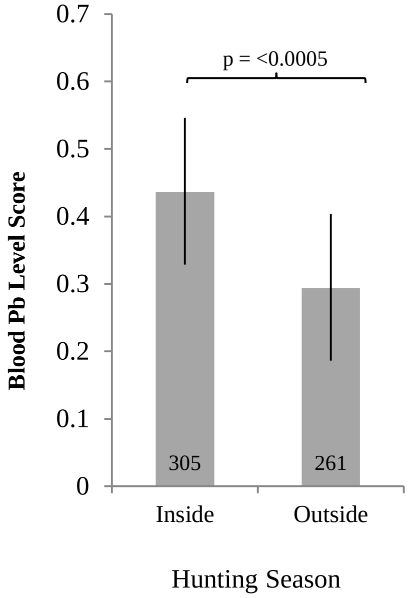
Pb Levels in relation to hunting activity

Table 2. Descriptive statistics, with upper and lower 95% confidence intervals (CI) of mean blood Pb levels (µg/dl) of 566 African white-backed vultures *Gyps africanus* captured and sampled in Botswana. Blood samples were collected inside and outside of hunting areas, inside and outside of the hunting season. Yes = inside hunting area, No = outside hunting area.

Hunt Area	Hunt Season	*n*	Mean	Median	Mode	SD	Min	Max	95% CI	
									Lower	Upper
Yes	-	197	10.72	7	1.6	11.06	1.6	66	9.79	11.65
No	-	369	10.70	7.05	1.6	10.97	1.6	66	9.79	11.61
-	Inside	261	10.67	4.8	4	13.50	1.6	54.2	4.78	16.46
-	Outside	305	10.62	7.1	1.6	10.93	1.6	66	9.74	11.60
Total samples		566	10.70	7.0	1.6	10.97	1.6	66	9.79	11.61

Hunting area and season had a significant influence on BLLs. Firstly, Pb levels were higher during the hunting season compared with the non-hunting season (χ^2 = 17.99, df = 2, $p < 0.0005$) (Figure 4a), and secondly, BLLs were significantly higher for vultures sampled inside hunting areas compared with vultures sampled outside of these areas (χ^2 = 5.76, df = 1, $p < 0.05$) (Figure 5a); although, these spatial differences were less extreme (Figure 5b). Additionally, there was a significant interaction between hunting season and hunting area. Although BLLs were significantly less in both areas outside of the hunting season (hunting areas: χ^2 = 20.85, df = 1, $p < 0.0005$ non-hunting areas: χ^2 = 5.74, df = 1, $p < 0.05$) the decline between the seasons was far greater inside than outside of hunting areas (Figure 6). Indeed, analysing BLLs for birds captured only outside of the hunting season, BLLs inside and outside of hunting areas were not significantly different (χ^2 = 1.47, df = 1, $p = 0.5$) (Figure 6). However, analysing BLLs for birds captured only inside the hunting season, BLLs in hunting areas were significantly higher (χ^2 = 13.51, df = 2, $p < 0.005$) (Figure 6).

4.a.



4.b.

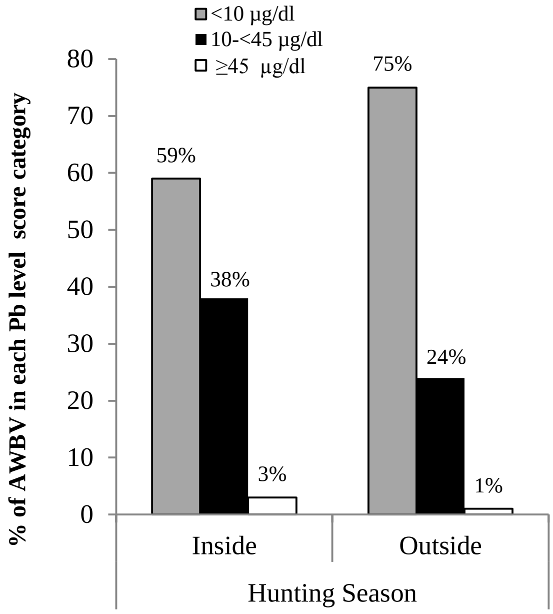
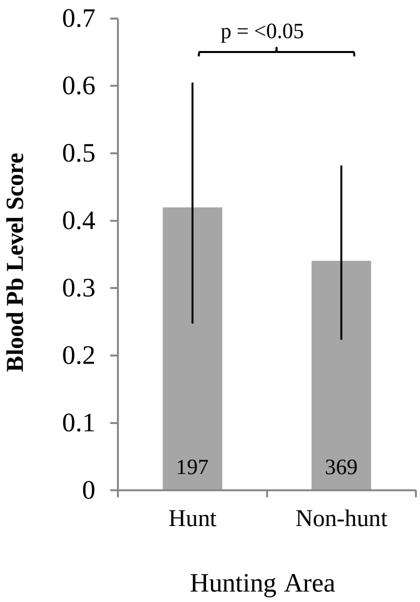


Figure **4.a.** Mean (with 95% credible intervals) blood Pb level scores (µg/dl) for 566 African white-backed vultures *Gyps africanus* captured and sampled in Botswana inside and outside of the hunting season, **4.b.** Percentage of blood Pb samples of African white-backed vultures within each blood Pb level score category inside and outside of the hunting season in Botswana. Values inside bars = sample size.

5.a.



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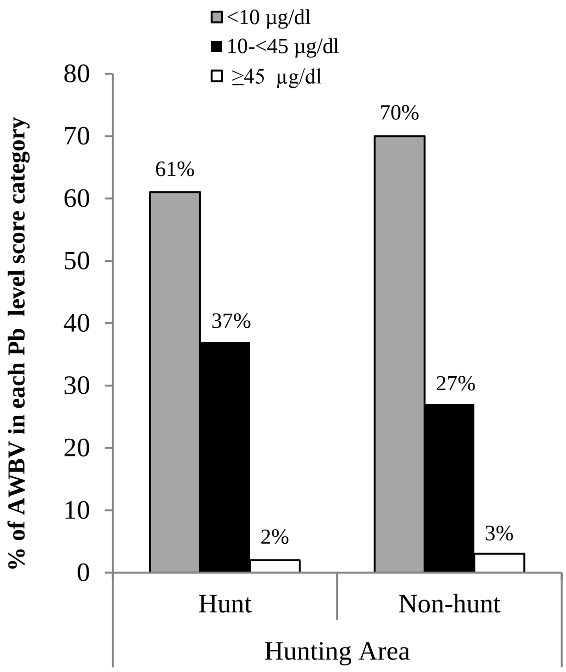


Figure **5.a.** Mean (with 95% credible intervals) blood Pb level score (µg/dl) of 566 African white-backed vultures *Gyps africanus* sampled and captured in Botswana inside and outside of hunting areas, **5.b.** Percentage of blood Pb samples of African white-backed vultures within each blood Pb level score category inside and outside of hunting areas in Botswana. Values inside bars = sample size.

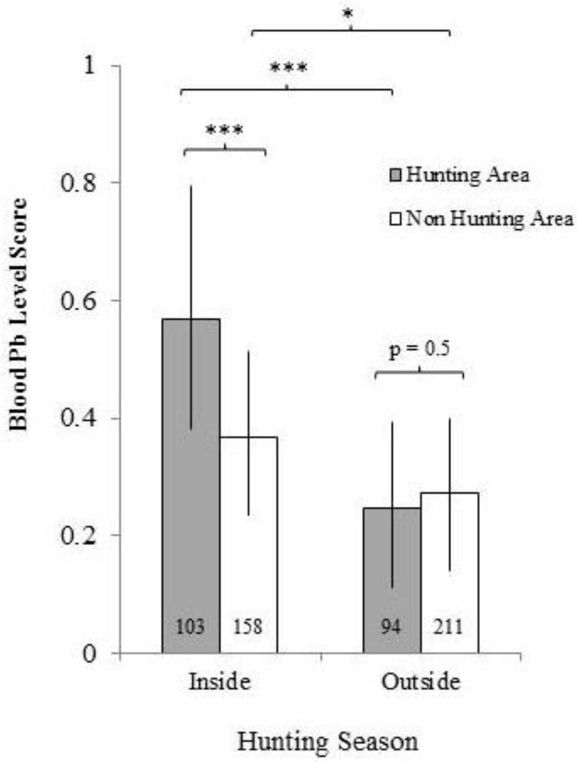
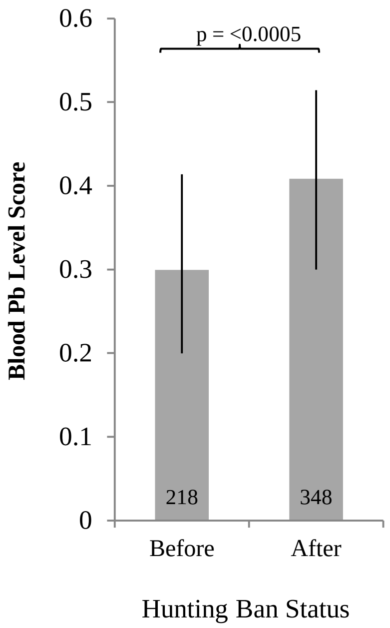


Figure 6. Mean blood Pb level index score (µg/dl) with 95% credible intervals of 566 African white-backed vultures *Gyps africanus* that were captured and sampled inside and outside of hunting areas within the hunting season, and inside and outside of hunting areas outside of the hunting season in Botswana during 2012 - 2015. *=p<0.05, ***=p<0.005. Values inside bars = sample size.

Pb Levels in relation to hunting ban

I conducted captures before and after the hunting ban came into force. For AWBVs, 217 (38%) blood samples were taken before the hunting ban and 349 (62%) were taken after the hunting ban (Figure 7a, Appendix 2). I found no evidence for a reduction in BLLs in AWBVs after the national hunting ban on government owned land (i.e.,, post 2014). In fact, after controlling for hunting season, hunting area, and their interaction, which influenced Pb levels, I actually found that BLLs were significantly higher after the ban was introduced (χ^2 = 20.63, df = 1, $p < 0.0005$).

7.a. 7.b.



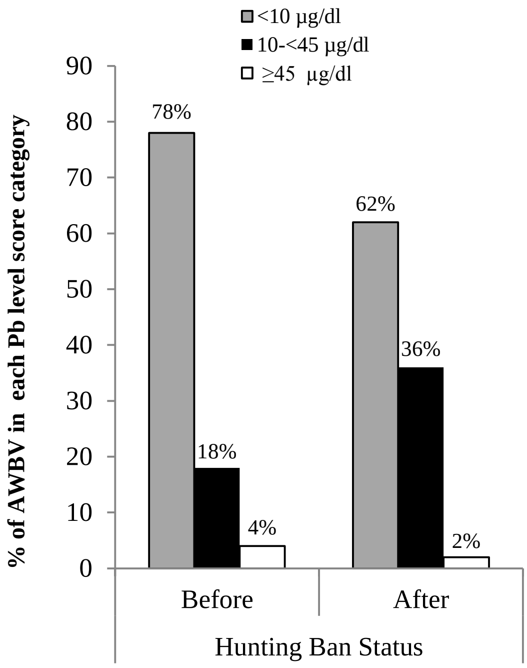


Figure **7.a.** Mean (with 95% credible intervals) blood Pb level score (µg/dl) of 566 African white-backed vultures *Gyps africanus* captured and sampled in Botswana before (n=218) and after (n=348) the hunting ban, **7.b.** Percentage of Pb blood samples of African white-backed vultures within each blood Pb level score category that were captured and sampled in Botswana before (2012-2013) and after (2014-2015) the hunting ban in Botswana. Values inside bars = sample size.

Discussion

This study, as far as I know, represents the first direct attempt to test for an association between hunting activity and BLLs in wild birds in Africa. My results support the growing body of evidence globally that suggests elevated Pb levels in wild scavenging birds are associated with uptake of spent Pb ammunition from hunting (Helander et al., 2009; Lambertucci et al., 2011; Finkelstein et al., 2012). The pattern of my results strongly supports the hypothesis that elevated BLLs in AWBVs in Botswana resulted from the ingestion of spent Pb ammunition.

This study therefore reinforces preliminary findings on AWBVs with elevated BLLs from Kenny et al. (2015), but with a considerably increased sample size. Worryingly, my data show that across all captures, 32% of AWBVs had either sub-lethal or potentially lethal

BLLs. During the hunting season, over 40% of birds had Pb levels above background exposure levels.

Across all tests, the results were consistent with my hypothesis that ingestion of Pb ammunition in hunted carcasses was the likely caused of elevated BLLs in AWBVs. As predicted, BLLs were higher inside the hunting seasons and for birds captured inside rather than outside of hunting areas. The overall differences were greatest from the temporal comparison (i.e.,, comparing seasons) rather than the spatial comparison (i.e.,, comparing areas), which I expected given the far ranging behaviour of vultures (Murn and Anderson, 2008; Phipps et al., 2013; Spiegel et al., 2013), and the relatively immediate measure of Pb exposure that BLLs provide. This said, it was interesting that I found some birds had elevated BLLs outside of the hunting season. The GPS tracking data from tagged vultures in Botswana shows that vultures range widely across international borders throughout the year (Chapter 4), so it is possible that elevated BLLs outside of hunting season result from Pb exposure in other countries.

Hunting seasons in southern Africa vary by country and are largely determined by environmental conditions and the breeding status of game animals. In some areas hunting occurs throughout the year (MET, 1996; Provincial Gazette, 2017; Zambia Wildlife, 2015). Besides recreational hunting, Pb for vultures may originate from private farming, where Pb ammunition may be used for population control and culling for meat sales or personal consumption. Poaching occurs across Botswana and may therefore also represent a significant source of Pb (Statistics Botswana, 2015). Human wildlife conflict (HWC) activities likely also contribute to levels of available Pb and may also peak during the hunting season, which would further explain elevated BLLs of vultures during this time.

I found that elevated BLLs did not differ greatly between the different age classes. Thus, it appears that the likelihood of Pb exposure does not differ according to age; although this may not be consistently the case throughout the year. For example, adults (particularly breeding birds) range less widely during the breeding season, as is known for other vulture species (Krüger et al., 2014) and is highlighted in chapter 4. However, the spatial resolution of my sampling did not allow me to distinguish whether this was the case.

The interaction between the temporal and spatial aspects of hunting activity provided further support for my hypothesised source of Pb exposure. I observed that the decreases in BLLs inside and outside of the hunting season were far greater for birds captured within hunting areas, than for birds captured outside of hunting areas. When I parsed the data by hunting and non-hunting season samples, I found significant differences between these areas during the hunting season, but outside of the hunting season these differences were no longer apparent. Thus, differences were largely driven by the considerably elevated Pb levels for birds captured inside the hunting season within hunting areas. Hunting seasons in other parts of the world also appear to be the main variable associated with elevated Pb levels of other raptors (Bedrosian et al., 2012; Pain et al., 1997), indicating that the pattern I have observed in vultures in Botswana is far from unusual.

Abnormally high environmental levels of Pb in South Africa have been attributed to leaded fuels (phased out in 2006) and mining activity (Naidoo et al., 2017). However, as Naidoo et al.'s (2017) study suggests, these probably do not represent the principle cause of Pb exposure for wild-ranging vultures. Although bioavailable Pb is present in other environmental sources, these sources alone are likely not sufficient enough to explain the elevated BLLs recorded for vultures to date (Hernandez and Margalida, 2009; Naidoo et al., 2017). Such a route, would also not explain why the elevated levels in the AWBVs sampled in this study would be associated so strongly with hunting season and hunting areas.

In a regional context, mean BLLs in Botswana vultures are lower than those found in neighbouring countries. For example, from 14 sites sampled in South Africa and Namibia in Naidoo et al's., (2017) study, 12 of them (with a sample size of 203 vultures) produced higher mean Pb levels than those in my study. Nonetheless, overall mean Pb levels of vultures in the Naidoo et al., (2017) study were not starkly different from mine, although my much larger sample size (almost three times as many birds sampled) suggests that individual BLLs were considerably lower in my study. Comparing BLLs of vultures in this way shows that the higher BLLs were found in countries where hunting still occurs at a significant level (South Africa and Namibia). This suggests that regional availability of Pb ammunition (Lindsey et al., 2006, 2007b) is the factor most prevalent to Pb exposure for vultures, and is not just attributed to in-country use of Pb ammunition.

My results link hunting and elevated BLLs in AWBVs. This study was limited by several factors: firstly, the BLL analyses were limited by lack of in-country facilities for laboratory testing, therefore the most appropriate method of analysis meant that blood Pb levels below <3.3 and >66 required assigned values. These values resulted in clumped data and the resulting distributions of data impeded analysis of actual blood Pb levels (as a continuous variable) as opposed to Pb index scores. Secondly, lack of in-country resources also hindered the use of isotope analyses (of ammunition and BLL) which would obtain more conclusive results with respect to identifying sources of Pb exposure (Berny et al., 2015; Finkelstein et al., 2012). In future, such an analysis could provide a further test of my hypothesis.

Although I anticipated that the Botswana hunting ban would reduce BLLs, this was not the case; possibly because the ban only applies to hunting on government land and not on private game farms. Kramer and Redig (1997) found BLLs of bald eagles *Haliaeetus leucocephalus* and golden eagles *Aquila chrysaetos* to be lower after a State wide hunting ban was enforced, but found that the actual number of birds with elevated BLLs did not reduce. This study suggests either that there were other sources of possibly lower-level Pb exposure (besides Pb ammunition), or alternatively, that eagles were exposed to Pb from hunting in other states where no hunting ban existed. Significant declines of BLLs in other raptor species following State wide bans on Pb ammunition (Kelly et al. 2011) could be indicative of minimal hunting activity in surrounding areas (that do not enforce a ban on Pb) or may be attributed to more confined ranging behaviours and different feeding ecology of species (i.e.,, not wholly dependent on carrion), resulting in differing levels of exposure to Pb. The fact still remains that such bans may only control the geographical distribution of spent Pb ammunition, but not the overall abundance or availability within a country, and thus for vultures and other scavenging raptors that range widely, regional bans are likely insufficient. The recovery of the California condor for example, may be most attributed to intensive population recovery programmes rather than the State ban on Pb ammunition (Finkelstein et al., 2012), particularly as California only represents a proportion of their range (Green et al., 2008).

For unexplained reasons, BLLs of AWBVs actually increased following the Botswana hunting ban. It is possible that the ban resulted in a spatial concentration of hunting activity, and produced a more easily identifiable and accessible food source for vultures, therefore contributing more biomass (containing Pb) to their diet. Discarded ‘gut piles’ and carcasses from hunting essentially replicate ‘vulture restaurants’, on which vultures can become reliant upon (Deygout et al., 2009; Kane et al., 2015). Therefore, even though the geographical spread of carcasses containing Pb ammunition may have been reduced by the Botswana ban, the quantity being eaten by vultures may be the same or greater than before the ban. Furthermore, the capacity of the ban to decrease the availability of Pb for vultures on a regional scale is likely to be small (as with the California condor), because hunting remains prevalent across the region, and still occurs within Botswana. There is also the possibility that poaching may have increased in areas where the ban is implemented, to replace the lost income that local communities may have suffered as a result of the removal of commercial (recreational) hunting (Lindsey et al., 2007b; Mbaiwa, 2008; Mbaiwa, 2018). Even prior to the ban, hundreds of animals were being poached each year (Statistics Botswana, 2015), which reiterates the likely contribution of poaching to Pb available for vultures.

Is the level of hunting in Botswana really sufficient to account for the extremely high proportion of vultures that showed elevated BLLs in my study? To examine this, I replicated the approach that Stokke et al., (2017) took to explore this for moose hunting in Europe. To do this I accessed information on numbers of hunted and poached animals collected annually from private game farmers in Botswana after the hunting ban was enforced. Assuming that the majority of ammunition used in Botswana is Pb core and that less than two bullets were used to kill each animal, I estimated that 14kg of Pb could be available each year for vultures in ‘gut piles’ from recreational hunting and known poaching on private game farms (from 47kg of Pb in carcasses). According to Pattee et al., (1981), this potentially constitutes a minimum of 7000 lethal doses for vultures and other scavenging birds. To put this into context, this could be enough to kill almost the entire population of lappet-faced vultures *Torgos tracheliotos* in Africa. Although this is an extremely crude estimation due to the relatively low quality of information on carcass availability; it is, if anything, probably a large underestimate of the actual amounts of Pb that is still available for vultures from spent Pb ammunition in Botswana.

Even relatively low BLLs may have sub-lethal consequences and serious physiological effects caused by bioaccumulation of Pb in other bodily tissues (Buekers et al., 2009; Pikula et al., 2013). Therefore, BLLs may not always reflect the severity of exposure and should be regarded as a modest representation. Because vultures are long-lived, they are predisposed to bioaccumulation of heavy metals such as Pb (Behmke et al., 2015). Although vultures appear quite tolerant of Pb (Kelly and Johnson, 2011; Naidoo et al., 2017), sub-lethal effects can reduce overall fitness and reduce reproductive output of raptors (Gil-Sánchez et al., 2018; Vallverdú-Coll et al., 2016). If this is occurring in African populations then this non-lethal Pb exposure could hinder vulture populations from recovering from mass poisonings as well as threatening overall population sustainability through reduced productivity. Yet, unlike mass poisonings, the likelihood of discovering birds that have died from Pb poisoning is small, and detecting the effects of Pb exposure on breeding performance is challenging.

A wealth of literature now links Pb ammunition to Pb exposure in wildlife species around the world. The threat of Pb ammunition is clearly acknowledged in the Convention on Migratory Species (CMS) resolution 11.15 (Preventing Poisoning of Migratory Birds), which aims to phase out Pb ammunition worldwide by 2020 (CMS, 2014). Although Botswana is not a signatory to the CMS, I would strongly recommend that it too should move towards a complete ban on Pb ammunition along with all other southern African countries. Non-Pb ammunition alternatives are available and are becoming more widely accredited for use in recreational hunting (Knott et al., 2009; Thomas, 2013).

Conclusions

This study has shown that a relatively large proportion of vultures in Botswana are at risk of Pb exposure and that it likely poses a significant additional threat alongside the mass poisoning events that are currently thought to be the greatest threat to this group of birds (Ogada et al. 2015). Because of the irreversible damage caused by Pb exposure, ultimately, no tolerable threshold level for Pb exposure exists for either humans or wildlife (Pattee et al., 2006; Pain et al., 2010; Centers for Disease Control and Prevention, 2012). Unlike some of the other challenges facing vultures in Africa (e.g., illegal poisoning), the prevalence of Pb ammunition is relatively easy to address through legislation. Banning Pb ammunition would likely be of great benefit for the conservation of this important group of birds, as well as for other scavenging wildlife species and humans. I therefore strongly urge countries in Africa with vulture populations to urgently adopt such changes.

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Appendices

Appendix 1. Description of model structures and data sets used in analyses of blood Pb level index exposure categories (µg/dl) showing BLLs of 566 African white-backed vultures *Gyps africanus* that were captured and sampled in Botswana inside and outside of hunting areas, inside and outside of the hunting season during 2012 – 2015.

Model	Response variable	Distribution (Link)	Explanatory variable	Random term	Data set
1)	Pb Index	Ordinal	Age	Capture site	All BLLs
2)	Pb Index	Ordinal	Hunting season	Capture site	All BLLs
3)	Pb Index	Ordinal	Hunting area	Capture site	All BLLs
4)	Pb Index	Ordinal	Hunting season*hunting area	Capture site	All BLLs
5)	Pb Index	Ordinal	Hunting season, hunting area, hunting ban, hunting area*hunting season	Capture site	All BLLs
6)	Pb Index	Ordinal	Hunting area	Capture site	Out of hunting season BLL
7)	Pb Index	Ordinal	Hunting area	Capture site	In hunting season BLLs
8)	Ageclass	Ordinal	Hunting area	Capture site	BLLs by hunting area
9)	Ageclass	Ordinal	Hunting season	Capture site	BLLs by hunting season

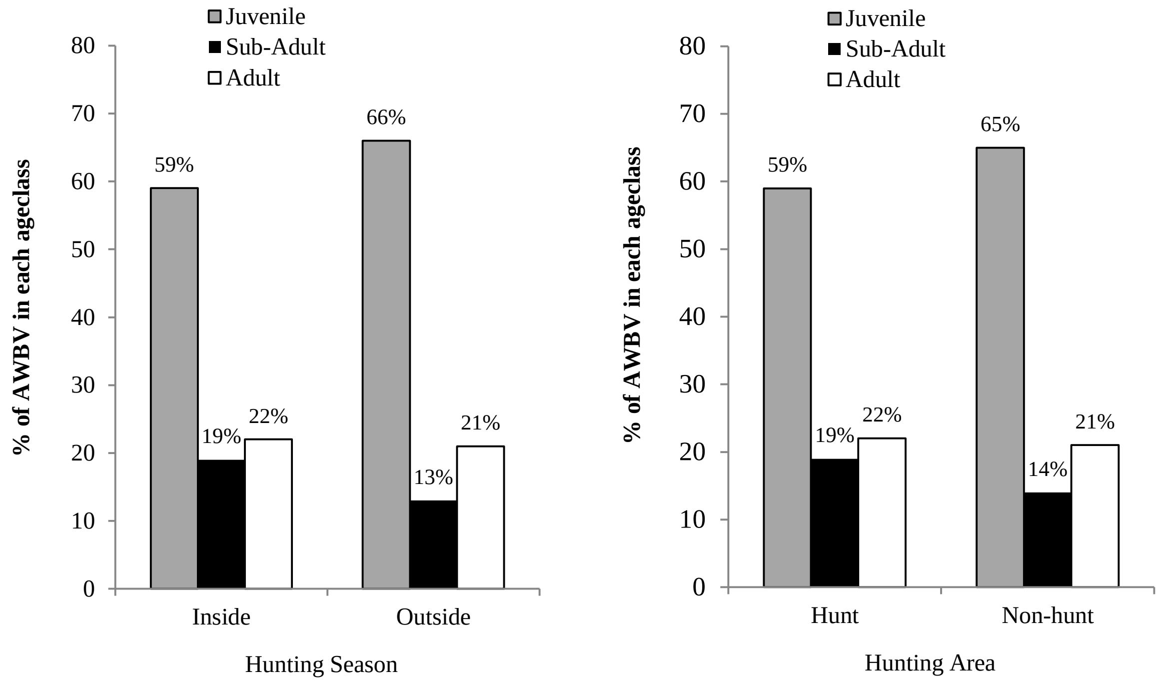
BLLs = blood Pb levels

Appendix 2. Details on 33 separate captures of 566 African white-backed vultures (AWBV) *Gyps africanus* in Botswana, showing capture dates, numbers of vultures caught during each capture, numbers caught of different age classes and hunting activity at time of capture (e.g., in or out of hunting season) and by location (e.g., in or out of hunting area). L = lappet-faced vulture *Torgos traceliotos*, WH = white-headed vulture *Triconoceps occipitalis*, H = hooded vulture *Necrosyrtes monachus*, C = cape vulture *Gyps coprotheres*. Unk = birds ages that were not recorded.

Capture Date	Capture Location	No. of AWBV captured	No. of Juvenile AWBV	No. of Sub-adult AWBV	No. of Adult AWBV	No. of other vulture species captured	Hunting Season (in/out)	Hunting Area (yes/no)	Hunting Ban (before/ after)
12-06-2012	Bokomoso	6	-	4	2	-	In	Yes	Before
14-06-2012	Bokomoso	12	unk	unk	unk	1L	In	Yes	Before
18-03-2013	Bokomoso	10	9	1	-	-	Out	Yes	Before
19-03-2013	Bokomoso	12	8	-	3	-	Out	Yes	Before
25-03-2013	Tautona	40	33	1	6	-	Out	Yes	Before
27-03-2013	Grasslands	34	31	-	3	-	Out	No	Before
28-03-2013	Grasslands	22	10	8	4	2L	Out	No	Before
03-05-2013	KTP	10	8	-	2	-	In	No	Before
06-05-2013	KTP	7	6	-	1	3L	In	No	Before

Appendix 2 continued.

Capture Date	Capture Location	No. of AWBV captured	No. of Juvenile AWBV	No. of Sub-adult AWBV	No. of Adult AWBV	No. of other vulture species captured	Hunting Season (in/out)	Hunting Area (yes/no)	Hunting Ban (before/ after)
09-05-2013	Kalahari Rest	21	7	9	5	-	In	Yes	Before
12-05-2013	Khutse	1	1	-	-	3L, 2WH	In	No	Before
12-09-2013	Makgadikgadi	5	5	-	-	-	In	No	Before
13-09-2013	Makgadikgadi	20	14	4	2	-	In	No	Before
16-09-2013	CKGR site 1	17	10	2	5	3L	In	No	Before
30-01-2014	Kanana	1	-	-	1	-	In	Yes	After
12-03-2014	Santawani	18	11	-	7	2L	Out	No	After
15-03-2014	Santawani	-	-	-	-	3H	Out	No	After
17-03-2014	CKGR site 2	29	21	-	8	1WH	Out	No	After
18-03-2014	CKGR site 2	12	10	-	2	-	Out	No	After
30-08-2014	Kanana	11	4	3	4	-	In	Yes	After
31-08-2014	Kanana	22	8	9	5	1L	In	Yes	After
01-09-2014	Thakadu	20	14	1	5	-	In	No	After
02-09-2014	Thakadu	19	11	2	6	-	In	No	After
15-11-2014	Kalahari Rest	19	11	4	5	-	Out	Yes	After
18-11-2014	Grasslands	37	18	12	7	2L	Out	No	After
19-11-2014	Grasslands	36	20	10	5	-	Out	No	After
12-03-2015	Khama Rhino	23	12	-	11	1C	Out	No	After
17-03-2015	Lesegolame	11	5	3	3	2L, 1C	Out	Yes	After
20-05-2015	Makgadikgadi	11	6	1	4	1L	In	No	After
21-05-2015	Makgadikgadi	-	-	-	-	2L, 1C	In	No	After
16-07-2015	Bokomoso	31	22	2	7	-	In	Yes	After
21-07-2015	Grasslands	34	23	5	6	1L	In	No	After
25-07-2015	Khwai	15	9	6	1	1H	In	No	After
Total	33	566	347	87	120	33	-	-	-



Appendix 3. Proportions of African white-backed vultures (*Gyps africanus*) in each of the three different age classes (juvenile, sub-adult and adult) (n = 554) that were captured and sampled inside and outside of hunting season and inside and outside of hunting areas in Botswana. All vultures with unknown ages were omitted from the dataset. The proportion of birds in each age class was not significantly different ($p > 0.05$).

Appendix 4. The number of other vulture species that were captured and sampled in Botswana showing the number of samples for each species within each blood Pb level score category (µg/dl), the total percentage of samples in each blood Pb level score category, and the mean blood Pb level of each of the four species.

	Number of other vulture species in each blood Pb level score category			
Species	<10 µg/dl	10 to <45 µg/dl	≥45 µg/dl	Mean Pb Level µg/dl
Lappet-faced vulture *Torgos tracheliotos*	20	2	1	6.3
White-headed vulture *Trigonoceps occipitalis*	3	-	-	1.6
Hooded vulture *Necrosyrtes monachus*	3	1	-	9.2
Cape vulture *Gyps coprotheres*	1	2	-	14.8
Total	27 (82%)	5 (15%)	1 (3%)	-

Chapter 4:

Ranging behaviour of breeding and non-breeding lappet-faced vultures: challenges for the conservation of this endangered scavenger

"Life on the thermals"

Abstract

Effective conservation strategies should adequately protect all demographics of a population. 'Full-cycle' conservation aims to protect a species during both the breeding and non-breeding season. For species that have both a breeding and non-breeding population, or in which some adults do not attempt to breed annually, understanding the resource requirements of all sectors of the population is vital. Many vulture species in Africa are declining at unprecedented rates due to human activities and urgent conservation action is required. The endangered lappet-faced vulture *Torgos tracheliotos* is declining throughout its range, yet little is known about its movements or habitat use, and how these differ inside and outside of the breeding season and between breeding and non-breeding individuals. I compare the ranging behaviour of breeding and non-breeding adults across the breeding and non-breeding seasons for 14 adult lappet-faced vultures in Botswana using data collected from 2012 to 2017. The home range size (95% kernel density estimate, KDE) of breeders during the breeding season was eight times smaller than non-breeders (95% KDE: 16,968 km^2 vs 139,499 km^2). Differences between home range size of breeders and non-breeders lessened, but remained significant during the post-breeding season (95% KDE: 70,207 km^2 vs 176,919 km^2). Despite these large differences in ranging behaviour, the percentage of protected area use was similar for breeders and non-breeders, and between the breeding and non-breeding season, with an average use of 27% ± 24%. Breeders showed a significant selection for protected areas during both the breeding and non-breeding season, whilst non-breeders selected protected areas more only during the breeding season. My study suggests that different conservation approaches are likely required in order to protect different sectors of the population. I argue that together with a 'full cycle' approach, conservationists should also consider a 'full spectrum' approach that would address the conservation of both breeders and non-breeders, when they have markedly different resource requirements.

Introduction

Understanding how animals utilise their environment is important for conservation (Berger-Tal et al., 2011). Information on ranging behaviours is central to establishing appropriate conservation strategies, protecting crucial resources, and mitigating key threats (Cooke 2008; Wilson et al., 2008). Where species range widely, conservation can be particularly challenging and protected areas may be insufficient (Batbayar et al., 2008; Trierweiler et al., 2014), particularly for species not restricted by political or geographical boundaries (Maxwell et al., 2011; Lambertucci et al., 2014).

Many factors influence wildlife movement patterns (Spiegel et al., 2017). Distribution of resources often drives temporal and spatial patterns of movement (Monsarrat et al., 2013; Zhang et al., 2017). In keeping with the central placed foraging theory (Carrete and Donázar 2005), ranging behaviour often contracts during the breeding season for many species, particularly birds, when a breeding location may more intensively constrain breeders (Krüger et al., 2014; Antolos et al., 2017; Hector and Fernando, 2017). For migratory birds, ranging behaviour and habitat use during the breeding and non-breeding seasons may differ more starkly than for other species (López-López et al., 2013; Stanley et al., 2015; Buechley et al., 2018). As such, research and conservation strategies should focus on protecting a species' over their 'full-cycle' of life (Marra et al., 2015).

Healthy populations of long-lived birds, such as raptors, often contain many non-breeding individuals (Hunt 1998; Tanferna et al., 2013). These 'floaters' include individuals that fail to secure territories due to competition with territory holders or as a strategy to enhance longer term fitness (Sergio et al., 2009). Whilst these individuals do not contribute offspring to the population, they are nevertheless vital to the long-term persistence of a population and can act to buffer negative effects on the breeding population (Penteriani et al., 2011; Robles and Ciudad 2017). For some large birds, such as raptors or albatrosses that display extended juvenile care, a single breeding season can span almost an entire year (Krüger et al., 2014; Murn and Holloway, 2014; Van Eeden et al., 2017). These species often forgo breeding in the year following a successful breeding event. Thus, for many species, a population includes both breeders and non-breeders, and the movements of these birds can differ substantially (Tanferna et al., 2013; Krüger et al., 2014; Weimerskirch et al., 2014; Holland et al., 2017; Van Eeden et al., 2017).

In the absence of reproductive constraints, non-breeding birds often range more widely than breeders because they have no main return point (García-Ripollés et al., 2011; Zurell et al., 2018). Several studies have examined the ranging behaviours of birds during the breeding season and the non-breeding seasons (Amat et al., 2005; Gutowsky et al., 2015; Holland et al., 2017), but relatively few have compared behaviours of breeders and non-breeders during the breeding season or in the subsequent non-breeding season (Tanferna et al., 2013; Zurell et al., 2018; Buechley et al., 2018). However, understanding how these two different sectors of the population differ in their space use is crucial to developing informed conservation strategies to protect an entire population – an approach we term ‘full spectrum’ conservation.

African vultures have recently received heightened conservation concern due to the decline of many species throughout their range (Ogada et al., 2015). Of the 11 species in Africa, seven are now classified as either endangered or critically endangered by the International Union for Conservation of Nature (IUCN) (Ogada et al., 2015; IUCN 2017). Throughout Africa the biggest threat to vultures comes from the illicit poisoning used to kill vultures either intentionally by poachers seeking to conceal their illegal activities from authorities (Ogada, Botha, and Shaw, 2016), or unintentionally, by livestock farmers targeting predators but killing vultures in the process (Ogada 2014).

The lappet-faced vulture (LFV) *Torgos tracheliotos* is declining rapidly across much of its range leading to its recent up-listing to globally endangered (IUCN 2017). Its range extends throughout much of Africa, but at one of the lowest population density of all African vultures (Mundy et al., 1992; IUCN 2017). The species has shown particularly large declines outside of protected areas (Ogada et al., 2015; Thiollay 2007; Virani et al., 2011). Recent declines have also been documented in Botswana (Garbett et al., 2018a). Currently, very little is known about the movements of this species. It was previously assumed that adults occupied relatively small home ranges, but is now recognised that they range over vast distances, regularly spending time across international borders (Shobrak 2014; Spiegel et al., 2015), to such an extent they are now considered to be partial migrants (Botha, et al., 2017). Lack of knowledge on the movement ecology of this species however, hinders effective conservation (Berger-Tal et al., 2011). Vultures often occur largely outside of protected areas (Herremans and Herremans-Tonnoeyr 2000), exposing them to wide-scale threats (Thiollay 2007). For some vulture species, protected areas are critical for their existence (Murn et al., 2016), but the overall importance of protected areas for LFV remains poorly understood.

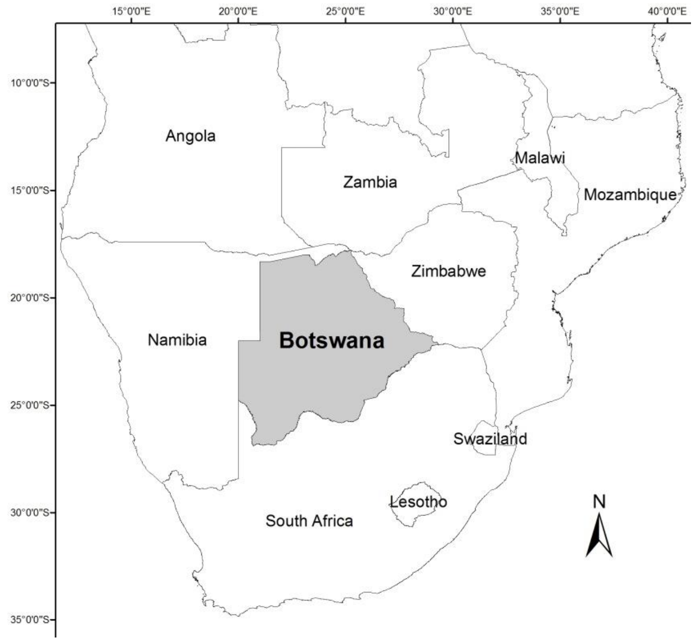
In this study, I explore the ranging behaviours of adult LFVs in Botswana tracked using Global Positioning System (GPS) satellite transmitters from 2012–2017. I use these data to describe the species’ home ranges and core use areas and their use and selection of protected areas. Specifically, I investigate whether these differ for breeding and non-breeding birds, both inside and outside of the breeding season.

Methods

Study area and species

Southern Africa is the southern-most part of Africa and includes ten countries: Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Zambia and Zimbabwe. It is a semi-arid tropical region that contains a wide diversity of ecoregions such as: tropical and subtropical grasslands, savannahs and shrublands, Mediterranean forest, woodland and scrub, and deserts and xeric shrublands, all of which sustain important global biodiversity (Olson and Dinerstein 2002; Rutherford et al. 2006). Southern Africa is one of the most drought-vulnerable regions in the world and is highly characterised by variable rainfall (Leichenko and O’Brien 2002). Botswana is centrally located within southern African and is part of the ‘drylands’ ecoregion consisting of mainly semi-arid Kalahari desert (Ringrose et al. 2003; Abson et al. 2012). It is therefore land-locked by bordering Angola, Namibia, South Africa, Zambia and Zimbabwe and covers an area of around 580 000 km^2 (Commonwealth Network 2017). Rainfall in Botswana occurs in the Austral summer between November and April (the wet season) (Barnes 2001). Land use throughout the country is predominantly communal and commercial farmland, but several game ranches, wildlife management areas (WMAs) and protected areas (Mordi, 1989; Perkins, 1996; Mbaiwa, 2005) (Figure 1) support a variety of free-ranging large ungulate herbivores (Statistics Botswana 2015). Protected areas cover around 20% of the country and with the addition of WMAs, 40% of the country is dedicated for wildlife conservation (Mbaiwa, 2005).

1.a.



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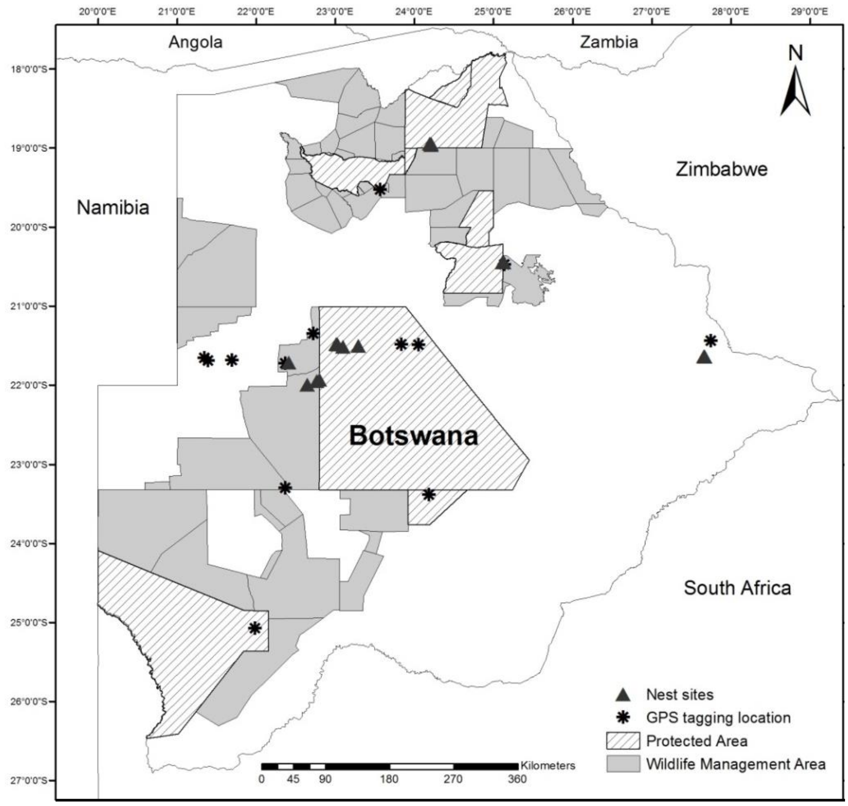


Figure**1.a.** Shows the wider study area – the ten countries that make up southern Africa, where lappet-faced vultures range widely throughout the region, and **1.b** Botswana is centrally located in southern Africa and is the focal study area. The map shows GPS tagging and nesting locations in Botswana of 14 adult lappet-faced vultures, as well as the areas of Botswana dedicated to wildlife conservation e.g., officially protected areas and Wildlife Management Areas (WMAs) that cover around 40% of the country.

The LFV is a non-territorial obligate scavenger that inhabits semi-arid and arid areas (Mundy et al., 1992). Ninety-five percent of the global population occurs in Africa (approx. 8,000 individuals), with the remainder occurring in the Middle East (approx. 500 individuals) (Mundy et al., 1992; BirdLife International 2017). Nests are usually located in solitary trees in remote areas, which may be re-used over consecutive years (Mundy et al., 1992), and breeding pairs perform bi-parental care (Pennycuick 1976).

Vulture capture and tagging

I captured LFVs at several locations throughout Botswana (Figure 1) between 2012 and 2015 using a gas-propelled canon net system (WCS NetBlaster™, Wildlife Control Supplies, East Granby, CT 06026, USA) with a portable nitrogen tank to charge the canon and a 13 x 17.3 m braided nylon net with a 5.1 cm^2 mesh and 21.8 kg breaking strain (Garbett et al., 2018b). Traps were baited with ungulate carcasses (Garbett et al., 2018b; Gil-Sánchez et al., 2018). I used 70 g solar-powered GPS PTT-100 tags (Microwave Telemetry Inc., Maryland, USA), representing less than 1% of a LFVs total body weight (7-8 kg). GPS tags were attached via harnesses in a backpack design using 8 mm Teflon ribbon (Bally Ribbon Mills, Bally, Pennsylvania). I identified adult LFVs by the uniform white plumage on their legs and collar and by a white bar of feathers running along the leading edge of the underwing (BirdLife International 2017). I also fitted vultures with uniquely numbered patagial tags and steel leg bands (see Garbett et al., 2018b) for individual identification.

Identification of breeding birds

To identify active breeding birds I subset all complete data for May and June in each year for each bird. Breeding birds are most heavily constrained to a nest location during these months due to egg-laying and incubation. Using this subset of data, I allocated fixes into a grid of 10 km x 10 km squares, and identified the most used grid squares for each bird for each year, calculating the percentage of use within that square. I presumed that breeding birds would concentrate space use within a single square more than non-breeders, and I could thus set a threshold, above which I would be confident that the bird was a breeder. To confirm this, I also actively monitored a selection of birds (eight) in the field and used these data to confirm my ability to distinguish active breeders (seven) from non-breeders (one) objectively. I actively monitored birds that appeared to be breeders (e.g., GPS fixes indicated a regular return to the same location) at the beginning of each breeding season (April/May). In this way I continued to monitor the seven confirmed breeders (confirmed by an adult bird sitting on a nest or the presence of an egg in a nest) throughout the breeding season. I ceased monitoring birds for that season that were identified as not being breeders (through ground surveys at the beginning of the breeding season) e.g., if there was no nest at or within close vicinity to the GPS location that was suspected to be a nest site (point of regular return). I also ceased to ground monitor breeding birds for the remainder of the breeding season after they were found to have failed.

Home range estimations

I filtered tag location data to remove outliers, inconclusive fixes ("No Fix", "Low Voltage" and "Batt Drain"), and long periods of intermittent data. For spatial analyses, I projected GPS fixes to the UTM coordinate system (WGS 1984 UTM Zone 34S). I used the 'adehabitatHR' package (Calenge 2006) to estimate utilisation distributions by means of the kernel density estimate (KDE) approach for each bird by each annual season (breeding: April – November; non-breeding; December – March) and for each month in each year. KDEs of 95% and 50% were calculated using the href method (grid = 150 m). I used the package 'rgdal' (Bivand et al., 2017) to process spatial data. I also estimated overall foraging ranges of each individual using 100% Minimum Convex Polygons (MCPs). Although an outdated method (Börger et al. 2006), MCPs provide an indication of the overall foraging area and allow comparisons with older studies.

To investigate whether monthly home range sizes differed for breeding and non-breeding LFVs throughout the year, I calculated 95% and 50% monthly KDE estimations for each breeding and non-breeding individual for each month. Each individual had > 200 GPS fixes per month of tracking data which was considered sufficient for delineating monthly home ranges estimates. I classified a year as a 'bird year' that ran from April to March, i.e., the beginning of the breeding season until the end of the non-breeding season. For analyses of overall breeding season and non-breeding season KDEs of breeding and non-breeding birds, I omitted any breeding failures (e.g., birds that changed breeding status part-way through the breeding season – judged either by monitoring in the field or a dramatic change in their movement patterns during the breeding season) so that any changes in movement patterns did not influence results. For monthly KDE analyses, I included birds that failed during the breeding season in analyses, and allowed them to change status between months following failure, thereby increasing my sample size and power.

Protected area use

To investigate use of protected areas by breeders and non-breeders, I overlaid GPS fixes of each individual onto a GIS layer of protected areas. I modified this GIS layer sourced from The World Database on Protected areas (IUCN and UNEP-WCMC 2016) and only included officially protected areas in southern Africa; it did not include WMAs. This layer covered the broader region (not just Botswana), because ranging of the tagged birds extended beyond the Botswana border (see results). I extracted numbers of GPS fixes located inside and outside of protected areas using the ‘raster’ package in R (Hijmans 2016).

Statistical analyses: home range estimations

I performed all statistical analyses in R version 3.3.0 (R Core Team, 2016). Please refer to Appendix 1 for a list of all analyses and model structures. To examine differences in KDEs I used a Linear Mixed Model (LMM) with Wald chi square tests within the ‘lme4’ package (Bates et al., 2015). I generated mean estimates ± 95% confidence intervals (CI) between categories of interest in the ‘lsmeans’ package (Lenth 2016). To test whether the overall KDE of all birds irrespective of breeding status differed significantly between the breeding and non-breeding season I used an LMM fitted with the 95% KDE of each season as the response variable and the breeding season (in or out) as the explanatory variable, with ‘bird id’ and ‘year’ as random terms. Next, I tested whether KDEs (95% and 50%) of breeders or non-breeders were different from each other inside vs outside of the breeding season. For this analysis, I calculated KDEs for each individual per month, for each year of tracking, and used LMM models with breeding status, breeding season, and the interaction of breeding status by season as explanatory variables, with ‘bird id’, ‘year’ and ‘month’ fitted as random terms in the model. Lastly, I used these same data to explicitly compare 95% KDEs for each month, according to the breeding status of the bird. For this, I used the same monthly KDEs as the response variable, but month and breeding status, plus their interaction were included as explanatory variables, with ‘bird id’ and ‘year’ fitted as random terms.

Statistical analyses: habitat use

I used LMMs to explore the use of protected areas by breeding and non-breeding individuals, with ‘year’ and ‘bird id’ included as random terms. I calculated the proportion of fixes inside protected areas in each annual season (breeding and non-breeding), and then transformed these proportions via an arcsine square root transformation to normalise these data, which I then fitted as the response variable. The interaction between breeding status (breed/non-breed) and breeding season (in/out) was fitted as the explanatory variable. Mean estimates were generated in the 'lsmeans' package (Lenth 2016), which I subsequently back-transformed into proportions.

Statistical analyses: selection of protected areas

My previous analysis explored only the use of protected areas by breeders and non-breeders between the seasons, but did not account for availability of this habitat class, and thus I could not explore differences in selection between the seasons. To explore selection of protected areas, I first created a series of pseudo-absence points that I randomly generated for each individual within their MCP (Reid et al., 2015). These pseudo-absence points therefore described the availability of protected areas for each bird. I generated three times as many pseudo-absence points as I had GPS fixes (Reid et al. 2015) using the 'sp' package in R (Pebesma and Bivand 2005). The 'raster' package (Hijmans 2016) in R was then used to classify each point as either 'inside' or 'outside' the boundary of a protected area. To test for differences in selection of protected areas by breeding birds, I used a Generalised Linear Mixed Model (GLMM) specifying a binomial response variable (vulture GPS points = 1; pseudo-absence points = 0), with two interactions between 1) area (protected or non-protected) and season (in or out), and 2) distance to nest site (standardised and centred) and season, fitted as the explanatory variables. 'Year' and 'bird id' were included as random terms in the models and pairwise comparisons were generated in the 'lsmeans' package (Lenth 2016). I used the same model for non-breeders, but excluded nest distance from the models, which obviously did not apply for these birds. Analyses were thus undertaken separately for breeders and non-breeders, which was necessary since nest site location is known to influence space use (Reid et al., 2015). This unfortunately meant that I could not compare differences in habitat selection between breeders and non-breeders, but could at least contrast the strength of any selection of protected areas between the seasons within each category of bird.

Results

I captured and tracked 14 adult LFVs between 2012 and 2017 for a mean (± SD) of 678 ± 218 days (range = 281 - 972 days; Appendix 2). GPS locations (fixes) of tracked birds were recorded in five southern Africa countries (Appendix 3 & 4). The mean percentage of fixes that fell outside of Botswana was 49% ± 23%. Of the total number of GPS fixes of breeding birds, only 10% were outside of Botswana. For non-breeding birds, 44% of their total fixes were outside of the country. Tracking data for at least one whole breeding season (April - November) were available for all birds and included breeding attempts between 2013 and 2017 (data for 2012 included only one month – December, and was therefore not used). During the tracking period, one bird died of confirmed poisoning and two of suspected poisoning, another one was assumed dead (unconfirmed), two tags fell off birds and were recovered with no birds observed on tag recovery, and a further two tags stopped transmitting altogether , which meant that no tag or bird recovery was possible (Appendix 2).

Identification of breeding birds

I identified two distinct patterns of maximum use within the 10 km grid squares overlaid onto the range of each individual in May and June of each year: a low range of maximum use of 7-23% and a high range of maximum use of 47-68% (Figure 2). The marked difference between the two ranges corresponded well with breeders and non-breeders. For the seven birds that I identified as active breeders through monitoring, all were above the 45% maximum use range. Thus, I set the parameter to identify a breeding bird as having ≥45% of fixes within the most used 10km grid square and non-breeders as those that fell below this (<45% fixes within the most used grid square) (Figure 2). Throughout the tracking period, seven LFVs bred at least once and seven did not. The seven LFVs that did not breed, bred at no time during data used for analyses, and the seven breeding birds had no ‘bird years’ where they did not attempt to breed (Appendix 2).

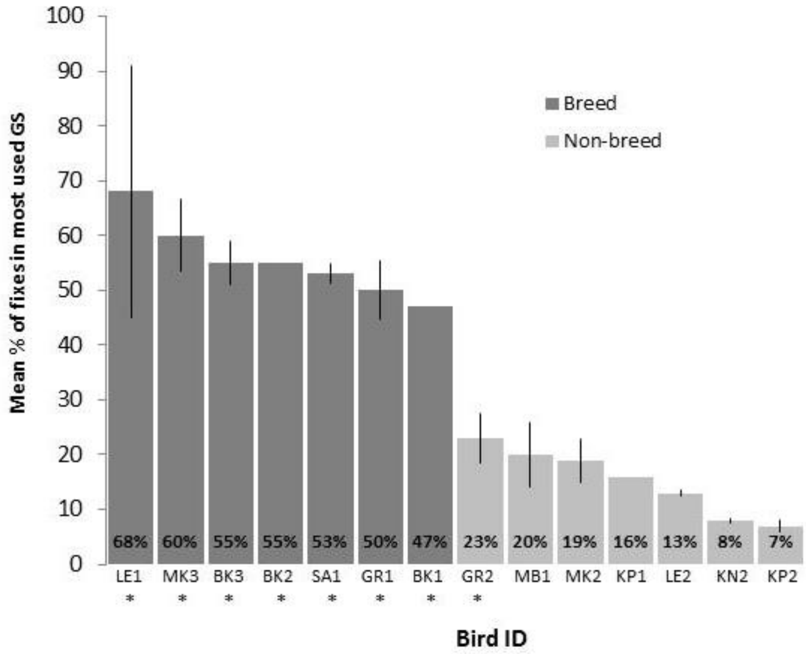


Figure 2. Summary of analysis used to identify breeding adult lappet-faced vultures in Botswana (± SE), using GPS tracking data to calculate the % of fixes in the most used 10 km grid-squares (GS) for each bird. The parameter for identifying breeding birds was thus set at >45% of mean individual fixes in the highest use DGS, which correlated with the DGS in which the nest was located. * = birds that were ground monitored in the years that they were breeding. This includes one bird that was suspected to be breeding in one year but was identified as being a non-breeder through ground surveys at the beginning of the breeding season, and was therefore not monitored for the remainder of the season.

Home range estimations and breeding activity

Mean 100% MCP (± SD) for all individuals was 248,986 ± 205,447 km^2. Mean overall 95% and 50% kernel density estimates (KDE ± SD) were 194,813 ± 168,353 km^2 and 27,955 ± 31,704 km^2, respectively. The 95% and the 50% KDEs of all birds, irrespective of their breeding status, differed significantly inside and outside of the breeding season (Table 2 & 3). Furthermore, the 95% and 50% KDEs during the breeding season were around eight to ten times smaller for breeders than for non-breeders (Appendix 3 & 4). Outside of the breeding season, the 50% and 95% KDEs of birds that were breeders were two to three times smaller than birds that had not bred (Appendix 3 & 4). The differences between 95% and 50% KDEs of breeders and non-breeders were significant, but the differences between seasons were not, nor was there an interaction between season and breeding status, suggesting that these differences between the breeders and non-breeders remained similar between the seasons (Table 2 & 3, Figure 3).

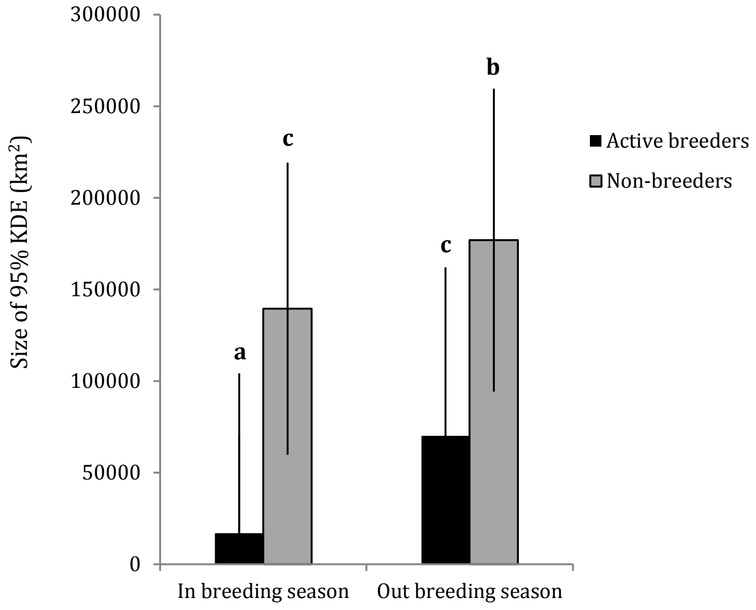
Examining the difference in the size of KDEs per month, I found no significant difference between 95% KDEs of breeders and non-breeders in any month (Figure 4). However, KDEs of breeding birds contracted considerably during the breeding season and increased outside of the breeding season, but with the mean always remaining consistently smaller than KDEs of non-breeders (Figure A.1), and large confidence estimates due to considerable within individual variation (Figure 3 & 4).

When I explored the 95% KDEs in each year for a few individual breeders and non-breeders that had most data for consecutive years, I found that there was a degree of overlap of individual KDEs in each year (Appendix 4). The percentage of KDE overlap for each vulture ranged from 21% to 65% inside and outside of the breeding season, respectively. The amount of overlap was largely consistent for each individual across both seasons (inside and outside of breeding season).

Table 2. Summary of 95% and 50% (± SD) kernel home range (KDE) sizes for 14 GPS-tagged adult lappet-faced vultures in Botswana. Home ranges of all individuals combined and breeding and non-breeding birds separately were calculated both inside and outside of the breeding season respectively.

Analyses	95% KDE (± SD)		50% KDE (± SD)	
Mean KDEs of all individuals	194,813 ± 168,353 km^2		27,955 ± 31,704 km^2	
Mean KDEs of breeding and non-breeding birds inside breeding season	16,968 ± 21,719 km^2 active breeders 139,499 ± 148,131 km^2 non-breeders		2,938 ± 13,737 km^2 active breeders 28,687 ± 34,436 km^2 non-breeders	
Mean KDEs of breeding and non-breeding birds outside breeding season	70,207 ± 92,324 km^2 active breeders 176,919 ± 185,507 km^2 non-breeders		14,544 ± 29,901 km^2 active breeders 39,145 ± 47,712 km^2 non-breeders	
	In breeding season	Out of breeding season	In breeding season	Out of breeding season
Mean KDEs of all birds in and out of the breeding season, irrespective of breeding status	82,988 ± 110,886 km^2	127,816 ± 147,738 km^2	16,764 ± 34,945 km^2	27,916 ± 35,607 km^2

3.a.



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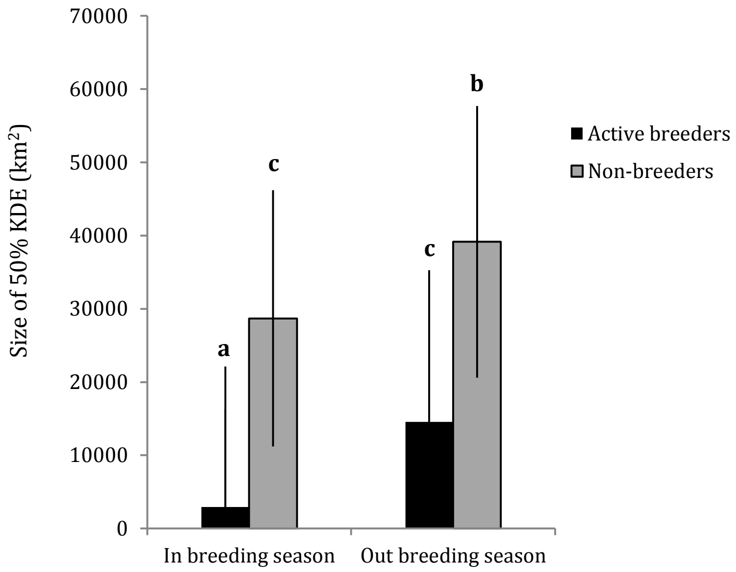


Figure 3. **(a)** Sizes of 95% and **(b)** 50% kernel home ranges (KDE) in km^2 of GPS-tagged adult lappet-faced vultures in Botswana with 95% confidence intervals. Data show KDEs of breeding and non-breeding birds inside and outside of the breeding season. Different letters indicate significant differences.

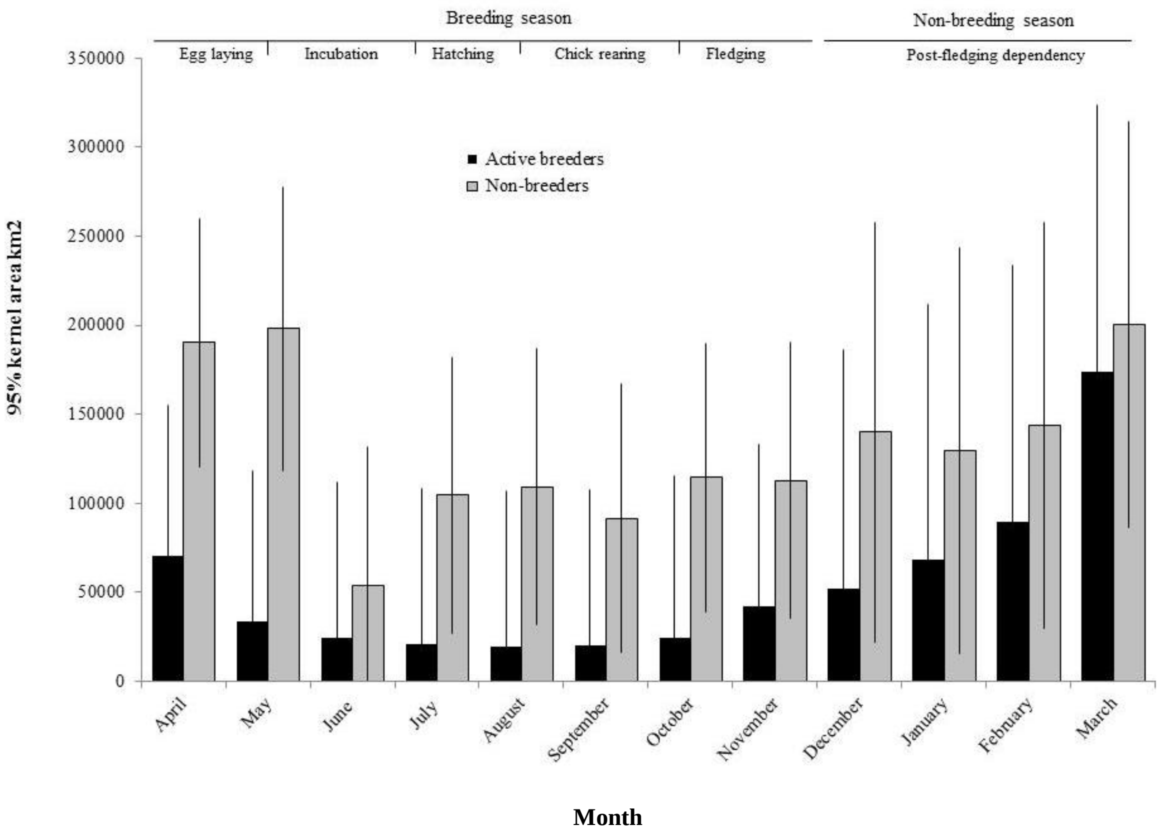


Figure 4. Mean estimates of 95% kernel home ranges (KDE) in km^2 with 95% confidence intervals of GPS-tagged adult lappet-faced vultures in Botswana. Data show 95% KDEs of breeding and non-breeding birds during each month of the breeding and non-breeding seasons. Different stages of the 'bird year' e.g., breeding and non-breeding season and different stages of the breeding cycle e.g., chick rearing and fledging, are shown.

Table 3. Summary of model outputs shown in Appendix 1. Model variables: breedstat (status: breeding = br, or non-breeding = nb), area (protected = PA or unprotected = Non-PA), breedseas or season (season: in or out), nest_dist. (distance of GPS fixes from known nest location, for breeding birds only). : = interaction term.

Analysis	Response variable	Variables	β	SE	df	χ^2	P
Differences between overall mean KDEs of all birds in and out of the breeding season irrespective of breeding status	95% KDE	Intercept	82989	31553			
		Breedseas	44828	15623	1, *231*	8.23	0.004
	50% KDE	Intercept	16765	6821			
		Breedseas-out	11151	4010	1, *231*	7.73	0.005
Differences between home ranges of br/nb birds in and out of breeding season	95% KDE of br/nb birds inside vs outside of breed season	Intercept	139499	36846			
		Breedstat-br	-122531	51682		5.62	0.01
		Breedseas-out	37420	23320		2.57	0.10
		Breedstatbr:seasout	15818	31288	1, *229*	0.25	0.61
	50% KDE of br/nb birds inside vs outside of breed season	Intercept	28687	8120			
		Breedstat-br	-25749	11262		5.22	0.02
		Breedseas-out	10458	6255		2.79	0.09
		Breedstatbr:seasout	1148	7999	1, *229*	0.02	0.88
Differences between use of PAs by br/nb birds in and out of breed season	Proportion of GPS fixes in and out of PAs (arcsine transformed) in and out breed season for br/nb birds	Intercept	0.36479	0.07487			
		Breedstat-nb	0.11233	0.07006		2.57	0.10
		Breedseas-out	-0.06105	0.05326		1.31	0.25
		Breedstatnb:seasout	-0.06127	0.07076	1, *50*	0.74	0.38
Differences between selection of PAs and Non-PAs by br/nb birds	Real and pseudo-absence points of br birds	Intercept	-0.610504	0.114357			
		Areaout	-0.701654	0.019262		1326.98	<0.0005
		Seasonout	0.058606	0.026407		4.95	0.02
		Nest_dist.	-0.305191	0.009517		1028.34	<0.0005
		Areaout:seasout	0.230800	0.031610		53.31	<0.0005
		Seasout:nest_dist	1.877904	0.035282	1, *127928*	1833.68	<0.0005
	Real and pseudo-absence points of nb birds	Intercept	-0.85859	0.01334			
		Areaout	-0.30138	0.01323		519.28	<0.0005
		Seasonout	-0.27792	0.02059		182.11	<0.0005
		Areaout:seasout	0.34698	0.02279	1, *296796*	231.72	<0.0005

Habitat use

Mean (± SD) percentage of each individual's total tracking fixes inside protected areas (PAs) was 27% ± 24%. All individuals used PAs to some extent; however, only two of the 14 tracked birds spent >50% of their time inside PAs (Appendix 1). Use of PAs did not differ between breeding and non-breeding birds, nor between the breeding and non-breeding season, nor was there an interaction between season and a birds breeding status (Table 3, Figure 5).

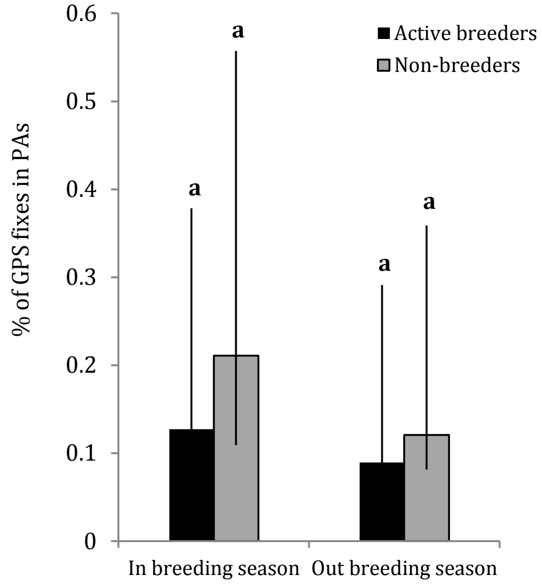
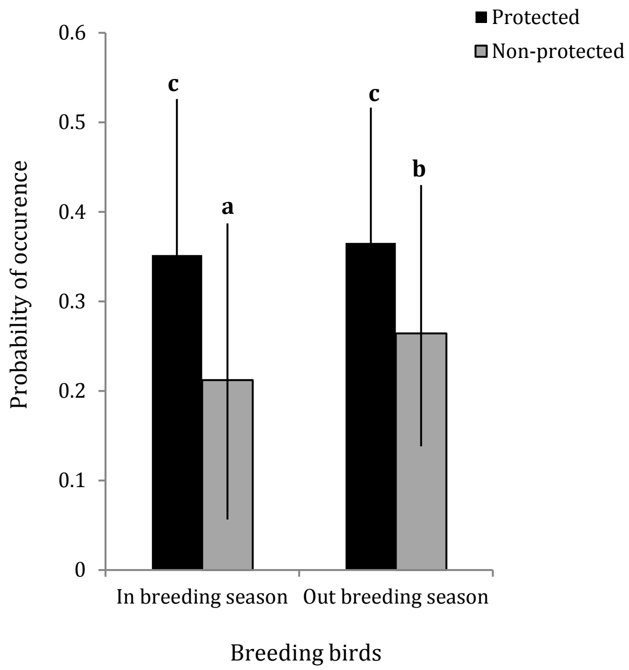


Figure 5. Mean estimated percentage of GPS fixes with 95% confidence intervals of breeding and non-breeding adult lappet-faced vultures in Botswana that are within protected areas in southern Africa. Estimates are back transformed from the model estimates (see Table 3, Appendix 1). Different letters indicate significance differences.

Habitat selection

Relative to availability and after accounting for distance to nest sites (Figure 2, Table 3) breeders showed a significant preference for PAs during both the breeding and non-breeding season, as appose to non-PAs (Table 3, Figure 6a & 6b). However, there was an interaction between protected area status (PA or non-PA) and breeding season status (breed or non-breed), which indicated that the relative difference in selection for protected areas was greater in the breeding season than in the non-breeding season (Table 3, Figure 6a). Furthermore, the interaction between nest distance and breeding season status was also significant, suggesting that the influence of nest site differed between the two seasons (Table 3). Non-breeders showed a significant preference for protected areas only during the breeding season, whereas they showed a slight avoidance for these areas outside the breeding season (Table 3, Figure 6b).

6.a.



6.b.

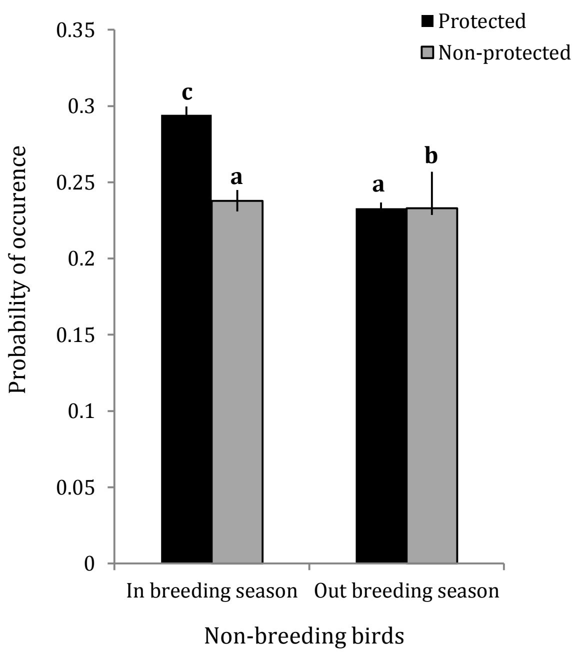


Figure 6. Mean probability estimates with 95% confidence intervals of habitat selection in relation to protected areas in southern Africa in accordance to their availability by adult lappet-faced vultures in Botswana. Selection if shown for **a)** breeding birds and **b)** non-breeding birds both inside and outside of the breeding season. Different letters indicate significance differences.

Discussion

My key findings were that LFVs use very large home ranges, but most importantly that range sizes differ greatly between breeding and non-breeding adults, with breeders using much smaller ranges. Use of protected vs non-protected areas did not differ significantly between breeding and non-breeding birds, but after taking into account availability, I found that during the breeding season both groups of birds selected protected areas.

Home range maps also revealed these large differences between breeders and non-breeding floaters as well as showing considerable regularity of space use between years (Appendix 4 & 5), especially for breeding birds, suggesting that these birds maintained a permanent home range. Non-breeding birds also used the same general areas across consecutive years, which could suggest a level of site or home range fidelity; although this generally contrasts with typical floater behaviour (Robles and Ciudad 2017). These findings were strikingly similar to those of Zurell et al. (2018) that investigated home ranges of breeding and non-breeding white storks. Their study also showed an apparent co-occurrence between breeder and floater populations, in that there was no obvious segregation between their movements, which is similar to my findings. Zurell et al. (2018) also found differences between home range sizes of breeders and non-breeders, comparable with those that I found.

Comparisons of home ranges

The vast home ranges of adult LFVs in my study were generally much larger than those identified for this species in Africa so far. GPS-tagged LFVs in East Africa were found to have an average home range size of 22,000 km^2, which is comparable with range sizes that I identified for breeding birds within the breeding season. The larger ranges of adult non-breeders in my study were a similar size to those of immature LFVs in Saudi Arabia (Shobrak 2014). However, I found much larger home ranges than those recorded for other adult vulture species. For example, LFVs ranges were on average 38-92% larger than those recorded for adult cape vultures *Gyps coprotheres* (Bamford et al., 2007; Phipps et al., 2013), 62% larger than ranges of adult Rüppell's vultures *Gyps rueppellii* (Virani et al., 2012) and 99% larger than adult bearded vulture ranges *Gypaetus barbatus* (Krüger et al., 2014). Ultimately, the ranges sizes I found for adult LFVs were most comparable with those of immature vulture range sizes of LFV and of other vulture species (Phipps et al., 2013a, b; Shobrak 2014; Spiegel et al., 2015).

Given these large home ranges, particularly for non-breeders or during the non-breeding season, conservation strategies for adult LFVs probably need to differ from those for other adult vulture species. For example, the reliance on protected areas or discrete vulture safe zones, as used for Asian vultures (Mukherjee et al., 2014) might not be appropriate for this species, but would certainly be worth exploring (see chapter 5). It may be more appropriate to consider approaches used for immature, non-territorial vultures or overwintering migrants. For example, migratory Egyptian vultures in Africa, that had range sizes similar to some floaters in my study, may benefit most from conservation strategies aimed at protecting core use areas (Buechley et al., 2018). However, for vultures, the best approach may require a broader conservation program aimed at changing human behaviour (e.g.,, reduced poison use at a wider scale) and activities outside of protected areas, rather than creating a few safe havens, especially to protect the wider ranging populations of non-breeding floaters (Sergio et al. 2005).

LFVs tagged in Botswana used all neighbouring countries and spent nearly half of their time outside of Botswana (Appendix 2). This may be evidence of partial migratory behaviours that have also been observed in other populations of LFVs (Shobrak 2014; Botha, et al., 2017), which predisposes this species to large gaps in their protection (Gillingham et al., 2015; Schuster et al., 2018). This finding emphasises the need for cross-border conservation action, highlighting the importance of schemes like the Multi-species Action Plan (MsAP) formed by the Convention on the Conservation of Migratory Species (CMS). A key conclusion from this plan was the need to implement conservation management coordinated across broader scales in order to halt widespread vulture declines occurring in different geographic regions (Botha et al., 2017).

Home ranges and breeding

As expected, home ranges of breeding LFVs in my study were consistently smaller during the breeding season than those of non-breeding birds. These differences diminished following the end of the breeding season, which corresponds to the period of post-fledging dependency and subsequent independence of offspring. Kane et al. (2015) predicted that based on energetics and nest constraints home range sizes of breeding vultures might be around five times smaller than non-breeders. This estimation thus corresponds well (albeit slightly less) with the differences I found; with home ranges of breeding birds inside of the breeding season being around 8-10 times smaller than non-breeders.

The results from my study also correlate well with those found by Tanferna et al. (2013), who explored home range sizes of breeding and non-breeding floaters in a black kite *Milvus migrans* population in Spain. They found that the average size of 95% KDEs for breeding males and females combined was seven times smaller than those of floaters. Buechley et al. (2018) described home ranges of breeding and non-breeding Egyptian vultures *Neophron percnopterus* as being around six times smaller for adult breeders than non-breeders. Similarly, Krüger et al.'s (2014) study on bearded vulture also found distinctly smaller (three times smaller) home ranges for breeding adults compared with non-breeding adults.

The most obvious explanation for the vastly smaller home ranges of breeding birds in my study, particularly the extreme contraction in size observed during the breeding season, is that they are constrained by the presence of a nest site (Tanferna et al., 2013). Feeding rates of adult LFVs to their chicks is not known, but for African white-backed vultures, adults fed chicks on average 0.7 times per day, thus adults are heavily confined to a nest site and cannot travel great distances away from it (Kane et al., 2015; Maphalala and Monadjem 2017). Furthermore, during the early stages of breeding, nest attendance must be near continuous in order to incubate and protect chicks when they are most susceptible to mortality, largely due to their inability to thermo-regulate at this early stage (Xirouchakis and Mylonas 2007; Katzenberger et al., 2015). The coldest winter months (June - August) in Botswana coincide with this particularly vulnerable breeding phase (weeks following hatching) and are also when home range sizes of breeders were smallest. Based on this species' mass, predictions from Katzenberger et al.'s (2015) study suggest that the intensive brooding period would last around 40 days. The gradual increase in range size of breeders in my study as the breeding season concluded coincides with decreased chick dependency (post-fledging stage) (Bassi et al., 2017).

All LFVs captured had adult plumage, and I was surprised by the proportion that never attempted to breed. Around half of the individuals I tracked did not breed throughout the entire tracking duration. These non-breeding birds had the largest individual home ranges of all tracked birds (Appendix 2). So whilst some bird species may forgo breeding after successful reproduction in the previous year (Hustler and Howells, 1987; Snyder and Snyder, 2000; Jouventin & Dobson, 2002), it appears that the majority of non-breeders in this study were actually non-breeding floaters, that are common in many raptors populations (Tanferna et al., 2013; Ferrer et al., 2015; Lieury et al., 2015). These non-breeding floaters may be birds that are yet to find a mate or might be older birds no longer capable of breeding through senescence (Murgatroyd et al., 2018; Sergio et al., 2009; Penteriani et al., 2011). From the behaviours of breeding birds in my study, it appears that this species is in fact an annual breeder; from the seven breeding birds, all attempted to breed in each year. This information was previously unknown, but is suspected in other vulture species, such as the white-headed vulture *Trigonoceps occipitalis* (Hustler and Howells, 1988). Breeding activity of most vulture species remains poorly understood, primarily because long-term monitoring is lacking. Information that does exist can vary; for example, for bearded vultures, both annual and bi-annual breeding activity is believed to occur (Donazar et al., 1993; Margalida and Bertran, 2008; Krüger et al., 2014). Weather conditions, particularly rainfall, is an important factor driving variations in vulture breeding ecology (Hustler and Howells, 1990; Bridgeford and Bridgeford, 2003; Herholdt 2006; Virani et al., 2012), and therefore fluctuating environmental conditions may influence breeding parameters of species. As a result, the annual breeding attempts of breeders in my study could reflect more favourable weather conditions for breeding in those years e.g., less or moderate rainfall. Conversely, adverse weather conditions (significantly increased rainfall or increased intensity of rainfall events) could have contributed to nest failures and consequently driven consecutive breeding attempts. However, there is no obvious pattern to annual nest failures of birds in this study. Furthermore, some birds bred in consecutive years even when breeding was successful the previous year. Investigations into weather conditions in relation to lappet-faced vulture breeding would be valuable, particularly given the vulnerability of much of their range in southern Africa to climate change (Leichenko and O'Brien 2002; Abson et al., 2012).

Ranges of non-breeders were largest during March to May (leading up to egg-laying), which could indicate failed wide-ranging attempts to find breeding partners (Spiegel et al., 2015). Younger birds are more prone to wide-ranging and exploratory behaviours and therefore age variation in LFVs in my study could further explain differences in range sizes (Sergio et al., 2009; Tanferna et al., 2013; Votier et al., 2017).

Use of protected areas

Most LFVs in my study spent most of their time outside of PAs (around 75% of all GPS fixes). However, I found no significant difference in proportional use of PAs between breeders and non-breeders, nor where there large differences between PA use inside or outside of the breeding season. When I investigated selection of PAs relative to availability, I found selection for PAs, with the pattern of selection differing between seasons for breeders and non-breeders respectively. Breeders showed a significant preference for protected areas during both the breeding and the subsequent non-breeding season, whereas non-breeders selected PAs only during the breeding season, and slightly avoided PAs during the non-breeding season. Although we know little about the distribution of LFV nest sites, many likely occur within PAs. Over half the nests of breeders in this study occurred within or at the border of a protected area, although this may not be indicative of an active selection given the relatively large proportion of PAs in the country and thus a significant likelihood of nests being within PAs. Nonetheless, non-breeding vultures may be more attracted to these areas during the breeding season by the activities of their co-specifics. Alternatively, food resources are an important predictor of habitat use (Raynor et al., 2017; Hongo et al., 2018). Therefore, breeders may select areas that provide more reliable year-round food resources (Sergio et al., 2005). However, breeders in this study consistently preferred to use protected areas even though prey may be most abundant outside of these areas (Wallgren et al., 2009). Kendall et al. (2014) suggest however, that mortality rates of prey species rather than their abundance may drive habitat use by vultures, which could explain why vultures may choose areas with perceived lower food opportunities (e.g., less prey biomass).

Conclusions

My results suggest using caution when describing the home range size of a species, since range sizes of non-breeding floaters within a population may inflate estimates of home range size for the species as a whole. Range contraction by breeding birds seems obvious when considering nest constraints, and is in-line with other studies that compare ranging behaviours of breeders and non-breeders (Tanferna et al., 2013; Krüger et al., 2014; Kane et al., 2015).

My findings highlight the challenges of protecting wide-ranging species. They stress the importance of species-specific conservation approaches that effectively address the protection of independent groups within a population through 'full-cycle' protection. Furthermore, my results highlight the importance of understanding how conservation requirements of a population may differ temporally. My study illustrates differences in the movement ecology within a wide-ranging vulture population, suggesting that a blanket-approach to conservation e.g., one that does not address differences within a population, might prove ineffective for this group of birds. The relatively low proportion of time spent within protected areas, even in an area with a relatively high proportion of protected area coverage, suggests that these areas alone are likely inadequate to protect African vultures and other wide ranging wildlife (De Klerk et al., 2004; Fynn and Bonyongo 2010; Geldmann et al., 2013). Many wide-ranging species are increasingly at risk of extinction. Targeted conservation may be suitable for breeding populations, but will likely be ineffective for non-breeding segments of a population, unless there is significant overlap in space and resource use between the two groups. Thus, conservation approaches tailored for 'full-cycle' and 'full-spectrum' protection of a population must be given priority.

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Appendices

Appendix 1. Description of statistical analyses methods used in analyses of GPS tracking data for 14 adult lappet-faced vultures in Botswana. KDE = kernel density estimate, LMM = linear mixed model, GLMM = generalised linear mixed model. Variables: seas = breeding season: in or out, breed stat = breeding status: breed or non-breed, area = protected or non-protected area: PA or non-PA, nest dist. = nest distance (from each GPS point for breed birds).

Dataset used in analysis	Analysis	Response variable	Explanatory variables	Random terms	Distribution	Model
Total 95% KDE of each individual inside and outside of breed season. - data excluded months that were not a complete breed or non-breed season.	Differences between 95% KDE of all individuals in and out of the breed season, irrespective of breeding status	95% in km^2	Breed season	Bird id & year	Normal	LMM
Total 50% KDE of each individual inside and outside of breed season. - data excluded months that were not a complete breed or non-breed season.	Differences between 50% KDE of all individuals in and out of the breed season, irrespective of breeding status	50% in km^2	Breed season	Bird id & year	Normal	LMM
95% KDE of each bird in month in each year. - data excluded failed breeders and the non-breeding season when a bird was tagged during non-breeding months. Data only includes complete 'bird years'.	Differences between 95% KDE of breeding and non-breed birds inside vs outside of the breeding season	95% in km^2	Breed stat*seas	Bird id, year, month	Normal	LMM
50% KDE of each bird in each month in each year. - data excluded failed breeders and the non-breeding season when a bird was tagged during non-breeding months. Data only includes complete 'bird years'.	Differences between 50% KDE of breeding and non-breed birds inside vs outside of the breeding season	50% in km^2	Breed stat*seas	Bird id, year, month	Normal	LMM
95% KDE of each bird in each month in each year. - data excluded the non-breeding season when a bird was tagged during non-breeding months.	Differences between 95% KDE of breeding and non-breed birds each month	95% in km^2	Breed stat*month	Bird id & year	Normal	LMM
Total number of GPS fixes in each tracking year for each bird (inc. breed status) inside and outside PAs, inside and outside of the breed season. - data excluded failed breeders and the non-breeding season when a bird was tagged during non-breeding months.	Differences between use of PAs and non-PAs of breeding and non-breed birds inside and outside of the breeding season	Arcsine transformed proportion of fixes in PAs and non-PAs	Breed stat*seas	Bird id & year	Normal	LMM

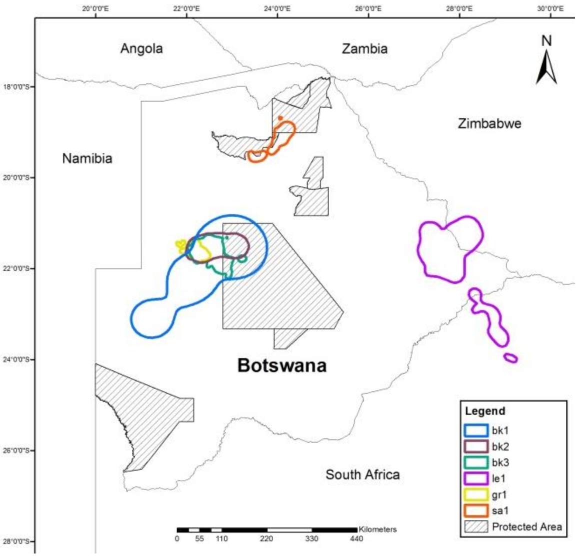
Appendix 1 continued

Dataset used in analysis	Analysis	Response variable	Explanatory variables	Random terms	Distribution	Model
All tracking data for breeding birds with 3 x the amount of pseudo-absence points as there were GPS fixes for each bird within the 100% MCP. - data for standardised nest distance included - data excluded failed breeders and the non-breeding season when a bird was tagged during non-breeding months.	Differences between habitat selection of **breeding** birds inside and outside of the breeding season	1/0 – binary (GPS fix / pseudo-absence)	Area*seas+nest_dist*seas	Bird id & year	Binomial	GLMM
All tracking data for non-breeding birds with 3 x the amount of pseudo-absence points as there were GPS fixes for each bird within the 100% MCP. - data excluded failed breeders and the non-breeding season when a bird was tagged during non-breeding months.	Differences between habitat selection of **non-breeding** birds inside and outside of the breeding season	1/0 – binary (GPS fix / pseudo-absence)	Area*seas	Bird id & year	Binomial	GLMM

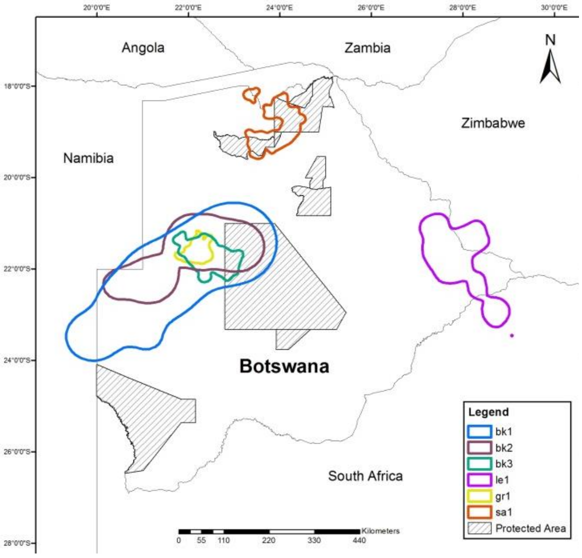
Appendix 2. Summary of GPS tracking data used to identify kernel home range sizes (KDE) and breeding activity for 14 adult lappet-faced vultures *Torgos tracheliotos* that were tagged in Botswana. Summary shows breeding status of each bird in each year and whether a breeding attempt was successful or not (suc/fail). Breeding activity data were collected through a combination of GPS tag data and ground surveys. KDEs are shown for data over full 'bird years' (bird year = April – March), which includes the breeding season followed by the consecutive non-breeding season or post-fledging dependency stage. PAs = protected areas. Data for failed breeders and incomplete 'bird years' were not used for seasonal analysis.

Vulture ID	Tracking dates	No. of total GPS fixes	% of GPS fixes inside PAs	No. of total tracking days	Breeding activity in each bird year	GPS tag status	100% MCP km^2	95% KDE inside breed season	95% KDE outside breed season
BK1LF	01/12/2012 – 30/04/2014	4526	55%	515	2013-br-suc	2014-UP	145 762 km^2	38,580 km^2	88,637 km^2
BK2LF	01/12/2012 – 08/02/2014	4091	47%	434	2013-br-suc	2014 - ST	63 208 km^2	7751 km^2	40,192 km^2
BK3LF	01/12/2012 – 30/04/2015	8092	8%	880	2013-br-suc 2014 br-fail	2014 - TO	110 567 km^2	6508 km^2	10,921 km^2
MB1LF	01/04/2013 – 29/06/2014	10289	15%	281	2013-nb 2014-nb	2014 - CP	49 708 km^2	21,992 km^2	21,223 km^2
GR1LF	06/04/2013 – 29/05/2015	6680	0.3%	783	2013-br-suc 2014-br-suc 2015-br-fail	2015 - TO	127 845 km^2	2274 km^2 6785 km^2	3942 km^2 6447 km^2
KP1LF	16/09/2013 – 30/10/2014	8633	42%	409	2014-nb	AC-INT	482 822 km^2	205,281 km^2	480,508 km^2
KP2LF	01/10/2013 – 30/04/2016	20686	41%	942	2014-nb 2015-nb	2016 - ST	473 533 km^2	181,498 km^2 158,232 km^2	328,645 km^2 163,677 km^2
SA1LF	01/04/2014 – 30/09/2016	20844	75%	908	2014-br-fail 2015-br-suc 2016-br-suc	2016 - UP	29 110 km^2	3472 km^2	11,106 km^2
KN2LF	01/09/2014 – 30/04/2017	22086	0.3%	972	2015-nb 2016-nb	AC	208 367 km^2	225,329 km^2 195,683 km^2	220,493 km^2 229,815 km^2
LE1LF	01/04/2015 – 30/04/2017	6087	3%	760	2015-br-suc 2016-br-suc	AC	66 390 km^2	23,453 km^2 21,132 km^2	24,221 km^2 40,544 km^2
LE2LF	01/04/2015 – 30/04/2017	16643	11%	760	2015-nb 2016-nb	AC	691 213 km^2	65,799 340,006	414,863 401,297
MK2LF	01/06/2015 – 30/04/2017	10310	44%	699	2015-nb 2016-nb	AC	439 444 km^2	253,752 km^2 323,923 km^2	47,417 km^2 47,177 km^2
MK3LF	01/06/2015 – 26/10/2016	7716	34%	512	2015-br-fail 2016-br-fail	2016 - unk	347 575 km^2		
GR2LF	01/08/2015 – 30/04/2017	9589	2%	638	2016-nb	AC	250 262 km^2	88,299 km^2	87,767 km^2
Total	-	156, 272	μ 23.4% ± 25.4%	9493	-	-	μ 248 986 km^2 ± 205 447 km^2	-	-

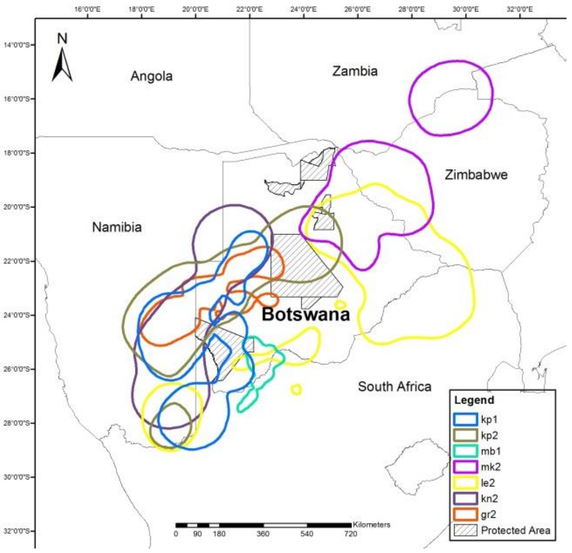
The cut-off date for GPS data used in analyses was the 30/04/2017. Br = breeding / nb = non-breeding.
GPS tag status: AC = still active, AC-INT = active but tag recording is intermittent, UP = unconfirmed poisoning, ST = stopped transmitting, TO = tag fell off, CP = confirmed poisoning, unk = unknown (no tag or bird recovered).



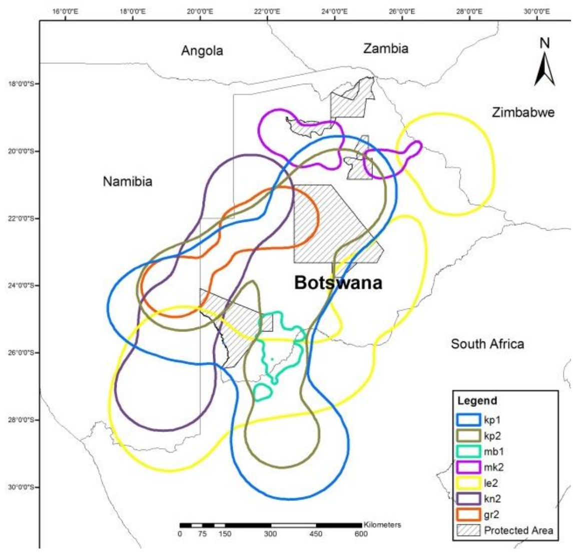
a. Ranges of each of the six breeders inside of the breeding season in a year in which they successfully bred.



b. Ranges of each of the six breeders outside of the breed season, in a year in which they successfully bred.

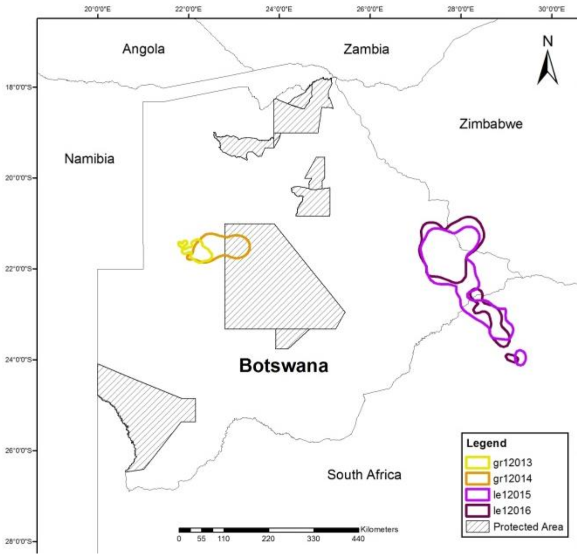


c. Ranges of each of the seven non-breeders inside the breeding season in a year in which they were tracked.

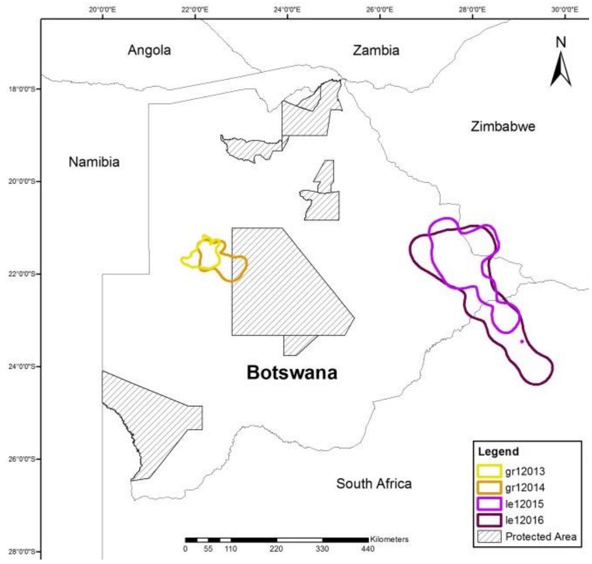


d. Ranges of each of the seven non-breeders outside the breeding season in a year in which they were tracked.

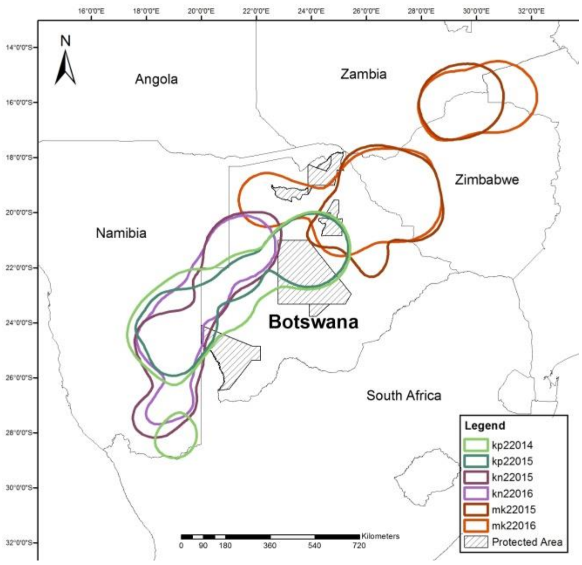
Appendix 3. (a-d) Visual representation of 95% kernel home ranges (KDE) for 1 'bird year' for each of the 13 (MK3LF excluded due to consecutive breeding failures across tracking data) GPS tracked adult lappet-faced vultures in Botswana. Data show 95% KDEs for breeding and non-breeding birds inside and outside of the breeding season respectively. Use of similar areas by birds is shown by consistent overlap of individual ranges. Range overlap with protected areas can also be seen.



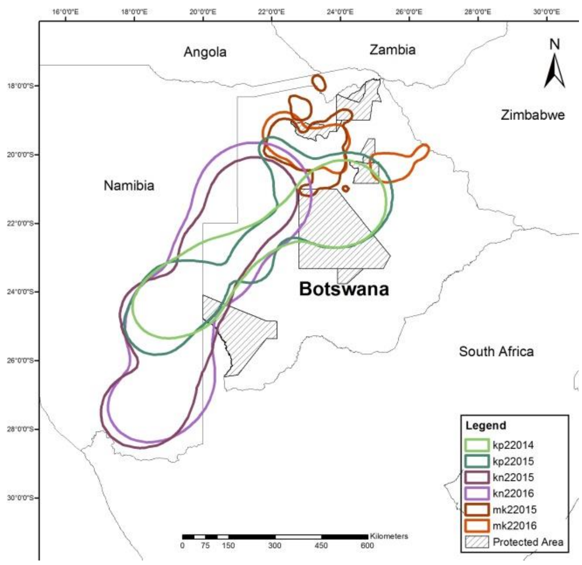
d. Ranges of two breeders in two consecutive years inside the breeding season



b. Ranges of two breeders in two consecutive years outside of the breeding season



c. Ranges of three non-breeders in two consecutive years inside of the breeding season



d. Ranges of three non-breeders in two consecutive years outside of the breeding season

Appendix 4. (a-d) Visual representation of 95% kernel home ranges (KDE) for breeding and non-breeding adult lappet-faced vultures in Botswana that had the most number of GPS tracked 'bird years'. Data show 95% KDEs inside and outside of the breeding season for the two different bird groups (breeders and non-breeders). Overlap of KDEs in each year for each individual were calculated and are shown in Appendix 5.

Appendix 5. Summary of the proportion of overlap of annual 95% kernel home ranges (KDE) for each GPS-tagged adult lappet-faced with ranges visually represented in Appendix 4. Table shows percentage of overlap for each breeder and non-breeder shown in Appendix 4, for both inside and outside of the breeding season respectively. * = breeders.

Vulture ID	% of overlap of annual 95% KDEs within breed season	% of overlap of annual 95% KDEs outside breed season
LE1*	58%	50%
GR1*	21%	33%
KP2	41%	36%
KN2	50%	58%
MK2	65%	48%

Chapter 5:

Exploring the use of Vulture Safe Zones for African vultures: a case study with lappet-faced vultures in Botswana

"Lappet love"

Abstract

The protection of highly mobile species poses complex challenges. Spatially targeted conservation may be the most effective way of protecting these species. In this way, conservation actions can be directed at protecting crucial resources and life stages of a population. This approach may be particularly important for threatened species. Vulture Safe Zones (VSZs) as focal areas for conservation of vultures have been used successfully in Asia to aid the recovery of three *Gyps* species that were driven to near extinction through poisoning (by veterinary drug - diclofenac). In Africa, vultures are in catastrophic decline, mainly due to illegal poisoning with pesticides. To explore whether VSZs could work for protecting vultures in Botswana, I used three 'bird years' of GPS tracking data for 13 adult lappet-faced vultures *Torgos tracheliotos* to identify areas most used by: 1) all birds 2) breeders and 3) non-breeders. I did this by calculating the cumulative percentage of GPS fixes of all individuals in each 1-degree grid-square (DGS) within Botswana (a total of 59 DGSs) and then ranking these DGSs according to the highest percentage of use. From these, I selected the top five DGSs (which formed the VSZs) for each bird group; resulting in three separate VSZs. I used five DGSs (50,000 km^2) because this area is spatially relevant to range sizes of adult lappet-faced vultures (see Chapter 4) and is realistically manageable. Furthermore, non-connected DGSs within the VSZs could offer multi-site protection of important areas and habitat, which is particularly important for conserving threatened species. I found that the three VSZs protected a cumulative total of 56% of 'all individual's' fixes and 54% of non-breeder's fixes. The most amount of protection was achieved by the VSZ aimed at protecting breeding birds, with 87% of their total fixes being protected. I found that VSZs offered similar amounts of protection inside and outside of the breeding season for all three bird groups. To test whether my targeted approach was better than a random approach, I compared the cumulative proportion of fixes that would be protected by randomly selected DGSs. Five randomly selected DGSs only protected 8% of cumulative fixes. Furthermore, it took 33 randomly selected DGSs to achieve the same level of protection as the least protective top five DGSs, which was the VSZ for non-breeders (54.2%). Thus, strategically designed VSZs aimed at protecting movements of breeders could be a viable conservation tool for adult lappet-faced vultures, or similarly wide-ranging species in Africa. However, the success of VSZs would rely heavily upon effective implementation and collaborative

conservation effort throughout the region, as well as on the effectiveness of other conservation activities outside of VSZs.

Introduction

An ongoing challenge in conservation is to adequately protect threatened species with limited resources available to do so (Margules and Pressey, 2000). Protected areas are the cornerstone of global biodiversity conservation (Gaston et al., 2008; Watson et al., 2014). The proposed expansion of the global protected area network by 2020 (from 13% to 17% land coverage) is aimed at halting the rapid decline of global biodiversity (Venter et al., 2014). However, increasing surface area coverage of protected areas may still fail to protect important biodiversity that may be more reliant upon area connectivity or habitat quality (Chape et al., 2005; Greve et al., 2011).

Therefore, for many wide-ranging species, protected areas alone may be inadequate conservation tools (Graham et al., 2016; Rabinowitz and Zeller, 2010). Such spatially explicit areas can hinder large-scale movements of species', which can threaten future population viability (Di Minin et al., 2013). In contrast, migratory species for example, often traverse international borders, and thus much of their range is not protected (Ito et al., 2006; Klaassen et al., 2014).

Using targeted areas for conservation such as Key Biodiversity Areas (KBAs) aims to be a more cost effective way in which to prioritise important areas for preserving global biodiversity (Eken et al., 2004). This type of site-specific conservation is increasingly being considered a more effective conservation approach for wide-ranging species, particularly for birds (Greve et al., 2011; López-López et al., 2007). There appears to be an increasing need for the use of priority conservation areas that focus on protecting optimal habitat and important life-cycle stages of species in order to 'fill gaps' in the protection of biodiversity (Abellán et al., 2011; Venter et al., 2014). For some species, a combination of both protected areas and additional site-based conservation may work best (Guixé and Arroyo, 2011; Sergio et al., 2005).

In Asia, contamination of carcasses with veterinary drug – diclofenac caused the near extinction of three species of *Gyps* vulture (Prakash et al., 2012). To help facilitate the recovery of these species, conservationists in Asia have established Vulture Safe Zones (VSZs). VSZs are essentially priority areas where conservation efforts can be concentrated, such as mitigating diclofenac poisoning and relieving pressures on breeding populations (Chaudhary et al., 2010; Murn et al., 2015). Vulture restaurants (supplementary feeding of vultures with carcasses or 'gut piles') have been used as the central concept of VSZs in Asia, to help reduce foraging by vultures outside of VSZs, thus alleviating their exposure to diclofenac-contaminated carcasses (Chaudhary, 2010). However, there is substantial controversy surrounding the use of vulture restaurants with regards to their capacity to effectively reduce mortality from poisoning and as to whether their use can negatively impact natural movement behaviours of vultures (Cortés-Avizanda et al., 2016; Deygout et al., 2009; Lieury et al., 2015).

In Africa, vultures have also undergone catastrophic declines in recent decades. As a result, most vulture species in Africa are heading towards extinction (Ogada et al., 2015). Poisoning by poachers or livestock owners is the biggest killer of African vultures and the use of poisons accounts for 61% of vulture deaths recorded on the continent (Buechley & Sekercioğlu, 2016; Ogada et al., 2016; Ogada et al., 2015). Furthermore, lead (Pb) poisoning from the ingestion of hunting ammunition left over in carcasses, has recently been identified as an additional threat that needs addressing (Garbett et al., 2018). Other significant causes of decline for African vultures include targeted poaching for belief based use of body parts, and collisions with electrical infrastructure (Ogada et al., 2015). Thus, addressing these threats are the most important actions that conservationists must tackle in order to help safeguard vulture populations into the future.

Most African vulture species range widely (Bamford et al., 2007; Krüger et al., 2014; Phipps et al., 2013; Virani et al., 2012) and protected areas alone are unlikely sufficient for protecting most species (Thiollay, 2007; Virani et al., 2011). Thus, conservationists in Africa are faced with a dilemma on how to allocate resources to tackling the threats across the ranges of different species. A similar approach to that adapted in Asia with VSZs has also been suggested as a potential conservation method for African vultures (Bowden, 2017). Within such VSZs, increased conservation measures would be enacted, actions could include education and enforcement to reduce poisoning (Ogada et al., 2016; Santangeli et al., 2016), rapid reaction teams to clear up poisoning incidents (Murn and Botha, 2017), removal of Pb ammunition (Garbett et al., 2018), and the mitigation of electrical infrastructure for example through marking of power lines (Shaw et al., 2010).

For such an approach to be successful in Africa, it is necessary to understand whether directing conservation actions within a certain area adequately protects a good proportion of the population and specifically whether such an approach would offer greater protection than a more dispersed 'scattergun' approach of non-targeted actions. It is also important to understand whether all sectors of the population are protected equally using such an approach and how easy it would be to identify the areas in which to target such actions.

In this study, I use tracking data collected between 2012 and 2017 from 13 adult lappet-faced vultures to explore the potential effectiveness of using Vulture Safe Zones as a conservation tool for this species in Botswana. The aim of this study is to explore whether I can identify the most used areas from these tracking data, and to explore what proportion of the population would be protected if conservation actions were targeted in these areas, and to select a reasonably sized area. I then contrast this approach with the alternative of allocation of resources to random areas, not informed by the tracking data. Lastly, I explore whether different sectors (breeders and non-breeders) of the population were equally well protected using such an approach (Chapter 4), and also whether protection differed by season (breeding and non-breeding). For example, because non-breeding floaters range more widely than breeding birds, VSZs may be a more viable tool for protecting the breeding population than for the non-breeding floating population, particularly given that breeder's ranges contract even more during the breeding season.

Methods and materials

Vulture Capture and Tagging

Between 2012 and 2017 I captured 14 adult lappet-faced vultures (LFV) at multiple locations distributed throughout Botswana (Figure 1). Trapping used the same methods as those described in chapter 4. All birds were fitted with 70 g solar- powered Global Positioning System (GPS) PTT-100s tags (Microwave Telemetry Inc., Maryland, USA), numbered patagial tags and ringed with steel leg bands for long-term monitoring.

Capture locations were distributed across the country, the aim being that the tracking data would be representative of the population as a whole rather than just the movements of a local population (Figure 1). However, there was some bias in the distribution of birds captured, with multiple birds sometimes being captured in the same area. Thus, if use of an area was strongly linked to the proximity of a capture location, any heavily used area might simply be a function of being closer to areas where more birds were captured, rather than representing a heavily used area for the population more generally. To explore this, for each GPS fix for each bird, I calculated the distance from that location to the location where the bird was captured, and then allocated the proportion of fixes for each bird to 100 km bands (up to 1000 km). I then calculated the mean ± 1 SD of fixes within each band and examined these data visually to ensure that there was not strong clustering of area use by each bird in close proximity (i.e., within a few 100 km) of the capture location.

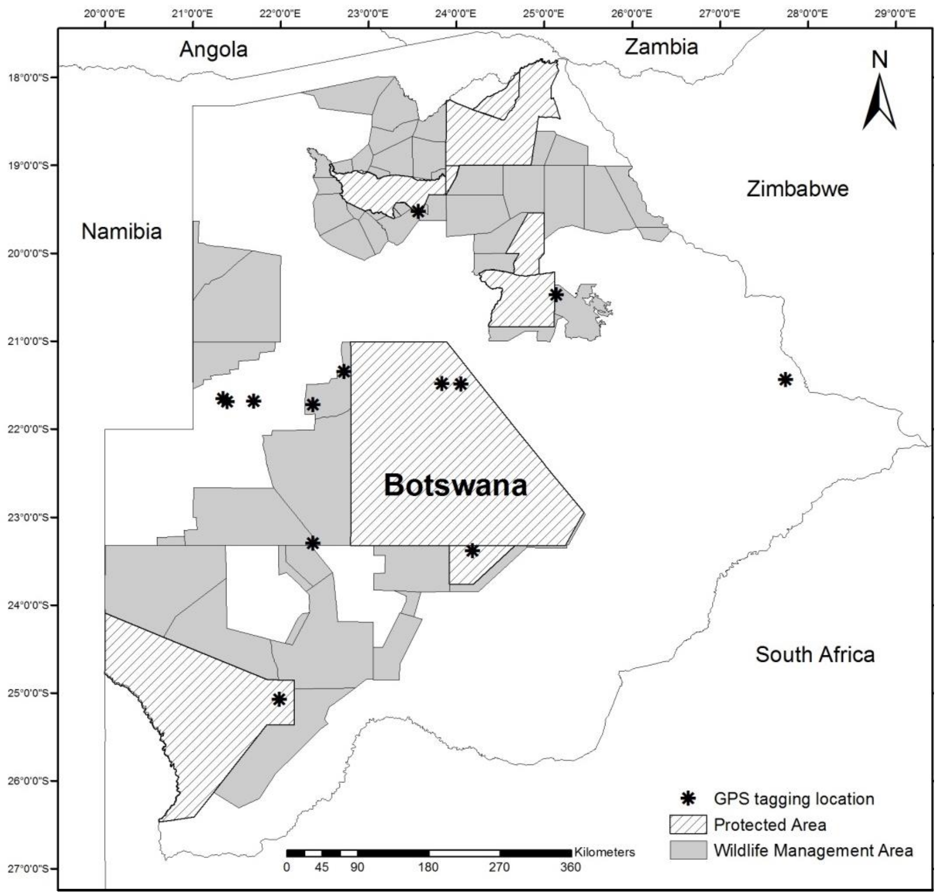


Figure 1. Study area showing the distribution of GPS tagging locations in Botswana of the 14 adult lappet-faced vultures captured. Data for 13 individuals were used for analyses due to consistent annual breeding failures of one individual across all tracked 'bird years' (Bird year = April – March). Areas designated as officially protected areas and Wildlife Management Areas (WMAs) are highlighted. These areas cover around 40% of the country. Tagging locations were largely within protected areas or WMAs.

Vulture safe zones

Methods used to identify breeding birds are described in chapter 4. The breeding status of individual birds for each breeding season were allocated across a 'bird year' that ran from April (the beginning of a breeding season), until March (the end of the non-breeding season), in the same way as in chapter 4. Only data for complete 'bird years' were used for VSZ analyses. To investigate whether vulture safe zones (VSZs) could be used for lappet-faced vulture conservation in Botswana, I explored the proportional use of each 1-degree grid square (DGS) that fell within Botswana. Whole DGS were used in this analysis, even those which only partially fell inside the boundary of Botswana. At this latitude a DGS is approximately a 100 km x 100 km square. Whilst a large proportion of fixes fell outside of Botswana (Chapter 4), for the purpose of this analysis, I explore only the fixes in DGSs that are within Botswana, specifically the 59 DGSs (ca 10,000 km^2 per DGS) located between latitude S18-27° and longitude E20-29° (Figure 1), thus the protection offered by VSZs in this study should be considered proportional to overall space use. Only data in Botswana were used in order to present the idea of VSZs for vulture conservation in Africa across a relatively manageable area that already contains a large network of protected areas. Spatial analysis was conducted in ArcMap v.10.2 (ESRI, Redlands, USA), and proportions of fixes in each DGS were analysed using the 'raster' package in R (Hijmans, 2016).

The percentage of GPS fixes (to account for the different numbers of fixes between birds) for each LFV was allocated to each DGS, then summed for each square, giving the cumulative percentage of use. I then ranked the squares from most to least used. This exercise was repeated for three separate categories: 1) all birds (irrespective of breeding status), 2) breeders 3) non-breeders (or floaters) (see Chapter 4). Breeding birds bred in all complete 'bird years' – and were classified as breeders, and non-breeders never bred in any of the 'bird years' they were tracked and were classified as non-breeders for the purpose of this study. One individual LFV had data omitted from analysis due to consistent annual breeding failures across all of its tracked 'bird years', resulting in the analysis of data for 13 LFVs.

For this study I envisaged a scenario where five DGSs (8.5% of squares), which would cover an area of 50,000 km^2, would be a realistic size to form VSZs for this species. Thus for each category of birds I used the ranked list of DGS usage to identify the five DGSs that contained the highest cumulative mean percentage of fixes; these acted as the VSZs for further calculations. I then explored what percentage of all fixes and of each individual would be protected by the respective VSZ, and how much this differed for all three bird categories (all birds, breeders and non-breeders). Additionally, I explored how consistent this level of protection was between the breeding season (April - November) and non-breeding season (December - March), by examining the percentage of fixes that were protected during these periods by the designated five DGSs that made up the VSZs. Lastly, I examined how much each of the three VSZs overlapped with protected areas and WMAs, performing all spatial analysis in ArcMap v.10.2 (ESRI, Redlands, USA).

To test how much better informed targeted selection of DGSs was compared to a non-informed targeted approach, I generated 50 random selections of DGSs, ranging from 50 samples of 1 DGS to 50 samples of the 59 squares in Botswana, and estimated the average (± 1 SD) percentage of fixes (and thus protection) each of the 50 samples protected. These random selections of DGSs were generated using the ‘sp’ package in R (Pebesma and Bivand, 2005).

Results

I used data for 13 LFVs that spanned a total of three different 'bird years' (see methods). Six LFVs were breeders and seven were non-breeders. Only data from inside Botswana were used for this study (Table 1).

Table 1. Summary of tracking data for the 13 GPS tracked lappet-faced vultures *Torgos tracheliotos* in Botswana showing the six breeders (*) and seven non-breeders, and the breeding activity of each bird within each 'bird year', as well as the breeding outcome (success or fail). Total numbers of GPS fixes inside Botswana for each bird show the data that were used for Vulture Safe Zone (VSZ) analysis. The proportion of total fixes of each bird within Botswana shows how much of their total tracking data were within Botswana and therefore gives an indication of how much overall protection (of total tracking data) might be achieved by VSZs in Botswana. Data for failed breeders and incomplete 'bird years' were omitted from analysis.

Vulture id	No. of total GPS fixes	No. of total tracking days	No. of total GPS fixes within Botswana	% of GPS fixes within Botswana	Breeding activity
BK1LF*	4526	515	2601	57%	2013-br- success
BK2LF*	4091	434	2926	71%	2013-br-success
BK3LF*	8092	880	3370	41%	2013-br- success 2014-br-fail
MB1LF	10289	281	5820	56%	2013-nb 2014-nb
GR1LF*	6680	783	5208	77%	2013-br-success 2014-br-success 2015-br-fail
KP1LF	8633	409	4007	42%	2014-nb
KP2LF	20686	942	9868	41%	2014-nb 2015-nb
SA1LF*	20844	908	10355	75%	2014-br-fail 2015-br-success 2016-br-success
KN2LF	22086	972	9364	42%	2015-nb 2016-nb
LE1LF*	6087	760	4840	79%	2015-br-success 2016-br-success
LE2LF	16643	760	6369	38%	2015-nb 2016-nb
MK2LF	10310	699	4326	42%	2015-nb 2016-nb
GR2LF	9589	638	3424	36%	2016-nb

I first explored whether fixes from individual birds were closely associated with their capture location. I found that the distribution of fixes in relation to distance from the capture locations was not strongly associated with the capture location, with on average 50% of fixes being found over 1000 km away from the capture location (Figure 2). Thus, I could be confident that the DGSs identified as those with the highest use, were not simply due to the influence of capture locations.

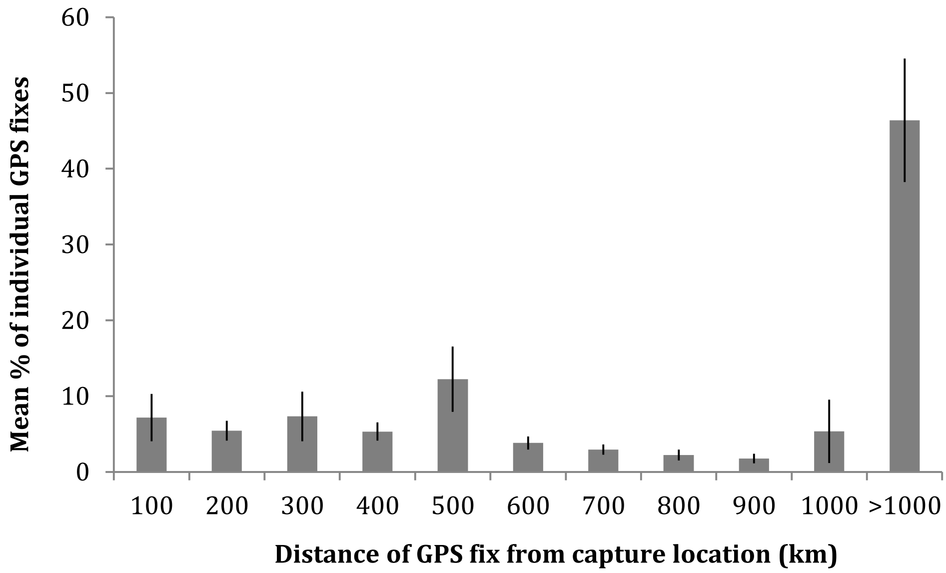


Figure 2. Summary of the mean % of each lappet-faced vulture's *Torgos tracheliotos* GPS fix data (± 1 SE) that were within each distance band radiating away from their capture location in Botswana at intervals of 100 km. This was done to investigate the potential influence of capture location on location of GPS fixes for all individual lappet-faced vultures. Fixes >1000 km away from the capture location were grouped into one category for the purpose of this analysis. All data (including fixes outside of Botswana) were used for this analysis.

Protection offered by vulture safe zones

As the number of DGSs selected increased, the additional proportion of fixes protected by them decreased, thus a cumulative curve was apparent (Figure 2). This indicates that fixes were not evenly distributed across all DGSs. The curves were similar for 'all birds' and 'non-breeders', but was steeper for breeding birds, indicating that a higher proportion of fixes could be protected with fewer DGSs. The top five ranking DGSs (i.e., 8.5% of all 59 DGSs in Botswana) protected nearly 57% of fixes in Botswana of 'all birds' (Figure 2 & 3a). For breeding birds, the five top ranking DGSs protected 88% of their fixes in Botswana (Figure 2

& 3b). For non-breeding birds, the top five DGS protected only 54% of their fixes inside Botswana (Figure 2 & 3c). Unsurprisingly, the randomly sampled DGSs offered far less protection than any of the strategically selected VSZs. The 50 samples of five randomly selected DGSs only protected on average 7.9% ± 5.8% (± 1 SD). To achieve 54% (i.e., the level of protection offered by VSZs for non-breeders) of protection with randomly sampled DGSs took 35 DGSs, and to achieve 88% protection (i.e., VSZs targeting breeders) took almost all (53) DGSs in Botswana (Figure 3).

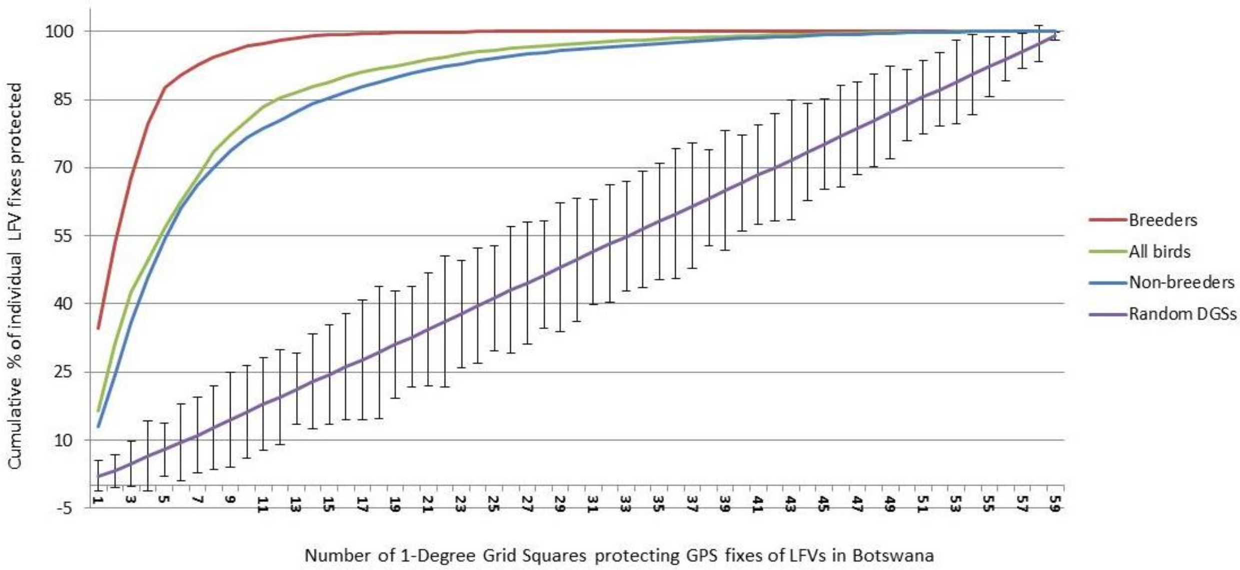
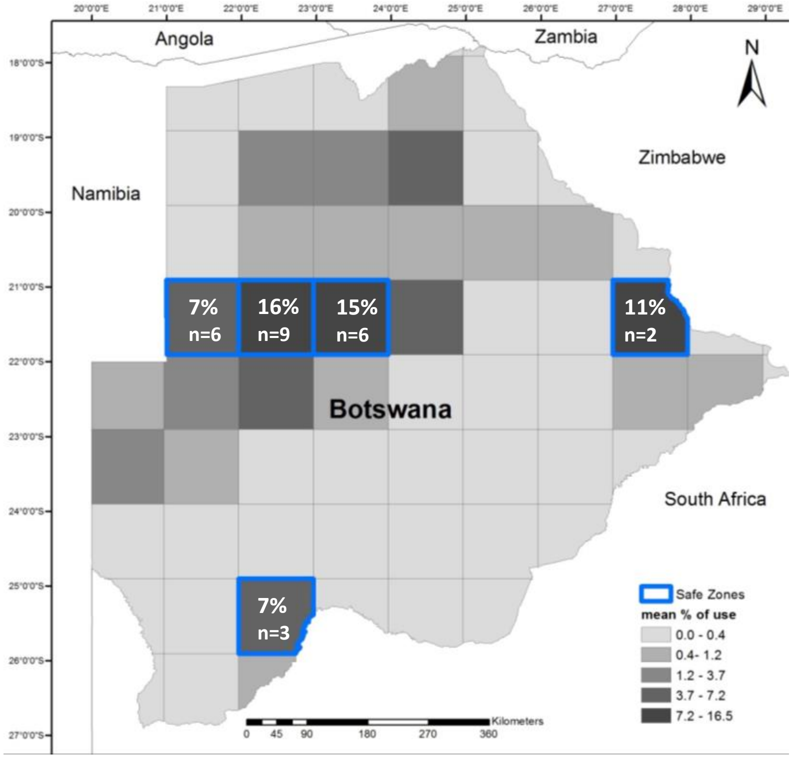
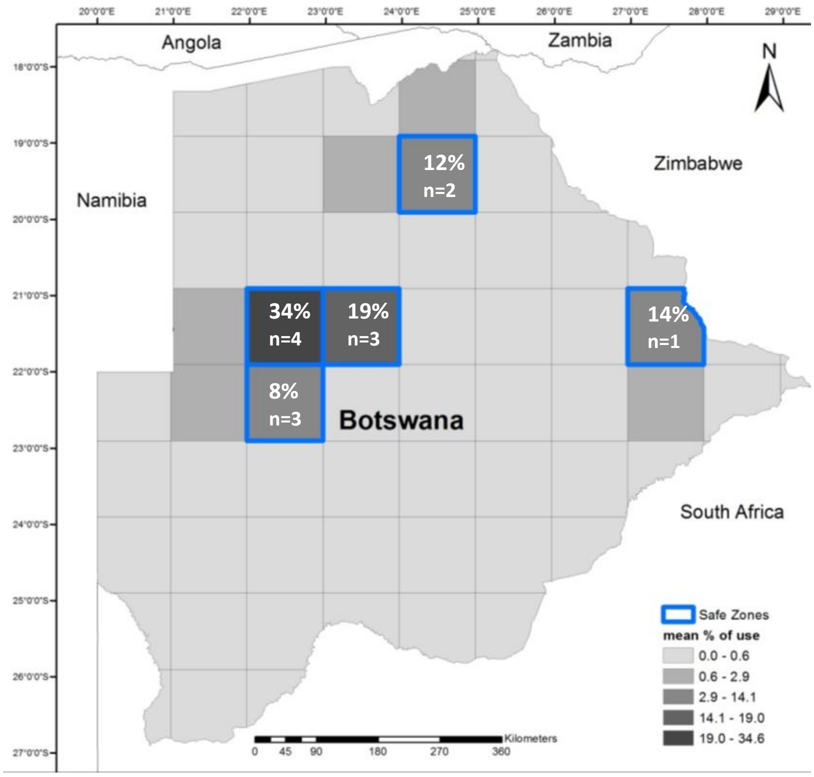


Figure 3. Curves showing the cumulative percentage (± 1 SD) of individual lappet-faced vulture's *Torgos tracheliotos* (LFV) fixes protected by increasing numbers of 1-Degree Grid Squares (DGS) in Botswana; from 1 DGS up to 59 (all the DGSs in Botswana). Different coloured curves indicate levels of protection that could be achieved for the three different bird groups: 'all birds', 'breeders' and 'non-breeders', within a population in Botswana, as well as showing the level of protection that could be offered using randomly selected DGSs. The top five DGSs were used to identify Vulture Safe Zones (VSZs) (an area of around 50,000 km^2) for each of the three bird groups. Data for 13 individual LFVs over a maximum of 3 'bird years' were used for analysis.

4.a.


Angola
Zambia
N
Zimbabwe
Namibia
7%
n=6
16%
n=9
15%
n=6
11%
n=2
Botswana
South Africa
7%
n=3
Safe Zones
mean % of use
0.0 - 0.4
0.4- 1.2
1.2 - 3.7
3.7 - 7.2
7.2 - 16.5
Kilometers
0 45 90 180 270 360

4.b.


Angola
Zambia
N
12%
n=2
Zimbabwe
Namibia
34%
n=4
19%
n=3
14%
n=1
8%
n=3
Botswana
South Africa
Safe Zones
mean % of use
0.0 - 0.6
0.6 - 2.9
2.9 - 14.1
14.1 - 19.0
19.0 - 34.6
Kilometers
0 45 90 180 270 360

4.c.

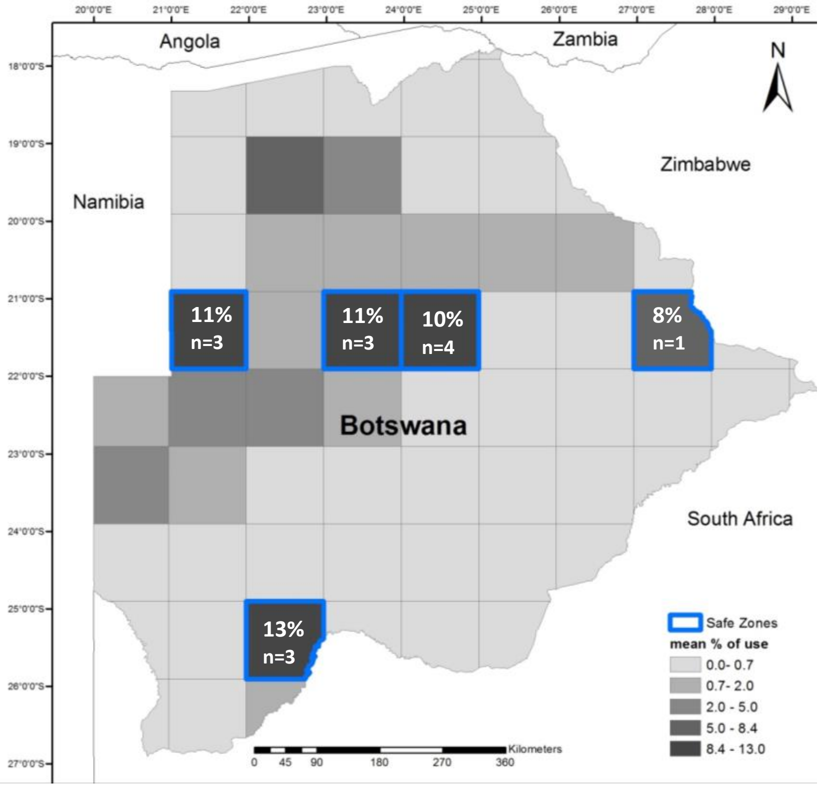


Figure 4 (a-c) Maps of Vulture Safe Zones (VSZs) e.g., the top five 1-Degree Grid Squares (DGS) with the highest mean % of individual coverage of GPS fixes for three different groups within a lappet-faced vulture *Torgos tracheliotos* population in Botswana: **a)** all birds **b)** breeding birds, and **c)** non-breeding birds. Percentages shown in VSZ squares (highlighted squares) are the cumulative % of individual use for that VSZ square. Percentages were rounded to whole numbers. VSZs protected a cumulative amount of 56.6% of **a)** all individual's fixes, 87.6% of **b)** breeding bird's fixes, and 54.2% of **c)** non-breeding bird's fixes. n = sample size.

The percentage of individual protection provided by the VSZs aimed at protecting 'all birds' ranged from 0% to 97% (Table 2), and the VSZs targeting breeders protected 71% to 93% of individual's fixes. Individual protection of the VSZs targeting non-breeders ranged from 0.4% to 89% (Table 3). Thus, VSZs targeting breeders offered the most cumulative and individual protection of fixes.

When I investigated whether levels of protection of VSZs differed inside and outside of the breeding season, I found that individual levels of protection remained largely the same across both seasons for all three groups of birds (Table 2 & 3). The only apparent difference was that for a few birds in the 'all birds' and 'non-breeder' categories, levels of protection by VSZs decreased quite substantially outside of the breeding season (Table 2 & 3). However, for breeders, the level of individual protection from VSZs remained similar inside and outside of the breeding season (Table 3).

Table 2. Summary of the total % of fixes of each GPS-tagged lappet-faced vulture *Torgos tracheliotos* in Botswana that were protected by the Vulture Safe Zones (VSZs) targeted at protecting 'all birds'. Summary shows the percentage of protection achieved for each bird a) throughout the whole year, b) inside the breeding season, and c) outside the breeding season. * = breeding birds.

VSZs for 'all birds'			
Bird ID	% of individual protection throughout the year	% of individual protection inside breeding season	% of individual protection outside breeding season
GR1LF*	96.6%	97.9%	91.7%
BK1LF*	91.8%	95.5%	72.7%
BK2LF*	94.1%	97.8%	80.6%
MB1LF	88.4%	89.8%	86.2%
LE1LF*	84.6%	84.6%	14.3%
KN2LF	80.0%	85.6%	63.0%
LE2LF	59.0%	64.4%	14.3%
BK3LF*	52.3%	43.5%	69.0%
KP2LF	47.9%	52.3%	41.3%
KP1LF	36.7%	41.1%	33.1%
GR2LF	4.4%	4.6%	4.2%
MK2LF	0.6%	0%	0.7%
SA1LF*	0%	0%	0%

Table 3. Summary of the total % of fixes of each GPS-tagged lappet-faced vulture *Torgos tracheliotos* in Botswana that was protected by the Vulture Safe Zones (VSZs) targeting protection of 'breeders' and 'non-breeders' respectively. Summary shows percentage of protection achieved for each bird a) throughout the whole year, b) inside the breeding season, and c) outside the breeding season.

VSZs for breeding birds				VSZs for non-breeding birds			
Bird ID	% of individual protection throughout the year	% of individual protection inside breeding season	% of individual protection outside breeding season	Bird ID	% of individual protection throughout the year	% of individual protection inside breeding season	% of individual protection outside breeding season
BK1LF	92.3%	95.5%	76.0%	MB1LF	88.4%	89.8%	86.2%
BK2LF	93.0%	97.5%	77.4%	KN2LF	79.3%	84.6%	63.0%
BK3LF	97.8%	99.1%	95.2%	KP1LF	69.1%	81.0%	57.6%
GR1LF	86.0%	86.5%	84.2%	KP2LF	81.7%	80.6%	83.3%
LE1LF	84.6%	84.6%	84.6%	LE2LF	59.6%	65.1%	14.3%
SA1LF	71.2%	67.0%	82.2%	MK2LF	1.2%	2.5%	0.9%
-	-	-	-	GR2LF	0.4%	0.6%	0.3%

On exploring the percentage of overlap of each of the three VSZs with officially protected areas (PAs) and WMAs in Botswana, I found that VSZs for all birds overlapped with PAs by 22%, that those for breeders overlapped by 28%, and that VSZs for non-breeders overlapped by 25%, thus all three VSZs showed similar percentages of overlap with PAs, with a mean overlap of 25% ± 2.4% (± 1 SD). For WMAs, the overlap of all bird VSZs was 20%, for breeder VSZs was 37%, and for non-breeder VSZs was 10%, producing a mean overlap with WMAs of 22% ± 11.1% (± 1 SD).

Discussion

My aim was to explore the feasibility of using VSZs as targeted conservation measures aimed at safeguarding LFVs in Botswana, which have rapidly declined in parts of the country over the last 20 years (Garbett et al. 2018). My results suggest that VSZs could be a potentially viable conservation tool for breeding LFVs in Botswana. VSZs targeting breeders protected more than 80% of their total movements within an area of 50,000 km^2, whilst also protecting between 70% - 90% of each breeding bird's movements within Botswana. The potential for VSZs to protect breeding LFVs is strengthened by the consistent levels of protection offered during both the breeding and non-breeding season, as well as the fact that almost all movements of breeders were within Botswana (90% of total movements), and are therefore almost entirely captured within this study. Although VSZs targeting 'all birds' and 'non-breeders' both offered over 50% of cumulative protection of fixes, their ranges of protection per individual were far less than those of VSZs aimed at protecting breeders. Furthermore, because around half of non-breeder movements (44%) were outside of Botswana, achieving a similar level of protection of their transboundary movements is optimistic. VSZs for 'all birds' and 'non-breeders' gave some individuals little to no protection at all. Nonetheless, over 70% of individual birds in each of these two groups ('all birds' and 'non-breeders') had more than 50% of their movements protected by their respective VSZs, indicating that these VSZs failed to protect a relatively small proportion of individuals. My results show that VSZs would be most effective for protecting breeding birds, and could potentially offer effective 'full-cycle' protection (protection across the breeding and non-breeding season). However, because VSZs may only be effective for protecting breeding birds, this approach may fail to achieve 'full-spectrum' protection of a population; 'full spectrum' being a term that I have used to describe the protection of different sectors within a population e.g., breeders and non-breeders. This alone, may question the viability of VSZs for protecting vultures in Botswana.

Vulture Safe Zones in Asia have been successfully used to aid the recovery of *Gyps* vulture populations that were driven to near extinction through feeding on carcasses containing veterinary drug, diclofenac, which is fatal to *Gyps* vultures (Chaudhary et al., 2010). The central concept of VSZs in Asia is the protection of wild breeding vulture colonies and the provision of 'clean meat' at vulture restaurants as a safe food resource (Mukherjee et al., 2014). The consequential increases in targeted Asian vulture populations show that they are important for breeding individuals and have likely decreased mortality rates (Gilbert et al., 2007). Observations from VSZ monitoring in Asia show that vultures use VSZs largely during important breeding stages such as hatching and early nestling dependency, but that their use decreases during the course of the breeding season and is at its lowest during and following the post-fledgling dependency stage (non-breeding season) (Gilbert et al., 2007).

Lappet-faced vultures are solitary, low density breeders (Bridgeford and Bridgeford, 2003) unlike the colonial breeding species that Asian VSZs target (e.g., oriental white-backed vultures) (Murn et al., 2015). However, unlike such colonially nesting vultures, we do not even know the most important nesting areas for this species in Botswana and only know of a handful of nests of this species. Thus, a breeding site based approach would not currently work for such a low density breeder. However, given the relatively confined ranging behaviours of breeding lappet-faced vultures (Chapter 4), there may be potential for VSZs to capture important breeding and foraging areas.

Although strategies based primarily upon the protection of nesting habitat may not work for lappet-faced vultures, they could be useful for conserving other vulture species such as the endangered cape vulture *Gyps coprotheres*. The colonial breeding behaviours of cape vultures mean that concentrated breeding colonies occur sparsely throughout the region (Boshoff et al., 2010; Wolter, 2017) and would therefore be relatively easily encompassed and managed through the use of 'safe zones'. However, the ranging behaviour of cape vultures from the breeding location is also not symmetrical (Bamford et al., 2007), and thus a similar approach as taken here (but with a finer scale –e.g., 10 km squares) could perhaps be applied to buffer areas around such colonies, where tracking data exist.

Artificial feeding sites (vulture restaurants) are used within VSZs in Asia (Gilbert et al., 2007) and are a potentially effective conservation tool for African vultures. Vulture restaurants may be useful in reducing exposure to poisoning; however the benefits for adult birds in particular have been mixed (Martínez-Abraín et al., 2012; Oro et al., 2008; Piper et al., 1999). Within southern Africa there has been little research on vulture restaurants, but evidence does suggest that they could have long-term value for vulture populations by providing safe and reliable food resources and by facilitating improved population survival (García-Ripollés and López-López, 2011; Kane et al., 2015; Lieury et al., 2015; Murn et al., 2015). However, supplementary feeding can be detrimental to vultures by creating an evolutionary trap that can lead to population declines (Fluhr et al., 2017). Vulture restaurants do however, have the capacity to act as centres for education and awareness, and for building capacity within local communities through eco-tourism (DeCandido et al., 2012; Houston and Piper, 2006). Furthermore, establishing well-managed vulture restaurants may help direct the largely unregulated network of vulture restaurants across southern Africa (Anderson and Anthony, 2005; Kane et al., 2015; Yarnell et al., 2015). Using vulture restaurants in conjunction with VSZs in Africa may help combat poisoning (pesticide, Pb and diclofenac or similar veterinary drugs) through regulation and monitoring of food sources, as well as through increasing education and awareness of, and building capacity for African vulture conservation. However, careful consideration would need to be given to their management e.g., size of restaurant, frequency of feeding, and risk of predation. The promotion and development of new VSZs, particularly for monitoring and mitigation in relation to key threats, is an important aspect of the framework for action in the Convention on Migratory Species (CMS) - Vulture Multi-species Action Plan (MsAP) (Botha et al., 2017).

Achieving complete protection of highly mobile species is challenging and goes beyond the scope of available resources and management capacity. Breeding birds are vital for population persistence, as well as for the physical recovery of populations suffering large declines, thus their protection is often the cornerstone of conservation strategies (Greenwood, 2003; Murn et al., 2016). Spatial limitations and more predictable behaviours of breeders during the breeding season alleviate some of the complexities associated with protecting them (Young et al., 2015). My study suggests that using VSZs as a tool for protecting lappet-faced vultures might be most viable for breeding birds, with the VSZ areas in this study offering substantially (c. 35%) more protection of movements for breeders than that provided to the more wide-ranging non-breeders (Chapter 4). Furthermore, because of the increased overlap of breeder VSZs with protected areas and WMAs when compared with non-breeder and all bird VSZ overlap, VSZs aimed at breeders may be a viable conservation tool for use alongside existing conservation management strategies, and may also help focus conservation action within existing conservation areas.

Perhaps equally as importantly, I found that this level of protection remained consistent during the breeding and non-breeding season meaning that full ‘life-cycle’ protection could be achieved. For other wide-ranging bird species, strikingly different ranging behaviours inside and outside of the breeding season warrant seasonally tailored conservation approaches (Amat et al., 2005; Morrison et al., 2013; Weimerskirch et al., 2014). The apparent indifference between seasons in heavy utilisation of specific areas by breeding birds in my study is advantageous to their protection through VSZs and may be evidence that VSZs contain important year-round habitat for lappet-faced vultures.

Most non-breeders in my study showed movement patterns similar to those of ‘floaters’. Adult floaters can act as surplus individuals able to quickly fill vacant positions within a population, for example, replacing breeding birds that die (Ferrer et al., 2003; Robles and Ciudad, 2017). Floaters in my study may therefore be acting as important buffers for population losses and it is now well established that such birds can play an important role in dynamics of a population (Monzón and Friedenberg, 2018; Penteriani et al., 2011), thus their conservation cannot be ignored at the expense of focussing solely on breeding birds (Robles and Ciudad, 2017). Although I found differences between home range sizes of breeders and floaters (or non-breeders) (Chapter 4), there was no obvious separation between geographical areas used by the two groups of birds, which can sometimes be true of floaters and breeders (Tanferna et al., 2013). Instead, I observed largely overlapping movements of both bird groups (Chapter 4), even though the intensity of area use differed. As a result, using VSZs aimed at protecting all birds within a population or all non-breeders, protected over half of the movements of each group, which could still prove to be highly valuable when used in combination with alternative conservation strategies, such as protected areas. In contrast, VSZs specifically targeting breeders only protected around 25% of movements of non-breeders, thus, it is still not entirely clear which would be the best strategy for the overall conservation of the species. Future population models might be useful in this regard to test the best approach to take.

My study was limited by the relatively small number of breeders and non-breeders. A larger samples size may have shown far less protection by VSZs as a consequence of increased individual variation of space use. Thus using larger sample sizes may better reflect the conservation capacity of VSZs. In addition, I only used data from within Botswana and therefore this evaluation does not account for movements outside of national borders, where a substantial amount of time was spent by the majority of study birds. My results could have been further influenced by the unbalanced amount of data for breeders and non-breeders and for inside and outside of the breeding season.

In contrast to strategically selected VSZs, randomly selected zones in my study offered far less protection for all three bird groups and would not be a viable or cost effective conservation approach. Conservation targeted at protecting key areas or life stages of highly mobile species can better sustain populations (Newton, 2010; Speed et al., 2010). This is particularly the case for wide-ranging birds (Newton, 2010; Schuster et al., 2018), although it has been suggested that dynamic protected areas which track movements of wide-ranging species, may be more effective than static or site-scale conservation areas (Bengtsson et al., 2016; Rayfield et al., 2008). However, the implementation and management of such areas would be considerably more challenging than strategies aimed at using permanent areas. Additionally, lack of ecological knowledge for many wide-ranging species would currently hinder the use of dynamic areas. In the current climate (i.e., wide-ranging threats and minimal protection by protected areas), additional focal conservation areas may prove to be our biggest asset for conserving African vultures (Buechley et al., 2018). With the potential for vast expansion of human infrastructure in southern Africa such as wind energy farms and powerline networks (Botha, et al., 2017; Reid et al., 2015), the necessity for areas that can safeguard regional vulture populations is increasing. However, the success of focal conservation areas is largely dependent upon factors operating outside of them e.g., threat mitigation and education of key stakeholders (Iwamura et al., 2013; Martin et al., 2007), therefore paralleled broad-scale conservation action would be necessary to complement the implementation of VSZs in Africa, and indeed, is also required alongside the use of existing protected areas.

My study shows that VSZs could be a potentially useful tool for conserving wide ranging vultures in Africa, particularly for breeding birds, but that caution should be used if applying this approach to other sectors of a population, particularly for birds of different age classes e.g., juveniles or immature birds, which are not represented in this study and likely range further than adults due to lack of breeding-motivated movements. Furthermore, assessing the usefulness of VSZs for larger number of individuals and other populations using the framework outlined in this study should be a pre-requisite for any conservation action resulting from this assessment. ‘Full-cycle’ and ‘full spectrum’ protection are fast being considered essential components of conservation strategies addressing wide-ranging species, especially those that are endangered. According to my findings, VSZs may be effective for ‘full-cycle’ protection but would likely fail to address ‘full spectrum’ requirements e.g., individual differences within a population, which may seriously depreciate their value for vulture conservation in Africa.

Conclusions

The results of this study highlight the challenges of protecting wide-ranging species and illustrates why protected areas that lack ecological focus are inadequate for the protection of many species. The study shows distinct differences between the ecology of individuals within a vulture population that suggests traditional conservation approaches are likely to be inefficient. With this in mind, my results support the increasing recognition for the necessity of more focussed conservation strategies alongside existing protected areas.

If VSZs were to be implemented in Africa, their success would largely depend upon broad-scale cooperation between key stakeholders and availability of resources that could be allocated for establishing and managing these areas (Guikema and Milke, 1999). Additionally, sound strategical planning and progress evaluation would be crucial for ensuring their efficacy (Kapos et al., 2008; Knight et al., 2006). Linking with projects in Asia and learning how to best establish VSZs in Africa would be a realistic starting point. Furthermore, working within the framework of the Vulture MsAP would facilitate the effective use of African VSZs through the provision of clear objectives relating to the protection of African vultures.

Acknowledgments

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Chapter 6: Synthesis

"A Kalahari winter"

Synthesis

This thesis stemmed from on-going research in Botswana working to fill knowledge gaps on raptor populations, specifically vultures, in light of their decline. My main thesis' aim was to shed light on how raptors in Botswana are faring compared to other regions, and to increase the capacity for effective conservation planning through increasing fundamental ecological knowledge and knowledge on key threats (Figure 1). Results were consistent with the deteriorating status of raptors observed elsewhere in Africa and highlight the need for urgent conservation prioritisation. My findings were incorporated into the convention on Migratory Species (CMS) Vulture Multi-species Action Plan (MsAP) (Botha et al., 2017). The existing MsAP framework can facilitate further assessment of potentially viable conservation strategies that arose from my research.

Historical information is important to establishing how a species or a population is faring (Plumptre and Cox, 2006; Yalden et al., 2007). The systematic raptor road surveys of Marc and Diane Herremans provided an ideal starting point to investigate the population status of raptors in Botswana. I repeated (Chapter 2) the northern section of the Herremans' road surveys to identify changes in abundance of raptor species over the last 20 years. As large-scale surveys are particularly suitable for raptors given their generally low density (Buij et al., 2013; Keys et al., 2012), they have been used in Africa to provide most of the historical information available on raptor population trends and have been integral to identifying declines of African raptors (Ogada et al., 2015; Thiollay, 2007a; Virani et al., 2011). The importance of using comparable monitoring methods is stressed by Ogada et al.'s (2015) study that amalgamated data from different surveys, made possible by the use of similar techniques in the different studies. This is an important consideration for future, long-term monitoring efforts across the continent, as highlighted by research priorities for African vultures (Botha et al., 2012).

African raptor declines

In chapter 2, I identified abundance trends for 29 raptor species in northern Botswana and found that almost all species declined over the last 20 years. My findings are a concern given that Botswana is regarded favourably in terms of its conservation potential due to its low

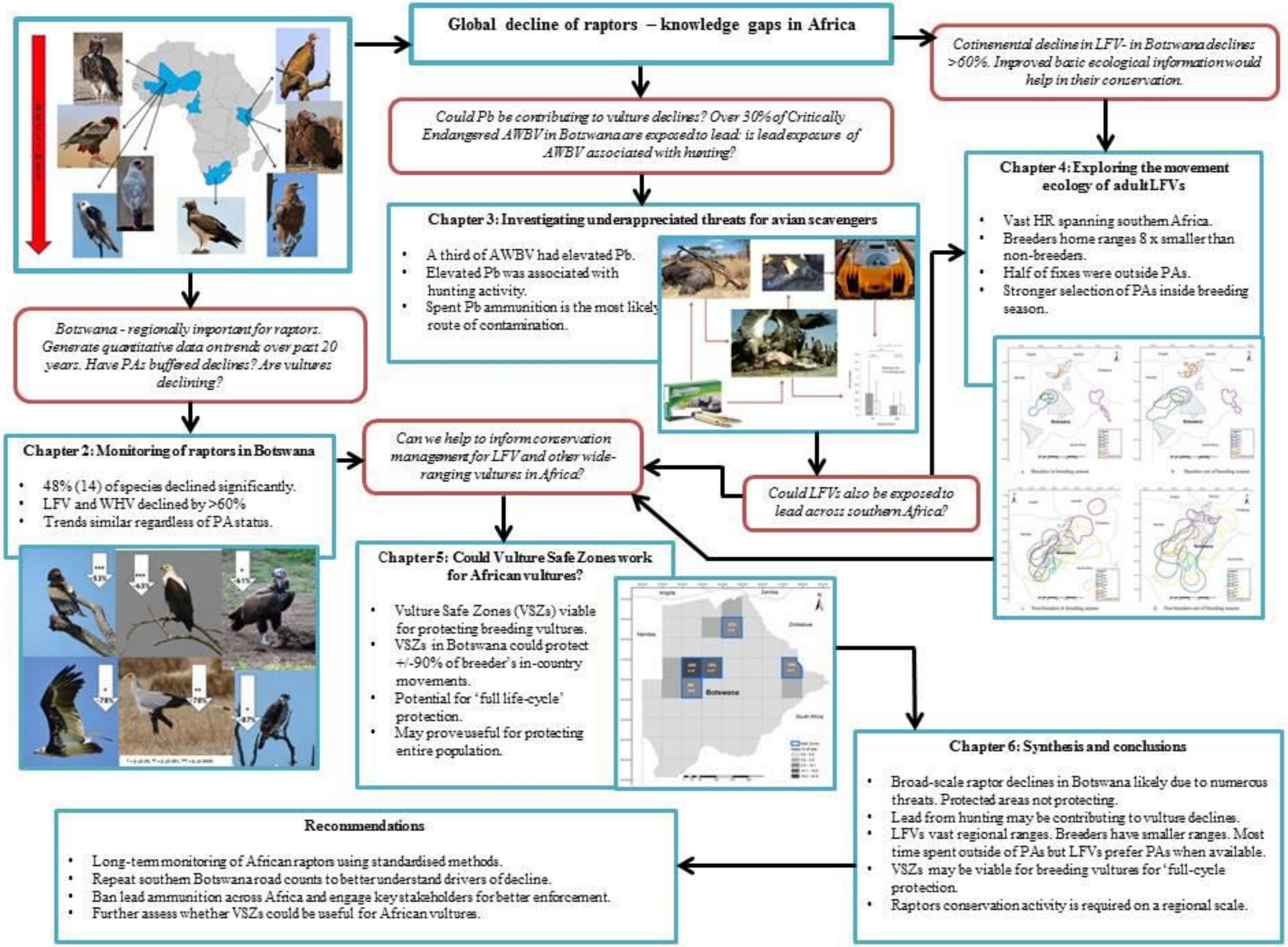

Figure 1. Infographic of research motivations and key questions forming the flow of thesis chapters, including principal findings of each chapter, main conclusions and recommendations arising from this research. Red boxes indicate research questions.

human population (2.3 million) and large proportion of areas designated for wildlife conservation (c. 40%) (Kootsositse et al., 2009; Statistics Botswana, 2011). Thus, whilst I expected that vulture populations may have declined in Botswana due to the large number of poisoning events that have occurred in the region over the last decade, I had expected populations of other raptor species to have fared better in Botswana, than elsewhere in Africa. However, this was not the case, with declines detected for many raptor species. These declines applied to species across the spectrum of life histories and ecological traits. Worryingly, and in stark contrast to other studies in Africa, I found decline levels were similar inside protected areas, suggesting that protected areas were failing to buffer declines. Only two surveyed species showed significantly different abundance trends inside vs outside of protected areas, suggesting that all other species are declining similarly across all areas. In this respect, my findings contrast starkly with raptor population trends in East and West Africa, where protected areas appear to act as important refuges for many raptor species, particularly for vultures (Ogada et al., 2015; Thiollay, 2007b; Virani et al., 2011). For example, within Botswana, lappet-faced *Torgos trachiliotos* and white-headed *Triconoceps occipitalis* vultures declined significantly by 61% and 78%, respectively, with no difference in trends inside vs outside of protected areas. However, in East and West Africa, these species have suffered disproportionately more outside of protected areas (Ogada et al., 2015). The same held for many large eagle species in West Africa, which have almost disappeared altogether outside of protected areas, with much lower declines occurring inside them (Thiollay 2007a, b). Nonetheless, the efficacy of protected areas for protecting wide-ranging species such as raptors is increasingly criticised, mostly because the magnitude of their ranges may far exceed the scope of protection that these areas can offer (Guixé and Arroyo, 2011; López-López et al., 2007; Pérez-García et al., 2011).

In Botswana, it seems that the factors driving raptor declines are acting in equal measure inside and outside protected of areas. This may be because the contrast between protected and non-protected areas is not that great due to low human density and consequent lack of land transformation; although agriculture is the predominant land use outside of protected areas (Darkoh and Mbaiwa, 2002; Dougill et al., 2016). If increased livestock numbers outside of protected areas are linked to increased food availability for vultures, as Wallgren et al., (2009) suggest, then this only emphasises the importance of mitigating poisoning outside of these areas. However, loss of biodiversity within protected areas may be associated with environmental changes rather than direct human pressures (Sinclair et al., 2002).

Climate change as a driver of decline?

Climate change is an increasing global concern, and Botswana, along with much of southern Africa, is particularly vulnerable to its effects (Abson et al., 2012; Leichenko and O'Brien, 2002). Raptors are often viewed as important bio-indicators (Machange et al., 2005; Rodriguez-Estrella et al., 1998), and the indiscriminate decline of raptors in Botswana could be an indication of deteriorating ecosystems as a result of climate change. However, if this were the case, I might expect to see declines for other avian species in Botswana, but many non-raptor bird species were found to have increased shortly before my surveys were conducted (Wotton et al., 2017). Nonetheless, the particular sensitivity of raptors to changing environmental conditions may act as an early indicator of climatic change that is not yet observable through changes in other species. Climate change may have already contributed to the disappearance of cape vultures *Gyps coprotheres* in the northern part of their range (Simmons and Jenkins, 2007), and as much as half of their current range could become unsuitable under future climate change scenarios (Phipps et al., 2017). Birds are one of the most vulnerable taxa to climate change and may respond to negative impacts through shifts in distribution and range contraction (Hickling et al., 2006; Jetz et al., 2007). African birds may be poor at adapting to climate driven changes within an area (Foden et al., 2013; Simmons et al., 2004) but may rather adapt through distributional shifts to more favourable areas (Erasmus et al., 2002; Huntley et al., 2006). Such distributional shifts of species could have resulted in the observed declines that I witnessed in my surveys. However, to determine if this is the case, similar monitoring in neighbouring countries is necessary. Monitoring activity could be focussed in areas where population shifts are initially thought to have been directed (Erasmus et al., 2002).

The growing effects of climate change are expected to reduce the suitability of static reserves, such as protected areas, for biodiversity conservation (Lovett et al., 2005; Phipps et al., 2017). Nonetheless, Important Bird Areas (IBAs) could play an increasingly important role in protecting threatened birds from the future effects of climate change (Willis et al., 2011). However, in Botswana, most IBAs are within protected areas (Kootsositse et al., 2009) and therefore the capacity for adaptive management strategies to address the effects of climate change in these areas, is limited. Encouragingly, Botswana has taken a positive stance on alleviating future impacts of climate change through the inclusion of relative objectives in the National Development Plan and the drafting of a Climate Change Response Policy (Koboto et al., 2015; SouthSouthNorth, 2017). This will mean the integration of climate change into future biodiversity and ecosystem management plans. Most importantly, the government readily acknowledges the necessity for adaptive management strategies and prioritisation of species particularly vulnerable to climate change. This is an essential step towards protecting raptors from the increasing negative impacts of climate change in Africa. Nonetheless, there is considerable evidence to suggest that we are already observing the impact of climate change on raptor populations in northern Botswana (Wichmann et al., 2004, 2003).

Poison and vultures in Botswana

For vultures, the drivers of decline in Botswana may differ from those for other raptor species, mainly due to vulture's unique feeding ecology (obligate scavenging) and vast ranging behaviours (Chapter 4). In the light of the catastrophic impact of poisoning throughout the region, I expected to find dramatic declines of African white-backed vultures (AWBV) *Gyps africanus*, which are the most frequent casualties of mass poisoning (Murn and Botha, 2017). However, I found them to have declined the least of all the vulture species (33%). This contrasts with findings from other surveys in Africa, where AWBVs have shown some of the greatest declines. However, because AWBVs range widely throughout the region, I suspect that influxes of transient individuals from other areas influenced my results (Phipps et al., 2013). The declining trend of resident breeding populations of AWBVs in northern Botswana (Leepile, 2018) also suggests that my results may have underestimated actual declines. The large decline of all other vulture species that were surveyed, suggests that poisoning could be a key factor in the decline of this highly specialised avian guild (Buechley and Sekercioğlu, 2016). Poisoning with the illegal use of pesticides is rife and increasing throughout Botswana and its neighbouring countries, with thousands of vultures having been killed over recent years (Aschenborn, 2013; Bradley and Maude, 2014; Groom, 2012; Hancock, 2016; Hartley et al., 2015; McNutt and Bradley, 2013; Murn and Botha, 2017). The growing trend in poisoning incidences is largely attributed to poachers intentionally killing vultures that signal their illegal activity – so called sentinel killing (Murn and Botha, 2017; Ogada et al., 2016). Poaching in Botswana has increased of late, potentially as a result of decreased resources for local communities following the national hunting ban (Mbaiwa, 2018). Poisoning attributed to human-wildlife conflict (farmers trying to kill predators) also occurs at relatively high rates throughout the country (Boast et al., 2016; Winterbach et al., 2014), unintentionally killing scavengers (McNutt and Bradley, 2016). An exercise mapping the use of poison by farmers in Namibia, shows similar risks (Santangeli et al., 2016). Poisoning by poachers permeates boundaries of protected areas and thus species within these areas are still at risk (Sergio et al., 2005). Vultures and other avian scavengers are at enormous risk of being extirpated if poisoning mortality continues at the same rate; in fact a recent Population Viability Analysis (PVA) suggested that at the current rate of poisoning and the current levels of productivity, resident breeding AWBV populations may go extinct within the next 10-15 years (Leepile, 2018). Twenty percent of GPS-tagged LFVs in this study died of either suspected or confirmed poisoning. Given that the overall annual population survival estimate, which also included mortality not thought to be attributed to poisoning was remarkably high (83%), substantial adult mortality may cause a rapid population crash. Potentially, this could be why LFVs in my study declined so greatly. Botswana's no-nonsense approach to poaching (e.g., shoot on site policy), has dramatically reduced historical poaching (Henk, 2005), but in a country with largely uninhabited and vast areas of wilderness, tackling poaching is challenging. There is a dire need for policy change to address the regulation of substances being used as poison and to heavily prosecute criminal offenders. Increased education and awareness may help to stem unintentional poaching but will do little towards reducing targeted illicit activity.

IUCN conservation status and raptor declines

Most raptor species that declined in the surveys are classified by the International Union for the Conservation of Nature (IUCN) as 'Least Concern', which means that they currently have a low conservation priority. This includes the species that I found to have declined the most (97%) - the lesser kestrel *Falco naumanni*. Such a decline is clearly unsustainable and growing evidence shows that migratory birds like the lesser kestrel face greater risks due to their complex movement ecology (Oppel et al., 2015; Rodríguez et al., 2009; Runge et al., 2015). Migratory birds are particularly at risk from threats associated with climate change, which could be driving their decline (Hurlbert and Liang, 2012; Jones and Cresswell, 2010). However, migratory species may also shift ranges in response to changing conditions throughout their range. For example, many migratory bird populations have shown northward shifts in-line with increasing global temperatures (Hitch and Leberg, 2007; Zuckerberg et al., 2009), or more sedentary movements, such as decreasing distances between wintering and breeding grounds (Fiedler, 2003; Visser et al., 2009). However, in relation to the IUCN status of many declining species, a species' conservation status can simply result from lack of sufficient information on population trends (Butchart et al., 2006). Thus, my results may be important for prompting re-evaluations of species' conservation status' and for influencing conservation action.

Despite the varied threats facing raptors, anthropogenic actions are primarily driving their decline (Anadón et al., 2010; Kruger et al., 2015; Ogada et al., 2015; Thiollay, 2007a), and protected areas in Botswana may not mitigate these threats. The African continent has one of the fastest rates of human population growth in the world (United Nations, 2015). Thus, other human-related threats that could be contributing to raptor declines, need to be urgently addressed.

Lead (Pb) and regional hunting activity

Besides illegal pesticides, other sources of anthropogenic poisons, such as toxic heavy metals, can represent a danger to vultures; in particular, lead (Pb) can pose a major risk (Mateo et al., 2016; Naidoo et al., 2012). My research showing that AWBVs in Botswana might be at risk from Pb exposure is of real concern, not least because there were uncertainties as to the source of Pb (Kenny et al., 2015). However, given the knowledge from other raptor populations around the world (Finkelstein et al., 2012; Gangoso et al., 2009; Mateo et al., 2001; Nadjafzadeh et al., 2013; Pain et al., 2008), it was viewed that the likely main source of Pb exposure in vultures was from Pb hunting ammunition that fragments throughout shot carcasses that are then eaten by vultures. In Africa, this source of Pb for vultures has been previously suggested by Van Wyk et al. (2001) and Naidoo et al. (2017). Thus for vultures, a significant source of Pb is likely to be discarded gut piles from hunting that vultures can become reliant upon as predictable and plentiful food (Deygout et al., 2009; Kane et al., 2015). Such gut piles may pose a serious risk for vultures due to the concentrated amount of Pb potentially available for ingestion (Stokke et al., 2017).

Thus, in chapter 3, I investigated the hypothesis that blood Pb levels (BLL) of 566 AWBVs caught in Botswana were associated with hunting activity. The fact that the Botswana government enforced a national hunting ban on government and tribal owned land part-way through this study (Mbaiwa, 2015) also gave me the unique opportunity to explore changes in BLLs before and after the ban. I found an association between Pb exposure in AWBVs in Botswana, and hunting activity. Over 30% of the tested vultures had elevated BLLs above background exposure levels, which confirmed the results of a previous study with a more limited sample size (Kenny et al. 2015). Beyond AWBVs, chapter 3 highlights that the threat of Pb exposure applies to other wide-ranging vultures and raptors. I showed BLL results for 23 lappet-faced vultures, 15% of which showed elevated BLLs. However, only data from AWBVs were used to test for an association with hunting activity due to the much greater sample size, which allowed comparison inside and outside of the hunting season and inside and outside of hunting areas.

My results showed higher BLLs were associated with hunting activity, both by season (BLLs higher inside the hunting season) and area (BLLs higher inside hunting areas). Essentially, this means that AWBVs and other vultures and scavenging raptors in Africa risk Pb exposure across the region because: 1) hunting is wide-spread, and 2) most raptors range across the entire region. However, AWBVs in Botswana had lower BLLs than those found for the same species in South Africa (Naidoo et al., 2017), which suggests that Pb exposure from hunting could also be somewhat localised given that hunting activity in Botswana is considerably lower than in South Africa. Nonetheless, vultures captured and tested within protected areas in Botswana still had high BLLs, which contrasted with vultures captured and tested in Etosha National Park in Namibia that had low BLLs consistent with background exposure (Naidoo et al., 2017). This is unexpected given that hunting in Namibia is extensive, much more so than in Botswana following the ban, but this could indicate two things: either vultures in Etosha move largely within the park boundaries, or areas surrounding Etosha are relatively free from hunting activity. Worryingly, I also found that BLLs of vultures increased after the Botswana hunting ban was enforced, reinforcing the regional nature of the threat. The reason for increases in BLLs after the ban could be due to gut piles being more spatially concentrated and thus easier for vultures to find. Additionally, recreational hunting is not the only source of Pb ammunition, which also originates from illegal poaching, anti-poaching and military activity, human-wildlife conflict, killing for meat sales, and farm management activities (such as culling), which occur throughout the region. When I estimated the amount of Pb that could still be available for vultures even after the hunting ban, I found that there could still be sufficient Pb from hunting and poaching on private farms to kill thousands of vultures. Therefore, a blanket ban on the use of Pb ammunition offers the most effective way to address Pb exposure for vultures (and other animals). To be effective, such a ban must occur across entire vulture ranges; in other words, on a regional (southern

Africa) level. Since Pb is detrimental to all life (i.e., it has no beneficial attributes), a global ban on the use of Pb would be ideal.

Pb-related vulture declines?

Currently, it is unclear whether Pb exposure has contributed to vulture declines, but compelling evidence suggests it might. The California condor *Gymogyps californianus* was driven to near extinction through Pb poisoning explicitly linked to ingesting Pb ammunition from hunted carcasses (Church et al., 2006). Substantial evidence also demonstrates that Pb poisoning represents a significant cause of mortality for raptors around the world (Helander et al., 2009; Kenntner et al., 2001; Kurosawa, 2000; Pain et al., 2007), and could therefore be killing African vultures. Although vultures may be more tolerant to the effects of Pb exposure than other species (Espín et al., 2014; Naidoo et al., 2012), sub-lethal effects, such as repressed reproduction and reduced overall fitness (Gil-Sánchez et al., 2018; Naidoo et al., 2012; Stauber et al., 2010), could currently be affecting African vulture populations (Ecke et al., 2017; Haig et al., 2014). In the context of additional huge losses from poisoning, this could be severely hindering population survival and the ability to recover from these enormous losses. Fortunately, the threat of Pb to scavenging birds is becoming more widely acknowledged, as reflected in the Convention on Migratory Species (CMS) resolution 11.15 (Preventing Poisoning of Migratory Birds) that aims to phase out Pb ammunition worldwide by 2020 (CMS, 2014). Because of its detriment to both humans and wildlife (Matz and Flint, 2009; Pain et al., 2010) many countries have already banned Pb ammunition (Avery and Watson, 2009). In the meantime, immediate action must be taken to alleviate the risk of Pb poisoning for vultures in Africa.

Compared to other threats (e.g., illegal pesticide poisoning), regulating the use of Pb ammunition should be relatively easy. Reducing the use of Pb ammunition has already benefited numerous scavenging species (Bedrosian et al., 2012; Green et al., 2008; Kelly et al., 2011), and it’s elimination from our ecosystems will benefit both humans and wildlife. The most effective way to swiftly address the use of Pb ammunition in Africa may be to focus the attention on the implications of Pb to humans; e.g.,, ingestion of Pb in game meat (Fachehoun et al., 2015), and hazardous effects of Pb on children (Nriagu et al., 1996). Pb and other toxic heavy metals can originate from other environmental sources, but sources such as soil and air borne Pb, do not sufficiently explain the high BLLs that have been found in other African vulture populations (Naidoo et al., 2017). However, heavy metal pollution in Botswana is apparent and is attributed to vehicle emissions (Mmolawa et al., 2011; Moreki et al., 2013), prevalent mining activity (Schwartz and Kgomanyane, 2005), and industrial development (Zhai et al., 2003). Although Pb toxicity is most applicable to raptor populations, their position at the top of the food chain makes them susceptible to bioaccumulation of a variety of heavy metals (Carneiro et al., 2015; Kavun, 2004; Movalli, 2000; Van Wyk et al., 2001) and therefore they are ideal sentinels for environmental prevalence of such substances. Banning Pb promises to help maintain the future integrity of ecosystems and thus has wider-reaching implications for other wildlife species.

Understanding an endangered vulture

Botswana may provide a stronghold for lappet-faced vultures (LFV) *Torgos tracheliotos* in the region due to most of the country being covered by their primary habitat - arid desert (Ringrose et al., 2003). In chapter 4, I attempted to better understand the movement ecology of LFVs to help inform conservation management. Some aspects of LFV ecology have previously received attention, but this has primarily focused on mechanistic processes (Kendall et al., 2012, 2014; Kendall, 2014; Spiegel et al., 2013; Spiegel et al., 2015). As a result, large fundamental knowledge gaps still hinder our ability to adequately conserve this species. In Saudi Arabia, Global Positioning System (GPS) data from immature LFVs was collected to help inform regional conservation management (Shobrak, 2014). I used data from 14 adult LFVs in Botswana fitted with GPS/satellite transmitters (herein after GPS tags) between 2012 and 2017 to delineate home range sizes and investigate space use. When GPS tags were first deployed in 2012, researchers believed the species to be largely sedentary, with adults showing nomadic tendencies (Shimelis et al., 2005). I therefore focused attention on adult LFVs for comparability and due to their importance for maintaining a population (Greenwood, 2003; Monadjem et al., 2013; Murn et al., 2016), thus emphasising the need to understand their movement ecology. My findings compare well with other current data for this species that shows wide ranging behaviours indicative of partial migration (Shobrak, 2014; Spiegel et al. 2015; Botha et al. 2017). Protecting LFVs is therefore particularly challenging and may require strategies similar to those used for migratory species (Runge et al., 2015).

I found stark contrasts in the ranging behaviours of breeding and non-breeding birds, with breeding birds using vastly smaller home ranges than non-breeding birds, particularly during the breeding season (April-November). These differences in range sizes were so large (breeders had 8-10 times smaller ranges than non-breeders), that LFVs likely require different conservation approaches for these two different sectors of a population. Similar differences have been found between breeders and non-breeders of several other wide-ranging raptor species (Carrete et al., 2006; Sergio et al., 2005; Tanferna et al., 2013; Van Eeden et al., 2017). The smaller and largely resident ranges of breeders that I found likely render their conservation easier, and protecting breeding individuals better supports population survival (Greenwood, 2003; Murn et al., 2016). I found that non-breeders displayed movement patterns largely consistent with 'floaters,' which are individuals that range widely and more randomly throughout the year (Penteriani et al., 2011). Floaters do not maintain a permanent territory or position within a population, but can often transition quickly to breeding individuals when necessary and therefore buffer population declines (López-Sepulcre and Kokko, 2005; Penteriani et al., 2011; Robles and Ciudad, 2017). I found large numbers of floaters and a breeder/floater ratio (i.e., approximately 1:1) similar to that usually regarded as a positive indicator of population stability (Monzón and Friedenberg, 2018; Penteriani et al., 2011). These results surprised me given the large decline of LFVs in chapter 2; although without other demographic information, the floater/breeder ratio may not provide a useful measure of population health (Monzón and Friedenberg, 2018).

The challenges associated with protecting floaters and indeed all sectors of a population remains an emerging topic (Tanferna et al., 2013; Van Eeden et al., 2017). Despite being a complex conservation challenge, the importance of adult survival is paramount to most wildlife populations, including both breeders and non-breeders (Marra et al., 2015; Schuster et al., 2018). Using a very crude method to calculate an annual population survival estimate (number of mortalities divided by number of tracked 'bird years') (Krüger, 2014), I estimated that the annual survival rate of the GPS-tagged LFVs is around 83%. However, this rate of adult survival emphasises the importance of adult individuals for population persistence and highlights that adult losses likely lead to rapid population declines. Similarly high survival rates have been identified for numerous *Gyps* species (Monadjem et al., 2013; Piper et al., 1999; Sarrazin et al., 1994), emphasising the need to protect adult vultures. Undoubtedly, individuals of other age classes play an important role in population dynamics and sustainability and thus it would be important to gather comparable spatial data for juvenile and immature birds. It may indeed have been beneficial to include different age classes in this study.

Protection of protected areas for vultures

In chapter 4, I also explored how breeding and non-breeding LFVs differed in their use of protected areas. Establishing this is useful because it indicates how important protected areas are for protecting different sectors of a population. I discovered that both groups showed a similar overall proportion of use of protected areas, which was relatively low at around 25%. However, when accounting for availability of protected areas within the MCPs of birds, I found that both groups selected protected areas significantly more than non-protected areas, but non-breeders only did this during the breeding season, while breeders selected protected areas more all year. Protected areas represent one of the cornerstones of global biodiversity conservation (Gaston et al., 2008), and contain important habitat for vultures, particularly for breeding birds (Monadjem and Garcelon, 2005; Murn et al., 2016; Roche, 2006). Over half of the breeding activity I recorded occurred within or at the boundary of protected areas, although this may not be indicative of protected area selection given the large proportion of land in Botswana that is classified as protected area. Furthermore, in other parts of Africa, protected areas often contain the only viable vulture populations (Pomeroy et al., 2014; Thiollay, 2007b). However, given the relatively low use of protected areas (even though they were preferred over non-protected areas), our findings add to the growing evidence suggesting that protected areas alone are largely inadequate for conserving wide ranging species such as LFVs (Graham et al., 2016; Sergio et al., 2005). Other focal conservation areas for birds in Botswana, such as IBAs, are mostly encompassed within protected areas (Kootsositse et al., 2009), which likely also decreases their effectiveness (Beresford et al., 2011). Nonetheless, the expansion of the global protected area network to better conserve global biodiversity is believed to be key (Venter et al., 2014), yet it could still fail to provide 'full-cycle' and 'full spectrum' protection for many species due to seasonal changes and individual-level variation in resource use (Fynn and Bonyongo, 2010; Gutowsky et al., 2015; Sheehy et al., 2010; Teitelbaum et al., 2015), that frequently results in the use of areas that are not protected.

Along with LFVs, numerous other species have shown behaviours that would require both a 'full spectrum' and 'full-cycle' conservation approach, whereby there have been pronounced differences between breed-status, sex and age, as well as variations between seasons (Amat et al., 2005; Gonzalez-Solis et al., 2000; Holland et al., 2017; López-López et al., 2016; Tanferna et al., 2013; Zurell et al., 2018). Therefore, more refined and targeted conservation approaches may be necessary for LFVs and other species with similar population characteristics, and should probably be increasingly used for conservation management. In this respect, potential methods are already suggested, such as investing in areas that contain the most suitable habitat or that are most intensively used (Abellán et al., 2011; Buechley et al., 2018; Soanes et al., 2013), or alternatively, use of dynamic areas that move with changing space and resource use of species' (Rayfield et al., 2008). The need for alternative approaches such as these to protect wide-ranging and ecologically complex species is fortunately, becoming increasingly acknowledged (Butchart et al., 2012; López-López et al., 2007; Runge et al., 2015). In Botswana, focussing management on protecting key resources for raptors in protected areas could be valuable, but assumedly already lies within the remit of IBAs, that are almost all within protected areas. Using existing Wildlife Management Areas may offer another option; thus assessing these areas for their conservation potential would be important. Ultimately, the best way forward for Botswana may be to focus on more ecologically sustainable land-use practices outside of protected areas and build strategies that incorporate wide-scale threat mitigation objectives, such as raptor friendly powerlines, holistic farming practices, poison-free ecosystems, and so on. In this way, healthier landscape networks could have wider benefits for many other wildlife species. This is similar to the formation of greater ecosystems such as those in the Serengeti and Yellowstone National Park. In these areas, harmonic land management practices inside and outside of protected areas form largely conserved landscapes that help sustain important biodiversity (Debinski et al., 1999; Hansen et al., 2016).

Knowledge is power: better protecting vultures

My findings from chapter 4 gave me the unique opportunity to investigate conservation strategies for LFVs in Botswana in chapter 5. Vulture Safe Zones (VSZ) are a cornerstone of conservation efforts in Asia that aim to recover *Gyps* vultures, whose populations were driven to near extinction through diclofenac poisoning (Chaudhary et al., 2010; Prakash et al., 2012). Using VSZs for African vultures has been suggested (Bowden, 2017). I found that VSZs might represent a viable conservation tool for protecting LFVs in Botswana, but would only really offer protection to the breeding section of the population. This finding therefore links back to the idea of ‘full-spectrum’ conservation proposed in chapter 4. Five 100 km x 100 km VSZs were imagined for Botswana which was a maximum size of area that was considered realistic in terms of management implementation. Using this approach I found these VSZs offered a reasonable level of a cumulative protection (>80%) within Botswana for breeding birds, as well as substantial protection per individual. However, this approach was not so effective at protecting the non-breeding section of the population with only 54% of fixes within Botswana protected using such an approach.

One weakness of this assessment of the use for VSZs was that I only incorporated fixes from within Botswana, and therefore my findings do not take into consideration the significant amount of time that GPS-tagged birds spent outside of the country. Nevertheless, the small and geographically similar annual home ranges of breeders (Chapter 4) indicate that VSZs could work for breeding birds, mainly because of their obvious constraint to a nest location during most of the year. Also encouraging, VSZs offered similar protection throughout the year and were not affected by breeding or non-breeding seasons, which means that they could in theory offer ‘full-cycle’ protection (Schuster et al., 2018). This targeted approach to focus conservation was more effective than a non-targeted approach. Yet existing protected area networks were created using a largely ‘adhoc’ approach, resulting in critical gaps in the protection of many species (de Klerk et al., 2004; Rodrigues et al., 2004). It would also be interesting to explicitly explore how well the protected area network within Botswana does at protecting fixes relative to the same areas of land selected at random. The VSZ approach offers a more efficient way of identifying areas for concentrated conservation effort, but whether this is sufficient to protect the species adequately is unclear. The amount of overlap that I found of VSZs with both protected areas and WMAs indicates that their complementary use may help target conservation action within existing conservation management areas by highlighting important areas of important habitat and space use by vultures. In this way, VSZs may help improve the efficacy of existing conservation strategies. Limited sample sizes in this study may have over-exaggerated the potential efficacy of VSZs to protect wide-ranging vultures. However, my analysis does at least provide a framework for exploring this issue and can be applied to other species in other regions of Africa where good tracking data exist.

Out with the old in with the new: novel information

Previously, the movement ecology of adults LFVs has been described in two different and contrasting ways; firstly, that they hold relatively small resident ranges (Shimelis et al., 2005; Spiegel et al., 2015), and secondly, that they are nomadic or a partially migrant species that ranges widely across international borders (Shimelis et al. 2005; Botha et al. 2017). My study supports both hypotheses, but for different sectors of the population. Breeders used smaller resident ranges than non-breeders or floaters, which used much larger transboundary ranges. Both breeders and non-breeders displayed significant range overlap across years, suggesting that this species may display some degree of non-exclusive, home range fidelity. The ratio (1:1) of breeders and floaters (based on the behaviours of the trapped birds) may reflect positively on future population viability (Monzón and Friedenberg, 2018; Penteriani et al., 2011), or may alternatively suggest some form of further limitation in the carrying capacity for breeders in the region (e.g., nesting trees or food availability). Although the breeding biology of LFVs has received some attention, breeding frequency is under-investigated (Bridgeford and Bridgeford, 2003; Mundy et al., 1992; Newton and Newton, 1996; Pennycuick, 1976; Shobrak, 2011). My study found that LFVs are annual breeders, contradicting suggestions that they breed biennially (Mundy et al., 1992). Thus, this species may have a breeding biology more similar to the smaller white-headed and hooded vultures *Necrosyrtes monachus* that also breed annually (Hustler and Howells, 1988; Mundy, 1982; Roche, 2006). This is unexpected for such a slow breeding, large-bodied raptor; although variations in breeding frequency can be associated with changing resource availability – i.e., higher frequency of breeding in food rich areas or times (Jouventin and Dobson, 2002). Chapter 4 suggests that breeders and non-breeding floaters may comprise distinct sectors within a population that do not frequently switch roles (e.g.,, breeders to non-breeders and vice versa). Alternatively, after a threshold number of years, breeders may switch to non-breeders, especially given that annual breeding may be particularly demanding for this large species. Longer-term tracking studies would be required to understand this aspect better.

LFVs are endangered throughout Africa, including Botswana (Ogada et al., 2015). The decline of this species in northern Botswana falls within levels of decline identified in West Africa (c. 60% - inside of protected areas) and East Africa (50%). However, in West Africa, they have disappeared altogether outside of protected areas (Thiollay, 2007b; Virani et al., 2011), whilst within our study region they do occur outside of protected areas. LFVs in

Uganda occur at a similar density to remaining populations within protected areas in West Africa (Pomeroy et al., 2014; Thiollay, 2007a). In southern Africa, this species looks to be declining across the region (Underhill and Brooks, 2014). Comparing sighting frequencies from other road surveys, northern Botswana has the lowest density of LFVs recorded so far in Africa (Pomeroy et al., 2014; Thiollay, 2007a; Virani et al., 2011). Information from repeat surveys in the south of Botswana would help us understand national vulture trends. Such information is needed to compile a Red List for all African vulture species (Botha et al., 2012) that would provide a more comprehensive record of the status of vultures in Africa.

As with other vulture African species, the most profound threat for LFVs is illegal poisoning (Ogada et al., 2015), for which Botswana is a regional hotspot (African Raptor Databank, 2017). Species that persist at low population densities, such as the LFV, struggle to sustain adult mortality as well as more populous species (the AWBV) (Ferrer et al., 2003), and therefore adult losses through poisoning may result in a more detectable decline, such as the one I observed in this study. Action to address poisoning in Botswana has already begun. Non-governmental conservation organisations (NGOs) are working with the government to form guidelines for managing and reporting on poisoning sites. Provision of education and increasing awareness is heavily integrated into the framework of both NGOs and government departments. Raptor conservation NGOs such as Raptors Botswana and BirdLife Botswana are collaborating with the Botswana government to address poisoning by conducting and facilitating activities aimed at educating and empowering key stakeholders within the community.

Conservation in Botswana – a broader approach

In Botswana, my road surveys suggest that unlike other parts of Africa, protected areas have limited value for protecting vultures and other raptor species. Botswana created its protected areas over a half a century ago, many of which were conceived with very limited ecological knowledge (Campbell, 1973). The assumed favourable conservation status of the country due to the amount of protected area coverage may therefore be misleading for some wildlife However, what may be most important for the future in terms of protected areas, is preserving critical habitat within them, that may deteriorate under the growing effects of climate change. Climate change could determine the future suitability of these areas for protecting wildlife. Furthermore, protected areas in Botswana are unlikely to fulfil year-round species requirements (Fynn and Bonyongo, 2010; Selebatso et al., 2017), much like the failure of strategies to provide ‘full-cycle’ protection for a species (Marra et al., 2015). Considering the largely un-informed and outdated conception of protected areas in Botswana, their capacity to encompass ‘full spectrum’ protection for the majority of species is also doubtful. IBAs also likely do not achieve either level of protection (full-cycle or full-spectrum), mainly because they are located within protected areas. As long ago as the 1970s, some ecologists called for expanding and better managing Botswana’s protected areas to effectively buffer increasing human activity outside of them, particularly agricultural activity (Campbell, 1973), but more recently, there is a realisation that focusing attention on broader landscapes could be more beneficial (Olson and Dinerstein, 2002). For example, the ‘Nature Needs Half’ movement calls for 50% protection of the terrestrial biosphere in order to address the global loss of biodiversity (Dinerstein et al., 2017). Range connectivity is important for migratory and wide-ranging species that spend time at different geographical locations and in areas of high risk (Clergeau and Burel, 1997; Iwamura et al., 2013; Martensen et al., 2008). At present, Botswana’s protected areas are not well connected and surrounding landscapes pose multiple risks for raptors (Abrahms et al., 2017; Bartlam-Brooks et al., 2011). Thus, creating better connectivity could be a sensible and wider-reaching conservation approach.

Outside of the 40%: non-protected areas in Botswana

Over the last 40 years, agricultural activity in Botswana has increased enormously (Botswana Dept. of Wildlife and National Parks, 2015) and currently livestock farming is the most predominant land-use outside of protected areas (Central Statistics Office, 2013). Increased farming has contributed to the degradation of rangelands (Darkoh, 1999; Darkoh and Mbaiwa, 2002), which is generally associated with loss of biodiversity (Diniz-Filho et al., 2009) – a key threat for many African vultures (Botha et al., 2017; Herremans, 1998). Edge effects in protected areas in Africa caused by increasing anthropogenic pressures at their boundaries, can negatively impact wildlife populations (Newmark, 2008; Woodroffe and Ginsberg, 1998). The ecological interactions between protected areas and surrounding landscapes can effectively help identify ‘greater ecosystems’, likely a much better approach for protecting wide-ranging species (Hansen and Defries, 2016; Serneels and Lambin, 2001). Thus, protecting African wildlife may largely depend on land use policies outside of protected areas (Fjeldså et al., 2004; Fynn and Bonyongo, 2010; Hansen and Defries, 2016;

Herremans, 1998). With much land in Botswana being communally owned, sub-optimal land management practices are often used and relatively few incentives for wildlife conservation exist (Dougill et al., 2016; Mbaiwa, 2005). Thus, little consideration is given to maintaining overall ecosystem integrity. Since the hunting ban was enforced in 2014, local communities within Wildlife Management Areas (WMAs) have lost important revenue (Mbaiwa, 2018) and thus we can expect more emphasis on income generated through agriculture. Therefore, land use practices outside of protected areas within Botswana should receive attention as a move towards creating 'greater ecosystems' approach that will benefit wide-ranging species and numerous other biodiversity. Furthermore, acting against the CBD Aichi Targets 5 and 7 (CBD, UNEP, 2010), the Botswana government should initiate actions for the assessment and regeneration of degraded landscapes so that important biodiversity can be supported outside of protected areas. Detrimental effects on communities from the hunting ban should be more carefully considered relative to increased poaching and the growing use of poisons by poachers. Community-Based Natural Resource Management (CBRNM) programmes focused on incorporating raptor-based tourism activities should be established as a catalyst for preserving local raptor populations. The potential economic and tourism value of vultures in particular can be considerable (Moleón et al., 2004), and should therefore be maximised, thus also creating an additional route for educational activities. Laws protecting important raptor breeding areas within the breeding season could be established and potentially policed at a local level to encourage active involvement e.g., by communities. Furthermore, building local capacity for participation in citizen science projects, such as the Southern African Bird Atlas Programme (SABAP) (Underhill and Brooks, 2014) and the Wild Bird Index (Wotton et al., 2017), would both empower communities and benefit conservation.

Study limitations

Time and resources constrained repeating all of the Herremans' road surveys. The repeat of only the northern section of the surveys hindered my ability to draw conclusions for national population trends.

The sample size of blood Pb levels of AWBV was adequate enough to draw conclusions that lead exposure is an issue for this species in Botswana, and that hunting activity is associated with higher lead levels. However, larger sample sizes for other species, such as the lappet-faced and hooded vultures, would be useful. The ‘snapshot’ nature of using BLLs to assess lead exposure means that BLLs could have increased or decreased with time. Lack of laboratory within Botswana facilities also hindered me from using alternative analysis methods such as isotopes, which could have helped confirm the source of the lead exposure. Another limiting factor of sampling a wild-ranging population was my inability to monitor birds with elevated lead levels post sampling. Re-testing and monitoring birds with elevated lead levels could provide a better understanding on the physiological implications of lead exposure, as well as establishing knowledge on threshold lead tolerance levels for African vultures. Ideally, it would have been useful to follow these birds and to have monitored both their survival and their breeding performance.

GPS tag data spanned six years, which enabled me to elicit previously unknown information on LFV home range sizes and movement ecology. Data for breeding birds was relatively time restricted and more years of data would have contributed to identifying changes between breeding and non-breeding status. Although I GPS-tagged in different geographical locations, most were concentrated in northern Botswana, therefore tagging more birds in the south may have added value and provided a more comprehensive understanding of space use, which might have provided better data for chapter 5 (VSZs). Sexing of individuals would have allowed for a more in depth interpretation of results and reporting on potential sampling effects. Lack of laboratory facilities (for toxicity testing) and government permissions (for movement of biological material) prevented us from identifying the majority of mortality identified by the GPS tags. However, some mortality helped to locate large-scale poisoning incidences which were then investigated and causes of death could be identified (through evidence of poison use at the scene).

Management recommendations

This thesis provides information on a variety of important topics that can help to better conserve raptors and particularly vultures in southern Africa. Directing conservation action using this information is the only way in which we can effectively address ongoing conservation issues and issues that have been highlighted by this thesis. Therefore, I outline management recommendations that have the best chance of achieving maximum conservation impact in relation to the focus of each data chapter (2-5), as well as focusing on addressing known major threats such as poisoning.

Recommendations aimed at mitigating lead exposure for vultures

- Implement a regional ban on the use of lead ammunition in southern Africa driven by applied research results, accompanied by Botswana signing the Convention on Migratory Species.

- Appropriate government agencies and conservation NGOs to engage with important stakeholders e.g., key people within the hunting fraternity, land owners, and local communities across the region to educate as to why a ban is needed, build capacity for a switch to non-lead ammunition.

Recommendations aimed at mitigating all substance poisoning

- Appropriate government agencies and NGOs to help increase education and awareness, targeting communities, of the importance of raptors and vultures for human ecosystems and human health, aimed at reducing the use of poison and lead ammunition by communities, mitigating nest disturbance and halting killing of raptors. We include and build upon existing vulture restaurants as an outlet for this.

- Strict regulation of sales of agricultural pesticides and banning those that can be used for poisoning wildlife e.g., Carbofuran. Regulations should apply throughout the region and must receive consistent national enforcement. A ‘zero tolerance’ approach to wildlife poisoning resulting in stiffer penalties and strict enforcement for criminal offenders. Furthermore, the extension of these penalties to people found in possession of banned pesticides.

- Work with landowners to find other solutions to human-wildlife conflict other than poisoning.
- Incorporate management of poisoning sites into the remit of anti-poaching strategies in Botswana, (both government and NGO) including the provision of relative training.

To be initiated by government departments and NGOs. Target anti-poaching in known poisoning 'hotspot' areas.

- Build capacity within communities through training and resource provision to identify poisoning sites and be able to swiftly address them in order to minimise the damage for wildlife. Particularly focus this in areas most prone to poaching.

- Identify the main incentives for poaching and therefore poisoning e.g., large-scale organised poaching or localised poaching, in order to establish the most effective approaches to tackle them.

- Localised poaching could be mitigated by incorporating village 'game scouts' into the legal framework addressing poaching, thereby creating financial incentive and increasing detection capacity. This authoritative presence within communities could also help deter localised poaching stemming from them.

- Gang or large-scale poaching organisations leading to mass poisoning ultimately needs to be tackled through law enforcement but increased resources would increase the efficiency of current anti-poaching efforts. Generating international awareness and support would help fund campaigns and issue a warning to poachers. Working with other cross-border organisations would be most useful, particularly where international patterns of poaching are evident.

- Reintroduce controlled subsistence hunting for communities within WMAs may help to alleviate poaching and thus poisoning. This must be non-lead based hunting which may pose additional challenges. An assessment of wildlife populations in these areas would first be required and strict quotas and ongoing monitoring would need to be sustained and effectively enforced.

- The Botswana government is currently considering a motion to reinstate elephant hunting. This is unlikely to help alleviate in-country poisoning, as few national poisoning incidences (to date) have been associated with elephant carcasses. However, outside of Botswana poached and poisoned elephants have killed thousands of vultures. Thus, this motion, should it be accepted, may help stem regional poisoning by replacing financial incentive to conserve elephants and potentially providing a food resource for communities. However, given the detriment of lead ammunition, should elephant hunting re-open, the use of lead-free ammunition must be enforced.

Recommendations aimed at generating conservation support

- Create incentives for local communities to conserve vultures and raptors. For example, in Botswana this could involve community projects integrated with photographic safari companies, whereby dedicated hides for raptor viewing and photography are run by local communities in areas with rich raptor abundance.
- Botswana government to encourage more raptor focussed research and use of resources for raptor conservation by non-raptor NGOs. Possibly by incorporating it as a research or contributory requirement within research permit requirements.

- Botswana government and NGOs Collaborative to establish a raptor rehabilitation centre in the north and south of Botswana to care for and re-release injured or poisoned raptors.

Recommendations aimed at future conservation management

- Use of targeted conservation approaches for wide-ranging raptors such as vultures that encompass 'full life-cycle' protection and focus on mitigating key threats (e.g.,, powerlines and poisoning by diclofenac, lead and pesticides). Perhaps in the form of strategically selected areas, such as VSZs or potentially geographically changing areas, that better track movement ecology. Transboundary collaboration is essential.

Future research recommendations

This study highlights numerous aspects that could be addressed by further research activities in order to enhance conservation potential for African raptors. Broadly, these could include improving research methods, increasing focus on key areas of concern, and building upon existing data and conservation resources. As such, I propose future research recommendations as follows:

- Since conclusions were drawn using only raptor population trends in the north of Botswana, a repeat of the southern road surveys is highly recommended to identify if this study's findings reflect national trends and to better understand the causes of decline for different species.

- Use standardised methods for all monitoring surveys on the continent so that we can easily compare findings in different areas, sustainable long-term monitoring of raptors should be implemented in 'gap' areas. More monitoring in protected areas and IBAs would provide more detailed information on their efficacy for raptors and other wide-ranging birds.
- Increase research attention to species shown to decline most in this study. GPS tagging is expensive and provides information from relatively few individuals, therefore existing initiatives such as SABAP and the Wild Bird Index could help us understand more wide-spread raptor population trends and possible population shifts resulting in observed declines in some areas. Build local capacity for research and conservation.

- Conduct more research on blood Pb levels of raptors and other wildlife species. Studies using isotope analysis would be valuable for determining explicit sources of lead.

- Conduct research into the physiological effects of lead in different species to help understand how BLLs already impact vulture populations (e.g.,, to what extent they could be contributing to declines). This may involve using captive facilities for temporary monitoring of individuals.
- Use patagial tags attached during the capture of all AWBV and LFV in this study to gather survival data through the use of re-sighting data (captured locally and by the SAFRING database). Doing so will require increased efforts to obtain re-sighting data in Botswana.

- Assess the use of VSZs or targeted conservation approaches for other African vulture species using existing tracking data, particularly for species for which these approaches could be most effective; e.g., the cape vulture (colonial breeder) and possibly hooded and bearded vultures (relatively small territorial home ranges). By pooling tracking data for species in Africa we should also investigate how targeted protected areas could help multiple species.

- Research main prey species and identify food-rich areas for vultures in Botswana to help secure 'safer food' resources e.g., help facilitate checks for use of veterinary drugs (in livestock), potential environmental pollutants, lead and the use of poison.

Conclusions

The majority of raptors in northern Botswana are suffering, some disproportionately more than in other parts of Africa, and vultures are no exception. Although Botswana has the potential to significantly contribute to raptor conservation, it is currently failing many species. Numerous drivers of decline are evident and are likely associated with both environmental and human-induced changes. Vultures in particular, are widely exposed to poisoning and lead from hunting across the region and their vast ranges make them difficult to protect, particularly because they move largely outside of protected areas. To exacerbate this further, for some vulture species, breeders and non-breeders may have different ranging behaviours, which can change throughout the year. Greater effort should be made towards 'full-cycle' and 'full-spectrum' conservation of species and in order to do this, current conservation management strategies may need to be revised.

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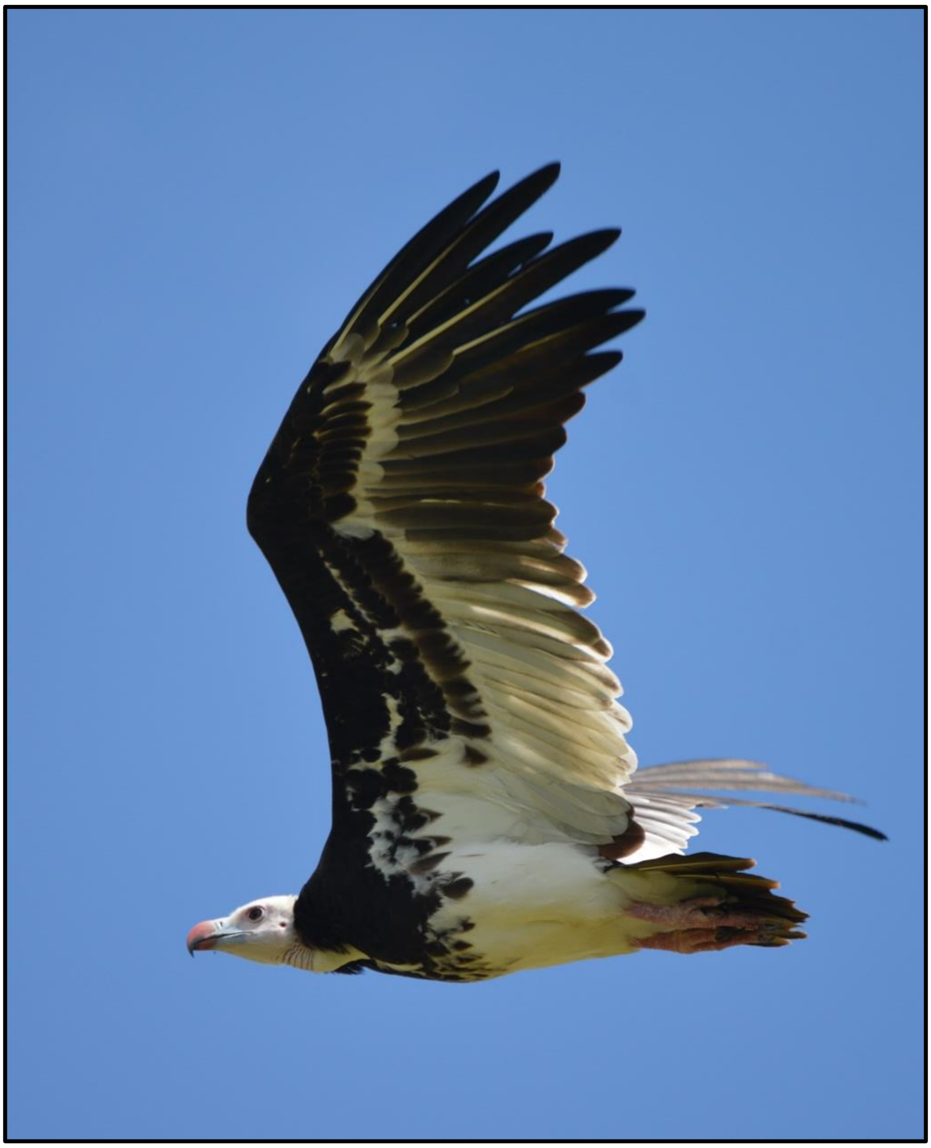

'In the end we will conserve only what we love, we will love only what we understand, and we will understand only what we are taught'