The role of supplementary feeding sites in vulture conservation in South Africa

Photo: Bettina Boemans

Christiaan Willem Brink

Thesis Presented for the Degree of

DOCTOR OF PHILOSOPHY

in the Department of Biological Sciences

UNIVERSITY OF CAPE TOWN

July 2021

The role of supplementary feeding sites in vulture conservation in South Africa

Christiaan Willem Brink

A thesis submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

(Conservation Biology)

FitzPatrick Institute of African Ornithology, University of Cape Town

Rondebosch, 7701, South Africa

27th July 2021

Supervisor: Dr. Robert Thomson

Co-supervisor: Dr. Andrea Santangeli

Co-supervisor: Dr. Arjun Amar

PLAGIARISM DECLARATION

1. I know the meaning of plagiarism and declare that all of the work in this dissertation, save that which is properly acknowledged, is my own.
2. Each contribution to and quotation in this dissertation from the work (s) of other people has been attributed, cited and referenced.
3. I acknowledge that copying someone else's assignment or essay or part thereof, is wrong and that this dissertation, is my own.
4. I have not allowed and will not allow anyone to copy my work with the intention of passing it on as his or her own work.

This thesis is based on the following articles:

- **Chapter 2:** Brink, C. W., A. Santangeli, A. Amar, K. Wolter, G. Tate, S. Krüger, A. S. Tucker, and R. L. Thomson. 2020. Quantifying the spatial distribution and trends of supplementary feeding sites in South Africa and their potential contribution to vulture energetic requirements. *Animal Conservation* 23: 491–501. doi:10.1111/acv.12561.
- **Chapter 3:** Brink, C. W., A. Santangeli, A. Amar, K. Wolter, G. Tate, S. Krüger, A. S. Tucker, and R. L. Thomson. 2020. Perceptions of vulture supplementary feeding site managers and potential hidden risks to avian scavengers. *Conservation Science and Practice* 2: e237. doi:10.1111/csp2.237.
- **Chapter 4:** Brink, C. W., R. L. Thomson, A. Amar, M. Girardello, and A. Santangeli. 2021. Prevalence and drivers of poison use by South African commercial farmers and perceptions of alternative livestock protection measures. *Ambio* 50: 1211–1221. doi:10.1007/s13280-020-01461-2.
- **Chapter 5:** Brink, C. W., R. L. Thomson, A. Amar, and A. Santangeli. Relationship between supplementary feeding and breeding success in Cape Vultures, *Gyps coprotheres* (Manuscript).

I, Christiaan Willem Brink, had the principal responsibility for data collection, analysis, and completion of the manuscripts throughout this thesis. Chapters were designed collaboratively between myself and my supervisors (Robert Thomson, Arjun Amar and Andrea Santangeli). Contact details of feeding site managers were supplied by VulPro, The Endangered Wildlife Trust and Ezemvelo KZN Wildlife. Some initial data collation regarding these contact details was done by Jordan-Laine Calder. Marco Girardello provided guidance and oversight on the statistical analysis of Chapter 4. Tapiwa Zimunya provided conceptual guidance to the analysis of Chapter 5. Data collection for Chapter 5 was done by various organisations of which the persons responsible were Kevin Shaw, Andy Ruffle and Kerri Wolter. All authors in each article contributed to the manuscript preparation or were responsible for initial data collection.

ABSTRACT

Supplementary feeding is a management application often used to support declining wildlife populations or facilitate reintroductions. Nowhere is it perhaps more popular, than in vulture conservation. Vulture supplementary feeding sites (SFS), also known as vulture restaurants, are specific locations where carcasses and unwanted animal parts are provided for vultures to feed on. This is proposed to be a win-win scenario in that contributors to the site receive a free carcass disposal service while simultaneously supporting vulture populations. SFS are assumed to benefit vultures through enhancing demographic parameters such as breeding success and survival. While there is some evidence for such effects, more recent critical assessments are questioning assumptions that these effects are ubiquitous. Additionally, research has begun to identify unintended negative consequences to both target and non-target species and the larger ecosystem. SFS may consequently be counterproductive to conservation goals in some cases. Most of these critical assessments have been conducted in Europe, and southern Africa, the supposed birthplace of SFS, remains understudied.

In light of the ongoing African vulture crisis, which has seen vulture populations plummet across the continent, effective investment of conservation resources is critical in preventing the extinction of this functional group. The main aim of this thesis was therefore to evaluate what role SFS play in vulture conservation in a southern African context. I specifically focus on South Africa, where SFS is widespread and have a long history. To understand the value of SFS I needed to verify the proposed positive effects of this conservation measure and assess any potential negative consequences of the practice. First, this required base-line information on the scale and extent of the practice. Secondly management practices and the motivations of managers needed to be reviewed to understand the context in which these sites function and whether there are any risks to vultures using these sites. Thirdly, the distribution of the major threat to vultures (i.e., poisoned carcasses), which SFS are proposed to mitigate, needed to be determined. And finally, the presumed positive effect of SFS on vultures needed to be tested. I could then examine the potential trade-offs of this management practice.

In this thesis I first describe the distribution and contribution of SFS to vultures at a national level. I do this by compiling records and databases from various organisations involved in vulture conservation. Then, using a snow-ball survey method and telephonic and email interviews, I verify the activity and history of all recorded and newly discovered SFS. Using

this method, I identify 143 currently active SFS across the country, feeding an average of 64.6 kg per day. Overall provisioning at SFS amounted to an estimated 3301 tonnes of food per year. An amount equivalent to 83% of the food requirements of all vultures in the region. I show that different vulture species have varying access to this resource depending on their range. Food provisioning was highly skewed to only 17% of SFS which are providing 69% of the food. Consequently, species with smaller home ranges have relatively poor access to food provided at SFS when compared to further ranging species. In this first chapter, I provide the necessary base-line information that has previously hampered the critical assessment of the effects of this intervention.

Using information from the survey conducted with SFS managers I then investigate the context in which these SFS function and their adherence to best management practices. Half of the SFS surveyed were associated with livestock farming and the majority were private individuals not officially affiliated with any conservation organisation. The pervasive sentiment under managers is that SFS are beneficial (84% of managers) and most managers are unable to indicate any disadvantages to themselves in the running of SFS. The cleaning service provided by the vultures is the most widespread perceived benefit. While managers may receive benefits from this practice, I show that their low awareness of vulture conservation issues may lead to practices that are harmful to vultures. For example, despite experts identifying unintentional and intentional poisoning from poison laced carcasses as the most critical threats to vultures, only 47 and 24% of managers, respectively, listed these as potential threats to vultures. Additionally, while most managers (85%) assess carcasses for provisioning suitability based on whether they had been treated with veterinary drugs, relatively few managers (10%) did the same for lead (Pb) contamination. Worryingly, only 30% of managers consider threats to vultures, such as the proximity of power lines, when deciding on a location for their SFS. Overall, current management practices are not adequate to guarantee the safety of vultures using SFS. I therefore advise that increased awareness and training is required and perhaps more stringent guidelines and regulation of the practice. As I show a correlation between the numbers of vultures seen at SFS and the amount of food provided there, the initial focus for such training and regulation should be the SFS with the highest provisioning rates.

More formal regulation of this practices will also allow for its targeted application in relation to threats in the landscape. To inform such management and to control for the major cause of vulture declines in subsequent analysis, I investigate the prevalence and motivations for using poison as a predator control method under livestock farmers. I do this via face-to-face surveys using a specialised questioning technique and ad hoc quantitative methods. This reveals that an estimated 22% and 31% of farmers use poison over a 1-year and 5-year period, respectively. Poison use hotspots generally coincide with small stock farming areas and the strongest predictor for its use is its perceived prevalence under peers. My results, however, indicate that farmers are less likely to use poisons if they frequently encounter vultures on their farm. The widespread positive attitude displayed towards vultures along with the other findings provide leverage points to change behaviours and mitigate this threat.

In addition to the proposition that SFS mitigate the threat from poison laced carcasses, they are also proposed to assist breeding vultures and increase their success in raising young. To test this, I use monitoring data on South African Cape vulture colonies spanning over two decades, to model the effects of SFS on breeding success, while accounting for threats such as poison-use and the provisioning of Pb contaminated food. I also test whether Pb contaminated food potentially proved at SFS is affecting breeding success. I show that the amount of food provided annually at SFS is weakly positively associated with breeding success, but that these results are not significant. I find that a reduced proximity of SFS to vulture colonies is negatively associated with breeding success, but this result is also not significant. Lastly, I find no evidence that the amount of potentially Pb contaminated food provided at SFS, nor the average prevalence of carcass poisoning in the area, affected local breeding success. These results cast doubt on the current dominant narrative in the conservation sphere, which asserts that SFS have positive effects on vulture demographic parameters, such as breeding success.

In this thesis, I show that some a priori assumptions about the benefits of SFS in vulture conservation may be overvalued and unjustified. Furthermore, I uncover that current management practices may be endangering vultures feeding at these sites, the problem of which is heightened by the identified widespread use and level of provisioning occurring at a landscape scale. It is therefore an urgent matter to examine other effects, both positive and negative, that SFS have on vultures and the rest of the ecosystem. In this thesis I have provided the necessary information to conduct such research. Until a net benefit to vultures is shown a refocussing of conservation efforts on directly combatting the major causes of vulture declines may be warranted to ensure the effective spending of limited conservation resources.

ACKNOWLEDGEMENTS

At the end of the long and windy road that is a doctorate study there are many people to thank. First and foremost, are my supervisors, Dr. Robert Thomson, Dr. Arjun Amar and Dr. Andrea Santangeli. Although some of your manuscript comments have made me want to test the aerodynamics of my laptop, your guidance and support has been invaluable in carrying across the finish line. Specifically, I'd like to thank Robert for being the most approachable supervisor I have ever had, Arjun for his ever present and much needed critical eye and Andrea, for being the fastest gun in the west (no student could ever wish for faster responses and feedback).

I would like to thank the funders that made this thesis possible. This thesis was funded by the NRF-DST Centre of Excellence funding to the FitzPatrick Institute of African Ornithology and A. Santangeli was funded by the Academy of Finland (grant no. 307909). I would like to thank the following people and their respective institutions for sharing data that was used in this thesis: Kevin Shaw (Cape Nature), Andy Ruffle (Oribi Vulture Viewing Hide), Kerri Wolter (VulPro), Gareth Tate (Endangered Wildlife Trust) and Sonja Krüger (Ezemvelo KZN Wildlife). I would like to thank Jordan-Laine Calder for her contribution in the early phases of this project and Tapiwa Zimunya for his contribution towards the statistical approach taken in Chapter 5. Nico Lübcker and Mathew Lewis for their assistance and guidance in exploring isotopic analysis as an avenue of research for this thesis. Hillary Buchanan, for her always kind and friendly support to wayward students navigating the administrative labyrinth of the University. Furthermore, Ben J. Dilley, for his carpentry skills and assistance in kitting out my research vehicle, the man always finds a solution to any problem.

I want to thank all the respondents in that took part in the surveys I conducted in this thesis. To those who scoffed me aside in irritation or who perceived me to be a salesman or conman after their money, I can only say I understand, I might have done the same had the roles been reversed (so no hard feelings). I would like to thank the following individuals for showing a lonely traveling researcher that there still are "homely houses east of the sea" and that rural hospitality is far from dead, even in these dangerous times. First to Vivienne and Mike van Breda for the luxury accommodation and world class homecooked meals. Secondly to Sonja and Jutta Moxham and Rory Evans, for the authentic farmhouse experience and stimulating conversation spanning from otters to the existence of extra-terrestrials. Lastly to Kabous Louw, for the best "rooi sand in jou sokkies" Kalahari braai I've ever had.

Finally, I would like to thank my friends and family for putting up with my self-pity and doubt over whether I would ever finish this thesis and a special thanks to those who supported my decision to do it in the first place. A very heartfelt thank you to those who recognised my scepticism and fondness for debate and the testing of ideas, as a commendable and even stimulating characteristic. Thank you to my parents, who funded my education longer than they needed to, and to my grandmother who is always there to lend an ear and have an honest and direct conversation (after the restraints of civility have been sufficiently dismantled). I would also like to thank those of my friends that supported me while I was a poor student, and they were becoming financially stable. Especially Roelof Schoeman who treated me to fancy restaurants I couldn't afford and Wietsche Penny for our weakly KFC tradition and his very good advice, "there are only two types of PhD's, perfect ones or finished ones".

TABLE OF CONTENTS

CHAPTER 1:

Introduction

Photo: White-backed vulture electrocuted by a powerline on a seldomly used farm road.

1. Conservation science and management

Conservation biology is a discipline that applies science to conservation problems (Soulé, 1985). It differs from other biological sciences in that it is often a crisis discipline requiring action even when information to guide management recommendations is severely limited (Soulé, 1985). Given the rapid loss of biodiversity and habitat transformation in often understudied systems, a certain level of tolerance for uncertainty in this field is a necessity. However, since the advent of the discipline, science has made leaps and bounds in the field, but some management practices have stubbornly refused to sway to new information.

Despite the increase in relevant conservation science information, there seems to be a large disconnect between this information and conservation managers on the ground. Research indicates that most manager make decisions based on what they "know", relying on experience rather than evidence when making management decisions (Pullin et al., 2004). A review of the management of over 1000 protected areas in Australia indicated that around 60% of management decisions relied on experience-based information and very few managers used evidence-based information (Cook et al., 2010). An assessment of fen management across 2996 ha in eastern England indicated that only 2% of management actions were based upon verifiable scientific evidence (Sutherland et al., 2004). Therefore, much of the current conservation management is based upon beliefs and opinions rather than a systematic appraisal of scientific evidence and this is an obstacle to effective conservation.

Research in the medical field comparing recommendations drawn from systematic and scientific review to those from "conventional expert wisdom" has shown the terrible mistakes that rely on expertise rather than evidence can make (Stevens and Milne, 1997). In the wake of this realisation and considering the many lives that were unnecessarily lost, radical changes took place in the medical industry to review even commonly used procedures and therapies which had previously not been well evaluated (Antman et al., 1992). A similar revolution may be needed in conservation as well. Given the current global biodiversity crisis we cannot afford to spend limited conservation resources on ineffective measures.

The reasons for the preferential reliance on experience are varied. One contributing factor is that systematic reviews of research results are rare and dissemination of findings to managers even more so (Sutherland et al., 2004). Although increased scientific communication would be valuable, the inertia of established beliefs in certain management actions may prevent managers from ceasing current actions or switching to evidence supported ones (Sutherland et al., 2004).

A part of this problem is that the consequences of conservation actions are rarely documented and continued monitoring after implementation is rare. This situation could leave managers with false impressions of the impact of their actions. Information alone is thus often insufficient to inspire behavioural change in a person with an existing reference framework, as social and environmental psychology suggests (Abrahamse et al., 2005). Addressing the motivational foundations for certain behaviours and the perceptions that shape them may therefore be required to effect such behavioural change (Osbaldiston and Schott, 2012). This is especially needed when engaging with members of the public who, since they are not generally trained in science nor conservation, may be less easily swayed by evidence-based information.

Members of the public, such as private landowners specifically, are becoming an increasingly important focus of conservation initiatives as there is a growing realisation that protected areas will be insufficient to achieve biodiversity goals (Norton, 2000). The protection of wide-ranging threatened species whose individuals routinely traverse park boundaries, such as vultures, is especially difficult (Lambertucci et al., 2014). Gaining landowner buy-in into conservation initiatives for such species is therefore key, but these initiatives need to be evidence-based.

2. Vultures

Many ecosystems provide large numbers of animal carcasses through various mechanisms of mortality (Barton et al., 2019; Kane et al., 2015). To exploit this resource many meat-eating vertebrates are facultative scavengers (Gutiérrez-Cánovas et al., 2020). Conversely, vultures are fully invested in a scavenging lifestyle and are the only obligate vertebrate scavengers in the world (Ruxton and Houston, 2004). They have evolved highly specialised physiologies and behaviour that enable them to exclusively exploit this evanescent food resource which is scarcely distributed throughout the landscape (Ruxton and Houston, 2004). The main adaptation that has enabled this, is the ability of energetically inexpensive soaring flight, which came at the cost of the ability to efficiently dispatch prey (Ruxton and Houston, 2004). Vultures also evolved large bodies and some members of the group, like the Cinereous Vulture, *Aegypius monachus*, and the Andean Condor, *Vultur gryphus*, are some of the heaviest flying birds in the world (Mundy et al., 1992). This enables them to consume more food when discovering a carcass and carry greater body reserves (Ruxton and Houston, 2004). Being heavier also means that they can forage over a greater surface area due to the relationship between mass and flight speed during soaring flight (Pennycuick, 1972). Furthermore, grouping behaviour such as communal roosting and feeding, allows information transfer regarding resources and increases the likelihood of finding a meal (Dermody et al., 2011). Along with this, extreme visual acuity (Jones et al., 2007) or olfactory abilities (Houston, 1986) help vultures discover carcasses. Finally, an extremely acidic stomach enables them to safely exploit carcasses that are host to a large variety of disease-causing pathogens (Houston and Cooper, 1975).

Globally there are 23 species of extant vultures which occur on every continent except for Australia and Antarctica. Vultures in the Old World (Africa, Europe, and Asia, 16 species) belong to the taxonomic order Accipitriformes and they differ phylogenetically from New World vultures (Americas, 7 species), which reside in a sister clade in the order Cathartiformes (Prum et al. 2015). Excluding *Falconiformes* (the kestrels and falcons) and Cathartiformes, Accipitriformes includes all diurnal birds of prey (or raptors).

3. Vulture and global biodiversity declines

3.1. Vultures in the context of global biodiversity declines

It has been proposed that earth has entered a new geological epoch, the Anthropocene, due to the profound influence of human activity on the global environment (Lewis and Maslin, 2015). Human activity is now impacting even the furthest most isolated corners of the globe (Munari et al., 2017; van Franeker and Bell, 1988) and is now the dominant cause of most contemporary environmental change affecting a wide range of earth's biophysical components (e.g., atmospheric composition, nitrogen cycle, carbon cycle, climate change, riverine flow, and land cover) (Steffen et al., 2008).

With the human population having grown to more than 7.7 billion by 2019 and expected to reach up to 10.9 billion by the end of the century (United Nations, 2019), such pressures on the environment will likely continue to increase in future. These environmental changes have led to what is now considered Earth's 6th Mass Extinction event (Barnosky et al., 2011). The first in earth's history to be caused by a single biotic entity, *Homo sapiens* (Barnosky et al., 2011). Currently extinction rates are 1000 times higher than background extinction rates (Pimm et al., 2014).

Across all bird species, 44% have declining populations and 13% are threatened (McClure et al., 2018). With more than half of the world's 557 raptor species having declining global populations and 18% being at risk of extinction, they are more threatened than the average bird species (McClure et al., 2018). Vultures as a group, specifically, are the most threatened group of raptors and birds in general (Buechley and Şekercioğlu, 2016). Old World vultures specifically, are doing the worst, with 69% of species being threatened and 81% with a declining population (McClure et al., 2018).

3.2. An Asian vulture crisis (diclofenac)

Around the year 2000, a catastrophic collapse of Indian white-backed, *Gyps bengalensis*, and long-billed, *Gyps indicus*, vulture populations were detected in India (Prakash et al., 2003). Initially, due to the observation of apparently sick birds, an epidemic disease was suspected (Prakash et al., 2003) but later the ingestion of the veterinary drug- diclofenac was identified as the cause (Oaks et al., 2004). This drug had been widely used to treat ailing cattle since the 1990s, but inadvertently caused visceral gout and renal failure in the vultures that fed on the carcasses of these cattle (Oaks et al., 2004). By the time legal action had been taken to ban the drug in 2006 (Cuthbert et al., 2011), Indian white-backed vultures, *Gyps bengalensis*, had already declined by 99.9%, and the long-billed, *Gyps indicus*, and slender-billed vultures, *Gyps tenuirostris*, declined by a combined 96.8% (Prakash et al., 2007). Although some of these populations have started increasing again since the ban (Chaudhry et al., 2012), it will be many years before these populations recover. Given this catastrophe, there is strong opposition against the legalisation of this drug in Africa (BirdLife International and VCF, 2014) where another continental vulture crisis is underway (Ogada et al., 2016).

3.3. African Vulture Crisis

3.3.1. African Vultures

Spanning roughly 30 million square kilometres, Africa is a huge continent and unique in that it is the only continent to straddle the tropics. Africa's expansive and diverse landscape hosts the largest vulture diversity in the world, with 11 different species inhabiting mostly its woodlands, savannas, grasslands, and arid areas. During the last decade 70% of Africa's vulture species have been uplisted to Critically Endangered or Endangered by the International Union for Conservation of Nature (IUCN) (Amar et al., 2018). Over the last 30 years, eight of these vulture species declined by an average of 62% (Ogada et al., 2016). Southern Africa boasts up to 8 different vulture species, including the endemic Cape Vulture, *Gyps corprotheres*.

3.3.2. Historical persecution

When Europeans first started settling southern Africa, vultures were plentiful (Mundy et al., 1992). Although hostile attitudes toward dangerous predators and damage causing animals have likely been ubiquitous throughout the centuries, these settlers brought with them an extermination mentality which had not necessarily previously existed on a wide scale in Africa (Mundy et al., 1992). As with other large raptorial birds in the settlers' countries of origin, vultures were regarded as significant predators of livestock (Mundy et al., 1992), a sentiment that, although rare, persists today (Chapter 4). When Ostrich farming started in the Cape Province in the 1860s, the ability of Egyptian Vultures, *Neophron percnopterus*, to crack open ostrich eggs with rocks reinforced such negative notions.

Naturally, these negative sentiments resulted in widespread persecution of vultures, with poison (specifically strychnine) being a favoured method (Mundy et al., 1992). South Africa has a long history of state sponsored lethal control of problem animals that extended into the 1990's and which at some stages endorsed poison-use (Endangered Wildlife Trust, 2006). In fact, "poison-clubs" specifically aimed at addressing the "vulture problem" existed (Boshoff and Vernon, 1980). By 1923 the Egyptian Vulture was extinct as a breeding species in southern Africa (Mundy, 1978) and throughout the century notable vulture colonies also started disappearing, such as the once prominent colony at Nelspoort in the Karoo (Mundy et al., 1992).

3.3.3. Modern major causes of African vulture declines

Attitudes of black African cultures towards vultures differ widely. Although vultures are consumed by some as a food source, they are also harvested for belief-based use due to the superstitious belief that they harbour magical properties (Ogada et al., 2016). The major applications of vultures in belief-based use in sub-Saharan Africa are to provide the user with foresight or clairvoyance, to imbue racehorses with greater swiftness and to attract customers (Mundy et al., 1992). These effects are inferred from the ability of vultures to find carcasses quickly with their superior visual acuity, the swiftness of their flight and their ability to gather in great numbers at carcasses (Mundy et al., 1992). All vulture species are vulnerable to such exploitation, which accounts for 29% of vulture mortalities (Ogada et al., 2016). This trade seems to be growing and may be stimulated by the opportunities presented by sentinel poisoning (Mateo-Tomás and López-Bao, 2020).

Sentinel poisoning entails poachers intentionally poisoning vultures to stop these birds from attracting the attention of nature authorities to the carcasses of poached animals (Ogada et al., 2016). It seems that poachers are now using such opportunities or to harvest vulture parts, or deliberately poisoning vultures for the purpose of harvesting them (Henriques et al., 2020; Mateo-Tomás and López-Bao, 2020). Before 2012 vulture poisoning was mostly unintended collateral during illegal predator control by livestock owners and this remains a prominent issue (Ogada et al., 2016; Santangeli et al., 2016b). Whatever the origin of the poison, poisoning is now the number one cause of vulture declines, accounting for 61% of mortalities (Ogada et al., 2016).

Another mounting concern regarding food safety for vultures is the use of lead ammunition in hunting activities (van den Heever et al., 2019). Although lead poisoning is a well-documented concern among large raptors and scavengers (Gangoso et al., 2009; van den Heever et al., 2019), the population level effects of mortalities due to this threat remains to be quantified across much of Africa. High blood-lead levels are, however, being detected across parts of southern Africa and warrants concern (Garbett et al., 2018; van den Heever et al., 2019).

Not only food safety, but also food availability has been suggested to contribute to vulture declines (Krüger et al., 2015; Williams et al., 2017). Wild ungulate herds have largely been replaced by livestock across Africa. Livestock have lower mortality rates, and their carcasses are generally used by their owners. This situation is proposed to result in an overall decrease in the number of carcasses that are available to vultures (Mundy et al., 1992).

Deaths associated to electrical infrastructure account for a further 9% of vulture demises and occur due to electrocutions or collisions with powerlines and wind turbines (Ogada et al., 2016; Rushworth and Krüger, 2014). A minimum of 80 Cape vultures are estimated to be killed by powerlines annually in the Eastern Cape province of South Africa and pressures from powerlines alone are predicted to cause the extinction of colonies in some areas within 50 years (Boshoff et al., 2011). With Africa's increasing population and power needs, power infrastructures are set to expand and therefor also the distribution of this threat throughout the continent (Bazilian et al., 2012; Rushworth and Krüger, 2014).

4. The ecological relevance of vultures and their anthropogenic value

Scavenger communities are often highly structured and can require specialized scavengers to facilitate scavenging by other species (Selva and Fortuna, 2007). The removal of key species in the scavenger community can thus lead to the deterioration of critical ecosystem services (Olson et al., 2012). Vultures are such specialised scavengers and although their specialisation may increase their vulnerability to extinction (Sekercioğlu et al., 2004), it makes them a key player in nutrient cycling and carcass decomposition (DeVault et al., 2003). Vultures greatly increase the rate at which carcasses are decomposed and, in their absence, it can take nearly three times as long for a carcass to disappear (Ogada et al., 2012a). This results in increased mammalian scavenger at carcasses, increased number of interactions between these scavengers and as a result likely increases disease transmission (Ogada et al., 2012b). Such a situation can have dire consequences on human well-being. In the wake of the Asian vulture crisis for example, feral dog, *Canis familiaris*, and rat, *Rattus rattus*, populations may have increased (Pain et al., 2003; Prakash et al., 2003). The expected resulting increase of rabies cases is estimated to have added an economic cost of $34 billion on India's health care system (Markandya et al., 2008).

Further economic losses may also be incurred in the form of livestock losses. The loss of apex scavengers such as some vulture species may result in mesoscavenger release (O'Bryan et al., 2019; Ogada et al., 2012b). As many of these mesoscavengers are also mesopredators (like black-backed jackal, *Canis mesomelas*, for example) such increases in their numbers can conceivably lead to increased predation on livestock. This may in turn inspire intensified predator persecution, including poisoning, which conceivably can cause further escalation of vulture declines and reinforce mesopredator increases.

5. Vulture conservation and supplementary feeding

5.1. Supplementary feeding

Survival, growth, and reproduction are all life history events which compete for the limited resources available to an organism. All organisms attend trade-offs when investing energy and resources into their own development and homeostasis versus reproductive effort. Strategies for energy allocation are therefore determined by the availability of resources.

Breeding is the most energetically costly activity of many species' lifecycle and thus the period when maximum resource availability is required (Martin, 1987). Animals generally adjust their breeding patterns to coincide with the period in the season when resources are most plentiful (Sinclair et al., 2006). In birds, for example, the timing of breeding is closely associated with the seasonal variation in food supply (Perrins, 1970). Variation in resource availability provides animals with information on, when and where to breed, as well as how much energy to invest into offspring (Korpimäki and Norrdahl, 1991; Martin, 1987). The environmental cues of food availability may thus shape population dynamics. In theory it is therefore expected that organisms that are food limited will increase their productivity if provided with more resources (Martin, 1987).

An increase in productivity in response to increases in food availability has been demonstrated by, for example, the correlation between breeding success in predators and the population fluctuations in their prey (Korpimäki and Norrdahl, 1991; Korpimäki and Wiehn, 1998). Pulsed events of greater resource availability such as insect outbreaks (Hogstad, 2005) and seed mast events (Curran and Leighton, 2000) have also been correlated with increased fecundity in birds. Pulsed events and dramatic fluctuations in food availability are however special cases that do not capture the subtle differences in food availability that occur in the absence of such strong environmental cues. Additionally, although such correlations allow for inference, they are not demonstrably causative. Experimental supplementation of food does however provide the opportunity to assess the causative nature of such effects.

Before the 1990s studies on supplementary feeding were strongly biased toward small-bodied herbivores in the northern hemisphere. These studies found that supplemental food resulted in smaller home ranges, increased body weight and earlier breeding (Boutin, 1990). Later avian studies have also produced similar results. Supplementary feeding for example improved the breeding performance in Eurasian Eagle Owl, *Bubo bubo*, including earlier egg laying and an increased probability of producing young (Pearson and Husby, 2021). Analysis of 15 years of individual-based demographic data for 161 red-billed chough, *Pyrrhocorax pyrrhocora*, showed substantial increases in adult survival and breeding success for supplementary fed individuals (Fenn et al., 2020). In the Northern Goshawk, *Accipter gentilis atricapillus*, supplementary feeding resulted in higher nestling survival (Dewey and Kennedy, 2001; Ward and Kennedy, 1996).

A meta-analysis of studies on birds indicates that although supplementary feeding has a mostly positive effect on reproductive parameters, such effects are variable (Ruffino et al., 2014). While most studies in the meta-analysis reported earlier laying dates, increase in growth rates and breeding success in birds in response to supplementary feeding, contradictory results are also common and the reasons for them not clearly understood. The analysis did, however, show that the effects of supplementary feeding are modulated by environmental conditions. Existing high food abundance in the environment, for example, was associated with reduced effects on reproductive parameters. Supplementary feeding also had a more pronounced effect on clutch size in birds who cache food. Competitive relationships may in some cases explain the lack of any beneficial supplementary feeding effects as differences in body mass has been indicated to influence dominance hierarchies, with heavier species monopolising supplementary food resources (Francis et al., 2018). Additionally, individual variation in behavioural responses to supplementary feeding may dilute population-wide patterns, thereby masking important population management considerations (Steyaert et al., 2014). Feeding can also negatively affect health parameters through inducing higher contact rates, stress and exposure to food contaminants which may counteract the benefits of additional food resources (Murray et al., 2016).

The distribution of food in the landscape may also affect the foraging patterns, behaviour, and distribution of animals. When high-quality or quantities of food are consistently available at specific locations, such areas may experience high population densities because animals move to and concentrate their activities around these sites (Cooper et al., 2006; Sahlsten et al., 2010). Supplementary feeding has consequently been indicated as a potential measure to change animal movements, including migration patterns (Jones et al., 2014), and distribution across a range of taxa (López-Bao et al., 2008; Sahlsten et al., 2010). Supplementary feeding has also been used in reintroductions and has increased site fidelity and persistence of reintroduced animals (Bannister et al., 2016).

This conservation measure can have consequences on animal behaviour in subsequent seasons, even if supplementary feeding has ceased (Jones et al., 2014). Supplemental feeding for example can alter the migration of elk, *Cervus elaphus*, decreasing their access to quality foraging (Jones et al., 2014). Additionally, supplementary feeding can strongly influence dispersal timing and distance, especially in animals that have condition dependent natal dispersal, such as juvenile northern goshawks (Kennedy and Ward, 2003). The long-term consequences of this activity thus need to be monitored if this measure is to be applied in a responsible manner, especially when it concerns its application on species with a high risk of extinction.

Supplementary feeding, in a conservation context, refers to the management tool whereby additional food resources are provided to presumed food-limited populations of conservation concern to reverse population declines. Such supplementary feeding schemes have been implemented for a wide range of animals and are often a standard component of reintroduction schemes. Evidence of the case-specific usefulness of this conservation measure has resulted in its application becoming commonplace (Ewen et al., 2015).

Wildlife also access anthropogenic food in a context unrelated to conservation activities and in human dominated world anthropogenic food sources are often readily available. While much of such anthropogenic food sources may include crop raiding, livestock predation and scavenging on human garbage, humans regularly provide food specifically for wild animals (Newsome and Rodger, 2008). Back-yard bird feeding for example is extremely common throughout the Western world (O'Leary and Jones, 2006), more than half of households in the United Kingdom feed birds (Davies et al., 2012). Unmanaged feeding can put wildlife and people at risk (Newsome et al., 2004; Semeniuk and Rothley, 2008). Potential problems with feeding of wildlife include habituation, disruption of normal activities, increased aggression, and nutritional problems. Food availability effects almost all aspects of an animal's life history. It is therefore a primary regulator of avian populations and supplementary feeding can consequently change avian community structure (Galbraith et al., 2015). This can include favouring invasive species and negatively effecting the abundance of native species (Galbraith et al., 2015). Given such environmental costs, the informal application of supplementary feeding by members of the public is inadvisable.

5.2. History of supplementary feeding in vulture conservation

People have been intentionally leaving meat for vultures for centuries. Traditions such as that of Mongolian and Tibetan Sky burials, where human corpses are fed to vultures, have histories spanning thousands of years (Martin, 1996). The modern concept of providing supplementary food to vultures for conservation purposes (also known as a vulture restaurant), however, is proposed to have originated in South Africa in 1966. At this time, a supplementary feeding site (SFS) was created to support Bearded Vultures in Giant's Castle Game Reserve (Mundy et al., 1992). Abattoirs also started making use of vultures around this time to get rid of unwanted meat and in the late 1970s this became a favoured conservation tool for Cape Vultures, *Gyps coprotheres*, in the Magaliesberg mountains in the then Transvaal province. It was during 1977 that vulture conservation came to the forefront in South Africa as the Vulture Study Group (VSG), a working group of the Endangered Wildlife Trust, was officially formed and became the first organisation solely dedicated to the study and conservation of vultures (Mundy et al., 1992). The VSG developed from a group of enthusiastic bird ringers involved in the first organised bird-ringing scheme in Africa, which annually ringed Cape Vulture at the Kransberg colony. Vulture studies in the region however started back in 1948 and was originally focussed on the Magaliesberg vulture colonies.

The VSG undertook a major project on SFS in the early 1980s and delivered carcasses to various sites themselves. As this system was later found to be economically impossible, they shifted to motivating landowners to start their own sites provided with animals that died locally. By 1988 there were 40 recognised SFS in southern Africa as well as other privately run ones, notably in Lichtenburg, Lydenburg and Thabazimbi.

Osteodystrophy syndrome was later detected in Cape Vulture chicks, which was assumed to indicate insufficient calcium in the diet of these birds. The cause was suggested to be the elimination of spotted hyena from the area due to their perceived incompatibility of this species with livestock farming. This resulted in a reduction in the amount of bone fragments available to vultures. The VSG and other SFS managers therefore made such bone fragments available at SFS and these sites therefore started playing an important role in nutrient provisioning for the affected vulture colonies. The VSG also used SFS to assist in research and environmental education regarding the usefulness and the plight of vultures.

The demonstrated utilities of this conservation measure helped cement it as an advisable action for supporting vulture colonies. Consequently, the VSG and some conservation organisations have urged private landowners to start and run their own SFS all over South Africa (Anderson et al., 2005; Mundy et al., 1992). This was proposed to be a cost-effective waste management solution for landowners that simultaneously supported endangered vulture species. As a result, SFS are now commonplace and many informal feeding sites likely remain undocumented as the practice is un-regulated (Craig et al., 2018; Pfeiffer et al., 2015b).

Further afield, SFS have also historically been used to address changes in sanitary policies affecting vulture food availability (Margalida and Colomer, 2012), for population recovery (Ferrer et al., 2018) and to assist in the reintroduction of species such as the California Condor, *Gymnogyps californianus* (Kelly et al., 2014), and the Bearded Vulture, *Gypaetus barbatus* (Carrete et al., 2006b). They played a pivotable role in reversing the extinction of the California Condor. During their reintroduction to southwestern United States and Mexico, SFS acted as substitutes for parental care for released fledglings, enabled the capture and release of condors for monitoring and treating blood lead levels and enabled the deployment of tracking devices (Kelly et al., 2014). In the Pyrenees Mountains of France and Spain as many as 25 SFS were created between 1988 and 2002 which were providing up to 15 tonnes of bone per year for the last 40 pairs of bearded vultures (Margalida et al., 2014). This is largely believed to have benefited pre-adult survival rates and contributed to the population recovery (Oro et al., 2008). Such early successes have fuelled the application of this conservation measure as a standard response to declining vulture populations.

5.3. Do SFS work as advertised?

The two main aspects that SFS are proposed to positively effect are survival and breeding success. One of the reasons that these effects are expected is due to the assumption that populations are limited by food availability, due to the large-scale habitat transformation and replacement of natural ungulate herds to livestock. An increase in food availability will thus intuitively have positive effects on these parameters. Assumptions of low food availability do not always hold up under direct investigation (Kane et al., 2015) but SFS are also proposed to buffer vultures against poisoning (Mundy et al., 1992) and thereby increase the survival of adult vultures and inadvertently the survival of the chicks they are raising.

Food availability is closely linked to breeding success and survival in the conservation zeitgeist, as is illustrated by Objective 8 of the Multi-species Action Plan to Conserve African-Eurasian Vultures. This objective aims to ensure an appropriate level of safe food to sustain healthy vulture populations with the main proposed means of verification of food availability being measures of breeding success and overall survival estimates (Botha et al., 2017). There are indeed studies showing that some populations and species, especially those that are food limited, SFS may be effective in increasing these measures.

A supplementary feeding program for Spanish imperial eagles led to the recovery of breeding success after a period of low prey availability after a haemorrhagic disease outbreak (González et al., 2006). SFS increased the number of fledglings per brood through reducing sibling aggression. The authors concluded that for this species SFS were an effective emergency conservation measure for the species as their reproductive output was food limited.

The majority of Old-World vultures, however, only lay a single egg (Mundy et al., 1992), the mechanism of increasing the number of fledglings raised in a single brood is thus not available for them. Coincidently, much of the evidence for a positive effect on breeding success in Old World vultures comes from the species that do indeed lay two eggs, such as the Bearded vulture and the Egyptian vulture, *Nephron percnopterus*. For a breeding population of Egyptian vultures in the Italian peninsula, nesting site occupation rate, percentage of breeding attempts with at least one success and the mean number of fledged young was found to be negatively correlated with the distance to SFS (Liberatori and Penteriani, 2001). A small population of Bearded vultures in northeast Spain showed a seven-fold increase in the average annual production of young during a period of supplementary feeding compared to a period without in a small population (Ferrer et al., 2014).

Other Old World vulture species have, however, shown similar positive responses in breeding parameters. The establishment of a feeding scheme in Dadia Forest, Greece, coincided with threefold increase in Cinereous vultures, *Aegypius monachus*, wintering in the area, breeding pairs doubled and breeding success increased from 40% to 95% (Vlachos et al., 1999). Schabo et al. (2017) assessed long-term data on a single Cape Vulture colony and found that although SFS did not increase breeding success, there was a significantly positive effect during the nest-building stage on the number of breeding pairs at the colony.

The beneficial effects of SFS are however not ubiquitous to vultures on a geographic level, as a group, nor even within a single species, a nuance that is often overlooked by conservationists and which can have important consequences. For example, in contrast to results above for the Italian Peninsula mentioned above, Oppel et al. (2016a) found no indication that supplementary feeding and nest guarding increased Egyptian vulture breeding propensity, breeding success, the number of fledglings raised or adult survival in the Balkans. Also, in Spain, modelling indicates that SFS only increases the survival of pre-adult Bearded vultures, also buffering them from the effects of poisoning, but not so for adults (Oro et al., 2008).

The extent to which a population is food limited will determine to what extent SFS affect demographic parameters. In most studies no direct estimates of food availability are available and a shortage is inferred due to historical large-scale replacement of the scavengers' natural food source by domestic cattle. A lack of response in the presence of SFS may indicate that food availability is not the limiting factor for these populations and that SFS may thus not be the most effective conservation response. Margalida (2010) experimentally provided additional food for Bearded vultures in the Spanish Pyrenees mountains during the chick-rearing period but found no significant increase in breeding success between non-provisioning and provisioning periods. Other studies have concurred with these results but have indicated that SFS were useful in promoting range expansion (Arroyo et al., 2021; Margalida et al., 2009).

Even in the presence of food limitation supplementary feeding is not automatically the most efficient conservation management investment as other factors may be a stronger driving force behind population declines. For example, Martínez-Abraín et al. (2012) found that although food scarcity due to the cessation of supplementary feeding during the European bovine spongiform encephalopathy epidemic did negatively effect fecundity of Griffon vultures, *Gyps fulvus*, wind farms had a much larger negative effect on this demographic parameter. In some cases, SFS may even be harming conservation goals by having a negative effect on the very measures they are purported to enhance. SFS have led to changes in Bearded Vulture mating systems due to social 'overcrowding' (increased formation of polyandrous trios) in Spain which has caused a reduction in breeding success (Carrete et al., 2006a; Margalida et al., 2014). Such findings have led to some controversy in the conservation and research sphere (Stoynov, 2016; Oppel et al., 2016b) and this highlights the need to critically assess the case-specific effects of this conservation measure.

5.4. Caveats and best management practices

Food availability can affect about every aspect of bird ecology, including reproduction, behaviour, demography and distribution (Robb et al., 2008b). This highlights the fact that, while a lack of the desired beneficial effects from SFS may represent misspent conservation resources, this endeavour is not risk free, and may also have negative consequences on other aspects of bird ecology. This thus calls into question the current informal application of this conservation tool. There is a need to consider various trade-offs and the effects of within target populations as well as on non-target species and the system as a whole (Cortés-Avizanda et al., 2016). The net benefit of SFS need to be conclusively shown to justify their current wide-spread implementation.

5.4.1 Changes in foraging behaviour

Carcasses are a pulsed resource that usually appear randomly in the landscape and present a large amount of food that is only available for short period of time (Yang et al., 2008). Vulture behaviour and foraging strategies, as well as competitive relationships within the scavenger guild, have evolved to reflect this (Ruxton and Houston, 2004). SFS, especially those with high provisioning rates are therefore a very unnatural scenario because food resources are centrally located and may be near permanent. Consequently, there are concerns that such provisioning may disrupt the competitive equilibriums with the scavenger assemblage and the ecological scavenging service provided by vultures. Concerns are often related to the development of habituation, dependence and monopolisation of food provided at SFS (Deygout et al., 2009; Fluhr et al., 2017).

The development of habituation and dependence can be inferred from changes in foraging movements in the presence of feeding sites. An analysis of the tracking data of 38 Griffon vultures, *Gyps fulvus*, in the Grand Causses, France, indicated that these vultures preferred feeding sites over the rest of their habitat where carcasses were unpredictable (Monsarrat et al., 2013). SFS were specifically preferred during seasonal resource scarcity or when flight conditions were poor. When flight conditions were optimal, however, these vultures still displayed natural foraging behaviour over areas with unpredictable resources. This suggests that although SFS influences foraging behaviour, birds do not lose their ability to forage naturally.

Carrete et al. (2006b) found that in Spain, SFS encouraged floater Bearded Vultures to settle in their natal area rather than dispersing further afield. Concurring with these findings, Fluhr et al. (2017) showed that SFS with high provisioning rates tended to increase the level of routine behaviour in Griffon vultures. Feeding sites were visited more often than would be expected if vultures were foraging randomly. Gilbert et al. (2007) found that the three GPS tagged Oriental

White-backed Vultures, *Gyps bengalensis*, that fed at SFS showed a reduction of home-range size by 23-59% upon discovering an experimental SFS. Contrastingly, Kane et al. (2016), who investigated Cape Vulture movements, found no significant change in home range size when compared to measurements before the inception of SFS. Their analysis did, however, show that aside from roost sites, SFS were the most important explanatory factor for vulture movements.

5.4.2 Changes in competitive relationships

The coexistence of species in the scavenger guild is enabled through competitive and faciliatory processes between facultative and specialist scavengers (DeVault et al., 2003). This results in ordered resource-partitioning within the scavenger guild (Houston, 1987). Such processes are modulated depending on the species present and their relative numbers. Smaller vultures for example may benefit from the presence of larger scavengers that are able to tear open tough carcass skins, resulting in increased access to the carcass (Meretsky and Mannan, 1999). However, when larger species outnumber smaller ones at a carcass they may monopolise the resource to the detriment of smaller species (Meretsky and Mannan, 1999; Moreno-Opo et al., 2015a).

An experiment has shown that predictable carcasses may unbalance the relative abundances of scavenger species and that facilitatory interspecific processes mentioned above is enabled by unpredictable carcasses (Cortés-Avizanda et al., 2012; Moreno-Opo et al., 2015a). Under predictable food availability conditions, dominant Griffon Vultures arrived earlier and in larger numbers, effectively monopolising the food resource. SFS with high provisioning rates may thus constitute an ecological trap for smaller and generally more endangered vulture species, who congregate at these sites but have restricted access to the resources available there (Cortés-Avizanda et al., 2012). Smaller vulture species are often more endangered and therefore SFS management practices should address such imbalances.

Given that supplementary feeding sites can disturb the dynamics between scavengers, Cortés-Avizanda et al., (2010) suggests that supplementary feeding should ideally mimic the spatiotemporal unpredictability of natural carcasses as to maintain natural inter-species competitive relationships. They advise that numerous feeding stations offering low quantities of food is ideal. Carcass size and fine scale distribution can also determine which species get to feed and small carcasses or the scattering of pieces of the carcass over a wider area can be used to ensure smaller vulture species are also supported by SFS (Cortés-Avizanda et al., 2010; Moreno-Opo et al., 2015a, 2015b).

Feeding methods can also modulate intra-species competition between different age classes (Duriez et al., 2012; Meretsky and Mannan, 1999; Moreno-Opo et al., 2015a). Young Griffon Vultures compete with older more dominant conspecifics at carcasses. This results in younger birds having access to a lower quantity and quality of resources than adults at high intensity feeding sites close to vulture colonies (Duriez et al., 2012). Similarly, when chicken carcasses were provided at feeding sites in the Negev Desert, Israel, adult Egyptian vultures could dominate these carcasses and fed in higher proportions than younger birds (Meretsky and Mannan, 1999). Adults were however not able to dominate feeding events where large carcasses and scattered scraps were provided and therefore did not feed preferentially. In this experiment large and infrequent feeding did not favour any age class.

SFS may affect selection pressures allowing unfit individuals to survive and therefore negatively influence population genetic health (García-Heras et al., 2013). Additionally, they have been shown to affect sex ratios in other birds (Clout et al., 2002), while in vultures they can be favoured by a specific sex, potentially causing sex differences in exposure to threats such as poisoning (Gangoso et al., 2009).

5.4.3 Food safety and health

One of the major benefits that SFS potentially provide is that they reduce the probability of vultures encountering unsafe food sources which may affect their survival and fitness (Margalida et al., 2014). Food safety relates to three threats already discussed: poison, veterinary drugs, and lead. SFS have successfully been implemented in response to the Asian vulture crisis in order to reduce their exposure to the toxic veterinary drug, diclofenac, which helped increase survival in relation to this calamity (Gilbert et al., 2007). The ban and identification of an alternative vulture-safe non-steroidal veterinary drug (Swarup et al., 2007) will likely reduce the need for SFS which were implemented as a short-term response to buy time, but these results provide a proof of concept that can be extended to other food contaminants.

This poisoning-risk reduction effect is based on the assumption that food provided at SFS are safe and contaminant free. However, because SFS are not necessarily formally regulated, as in South Africa, whether carcasses provided at SFS are free from any harmful contaminants will depend on how aware managers are of best management practices and how willing they are to stick to them. Well-meaning management strategies not adhering to scientifically based best management practices can have the opposite effects than intended on the target species (Blanco et al., 2011). A two decade long supplementary feeding initiative to increase the productivity of the highly endangered Spanish Imperial Eagle, *Aquila adalberti*, had unintentionally been dousing the birds with pharmaceuticals (antibiotics and antiparasitics) that were contained in the carcasses provided at the SFS. This resulted in depressed immune systems and a higher diversity and load of pathogens on individuals. Therefore, the supplementary feeding initiative was likely increasing the extinction risk of this species (Blanco et al., 2011). Pathogens can also be transmitted directly from carcasses supplied at SFS, some vultures have for example been shown to contract antimicrobial resistant *Salmonella* from swine carcasses fed at SFS (Blanco, 2018; Marin et al., 2018).

5.4.4 Effects on non-vulture species

Food provided at SFS can also be exploited by non-target species. Such increases can also have notable knock-on effects for the rest of the ecosystem, causing increased predation pressures for other animals, such as ground nesting birds (Cortés-Avizanda et al., 2009) and perhaps exacerbate human wildlife conflict. In South Africa food provisioning led to an increase of mammalian scavengers which are often in conflict with livestock owners, namely the brown hyaena, *Hyaena brunnea*, and the black-backed jackal, *Canis mesomelas* (Yarnell et al., 2015). As discussed with regards to the Asian Vulture Crisis, this circumstance can lead to increased disease transmission and detrimental effects on human well-being but also notably increased human-wildlife conflict.

Localised increases in the mammalian scavengers can intuitively lead to increases in livestock losses due to predation. This may in turn inspire retaliatory poisoning by livestock owners. It is due to these factors that providing a fence around feeding sites is advised so that mammalian scavengers can be excluded from these sites. These fence lines should however encapsulate a large enough area for vultures to safely take off and land, otherwise these vultures run the risk of becoming entangled in these structures. Additionally, SFS should be placed away from other dangerous structures such as powerlines and wind farms, which pose an electrocution and collision risk to vultures (Martínez-Abraín et al., 2012) and other species, such as Marabou storks, *Leptoptilos* crumenifer, which are also often seen at feeding sites (Monadjem et al., 2012).

6. My Research

6.1. Thesis aims

Africa is currently experiencing a vulture crisis with most vulture species on the continent facing the risk of extinction. Supplementary feeding sites have become a popular conservation tool and private landowners have been motivated to manage such sites themselves. This is done despite a lack of clarity on how effective this conservation measure is or what the potential trade-offs, non-intended consequences and knock-on effects to non-target species and the rest of the ecosystem may be. There is thus an urgent need for research into this conservation measure. A lack of robust data on feeding sites has previously hampered the critical assessment of these aspects. The aims of this thesis are therefore 1) to provide robust data on SFS in South Africa and how much food they provide which will facilitate future research into a range of aspects, 2) to determine how well the managers of these sites adhere to best management practices that ensure SFS are safe for vultures, 3) identify the severity of the threat of poison use, the major cause of vulture declines, in the agricultural landscape, and 4) test whether the main proposed benefit of increasing breeding success holds true in the endemic Cape Vulture while accounting for the before mentioned confounding factors. This information is aimed to help inform conservation decisions as to the most effective use of conservation resources in saving vultures and to refine the application of SFS as conservation tool.

6.2. Thesis overview

The main body of this thesis consists of four data chapters (Chapter 2-5) which serve as stand-alone research articles. This has been done to facilitate publication and indeed three of the chapters in this thesis (chapters 2 -4) have already been published in peer-reviewed journals at the time of submission of this thesis. While this approach has greatly increased the impact of this work and is also more efficient, this does result in some slight repetition of this introduction. Figure 1.1 illustrates the rationale for the thesis and how chapters link together and culminate in the synthesis. An overview of each data chapter is provided below.

Chapter 2 collates, compiles, and verifies records of SFS in South Africa. Through surveying the managers of these sites, I establish a spatiotemporally accurate national SFS database. This database includes critical information on the provisioning rate of SFS which is required to investigate their effect. This is then put into the context of vulture food requirements to get a sense of whether vultures have a sufficient food supply. Data from this chapter provides the corner stone for the chapters that follow it.

Chapter 3, stemming from the same survey as Chapter 2, examines the motivations, perceptions, and awareness of best management practices of SFS managers. I identify potential hidden risks vultures may be exposed to at SFS due to a lack of awareness of safe management practices and identify the best motivational avenues to leverage manager behaviours to adhere to vulture safe practices.

Chapter 4 investigates the prevalence of poison-use by commercial farmers in South Africa. As this is the main cause of vulture mortalities and SFS can potentially lure vultures to an area with higher poison use, we quantified the prevalence of this practice through surveys with farmers which allowed us to account for this effect in Chapter 5 and isolate only the effects of SFS on breeding success.

Chapter 5 models the effects of SFS on vulture breeding success. We investigate this effect in Cape Vultures and at the scale of the colony, using vulture monitoring data from the past 20 years. Data from all preceding chapters inform this model as to have the most accurate picture of the effect of these SFS on vultures.

Chapter 6 synthesises our results and provides management recommendations in line with our findings.

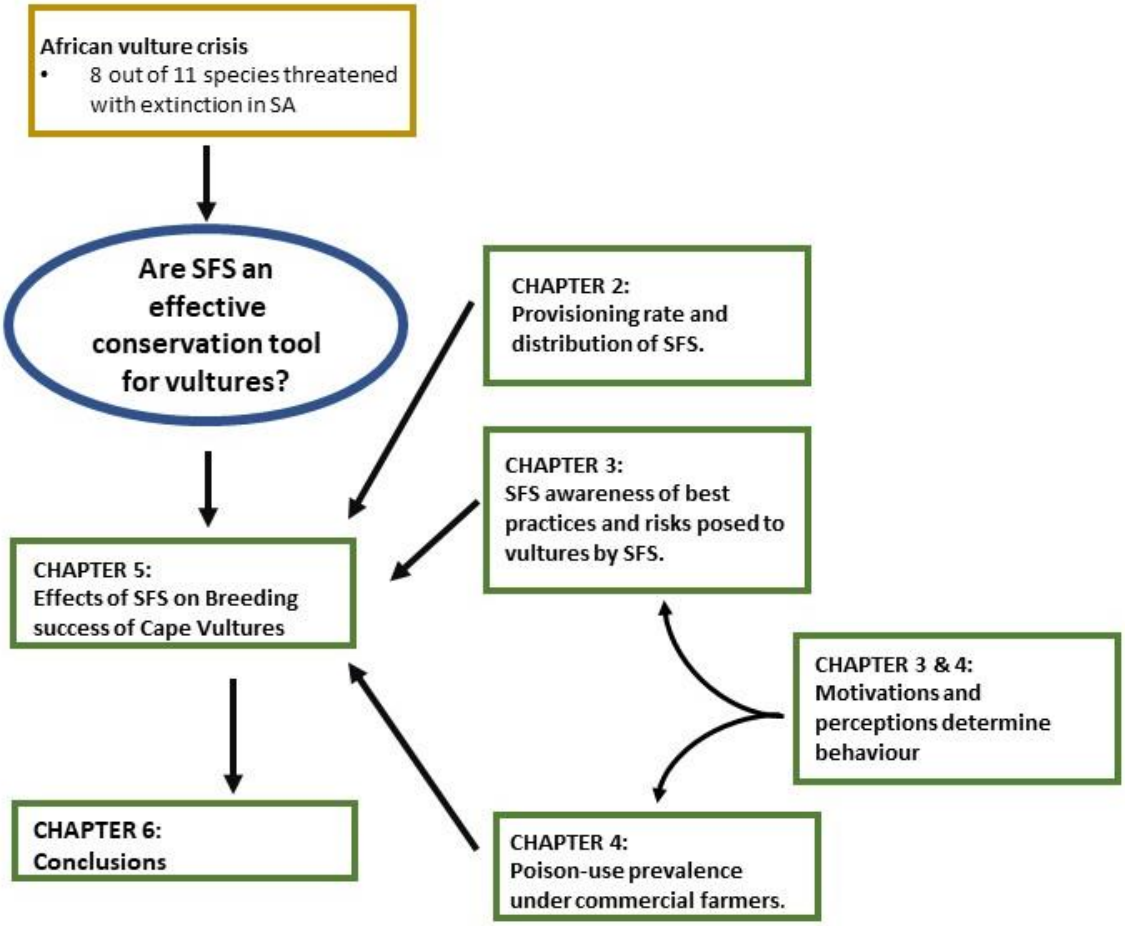


Figure 1.1: Schematic diagram showing the outline of research questions and how data chapters interlink to answer these questions.

CHAPTER 2:

Quantifying the spatial distribution and trends of supplementary feeding sites in South Africa and their potential contribution to vulture energetic requirements.

Photo: Farmer providing unwanted meat to vultures at SFS (Photo by Robert Trollip).

Abstract

Old World vultures are the most threatened group of raptors globally. Supplementary feeding sites (SFS) are a popular conservation tool, widely used to assist vulture populations. Despite their popularity, the impact of SFS on vultures remains largely unstudied. A lack of knowledge on the number, distribution and management of SFS is a key factor hindering such research. In this study, I compile records of SFS in South Africa and conduct questionnaires with SFS managers to characterise SFS. I identify 143 currently active SFS. My data suggest that SFS numbers have been stable over the last decade. The average provisioning rate for all SFS was 64.6 kg/day. Overall SFS provide an estimated 3301 tonnes of food to scavengers each year, the equivalent of 83% of the energetic needs of all vultures in the region. This contribution was highly skewed, however, with just 17% of active SFS sites providing 69% of all food. Furthermore, these resources were not equally distributed, with SFS in Limpopo, North West and Kwazulu-Natal provinces providing 83% of the total meat provisioned. The three most common meat types provided at SFS were beef (39%), pork (33%) and game (19%). Worryingly, I found that 68% and 28% of SFS managers were unaware of the potential harmful effects of lead and veterinary drugs, respectively, which highlights potential poisoning risks associated with SFS. Examining exposure to SFS by different vulture species, I found that whilst SFS are accessible across the distribution range of vultures with large home ranges (e.g., African white-backed and Cape vultures), those species with smaller home ranges have relatively poor accessibility. With this study I demonstrate the potential importance, but also associated risks, of SFS to vultures in South Africa, and provide the information-base to assess the impacts of this popular but as yet largely un-assessed conservation tool.

Introduction

The decline of biodiversity often requires the implementation of intensive management actions (Butchart et al., 2010; Barnosky et al., 2011). Because of the inherent uncertainty in how biological systems will react to conservation interventions (Keith et al., 2011), some management actions can cause unintended negative effects on target species or ecosystems (Cortés-Avizanda et al., 2009; Wittmer et al., 2013). Validating the beneficial outcome of such interventions is thus a crucial role of conservation science. To facilitate such inquiry, responsible management should entail continuous monitoring and assessment. This is the only way in which to ensure that limited conservation resources are not wasted on ineffective or detrimental interventions (Santangeli and Sutherland, 2017).

Food supplementation is an intensive management intervention often meant to help threatened species. While its effects in a conservation context are in many cases unknown, unintended negative ecological effects of food supplementation have been reported (Robb et al., 2008a; Milner et al., 2014). These include changes in social and movement behaviour (Duriez et al., 2012; Jones et al., 2014; Fluhr et al., 2017), predation and selection pressures (Schmidt and Hoi, 2002; Cortés-Avizanda et al., 2009), interspecific relationships (Carrete et al., 2010; Cortés-Avizanda et al., 2012) sex ratios and reproductive performance (Clout et al., 2002; Carrete et al., 2006b) and various health factors (Blanco et al., 2011; Sorensen et al., 2014).

Almost seventy percent of old-world vulture species are threatened with extinction (IUCN, 2019), the most rapid population declines occurring in the vulture-rich regions of Asia and Africa (Ogada et al., 2016). Over the last decade, the unnatural and accelerated mortality rates of vultures across Africa have led to the International Union for Conservation of Nature (IUCN) uplisting seven out of ten of the continent's vulture species to Critically Endangered and Endangered (Amar et al., 2018). While this can be attributed to various threats (Anderson et al., 1999; Boshoff et al., 2011; McClure et al., 2018), the most prevalent of these is poisoning. This risk of poisoning include: intentional poisoning - for traditional belief-based use of vulture parts (Mckean et al., 2013), or "sentinel poisoning", whereby poachers target vultures as they provide rangers with a clear sign of poaching events (Ogada et al., 2016), and unintentional secondary poisoning - where vultures are the unintended victims of the poisoning of so-called problem carnivores (Santangeli et al., 2016b). Similarly, vultures may be poisoned by feeding on livestock treated with veterinary drugs, specifically those treated with non-steroidal anti-inflammatory drugs (Gilbert et al. 2002; Oaks et al. 2004) or lead contaminated carcasses (Bounas et al. 2016; Garbett et al. 2018), which may even lead to catastrophic population level impacts (Green et al., 2004).

The high mobility and wide ranging behaviours of vultures make conserving them challenging because conventional conservation measures, such as protected areas, may be insufficient (Santangeli et al., 2019). In South Africa, there has been a strong emphasis on providing additional food through supplementary feeding sites (SFS; often also referred to as "vulture restaurants", Cortés-Avizanda et al., 2016). These measures have been implemented because providing such food is typically assumed to reduce poisoning risk (Gilbert et al., 2007), with some evidence indicating it can also increase breeding success and survival (González et al., 2006; Oro et al., 2008). However, such effects are not ubiquitous and, in some cases, SFS show no effects (Krüger et al., 2015; Oppel et al., 2016a). SFS therefore remain a debated conservation tool (Oppel et al., 2016b).

Anderson and colleagues (2005) previously estimated that there were around 140-145 active SFS in South Africa, with an annual increase of 9% per year. The majority of SFS are established informally by land managers, particularly as an easy and inexpensive form of carcass disposal (Mundy et al., 1992; Piper, 2004b). Therefore, many SFS are potentially operated without following best-practice guidelines (Piper, 2004a). Essential information on the number, status (active - providing food, or closed), location and provisioning rate of SFS is lacking and not collated into a systematic centralised database. This hinders investigations on the effects of SFS on vultures in Africa (e.g., Kane et al., 2015), which is essential to understand the conservation outcomes of SFS. The first step in quantifying the effectiveness of SFS is thus to systematically gather this information.

Here, I aim to fill this knowledge gap in South Africa and lay the basis for future studies on this common, yet un-assessed conservation tool. Specifically, I aim to i) determine the current and historical number and distribution of active SFS in South Africa; ii) quantify the amount and type of food resources being provisioned at these SFS; iii) estimate the contribution of SFS resources towards filling the energetic needs of the different vulture species based on their potential access to SFS.

Methods

Ethics statement

This study was approved by the Faculty of Science Research Ethics Committee at the University of Cape Town (Approval code: FSREC 83 – 2017). Participants provided informed verbal consent, as approved by the ethics committee.

Supplementary feeding site data

We used existing datasets on SFS from three organisations in South Africa which are extensively involved in vulture conservation (VulPro, The Endangered Wildlife Trust and Ezemvelo KwaZulu-Natal Wildlife). These datasets were out-dated to various extents and the information they contained had not been verified during recent years. I consolidated all three databases.

We conducted a survey with the managers or affiliated persons of each SFS. The survey was conducted by a single interviewer (CWB) over the telephone or email, using an open-ended questionnaire (see Appendix 2.1). Surveys were conducted between November 2017 and October 2018. Respondents were asked to provide a range of information regarding their SFS, most notably coordinates of the site, the status of the SFS (whether the site was active, i.e., provisioning food, or closed and no longer provisioning) their provisioning rates (tonnes per year), type of carcasses used, their date of establishment and closure and reasons for establishment and closure. SFS managers were also presented with a multiple-choice question regarding whether they believed that lead from spent ammunition or veterinary drugs present in carcasses could have any potential harmful effects on vultures.

Provisioning rate calculations

Respondents were asked to specify, as accurately as possible, the type and quantity of food (a combination of whole carcasses and offal) that they provide at their SFS within a given time unit. When respondents provided weights per carcass or specified the amount of offal in kilograms (the parts of an animal carcass that is discarded after butchering or dressing), these amounts were used. In cases where respondents provided a quantity range, the mid-point of this range was used to calculate provisioning rate. However, when livestock carcass weights were not provided but only the numbers of carcasses, I used the body mass of animals from the literature averaged across breeds within a specific livestock type (Cloete and De Villiers, 1987; Cloete et al., 2000; Wells and Krecek, 2001; Sheridan et al., 2003; Scholtz, 2010; Snyman, 2014a, 2014b, 2014c, 2014d, 2014e; Andrew Tucker unpubl. data).

To determine provisioning rate of game animals, the average mass of game species was derived from the 2016 South African hunting statistics (available from the Department of Environmental Affairs) and published weights (Stuart and Stuart, 2015). When respondents indicated an amount provisioned during the hunting season, I assumed that this was provided over the average winter hunting season, which is three months in duration.

To calculate the amount of offal provided I used averaged dress out percentages (ratio of slaughtered and vicerated carcass to live weight) from the literature for each animal group. This was only needed for the game and pork category as all other livestock offal amounts were indicated in weights. South African dress out percentage for a range of ungulate species falls within a 52-61% of body weight (Von La Chevallerie 1970; Hoffman 2000; van Zyl and Ferreira 2004; Hoffman and Wiklund 2006; Hoffman et al. 2009; Swanepoel et al. 2016). Offal thus accounts for between 39-48% of live weight. I used the conservative measure of 40% of live weight for my calculations of offal weight as some offal is commonly used for human consumption. Dressing weights for domestic pigs were between 72-84% (Latorre et al. 2009; Warriss et al. 1990; Boler et al. 2012; Virgili et al. 2003), thus for pigs I used 20% as percentage offal of live weight. QGIS was used for all spatial analyses (QGIS, 2019).

Calculation of vulture energetic needs

To contextualise the total amount of food being provided by SFS, I calculated the total annual food requirements of all vultures in the South Africa, Lesotho and eSwantini region (Appendix 2.2). I used adult vulture population estimates and indications of the proportion of the population that are adults to calculate the total population size. Daily food requirements from the literature were then used to calculate food requirements for the entire population on an annual basis (Appendix 2.2). In addition to the SFS within South Africa, provisioning rates from two verified SFS in Lesotho and two in eSwatini were then used to calculate what percentage of the annual food requirements were already provided by SFS. The species evaluated included the IUCN Critically Endangered African white-backed vulture, *Gyps africanus*, Endangered Cape vulture, *Gyps corprotheres*, Endangered lappet-faced vulture, *Torgos tracheliotos*, Near Threatened bearded vulture, *Gypaetus barbatus*, Critically Endangered hooded vulture, *Necrosyrtes monachus*, and Critically Endangered white-headed vulture, *Trigonoceps occipitalis* (IUCN, 2019).

Coverage of species range by SFS

Adult vultures often have smaller home ranges than non-adults and thus their access to SFS is more restricted (eg. Krüger, Reid, and Amar, 2014). The extremely wide-ranging nature of immature vultures means that they effectively have complete access to all SFS in South Africa Thus to make useful comparisons between species regarding their access to SFS, I focussed this analysis on adults only. I quantified the proportion of each species' distribution range that is accessible to SFS in the following way. First, I collated home range estimates for each species from the literature (Krüger et al., 2014; Kane et al., 2016; Garbett, 2018; Reading et al., 2019). Such estimates were unavailable for adult African white-backed vultures, but as evidence suggests they display similar movement behaviour as lappet-faced vultures (Spiegel et al., 2013), I thus used lappet-faced vulture estimates as a proxy. The average across all species was used for white-headed vultures for which data were also unavailable. Assuming uniform circular home ranges, I converted these species-specific home range estimates to minimum and maximum buffers for each species (Appendix 2.3). I used 95% Kernel Density Estimates (KDE), 90% in the case of bearded vultures, for the calculation of the maximum buffer radiuses and 50% KDE for the minimum buffer radius of each species. These species-specific radiuses were then used to create buffers around each active SFS in the region. Finally, I calculated the proportion of each vulture species' range covered by the minimum and maximum buffer surrounding SFS in the region. This yielded a minimum and maximum proportion of species range coverage by SFS. I repeated the above analyses using only SFS with high provisioning rates (>40 kg/day).

Results

We were able to contact 92.4% of the SFS for which I had working contact details. The remainder either refrained from responding to all attempts at communication or had closed so long ago that no relevent respondent could be found. Of those I did contact, 72.4 % participated in the study beyond just simple verrificaion of the status of their SFS. Among verified and currently active SFS, I had a response rate of 94.3%.

State of SFS in South Africa

We verified the status of 232 SFS records in South Africa, including 25 new sites (i.e., not present in the three original datasets) that were mentioned by respondents and verified on an ad-hoc basis. Among verified SFS, 143 were active (Figure 2.1), and 89 were closed. Ninety entries remained unverified, due to out-dated contact information. Given the age of the databases and their entries, these were assumed to be closed.

Trend and motivations of SFS establishment

We gathered information on establishment and closure dates of 104 currently active and 39 closed SFS. The earliest reported establishment date was 1933. From 1975 numbers of active SFS increased sharply but have remained relatively constant since around 2009 (Figure 2.2). The main motivation for establishing an SFS was for conserving vultures (65% of 159 total responses) and for the cleaning benefits vultures provide (26%). Other reasons were the personal pleasure of running an SFS (12%) and ecotourism (11%). Reasons for closing SFS were: managers moving away (22% out of 55 responses), low vulture visitation rates (13%), relocation of SFS (11%), carcass contamination concerns and lack of control regarding dumping by general public (11%), lack of carcasses for provisioning (7%), and occurrence of powerline mortalities (7%).

Provisioning Rates

We obtained information on provisioning rates from 132 of the 143 active SFS. Of these, 24 provided both livestock and game, 82 provided livestock only and 26 provided game only. Eight SFS that only provided game, indicated that their SFS was solely active during the hunting season. There was high variability in provisioning rate among SFS, with a mean ± S.D. of 23.58 t/y ± 38.84 (range: 0.32 – 208.57 t/y), equivalent to 64.61 kg/day ± 106.42. Across all SFS for which data was collected, I estimated that 3113 tonnes of food are provided each year. If extrapolated across sites with unknown provisioning rates, using the average of similar types of sites in the same province (or across the entire country in the case of Nature and Game Reserves), then 3301 tonnes of food are provided across all known active SFS.

The contribution of food provisioned was highly skewed, with just 17% of active sites providing 69% of reported total annual provisioned food (Appendix 2.4). Sites with highest provisioning rates are generally affiliated with intensive livestock farms, abattoirs or Non-Governmental Organisations (NGO) who source carcasses from such operations. Sites that provided little food annually are represented more often by small-scale livestock farms. I report high variation in resource contribution by SFS across South Africa, with Limpopo, KwaZulu-Natal and North West provinces providing the majority of food resources (Figure 2.3). Across South Africa, most of the total food provisioned consisted of beef (39.2%), pork (33.3%) and game (19.4%, Appendix 2.5). Less common meat sources included sheep (3.6%), horses/donkeys (2.2%), chicken (1.0%) and goat (0.2%).

Potential energetic contribution of SFS

We estimated that the extrapolated total provisioning rate of 3301 t/y, plus 16 t/y provided at SFS in eSwatini and Lesotho, is enough to potentially fulfil about 83 % of the annual food requirements for vultures in South Africa.

Food safety

Out of 111 respondents answering the question on the health risks posed to vultures from providing contaminated food, 32% of managers believed that lead from spent ammunition could be dangerous to vultures, 35% were not sure and 32% were convinced otherwise. For veterinary drugs, 72% believed that they could have harmful effects, 20% were unsure and 8% were convinced otherwise.

Vulture range coverage by SFS

The South African range of lappet-faced vultures, African white-backed vultures and Cape vultures had highest accessibility to SFS, with 100% of their range being covered by any SFS, and 79% to 81% when considering only SFS providing more than 40 kg/d (Table 2.1). Conversely, hooded and bearded vultures had the lowest SFS range coverage (Table 2.1).

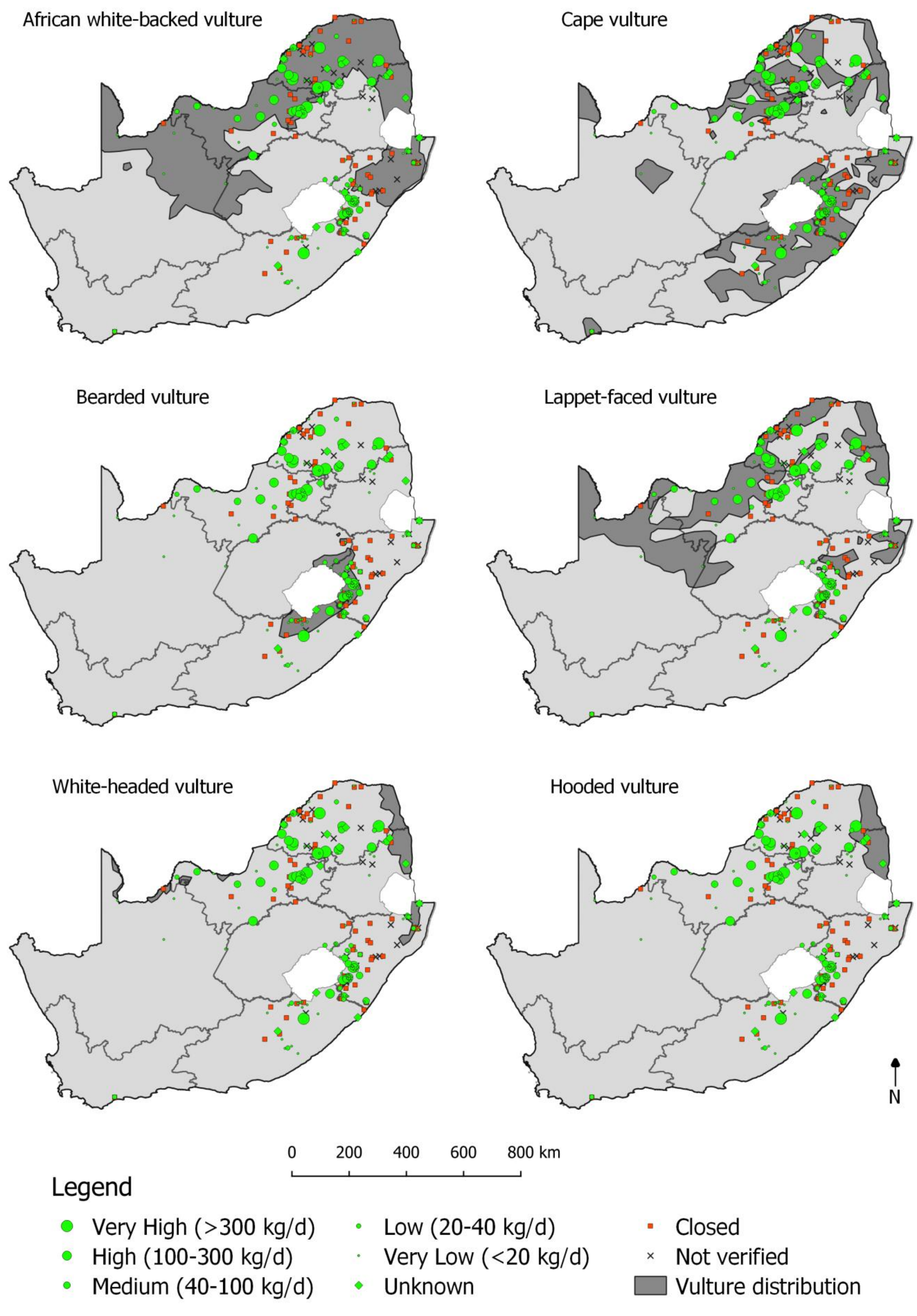


Figure 2.1: The distribution and status of vulture supplementary feeding sites in South Africa as verified by the present study. Active (green), closed (red) and unverified (black cross) supplementary feeding sites are indicated. The average daily food provisioning rate category of active sites is indicated by the size of the green circles, green diamonds indicate active supplementary feeding but with unknown provisioning rates. The distribution of each of

six vulture species occurring in South Africa is shown in dark grey (data obtained from BirdLife International and NatureServe 2015).

.

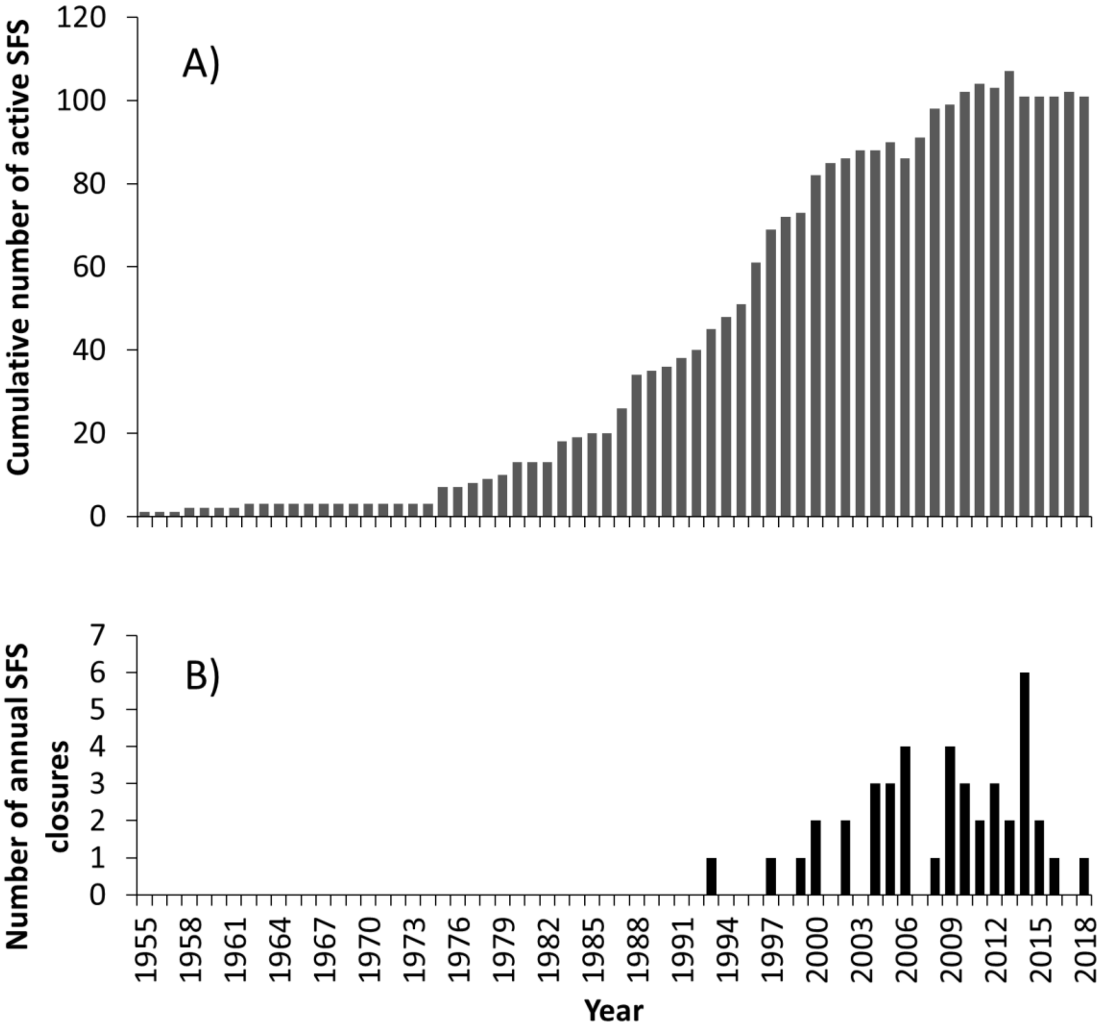


Figure 2.2: A) Cumulative number of active SFS over time in South Africa, and B) the number of annual SFS closures. This is based on information of opening and closing dates obtained from 155 SFS. I start the timeline at 1955 for brevity, because between 1933 and 1955 only a single SFS was reported as active. Sites that did not provide this information were excluded here.

.

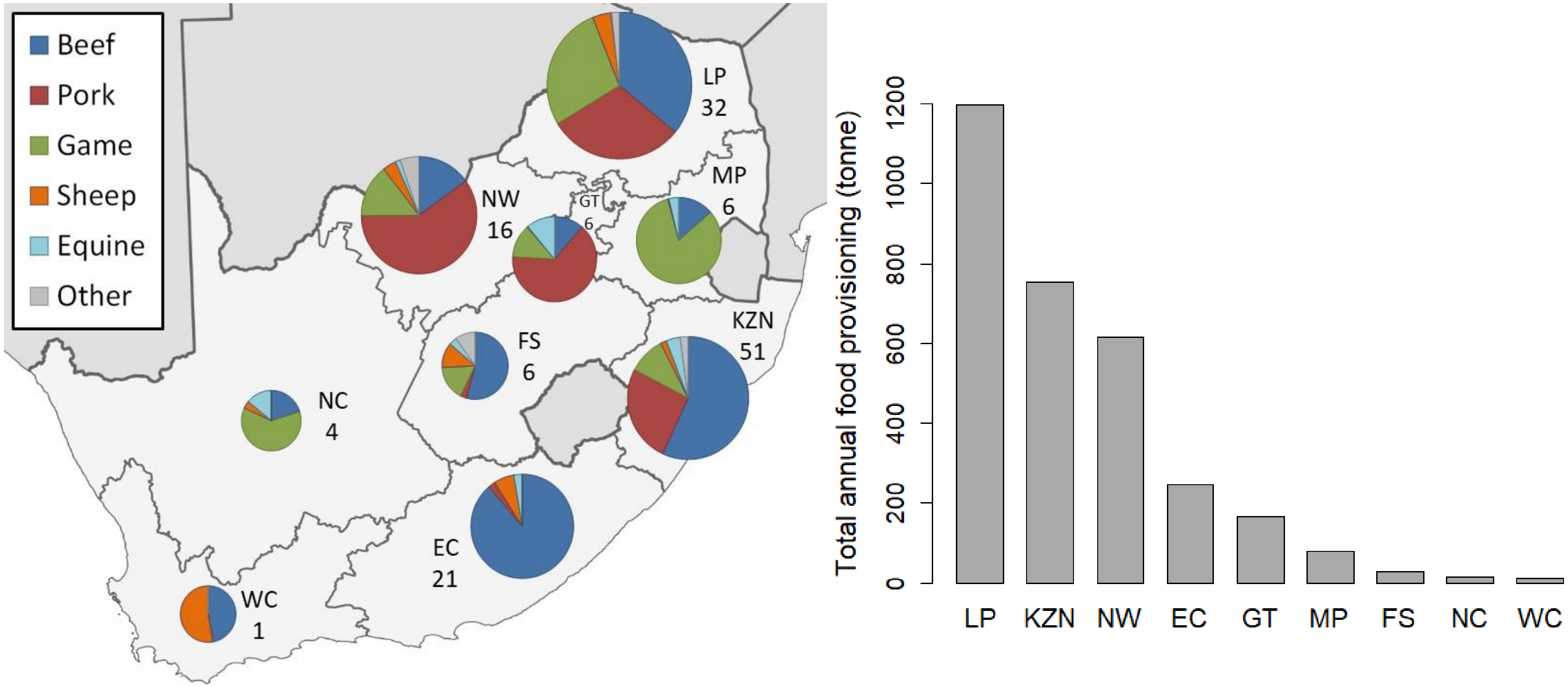


Figure 2.3: Proportional contribution of each meat type to the total food provisioned at supplementary feeding sites in each province in South Africa (shown by the pie charts within each region in the map). The size of each pie chart is proportional to the total amount of food provisioned in each province per year (log transformed to ease visualisation). Numbers below the name of each province in the map indicate the number of active supplementary feeding sites in that province. The total amount of food provided at supplementary feeding sites in each province in tonnes per year is reported in the histogram to the right. (LP = Limpopo, KZN = KwaZulu Natal, NW = North West, EC = Eastern Cape, GT = Gauteng, MP = Mpumalanga, FS = Free State, NC = Northern Cape, WC = Western Cape).

Table 2.1: The percentage area of vulture species' South African distribution range that is within adult vulture maximum (based on 95% Kernel Density Estimates, except for bearded vultures which is based on 90% Kernel Density Estimates) and minimum (based on 50% Kernel Density Estimates) home range distances from SFS and SFS with higher provisioning rates respectively.

				All SFS		Higher provisioning rate SFS (>40 kg/d)	
Species	Maximum buffer radius (km)	Minimum buffer radius (km)	South African distribution range (km^2)	Percentage area within maximum home range distance (%)	Percentage area within minimum home range distance (%)	Percentage area within maximum home range distance (%)	Percentage area within minimum home range distance (%)
Lappet-faced vulture	249	94	243927	100	84	79	45
African white-backed vulture	249	94	399801	100	81	81	46
Cape vulture	187	56	285533	100	72	80	41
White-headed vulture	120	41	34717	92	41	56	5
Hooded vulture	35	10	37888	33	5	14	2
Bearded vulture	10	4	35898	24	6	7	2

Discussion

My study shows that use of SFS in South Africa is widespread, and they provide enough food to potentially fill almost all the energetic needs of the entire South African vulture population. Provisioned food was not distributed evenly, with some species having low access to SFS through their range. Therefore, vultures in the area are exposed to varying amounts of provisioned meat quantities and types, and the associated risks of provisioned food of which many SFS managers remain unaware. The numbers of active SFS have remained stable over the past decade.

SFS trends

The initial increase in SFS from the 1970s onwards can likely be ascribed to various awareness campaigns promoting the establishment of SFS to local landowners and the general public (Mundy et al. 1992). Combined with increased awareness of vulture declines, this may have accounted for the growing adoption of SFS by landowners. If the growth rate of SFS remained consistent since that of 2002, then today there would be 430 active SFS in South Africa (Anderson et al., 2005). My results show a similar increase up to the year 2002, but a reduction in this rate afterwards, with SFS numbers plateauing in 2009.

Adherence to best practices

Livestock dominates the food provisioned by SFS in most areas. Due to widespread use of veterinary drugs in livestock production, many scavenger species may be exposed to these substances (Blanco et al., 2016; Blanco et al., 2017) in a similar way as reported for Asian vultures (Shultz et al., 2004). Other veterinary drugs such as antibiotics may have unidentified long term sub-lethal effects that can influence the fitness of scavengers (Pitarch et al., 2017). Game meat was provisioned at 34% of SFS and mostly originates from hunting activities. This provisioned meat may therefore contain lead fragments from spent lead ammunition. This is problematic as the harmful effects of lead on avian taxa are well documented (Haig et al., 2014). Lead is known to accumulate in vultures in southern Africa and a worrying number of individuals display lead levels consistent with subclinical to severe clinical effects (Garbett et al., 2018; Krüger and Amar, 2018; van den Heever et al., 2019). Ingestion of lead fragments in carcasses have been indicated as the most likely cause of these elevated lead levels as these elevated levels were not found in non-scavenging species and were also associated with hunting season and areas (Garbett et al., 2018; van den Heever et al., 2019).

The safety of the food provided at SFS depends on how aware managers are of threats, and how seriously they take them. In South Africa, my survey suggested that 28% of SFS managers were unaware of potential harmful effects of veterinary drugs and 68% were unaware of the harmful effects of lead. Consequently, carcasses provided at many SFS could be contaminated with these harmful substances, which could have a negative impact on the vultures that consume them. Another indication that best practice is not always followed is illustrated by the small percentage of SFS that are providing poultry carcasses, potentially exposing vultures to avian influenza (Ducatez et al., 2007). Some respondents also reported powerline associated mortalities at their sites which represents a main contributing factor for the closure of 7% of SFS. This indicates that some SFS may potentially increase the collision and electrocution risks to vultures. I suggest that conservation practitioners should work more in connection with SFS managers in order to increase their awareness of these unintended consequences and reduce their likelihood through promoting best management practices. In cases where negligent management practices are resulting in mortalities of endangered species, the relevant authorities should intervene.

Temporal variation in SFS provisioning: a paradox

Our updated information on distribution and food provision of SFS in South Africa will allow in-depth analyses of how SFS may influence space use of vultures. Vultures have historically evolved to use temporally variable and unpredictable food resources (Monsarrat et al., 2013). Conversely, regular feeding at SFS associated with intensive livestock farming operations, could lead to the development of routine behaviours and dependence (Fluhr et al., 2017). Within an African context, limited information exists on this potential impact of SFS on vulture behavior. Anecdotal knowledge in Southern Africa suggests this may be species-specific. For example, dependence on SFS seems low for the Cape vulture (Kane et al., 2016), but high for non-adult bearded vultures (Reid et al., 2015).

Paradoxically, while foraging naturally, vultures may have an increased risk to come into contact with carcasses that have been laced with poison (Monadjem et al., 2018). Regular and copious provisioning of safe food at SFS could thus lead to a reduction in poisoning risk. Initially, SFS were only viewed as a temporary means to 'buy time' for addressing the ultimate threats that are causing vulture declines. Unfortunately, after 40 years since the introduction of SFS, the threat of poisoning is still high, and SFS have become an established tool for general application.

Expansion of the SFS network

Many conservation organisations promote the establishment of SFS (Birds of Prey Programme, 2007). They do so based on different unverified assumptions e.g. that SFS reduces localized poisoning risk, that SFS can divert vultures from areas of high risk and that in the absence of SFS, vulture populations experience food shortages. In order for the expansion of the existing SFS network to be evidence-based, such assumptions first need verification through scientific investigation. Once evidence for a measurable net positive impact on vulture demographic parameters has been obtained, then this tool can be considered on a case-by-case basis. Given the current lack of such evidence, decisions on SFS establishment are made in the dark (Cook et al., 2010).

Future research

Parts of the SFS database were already being used in research prior to this study and thus prior to my verification (e.g., Krüger et al., 2015; Kane et al., 2016). A visual comparison of the results of this study and the locations used by Kane et al. (2016) suggests that roughly 22% of the 110 SFS included in their study were miscategorised. Their study also omitted at least 70 active SFS. One of the aims of the present study is therefore to provide up to date information that can assist future analyses exploring the influence of SFS on vulture behaviour or demographics.

Future studies need to verify the basic assumptions on the demographic effects of SFS on vulture populations. In addition, research should focus on quantifying the role of SFS in reducing poisoning risk to vultures, e.g., by studying impacts on ranging behaviours. For example, it may be that SFS could be strategically located to divert vulture movements away from areas with a high threat of poisoning or wind turbine collision (Reid et al., 2015). Finally, the effects of different feeding methods (regular vs. irregular feeding, whole carcasses versus small food parcels) on the above factors and the structure and functioning of the South African scavenger guild could be assessed. In Europe, increased predictability of resources at SFS favoured more dominant species to the detriment of less competitive and often more threatened vulture species (Cortés-Avizanda et al., 2012). Feeding methods could thus play an important role when SFS are aimed at supporting a particular species in a particular area.

Although I hope this study can assist in future research, SFS security is a concern. There are fears that if SFS locations are made freely available, they could be exploited by poachers for vulture harvesting, or that provided carcasses would be taken for human consumption. Parties interested in using this data for research or management planning are therefore encouraged to contact the authors directly so relevant data-agreements can be arranged.

Conclusion

To assess the effectiveness of conservation interventions, it is crucial to know where, when and how such interventions are implemented. A lack of this information prevents such assessments, ultimately leading to a potential waste of scarce conservation resources that, in the case of vulture SFS, may even have counterproductive effects. In this study, I provide the necessary information to enable such research and provide conservation managers with an updated view of the South African SFS network.

Appendix 2

Appendix 2.1 : Questionnaire used in survey.

Christiaan Willem Brink

PhD Candidate

FitzPatrick Institute

University of Cape Town

christiaanwillembrink@gmail.com

0817317643

Questionnaire

Date:

VR_Code (for office use):

VULTURE RESTAURANT SURVEY:

Hello, my name is Christiaan W. Brink and I am a PhD student at the University of Cape Town researching the contribution of vulture restaurants to vulture conservation in South Africa. I found your contact details on our existing database in relation to a vulture restaurant / feeding site, and would appreciate it if you took part in our survey that will aid vulture conservation and which will ultimately benefit vultures and landowners. Your participation would be appreciated whether you are currently feeding vultures or have stopped doing so.

As part of my thesis I am updating the current database with the information of vulture restaurant managers. This information will not be published or made freely available to the public and will only be distributed to the relevant people in vulture conservation and research (eg. VulPro, EWT, Ezemvelo KwaZulu-Natal wildlife, all of which have contributed to, or is a collaborator on this project). Do you give consent for your information to be shared with the before mentioned people?

Participant agreed (Please remove if you disagree)

At the same time we would like to get an understanding of what motivates people to run vulture restaurants. Please answer the questions below. Please note that the answers from these questions (excluding the Basic Info) will not be included in the database but rather kept confidential. When the research is published, none of your answers will be linked with your name or name of your farm and so will remain anonymous.

Please note that your participation in this interview is completely voluntary.

Do you agree to participate in this interview?

Participant agreed (Please remove if you disagree)

A. Basic info/demographics

1. **Name:**
2. **Position/role at the property: (i.e.: owner, manager):**
3. **Occupation:**
4. **Property owner name:**
5. **Name of property/farm:**
6. **Vulture restaurant property address:**

7. **Email:**
8. **Preferred contact number:**
9. **Coordinates of Vulture Restaurant (if not available, coordinates of property-please specify the structure for which coordinates are given):**

B. Vulture Restaurant (VR):

10. **Is the vulture restaurant still active, are you still feeding vultures?**

[if closed] :____

11. **When did you stop putting out food for vultures?**

12. **What were the reasons why you stopped?**

---

13. **When did you start feeding vultures? (year and month if possible)**

14. **What was the motivation behind establishing and maintaining the vulture restaurant**?

15. **Please provide as accurate an estimate and description of what is provided at the vulture feeding site as possible: (eg. 2 Adult pigs per year (200-300kg per carcass); 10kg of Beef offal per day; 5 new born calves per month; Offal from 50 game carcasses during hunting season). We are fully aware that this may depend on stock losses and be variable but please make an attempt at providing some sort of rough estimate. Number of carcasses provided over the last year might be easiest. If closed please provide an indication of how much you used to feed.**

16. **Where is/was this food sourced from? (eg. My own property; neighbouring farmers donate; SPCA)**

17. **In your opinion do carcasses containing lead from spent ammunition pose any potential health threats to vultures (eg. Feeding on animals shot during hunting)? Please highlight chosen answer**

    a. **Yes**
    b. **No**

c. **I don’t know**

18. **In your opinion can veterinary drugs present in carcasses have any negative effects on vulture health? Please highlight chosen answer**
    a. **Yes**
    b. **No**
    c. **I don’t know**

Appendix 2.2: South African population size and total annual food requirement estimates for six vulture species.

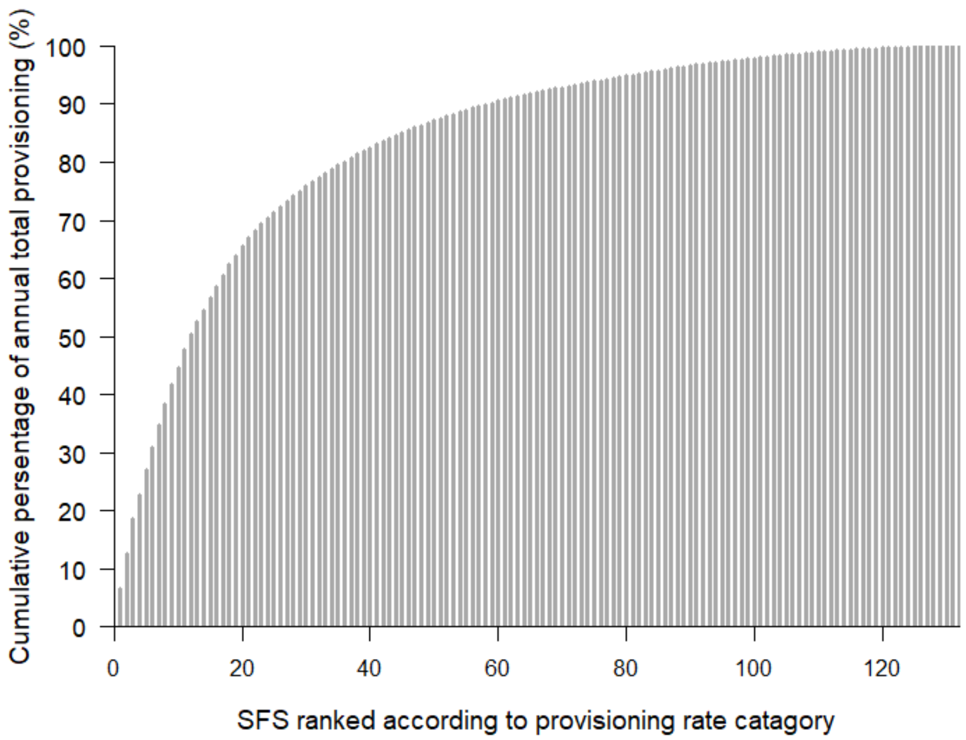
Common name	Scientific name	Number of adult vultures	Proportion adults	Population estimate	Daily food requirements (kg)	Annual food requirement (t)	Annual provisioning in species distribution (t/y)
African white-backed vulture	*Gyps africanus*	7350[a]	0.67[b]	10970	0.4[c]	1601.6	2218.0
Cape vulture	*Gyps corprotheres*	8800[a]	0.75[d]	11733	0.52[c]	2227.0	2448.9
White-headed vulture	*Trigonoceps occipitalsis*	158[a]	0.75[e]	211	0.35[c]	27.0	84.6
Lappet-faced vulture	*Torgos tracheliotos*	338[a]	0.81[e]	417	0.5[c]	76.1	1190.0
Hooded vulture	*Necrosyrtes monachus*	150[a]	0.65[f]	231	0.35[c]	29.5	120.1
Bearded vulture	*Gypaetus barbatus*	233[a]	0.6[f]	388	0.3[g]	42.5	737.4
TOTAL		17029		23950		**4003.6**	

[a]Taylor et al. 2015, [b]Murn and Botha 2018, [c]Mundy et al. 1992, [d]Robertson 1984, [e]Kemp and Begg 2001, [f]Brown 1997, [g]Donázar 1993

Appendix 2.3: Vulture species home range sizes used for the calculation of SFS range coverage. The maximum buffer radius corresponds to the 95% Kernel Density Estimates (KDE) for the given species. Only a 90% KDE was available for bearded vultures. For the minimum buffer size, 50% KDE was used.

Species	Scientific name	Average home range (km^2)	Maximum buffer radius (km)	Minimum buffer radius (km)	References
Lappet-faced vulture	*Torgos tracheliotos*	194 813	249	94	Garbett, 2018
African white-backed vulture	*Gyps africanus*	-	249[i]	94[i]	Spiegel, Getz, & Nathan, 2013
Cape vulture	*Gyps corprotheres*	110 181	187	56	Kane et al., 2016
White-headed vulture	*Trigonoceps occipitalsis*	-	120[ii]	41[ii]	-
Hooded vulture	*Necrosyrtes monachus*	3913	35	10	Reading et al., 2019
Bearded vulture	*Gypaetus barbatus*	286	10	4	Krüger, Reid, & Amar, 2014

[I] Data unavailable, lappet-faced vulture values used here based on literature suggesting similar movement behaviour.
[ii] Data unavailable, average values of all other species for which data was available used.



Appendix 2.4: Supplementary feeding sites (SFS) ranked according to their annual provisioning rates, from highest to lowest, in relation to the cumulative contribution of each additional site, to the national total annual provisioning rate (expressed as a percentage).

Appendix 2.5: Summary of the composition and distribution of the 3113 tonnes (t) of annually (y) provided food, at 143 verified active SFS, across all South African provinces. (LP = Limpopo, KZN = KwaZulu Natal, NW = North West, EC = Eastern Cape, GT = Gauteng, MP = Mpumalanga, FS = Free State, NC = Northern Cape, WC = Western Cape).

Province	Verified active sites	TOTAL t/y	% of TOTAL	% Beef	% Game	% Pork	% Sheep	% Equine	% Other
LP	32	1198.7	38.5	35.9	27.6	30.4	4.1	0.2	1.7
KZN	51	752.4	24.2	56.4	10.9	25.3	1.6	3.7	2.1
NW	16	616.5	19.8	15.0	14.6	59.9	3.8	1.4	5.3
EC	21	246.8	7.9	89.1	0	2.2	5.9	2.7	0.0
GT	6	165.1	5.3	11.4	12.7	64.5	0.3	11.1	0.0
MP	6	78.4	2.5	13.6	82.2	0.0	0.4	3.8	0.0
FS	6	26.2	0.8	54.2	16.8	3.2	12.2	3.8	9.8
NC	4	16.2	0.5	20.2	61.9	0.0	3.9	14.1	0.0
WC	1	12.6	0.4	47.2	0.0	0.0	52.8	0.0	0.0

CHAPTER 3:

Perceptions of vulture supplementary feeding site managers and potential hidden risks to avian scavengers.

Photo: Vultures reduce cow to skin and bone in less than a day, before farmer could even move carcass to feeding site (Photo by C.W. Brink).

Abstract

Under the current African vulture crisis, supplementary feeding sites (SFS), which provide carrion resources, have become a popular conservation tool to address vulture declines. In South Africa, this practice is unregulated and the context in which SFS operate and their adherence to best management practices is currently unknown. In this study, I conducted a survey with SFS managers regarding the management of their SFS to evaluate potential conservation implications of different practices. Half of the SFS surveyed were associated with livestock farming. Overall, most managers (84%) perceived some benefit from running an SFS, largely attributed to cleaning services provided by vultures. Over half of the managers perceived no disadvantages from running SFS. I found a positive correlation between numbers of vultures seen at SFS and the amount of food provided there. Despite unintentional and intentional poisoning being identified by experts as the most critical threats to vultures in Southern Africa, only 47% and 24% of managers, respectively, listed these as potential threats to vultures, highlighting limited understanding of current vulture conservation issues. Most managers (85%) vetted carcasses for provisioning suitability based on whether they had been treated with veterinary drugs, but relatively few managers (10%) did the same for lead (Pb) contamination. Only 30% of managers considered threats to vultures when they decided on a location for their SFS. Overall, this study unveils that at many SFS, safety conditions are not met, and vultures may be exposed to risks, such as the ingestion of toxic substances (e.g. Pb) or electrocution by energy infrastructure. To minimise unintended negative consequences from SFS it will be essential to increase the interaction between SFS managers and conservation practitioners, to increase the flow of information on best management practices and enforce stringent and clear guidelines that minimise any risks to vultures.

Introduction

Community and stakeholder engagement is often a prerequisite for the success of conservation initiatives (Hulme and Murphree, 1999; Kumasi et al., 2010). As a result, many conservation programs have shifted from top-down regulatory approaches to bottom-up voluntary initiatives that foster stewardship and the appreciation of ecosystems and their services (Santangeli et al., 2016a). In many cases, local communities rather than the government or organisations are responsible for the implementation of conservation initiatives, a situation which is easier to establish if there is some benefit to participating individuals (Naidoo et al., 2016). Community involvement in conservation initiatives has considerable potential (Olsson and Folke, 2001; Nelson et al., 2010), but these benefits can be tempered by the competence of community members and the extent to which best practices are followed. When best practices are poorly applied, such initiatives may have detrimental ecological effects (Blanco et al., 2011). In such cases, detrimental effects on the target species or system may occur, while still providing short term benefits to participating community members, conceivably resulting in these practices being perpetuated.

Graphical Abstract: Summary of supplementary feeding site manager perceptions regarding the benefits and disadvantages of running a supplementary feeding site, as well as the most commonly perceived threats to vultures. Arrows are scaled to the percentage of respondents that mentioned the element.

Vulture supplementary feeding sites (SFS, also referred to as vulture restaurants) are a popular tool implemented under the assumption that they can help avert the dramatic declines of old-world vultures (Cortés-Avizanda et al., 2016; Chapter 2). The popularity of SFS is likely because they conceptually present a win-win scenario for landowners and vultures. SFS provide a cost-effective carcass disposal method for landowners who would otherwise have to burn or bury their carcasses to ensure biosecurity on their farms. Alternatives often require expensive equipment, such as earth moving vehicles or industrial scale incinerators, which also have operating costs along with transportation costs, compared to SFS that in many cases only require transport costs. Additionally, SFS may provide a tourism attraction that can help attract customers for landowners that offer hospitality services. Among the proposed benefits to vultures is a reduced poisoning risk, the main threat driving vulture declines. Although based on a sample of only six Oriental white-backed vultures, *Gyps bengalensis*, Gilbert and colleagues (2007) found reduced diclofenac poisoning related mortality rates in response to SFS establishment, thereby providing some support for this tool in conservation. Other proposed positive effects include improved breeding success and survival (Margalida et al., 2014; Botha et al., 2017). These effects have, however, not been ubiquitously or conclusively demonstrated (Schabo et al., 2017), and in many cases, SFS establishment is based on assumptions rather than science (Oppel et al., 2016a).

Worryingly, SFS may even result in unintended negative consequences. These may include changes in foraging patterns or habituation (Gilbert et al., 2007; Fluhr et al., 2017), negative health consequences and disease transmission (Blanco et al., 2011; Botha et al., 2017; Chapter 2), decreasing productivity (Carrete et al., 2006b), and the monopolization of resources by certain age classes or species (Cortés-Avizanda et al., 2012; Duriez, et al., 2012). SFS may also have cascading effects on non-target species by increasing local predation pressure (Cortés-Avizanda et al., 2009). There are thus likely many benefits and disadvantages from SFS which should be considered before assuming a net gain (Cortés-Avizanda et al., 2016).

In South Africa, conservation organisations have long promoted the establishment of informal and privately run SFS (Mundy et al., 1992; Anderson et al., 2005). These are proposed as a cost-effective waste management solution that also supports endangered avian scavenger species, especially vultures. The use of supplementary feeding sites is now commonplace. A recent study (Chapter 2) consolidated records of SFS in South Africa from various conservation organisations and surveyed their managers. This study verified 143 active SFS across the country that provide an estimated 3301 tonnes of food annually, equivalent to 83% of the food requirements of all vultures in the region. Additionally, many informal small SFS likely remain undocumented (Pfeiffer et al., 2015b; Craig et al., 2018). In South Africa, landowners are free to dispose of unwanted animal carcasses by providing them to scavengers, and this practise is currently un-regulated. It is likely therefore that this practise is commonplace for landowners in areas where vultures and other scavengers are present. SFS seem to be an ideal scenario, perfectly aligned with UN Sustainable Development Goal 15 “Life on Land” which aims to facilitate development while protecting biodiversity. However, for SFS to deliver sustainability outcomes, as mentioned above, they should provide a net benefit for vultures and for people.

If SFS are not managed responsibly, these sites might not have the desired beneficial effect on vultures and other scavenger species. For example, the safety of carcasses provided at SFS is a concern. Lead (Pb) is toxic to animals, including vultures (Naidoo et al., 2012; Pikula et al., 2013), and has been documented to accumulate in African vultures with the likely source of contact being lead shot contained within the carcasses of hunted animals (Garbett et al., 2018; van den Heever et al.,2019). This source of lead nearly drove the California condor, *Gymnogyps californianus,* to extinction in North America, and the use of lead ammunition within condor habitat has consequently been banned (Finkelstein et al., 2012). The ingestion of veterinary drugs can also have dramatic impacts on vulture populations, as shown by the catastrophic declines in Asian vulture populations due to the anti-inflammatory drug, diclofenac (Green et al., 2004; Shultz et al., 2004). The effect of many routinely used veterinary drugs on vultures, such as antibiotics, remain unassessed. Gómez-Ramírez et al. (2018) found that despite farmer assurances that carcasses provided at SFS in southeastern Portugal were not treated with antibiotics, 29% of meat samples contained antibiotic residues. In South Africa, 68% of SFS managers were unaware that lead, and 28% were unaware that veterinary drugs, can have negative health consequences for vultures (Chapter 2). Vultures may thus routinely be ingesting these substances at SFS. Besides the provisioning of contaminated food, other unsafe management practices would include placing SFS in close proximity to powerlines or fences and bird un-friendly reservoirs, leading to potential collisions/electrocutions and drowning respectively (Piper, 2004a). Best management practices for SFS therefore aim to reduce vultures' exposure to the above-mentioned threats (Birds of Prey Programme, 2007). This includes taking steps to ensure that food provisioned is free from contaminants and ensuring that SFS placement does not expose vultures to threats.

If conservation practitioners want to influence the management practices of private individuals using this unregulated conservation tool, then they need a good understanding of the perceptions, motivations and knowledge base of the individuals engaging in this practice (Kareiva and Marvier, 2012). In this study I aim to fill this knowledge gap by; 1) Providing information on the land management context in which SFS function; 2) Determining vulture visitation and how this may be affected by provisioning rates; 3) Determining the level of awareness of SFS managers to the anthropogenic threats vulture face and their knowledge of best practices as applied to SFS. This information will provide useful insights to inform future interactions between conservation managers and SFS managers. It will also serve as an urgent call to the conservation community to evaluate the application of this conservation tool. Although SFS have many potential conservation benefits, it also has the potential to negatively affect an entire and highly threatened guild, with potential cascading effects on the ecosystem.

Methods

In Chapter 2 I collated, updated and verified a national SFS database for South Africa. This database contains information from various organisations extensively involved in vulture research and conservation (FitzPatrick Institute of African Ornithology, VulPro, Ezemvelo KwaZulu-Natal Wildlife and the Endangered Wildlife Trust). The data for this present study were simultaneously collected alongside that project. Thus, at the same time as confirming if the SFS was active (supplying at least one carcass per year), I surveyed the managers or affiliated personnel of these SFS. The survey was conducted by a single interviewer (me) over the telephone or email, via an open-ended questionnaire (supplementary material) between November 2017 and October 2018. Telephonic contact was always first attempted, and email was only used if requested by the respondent or if telephonic contact could not be established. Although different survey methods may affect the results, these effects are not ubiquitous and usually small (Elliott et al., 2009; Rutherford et al., 2016). Self-administered questionnaires generally suffer more from non-response bias while interviewer facilitated methods suffer more from social desirability bias, which is more prominent if the subject matter is sensitive (De Leeuw, 2005). Mixed-mode strategies (e.g., telephonic interviews and self-administered email questionnaires) are consequently often used to compensate for the weaknesses of each individual mode (De Leeuw, 2005). Because my questionnaire did not contain any particularly sensitive questions, I assumed that reduction in non-response bias due to a mixed-mode approach would outweigh any potential differences in social desirability bias between the two techniques. Respondents were asked a range of questions pertaining to the context in which their SFS was operated, the carcasses they provided, their perceptions regarding the benefits and disadvantages of running a SFS, perceived trends in number of visiting vultures, knowledge on the current threats to vultures, and their awareness of best management practices. I also asked SFS managers to provide an indication of the average number of vultures present during a feeding event (Question 15, Appendix 3.1). For the full list of questions see Appendix 3.1.

Only SFS verified as active were included in my questionnaire study. As these were open-ended questionnaires, some responses were not relevant and were excluded from analyses. For example, when respondents were asked to list all the threats to vultures in South Africa that they knew about (Question 20, Appendix 3.1), only threats of anthropogenic origin and those mentioned in the Multi-Species Action Plan (MSAP) were considered relevant (Botha et al., 2017). These threats include unintentional poisoning (secondary poisoning during predator control attempts), intentional poisoning (for belief-based use or as part of sentinel poisoning), powerline electrocutions, collisions with power infrastructure, food scarcity, habitat loss and degradation, disturbance from human activities, climate change and other less prevalent threats such as drowning in farm reservoirs. Afterwards, I pooled similar answers into categories or themes. For simplicity, only categories that were mentioned by more than one respondent are reported.

We expected differences in the perceptions (e.g., threats or benefits) of SFS between managers whose main income relates to livestock farming as compared to hunting activities. The financial capital of livestock farmers is directly influenced by the effects from carcasses (such as increased predator numbers or disease prevalence) either at SFS or on the farm in general, as they may influence livestock mortality rates. Farmers are thus required to manage carcasses to protect their livestock, but carcass management can be costly and labour intensive. SFS thus provides a relatively cheap and convenient method that SFS managers can exploit. People whose main income comes from hunting do not contend with these risks to the same extent and carcass management is thus less of a required management practice. Consequently, I thus expect them to have different attitudes towards SFS than livestock farmers. I predict that hunting operators would perceive more benefit from ecotourism and farmers more benefit from the cleaning services provided at SFS. I also predict that farmers will perceive more disadvantageous to running an SFS than hunting operators.

Based on responses from the questionnaire, I calculated two awareness scores for each SFS related to two different concepts. One was related to the number of population-level threats to vultures that managers could name, providing an estimate of manager knowledgeability on vulture conservation issues in a broad sense. The other was related to managers' awareness of two known food safety risks that can negatively impact vulture health and was thus directly related to potential risks experienced at individual SFS. The awareness score for each concept was calculated as follows:

1) Broad knowledge of threats: I calculated the proportion of threats that a manager could name from those listed in the MSAP, thereby providing a score between zero and one (one being assigned when all threats, $n = 9$, in the MSAP were listed by the respondent).

2) Awareness of food safety risks: this was also calculated as a score from 0-1, where managers received 0.5 points for indicating that lead, and another 0.5 points for indicating veterinary drugs in carcasses could have a harmful effect on vultures (a score of 1 was thus given if they indicated both lead and veterinary drugs).

These two scores were then summed and divided by two to provide a score from 0 to 1, where one indicated full awareness of all threats to vultures (this term is hereafter 'Awareness'). To spatially visualise these Awareness levels, I used inverse distance weighting interpolation (Santangeli et al., 2016) on the Awareness score for each SFS based on its known coordinates and mapped the results. Inverse distance weighting assumes that each provided data point has a localised influence that diminishes with distance from that point. Using this assumption this method then calculates scores for each spatial point for which there is no data, while giving greater weight to scores from datapoints closest to itself (Lu and Wong, 2008). The same approach was also recently used to interpolate poison use prevalence across Namibia (Santangeli et al., 2016b; Craig et al., 2018). I used QGIS (QGIS, 2019) to construct this map.

Statistical analysis

To evaluate whether there were differences in the perceived benefits, disadvantages and awareness of each threat between SFS who generated income from livestock farming versus hunting, I used Generalised Linear Models (GLM) with a binomial error structure and a logit-link function. Each identified benefit, disadvantage and threat was modelled in isolation as a binary response variable (indicating whether it was mentioned by a manager or not) with SFS type (either livestock farming or hunting) as the predictor variable. The probabilities and 95% confidence intervals were then calculated for each predictor using the estimated marginal means. These analyses were conducted using the stats and the emmeans package in the statistical software R (version 3.6.1) (R Core Team, 2019; Lenth, 2020). Some of the models did not run due to convergence problems caused by one or both categories in the predictor variable containing only zeros in the response data.

I explored the association between vulture visitation rate at SFS (obtained with the present survey) and food provisioning rates at the same SFS (kilograms of meat or carcasses provided annually), obtained from Chapter 2. For this analysis, I used a Pearson's product-moment correlation test.

Ethics statement:

This study was approved by the Faculty of Science Research Ethics Committee at the University of Cape Town (Approval code: FSREC 83 – 2017) and participants provided informed verbal consent for participation.

Results

Of the 143 active SFS contacted, 114 (80%) participated in this survey. Although participation rate was high, not all respondents answered every question in the survey, resulting in varying sample sizes for each question. In most cases, categories were not mutually exclusive, and respondents often reported multiple categories. Over half of the questionnaires were conducted over the phone (61%) and the remainder via email (39%).

Land management context in which SFS operate

Livestock farming was the most common main income-generating activity, reported by 50% of managers (Appendix 3.2). The second most common income-generating activity was tourism and hospitality, reported by 25% of managers, followed by hunting (20%) and game breeding (19%). These criteria were not mutually exclusive, and managers often reported multiple income sources. Viewing hides were present at 28% (of 105 respondents) of SFS (although 6% specified that these were for private use only).

Perceived benefits and disadvantages

The cleaning service provided by vultures at SFS was mentioned by 44% of managers, making it the most widely perceived benefit (Figure 3.1). Despite this, few managers seemed to link this benefit to disease prevention, as this was only mentioned by 2% of managers (Figure 3.1). Thirty percent of managers also derived personal pleasure or a feeling of satisfaction through running an SFS. Ecotourism was perceived as a benefit by 21% of managers. Some respondents (16%) perceived no benefits from the use of SFS. Less common benefits included facilitating research (7%) and the presence of vultures assisting in locating dead animals (2%). There appeared to be only a limited difference in the perceived benefits between SFS mangers that were principally involved in livestock farming as compared with those involved in hunting. Ecotourism was the only perceived benefit that I analysed, which differed between these two types of SFS sites (z-value = 2.461, p = 0.01, Appendix 3.3), with SFS managers on hunting farms being 6.8 times more likely to perceive ecotourism as a benefit compared to livestock farmers (Figure 3.2A, Appendix 3.3). Furthermore, locating mortalities was only mentioned by managers on hunting farms (5.3%, 95% CI = 0.7% - 29.4%) and disease prevention was only mentioned by managers on livestock farms (1.9%, 95% CI = 0.3%-12.4%, Appendix 3.3).

Over half of all managers (56%) reported no disadvantages to managing an SFS (Figure 3.1). The two most commonly identified disadvantages were increases in problem animals such as jackal (15%), and the effort in cleaning and maintaining the site (15%). Site security was the third most frequently expressed concern (10%, Figure 3.1), with some managers reporting increased trespassing on their properties caused by the SFS, which was also associated with carcass and infrastructure theft, as well as uncontrolled dumping at the site. The general "dirtiness" and "untidiness" of the site (9%), often related to the number of bones lying around, was also cited as a concern by some managers. Less common concerns included offensive smells emanating from SFS (6%), fears of disease spread (6%) with two managers stating that they fear their cows may become sick from chewing on bones (the most likely cause being botulism), and challenges concerning carcass sourcing (4%).

There were again little differences in the perceived disadvantages between SFS mangers that were principally involved in livestock farming as compared with hunting SFS sites. Managers from hunting associated SFS were 1.6 times more likely to perceive no disadvantage from having an SFS when compared to livestock farmers (z-value = 2.107, p = 0.035, Appendix 3.4) (Figure 3.2B). Furthermore, increases in problem animals (19.2%, 95% CI = 10.7% - 32.2%) and carcass sourcing (3.9%, 95% CI = 1.0%-14.1%) were disadvantages only mentioned by managers on livestock farms.

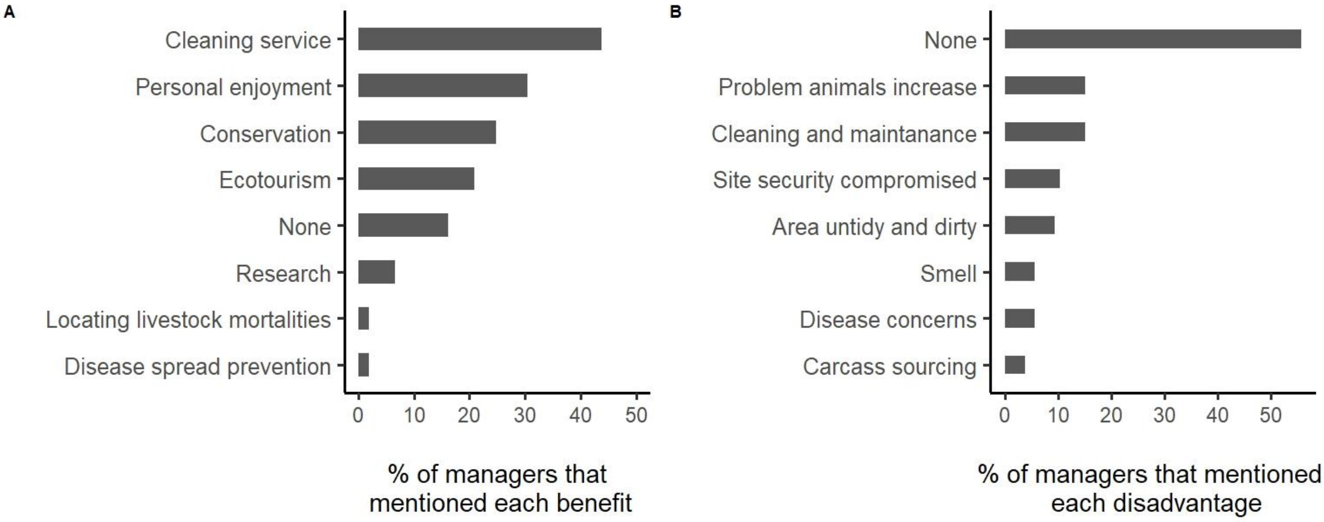


Figure 3.1: Benefits (n=105, A) and disadvantages (n=106, B) to having a supplementary feeding site as expressed by managers of active supplementary feeding sites in South Africa. Data were acquired via email and telephonic questionnaires. The categories in these graphs are not mutually exclusive.

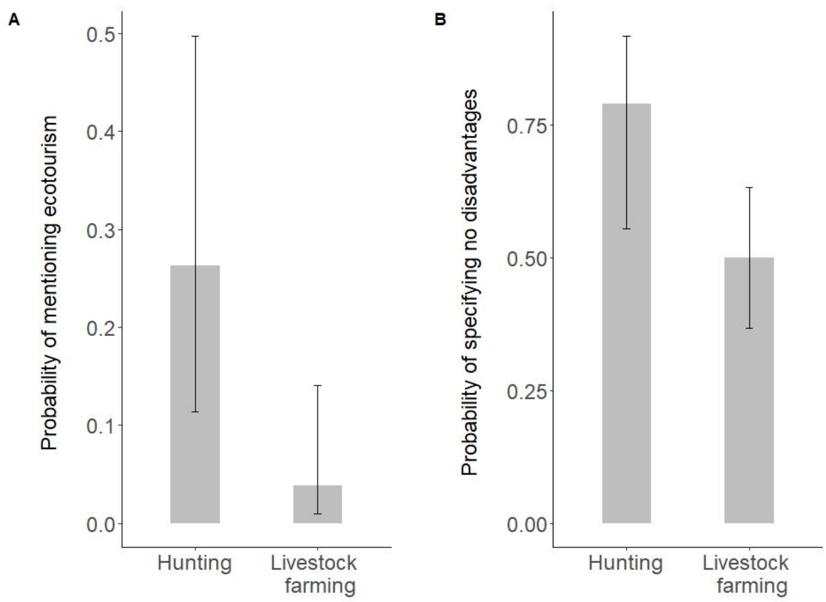


Figure 3.2: The probability that managers of differing supplementary feeding site types (livestock farming or hunting) would mention (A) ecotourism as a benefit of running a supplementary feeding site or (B) that there are no disadvantages to running a supplementary feeding site. Error bars indicate 95% confidence intervals.

Carcass sourcing

Over half of the managers (58%) provided carcasses exclusively from their own properties, 28% provided from their own and other properties and 15% provided only carcasses originating from other properties. Of the carcasses that came from other properties, the vast majority (85%) were provided by neighbouring farmers, followed by abattoirs and butcheries (22%). Other uncommon sources were veterinarians and the Society for the Prevention of Cruelty to Animals (animal welfare NGO) (3%), roadkill (2%) and police and security services confiscating stolen and poached animals (2%).

Contamination risk mitigation

When asked about whether there were some carcasses that managers considered unsuitable to be provided at their SFS (Question 12, Appendix 3.1), the majority of respondents (70%, of 103 respondents) indicated that there were some criteria with which they judged carcass suitability; the remaining 30% indicated that they provide all carcasses that become available. The presence of veterinary drugs in a carcass was the most common criteria by which SFS managers judged carcasses as unsuitable (Figure 3.3). Although managers commonly referred to veterinary drugs in general, some specifically mentioned drugs included non-steroidal anti-inflammatories (NSAID), antibiotics, tranquillizers and cortisone (Figure 3.3). Moreover, some managers avoided providing carcasses of animals dying from disease, preferring to dispose of such carcasses in a more direct manner (incineration or burying).

Only 10% of all managers mentioned that they actively avoided lead contamination in their carcasses. When considering only managers that provide game at their SFS (for which the issue of lead contamination will principally apply – i.e., from lead ammunition), 11% (of 38 respondents) indicated they avoided putting out lead-contaminated carcasses.

Managers' awareness of threats and unintended risks

When choosing the location for establishing the SFS, only 30% of SFS managers considered possible threats to vultures (Appendix 3.5). The most common criterion used when choosing a location, mentioned by 61% of managers, was the accessibility of the site to vultures (Appendix 3.5 and 3.6), followed by the accessibility of the SFS to farm staff, mentioned by 40% of managers. Some managers (19%) considered the ease of use of the sites for vultures when deciding on a location, which included having perching and roosting structures and having a water source close by. Most SFS (n=65) did indeed have a water point nearby (40%) or at the SFS (32%), but 28% had no water point.

Respondents (n=108) mentioned an average of three applicable threats (i.e., those identified by the MSAP) (range: 0-9). The most commonly mentioned threats by managers were in order:

power lines, belief-based use and unintentional poisoning (i.e., pertaining to secondary poisoning aimed at predator control) (Figure 3.4). For testable threats, the awareness of each threat did not differ significantly between livestock and hunting associated SFS, but some threats were mentioned solely by managers on livestock farms, including food availability (15.4%, 95% CI = 7.9%-27.9%), wind turbines (7.7%, 95% CI = 2.9%-18.8%), human disturbance (3.9%, 95% CI = 1.0%-14.1%), drowning (1.9%, 95% CI = 0.3%-12.4%), and disease (1.9%, 95% CI = 0.3%-12.4%), (Appendix 3.7). Vehicle collisions (5.3%, 95% CI = 0.7%-29.4%) was only mentioned by managers on hunting farms (Appendix 3.7). Awareness of threats showed a patchy spatial distribution, with hotspots of low awareness occurring along South Africa's northern border, eastern KwaZulu Natal and throughout much of the Eastern Cape (Figure 3.5).

Perceived population trends and vulture visitation at SFS

When asked about local vulture population changes of the last 10 years (Question 16, Appendix 3.1), managers (n=92) were equally divided between those that believed numbers had increased (38%), were stable (33%) or had declined (27%), with a further 2% indicating that there was no discernible trend due to varying numbers. The mean reported vulture visitation rate at SFS was 72 vultures per feeding event (n=98, range: 0-300]. There was a positive correlation between the average number of vultures visiting the SFS during feeding events and annual provisioning rate ($r= 0.398$, $t = 4.268$, $df = 97$, p-value <0.001, Appendix 3.8).

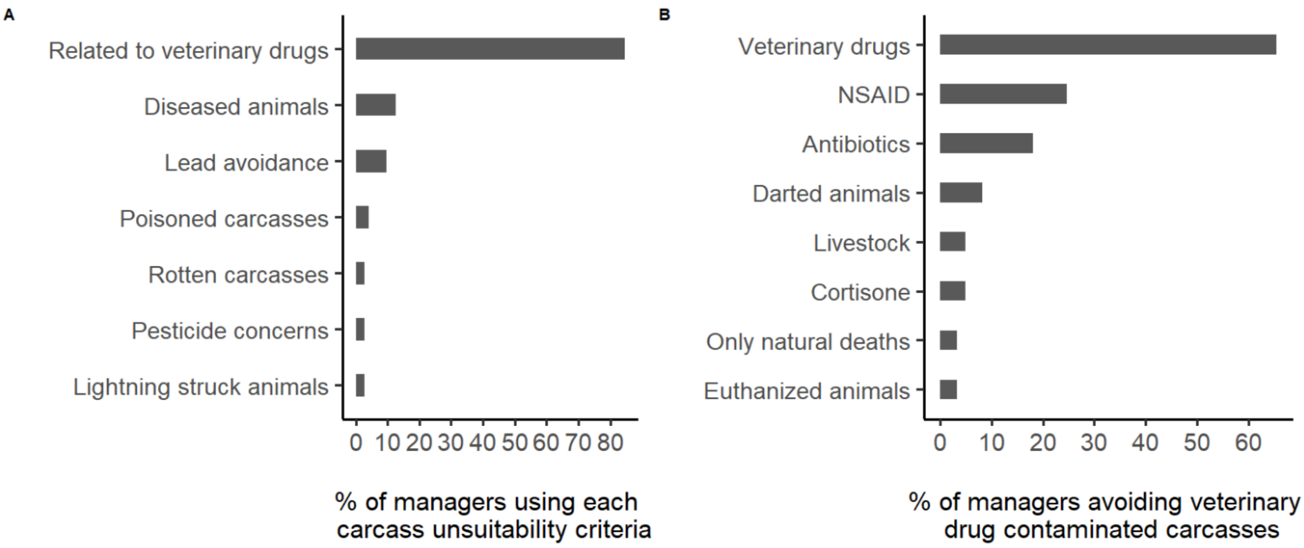


Figure 3.3: Carcass criteria that managers of active supplementary feeding sites in South Africa considered as unsuitable to provide to vultures (n=72, A). Criteria related to veterinary drugs reported by managers who attempted to avoid providing veterinary drug contaminated carcasses at their feeding sites (n=61, B). These are the constituents of the "Related to veterinary drugs" criteria in the figure to the left. None of the criteria in these graphs are mutually exclusive.

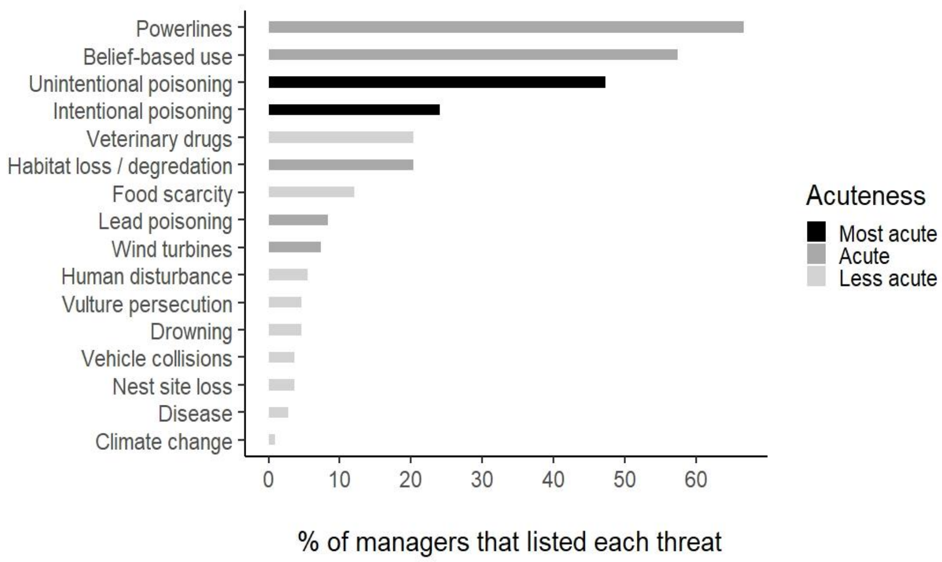


Figure 3.4: Percentage of supplementary feeding site managers (n=108) that are aware of each threat listed by the Vulture MSAP. The relative acuteness of each threat in southern Africa (as specified by the MSAP) is indicated by the grey shading.

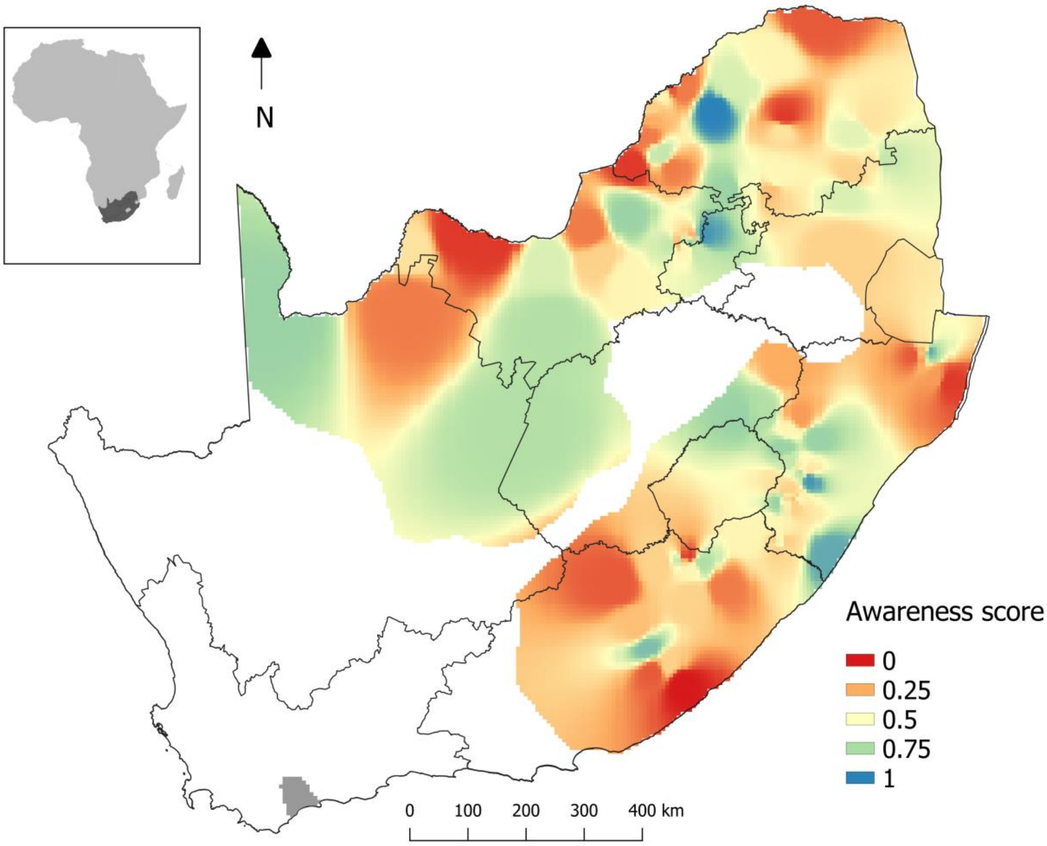


Figure 3.5: Awareness of supplementary feeding site managers of vulture threats and food safety concerns in South Africa, the coloured and grey area indicates the cumulative distribution of six vulture species. The grey shaded area contained only a single supplementary feeding site and these results were therefore excluded for anonymity reasons. The map was derived using inverse distance weighting interpolation of calculated awareness scores (see methods) which were based on the number of relevant threats managers could list and whether they were aware of the risks of food contaminated with lead (Pb) and veterinary drugs to vultures. Higher scores indicate higher awareness.

Discussion

Our results suggest that managers perceive various benefits from their SFS, while perceiving few disadvantages. I also identified a worrying lack of knowledge on best management practices meaning that some SFS may pose a risk to vultures. Several managers have low awareness of the main threats to vultures. As a result, often managers do not consider threats when choosing a location to place their SFS. Additionally, and perhaps of most concern, many SFS managers are not selective in the food they provide to the vultures, which may lead to vultures ingesting veterinary drugs or lead when feeding at SFS.

Context in which SFS operate

The main income-generating activities (livestock farming, tourism and hospitality, hunting, game breeding and crop farming) indicate that the vast majority of SFS are either being run from farmland or privately-owned reserves. Livestock farming is intuitively the nexus around which SFS operate everywhere where they exist. For example, in France, 95% of the 105 SFS are run by livestock farmers (Fluhr et al., 2017), while in northern Spain, livestock farmers suggested food provisioning as the best way to conserve the Egyptian vulture population (Cortés-Avizanda et al., 2018).

The context in which SFS operate can both influence how managers perceive risks to vultures associated with their SFS and determine what the best strategies for conservationists are to influence these perceptions. The majority of South African SFS are strictly for private use and do not provide carcasses sourced from other properties. Some managers expressed that this is because they want to maintain strict control of carcasses provided to vultures to ensure that the food is safe. If managers already foster such concerns, then alleviating risks from contaminated carcasses, which my questionnaire suggests might be an issue, should be a simple case of ensuring that managers are well informed of which substances would be harmful to vultures. Unfortunately, most hunters in South Africa and elsewhere still ignore the threats that lead ammunition can pose to scavengers, and other wildlife (Epps, 2014; Cromie et al., 2015). This situation can be exacerbated by the reluctance of organisations trusted by the hunter community, to acknowledge the threats of lead ammunition to avian scavengers. For example, the South African Hunters and Game Conservation Association, have an official stance that although they recognise the studies indicating increased blood lead levels in vultures, studies have in their opinion not sufficiently managed to link this to lead ammunition in carcasses (van de Geissen, 2019). Getting such organisations to promote best management practices and engaging properly with such stakeholders must be a priority if we are to ensure food placed at SFS is safe for vultures. Encouragingly, the recently established South African Lead Task Team of the National Wildlife Poisoning Prevention Working Group includes several stakeholders from the South African hunting industry.

We found that most managers perceive at least some benefits from running an SFS. This suggests that most managers recognise and value some of the ecosystem services provided by vultures. These services fall mostly within a regulation and maintenance (related to carcass disposal) or cultural theme (related to the aesthetic and existence value of vultures) (Potschin and Haines-Young, 2011). The most widely perceived benefit was the cleaning service provided by vultures. This ecosystem service seems to be recognised elsewhere too (Santangeli et al., 2016b; García-Alfonso et al., 2018; Morales-Reyes et al., 2018). In South Africa, other carcass disposal methods are burning or burying (personal observation) which is widely viewed as a good farm management practice, because carcasses are considered potential points of origin for diseases (e.g., botulism) which may cause stock losses (Radostits et al., 2007). Carcass disposal can be a laborious and costly task, especially for intensive farming operations, therefore, using vultures is likely a more affordable and logistically feasible alternative. Most other perceived benefits fall under cultural ecosystem services, such as personal enjoyment in running an SFS. I can assume that managers that indicated that they receive no benefit from their SFS run them purely because they feel some sort of moral imperative to do so. Similarly, those managers that highlight conservation or environmentalism as a benefit, may run an SFS at least partly, for altruistic reasons, e.g., for a sense of biophilia (Kellert and Wilson, 1993), and their participation in this activity may thus contribute to a sense of moral wellbeing.

Many of the perceived benefits and disadvantages of running SFS seem to correspond to the context in which they function. An understanding of how these contexts cause knowledge/attitude differences will enable conservation management to influence the managers of these sites. Managers from hunting SFS were for instance more likely to perceive ecotourism benefits from SFS. This may thus be a good avenue with which to influence such managers. Similarly, the most frequently mentioned disadvantage of SFS was that they cause an increase in problem animals such as predators that may attack livestock (e.g., black-backed jackals, *Canis mesomelas*). No manager of hunting SFS saw this as a disadvantage. Indeed, those managers, seemed to be less affected by their SFS, with a higher proportion of them perceiving both no disadvantages as well as no benefits.

SFS use and manager perceptions of vulture trends

Considering the current vulture declines experienced in Africa (Ogada et al., 2016), it is surprising that over a third of mangers in South Africa perceived a local increase in vulture numbers at their SFS. This perception was also recorded in Namibia, where 68% of farmers perceive vultures to have increased on their farms during the previous 5 years (Santangeli et al., 2016b). One explanation for the contrast in perception with known population trends, may be the localised increase of vultures at sites after the initiation of an SFS. One manager, with a very high provisioning rate, explained that after a year of food provisioning without any vulture visits, they now observe between 100-300 vultures daily. This may explain why many managers assume, despite no scientific evidence, that their SFS are helping to increase vulture populations (personal observation). Increased activity at SFS may, however, not be an indicator of vulture population trends in the area, but rather the consequence of a shift in foraging activity towards SFS as opposed to other areas.

We found a correlation between number of vultures and the amount of food provisioned. This result may stem from vultures responding to the amount of food supplied at an SFS, or alternatively because the amount of food managers supply is reactionary to the numbers of vultures. If the former, it would suggest that vultures foraging behaviour is being altered by SFS. Had vultures been foraging naturally I would expect single feeding events to be drawing similar vulture numbers irrespective of the provisioning rate at SFS. If vultures are becoming dependent or habituated to this artificial food source, this may have important management implications (Fluhr et al., 2017). The latter might be less likely, since managers are likely to be restricted in their provisioning to their stocking and mortality rates, and thus only intensive farming operations will have the resources to respond to vulture numbers in any significant way. I therefore speculate that vultures responding to varying provisioning rates is a more likely hypothesis for the observed correlation.

The potential costs to vultures from SFS

Species-centred conservation may have greater support when stakeholders better understand the value of the species in question. This can be achieved by highlighting the ecosystem services that vultures provide (Gangoso et al., 2013). The notion being that the species will be valued and protected in response.

With an average of 72 vultures visiting during each feeding event, and the ability to draw more than 300 vultures, SFS provide food for a considerable number of vultures. Indeed Chapter 2 suggested that South African SFS may be fulfilling up to 83% of the total energy requirements of vultures in the region. This combined with the potential for dependency or habituation, means that SFS, if poorly managed, may have considerable population-level effects on vultures in the region, through luring vultures into areas with increased risk of mortality and exposure to unsafe food.

Many SFS managers do not have good awareness about the threats currently facing vultures, with managers on average only being able to name about three of the nine applicable threats (as identified by the MSAPs). Threat knowledge also did not correspond well to the importance of the threat in the region. Poisoning, for instance, is widely recognised as the main threat to vultures. On farms, this specifically relates to the use of poisons for predator control. More than half of managers seem to be unaware that this behaviour threatens vultures, or perhaps they do not believe that it commonly occurs. Some managers indicated that they use poison to target predators, however, they believe they do so in a way that removes any risk to vultures (e.g., using small parcels of poisoned bait). In Namibia, 88% of interviewed commercial farmers indicated that they used poisoned baits in a similar way and 12% indicated that they poisoned larger carcasses (Santangeli et al., 2016b). If poison-use rates in South Africa are comparable to those in Namibia, this would pose a severe hurdle to ensuring that vultures persist in the country. Worryingly, increases in problem animals (referring to predators) was the most cited disadvantage of SFS. This was already shown in previous studies (Yarnell et al., 2015). Consequently, SFS may cause increased predator numbers, leading to higher stock losses and increased likelihood of managers or neighbouring farmers to use poison. In this way SFS may exacerbate human-wildlife conflict.

Other safety concerns relate to the food provided at SFS themselves. Previous studies show that few SFS managers consider lead to be harmful to vultures (Chapter 2). This will however mostly be a concern at the 38% of SFS that provide hunted game carcasses (Chapter 2). Surprisingly when I asked these game providing managers what criteria they use to screen carcasses for provisioning, only 11% mentioned lead avoidance (Question 12, Appendix 3.1). When asked directly whether they believed lead could have detrimental health effects on vultures, however, 41% of these managers agreed that lead could have detrimental effects on vulture health (Chapter 2). It thus seems that although some managers know that lead is harmful to vultures, they do not necessarily translate this knowledge into actions to minimise risks from lead contamination. Vultures are likely exposed to lead at SFS. A recent study showed how widespread lead exposure was for vultures in South Africa (van den Heever et al., 2019). Contamination at SFS may contribute to the above-mentioned results and explain why lead levels in South Africa are so much higher than for other regional populations (Garbett et al. 2018 compared to van den Heever et al. 2019). Moreover, it is still common for statutory conservation agencies to provide animals from culling operations or animals that were poached, which also likely contain lead, for vultures to feed on.

SFS managers recognise the potential toxicity of veterinary drugs to vultures (Chapter 3) and this is the most widespread consideration in terms of determining if carcasses are suitable to be fed to vultures. However, 28% of SFS managers remain unaware of the potential negative effects of veterinary drugs (Chapter 2). It is also worrisome that some SFS provide carcasses originating from the Society for the Prevention of Cruelty to Animals and veterinarians who routinely euthanize animals. Despite most SFS managers being aware of the immediate threat of veterinary drugs to vulture health (Chapter 3), few considered it to be a real threat to vultures in a more general sense. It is also important to note that sentiments about which drugs are safe for vultures and which are not, may differ widely. The risks associated with veterinary drugs may be ameliorated by the influence of veterinarian professionals, one respondent, for instance, specified that although they provide all carcasses that become available, they have switched some of their medicines to those that their veterinarian advised is safe for vultures. This could be true for other SFS as well, but a further complication is that vultures can contract multi-antibiotic resistant pathogens from carcasses provided at SFS which potentially pose mortality and fitness risks (Blanco, 2018; Marin et al., 2018, Plaza et al., 2020).

SFS managers recognised the threat of power lines to vultures, but only a few managers indicated that they considered the proximity to powerlines when selecting a location for their SFS. It might be that many managers just did not need to consider this as power lines were not present in their candidate areas. Some SFS, however, do occur near powerlines despite managers being aware of powerline associated vulture mortalities at these sites (personal observation).

SFS may also be easy targets for criminals aiming to harvest vultures for the belief-based use market (McKean et al., 2013; Mateo-Tomás and López-Bao, 2020). One SFS manager divulged that they had once discovered a sack full of vulture parts on the side of the road next to their property. Another had apprehended persons with a live and injured vulture. Such incidences may become more common as it has been suggested that the current rise in sentinel poisoning may stimulate the illegal trade in vulture parts (Mateo-Tomás and López-Bao, 2020).

Currently, SFS are unregulated and left to the discretion of single private individuals. I show that some of these individuals are unaware of the risks their management decisions pose to vultures and many do not conform to best management practices. This should be urgently addressed to avoid a situation where SFS cause issues for vultures and it is the role of the scientific community to deliver the knowledge and tools necessary to ensure sustainable use of such ecosystem services. This could either be done through increasing educational awareness and training from the conservation NGOs that are involved with several of these sites, or if this measure fails, government regulation of SFS.

Conclusion

In South Africa, SFS mostly operate within a farming context and the free cleaning service provided by vultures is a widely valued benefit. SFS managers seem to experience minimal disadvantages in running such operations. Although SFS may have beneficial effects on vulture populations some costs need to be considered as well. Many such costs will stem from the fact that SFS managers seem to have a low awareness of the threats vultures may face and how their feeding sites may contribute to this risk, especially with regards to food safety. I suggest increased interaction and communication between conservation practitioners and SFS managers. Such efforts may be particularly urgent in those areas I have identified as associated with low SFS manager awareness of vulture threats and the food contamination risks, particularly in the North-Eastern region of South Africa which also represents a global priority for vulture conservation (Santangeli et al., 2019).

Appendix 3

Appendix 3.1: Questionnaire used in this study.

Date:
VR_Code (for office use):

VULTURE RESTAURANT SURVEY:

Hello, my name is Christiaan W. Brink and I am a PhD student at the University of Cape Town researching the contribution of vulture restaurants to vulture conservation in South Africa. I found your contact details on our existing database in relation to a vulture restaurant / feeding site, and would appreciate it if you took part in our survey that will aid vulture conservation and which will ultimately benefit vultures and landowners. Your participation would be appreciated whether you are currently feeding vultures or have stopped doing so.

As part of my thesis I am updating the current database with the information of vulture restaurant managers. This information will not be published or made freely available to the public and will only be distributed to the relevant people in vulture conservation and research (eg. VulPro, EWT, Ezemvelo KZN wildlife, all of which have contributed to, or is a collaborator on this project). Do you give consent for your information to be shared with the before mentioned people?

Participant agreed (Please remove if you disagree)

At the same time we would like to get an understanding of what motivates people to run vulture restaurants. Please answer the questions below. Please note that the answers from these questions (excluding the Basic Info) will not be included in the database but rather kept confidential. When the research is published, none of your answers will be linked with your name or name of your farm and so will remain anonymous.

Please note that your participation in this interview is completely voluntary.

Do you agree to participate in this interview?

Participant agreed (Please remove if you disagree)

A. Basic info/demographics

1. **Name:**
2. **Position/role at the property: (i.e.: owner, manager):**
3. **Occupation:**
4. **Property owner name:**
5. **Name of property/farm:**
6. **Vulture restaurant property address:**
7. **Email:**
8. **Preferred contact number:**
9. **Coordinates of Vulture Restaurant (if not available, coordinates of property- please specify the structure for which coordinates are given):**

B. Property:

10. **What are the main income generating activities on the property? (eg. farm (type?)/hunting/hospitality/residential/game reserve/ecotourism/conservation area etc.):**

11. **Please provide an indication of land use on the property and the percentage area each occupies (eg. 10% grazing; 40% cultivated maize fields, 50% natural area etc.)**

C. Vulture Restaurant (VR):

12. **Are/were there any carcasses that are considered unsuitable to be put out at the vulture feeding site or are all carcasses put out? Please specify what type of carcasses are considered unsuitable if any.**

13. **What benefits do/did you or the property owner derive from the vulture restaurant?**

14. **What disadvantageous are/were there to managing a vulture restaurant?**

15. **Can you give an estimate of the average number of vultures (per species) at a carcass?**

16. **How has vulture numbers (per species) changed over the last ten years at your feeding site? Increase, decrease, stayed the same?**

17. **Is there a viewing hide at the vulture restaurant?**

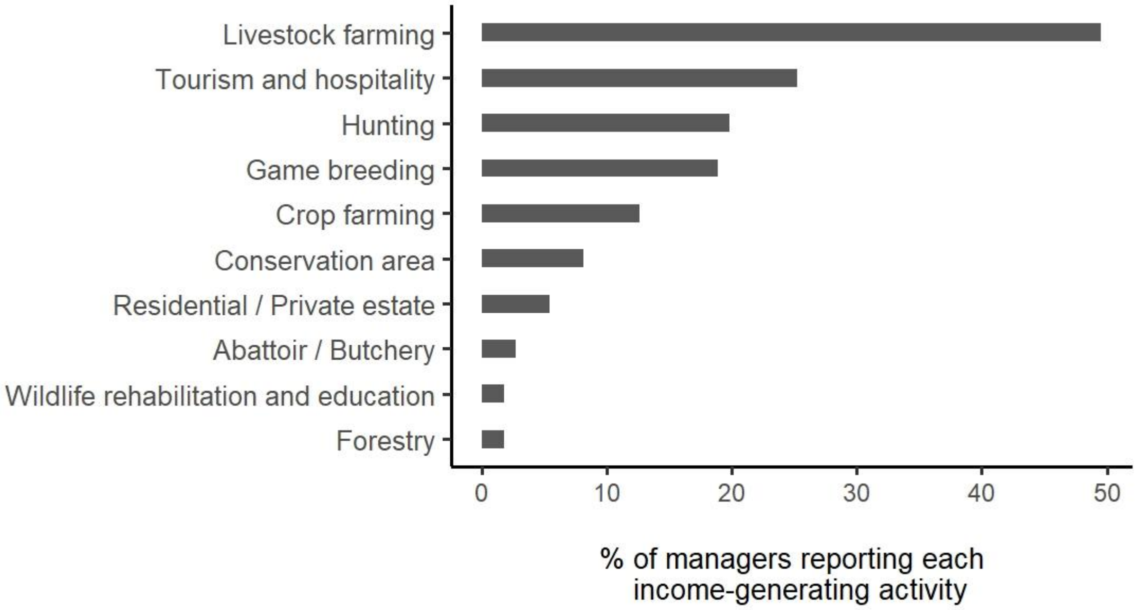
18. **How did you select the location for the vulture restaurant? What did you need to consider when deciding on a location?**

19. **Is there a water point that vultures can bathe in at the restaurant?**

D. Vulture Conservation:

PLEASE USE ONLY YOUR OWN GENERAL KNOWLEDGE AND OPINIONS TO ANSWER THIS SECTION-PLEASE NOTE THAT THESE QUESTIONS DO NOT SPECIFICALLY RELATE TO YOUR OWN PROPERTY OR AREA

20. **Please list all the threats to the conservation of vultures, across southern Africa, which you know about?**



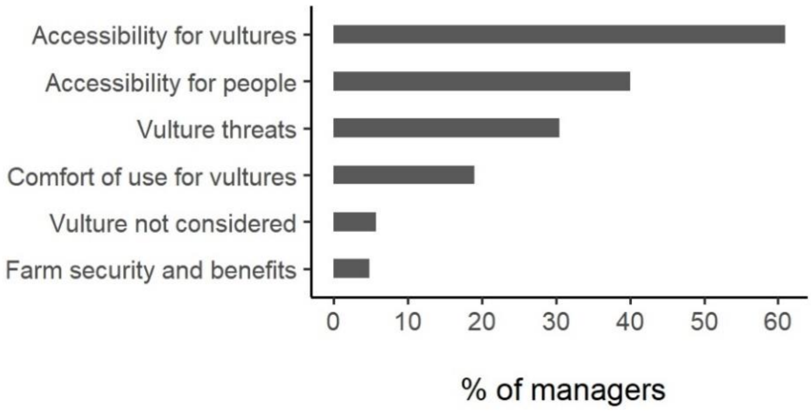
Appendix 3.2: Main income-generating activities on active vulture supplementary feeding site properties in South Africa, as reported by managers (n=111). These categories are not mutually exclusive, and some managers indicated multiple categories as their main sources of income.

Appendix 3.3: Results from eight Generalised Linear Models with a binomial error structure and a logit-link function where each perceived benefit was used as a response variable and the type of supplementary feeding site (SFS), either livestock farming (n=52) or hunting (n=19) as the explanatory variable. Probabilities and 95% confidence intervals (CI) were calculated using Estimated Marginal Means, test statistics and p-values provided from the model summary directory. Missing values indicate models which were unable to converge due to one or both of the categories in the predictor variable containing only zeros in the response data.

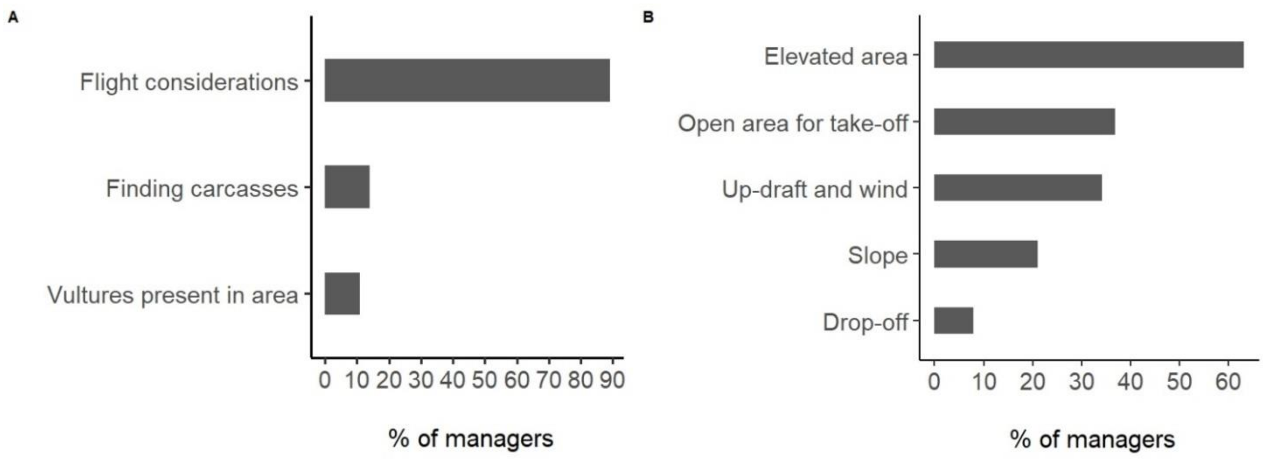
	Hunting SFS		Livestock farming SFS			
Response variable	Prob	95% CI	Prob	95% CI	Z-value	p-value
Cleaning service	0.368	0.187 ; 0.597	0.596	0.459 ; 0.720	-1.678	0.093
Personal enjoyment	0.263	0.114 ; 0.498	0.327	0.214 ; 0.464	-0.513	0.608
Conservation	0.105	0.027 ; 0.337	0.192	0.107 ; 0.322	-0.853	0.393
Ecotourism	0.263	0.114 ; 0.498	0.039	0.010 ; 0.141	2.461	0.014
None	0.263	0.114 ; 0.498	0.115	0.053 ; 0.234	1.485	0.137
Research	0.053	0.007 ; 0.294	0.019	0.003 ; 0.124	0.723	0.470
Locating mortality	0.053	0.007 ; 0.294	0.000	-	-	-
Disease prevention	0.000	-	0.019	0.003 ; 0.124	-	-

Appendix 3.4: Results from eight Generalised Linear Models with a binomial error structure and a logit-link function where each perceived disadvantage was used as a response variable and the type of supplementary feeding site (SFS), either livestock farming (n=52) or hunting (n=19) as the explanatory variable. Probabilities and 95% confidence intervals (CI) were calculated using Estimated Marginal Means, test statistics and p-values provided from the model summary directory. Missing values indicate models which were unable to converge due to one of the categories in the predictor variable containing only zeros in the response data.

	Hunting SFS		Livestock farming SFS			
Response variable	Prob	95% CI	Prob	95% CI	Z-value	p-value
None	0.789	0.554 ; 0.919	0.500	0.367 ; 0.633	2.107	0.035
Maintenance	0.053	0.007 ; 0.294	0.115	0.053 ; 0.234	-0.765	0.444
Problem animals	0.000	-	0.192	0.107 ; 0.322	-	-
Site security	0.053	0.007 ; 0.294	0.096	0.041 ; 0.211	-0.575	0.565
Untidy	0.158	0.052 ; 0.392	0.096	0.041 ; 0.211	0.721	0.471
Smell	0.053	0.007 ; 0.294	0.058	0.019 ; 0.164	-0.082	0.935
Disease	0.053	0.007 ; 0.294	0.096	0.041 ; 0.211	-0.575	0.565
Carcass sourcing	0.000	-	0.039	0.010 ; 0.141	-	-



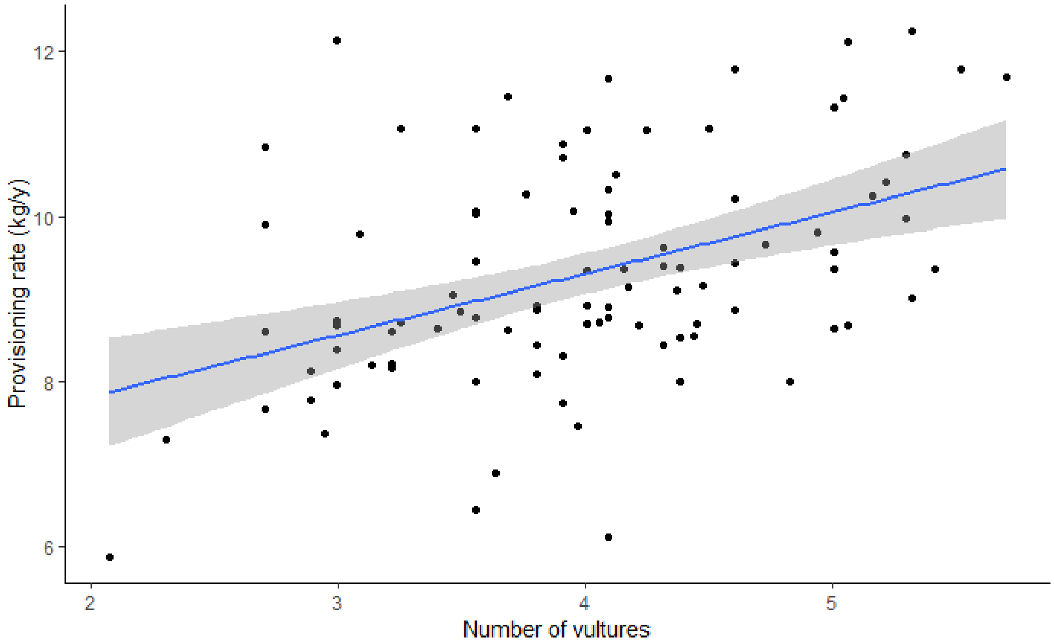
Appendix 3.5: Criteria used by managers of active supplementary feeding sites in South Africa when deciding on a location for their supplementary feeding site (n=105). The categories are not mutually exclusive.



Appendix 3.6: Composition of the "Accessibility for vultures" criteria in Appendix 4 (n=64, A). Composition of the "Flight considerations" criteria in the left graph (n=38, B). The categories in these graphs are not mutually exclusive.

Appendix 3.7: Results from 16 Generalised Linear Models with a binomial error structure and a logit-link function. Managers mentioning the threat was the response variable and the type of supplementary feeding site (SFS), either livestock farming (n=52) or hunting (n=19) was used as the explanatory variable. Probabilities and 95% confidence intervals (CI) were calculated using Estimated Marginal Means, test statistics and p-values provided from the model summary directory. Missing values indicate models which were unable to converge due to one or both categories in the predictor variable containing only zeros in the response data.

	Hunting SFS		Livestock farming SFS			
Response variable	Prob	95% CI	Prob	95% CI	Z-value	p-value
Powerlines	0.526	0.311 ; 0.732	0.654	0.516 ; 0.770	-0.975	0.329
Belief-based use	0.368	0.187 ; 0.597	0.500	0.367 ; 0.633	-0.979	0.328
Unintentional poisoning	0.316	0.149 ; 0.548	0.500	0.367 ; 0.633	-1.366	0.172
Intentional poisoning	0.105	0.027 ; 0.337	0.231	0.136 ; 0.364	-1.146	0.252
Veterinary drugs	0.105	0.027 ; 0.337	0.231	0.136 ; 0.364	-1.146	0.252
Habitat loss	0.263	0.114 ; 0.498	0.096	0.041 ; 0.211	1.725	0.084
Food scarcity	0.000	-	0.154	0.079 ; 0.279	-	-
Lead poisoning	0.053	0.007 ; 0.294	0.039	0.010 ; 0.141	0.262	0.794
Wind turbines	0.000	-	0.077	0.029 ; 0.188	-	-
Human Disturbance	0.000	-	0.039	0.010 ; 0.141	-	-
Vulture persecution	0.053	0.007 ; 0.294	0.019	0.003 ; 0.124	0.723	0.470
Drowning	0.000	-	0.019	0.003 ; 0.124	-	-
Vehicle collisions	0.105	0.027 ; 0.337	0.000	0.000 ; 1.000	-	-
Nest site loss	0.053	0.007 ; 0.294	0.019	0.003 ; 0.124	0.723	0.470
Disease	0.000	-	0.019	0.003 ; 0.124	-	-
Climate change	0.000	-	0.00	-	-	-



Appendix 3.8: Provisioning rate at active South African supplementary feeding sites plotted against the indicated number of vultures seen at an average feeding event. The regression line is indicated by the solid line and the 95% confidence interval by the shaded area. Values are presented at a log scale for both axes.

CHAPTER 4:

Prevalence and drivers of poison-use by South African commercial farmers and perceptions of alternative livestock protection measures

Photo: Farmers gather at a livestock auction (Photo by C.W. Brink).

Abstract

The use of poison to eliminate predators is causing African vulture populations to collapse. To understand the prevalence and motivations of this practice I conducted an extensive survey with South African commercial farmers. Using a specialised questioning technique and ad-hoc quantitative methods I found that an estimated 22% and 31% of farmers used poison over a one-year and five-year period, respectively. Poison-use hotspots generally coincided with small stock farming areas. The strongest predictor of poison-use was whether farmers believed the practice to be common amongst their peers. My results suggest that farmers' attitudes to vultures are primarily positive, and farmers are less likely to use poisons if they frequently encounter vultures on their farm. Overall, my findings provide an understanding on poison-use that provides leverage points to change farmers' behaviour and help avert the African vulture crisis and possible cascading ecosystem impacts.

Introduction

Under a human-managed world, changing human behaviour is essential to halt the current biodiversity crisis (Johnson et al. 2017). Broad-scale approaches, such as policy and regulation, may be the most efficient methods to establish pro-environmental practices (Gray and Shimshack 2011), but poor enforcement, especially in developing countries, often results in compliance being voluntary in practice (Rowcliffe et al. 2004). Changing human behaviour at the individual level is thus an important component of conservation efforts seeking to address such issues, but one that is rarely achieved.

Conservation initiatives targeting individual behaviours often rely on the fundamental premise that non-participation in pro-environmental behaviour is because of a lack of awareness (van der Ploeg et al. 2011). However, social and environmental psychology research suggests that information alone is insufficient in producing behavioural change (Abrahamse et al. 2005). Additional approaches that enhance the motivational foundation for pro-environmental behaviour are thus required (Osbaldiston and Schott 2012). To design and effectively implement such alternative approaches, research needs to move beyond the simple quantification of human environmental impacts, to examining the causative behaviours themselves. The realisation that human behaviour is a key component in effective conservation has been slow to penetrate the conservation science field and requires a larger research focus (Cowling 2014).

Environmentally destructive behaviours often take place within a human-wildlife conflict where wildlife cause a range of damages (Nyhus 2016). Responses to such damage can often be overly corrective and in some cases dramatic, such as bombing the offending animals (Cheke and El Hady Sidatt 2019). The use of poison is a widespread and popular method of retaliation or control to target almost any damage causing species (Ogada 2014). Beyond agricultural pests, the most common poisons used to target vertebrate species are agricultural pesticides, such as organophosphates and carbamates, because of their high availability (Ogada 2014). Their legitimate use and their use to target vertebrate species can have a range of both lethal and sub-lethal effects on non-target species, with cascading effects through the entire ecosystem (Ogada 2014).

The use of poison by livestock owners to kill predators that cause livestock losses is currently at the forefront of conservation discussions, specifically concerning its impacts on scavengers (Plaza et al. 2020). Being obligate scavengers, vultures are particularly vulnerable to poisoning and this is one of the main drivers of the population declines that have resulted in an African vulture crisis (Ogada et al. 2016). Currently, seven of the eleven African vulture species are listed as endangered or critically endangered (Ogada et al. 2016). The loss of vultures and their carcass disposal service could have cascading impacts on ecosystems and human wellbeing. Vulture declines have, for example, been linked to increases in mammalian scavengers, such as feral dogs (*Canis lupus familiaris*), which in turn may result in increases in human rabies infections (Markandya et al. 2008). Furthermore, this associated meso-predator release, may result in increased livestock depredation and further motivate the use of poisons.

Although poisoning predators is currently illegal in most countries, the practice remains widespread in 83% of African countries (Ogada, 2014). This is because of the large economic cost associated with livestock depredation, estimated to range between USD 22 – 171 million in South Africa annually (van Niekerk 2010; Statistics South Africa 2010). The consequent poison-use is estimated to kill more than 500 000 wild animals every year in this country (Endangered Wildlife Trust 2006). Understandably, livestock owners want to avoid such economic losses and, despite some evidence to the contrary (McManus et al. 2015), lethal predator control methods are still viewed as more effective and cheaper than alternative methods (Scasta et al. 2017). Of the lethal options, poisoning is likely the least labour-intensive and is therefore likely to continue if perceptions of the risks associated to this practice are not changed.

Given the large livestock losses associated with predation in South Africa, it is surprising that there are relatively few comprehensive studies investigating livestock protection measures in the region (Kerley et al. 2018). Some information on prevalence of specific livestock protection measures is available from surveys which used a direct questioning approach, but the authors of these studies highlighted that famers may be apprehensive to answer sensitive questions openly, out of fear of prosecution or confrontation (Badenhorst 2014). Estimating the prevalence of sensitive behaviours is notoriously difficult as social desirability and non-response bias may affect the results (Nuno and St. John 2015). Therefore, alternative methods have recently been developed that provide respondents anonymity with regards to their admittance to participating in a sensitive behaviour (Nuno and St. John 2015). Such techniques have been effectively used in elucidating the prevalence of illegal bushmeat trading (van Velden et al. 2020) and poison-use (Santangeli et al. 2016b).

Here I used specialised social science techniques that ensure respondent anonymity to investigate poison-use by livestock farmers in South Africa, a global hotspot for vulture conservation (Santangeli et al. 2019). I firstly aimed to provide a deep understanding of poisoning behaviour by determining its prevalence among commercial livestock farmers, which I expected to be comparable to Namibian commercial farmers who farm within similar cultural and circumstantial frameworks (Santangeli et al. 2016b). Secondly, I aimed to identify the context and attitudes that are associated with poison-use. I predicted that, similar to the Namibian study (Santangeli et al. 2016b), small stock farmers would be most likely to use poison as their livestock are most susceptible to predation. Thirdly, I explored the spatial patterns of poison-use across the country. Lastly, I investigated farmer perceptions of alternative livestock protection methods that may explain the persistence of poison-use. Given the widespread use of lethal control, I expected this to be perceived as the most effective method. I discuss how my results may be leveraged to curb poison-use and how the spatial distribution of poisoning may affect vulture conservation initiatives.

Methods

Protocol for data collection

To investigate the prevalence of poison-use in predator control, I conducted a survey with South African commercial livestock farmers between April and September 2019. Because of South Africa's political history, which enforced segregation on a racial basis, commercial farming areas tend to be spatially distinct from areas of communal farming. Previous studies have indicated that poisoning is more prevalent among commercial than communal farmers (Santangeli et al. 2016b; Craig et al. 2018); because of this and logistical constraints, I focussed this study on commercial farmers. All interviews were conducted in person (by CWB). Commercial farmers were approached at either agricultural retail stores, livestock auctions or agriculture fairs. I restricted my study to South Africa and focussed my sampling efforts to within 100 km of the range of any relevant vulture species in South Africa (African white-backed vultures, *Gyps africanus*, Cape vulture, *Gyps coprotheres*, bearded vulture, *Gypaetus barbatus*, hooded vulture, *Necrosyrtes monachus*, white-headed vulture, *Trigonoceps occipitalis*) (Chapter 2). Interviews took 10 to 30 min to complete and were conducted in either English or Afrikaans, depending on the respondent's preference. The overwhelming majority of respondents showed good familiarity with either language and I perceive no biases as a consequence of language comprehension in the study. Respondents either filled in the questionnaires by themselves or were read the questions and their answers transcribed.

General questions

We designed the questionnaire to include questions on factors that may be associated with a respondent's propensity to use poison (Appendix 4.1). Questions related to basic demography (e.g., age and education level), farming context (e.g., location of farm, size of farm, type and number of livestock on farm, percentage income from livestock farming, depredation numbers), attitudes (e.g., towards predators, game, vultures and farmworkers) and the perception of the effectiveness of alternative predator control methods. Attitude and perception questions were framed on a five-point Likert scale of agreement or effectiveness (ranging from strongly disagree to strongly agree or from very ineffective to very effective). I also asked farmers to indicate the percentage of their peers they believed used poison to control predators. Farmers indicated the locations of their farms on a map and the coordinates were extracted.

The list experiment

Using poison to target predators is illegal in South Africa (Thompson and Blackmore 2020). Therefore, I used an indirect questioning technique that provides anonymity to respondents and does not require them to directly admit to the illegal behaviour, thereby reducing biases inherent in direct questioning (Nuno and St. John 2015). The technique used here, referred to as either the unmatched count technique or a list experiment, has been successfully used to quantify illegal hunting prevalence in African communities (Whytock et al. 2018; van Velden et al. 2020). Respondents were randomly assigned to either a treatment or a control group. Each respondent was presented with a list of behaviours containing four non-sensitive behaviours, but in the case of the treatment group a fifth behaviour, the sensitive behaviour under investigation (poisoning), was added to the list (Appendix 4.1). Respondents were asked to indicate how many of the listed behaviours had been performed on their farm in the last year, and the last five years, without indicating the behaviours themselves. This resulted in two datasets, one for poison-use over a one-year period and another for a five-year period. All behaviours listed were related to farming practices and one very common and one very rare behaviour was included as is the advised experimental design to avoid ceiling and floor effects (Blair et al. 2019). The non-sensitive behaviours, or the control items, were the use of protective collars on livestock (rare behaviour), infrastructure such as fences (common behaviour), hunting of predators and using flock guarding animals such as Anatolian dogs.

Ethics statement

Informed consent was provided before each interview. To ensure anonymity of respondents this consent was obtained verbally. This study was approved by the Faculty of Science Research Ethics Committee at the University of Cape Town (Approval code: FSREC 19 - 2019).

Statistical analysis

Data analyses were done in R v.3.6.3 (R Core Team 2019), using the "list" package, which was specifically designed for analysing list experiments (Blair and Imai 2012). Data analyses were performed using the modelling framework provided by Blair and Imai (2012), which performs better than previous multivariate regression analysis approaches used for list experiments (Blair and Imai 2012). Within this framework I used the proposed Non-linear Least Squares (NLS) estimator and tested my models for assumption inherent to list experiments (Appendix 4.2 – 4.5. The one-year and the five-year timeframes were analysed separately. Please refer to Appendix 4.6 for a more detailed description of the statistical approach.

All predictors were tested for collinearity and only largely uncorrelated variables ($r < 0.4$) were used in my analysis (Appendix 4.7). Below I provide a description of the 15 variables included in the NLS models and the rationale for their inclusion. A subset of variables pertaining to farming context was included on the assumption that this context would influence a farmer's ability to protect his livestock from predators. These included farm size, and number and type of livestock. Stock type was included as small stock (sheep and goats) have a higher propensity to be predated in South African farmland where the main threat is medium sized predators. Poison-use was also strongly related to small stock farming in a previous study (Santangeli et al. 2016b). Game in the context of this study refers to medium to large wild ungulates.

High predation rates or the perception that predation is one of the main causes of livestock losses is intuitively expected to trigger predator control. Similarly, farmers with negative attitudes to predators or game were expected to more readily use poison, owing to the potential for these animals to cause financial damages (e.g. predation, crop damage). I expected that poisoning would be more prevalent amongst older farmers who started farming in an era when this behaviour was more widespread and acceptable (Ogada 2014). I assumed that a higher level of education would correlate with increased environmental awareness. I expected farmers to generally be aware that poisoning threatens vultures and thus would be more apprehensive to use poison if they saw vultures regularly on their farms. Similarly, positive attitudes towards vultures were expected to reduce propensity for poison-use. Strained relationships between farmers and their workers have been reported to result in unmotivated workers and in some cases vengeful behaviour that can exacerbate livestock losses (Rust et al. 2016). I therefore included a variable gauging the relationship of farmers with their workers. Lastly, I expected that farmers who perceived a higher prevalence of poison-use in their community were more likely to use poison themselves because of the false consensus effect, whereby people are likely to overestimate the prevalence of a behaviour that they participate in (Deutsch 1989). All variables were used as continuous variables except for education level and the main cause of livestock losses which were added as categorical variables with two levels (tertiary education/no tertiary education, predators / other).

Poisoning probability estimates were derived for each respondent and interpolated using Inverse Distance Weighting to show the spatial prevalence of poison-use across South Africa, following Santangeli et al. (2016b) and Craig et al. (2018).

Results

Respondent characteristics, farming context and farmer attitudes

Of all 1411 people approached 65% indicated that they were livestock farmers and 90% (n = 823) of them participated in the study, nine were excluded because they did not fit the criteria of commercial livestock farmers. Of the 814 respondents that participated, 98% were male, largely Afrikaans (78%), followed by English (12%), the rest were of other less represented groups (Appendix 4.1). Respondent age was 50 on average (±14 standard deviation), with 58% having tertiary education.

Respondents largely (76%) were full time farmers, and 52% earned over 60% of their income from livestock farming. Average farm size was 2773 ha with a mean of 1080 livestock, largely cattle (81%), followed by sheep (56%), goats (16%), game (15%), pigs (3%), chickens (2%) and lastly horses and donkeys (1%). Of the commonly farmed animals, game was the most predated, with an average of 6.7% of stocks being lost to predators, followed by sheep (4.4% of stocks), goats (2.7% of stocks) and cattle (0.5% of stocks). Overall mean predation rate was higher for small stock (sheep and goats; 4.1%) than large stock (cattle, game, horses and donkeys; 3.7%).

Farmers generally reported a positive relationship with their farmworkers (94%), favoured game on their farms (87%) but disliked predators (58%, Appendix 4.8). Attitudes towards vultures were broadly positive, 84% of respondents wanted vultures on their farm and only 6% of respondents believed that vultures kill livestock (Appendix 4.8). Although most respondents

(57%) agreed that vultures do not spread disease, many (31%) had no opinion on this issue (Appendix 4.8).

Prevalence and correlates of poison-use.

Poison-use prevalence across the whole sample of 814 respondents was 21.9% (95% CI: 11.6-32.2%) with reference to the one-year period, and 30.8% (95% CI: 19.7-41.8%) with reference to the five years period. Few respondents (6.6%) admitted directly to using poison. The most common poisons used were pesticides, specifically aldicarb (Appendix 4.9). Farmers' estimate of poison-use by their neighbours (direct question) was 13.5% on average (95% CI: 12.0-15.0%).

Model results indicated that various factors were associated with poison-use (Figure 4.1, Appendix 4.10 and 4.11). Poison-use was highest for farmers who perceived this practice to be common among neighbours, for farmers with a positive attitude towards vultures and those who own larger numbers of small stock (Figure 4.2). Other factors positively related to poison-use were farmer age, proportion of livestock predated and negative attitude to predators. Poison-use was also lower in areas where vultures were seen more frequently (Figure 4.1).

Spatial distribution of poison-use

Predicted poison-use was highest in the Eastern Cape, central Free State and the eastern section of the Northern Cape and was lowest in the northern half of the country (Figure 4.3, Appendix 4.12). While poisoning prevalence patterns in space are broadly consistent for the one and five-year periods, poison-use was much more widespread when assessed over a five-year period. Farmer perceptions of poisoning prevalence were generally lower than predicted by my model but similar in spatial distribution (Appendix 4.13).

Perceptions of alternative predator control methods

Three of four respondents (73.6%) believed infrastructures, such as fences and enclosures, are most effective in reducing livestock depredation (Figure 4.4). Lethal control, guarding animals and removing problem individuals were also regarded as effective by half of respondents, while other methods where broadly considered as less effective (Figure 4.4).

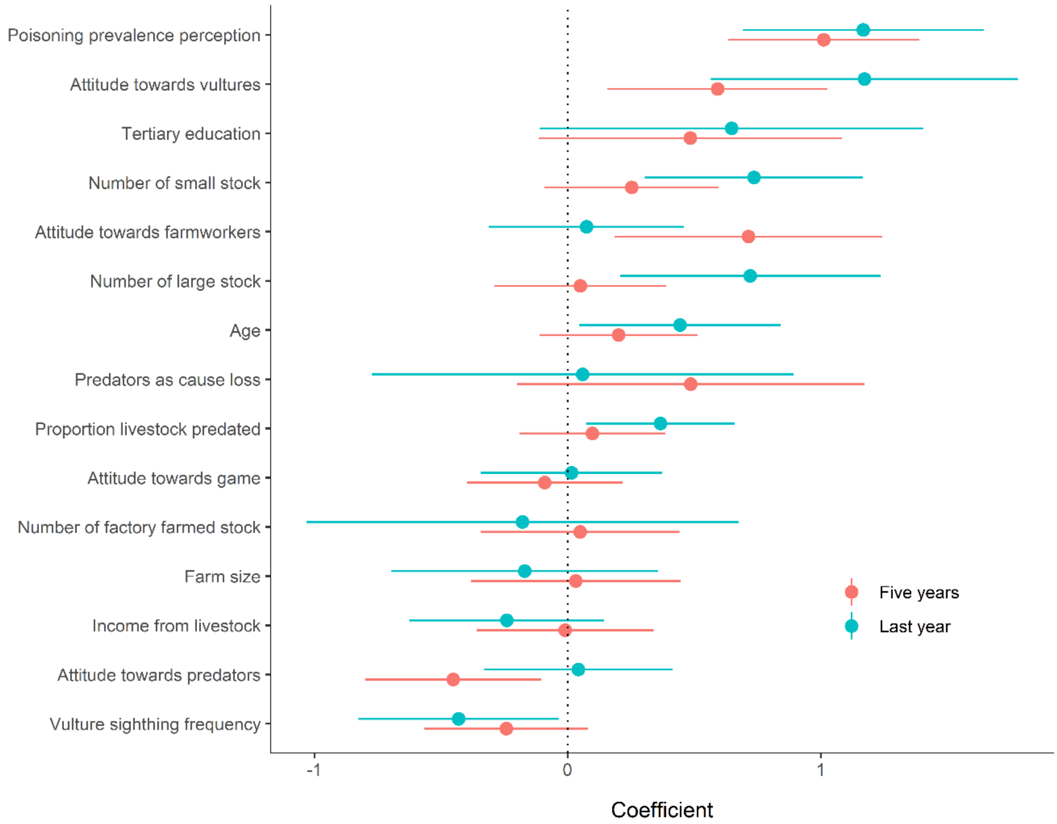


Figure 4.1: Factors associated to the use of poison by South African commercial livestock farmers over a one-year (blue) and five-year period (red) in the present study. Variable coefficients (dots) and standard error (lines) are derived from multivariate regression models using a non-linear least squares estimator.

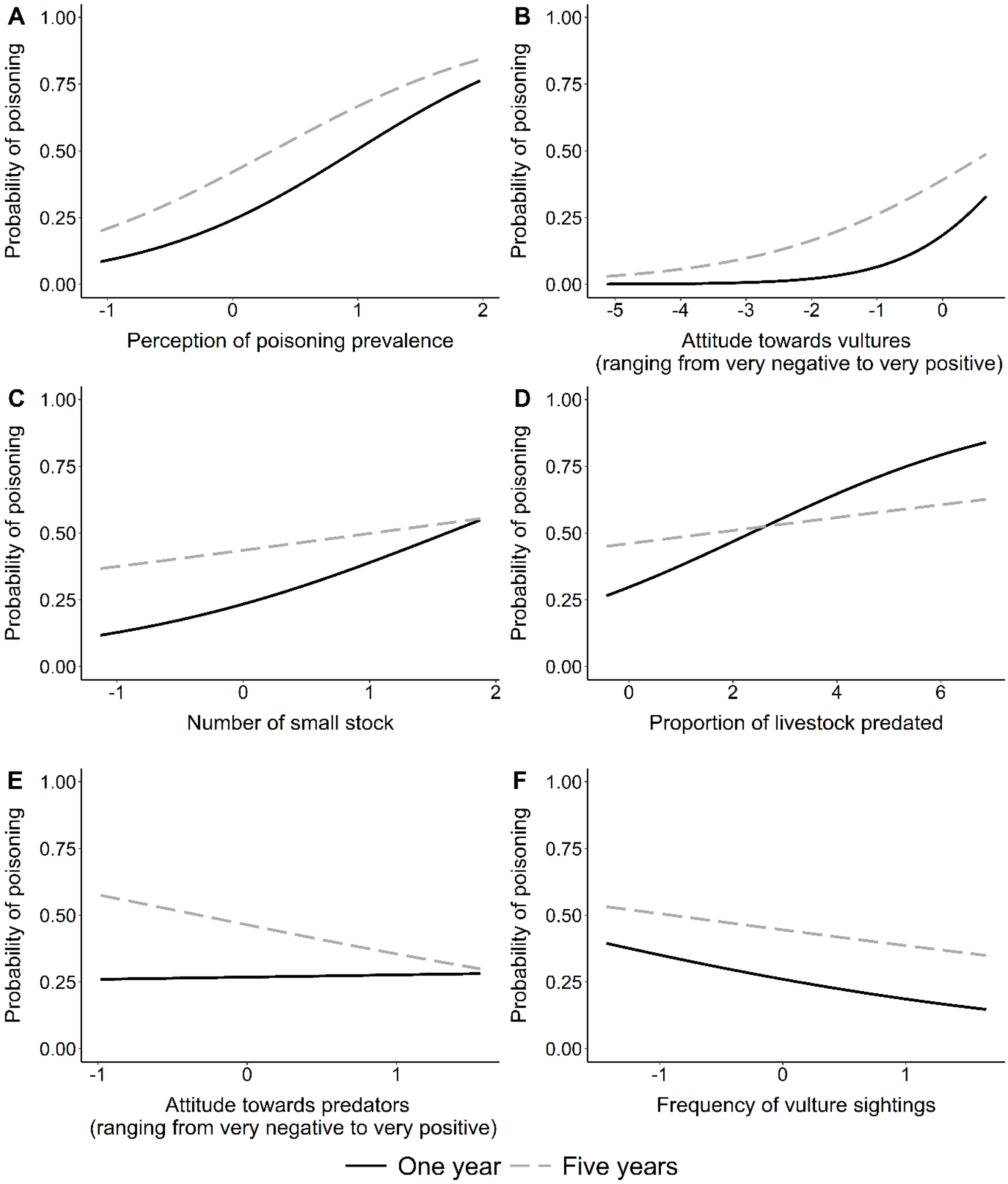


Figure 4.2: Partial dependence effects plots showing the association of different factors (x-axis) to the probability of poison-use among South African commercial livestock farmers over a one-year (solid line) and a five-year period (dashed line) in the present study. All variables have been logged and scaled. Variable effects displayed include farmer perceptions of the prevalence of poisoning under their neighbours (A), attitudes towards vultures (B), number of small stock (C), proportion of livestock predated (D), attitude towards predators (E) and frequency of vulture sightings (F).

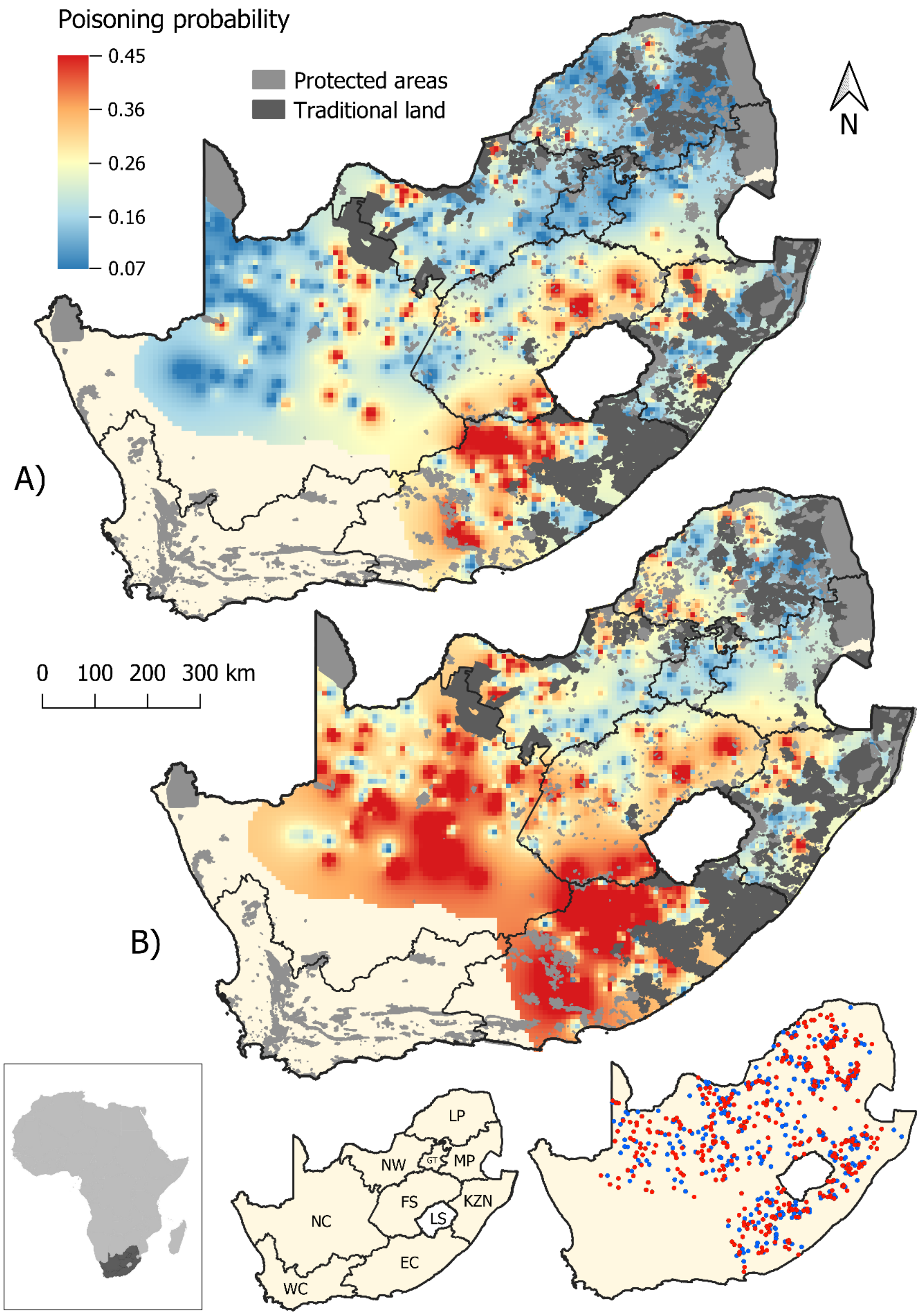


Figure 4.3: Interpolated predicted probabilities of poison-use over A) a one-year period, and B) a five-year period, from a multivariate regression analysis of a list experiment involving South African commercial livestock farmers. Poisoning probability is indicated by the colour shading, while protected areas and land under traditional authority (communal farmland) are in grey. Distribution of sampling points (bottom right map) is indicated for both the treatment (red dots) and control group (blue dots). South African provinces are denoted (bottom centre) as WC = Western Cape, NC = Northern Cape, NW = North West, LP = Limpopo, MP = Mpumalanga, GT = Gauteng, FS = Free State, KZN = KwaZulu-Natal, and EC = Eastern Cape (LS indicates the country Lesotho). To assist visualisation and interpretation the colour ramp was scaled to include 2%-98% of the data values.

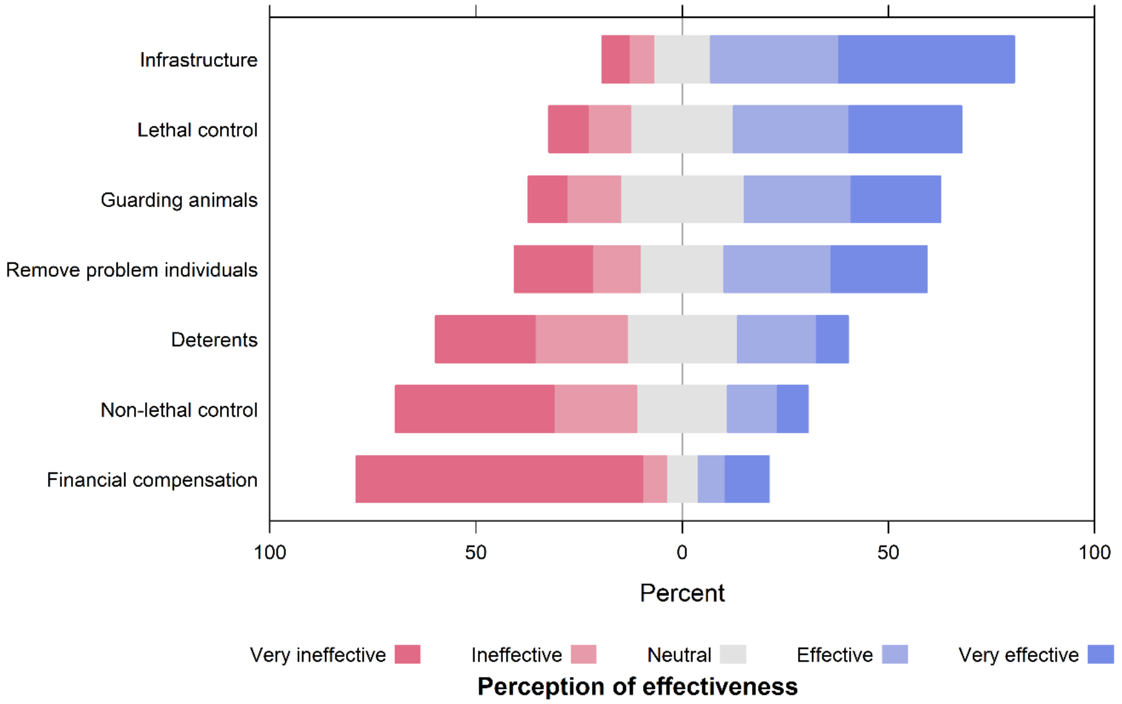


Figure 4.42: Farmer perceptions of the effectiveness of various livestock depredation avoidance methods. The percentage of farmers listing each method on a Likert scale varying from very ineffective to very effective is indicated.

Discussion

Here I use a specialised survey technique to characterise, quantify and map poison-use by commercial farmers across South Africa. I found that more than one in five farmers used poison over a one-year period and almost a third of farmers in a five-year period. This practice was positively associated with small stock farming and with the social environment, i.e., higher poison-use prevalence among neighbours favours this practice at the individual level. Poison-use was negatively associated with the presence of vultures. The continued widespread belief in the effectiveness of lethal control methods, over alternative livestock predation avoidance methods, likely contributes to the continued prevalence of poison-use in predator control.

Poison-use prevalence

Although poison-use has likely declined in the past thirty years, it remains a relatively common practice (Nattrass and Conradie 2018). Interestingly, my five-year estimate was very similar to the 34% poisoning prevalence recorded around 1988 among farmers in the southern and central

Drakensberg region (Brown and Piper 1988). This estimate, however, originates from a mail survey which used direct questioning and therefore likely underestimated poison-use. Poison-use seems to have shifted away from strychnine, used by 54% of poison users in the Brown and Piper (1988) study, and was only mentioned by a single self-proclaimed poison user in my study. Although few respondents indicated which poisons they used, more readily available pesticides such as carbamates were mentioned most in the present study (Appendix 4.9). Over a one-year period my poisoning prevalence estimate (22%) was very similar to the 20% poisoning prevalence recorded for Namibian commercial farmers using a similar questioning technique (Santangeli et al. 2016b).

The additional 10% increase in poisoning prevalence between my one-year and five-year estimates highlights the importance of incorporating longer time scales in such surveys. Poison-use is reactionary and if the specific conditions, such as a particularly problematic predator, were not present in the immediate past, then poisoning is unlikely to be recorded. Thus, this longer time scale may provide a more accurate representation of the spatial distribution of the threat of poison in the landscape.

Correlates of poison-use

Of the factors associated with poison-use, farmers perceptions of the prevalence of poison-use in their community was the strongest predictor. Farmers may thus be more likely to use poison if they believe the practice to be locally common. Alternatively, farmers that use poison may overestimate the number of their peers that use poison as a self-justification for their own behaviour (Deutsch 1989).

In my study, as in similar studies (Brown and Piper 1988; Santangeli et al. 2016b), small stock farming was more closely associated with poison-use than other types of livestock farming. Small stock, because of their size, are more prone to predation by medium sized and widespread predators (e.g., black-backed jackal, Canis mesomelas, and caracal, Caracal caracal), which are responsible for the majority of livestock losses in South Africa (Van Niekerk 2010). My results also provide evidence that poison-use increases with the proportion of livestock that is predated and a negative attitude towards predators. This suggests that the intensity of human-carnivore conflict triggers the use of poison.

The relationship between a positive attitude towards vultures and poisoning is counter intuitive. One explanation for this may be that farmers who use poison may try to compensate for their detrimental behaviour by showing a positive attitude towards vultures. Interestingly, as for Namibian commercial farmers (Santangeli et al. 2016b), farmers listed a range of measures they use to avoid mortalities in non-target species when using poison. These include using poison at night only, with small parcels of meat, and placed in strategic locations which are perceived to be less accessible to non-target species. These measures are still associated with high risks to non-target species (Santangeli and Arkumarev, pers. comm.).

Older farmers were more likely to use poison. This finding may be explained by younger generations being more environmentally conscious (Pérez Urdiales et al. 2016) or because older farmers, as some have indicated, are no longer able, or keen, to implement more labour-intensive means of predator control, such as shooting, thus reverting to poison-use.

Farmers who frequently observe vultures on their farms are less likely to use poison, likely because they are aware of its potential impacts on vultures. However, this result may also underscore a potential risk to vultures in areas where they are rarer and where farmers may feel a false sense of complacency for using poison.

Spatial distribution of poisoning

Predicted poisoning prevalence was highest in the southern parts of South Africa where small stock farming is most common (Van Niekerk, 2010). Because of this spatial pattern, the species at highest risk to poisoning are the Critically Endangered white-backed vulture, the Endangered lappet-faced and Cape vulture, and the only extant bearded vulture population of southern Africa (SABAP2 2007). Additionally, the high poison-use in the Eastern Cape represents an important threat for a planned bearded vulture reintroduction, two sites in this region have recently been identified as candidates for this reintroduction (Chapter 3).

Poisoning and attitudes to alternative predator control

There was widespread support among farmers for the effectiveness of fences, enclosures and other infrastructures in keeping animals safe from depredation. Denying predators access to livestock would present a simple solution for this human-wildlife conflict. Unfortunately, the large financial investment required to implement this measure effectively makes it unattainable for many farmers (Landman 2016).

Among other means of predator control, lethal methods are still perceived to be more effective than non-lethal ones. This perception likely supported the persistence of poison-use as reported in this study. Encouragingly, half of the farmers supported a problem individual approach rather than an indiscriminate one, likely stemming from the shift from the "vermin" or "pest species" mentality towards the idea that specific individuals disproportionately cause depredation (Linnell et al. 2008; Swan et al. 2017). There is evidence that, at least in some cases, selective predator management strategies can be effective (Swan et al. 2017). When successful, this strategy promotes co-existence between livestock farmers and individual predators which are perceived as non-problematic or even beneficial. Given that indiscriminate persecution of certain species is currently the norm in South Africa, the adoption of this strategy may reduce poison-use, which is incompatible with this approach.

Non-lethal predator control methods, such as translocation, did not carry much favour among farmers. Translocation of problem animals has not been very successful in the past (Linnell et al. 1997), which may explain the farmers' scepticism for this method. Guarding animals (Marker et al. 2005; Rust et al. 2013) and deterrents (Miller et al. 2016b) have been shown to effectively reduce livestock predation. However, these means require expertise, financial resources, and are logistically challenging, factors adding to the risk of failure (Rust et al. 2013).

Financial compensation when administered appropriately can be an effective measure for reducing retaliatory killings of predators (Miller et al. 2016a) but fails when administered ineffectively (Karanth et al. 2012) because of resulting growing intolerance in uncompensated livestock owners (Karanth et al. 2013). The latter is broadly the case in South Africa and may strongly explain the lack of faith in compensation schemes by the farmers.

Conservation solutions and behaviour change

The vast majority of interviewed farmers of this study had positive attitudes towards vultures. South African farmers, as also those from Namibia, in general seem to have an appreciation for the cleaning services provided by vultures and many make use of them for carcass disposal (Santangeli et al. 2016b; Chapter 3). Conservation work with these farmers may thus yield positive outcomes, i.e., aid the reduction of poison-use, by increasing their awareness of vultures' declines stemming from poisoning, and by suggesting alternative predator control means.

Among those farmers who use poison, many perceived they could do it in a responsible and selective way. It is thus important to make those farmers aware of the high potential risks that poison-use entails for any species in the surrounding landscape (humans, pets and livestock included), irrespective of the way it is used. This could be done by running awareness campaigns particularly in those areas of the southern half of South Africa which I identified as having a high prevalence of farmers using poison.

It is important for conservation initiatives to work directly with agencies trusted by farmers, such as farmer associations, and disseminate the required information through these channels. There is currently a large degree of distrust between farmers and conservation agencies in South Africa. Thus, a possible channel to work with farmers on issues related to poison-use could be through trusted bodies that are close to farmers interests, such as farmers associations and support bodies. This approach proved to be beneficial in conflicting situations between landowners and nature conservation (Santangeli et al. 2012).

Conclusions

An understanding of the motivations and perceptions leading to environmentally destructive behaviours is still largely lacking. Economic gain is often understood as the only relevant component and leverage points for behavioural change therefore remain undiscovered. This is particularly salient in the context of this study, which suggests that farmers who use poison may in general have a positive disposition to vultures and likely lack awareness of, or underestimate, the risks associated with their behaviour. For commercial farmland to become viable vulture habitat, guidance from conservationists may be needed, but a bottom-up approach with farmers as key stakeholders is a necessity (Redpath et al. 2013). Any campaign aiming to address poison-use prevalence should incorporate the environmental sensibilities uncovered in this study. Central to such a campaign would be convincing farmers of the risks that this behaviour, in all its forms, poses to highly endangered avian scavengers, the potential effectiveness of alternative methods if correctly applied and the potential ecosystem disruptions caused by the loss of vultures.

My study suggests that the presence of vultures represent a strong deterrent for farmers to minimise the use of poison. If vultures are lost, there may be no constraint for farmers in using poisons, with catastrophic consequences on a wealth of other scavenger and non-scavenger species. This may ultimately compromise the ecosystem balance to the detriment of wildlife and humans alike (Markandya et al. 2008).

Appendix 4

Appendix 4.1: Questionnaire for list experiment with livestock farmers

2018 Farming Practices Survey - University of Cape Town A3

Survey code:_____________________________ LC: ______________________

Thank you for taking the time to participate, this questionnaire is anonymous and none of the answers of any respondent will be connected to that respondent. Please answer all questions as far possible.

1. **Farm area and province:** ____

2. **Farm coordinates:** ____

NB! IF NOT AVAILABLE PLEASE INDICATE YOUR FARM LOCATION ON THE MAP TO THE RESEARCHER.

3. **What type of farmer are you?** *[Circle answer]*

Subsistence farmer / Small-scale farmer / Commercial farmer

4. **Are you a full-time farmer?** *[Circle answer]* Yes / No

If no, what is your other profession? ________________________

5. **What is your age?** ________

6. **What is your ethnic group?** *[Circle where applicable]*

Afrikaans, English, Zulu, Xhosa, Ndebele, Northern Sotho, Sesotho, Venda , Tswana, Tsonga, Swati, Cape coloured, Other ___

7. **Level of education** [*Tick applicable answer*]

primary school__
high school__
tertiary education__
no formal education__

8. **What is the % of your income coming from livestock / wildlife farming only?** [*Please tick only one*]

less than 10% __
between 10 and 20% __
between 20 and 40% __
between 40 and 60% __
between 60 and 80% __
between 80 and 90% __
more than 90% __

9. **Approximately how many hectares of land are you farming on?**___________________Ha

10. Please refer to the list of farming practices below. During the last 12 months, how many out

of these five practices were active/used on your farm? [*Please count each method only once, regardless of how many times the method was applied*]

____________________ out of the 5

11. Including those used in the last 12 months, how many of these methods were used on your farm during the last 5 years? [*Please count each method only once*]

____________________ out of the 5

Infrastructure
(eg. Any form of fencing,
a kraal or enclosures)

Killing predators with poison

Hunting predators
(eg. shooting jackal & lynx,
cage traps)

Flock guarding animals
(bv. Anatolian dog,
donkey, emu)

Protective collars
(non electronic,
physical protection only)

12. What is the largest cause of cattle / game deaths over the past 12 months:
[Please select only one]

Drought	Disease	Injury	Poisonous plants
Stolen	Lost	Unknown	Snake bites
Predator	Stillborn	Fell down hole	Other:

12b. What is the second most common cause of cattle / game deaths over the past 12 months:
[Please select only one]

Drought	Disease	Injury	Poisonous plants
Stolen	Lost	Unknown	Snake bites
Predator	Stillborn	Fell down hole	Other:

13.

Livestock on farm (eg. cattle, game)	**Number on farm**	**Number lost (last 12 months)**	**Approximate cost of losses**	**Number lost to predators**	**Compensation (Yes/No)**

14. Please rate the following statements on a scale of whether you agree or disagree with them
-2 is strongly disagree, -1 is somewhat disagree, 0 is neutral, +1 is somewhat agree, and +2 is strongly agree.

i. I get along well with my workers and farmhands -2 -1 0 +1 +2

ii. I like having **game** on my farm -2 -1 0 +1
+2

iii. I would like my farm to have **no predators** on it -2 -1 0 +1 +2

iv. I like having vultures on my farm -2 -1 0 +1 +2

v. Vultures spread disease -2 -1 0 +1
+2

vi. Vultures kill livestock -2 -1 0 +1
+2

15. Vultures are useful to have on my farm because: [tick if applicable to your farm]

They are not useful__
They clean up carcasses__
They are an important part of the ecosystem__
They make me aware of where animals died__
I enjoy seeing them__
They attract tourists__
They prevent disease spread__

16. How often do you see vultures on your farm? [*Please tick only one box*]
Never ___

Less than once per month __
Approximately once a month __
Approximately once a week __
Approximately once a day__

17. Estimate the % of farmers in your community (general surrounding area) that you think have purposefully used poison to kill predators in the last 12 months?

________________%

18. How do you discard carcasses, offal or other forms of unused animal meat on the farm?
[tick all applicable answers]
Burn___
Bury___
Compost___
Leave in the veld for scavengers (in various areas on my farm)___
Leave in the veld for scavengers (in a specific area)___
Vulture restaurant___
Drive to a dump___
Other (please specify):____

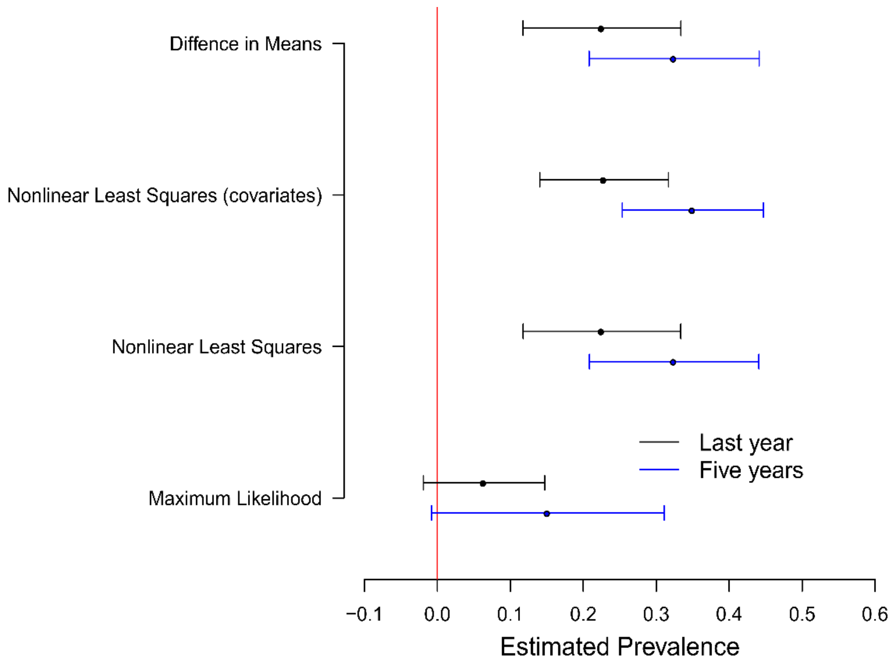
19. If you leave meat for scavengers please provide a rough indication of how many kilograms of meat you have provided over the last 12 months:

____________________ kg

20. In your opinion, how effective do you believe the following stock loss prevention methods are? Please provide a score between 1 and 5, where 1 is very ineffective and 5 is extremely effective *[circle answer]*

i.	Guarding animals (Anatolian dog, donkey, emu etc.)	1	2	3	4	5
ii.	Deterrents and repellents (light, sound)	1	2	3	4	5
iii.	Lethal control of predator numbers (eg. shooting jackal)	1	2	3	4	5
iv.	Non-lethal control (live capture and relocation)	1	2	3	4	5
v.	Removal of identified problem individuals only	1	2	3	4	5
vi.	Infrastructure to keep predators out (fences, enclosures)	1	2	3	4	5
vii.	Financial compensation by state or NGO	1	2	3	4	5

THANK YOU FOR YOUR PATIENCE AND PARTICIPATION



Appendix 4.2: The estimated prevalence of poisoning based on various regression analysis, including the simple difference in means estimator, maximum likelihood and nonlinear least squares regression estimators. The estimated prevalence of poisoning for a nonlinear least squares multivariate regression analysis, indicated with "(covariates)" is also shown.

Appendix 4.3: Estimated proportion of respondent types by the number of affirmative answers to the control and sensitive items in a list experiment on poison use. The table shows the estimated proportion of respondent type p(x, y) where x in p(x, y) indicates the number of affirmative answers to the control items and y indicates whether respondents answer yes, (x, 1), to participating in poisoning.

	One-year period		Five-year period	
	Est.	s.e.	Est.	s.e.
p(0, 1)	-0.007	0.007	-0.007	0.007
p(1, 1)	0.087	0.034	0.078	0.032
p(2, 1)	0.105	0.027	0.184	0.031
p(3, 1)	0.036	0.011	0.065	0.015
p(4, 1)	0.005	0.004	0.005	0.004
p(0, 0)	0.013	0.006	0.013	0.006
p(1, 0)	0.253	0.023	0.215	0.022
p(2, 0)	0.433	0.033	0.365	0.034
p(3, 0)	0.071	0.020	0.076	0.023
p(4, 0)	0.003	0.006	0.006	0.007
Difference in means	0.226	0.055	0.325	0.059

Appendix 4.4: Summary of responses to the number of behaviours they participate in in a list experiment on poison use over a one-year period. Responses for both treatment and control groups are indicated. The table illustrates likely low ceiling and floor effects with few respondents answering either zero or five in the treatment group.

Response	Control (n)	Control (%)	Treatment (n)	Treatment (%)
0	3	0.8	5	1.2
1	130	33.4	107	25.2
2	211	54.2	219	51.5
3	42	10.8	76	17.9
4	3	0.8	16	3.8
5	-	-	2	0.5
TOTAL	389		425	

Appendix 4.5: Summary of responses to the number of behaviours they participate in in a list experiment on poison use over a five-year period. Responses for both treatment and control groups are indicated. The table illustrates likely low ceiling and floor effects with few respondents answering either zero or five in the treatment group.

Response	Control (n)	Control (%)	Treatment (n)	Treatment (%)
0	3	0.8	5	1.2
1	111	28.5	89	21.2
2	215	55.3	187	44.5
3	56	14.4	109	26.0
4	4	1.0	28	6.7
5	-	-	2	0.5
TOTAL	389		420	

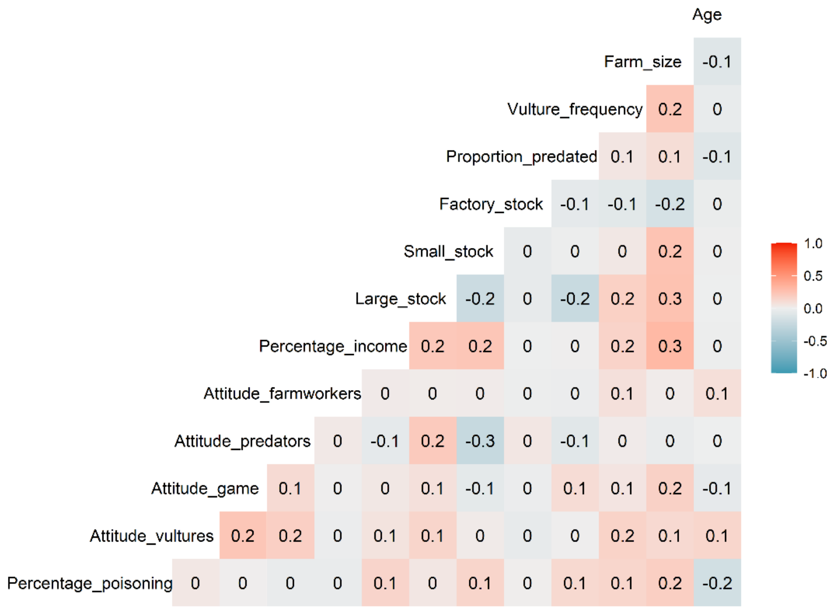
Appendix 4.6: Statistical analysis overview.

Data analyses were performed in R v.3.6.3 (R Core Team 2019), using the "list" package, which was specifically designed for analysing list experiments (Blair and Imai 2010). All analyses as detailed below where run separately using the list data referring to the one-year and the five-year timeframes (i.e. the number of behaviours engaged with during the past one or five years). Overall poisoning prevalence was calculated through a simple difference in means estimate between control and treatment groups using the full sample of farmers. Blair and Imai (2012) provide a modelling framework that performs better than previous multivariate regression analysis approaches used for list experiments (Blair and Imai 2012). Within this framework, two estimators were developed for the regression analysis, a Maximum Likelihood (ML) estimator, which is statistically more efficient, and a Non-linear Least Squares (NLS) estimator which is more robust. The ML model is more sensitive to assumption violations regarding measurement errors which, for example, can arise when a subset of respondents provide answers at random or choose maximal response values regardless of their truthfulness. This can induce severe model misspecification biases for ML models (Blair et al. 2019). We constructed models using both these methods and then tested for misspecification, using a Hausman test and a comparison of poisoning prevalence estimates with a robust base-line difference in means estimate (Appendix 4.3). Results from this test, the comparison, and convergence issues, indicated that ML models suffered from misspecification. A comparison between baseline ML models and NLS models indicated misspecification of the ML model for the one-year data (Hausman statistic = -14.768, df = 2, p-value = 0.001) but could not conclusively be shown for the five-year data (Hausman statistic = -4.857, df = 2, p-value = 0.088). ML models with covariates however did not converge for either the one-year or five-year data. The more robust NLS estimator was therefore preferred for the multivariate regression analysis.

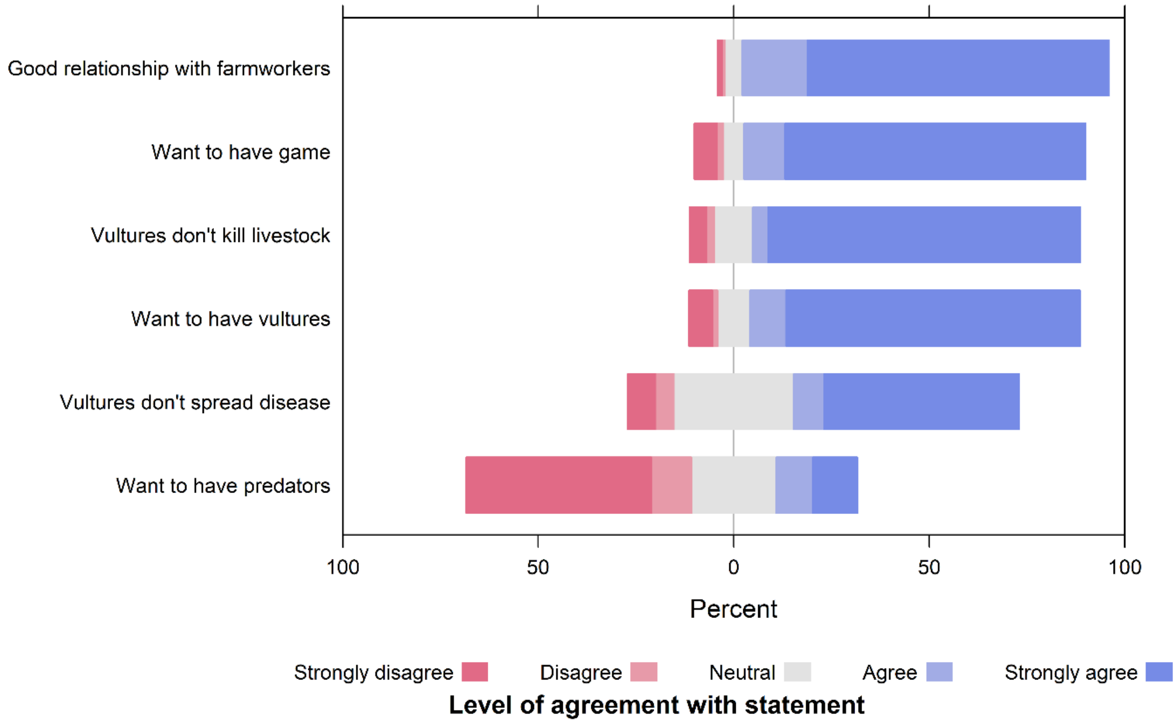
A key assumption of the list experiment is that the addition of the sensitive behaviour in the treatment list does not change the probability of respondent's affirming control items. Before conducting our analyses, we verified that no such design effect was present using the ict.test function (Blair and Imai 2010). We found no evidence for a design effect in our questionnaire in either the one-year (p=0.56) or our five-year (p=0.54) data. Estimated proportions of each response type indicated that poisoning was sufficiently prevalent to be assessed with a list experiment approach (Appendix 4.4). Although we designed our questionnaire to avoid it (see above), we also estimated the ceiling and floor effects in our model. Summaries of responses showed a very low percentage of respondent reporting either zero or four behaviours (Appendix 4.5 and 4.6), the opposite trend would have indicated potential ceiling and floor effects. Quasi-Bayesian approximation estimates of ceiling and floor effects indicate that 0.07% (SE: 0.005%) of respondents avoid honestly indicating five out of five behaviours (ceiling effect) and 0.1% (SE: 0.006%) of respondents falsely gave zero behaviours when poisoning is the only activity they participate in (floor effects). Ceiling and floor effects were consequently ignored. Model assumptions for collinearity were checked and the correlation coefficients of all included numeric variables were below 0.4 (Appendix 4.7).

We constructed two NLS models, one with the number of participated behaviours over a one-year period as the response and the other with the number of participated behaviours over a five-year period as response variables.

Poisoning probability estimates were derived with the predict function, for all respondents who provided the necessary information for inclusion in the multivariate regression modelling (some respondents did not answer all questions). These predicted poisoning probability estimates were interpolated using Inverse Distance Weighting to show the prevalence of poison-use spatially across South Africa, following (Santangeli et al. 2016b; Craig et al. 2018).



Appendix 4.7: Correlation coefficients for numeric variables used in a multivariate regression analysis of poison-use under commercial farmers in South Africa.



Appendix 4.8: Farmer attitudes to farmworkers, game, vultures and predators. The percentage of farmers that who responded with each level of agreement, ranging on a Likert scale from strongly disagree to strongly agree is indicated.

Appendix 4.9: Poisons used by farmers who admitted to poison-use. Poison names are displayed as they were reported by farmers. The unidentified poison refers to a single poison which is only known by the distributor's name, the distributor seems to be a single individual from the Eastern Cape, from where he distributes the poison to other provinces.

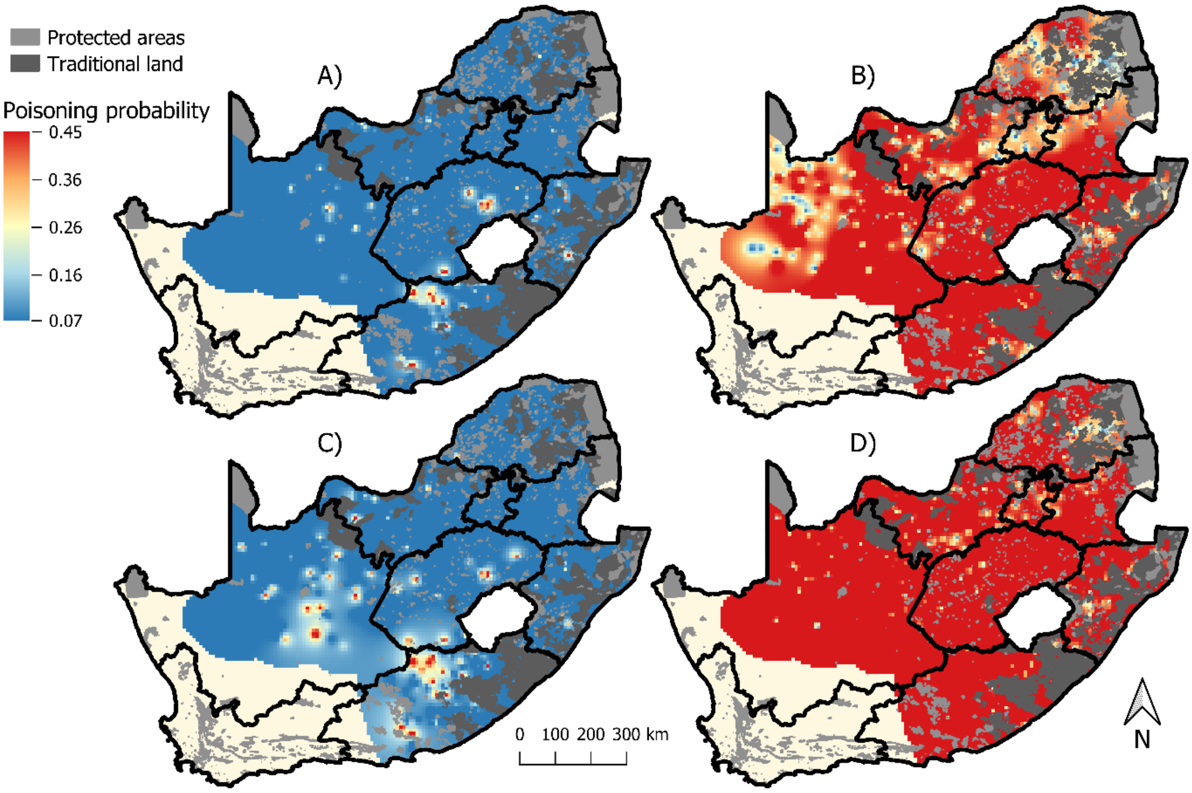
Name	Number	Percentage (%)
Temik/Aldicarb	14	33
Sneuklith Poison	13	30
Insecticide	9	21
1080	3	7
Strychnine	1	2
Xylitol	1	2
Cyanide	1	2
Animal dip	1	2
TOTAL	43	

Appendix 4.10: Results of a multivariate regression analysis of poison-use for predator control over a one-year period, by South African commercial farmers who participated in a list experiment. Model coefficients, standard error (S.E.) and p-values are indicated for both poison-use (the sensitive item) and control items.

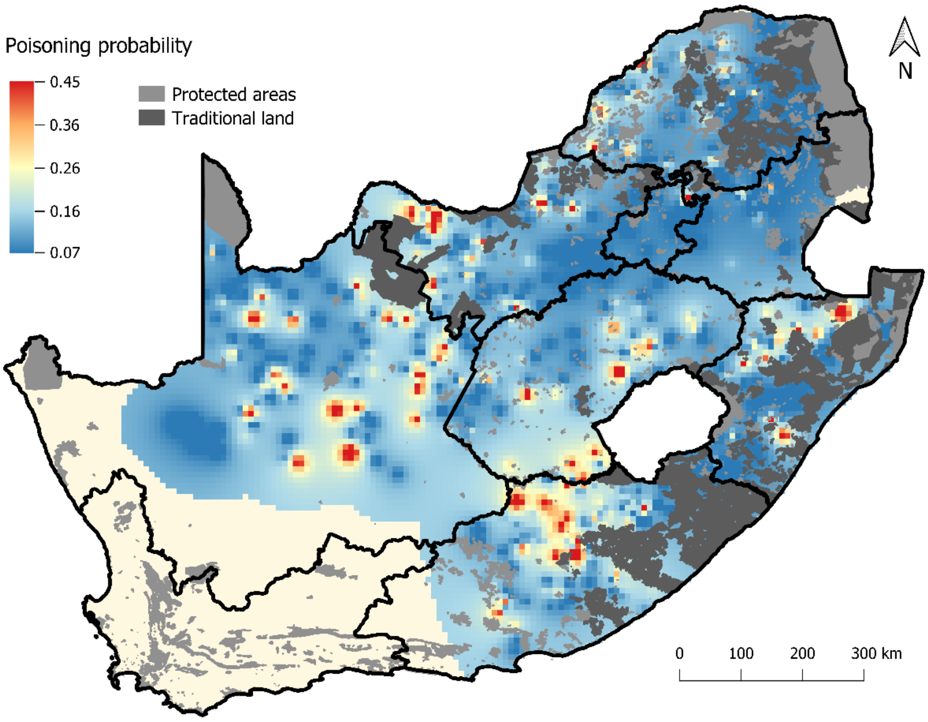
Variable	Sensitive item coefficients	S.E.	p-value	Control item coefficients	S.E.	p-value
(Intercept)	-2.601	0.876	0.003	-0.327	0.061	0.000
Percentage neighbours poisoning	1.168	0.475	0.014	0.063	0.033	0.051
Attitude towards vultures	1.173	0.607	0.054	-0.012	0.041	0.772
Attitude towards game	0.016	0.359	0.965	0.057	0.035	0.101
Attitude towards predators	0.042	0.373	0.910	-0.091	0.038	0.016
Attitude towards farmworkers	0.075	0.385	0.846	-0.022	0.024	0.348
Percentage income from livestock	-0.240	0.385	0.533	0.054	0.037	0.148
Number of large stock	0.722	0.514	0.161	0.037	0.041	0.363
Number of small stock	0.736	0.431	0.088	0.116	0.041	0.005
Number of factory farmed stock	-0.178	0.854	0.835	0.041	0.069	0.550
Proportion livestock predated	0.367	0.294	0.213	0.022	0.032	0.481
Main cause of livestock loss	0.059	0.832	0.943	0.287	0.079	0.000
Vulture sighting frequency	-0.430	0.395	0.277	-0.003	0.038	0.927
Farm size	-0.170	0.526	0.747	0.065	0.041	0.108
Age	0.444	0.397	0.264	-0.055	0.033	0.097
Tertiary education	0.648	0.757	0.393	-0.037	0.067	0.580

Appendix 4.11: Results of a multivariate regression analysis of poison-use for predator control over a five-year period, by South African commercial farmers who participated in a list experiment. Model coefficients, standard error (S.E.) and p-values are indicated for both poison-use (the sensitive item) and control items.

Variable	Sensitive item coefficients	S.E.	p-value	Control item coefficients	S.E.	p-value
(Intercept)	-1.810	0.686	0.009	-0.233	0.063	0.000
Percentage neighbours poisoning	1.012	0.377	0.007	0.041	0.033	0.222
Attitude towards vultures	0.593	0.435	0.173	-0.003	0.041	0.935
Attitude towards game	-0.091	0.307	0.768	0.076	0.035	0.032
Attitude towards predators	-0.453	0.348	0.193	-0.054	0.040	0.175
Attitude towards farmworkers	0.715	0.528	0.176	-0.042	0.026	0.105
Percentage income from livestock	-0.010	0.350	0.977	0.073	0.042	0.081
Number of large stock	0.050	0.340	0.882	0.056	0.044	0.203
Number of small stock	0.253	0.344	0.462	0.178	0.042	0.000
Number of factory farmed stock	0.050	0.393	0.900	0.020	0.064	0.755
Proportion livestock predated	0.098	0.289	0.734	0.026	0.033	0.432
Main cause of livestock loss	0.486	0.686	0.479	0.212	0.080	0.009
Vulture sighting frequency	-0.243	0.323	0.453	0.028	0.038	0.456
Farm size	0.032	0.413	0.938	0.029	0.044	0.506
Age	0.202	0.313	0.519	-0.065	0.034	0.057
Tertiary education	0.485	0.598	0.418	0.007	0.067	0.921



Appendix 4.12: Interpolated lower (A and C) and upper (B and D) limits of the predicted probabilities of using poison for predator control over a one-year period (A and B), and a five-year period (C and D), from a multivariate regression analysis of a list experiment in which South African commercial livestock farmers took part. Poisoning probability (colour shading) protected areas (light grey shading) and land under traditional authority, or communal farmland (dark grey shading) is indicated.



Appendix 4.13: Interpolated South African commercial farmer perceptions of the prevalence of poison-use for predator control under their neighbours. Estimated proportion of farmers using poison (colour shading), protected area (light grey shading) and land under traditional authority, or communal farmland (dark grey shading), is indicated.

CHAPTER 5:

Relationship between supplementary feeding and breeding success in Cape Vultures, *Gyps coprotheres*

Photo: White-wash from a Cape Vulture colony stains a distant cliff face (Photo by C.W. Brink).

Abstract

Supplementary feeding has become a popular, yet still debated, conservation tool to mitigate Old World vulture declines. This intervention is proposed to support vulture numbers by increasing various demographic parameters, but such effects have seldom been verified. I used monitoring data on ten South African Cape Vulture colonies spanning over two decades, to model the relationship between supplementary feeding sites within a 100 or 200 km radius and breeding success. I found that the amount of food provided annually at SFS surrounding a colony was weakly positively associated with breeding success, but these results were not significant. An index of the proximity of SFS within a given radius to vulture colonies was negatively associated with breeding success but this also was not significant. I found no evidence that the potential amount of lead contaminated food provided at SFS, nor the average prevalence of poisoning in the area, was associated with local breeding success. These results suggest that this conservation measure may currently be overvalued, with regards to its ability to enhance breeding success, in the South African conservation community. To ensure that conservation resources are not misspent the effect of SFS on other parameters need to be evaluated and the net benefit to vultures shown.

Introduction

Old World vulture populations have declined dramatically over the last three decades, and they are now the most threatened group of raptors and avian functional guild (McClure et al., 2018). Over 80% of vulture populations are declining (McClure et al., 2018), some at rates of up to 97% over three generations (Ogada et al., 2016). Following the catastrophic declines of vultures in South Asia due to the widespread use of an anti-inflammatory veterinary drug that is toxic to vultures (Oaks et al., 2004), Africa has followed suite with a continent-wide vulture crisis (Ogada et al., 2016). Of the eleven species found on the continent, two are Near Threatened, three are Endangered and four are Critically Endangered (IUCN, 2021). The loss of the carcass removal ecosystem service that vultures provide can have severe consequences for ecosystems and human wellbeing (Markandya et al., 2008). Without vultures, decomposition rates increase and mammalian scavengers proliferate (Ogada et al., 2012a). This can result in increased disease transmission between mammalian scavengers and result in a surge in human infections, resulting in both loss of life and severe economic costs (Markandya et al., 2008). Given all these effects protecting vultures should be a conservation priority.

Long generation times and slow breeding rates make most raptor populations vulnerable to the increased mortality rates caused by various anthropogenic activities, but vultures are especially susceptible (McClure et al., 2018). Their obligate scavenging behaviour makes them exceptionally vulnerable to poisoning, which accounts for more than 60% of recorded vultures found dead in Africa (Ogada et al., 2016). Although poisoning of vultures often occurs unintentionally when farmers put out poison for other damage causing animals (Ogada et al., 2012b), there has recently been a sharp increase in deliberate poisoning by poachers, who either aim to stop vultures from providing a sentinel role to nature protection authorities (Gore et al., 2020) or to harvest vultures for belief-based use (Henriques et al., 2020). Recent research is also highlighting the threat of lead (Pb) poisoning through the ingestion of carcasses containing spent ammunition (Garbett et al., 2018; Krüger and Amar, 2018; van den Heever et al., 2019). Other notable drivers of these declines include mortalities caused by power grid infrastructure (electrocutions and collisions), habitat loss and human disturbance (Botha et al., 2017), and the growing threat of collisions with wind energy (Reid et al., 2015), but food safety is generally viewed as being of the highest concern.

A reduction in food availability has also been suggested to accelerate vulture declines (Botha et al., 2017; Krüger et al., 2015). Large-scale agriculture intensification has occurred throughout Africa with livestock largely replacing wild ungulates, the natural food source of vultures (Hempson et al., 2017). This situation may lead to fewer carcasses available to vultures through reduced mortalities of ungulates due to better animal husbandry practices (Mundy et al., 1992); carcass disposal practices such as burying or burning carcasses (Margalida and Colomer, 2012); and increased competition with other scavengers that are associated with anthropogenic landscapes (Kushwaha et al., 2020). Despite a lack of data, a panel of conservationists and scientists overwhelmingly highlighted the decrease in the amount of carrion as the highest priority for conservation action to address Cape Vulture, *Gyps coprotheres*, declines in southern Africa in the mid-2000's (Boshoff and Anderson, 2006). Given such assertions, it is perhaps unsurprising that supplementary feeding has increasingly become a favoured conservation intervention for supporting declining vulture populations globally (Chapter 2; Gilbert et al., 2007; Oro et al., 2008). In South Africa alone there are currently at least 143 active vulture supplementary feeding sites (SFS) supplying a combined total of 3301 tonnes of meat annually (Chapter 2). These SFS are proposed to increase survival rates and breeding success, either through providing food to resource limited populations or by buffering vultures against the threat of unsafe food sources in the environment (Gilbert et al., 2007; Margalida et al., 2014).

There is some evidence that SFS can have beneficial effects. For example, Schabo et al. (2017) found a significant positive effect of supplementary food provided at a nearby SFS during the nest-building phase on the numbers of breeding pairs at a single Cape Vulture colony. Gilbert et al. (2007), suggested that SFS reduced mortality rates of Oriental white-backed Vultures, *Gyps bengalensis* by changing the ranging behaviour and thus exposure to carcasses contaminated by lethal veterinary drugs. Another study only found a positive effect on survival for pre-adult birds, suggesting that while SFS may support a large floater surplus, they fail to reduce poisoning risk among adults (Oro et al., 2008). Krüger et al. (2015) found an indication that proximity to SFS influenced the probability of Bearded Vultures territories remaining occupied, but only in one of their study regions. Given these positive indications, conservation organisations have often motivated livestock owners to establish SFS without consideration of the scientific evidence regarding the suitability of the practice (Cortés-Avizanda et al., 2016). Such dogmatic adoption of a conservation measure may overlook potential trade-offs associated with SFS that need careful consideration before this measure is adopted (Ewen et al., 2015). The indicated benefits to immature birds may, for example, lead to aggregations of non-breeding birds that can cause a reduction in productivity of nearby breeding birds (Carrete et al., 2006b). Additionally, positive effects of SFS are not ubiquitous. In the Balkan Peninsula food shortages were not limiting population trends as was originally assumed (Dobrev et al., 2016) and SFS did not affect productivity or survival (Oppel et al., 2016a). In this case SFS represented a waste of conservation resources. The fact that such results have led to discontentment from supporters of SFS is perhaps an early warning signal that the merits of the application of supplementary feeding may not always be assessed in an unbiased manner (Oppel et al., 2016b). The application of SFS can also lead to unexpected expose vultures to additional threats. In South Africa, a national survey with SFS managers showed that many SFS managers were unaware of the importance of screening carcasses for veterinary drugs, which caused the Asian vulture crisis, or Pb (Chapter 2). The physiological effects of Pb are well documented and affect normal nervous-system functioning, leading to health deterioration, behavioural change and mortality (Haig et al., 2014; Pokras and Kneeland, 2008). Pb contamination at an SFS could therefore likely affect the fitness of breeding adults, including their ability to effectively raise young and thereby result in reducedbreeding success. The low awareness under SFS managers of such factors are worrisome, especially so given that SFS provide more than 80% of the potential food requirements of the entire vulture population in this region (Chapter 2).

The predictability of food provided by SFS may also negatively affect vulture behaviour and foraging ecology. While Kane et al. (2016) concluded that SFS do not significantly influence the foraging movements of Cape Vultures, their results perhaps contradict this in that, besides roosting sites, SFS were the most important explanatory variable in their habitat selection models. Similarly, Reid et al. (2015) found that habitat selection by non-adult Bearded Vultures was influenced by SFS, but not so for adults. Fluhr et al. (2017) suggest that SFS with high provisioning rates may promote routine behaviours in vulture foraging. Gilbert et al. (2007) found that SFS reduced home-ranges, time in flight and daily distance travelled.

The research thus far conducted, suggests uncertainties on the effects of SFS on vultures. However, such studies are low in numbers, spatial and taxonomic breadth compared to the widespread use of SFS as a tool for vulture conservation. There is, therefore, an urgent need for studies aimed at quantifying the effects of this conservation tool on vulture fitness. This is particularly the case in South Africa, which has a long tradition of applying this conservation measure (Chapter 2). A major factor hindering such investigations thus far has been the availability of systematic and large-scale data on SFS locations and their provisioning. Here, for the first time, I make use of a recently compiled high resolution and up-to-date database on SFS, including the amounts of food and potential Pb contamination of this food provided at individual sites, across the whole of South Africa (Chapter 2), a hotspot for global vulture conservation (Santangeli et al., 2019). Additionally, I make use of another recently compiled spatial assessment on the predicted poisoning prevalence amongst commercial farmers in South Africa (Chapter 4). I combine the above databases with breeding success at ten Cape Vulture colonies monitored over more than two decades across their national distribution in South Africa. I aim to assess 1) the relationship between breeding success at the colony level and the amount of food provided at nearby SFS, 2) whether SFS in closer proximity to vulture colonies are more beneficial, 3) whether poor management practice of not screening carcasses for Pb-contamination may have negative effects on vulture breeding success, 4) whether estimated poisoning prevalence by commercial farmers in the vicinity of colonies may have negative effects on vulture breeding success. I predict that higher provisioning rates and the proximity of SFS to colonies will increase breeding success and that both higher potential poisoning prevalence and higher potential amounts of Pb contaminated food provisioning will decrease breeding success.

Methods

Study species

The Cape Vulture is a gregarious cliff-nesting raptor which is endemic to southern Africa. They lay a single egg which is incubated for approximately 57 days, followed by a nestling phase of about 140 days before fledging (Mundy et al., 1992). The average lay date varies between early May to the latter half of June depending on colony location and local rainfall seasonality (Mundy et al., 1992). Both South Africa and Lesotho are breeding strongholds for the species which is listed as Endangered on the IUCN Red List (BirdLife International, 2017).

Colony monitoring data

My study was focused on South Africa, where there is the best data on SFS and the most colony monitoring data (Figure 5.1). I sourced data on breeding success from various organisations that monitor Cape Vulture colonies during the breeding season, including the Vulture Programme (VulPro), Oribi Vulture Viewing Hide and Cape Nature. Monitoring protocols between organisations differed slightly. Most colonies were surveyed two to three times during the breeding season. However, the Potberg colony was surveyed monthly. I consequently standardized data from this colony to make it comparable to the survey protocol of the other colonies. To do this I used colony specific average laying dates, extracted from the literature (Mundy et al., 1992). For each colony I calculated the average number of days between its corresponding average laying date and the dates at which initially surveyed, then repeated this calculation for the last survey of the season. Initial surveys were done around 21 (range -19-73) days after the average laying date and the last survey, around 129 (range 73-172) days after the average laying date. I then applied these calculated timeframes to select which monthly surveys of the Potberg colony data to use as the initial and final survey for the calculation of breeding success estimates.

Colony monitoring broadly followed a standardized protocol developed by the Vulture Study Group (Benson et al., 2007). This protocol entailed scanning the vulture colony from a vantage point using telescopic aids and counting the number of breeding pairs and chicks during each survey visit. In general, colonies were first visited in May and June. During this visit any nesting, incubating or copulating behaviour was considered a breeding attempt, including occupation of a ledge by a pair of vultures where there was a suspicion that these birds were using the site as a nest. During later visits the number of chicks, nestlings or fledglings were counted (visually confirmed or inferred from adult behaviour). I assumed that all monitoring data sources followed a similar protocol. The average time between the first survey and the final survey was 108 days (range 46-157, ± 31 SD).

Supplementary Feeding Sites (SFS)

We used a recently compiled national SFS database (Chapter 2) and later augmented with accounts of SFS from a national survey about poison-use by farmers (Chapter 4). Notably, these data included estimates on the rates at which food was provisioned to individual SFS, a critical factor that previous studies using SFS data could not include (Kane et al., 2016; Krüger et al., 2015). As SFS differ drastically in how much food they provide this is essential information when determining the effects of SFS (Chapter 2). Additionally, these data included the establishment and closure dates of each SFS.

To assess the effect of SFS on breeding success I subset the SFS data for each colony so that it only included SFS that were active during the year that corresponds with a given breeding success estimate. Additionally, SFS were subset to only include those that were likely to be used by vultures from the colony in question. Adult Cape Vulture home range estimates range between 14 700 km^2 (radius of 68 km) and 110 181 km^2 (radius of 187 km)(Bamford et al., 2007; Kane et al., 2016; Pfeiffer et al., 2015a). I assessed SFS within two spatial scales from colonies, within a 100km buffer and within a 200 km buffer, which encapsulated either the lower or both lower and upper range estimates mentioned above.

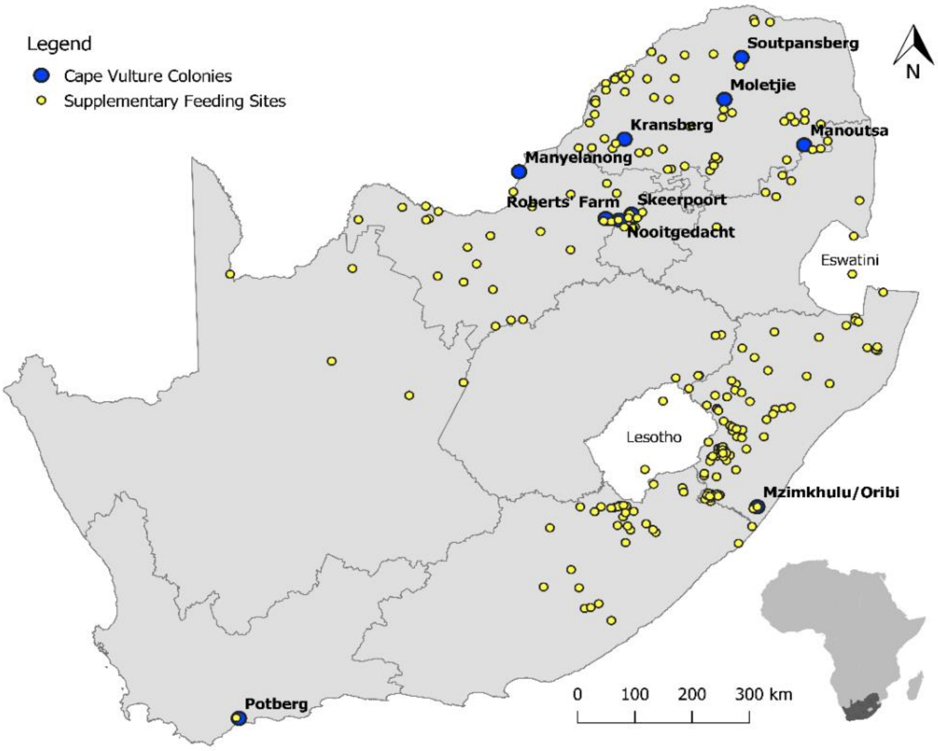


Figure 5.1: Map of South Africa showing the location of the Cape Vulture colonies and all supplementary feeding sites that were active at any point between 2001-2020.

Predictor variables:

Poison data

An average poisoning prevalence was calculated for each buffer centred around each colony. This used data from Chapter 4 which quantified poison-use under commercial livestock farmers using specialised social science methods designed to specifically survey sensitive and illegal behaviours.

Observation period

Observation period was calculated by determining the number of days between the first survey and the last colony survey in each year. Surveys with longer windows provide more opportunities for failure, and thus it is important to control for differences in the survey protocols when modelling breeding success.

Proximity index to supplementary feeding site

We used a proximity index (adapted from Esselstyn et al., 2004) to describe vulture colony proximity to one or more SFS. I assumed that SFS that were closer would be more accessible and therefore have a stronger effect on breeding success. The proximity index was calculated as:

$$PI = \frac{\sum_{i=1}^{n} \left[\left(\frac{1}{d^2} \right) \right]}{s}$$

Where PI = proximity index, d = distance to SFS in kilometres and s = number of SFS within the specific buffer. Initially the above proximity index was weighted by provisioning rate, but as this made no qualitative difference to the results, I decided to disentangle food proximity and quantity in the model and examine the effects of these aspects separately. I reasoned that this is conceptually less confounding and that given the mobility and flight efficiency of vultures all resources within a certain distance could likely be easily accessible.

Provisioning rate

Provisioning rates (kilograms per year) for each SFS were acquired from Chapter 2 and summed for each buffer. Provisioning rate estimates were originally recorded for the year 2018. Because there can be temporal variability in the amount to food provided at SFS due to changes in farming practises and stocking rates, it is likely that these estimates are more accurate for years nearer the time of the survey; and this was explored through the two-time scale models (10 years or 20 years).

Pb contamination risk

I determined the amount of game meat (which would stem from hunting) that was provided at SFS by managers who indicated that they did not believe that Pb from spent ammunition left in carcasses would have any detrimental effects on vultures. Using this criterion, I had a good justification to assume this game meat may contain Pb (Hampton et al., 2018).

Statistical Analysis

To assess the effect of SFS on breeding success, I fitted generalised linear mixed effect models (GLMM) with a binomial error structure using the 'lme4' package (Bates et al., 2015) in R version 3.6.3 (R Core Team, 2020). Breeding success, the response variable, was incorporated into the model in a binomial fashion as the number of successful breeding attempts in relation to the number of failed breeding attempts in any given year for any given colony. The number of successes was determined by the number of fledglings or chicks counted or inferred during the last survey. Failures were calculated by subtracting the successful breeding attempts from the initial survey of active breeding pairs. In some cases, subsequent surveys had higher chick counts than active nests reported in the initial survey. In such cases, I assumed that extra chicks were the result of breeding attempts initiated after the initial surveys. I therefore took this value to be a more accurate indication of the number of pairs and this resulted in breeding success values of 100% in some cases. Unfortunately, I was not granted access to nest site specific data which would have enabled us to calculate breeding success at the individual pair level. Such data would have removed the potential for late breeding attempt to interfere with colony level measure of breeding success. I explored the effect that these 100% estimates on the models by comparing models run with and without this data. Year and colony identity were included as random effects in all models to account for between-year variation in breeding success, and for the pseudo-replication arising from repeated observations of the same colony over time. Covariates included the estimated Poison-use prevalence, Observation period, Proximity index, Provisioning rate and Pb contamination risk, which are described above. Covariates were investigated for collinearity and excluded in models where they were highly correlated (coefficient >0.7). See Appendix 5.1 for the full model equation.

I investigated the effects of SFS at two spatial scales (100 km and 200 km buffers). I used breeding success data for the year 2001 to 2020, but also repeated analysis for a more recent time frame from 2011-2020, which better matched the predictors with regards to their relevance in time.

The basic structure above was used in all models, of which there were two variants. The first was a full model containing all predictor variables, including those that I hypothesized had a negative effect on breeding success (Pb contaminated food provisioning and poisoning prevalence). Unfortunately, no estimates for poisoning prevalence were available for the Potberg colony. Therefore, to make use of all available data and to focus on the effects of provisioning exclusively, I also constructed simpler models. These simple models solely investigated the effects of the amount of food provisioned and its proximity to vulture colonies while also controlling for the observation period.

Results

Summary results

Data consisted of 95 observations on annual breeding success spread over a period of 20 years from ten different vulture colonies located across South Africa (Figure 5.1; Table 5.1). The average breeding success across all these colonies and years was 77.0%, with a minimum of 21.4% and a maximum of 100%. The 100 km buffers contained an annual mean of 8 SFS (range: 2-15) and 262 tonnes (range: 18-654 tonnes) of food, with an estimated poisoning prevalence ranging between 16-27% of commercial farmers. The 200 km buffers contained a mean of 28 SFS (range: 2-57) and 800 tonnes of food (range: 25-1820 tonnes), with the mean poisoning prevalence ranging between 18-26% of commercial farmers. The average observation period (time between first and last survey) was 107.98 days (range 46-169 days).

Relationships with breeding success

Results varied little between the models for the two time scales (10 and 20 years) and two spatial scales (100 and 200 km, Table 5.2), with provisioning rate showing a positive relationship and proximity to SFS showing a negatively relationship with breeding success in all models (Figure 5.2). However, these effects were not statistically significant in any of the models; although for 200 km 20-year simple model, the relationships were only marginally non-significant ($P = 0.082$ and $p = 0.088$ respectively for provisioning rate and proximity).

Co-linearity between variables meant that the full model (i.e., models including potential Pb level and poisoning exposure) could only be run for the 10-year data at the 100 km buffer spatial scale. In this model, although showing a negative relationship in both cases, I found no significant effect of the estimated average poisoning prevalence and the provisioning of potentially Pb contaminated food on breeding success ($p=0.781$ and 0.730 respectively, Figure 5.3). Unsurprisingly, all models highlighted observation period as having the greatest effect on breeding success estimates, with breeding success decreasing over longer observation periods (Table 5.2; Appendix 5.2-5.4). The exclusion of datapoints with 100% breeding success estimates did not materially affect any of the results (Appendix 5.5-5.7).

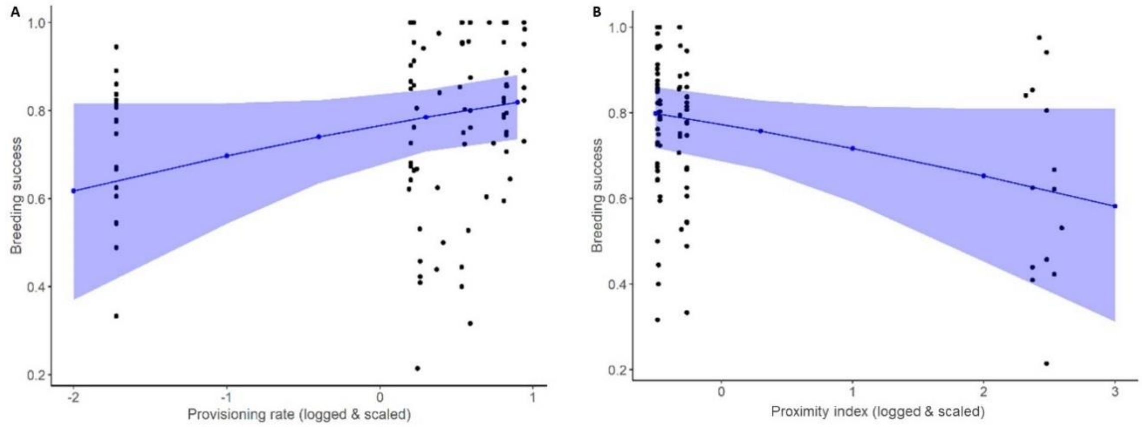


Figure 5.2: The fitted relationship, from a GLMM, between colony breeding success and provisioning rate, $p = 0.088$ (A), as well as the relationship between breeding success and the proximity of SFS to a given colony expressed as an index, $p = 0.082$ (B). These results stem from a GLMM including Provisioning rate and Proximity Index for SFS within a 200km buffer and 20 years of Cape Vulture colony breeding success data. The 95% confidence interval is indicated and raw data (black dots) is shown.

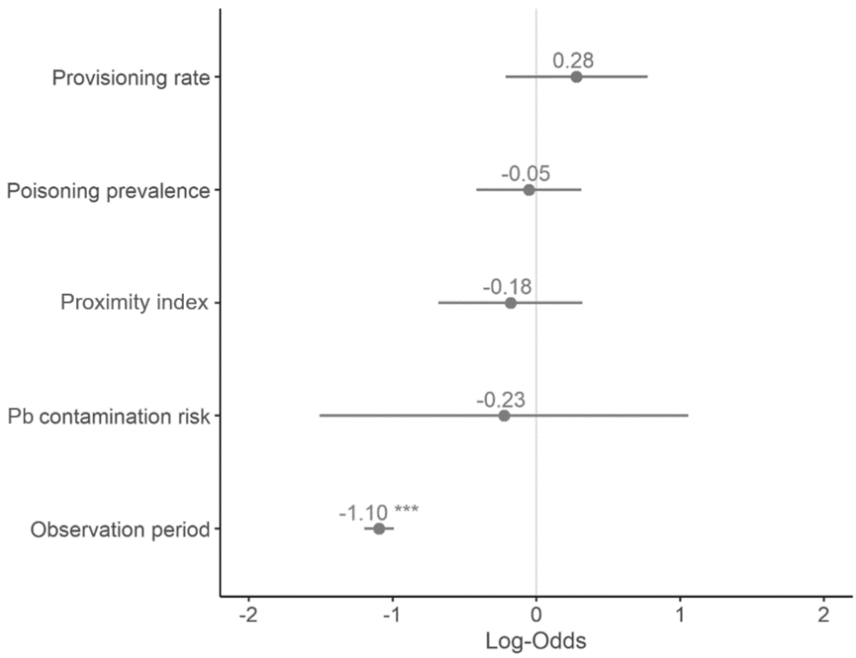


Figure 5.3: Results from generalised linear mixed effects model testing the effects of the full model (100 km buffer) on the breeding success of Cape Vulture colonies over a 10-year period.

Table 5.1: Summary of Cape Vulture colony monitoring data and data on supplementary feeding sites in either a 100 km or 200 km buffer zone. Mean estimates are indicated with the range shown in brackets.

Colony	Years	Number of pairs	Breeding success	Number of SFS: 100 km buffer	Number of SFS: 200 km buffer	Tons of food provided per year: 100 km buffer	Tons of food provided per year: 200 km buffer
Nooitgedacht	2010 – 2020	122 (82 -177)	0.83 (0.53-1.00)	11 (10-12)	29 (27-30)	605 (408-654)	1393 (1008- 1511)
Skeerpoort	2010 – 2020	259 (197-360)	0.79 (0.59-1.00)	10 (9-11)	32(30-33)	503 (307- 553)	1355 (969- 1473)
Roberts' Farm	2008-2011	7(5 -9)	0.65 (0.40-1.00)	12 (11-12)	26	421 (421-422)	946 (942- 957)
Manoutsa	2012-2019	603 (433 -775)	0.89 (0.66-1.00)	11	24	248	571
Kransberg	2011-2020	710 (608 -869)	0.86 (0.65-1.00)	15 (14-15)	48 (47-49)	514 (417- 538)	1738 (1314- 1820)
Soutpansberg	2012-2019	202 (182 -225)	0.79 (0.64-1.00)	2 (2-3)	20 (20-22)	18 (18-20)	552 (551-552)
Mzimkulu/Oribi	2001-2014	35 (17 -48)	0.63 (0.21-0.98)	13 (13-15)	55 (52-57)	117 (71-129)	660 (542-925)
Potberg	2001-2019	54 (20 -95)	0.73 (0.33-1.00)	2	2	25	25
Moletjie	2012 – 2018	15 (5- 21)	0.75 (0.32-1.00)	8	40 (39-40)	367 (365- 368)	995 (776- 1032)
Manyelanong	2017-2019	85 (82-89)	0.97 (0.95-1.00)	2	24	71	948

Table 5.2: Results from a Generalised Linear Mixed Effects Model with a binomial error structure examining the effects of supplementary feeding sites within a 100 km or 200 km buffer of vulture colonies on breeding success over a 20-year period. Predictors included in the model include an index of the proximity of SFS within a buffer zone to any given vulture colony, the amount of food provided within the buffer zone annually and the number of days over which the colony was monitored. Year and colony ID were added to the model as random effects.

	100 km buffer model				**200 km buffer model**			
Predictors	**Log-Odds**	**std. Error**	**CI**	**p**	**Log-Odds**	**std. Error**	**CI**	**p**
(Intercept)	1.27	0.20	0.88 – 1.65	<0.001	1.19	0.22	0.77 – 1.62	0.001
Proximity index	-0.18	0.15	-0.48 – 0.12	0.235	-0.30	0.17	-0.64 – 0.04	0.082
Provisioning rate	0.22	0.13	-0.04 – 0.48	0.097	0.36	0.21	-0.05 – 0.76	0.088
Observation period	-0.86	0.04	-0.94 – -0.77	**<0.001**	-0.86	0.04	-0.94 – -0.77	**<0.001**

Discussion

We tested the effects of supplementary feeding, the associated potential Pb exposure, and potential exposure to poison through its use by commercial farmers on Cape Vulture breeding success. I did not find support for my hypothesis that breeding success was positively affected by the proximity of SFS or the amount of food they provision. I also found no association between breeding success and the average poisoning prevalence and the amount of potentially Pb contaminated food provided at SFS. Overall, my study raises some questions as to whether breeding success in Cape Vultures is food limited in South Africa.

Although not significant, breeding success in Cape Vultures was positively associated with the amount of food provided at SFS in their foraging range. This positive relationship was present in all models (irrespective of time- or spatial-scale). This positive relationship concurs with various other studies that have indicated increases in raptor breeding success in relation to supplementary feeding (González et al., 2006; Rooney et al., 2015). In most bird species, breeding is a challenging and demanding period where temporal variations in resource availability may impact a wide range of breeding parameters (Hilgartner et al., 2014; Rooney et al., 2015). A stable food supply during breeding is known to positively impact a wide range of breeding parameters in many species (Amar and Redpath, 2002; Davis et al., 2005; Robb et al., 2008a). However, in cases where food is not a limiting factor such positive effects are unlikely and conservation resources may be better spent elsewhere. Hoodless et al. (1999) concluded that spring feeding cannot be advocated as a management technique to improve the breeding success of Ring-Necked Pheasants, *Phasianus colchicus*. Similarly, Margalida (2010) found that supplementary feeding during the chick-rearing period was ineffective at increasing breeding success in Bearded Vultures, *Gypaetus barbatus*, in the Spanish Pyrenees. Margalida (2010) suggested that for these Bearded Vultures other conservation actions should be prioritised to optimise the use of conservation resources. The low confidence in the positive relationship between supplementary feeding and breeding success found in my study fails to provide good support for the idea that a stable food supply is a limiting factor for the Cape Vulture colonies I investigated (Mundy et al., 1992).

One of the limitations of this study was that I was not able to control for other sources of food, such as natural food availability. Accounting for this may change results, and future studies should aim to quantify these food resources to establish food availability in the absence of currently active SFS. Such research will also allow the targeted application of SFS to only vulture populations that have been shown to be food limited. Currently, however, my results reflect other studies where initial examination of the effects of SFS suggested a positive effect that later more robust statistical techniques have refuted (Margalida et al., 2017).

The proximity of SFS did not significantly affect breeding success. A range of adaptations allow vultures to access resources spread across vast distances, the largest foraging range calculated for a Cape Vulture is, for example, 2 066 350 km^2 (Hirschauer et al., 2017). These adaptations include low energy flight, the ability to consume and store sizable quantities of food and singular offspring with slow growth rates (Ruxton and Houston, 2002). These characteristics help to make the proximity of food resources less important for vultures than in other avian groups (Ruxton and Houston, 2002).

I did not find a negative relationship between breeding success and the amount of potentially Pb contaminated food provided at SFS. Although I could not be certain that all game meat provided at SFS had been shot, I believe my indirectly measured exposure of Pb in this food type was realistic, since shooting is the primary method of killing game animals in South Africa. Furthermore, during the period of study, there has been very limited adoption of non-Pb ammunition. One possibility for any lack of affect, could be that when vultures feed at a carcass, only a small number may ingest Pb particles. The effect of Pb-poisoning mortalities may thus be diluted at the colony level which I investigated. A large proportion of Pb exposure in vultures may come from hunting activities that are unaffiliated to SFS and therefore not accounted for in my model. A large percentage of African vultures show elevated Pb levels, with Pb-shot having been identified as the most likely cause (Garbett et al., 2018; van den Heever et al., 2019). Although sub-lethal effects are likely affecting vulture fitness on an individual level (van den Heever et al., 2019), these effects may be outweighed by the short-term benefits of the additional food resource in some cases (Herring et al., 2020). Also, the harmful effects of lead ingested as a chick may only become evident in the long-term, after chicks have already successfully fledged.

We also found no effect of the potential exposure to poisoning by commercial farmers in the area surrounding colonies. For this variable to affect breeding success, breeding adults would have to be poisoned during the breeding season. Although poisoning events have the potential to cause huge vulture losses (Henriques et al., 2020), such events tend to be infrequent and randomly distributed at the landscape scale. My measure of poisoning prevalence is a measure of commercial farmers propensity to use poison and may not have been an adequate representation of poisoning events where vultures were killed. It is also possible that the large number of SFS around permanent and conspicuous Cape Vulture breeding colonies, are reducing the likelihood of vultures encountering poisoned carcasses, thereby mitigating the effect of this variable on breeding success in the model. Such a poison-risk buffering effect is a further potential positive benefit of SFS, but one that requires detailed modelling and empirical research to verify.

Management implications

As suggested by Chapter 2 the amount of food provided at existing SFS combined with natural food resources, is likely already exceeding the food requirements of vultures in the region. This could explain why I found no effect of SFS. In the absence of evidence that supplementary feeding is bolstering breeding South African vultures, it is important to verify other proposed positive impacts which may still validate the use of this conservation measure. In long-lived species like large raptors, management strategies that enhance survival rather than action which aim to address productivity, are more likely to affect population trends (Sæther and Bakke, 2000). If a vulture population is indeed food limited, it is likely that SFS will increase survival (Lieury et al., 2015). I could speculate that SFS have the ability to increase survival of recently fledged vultures or reduce poisoning risk by vultures preferentially feeding at this safe food source. However, such aspects require specific testing, and more research is needed to verify these effects. Short-term survival gains also need to be weighed against longer term negative effects. For example, SFS may allow birds to increase their fat deposits and therefore energy reserves, while at the same time causing neurological damage, through chronic exposure to Pb, that compromises individual fitness over the long-term. Such individual level effects can affect population demographics as older individuals (the more experienced breeders) suffer the effects of this exposure compounded over time.

The application of SFS was only ever meant to provide temporary support to vulture populations while the causes of their declines are addressed and should never be considered a long-term solution to the current African vulture crisis. If a net benefit to vultures cannot be shown, then conservation resources may be more wisely spent on directly combatting mortality causing threats, such as poison use and powerlines. This is especially poignant given my results and the fact that further research is needed on the effect of this measure on vulture behaviour, ecological structure, and the effects of substances that vultures may be exposed to at SFS. Additionally, there may be costs for less competitive but more threatened vulture species who may be attracted to SFS but where food is monopolised by larger and more dominant Cape Vultures (Cortés-Avizanda et al., 2010). It is therefore necessary to conduct species specific research on the effects of SFS.

My results and conclusions should be interpreted cautiously. My analysis was conducted at the landscape scale, and it is possible that some individual colonies may be benefiting from supplementary feeding due to localised food shortages. I therefore urge managers to conduct case-specific and experimental assessment of the impact of supplementary feeding at vulture colonies to determine the suitability of this conservation measure at their sites.

Conclusion

Our study did not provide evidence that SFS are benefitting Cape Vultures via the mechanism of enhanced breeding success, in South Africa. While I only investigated one of the potential benefits of SFS, these results viewed in light of the identified low awareness of vulture threats under managers, perhaps caution against the indiscriminate application of this conservation measure. The many potential negative consequences of anthropogenic supplementary feeding is still poorly understood. A case-by-case assessment of the justifications for its application, and the way it is applied, may therefore be a more responsible strategy than recommending it as a standard practice. If a net beneficial effect cannot be shown, then conservation resources are perhaps more effectively spent if directed towards combatting the causes of vulture mortalities directly. While supplementary feeding has the potential to play a supportive role in combatting the vulture declines, it should not be viewed as a solution to the current crisis.

Appendix 5

Appendix 5.1: Representation of model structure used in R.

Basic model: *glmer(cbind(success, fail)~ Proximity Index + Provisioning Rate + Observation Period + (1|colony) + (1|year), family=binomial)*

Full model: *glmer(cbind(success, fail)~ Proximity Index + Provisioning Rate + Observation Period + Lead provisioning + Poisoning Prevalence + (1|colony) + (1|year), family=binomial)*

Appendix 5.2: Summary of 100km buffer results for 10 year period. (only data that allowed us to model it)

Predictors	Log-Odds	std. Error	CI	p
(Intercept)	1.59	0.45	0.70 – 2.47	**<0.001**
Proximity index	-0.18	0.26	-0.68 – 0.32	0.479
Provisioning rate	0.28	0.25	-0.22 – 0.77	0.270
Pb contamination risk	-0.23	0.65	-1.51 – 1.06	0.730
Poisoning prevalence	-0.05	0.19	-0.42 – 0.31	0.781
Observation period	-1.73	0.08	-1.89 – -1.57	**<0.001**
Random Effects				
σ2	3.29			
τ00	0.57 year 0.28 colony			
ICC	0.21			
N	9 colony 10 year			
Observations	61			
Marginal R2/Conditional R2	0.264 / 0.415			

Appendix 5.3: Summary of 100km buffer results for 20 and 10 year period simple models.

Predictors	***Log-Odds***	***std. Error***	***CI***	***p***	***Log-Odds***	***std. Error***	***CI***	***p***
(Intercept)	1.27	0.20	0.88 – 1.65	**<0.001**	1.49	0.25	1.00 – 1.97	**<0.001**
Proximity index	-0.18	0.15	-0.48 – 0.12	0.235	-0.11	0.17	-0.45 – 0.23	0.508
Provisioning rate	0.22	0.13	-0.04 – 0.48	0.097	0.23	0.16	-0.07 – 0.54	0.137
Observation period	-0.86	0.04	-0.94 – -0.77	**<0.001**	-0.91	0.05	-1.00 – -0.82	**<0.001**
Random Effects								
σ^2	3.29				3.29			
τ_{00}	0.40 $_{year}$ 0.15 $_{colony}$				0.18$_{colony}$ 0.38 $_{year}$			
ICC	0.14				0.15			
N	10 $_{colony}$ 20 $_{year}$				10 $_{colony}$ 10 $_{year}$			
Observations	95				70			
Marginal R^2 /Conditional R^2	0.166 / 0.285				0.207 / 0.322			

Appendix 5.4: Summary of 200 km buffer results for 20 and 10 year period simple models

Predictors	***Log-Odds***	***std. Error***	***CI***	***p***	***Log-Odds***	***std. Error***	***CI***	***p***
(Intercept)	1.19	0.22	0.77 – 1.62	**<0.001**	1.42	0.27	0.89 – 1.94	**<0.001**
Proximity index	-0.30	0.17	-0.64 – 0.04	0.082	-0.16	0.20	-0.55 – 0.23	0.421
Provisioning rate	0.36	0.21	-0.05 – 0.76	0.088	0.30	0.21	-0.12 – 0.72	0.160
Observation period	-0.86	0.04	-0.94 – -0.77	**<0.001**	-0.91	0.05	-1.00 – -0.82	**<0.001**
Random Effects								
σ^2	3.29				3.29			
τ_{00}	0.40 year 0.21 colony				0.24 colony 0.38 year			
ICC	0.16				0.16			
N	10 colony 20 year				10 colony 10 year			
Observations	95				70			
Marginal R^2 / Conditional R^2	0.119 / 0.323				0.224 / 0.347			

Appendix 5.5: Summary of 100km buffer results for 10 year period when breeding success estimates of 100% are excluded.

Predictors	**Log-Odds**	**std. Error**	**CI**	**p**
(Intercept)	1.41	0.35	0.72 – 2.09	**<0.001**
Proximity index	-0.07	0.21	-0.48 – 0.35	0.756
Provisioning rate	0.20	0.22	-0.23 – 0.62	0.370
Lead contamination risk	-0.14	0.54	-1.19 – 0.91	0.794
Poisoning prevalence	0.01	0.15	-0.28 – 0.30	0.966
Observation period	-0.79	0.06	-0.90 – -0.68	**<0.001**
Random Effects				
σ2	3.29			
τ00	0.17 colony 0.24 year			
ICC	0.21			
N	9 colony 10 year			
Observations	49			
Marginal R2/Conditional R2	0.141 / 0.235			

Appendix 5.6: Summary of 100km buffer results for 20 and 10 year period simple models when breeding success estimates of 100% are excluded.

Predictors	***Log-Odds***	***std. Error***	***CI***	***p***	***Log-Odds***	***std. Error***	***CI***	***p***
(Intercept)	1.10	0.15	0.80 – 1.40	**<0.001**	1.35	0.17	1.02 – 1.68	**<0.001**
Proximity index	-0.15	0.12	-0.37 – 0.08	0.213	-0.01	0.13	-0.27 – 0.25	0.923
Provisioning rate	0.12	0.11	-0.10 – 0.33	0.283	0.16	0.12	-0.08 – 0.39	0.190
Observation period	-0.56	0.05	-0.66 – -0.47	**<0.001**	-0.61	0.05	-0.71 – -0.52	**<0.001**
Random Effects								
σ^2	3.29				3.29			
τ_{00}	0.08 colony 0.24 year				0.09 colony 0.16 year			
ICC	0.09				0.07			
N	10 colony 20 year				10 colony 10 year			
Observations	82				58			
Marginal R^2 /Conditional R^2	0.063 / 0.147				0.086 / 0.150			

Appendix 5.7: Summary of 200 km buffer results for 20 and 10 year period simple models when breeding success estimates of 100% are excluded.

Predictors	***Log-Odds***	***std. Error***	***CI***	***p***	***Log-Odds***	***std. Error***	***CI***	***p***
(Intercept)	1.05	0.17	0.72 – 1.38	<0.001	1.30	0.19	0.94 – 1.66	**<0.001**
Proximity index	-0.22	0.13	-0.47 – 0.03	0.090	-0.04	0.15	-0.34 – 0.25	0.771
Provisioning rate	0.23	0.16	-0.09 – 0.55	0.154	0.23	0.16	-0.08 – 0.54	0.142
Observation period	-0.56	0.05	-0.66 – -0.47	<0.001	-0.61	0.05	-0.71 – -0.51	**<0.001**
Random Effects								
σ^2	3.29				3.29			
τ_{00}	0.11 $_{colony}$				0.12 $_{colony}$			
	0.24 $_{year}$				0.16 $_{year}$			
ICC	0.10				0.08			
N	10 $_{colony}$				10 $_{colony}$			
	20 $_{year}$				10 $_{year}$			
Observations	82				58			
Marginal R^2 / Conditional R^2	0.082/ 0.170				0.100 / 0.171			

CHAPTER 6:

Synthesis

Photo: The sun sets over a SFS on top of a hill in the southern Drakensberg (Photo by C.W. Brink).

This thesis stems from the current widespread and favoured application of supplementary feeding in vulture conservation. The popularity of this conservation measure is currently not congruent to the level of conclusive scientific evidence of its beneficial effects on vulture populations. Many contradictory results have been published globally and knock-on effects on non-target species, the wider ecosystem and human-wildlife dynamics have rarely been considered. Additionally, previous assessments have often been localised studies or have been hampered by a lack of information on resource provisioning at feeding sites. My thesis therefore investigates the role of SFS in vulture conservation. I did this by firstly compiling base-line information on this practice in South Africa. I then attempt to verify some of the proposed beneficial effects of this conservation measure while accounting for potential trade-offs stemming from bad management practices and threats within the landscape. My thesis focuses on South Africa, the apparent birthplace of this conservation measure, but the outcomes of the thesis are also applicable further afield. These outcomes are meant to guide conservation management in adding to the growing discussion of the trade-offs of SFS for vultures and the wider ecosystem, as well as identifying and refining best management practices.

Summary of key findings

The infographic below illustrates the overall structure and key findings of my thesis (Figure 6.1). In the second chapter I describe for the first time the prevalence, distribution and resource contribution of SFS at a national level, thereby providing baseline information for all future research into this subject. Analysis of this data shows that SFS already contribute a significant amount of food to vulture populations, which calls into question current assumptions that vulture populations are food limited in South Africa. However, most of the food is provided by a small number of SFS with very high provisioning rates, and vulture species have varying access to these resources depending on their distributions.

Chapter 3 investigated the SFS managers themselves, who were identified to be mostly involved in livestock farming but also tourism, hunting and game breeding. SFS were perceived to have few disadvantages and to mostly benefit managers. Managers had a poor understanding of vulture conservation issues. I show that this low awareness could compromise the safety of vultures that visit these sites through, for example, the provisioning of food contaminated by veterinary drugs and/or lead.

Contaminants in meat provided at SFS are additional to the already widespread threat of poison use under livestock farmers. In Chapter 4 I show that this practice persists in nearly a third of South African commercial farmers and is most prevalent under small stock farmers. I found that farmers were mostly positively disposed to vultures and less likely to use poison if vultures were present on their farms. The strongest predictor for poison use was, however, whether the practice was perceived to be commonly used by peers, highlighting how perceived social acceptability may be shaping behaviour and could be leveraged for vulture conservation. Being the major cause of vulture mortalities in Africa, poison prevalence may impact breeding success at the colony level through the mortalities of parents with dependent chicks.

In Chapter 5 I use the baseline data on SFS from Chapter 1, while accounting for potential effects of unsafe food resources identified in Chapter 2 and 3, to test the effect that SFS have on the breeding success of vultures at a regional level, using Cape Vultures as a study species. I found no strong evidence for a beneficial effect of SFS on breeding success, but neither did I find any strong evidence for negative effects regarding food contaminants provided at SFS, nor the prevalence of poisoning in the surrounding commercial farmland.

Panacea or perilous management practice?

SFS are enthusiastically envisioned as a win-win scenario for both their managers and vultures. SFS managers are proposed to receive cost effective carcass disposal and disease prevention while vultures are proposed to benefit through increased survival and breeding success, as well as a reduced risk of poisoning. This is the common narrative in campaigns aimed at recruiting landowners into adopting this practice (The Endangered Wildlife Trust 2011). Unpacking these assumptions in the context of this thesis, however, shows that establishing such a mutually beneficial relationship is not necessarily easily accomplished.

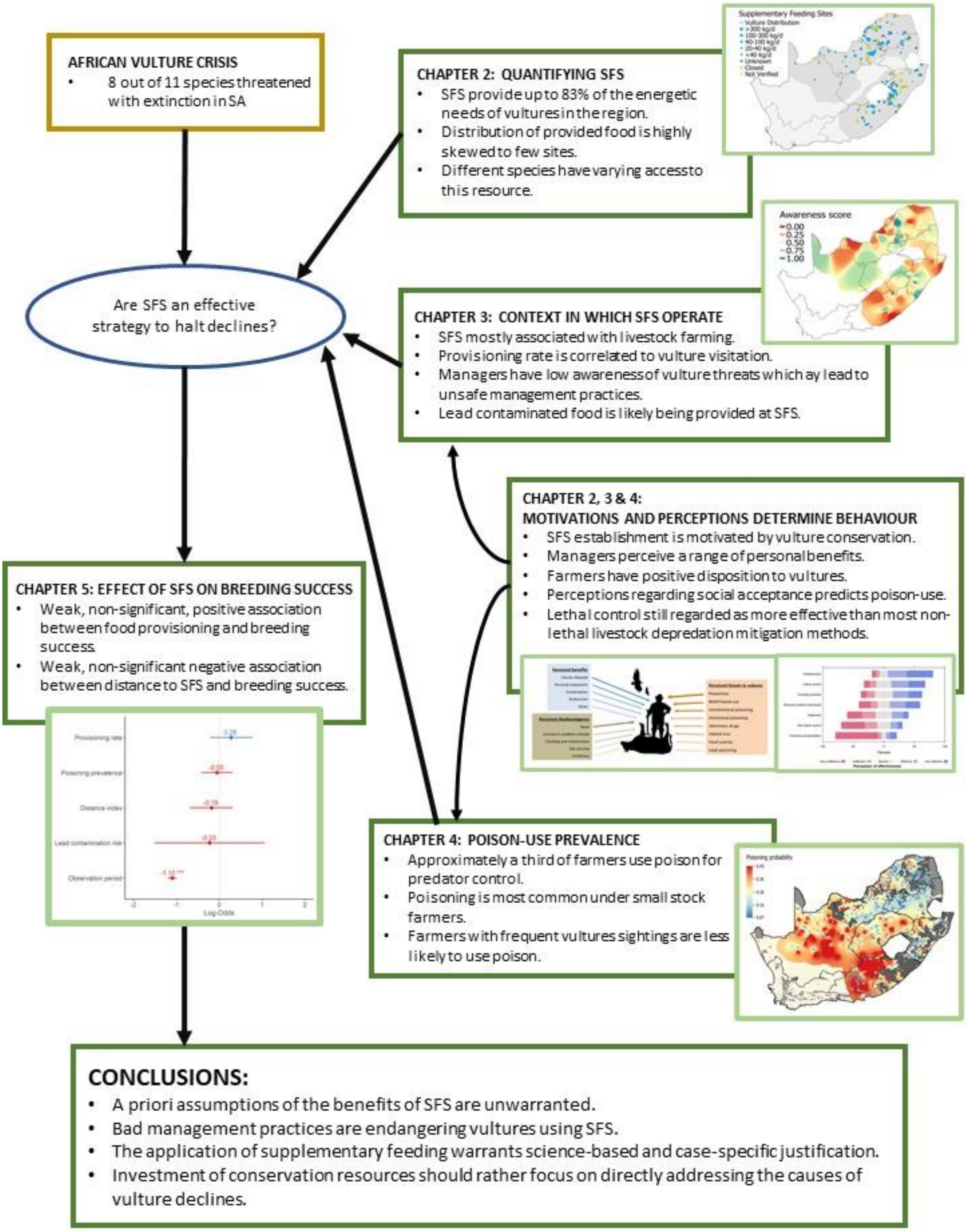


Figure 6.1: Schematic diagram showing the outline of my research question and how data chapters interlink to answer this question.

The majority of managers did indeed perceive SFS to be beneficial to themselves. More than half of managers specifically appreciated the cleaning service provided by vultures. Interestingly, only 2% of managers seemed to directly connect this with disease prevention, or at least specified this benefit. Vultures indeed live up to their reputation of being efficient cleaners and are able to effectively and quickly dispose of carcasses before pathogens manage to significantly replicate and transmit (van den Heever et al. 2021). Does this however translate to reduced disease spread for managers leaving carcasses out for vultures?

Historically perceptions that vultures spread disease were prevalent (Mundy et al. 1992). Perhaps this negative connotation is still embedded in the minds of landowners. The general survey I conducted under livestock farmers in Chapter 3 indicated that 43% of livestock farmers in South Africa do not disagree with the statement that vultures spread disease, albeit that 31% were undecided regarding whether they believed it to be an issue. Currently, the role vultures play as the vectors of pathogens is largely understudied (van den Heever et al. 2021). Their exceedingly acidic stomachs help to reduce their susceptibility to pathogens, but anthrax spores have been found in their faecal matter (Hugh-Jones and de Vos 2002) and colonisation by various zoonotic pathogens has been recorded (Plaza et al., 2020). It is therefore possible for vultures to spread pathogens over great distances given their wide-ranging habits, but the current consensus is that the disease spread prevention effect of functional vulture populations far outweighs any potential transmission risks (van den Heever et al. 2021). However, vultures rely on cues from conspecifics to find carcasses (Mundy et al. 1992) and a reduction in vulture densities in an area can therefore compromise the effectiveness of this ecosystem service by causing delays in carcass discovery and reduced consumption. This situation would allow additional opportunity for pathogens to colonise, replicate and, in the case of anthrax, *Bacillus anthracis*, to form spores (van den Heever et al. 2021). Consequently, landowners may, at least initially until vulture populations recover, experience higher disease prevalence if they leave carcasses for vultures rather than using other traditional carcass disposal methods such as burying or burning. The effectiveness of using vultures for carcass disposal and disease prevention will consequently depend on vulture prevalence and the amount of waste produced by a livestock production operation. Whether traditional methods of carcass disposal are more expensive also depends on these factors and the cost-effectiveness of SFS for intensive versus smaller scale livestock operations still requires investigation. SFS are not without their costs and they require infrastructure such as fencing and the transport of carcasses to specific sites.

Vultures themselves may also face the risk of disease and infection when making use of anthropogenic food sources. Vultures have been shown to be colonised by host-specific human and multi-antibiotic resistant pathogens, some of which are potentially influencing mortality risk and fitness (Plaza et al., 2020). SFS have been identified as the origin of many of these infections (Plaza et al., 2020) furthering the idea that there are likely trade-offs for vultures in using SFS. Comparably, Plaza and Lambertucci (2018) showed that black vultures, *Coragyps atratus*, in the Americas that fed from rubbish dumps had higher body mass on average and were less prone to dehydration than those in a more natural setting. However, the vultures that fed at rubbish dumps also displayed biochemical parameters suggesting nutritional problems that may be causing kidney damage or infections. This thesis may be comparable to the South African situation where I have identified that, due to low awareness under SFS managers, carcasses at SFS may contain contaminants (lead and veterinary drugs) that are known to be harmful to vultures (Chapter 3). In singular cases some SFS have even devolved into uncontrolled dump sites where all manner of waste, even inorganic waste is or was being dumped. While most managers seem to be aware of the dangers of veterinary drugs, awareness of the very real dangers of lead poisoning are exceedingly low. This is despite the toxicity of lead to all organisms, including vultures, being very well documented.

In this thesis I did not find evidence that SFS help to increase the breeding success of Cape Vultures at national level. Failure to find a signal for this effect at this large-scale builds on other critical assessments that are increasingly questioning the narrative that a beneficial effect is a standard response (Cortés-Avizanda et al. 2016; Oppel et al. 2016a). Such effects may be situational, requiring populations to be food restricted, which may not be the case at a landscape level in South Africa. If I had assessed a smaller and less dominant vulture species, then perhaps it could have been argued that I failed to find any effect because my thesis species was outcompeted by others at SFS. Cape vultures are however the largest vulture across much of their South African range. If such base level beneficial effects cannot be shown and the detrimental effects on the ecology of vultures and the rest of the ecosystem remain largely unknown, is supplementary feeding an advisable management strategy at the landscape level? More research is needed to verify how transferable my results are to other species and to test for other effects like increased survival. In the interim it may perhaps be advisable to limit the application of SFS to specific cases where low food availability has been demonstrated and SFS manager can be adequately trained.

The need for regulation

Much of the negative effects mentioned above relate to bad management practices. The low awareness of SFS managers of best management practices indicates a need for increased training and communication from the conservationists that are motivating landowners to adopt this practice. “Vulture restaurants” as they are more commonly known under livestock farmers, are however so widely known as a concept in South Africa that it is an activity that people engage in informally and at their own discretion. Many undocumented SFS therefore likely currently exist and will be established in future without consultation with conservation practitioners. Dangerous management practices will consequently be difficult to stamp out under the current structure of governance which is individual based. Formal regulation of SFS is therefore perhaps required to ensure that SFS do not endanger vultures. Such regulation would be most needed at the largest SFS which are likely having the strongest effect on vultures.

Regulation of SFS was implemented in Europe in response to the 2001 outbreak of bovine spongiform encephalopathy and new legislation severely restricted the use of carcasses and animal by-products (Donázar et al. 2009). The downside of such regulatory action may be that it discourages landowners to be involved with such initiatives. The resulting low participation may therefore lead to the closure of many existing sites. Given the potential contribution to vulture energetic needs I identified, such closures may result in food shortages as it did for European vultures. The new European sanitary legislation initially resulted in a decrease in breeding success and survival for vultures since these populations were mostly depended on domestic livestock (Donázar et al. 2009). Whether this would be the case in South Africa, where more wild ungulates still remain, is not yet clear.

An additional consideration is South Africa’s ability to enforce such regulation or legislation. Realistically there is likely a very low capacity to do so effectively. This means that the responsibility of ensuring that active sites are using best management practices falls to the conservation organisations who motivated managers to start this practice. Identifying what the best management practices are is however still open to debate, as the effects of SFS on vulture ecology and especially foraging ecology are still much debated.

Poisoning mitigation versus habituation: a catch-22

Assuming my findings regarding the lack of positive effects on breeding success are applicable to other species as well, then SFS could still be an advisable conservation response if they are shown to increase the survival of vultures. Potential trade-offs will then need to be considered. If SFS increase survival while also causing density dependent productivity depression, as has been the case in some instances (Carrete et al. 2006b), then a net benefit at the population level is not guarenteed.

One of the mechanisms for increased survival is through reducing the risk of vultures to be exposed to unsafe food resources such as poisoned carcasses (Gilbert et al. 2007). How supplementary feeding schemes are applied will, however, determine the acuteness of such effects. This highlights a certain extent of cognitive dissonance in the current conservation narrative. Awareness campaigns for livestock farmers are often focussed on educating farmers about the ecological role that vultures play by cleaning the environment of carrion and stopping diseases (The Endangered Wildlife Trust 2011). At the same time landowners are motivated to use SFS to reduce the risks of vultures encountering poisoned carcasses. This risk reduction is maximised by increasing dependence of vultures on SFS and the safe food sources provided there (Kelly et al. 2014). Such dependence is encouraged by the predictable and consistent provisioning of large amounts of food at SFS (Fluhr et al. 2017). However, if vultures are preferentially feeding at SFS this will compromise the ecosystem service that is highlighted as the most important motivation for conserving vultures in the first place. Some researchers have concluded that SFS do not compromise natural foraging behaviour (Kane et al. 2016), but if this is the case then the buffering effect of SFS against poisoning will be much reduced.

Evidence that SFS do indeed alter vulture movements is mounting (López-López et al. 2014; Fluhr et al. 2017). The placement of SFS is thus becoming an important management consideration that may determine whether vultures are being lured into or out of high-risk areas. This aspect requires further investigation. Many vultures are currently being tracked by various NGO’s and Universities in southern Africa, this presents an opportunity to test the effect of SFS on movement behaviour in an experimental manner. Vulture movement in the presence of predictable food sources can be compared with those when only unpredictable food resources are available. If any effect is found it would be advisable to also investigate how long the effects on movement behaviour continue after the cessation of predictable food provisioning. Once these effects have been determined the distribution of threats at a landscape level will become imperative for the proper planning of SFS placement. Such conservation management is however currently hampered by the lack of regulation and the informal way in which SFS function.

In this thesis I provide some information towards the future planning of SFS placement by spatially quantifying the risk of poisoning, the main threat to vultures, from commercial farmers to all susceptible vulture species in South Africa. This information will be invaluable for future conservation planning, but to effectively use it we first need to understand the net effects of SFS. For example, does placing SFS in areas with high poisoning risk reduce poisoning risk for vultures or result in an increase in population level mortality because vultures from further afield are lured into high risks areas? What is clear is that the current simplistic narrative surrounding SFS proposes benefits that may conflict with each other, are unsubstantiated, or do not include important technical considerations which are required for the responsible application of this conservation measure.

Conservation priorities

Given the potential of anthropogenic food resources to alter the ecology of wildlife, SFS were only ever intended as a temporary conservation measure to buy time for conservationists to address the causes of vulture declines (Moreno-Opo et al. 2015a). Since their inception, however, the main threats driving vulture declines remain unchanged (Botha et al. 2017). Addressing threats such as habitat loss, poison-use and belief-based use are complex, sensitive and multi-faceted. It is therefore tempting to focus on simplistic measures that are straightforward to apply, such as providing food for declining populations, rather than engaging directly with the root causes of declines. While establishing SFS may seem simplistic and feel like a valuable contribution, applying this measure effectively and responsibly is more complex than generally appreciated and may in many cases be a risky investment of conservation resources.

In South Africa SFS have evolved beyond a temporary measure and is likely thought by some to be a viable and permanent means of sustaining vulture populations. If we are to evaluate supplementary feeding as a non case-specific, standard response to vulture declines, then at best the science indicates that there is ambiguity as to whether SFS are beneficially affecting vulture populations. At worst it shows that SFS negatively impact vulture populations, alter their behaviour and ecology and may even constitute an ecological trap for some species. Given this ambiguity and the continued prevalence of severe threats to vultures, it is perhaps prudent for a shift in the vulture conservation zeitgeist away from a focus on supplementary feeding towards the investment of conservation capital into addressing threats to vultures directly. My thesis suggests, at least with regards to Cape Vulture breeding success, that conservation efforts would be more efficiently spent combating anthropogenic causes of vulture mortality.

Dogma and expert opinion versus scientifically informed management practices

Pro-active conservation initiatives should be managed in continual process of design, implementation, evaluation and re-evaluation cycles that are evidence based and targeted (Sutherland et al. 2004). Unfortunately, while interventions may often be evidence based, case-specific evaluation is often neglected (Fenn et al. 2020). This impedes effective and responsive conservation management.

Evidence for the positive effects of supplementary feeding have resulted in a priori assumptions that this is an efficient conservation practice for supporting vulture populations. Although early studies have indicated that SFS are appropriate conservation interventions for large avian scavengers, more recently critical reviews of their usefulness are emerging (Margalida et al 2010). The continued knee-jerk application of this conservation measure in response to species declines, despite these contrary indications, has resulted in supplementary feeding being highlighted as a conservation measure whose application has become dogmatic (Martínez-Abraín and Oro 2013). Justifications for its application should thus be critically assessed on a case-by-case basis and in a scientifically robust way.

The outcomes of management practices based on scientific evidence can be predicted, albeit to varying degrees of accuracy, but expectations regarding the outcome are backed up by evidence. Management practices that are based on dogma ignores contrary evidence, and they can thus lead to unexpected results (Martínez-Abraín et al. 2004), including negative ecological and economic consequences (Carwardine et al. 2008). Dogmatic management practices therefore constitute a bad allocation of the limited economic resources in the conservation sphere (Martínez-Abraín and Oro 2013). Given the current economic crisis and the crisis that is biodiversity decline, the wasting of such resources on ineffective measure are unjustifiable. There is currently an uneven distribution of conservation spending in relation to conservation priorities (Halpern et al. 2006). Vulture conservation managers should therefore be mindful that their management decisions regarding SFS do not become dogmatic and are evidence based. Further research will be necessary to determine whether supplementary feeding should be a priority in vulture conservation in South Africa.

Thesis limitations and research recommendations

The fact that I did not find a strong positive effect of SFS on breeding success, highlights the importance of investigating potential negative effects of this practice on vultures and the wider ecosystem. Such research will help refine the supplementary feeding methods used, to mitigate such negative effects, and help to caution the conservation community regarding a priori assumption about the suitability of this management technique (Blanco et al. 2011; Oppel et al. 2016b). In this thesis I only tested the effects of SFS on the breeding success of Cape Vultures. What effect supplementary feeding has on vultures and their populations is too large and diverse a question to address solely with this thesis. It will require a diverse array of research across a range of fields and on a variety of species and locations.

To ensure that such questions can be effectively assessed with the level of urgency warranted by the African Vulture Crisis, standardised monitoring protocols of vulture colonies and SFS are required. This information also needs to be shared between organisations and researchers to enable faster research outputs and broader-scale analysis. My thesis was hampered by the lack of standardised monitoring protocols, requiring post hoc and less effective standardisation or data exclusion. Additionally, refusals to share data prohibited the exploration of the effects of SFS on other species. The conservation need of vultures in Africa underlines the need for unreserved collaboration between organisations towards the common goal of saving vultures. In this thesis I provide the necessary baseline information on SFS that has hampered robust analysis of the effects of SFS, at least in a southern African context. In the view of the sentiment above, this will be made freely available to parties conducting relevant research or who can aid vultures in their conservation plight.

This information is however not without its own shortcomings. While I was able to provide estimates on food provisioning. These estimates likely become more and more inaccurate the further back in time or forward into the future they are projected. This is due to an increased likelihood of changes in farming practices, such as stocking rates or farming type. Further research could benefit from accurate records of feeding at SFS. Encouraging farmers to keep such records could enhance the confidence in the findings from research incorporating this information. Baseline information on food availability would also have been useful in my thesis. Currently no large-scale information on carcass availability exists and this was a complicating factor I could not account for in my modelling. Controlling for this will enable the identification of vulture colonies who do indeed have low food availability and could conceivably be affected more positively by supplementary food.

Different species may also respond differently to food supplementation for a variety of reasons, including differences in life history traits, environmental conditions and inter and intra-specific competition (Ruffino et al. 2014; Moreno-Opo et al. 2015). These factors are important to disentangle to effectively apply supplementary feeding initiatives that have the desired effects on target species. Currently Africa is lagging behind Europe regarding the identification of best management practices that incorporate such elements (Moreno-Opo et al. 2015).

Of specific interest is the differences in the effects of different feeding strategies and identifying which would be the preferred application in a given scenario. For example, is a feeding strategy that simulates a natural situation (spatially and temporally unpredictable spread of food) and therefore does not alter vulture behaviour preferable? Or should we rather be encouraging dependence through highly predictable food resources that may be more effective in reducing poisoning risk but have more acute unintended consequences?

Lastly an investigation of the nutritional quality of food provided at SFS needs investigation (Ruffino et al. 2014). SFS mostly provide domestic livestock, which has higher fat content than wild ungulates, and may contain various artificial hormones and veterinary drugs. These nutritional factors could potentially be affecting vultures in various ways.

Conclusion

My research adds to the increasing body of evidence that current a priori assumptions regarding the effectiveness of supplementary feeding in addressing vulture declines are unwarranted. Worryingly, the potential adverse effects of this management practice on vultures and the wider ecosystem are still poorly understood and rarely considered. These aspects require urgent research. What is clear is that the informal application of this conservation measure by untrained managers is potentially endangering vultures through dangerous management practices. Increased regulatory action or training can potentially address this concern. As the situation stands, a focus on food provisioning may be diverting scarce conservation resources and attention away from management actions which are potentially more effective. Specifically, directly addressing the causes of vulture population declines specifically should be a priority. In summary, supplementary feeding has the potential to be an effective conservation tool in specific cases, but its current application hints at having become dogmatic in nature. If the effects of SFS and their various trade-offs are not objectively assessed, then they may become counterproductive to conservation goals in some cases. In future case-specific research and continuous monitoring is needed to ensure this conservation measure is correctly applied and resulting in the desired outcomes.

REFERENCES

Abrahamse, W., L. Steg, C. Vlek, and T. Rothengatter. 2005. A review of intervention studies aimed at household energy conservation. *Journal of Environmental Psychology* 25: 273–291. doi:10.1016/j.jenvp.2005.08.002.

Amar, A., and S. M. Redpath. 2002. Determining the cause of the hen harrier decline on the Orkney Islands: An experimental test of two hypotheses. *Animal Conservation* 5: 21–28. doi:10.1017/S1367943002001038.

Amar, A., R. Buij, J. Suri, P. Sumasgutner, and M. Z. Virani. 2018. Conservation and ecology of African Raptors. In *Birds of Prey: Biology and conservation in the XXI century*, 419–455. doi:10.1007/978-3-319-73745-4_18.

Anderson, M. D., A. W. A. Maritz, and E. Oosthuysen. 1999. Raptors drowning in farm reservoirs in South Africa. *Ostrich* 70: 139–144. doi:10.1080/00306525.1999.9634530.

Anderson, M. D., S. E. Piper, and G. E. Swan. 2005. Non-steroidal anti-inflammatory drug use in South Africa and possible effects on vultures. *South African Journal of Science* 101: 112–114. doi:10.1098/rsbl.2004.0223.

Antman, E. M., J. Lau, B. Kupelnick, F. Mosteller, and T. C. Chalmers. 1992. A Comparison of Results of Meta-analyses of Randomized Control Trials and Recommendations of Clinical Experts: Treatments for Myocardial Infarction. *JAMA: The Journal of the American Medical Association* 268: 240–248. doi:10.1001/jama.1992.03490020088036.

Arroyo, B., J. Lafitte, E. Sourp, D. Rousseau, L. Albert, V. Heuacker, J. F. Terrasse, and M. Razin. 2021. Population expansion and breeding success of Bearded Vultures Gypaetus barbatus in the French Pyrenees: results from long-term population monitoring. *Ibis* 163: 213–230. doi:10.1111/ibi.12852.

Badenhorst, C. G. 2014. The Economic Cost of Large Stock Predation in the North West Province of South Africa. University of the Free State.

Bamford, A. J., M. Diekmann, A. Monadjem, and J. Mendelsohn. 2007. Ranging behaviour of Cape Vultures *Gyps coprotheres* from an endangered population in Namibia. *Bird Conservation International* 17: 331–339. doi:10.1017/S0959270907000846.

Bannister, H. L., C. E. Lynch, and K. E. Moseby. 2016. Predator swamping and supplementary feeding do not improve reintroduction success for a threatened Australian mammal, *Bettongia lesueur*. *Australian Mammalogy* 38: 177–187.

doi:10.1071/AM15020.

Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, et al. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471: 51–57. doi:10.1038/nature09678.

Barton, P. S., M. J. Evans, C. N. Foster, J. L. Pechal, J. K. Bump, M. M. Quaggiotto, and M. E. Benbow. 2019. Towards Quantifying Carrion Biomass in Ecosystems. *Trends in Ecology and Evolution* 34: 950–961. doi:10.1016/j.tree.2019.06.001.

Bates, B., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67: 1–48. doi:10.18637/jss.v067.i01.

Bazilian, M., P. Nussbaumer, H. H. Rogner, A. Brew-Hammond, V. Foster, S. Pachauri, E. Williams, M. Howells, et al. 2012. Energy access scenarios to 2030 for the power sector in sub-Saharan Africa. *Utilities Policy* 20: 1–16. doi:10.1016/j.jup.2011.11.002.

Benson, P., S. E. Piper, M. Neethling, C. J. Vernon, A. Botha, A. Boshoff, W. D. Borello, R. Borello, et al. 2007. *Cape Griffon Vulture Gyps coprotheres: breeding colony conservation and monitoring protocol*. Johannesburg: Endangered Wildlife Trust.

BirdLife International and NatureServe. 2015. Bird species distribution maps of the world. Version 4.0. BirdLife International, Cambridge, UK and NatureServe, Arlington, USA.

BirdLife International, and VCF. 2014. Ban veterinary diclofenac: *Technical summary*: 1–12.

BirdLife International. 2017. *Gyps coprotheres* (amended version of 2016 assessment). *The IUCN Red List of Threatened Species 2017*. doi:https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T22695225A118592987.en.

Birds of Prey Programme. 2007. *The Sasol guide to the establishment and operation of supplementary feeding sites for vultures.* Modderfontein, South Africa: The Endangered Wildlife Trust.

Blair, G., and K. Imai. 2010. List: statistical methods for the item count technique and list experiment. The Comprehensive R Archive Network (CRAN), available at http://CRAN.R-project.org/ package=list.

Blair, G., and K. Imai. 2012. Statistical Analysis of List Experiments. *Political Analysis* 20: 47–77. doi:10.1093/pan/mpr048.

Blair, G., W. Chou, and K. Imai. 2019. List Experiments with Measurement Error. *Political Analysis* 27: 455–480. doi:10.1017/pan.2018.56.

Blanco, G. 2018. Supplementary feeding as a source of multiresistant *Salmonella* in endangered Egyptian vultures. *Transboundary and Emerging Diseases* 65: 806–816. doi:10.1111/tbed.12806.

Blanco, G., A. Junza, and D. Barrón. 2017. Occurrence of veterinary pharmaceuticals in golden eagle nestlings: Unnoticed scavenging on livestock carcasses and other potential exposure routes. *Science of The Total Environment* 586: 355–361. doi:10.1016/J.SCITOTENV.2017.02.023.

Blanco, G., A. Junza, D. Segarra, J. Barbosa, and D. Barrón. 2016. Wildlife contamination with fluoroquinolones from livestock: Widespread occurrence of enrofloxacin and marbofloxacin in vultures. *Chemosphere* 144: 1536–1543. doi:10.1016/j.chemosphere.2015.10.045.

Blanco, G., J. A. Lemus, and M. García-Montijano. 2011. When conservation management becomes contraindicated: Impact of food supplementation on health of endangered wildlife. *Ecological Applications* 21: 2469–2477. doi:10.1890/11-0038.1.

Boler, D. D., J. Killefer, D. M. Meeuwse, V. L. King, F. K. McKeith, and A. C. Dilger. 2012. Effects of slaughter time post-second injection on carcass cutting yields and bacon characteristics of immunologically castrated male pigs. *Journal of Animal Science* 90: 334–344. doi:10.2527/jas.2011-4071.

Boshoff, A. F., and C. J. Vernon. 1980. The Past and Present Distribution and Status of the Cape Vulture in the Cape Province. *Ostrich* 51: 230–250. doi:10.1080/00306525.1980.9633570.

Boshoff, A. F., and M. D. Anderson. 2006. Towards a conservation plan for the Cape Griffon *Gyps coprotheres*: identifying priorities for research and conservation action. *Vulture News* 57: 56-59.

Boshoff, A. F., J. C. Minnie, C. J. Tambling, and M. D. Michael. 2011. The impact of power line-related mortality on the Cape Vulture *Gyps coprotheres* in a part of its range, with an emphasis on electrocution. *Bird Conservation International* 21: 311–327. doi:10.1017/S095927091100013X.

Botha, A. J., J. Andevski, C. G. R. Bowden, M. Gudka, R. J. Safford, J. Tavares, and N. P. Williams. 2017. *Multi-species Action Plan to Conserve African-Eurasian Vultures*. *CMS Raptors MOU Technical Publication No. 5.* Abu Dhabi, United Arab Emirates.

Bounas, A., M. Ganoti, and E. Giannakaki. 2016. First confirmed case of lead poisoning in the endangered Egyptian Vulture (Neophron percnopterus) in the Balkans. *Vulture News* 70: 22–29.

Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems and the future. *Canadian Journal of Zoology* 68: 203-220. doi:10.1139/z90-031.

Brink, C. W., A. Santangeli, A. Amar, K. Wolter, G. Tate, S. Krüger, A. S. Tucker, and R. L. Thomson. 2020a. Quantifying the spatial distribution and trends of supplementary feeding sites in South Africa and their potential contribution to vulture energetic requirements. *Animal Conservation* 23: 491–501. doi:10.1111/acv.12561.

Brink, C. W., A. Santangeli, A. Amar, K. Wolter, G. Tate, S. Krüger, A. S. Tucker, and R. L. Thomson. 2020b. Perceptions of vulture supplementary feeding site managers and potential hidden risks to avian scavengers. *Conservation Science and Practice* 2: e237. doi:10.1111/csp2.237.

Brink, C. W., R. L. Thomson, A. Amar, M. Girardello, and A. Santangeli. 2021. Prevalence and drivers of poison use by South African commercial farmers and perceptions of alternative livestock protection measures. *Ambio* 50: 1211–1221. doi:10.1007/s13280-020-01461-2.

Brown, C. J., and S. E. Piper. 1988. Status of Cape Vultures in the Natal Drakensberg and their Cliff Site Selection. *Ostrich* 59: 139–141. doi:10.1080/00306525.1988.9633714.

Brown, C.J. (1997). Population dynamics of the bearded vulture *Gypaetus barbatus* in southern Africa. *Afrian Journal of Ecology* 35: 53-63.

Buechley, E. R., and Ç. H. Şekercioğlu. 2016. The avian scavenger crisis: Looming extinctions, trophic cascades, and loss of critical ecosystem functions. *Biological Conservation* 198: 220–228. doi:10.1016/j.biocon.2016.04.001.

Butchart, S. H. M., M. Walpole, B. Collen, a. van Strien, J. P. W. Scharlemann, R. E. a. Almond, J. E. M. Baillie, B. Bomhard, et al. 2010. Global Biodiversity: Indicators of Recent Declines. *Science* 328: 1164–1168. doi:10.1126/science.1187512.

Carrete, M., J. A. Donazar, A. Margalida, and J. Bertran. 2006a. Linking ecology, behaviour and conservation: does habitat saturation change the mating system of bearded vultures? *Biology Letters* 2: 624–627. doi:10.1098/rsbl.2006.0498.

Carrete, M., J. A. Donázar, and A. Margalida. 2006b. Density-dependent productivity depression in Pyrenean Bearded Vultures: Implications for conservation. *Ecological Applications* 16: 1674–1682. doi:10.1890/1051-0761(2006)016[1674:DPDIPB]2.0.CO;2.

Carrete, M., S. A. Lambertucci, K. Speziale, O. Ceballos, A. Travaini, M. Delibes, F. Hiraldo, and J. A. Donázar. 2010. Winners and losers in human-made habitats: Interspecific competition outcomes in two Neotropical vultures. *Animal Conservation* 13: 390–398. doi:10.1111/j.1469-1795.2010.00352.x.

Carwardine, J., K. A. Wilson, M. Watts, A. Etter, C. J. Klein, and H. P. Possingham. 2008.

Avoiding costly conservation mistakes: The importance of defining actions and costs in spatial priority settings. *PLoS ONE* 3. doi:10.1371/journal.pone.0002586.

Chaudhry, M. J. I., D. L. Ogada, R. N. Malik, M. Z. Virani, and M. D. Giovanni. 2012. First evidence that populations of the critically endangered Long-billed Vulture *Gyps indicus* in Pakistan have increased following the ban of the toxic veterinary drug diclofenac in south Asia. *Bird Conservation International* 22: 389–397. doi:10.1017/S0959270912000445.

Cheke, R. A., and M. El Hady Sidatt. 2019. A review of alternatives to fenthion for quelea bird control. *Crop Protection* 116: 15–23. doi:10.1016/j.cropro.2018.10.005.

Cloete, S. W. P., and T. T. De Villiers. 1987. Production parameters for a commercial Dorper flock on extensive pasture. *South African Journal of Animal Science* 17: 121–127.

Cloete, S. W. P., M. A. Snyman, and M. J. Herselman. 2000. Productive performance of Dorper sheep. *Small Ruminant Research* 36: 119–135.

Clout, M. N., G. P. Elliott, and B. C. Robertson. 2002. Effects of supplementary feeding on the offspring sex ratio of kakapo: A dilemma for the conservation of a polygynous parrot. *Biological Conservation* 107: 13–18. doi:10.1016/S0006-3207(01)00267-1.

Cook, C. N., M. Hockings, and R. W. Carter. 2010. Conservation in the dark? The information used to support management decisions. *Frontiers in Ecology and the Environment* 8: 181–188. doi:10.1890/090020.

Cooper, S. M., M. K. Owens, R. M. Cooper, and T. F. Ginnett. 2006. Effect of supplemental feeding on spatial distribution and browse utilization by white-tailed deer in semi-arid rangeland. *Journal of Arid Environments* 66: 716–726. doi:10.1016/j.jaridenv.2005.11.015.

Cortés-Avizanda, A., B. Martín-López, O. Ceballos, and H. M. Pereira. 2018. Stakeholders perceptions of the endangered Egyptian vulture: Insights for conservation. *Biological Conservation* 218: 173–180. doi:10.1016/J.BIOCON.2017.09.028.

Cortés-Avizanda, A., G. Blanco, T. L. Devault, A. Markandya, M. Z. Virani, J. Brandt, and J. A. Donázar. 2016. Supplementary feeding and endangered avian scavengers: Benefits, caveats, and controversies. *Frontiers in Ecology and the Environment* 14: 191–199. doi:10.1002/fee.1257.

Cortés-Avizanda, A., M. Carrete, and J. A. Donázar. 2010. Managing supplementary feeding for avian scavengers: Guidelines for optimal design using ecological criteria. *Biological Conservation* 143: 1707–1715. doi:10.1016/j.biocon.2010.04.016.

Cortés-Avizanda, A., M. Carrete, D. Serrano, and J. A. Donázar. 2009. Carcasses increase the probability of predation of ground-nesting birds: A caveat regarding the conservation value of vulture restaurants. *Animal Conservation* 12: 85–88. doi:10.1111/j.1469-1795.2008.00231.x.

Cortés-Avizanda, A., R. Jovani, M. Carrete, and J. A. Donázar. 2012. Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: A field experiment. *Ecology* 93: 2570–2579. doi:10.1890/12-0221.1.

Cowling, R. M. 2014. Let's Get Serious About Human Behavior and Conservation. *Conservation Letters* 7: 147–148. doi:10.1111/conl.12106.

Craig, C. A., R. L. Thomson, M. Girardello, and A. Santangeli. 2018. The drivers and extent of poison use by Namibia's communal farmers: Implications for averting the African vulture crisis. *Ambio* 48: 1–10. doi:10.1007/s13280-018-1128-6.

Cromie, R., J. Newth, and J. Reeves. 2015. The sociological and political aspects of reducing lead poisoning from ammunition in the UK: why the transition to non-toxic ammunition is so difficult. *Proceedings of the Oxford Lead Symposium*, Edward Grey Institute, University of Oxford, UK, 10 December 2014.

Curran, L. M., and M. Leighton. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecological Monographs* 70: 101–128. doi:10.1890/0012-9615(2000)070[0101:VRTSVI]2.0.CO;2.

Cuthbert, R., M. A. Taggart, V. Prakash, M. Saini, D. Swarup, S. Upreti, R. Mateo, S. S. Chakraborty, et al. 2011. Effectiveness of action in India to reduce exposure of gyps vultures to the toxic veterinary drug diclofenac. *PLoS ONE* 6. doi:10.1371/journal.pone.0019069.

Davies, Z. G., R. A. Fuller, M. Dallimer, A. Loram, and K. J. Gaston. 2012. Household factors influencing participation in bird feeding activity: A national scale analysis. *PLoS ONE* 7. doi:10.1371/journal.pone.0039692.

Davis, S. E., R. G. Nager, and R. W. Furness. 2005. Food availability affects adult survival as well as breeding success of Parasitic Jaegers. *Ecology* 86: 1047–1056. doi:10.1890/04-0989.

De Leeuw, E. 2005. To Mix or Not to Mix Data Collection Modes in Surveys. *Journal of official statistics* 21: 233.

Dermody, B. J., C. J. Tanner, and A. L. Jackson. 2011. The evolutionary pathway to obligate scavenging in gyps vultures. *PLoS ONE* 6: 11–15. doi:10.1371/journal.pone.0024635.

Deutsch, F. M. 1989. The False Consensus Effect: Is the Self-Justification Hypothesis Justified. *Basic and Applied Social Psychology* 10: 83–99.

doi:10.1207/s15324834basp1001.

DeVault, T. L., O. E. Rhodes, and J. A. Shivik. 2003. Scavenging by vertebrates: Behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* 102: 225–234. doi:10.1034/j.1600-0706.2003.12378.x.

Dewey, S. R., and P. L. Kennedy. 2001. Effects of supplemental food on parental-care strategies and juvenile survival of Northern Goshawks. *Auk* 118: 352–365. doi:10.2307/4089797.

Deygout, C., A. Gault, F. Sarrazin, and C. Bessa-Gomes. 2009. Modeling the impact of feeding stations on vulture scavenging service efficiency. *Ecological Modelling* 220: 1826–1835. doi:10.1016/j.ecolmodel.2009.04.030.

Dobrev, V., Z. Boev, V. Arkumarev, D. Dobrev, E. Kret, V. Saravia, A. Bounas, D. Vavylis, et al. 2016. Diet is not related to productivity but to territory occupancy in a declining population of Egyptian Vultures Neophron percnopterus. *Bird Conservation International* 26: 273–285. doi:10.1017/S0959270915000155.

Donázar J.A. 1993. Los buitres Ibéricos. Biología y conservación. 1 ed., J.M. Reyero, Madrid.

Donázar, J. A., A. Margalida, M. Carrete, and J. A. Sánchez-zapata. 2009. Too Sanitary for Vultures. *Science* 326: 664.

Ducatez, M. F., Z. Tarnagda, M. C. Tahita, A. Sow, S. de Landtsheer, B. Z. Londt, I. H. Brown, D. M. E. Osterhaus, et al. 2007. Genetic characterization of HPAI (H5N1) viruses from poultry and wild vultures, Burkina Faso. *Emerging infectious diseases* 13: 611–3. doi:10.3201/eid1304.061356.

Duriez, O., S. Herman, and F. Sarrazin. 2012. Intra-specific competition in foraging Griffon Vultures *Gyps fulvus* : 2. The influence of supplementary feeding management. *Bird Study* 59: 193–206. doi:10.1080/00063657.2012.658640.

Elliott, M. N., A. M. Zaslavsky, E. Goldstein, W. Lehrman, K. Hambarsoomians, M. K. Beckett, and L. Giordano. 2009. Effects of survey mode, patient mix, and nonresponse on CAHPS ® hospital survey scores: Methods. *Health Services Research* 44: 501–518. doi:10.1111/j.1475-6773.2008.00914.x.

Endangered Wildlife Tust. 2006. *Prevention is the Cure. Proceedings of a workshop on holistic management of human-wildlife conflict in the agricultural sector of South Africa*. Edited by B. Daly, H. Davies-Mostert, W. Davies-Mostert, S. Evans, Y. Friedmann, N. King, T. Snow, and H. Stadler. Johannesburg, South Africa: CBSG Southern Africa. doi:10.13140/2.1.2237.0085.

Epps, C. W. 2014. Considering the switch: Challenges of transitioning to non-lead hunting ammunition. *The Condor* 116: 429–434. doi:10.1650/condor-14-78.1.

Esselstyn, J. A., G. J. Wiles, and A. A. Amar. 2004. Habitat use of the Pacific sheath-tailed bat (Emballonura semicaudata) on Aguiguan, Mariana Islands. *Acta Chiropterologica* 6: 303–308. doi:10.3161/001.006.0208.

Ewen, J. G., L. Walker, S. Canessa, and J. J. Groombridge. 2015. Improving supplementary feeding in species conservation. *Conservation Biology* 29: 341–349. doi:10.1111/cobi.12410.

Fenn, S. R., E. M. Bignal, A. E. Trask, D. I. McCracken, P. Monaghan, and J. M. Reid. 2020. Collateral benefits of targeted supplementary feeding on demography and growth rate of a threatened population. *Journal of Applied Ecology* 57: 2212–2221. doi:10.1111/1365-2664.13721.

Ferrer, M., I. Newton, R. Muriel, G. Báguena, J. Bustamante, M. Martini, and V. Morandini. 2014. Using manipulation of density-dependent fecundity to recover an endangered species: The bearded vulture Gypaetus barbatus as an example. *Journal of Applied Ecology* 51: 1255–1263. doi:10.1111/1365-2664.12308.

Ferrer, M., V. Morandini, G. Baguena, and I. Newton. 2018. Reintroducing endangered raptors: A case study of supplementary feeding and removal of nestlings from wild populations. Edited by Des Thompson. *Journal of Applied Ecology* 55: 1360–1367. doi:10.1111/1365-2664.13014.

Finkelstein, M. E., D. F. Doak, D. George, J. Burnett, J. Brandt, M. Church, J. Grantham, and D. R. Smith. 2012. Lead poisoning and the deceptive recovery of the critically endangered California condor. *Proceedings of the National Academy of Sciences of the United States of America* 109: 11449–11454. doi:10.1073/pnas.1203141109.

Fluhr, J., S. Benhamou, L. Riotte-Lambert, and O. Duriez. 2017. Assessing the risk for an obligate scavenger to be dependent on predictable feeding sources. *Biological Conservation* 215: 92–98. doi:10.1016/j.biocon.2017.07.030.

Francis, M. L., K. E. Plummer, B. A. Lythgoe, C. Macallan, T. E. Currie, and J. D. Blount. 2018. Effects of supplementary feeding on interspecific dominance hierarchies in garden birds. *PLoS ONE* 13: 1–13. doi:10.1371/journal.pone.0202152.

Galbraith, J. A., J. R. Beggs, D. N. Jones, and M. C. Stanley. 2015. Supplementary feeding restructures urban bird communities. *Proceedings of the National Academy of Sciences of the United States of America* 112: E2648–E2657. doi:10.1073/pnas.1501489112.

Gangoso, L., P. Álvarez-Lloret, A. A. B. Rodríguez-Navarro, R. Mateo, F. Hiraldo, and J. A.

Donázar. 2009. Long-term effects of lead poisoning on bone mineralization in vultures exposed to ammunition sources. *Environmental Pollution* 157: 569–574. doi:10.1016/j.envpol.2008.09.015.

Gangoso, L., R. Agudo, J. D. Anad??n, M. De la Riva, A. S. Suleyman, R. Porter, and J. A. Donázar. 2013. Reinventing mutualism between humans and wild fauna: Insights from vultures as ecosystem services providers. *Conservation Letters* 6: 172–179. doi:10.1111/j.1755-263X.2012.00289.x.

Garbett, R. A. 2018. Conservation of raptors and vultures in Botswana: with a focus on lappet-faced vultures Torgos tracheliotos. *Thesis*.

Garbett, R., G. Maude, P. Hancock, D. Kenny, R. Reading, and A. Amar. 2018. Association between hunting and elevated blood lead levels in the critically endangered African white-backed vulture *Gyps africanus*. *Science of the Total Environment* 630: 1654–1665. doi:10.1016/j.scitotenv.2018.02.220.

García-Alfonso, M., Z. Morales-Reyes, L. Gangoso, W. Bouten, J. A. Sánchez-Zapata, D. Serrano, and J. A. Donázar. 2018. Probing into farmers' perceptions of a globally endangered ecosystem service provider. *Ambio* 48: 900–912. doi:10.1007/s13280-018-1102-3.

García-Heras, M. S., A. Cortés-Avizanda, and J. A. Donázar. 2013. Who are we feeding? Asymmetric individual use of surplus food resources in an insular population of the endangered Egyptian vulture Neophron percnopterus. *PLoS ONE* 8: 1–7. doi:10.1371/journal.pone.0080523.

Gilbert, M., M. Z. Virani, R. T. Watson, J. L. Oaks, P. C. Benson, A. A. Khan, S. Ahmed, J. Chaudhry, et al. 2002. Breeding and mortality of Oriental White-backed Vulture *Gyps bengalensis* in Punjab Province, Pakistan. *Bird Conservation International* 12: 311–326. doi:10.1017/S0959270902002198.

Gilbert, M., R. T. Watson, S. Ahmed, M. Asim, and J. A. Johnson. 2007. Vulture restaurants and their role in reducing diclofenac exposure in Asian vultures. *Bird Conservation International* 17: 63. doi:10.1017/S0959270906000621.

Gómez-Ramírez, P., P. J. Jiménez-Montalbán, D. Delgado, E. Martínez-López, P. María-Mojica, A. Godino, and A. J. García-Fernández. 2018. Development of a QuEChERS method for simultaneous analysis of antibiotics in carcasses for supplementary feeding of endangered vultures. *Science of The Total Environment* 626: 319–327. doi:10.1016/j.scitotenv.2018.01.060.

González, L. M., A. Margalida, R. Sánchez, and J. Oria. 2006. Supplementary feeding as an effective tool for improving breeding success in the Spanish imperial eagle (Aquila adalberti). *Biological Conservation* 129: 477–486. doi:10.1016/j.biocon.2005.11.014.

Gore, M. L., A. Hübschle, A. J. Botha, B. M. Coverdale, R. Garbett, R. M. Harrell, S. C. Krüger, J. M. Mullinax, et al. 2020. A conservation criminology-based desk assessment of vulture poisoning in the Great Limpopo Transfrontier Conservation Area. *Global Ecology and Conservation* 23: 1–16. doi:10.1016/j.gecco.2020.e01076.

Gray, W. B., and J. P. Shimshack. 2011. The effectiveness of environmental monitoring and enforcement: A review of the empirical evidence. *Review of Environmental Economics and Policy* 5: 3–24. doi:10.1093/reep/req017.

Green, R. E., I. Newton, S. Shultz, A. A. Cunningham, M. Gilbert, D. J. Pain, and V. Prakash. 2004. Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. *Journal of Applied Ecology* 41: 793–800. doi:10.1111/j.0021-8901.2004.00954.x.

Gutiérrez-Cánovas, C., M. Moleón, P. Mateo-Tomás, P. P. Olea, E. Sebastián-González, and J. A. Sánchez-Zapata. 2020. Large home range scavengers support higher rates of carcass removal. *Functional Ecology* 34: 1921–1932. doi:10.1111/1365-2435.13619.

Haig, S. M., J. D'Elia, C. Eagles-Smith, J. M. Fair, J. Gervais, G. Herring, J. W. Rivers, and J. H. Schulz. 2014. The persistent problem of lead poisoning in birds from ammunition and fishing tackle. *The Condor* 116: 408–428. doi:10.1650/CONDOR-14-36.1.

Halpern, B. S., C. R. Pyke, H. E. Fox, J. Chris Haney, M. A. Schlaepfer, and P. Zaradic. 2006. Gaps and mismatches between global conservation priorities and spending. *Conservation Biology* 20: 56–64. doi:10.1111/j.1523-1739.2005.00258.x.

Hampton, J. O., M. Laidlaw, E. Buenz, and J. M. Arnemo. 2018. Heads in the sand: Public health and ecological risks of lead-based bullets for wildlife shooting in Australia. *Wildlife Research* 45: 287-306. doi:10.1071/WR17180.

Hempson, G. P., S. Archibald, and W. J. Bond. 2017. The consequences of replacing wildlife with livestock in Africa. *Scientific Reports* 7: 1–10. doi:10.1038/s41598-017-17348-4.

Henriques, M., R. Buij, H. Monteiro, J. Sá, F. Wambar, J. P. Tavares, A. Botha, G. Citegetse, et al. 2020. Deliberate poisoning of Africa's vultures. *Science* 370: 304. doi:10.1126/science.abd1862.

Herring, G., C. A. Eagles-Smith, J. A. Buck, A. E. Shiel, C. R. Vennum, C. Emery, B. Johnson, D. Leal, et al. 2020. The lead (Pb) lining of agriculture-related subsidies: enhanced Golden Eagle growth rates tempered by Pb exposure. *Ecosphere* 11: 1-17. doi:10.1002/ecs2.3006.

Hilgartner, R., D. Stahl, and D. Zinner. 2014. Impact of supplementary feeding on reproductive success of white storks. *PLoS ONE* 9: 1–8. doi:10.1371/journal.pone.0104276.

Hirschauer, M. T., K. Wolter, R. E. Green, and T. H. Galligan. 2017. Immature Cape Vulture *Gyps coprotheres* breaks species range record. *Biodiversity Observations* 8: 1–4.

Hoffman, L. C. 2000. The yield and carcass chemical composition of impala (Aepyceros melampus), a southern African antelope species. *Journal of the Science of Food and Agriculture* 80: 752–756. doi:10.1002/(SICI)1097-0010(20000501)80:6<752::AID-JSFA608>3.0.CO;2-L.

Hoffman, L. C. C., A. C. C. Mostert, M. Kidd, and L. L. L. Laubscher. 2009. Meat quality of kudu (Tragelaphus strepsiceros) and impala (Aepyceros melampus): Carcass yield, physical quality and chemical composition of kudu and impala Longissimus dorsi muscle as affected by gender and age. *Meat Science* 83: 788–795. doi:10.1016/j.meatsci.2009.08.022.

Hoffman, L. C., and E. Wiklund. 2006. Game and venison - meat for the modern consumer. *Meat Science* 74: 197–208. doi:10.1016/j.meatsci.2006.04.005.

Hogstad, O. 2005. Numerical and functional responses of breeding passerine species to mass occurrence of geometrid caterpillars in a subalpine birch forest: A 30-year study. *Ibis* 147: 77–91. doi:10.1111/j.1474-919x.2004.00338.

Hoodless, A. N., R. A. H. Draycott, M. N. Ludiman, and P. A. Robertson. 1999. Effects of supplementary feeding on territoriality, breeding success and survival of pheasants. *Journal of Applied Ecology* 36: 147–156. doi:10.1046/j.1365-2664.1999.00388.x.

Houston, C., and J. E. Cooper. 1975. The digestive tract of the Whiteback Griffon Vulture and its role in disease transmission among wild ungulates. *Journal of Wildlife Diseases* 11: 306–313.

Houston, D. C. 1986. Scavenging Efficiency of Turkey Vultures in Tropical Forest. *The Condor* 88: 318–323.

Houston, D. C. 1987. Competition for food between Neotropical vultures in forest. *Ibis* 130: 402–417.

Hugh-Jones, M. E., and V. de Vos. 2002. Anthrax and wildlife. *Revue scientifique et technique* 21: 359–383. doi:10.1002/9781118829417.ch9.

Hulme, D., and M. Murphree. 1999. Communities, wildlife and the “new conservation” in Africa. *Journal of International Development* 11: 277–285. doi:10.1002/(SICI)1099-1328(199903/04)11:2<277::AID-JID582>3.0.CO;2-T.

Isomursu, M., J. Koivusaari, T. Stjernberg, V. Hirvelä-Koski, and E.-R. Venäläinen. 2018. Lead poisoning and other human-related factors cause significant mortality in white-tailed eagles. *Ambio* 47: 858–868. doi:10.1007/s13280-018-1052-9.

IUCN. 2019. The IUCN Red List of Thretened Species. *Version 2019-2*.

IUCN. 2021. The IUCN Red List of Threatened Species. *Version 2020-1*.

Johnson, C. N., A. Balmford, B. W. Brook, J. C. Buettel, M. Galetti, L. Guangchun, and J. M. Wilmshurst. 2017. Biodiversity losses and conservation responses in the Anthropocene. *Science* 356: 270–275. doi:10.1126/science.aam9317.

Jones, J. D., M. J. Kauffman, K. L. Monteith, B. M. Scurlock, S. E. Albeke, and P. C. Cross. 2014. Supplemental feeding alters migration of a temperate ungulate. *Ecological Applications* 24: 1769–1779. doi:10.1890/13-2092.1.

Jones, M. P., K. E. Pierce, and D. Ward. 2007. Avian Vision: A Review of Form and Function with Special Consideration to Birds of Prey. *Journal of Exotic Pet Medicine* 16: 69–87. doi:10.1053/j.jepm.2007.03.012.

Kane, A., A. L. Jackson, A. Monadjem, M. A. Colomer, and A. Margalida. 2015. Carrion ecology modelling for vulture conservation: Are vulture restaurants needed to sustain the densest breeding population of the African white-backed vulture? *Animal Conservation* 18: 279–286. doi:10.1111/acv.12169.

Kane, A., K. Wolter, W. Neser, A. Kotze, V. Naidoo, and A. Monadjem. 2016. Home range and habitat selection of Cape Vultures *Gyps coprotheres* in relation to supplementary feeding. *Bird Study* 63: 387–394. doi:10.1080/00063657.2016.1214105.

Karanth, K. K., A. M. Gopalaswamy, R. DeFries, and N. Ballal. 2012. Assessing Patterns of Human-Wildlife Conflicts and Compensation around a Central Indian Protected Area. *PLoS ONE* 7: e50433. doi:10.1371/journal.pone.0050433.

Karanth, K. K., L. Naughton-Treves, R. Defries, and A. M. Gopalaswamy. 2013. Living with wildlife and mitigating conflicts around three indian protected areas. *Environmental Management* 52: 1320–1332. doi:10.1007/s00267-013-0162-1.

Kareiva, P., and M. Marvier. 2012. What Is Conservation Science? *BioScience* 62: 962–969. doi:10.1525/bio.2012.62.11.5.

Keith, D. A., T. G. Martin, E. McDonald-Madden, and C. Walters. 2011. Uncertainty and adaptive management for biodiversity conservation. *Biological Conservation* 144: 1175–1178. doi:10.1016/j.biocon.2010.11.022.

Kellert, S. R., and E. O. Wilson, ed. 1993. *The biophilia hypothesis*. Covelo, California: Island Press.

Kelly, T. R., J. Grantham, D. George, A. Welch, J. Brandt, L. J. Burnett, K. J. Sorenson, M. Johnson, et al. 2014. Spatiotemporal Patterns and Risk Factors for Lead Exposure in Endangered California Condors during 15 Years of Reintroduction. *Conservation Biology* 28: 1721–1730. doi:10.1111/cobi.12342.

Kemp, A. and Begg, K. 2001. Comparison of time-activity budgets and population structure for 18 large-bird species in the Kruger National Park, South Africa. *Ostrich* 72, 179-184.

Kennedy, P. L., and J. M. Ward. 2003. Effects of experimental food supplementation on movements of juvenile northern goshawks (Accipiter gentilis atricapillus). *Oecologia* 134: 284–291. doi:10.1007/s00442-002-1108-0.

Korpimäki, E., and J. Wiehn. 1998. Clutch Size of Kestrels: Seasonal Decline and Experimental Evidence for Food Limitation under Fluctuating Food Conditions. *Oikos* 83: 259–272. doi:10.2307/3546837.

Korpimäki, E., and K. Norrdahl. 1991. Numerical and Functional Responses of Kestrels, Short-Eared Owls, and Long-Eared Owls to Vole Densities. *Ecology* 72: 814–826.

Krüger, S. C., and A. Amar. 2018. Lead exposure in the Critically Endangered Bearded Vulture (Gypaetus barbatus) population in southern Africa. *Journal of Raptor Research* 52: 491–499.

Krüger, S. C., R. Simmons, and A. Amar. 2015. Anthropogenic activities influence the abandonment of Bearded Vulture Gypaetus barbatus territories in southern Africa. *The Condor: Ornithological Applications* 117: 94–107. doi:10.1650/CONDOR-14-121.1.

Krüger, S., T. Reid, and A. Amar. 2014. Differential Range Use between Age Classes of Southern African Bearded Vultures Gypaetus barbatus. *PLoS ONE* 9: e114920. doi:10.1371/journal.pone.0114920.

Kumasi, T. C., K. Obiri-Danso, and J. H. Ephraim. 2010. Community engagement in the sustainable management of rivers: Barekese catchment, Kumasi, Ghana. *Environment, Development and Sustainability* 12: 927–943. doi:10.1007/s10668-010-9232-1.

Kushwaha, S., A. Kumar, and A. Singh. 2020. Conflict Between Two Best Acquaintances of Man: Vultures and Dogs. *Journal of Wildlife Research* 8: 39–44.

Lambertucci, S. A., P. A. E. Alarcón, F. Hiraldo, J. A. Sanchez-Zapata, G. Blanco, and J. A. Donázar. 2014. Apex scavenger movements call for transboundary conservation policies. *Biological Conservation* 170: 145–150. doi:10.1016/j.biocon.2013.12.041.

Latorre, M. A., G. Ripoll, E. García-Belenguer, and L. Ariño. 2009. The increase of slaughter weight in gilts as a strategy to optimize the production of Spanish high quality dry-cured ham1. *Journal of Animal Science* 87: 1464–1471. doi:10.2527/jas.2008-1362.

Lewis, S. L., and M. A. Maslin. 2015. Defining the Anthropocene. *Nature* 519: 171–180. doi:10.1038/nature14258.

Liberatori, F., and V. Penteriani. 2001. A long-term analysis of the declining population of the Egyptian vulture in the Italian peninsula: Distribution, habitat preference, productivity and conservation implications. *Biological Conservation* 101: 381–389. doi:10.1016/S0006-3207(01)00086-6.

Lieury, N., M. Gallardo, C. Ponchon, A. Besnard, and A. Millon. 2015. Relative contribution of local demography and immigration in the recovery of a geographically-isolated population of the endangered Egyptian vulture. *Biological Conservation* 191: 349–356. doi:10.1016/j.biocon.2015.07.008.

Linnell, J. D. C., J. Odden, M. E. Smith, R. Aanes, J. E. Swenson, A. Ronn, and J. E. Swen. 2008. Carnivores and Predation Large carnivores that kill livestock : do " problem individuals " really exist? *Society* 27: 698–705.

Linnell, J. D. C., R. Aanes, J. E. Swenson, J. Odden, and M. E. Smith. 1997. Translocation of carnivores as a method for managing problem animals: A review. *Biodiversity and Conservation* 6: 1245-1257. doi:10.1023/B:BIOC.0000034011.05412.cd.

López-Bao, J. V., A. Rodríguez, and F. Palomares. 2008. Behavioural response of a trophic specialist, the Iberian lynx, to supplementary food: Patterns of food use and implications for conservation. *Biological Conservation* 141: 1857–1867. doi:10.1016/j.biocon.2008.05.002.

López-López, P., C. García-Ripollés, and V. Urios. 2014. Food predictability determines space use of endangered vultures: Implications for management of supplementary feeding. *Ecological Applications* 24: 938–949. doi:10.1890/13-2000.1.

Margalida, A. 2010. Supplementary feeding during the chick-rearing period is ineffective in increasing the breeding success in the bearded vulture (Gypaetus barbatus). *European Journal of Wildlife Research* 56: 673–678. doi:10.1007/s10344-010-0366-0.

Margalida, A., and M. À. Colomer. 2012. Modelling the effects of sanitary policies on European vulture conservation. *Scientific Reports* 2. doi:10.1038/srep00753.

Margalida, A., J. Bertran, and R. Heredia. 2009. Diet and food preferences of the endangered Bearded Vulture *Gypaetus barbatus*: A basis for their conservation. *Ibis* 151: 235–243. doi:10.1111/j.1474-919x.2008.00904.x.

Margalida, A., J. M. Martínez, A. Gómez de Segura, M. A. Colomer, R. Arlettaz, and D. Serrano. 2017. Supplementary feeding and young extraction from the wild are not a sensible alternative to captive breeding for reintroducing bearded vultures Gypaetus barbatus. *Journal of Applied Ecology* 54: 334–340. doi:10.1111/1365-2664.12541.

Margalida, A., M. À. Colomer, and D. Oro. 2014. Man-induced activities modify demographic parameters in a long-lived species: Effects of poisoning and health policies. *Ecological Applications* 24: 436–444. doi:10.1890/13-0414.1.

Marin, C., C. Torres, F. Marco-Jiménez, M. Cerdà-Cuéllar, S. Sevilla, T. Ayats, and S. Vega. 2018. Supplementary feeding stations for conservation of vultures could be an important source of monophasic Salmonella typhimurium 1,4,[5],12:i:-. *Science of the Total Environment* 636: 449–455. doi:10.1016/j.scitotenv.2018.04.310.

Markandya, A., T. Taylor, A. Longo, M. N. Murty, S. Murty, and K. Dhavala. 2008. Counting the cost of vulture decline-An appraisal of the human health and other benefits of vultures in India. *Ecological Economics* 67: 194–204. doi:10.1016/j.ecolecon.2008.04.020.

Marker, L. L., A. J. Dickman, and D. W. Macdonald. 2005. Perceived effectiveness of livestock-guarding dogs placed on Namibian farms. *Rangeland Ecology and Management* 58: 329–336. doi:10.2111/1551-5028(2005)058[0329:PEOLDP]2.0.CO;2.

Martin, D. 1996. On the cultural ecology of sky burial on the Himalayan Plateau. *East and West* 46: 353–370.

Martin, T. E. 1987. Food as a Limit on Breeding Birds : A Life-History Perspective. *Annual Reviews* 18: 453–487.

Martínez-Abraín, A., and D. Oro. 2013. Preventing the development of dogmatic approaches in conservation biology: A review. *Biological Conservation* 159: 539-547. doi:10.1016/j.biocon.2012.10.020.

Martínez-Abraín, A., B. Sarzo, E. Villuendas, M. A. Bartolomé, E. Mínguez, and D. Oro. 2004. Unforeseen effects of ecosystem restoration on yellow-legged gulls in a small western Mediterranean island. *Environmental Conservation* 31: 219–224. doi:10.1017/S0376892904001456.

Martínez-Abraín, A., G. Tavecchia, H. M. Regan, J. Jiménez, M. Surroca, and D. Oro. 2012. Effects of wind farms and food scarcity on a large scavenging bird species following an epidemic of bovine spongiform encephalopathy. *Journal of Applied Ecology* 49: 109–117. doi:10.1111/j.1365-2664.2011.02080.x.

Mateo-Tomás, P., and J. V. López-Bao. 2020. Poisoning poached megafauna can boost trade in African vultures. *Biological Conservation* 241: 108389. doi:10.1016/j.biocon.2019.108389.

Mateo-Tomás, P., P. P. Olea, I. S. Sánchez-Barbudo, and R. Mateo. 2012. Alleviating human-wildlife conflicts: Identifying the causes and mapping the risk of illegal poisoning of wild fauna. *Journal of Applied Ecology* 49: 376–385. doi:10.1111/j.1365-2664.2012.02119.x.

McClure, C. J. W., J. R. S. Westrip, J. A. Johnson, S. E. Schulwitz, M. Z. Virani, R. Davies, A. Symes, H. Wheatley, et al. 2018. State of the world's raptors: Distributions, threats, and conservation recommendations. *Biological Conservation* 227: 390–402. doi:10.1016/J.BIOCON.2018.08.012.

Mckean, S., M. Mander, N. Diederichs, L. Ntuli, K. Mavundla, V. Williams, and J. Wakelin. 2013. The impact of traditional use on vultures in South Africa. *Vulture News* 65: 15–36. doi:10.4314/vulnew.v65i1.2.

McManus, J. S., A. J. Dickman, D. Gaynor, B. H. Smuts, and D. W. Macdonald. 2015. Dead or alive? Comparing costs and benefits of lethal and non-lethal human-wildlife conflict mitigation on livestock farms. *ORYX* 49: 687–695. doi:10.1017/S0030605313001610.

Meretsky, V. J., and R. W. Mannan. 1999. Supplemental feeding regimes for egyptian vultures in the Negev Desert, Israel. *Journal of Wildlife Management* 63: 157–165.

Miller, J. R. B. B., K. J. Stoner, M. R. Cejtin, T. K. Meyer, A. D. Middleton, and O. J. Schmitz. 2016b. Effectiveness of contemporary techniques for reducing livestock depredations by large carnivores. *Wildlife Society Bulletin* 40: 806–815. doi:10.1002/wsb.720.

Miller, J. R. B., Y. V. Jhala, and J. Jena. 2016a. Livestock losses and hotspots of attack from tigers and leopards in Kanha Tiger Reserve, Central India. *Regional Environmental Change* 16: 17–29. doi:10.1007/s10113-015-0871-5.

Milner, J. M., F. M. Van Beest, K. T. Schmidt, R. K. Brook, and T. Storaas. 2014. To feed or not to feed? Evidence of the intended and unintended effects of feeding wild ungulates. *The Journal of Wildlife Management* 78: 1322–1334. doi:10.1002/jwmg.798.

Monadjem, A., A. Kane, A. Botha, C. Kelly, and C. Murn. 2018. Spatially explicit poisoning risk affects survival rates of an obligate scavenger. *Scientific Reports* 8: 4364. doi:10.1038/s41598-018-22632-y.

Monadjem, A., A. Kane, A. Botha, D. Dalton, and A. Kotze. 2012. Survival and Population Dynamics of the Marabou Stork in an Isolated Population, Swaziland. *PLoS ONE* 7: e46434. doi:10.1371/journal.pone.0046434.

Monsarrat, S., S. Benhamou, F. Sarrazin, C. Bessa-Gomes, W. Bouten, and O. Duriez. 2013. How Predictability of Feeding Patches Affects Home Range and Foraging Habitat Selection in Avian Social Scavengers? *PLoS ONE* 8: 1–11.

doi:10.1371/journal.pone.0053077.
Morales-Reyes, Z., B. Martín-López, M. Moleón, P. Mateo-Tomás, F. Botella, A. Margalida, J. A. Donázar, G. Blanco, et al. 2018. Farmer Perceptions of the Ecosystem Services Provided by Scavengers: What, Who, and to Whom. *Conservation Letters* 11: 1-11. doi:10.1111/conl.12392.
Moreno-Opo, R., A. Trujillano, Á. Arredondo, L. M. González, and A. Margalida. 2015a. Manipulating size, amount and appearance of food inputs to optimize supplementary feeding programs for European vultures. *Biological Conservation* 181: 27–35. doi:10.1016/j.biocon.2014.10.022.
Moreno-Opo, R., A. Trujillano, and A. Margalida. 2015b. Optimization of supplementary feeding programs for European vultures depends on environmental and management factors. *Ecosphere* 6: 1-15. doi:10.1890/es15-00009.1.
Munari, C., V. Infantini, M. Scoponi, E. Rastelli, C. Corinaldesi, and M. Mistri. 2017. Microplastics in the sediments of Terra Nova Bay (Ross Sea, Antarctica). *Marine Pollution Bulletin* 122: 161–165. doi:10.1016/j.marpolbul.2017.06.039.
Mundy, P. J. 1978. The Egyptian Vulture (Neophron percnopterus) in southern Africa. *Biological Conservation* 14: 307–315.
Mundy, P., D. Butchart, J. Ledger, and S. Piper. 1992. *The Vultures of Africa*. Edited by Eleanor-Mary Cadell. Randburg, South Africa: Acorn Books and Russel Friedman Books.
Murn, C. and Botha A. (2018). A clear and present danger: Impacts of poisoning on a vulture population and the effect of poison response activities. *Oryx* **52**, 552-558.
Murray, M. H., D. J. Becker, R. J. Hall, and S. M. Hernandez. 2016. Wildlife health and supplemental feeding: A review and management recommendations. *Biological Conservation* 204: 163-174. doi:10.1016/j.biocon.2016.10.034.
Naidoo, R., L. C. Weaver, R. W. Diggle, G. Matongo, G. Stuart-Hill, and C. Thouless. 2016. Complementary benefits of tourism and hunting to communal conservancies in Namibia. *Conservation Biology* 30: 628–638. doi:10.1111/cobi.12643.
Naidoo, V., K. Wolter, I. Espie, and A. Kotze. 2012. Lead toxicity: consequences and interventions in an intensively managed (*Gyps coprotheres*) vulture colony. *Journal of Zoo and Wildlife Medicine* 43: 573–578. doi:10.1638/2012-0060R.1.
Nelson, F., C. Foley, L. S. Foley, A. Leposo, E. Loure, D. Peterson, M. Peterson, T. Peterson, et al. 2010. Payments for ecosystem services as a framework for community-based conservation in Northern Tanzania: Conservation practice and policy. *Conservation*

Biology 24: 78–85. doi:10.1111/j.1523-1739.2009.01393.x.

Newsome, D., A. Lewis, and D. Moncrieff. 2004. Impacts and risks associated with developing, but unsupervised, stingray tourism at Hamelin Bay, Western Australia. *International Journal of Tourism Research* 6: 305–323. doi:10.1002/jtr.491.

Newsome, D., and K. Rodger. 2008. To feed or not to feed: A contentious issue in wildlife tourism. In *Too close for comfort: contentious issues in human-wildlife encounters*, ed. D. Lunney, A. Munn, and W. Meikle, 255–270. New South Wales, Australia: Royal Zoological Society of New South Wales. doi:10.7882/fs.2008.029.

Norton, D. A. 2000. Conservation biology and private land: Shifting the focus. *Conservation Biology* 14: 1221–1223. doi:10.1046/j.1523-1739.2000.01451.x.

Nuno, A., and F. A. V. St. John. 2015. How to ask sensitive questions in conservation: A review of specialized questioning techniques. *Biological Conservation* 189: 5–15. doi:10.1016/j.biocon.2014.09.047.

Nyhus, P. J. 2016. Human-Wildlife Conflict and Coexistence. *Annual Review of Environment and Resources* 41: 143–171. doi:10.1146/annurev-environ-110615-085634.

O'Bryan, C. J., M. H. Holden, and J. E. M. Watson. 2019. The mesoscavenger release hypothesis and implications for ecosystem and human well-being. Edited by Johannes Knops. *Ecology Letters* 22: 1340–1348. doi:10.1111/ele.13288.

O'Leary, R., and D. N. Jones. 2006. The use of supplementary foods by Australian magpies Gymnorhina tibicen: Implications for wildlife feeding in suburban environments. *Austral Ecology* 31: 208–216. doi:10.1111/j.1442-9993.2006.01583.x.

Oaks, J. L., M. Gilbert, M. Z. Virani, R. T. Watson, C. U. Meteyer, B. A. Rideout, H. L. Shivaprasad, S. Ahmed, et al. 2004. Diclofenac residues as the cause of vulture population decline in Pakistan. *Nature* 427: 630–633. doi:10.1038/nature02317.

Ogada, D. L. 2014. The power of poison: Pesticide poisoning of Africa's wildlife. *Annals of the New York Academy of Sciences* 1322: 1–20. doi:10.1111/nyas.12405.

Ogada, D. L., M. E. Torchin, M. F. Kinnaird, and V. O. Ezenwa. 2012a. Effects of Vulture Declines on Facultative Scavengers and Potential Implications for Mammalian Disease Transmission. *Conservation Biology* 26: 453–460. doi:10.1111/j.1523-1739.2012.01827.x.

Ogada, D., A. Botha, and P. Shaw. 2016. Ivory poachers and poison: Drivers of Africa's declining vulture populations. *ORYX* 50: 593–596. doi:10.1017/S0030605315001209.

Ogada, D., P. Shaw, R. L. Beyers, R. Buij, C. Murn, J. M. Thiollay, C. M. Beale, R. M. Holdo, et al. 2016. Another Continental Vulture Crisis: Africa's Vultures Collapsing toward Extinction. *Conservation Letters* 9: 89–97. doi:10.1111/conl.12182.

Ogada, D.L., F. Keesing, and M. Z. Virani. 2012b. Dropping dead: Causes and consequences of vulture population declines worldwide. *Annals of the New York Academy of Sciences* 1249: 57–71. doi:10.1111/j.1749-6632.2011.06293.x.

Olson, Z. H., J. C. Beasley, T. L. Devault, and O. E. Rhodes. 2012. Scavenger community response to the removal of a dominant scavenger. *Oikos* 121: 77–84. doi:10.1111/j.1600-0706.2011.19771.x.

Olsson, P., and C. Folke. 2001. Local ecological knowledge and institutional dynamics for ecosystem management: A study of Lake Racken watershed, Sweden. *Ecosystems* 4: 85–104. doi:10.1007/s100210000061.

Oppel, S., V. Dobrev, V. Arkumarev, V. Saravia, A. Bounas, E. Kret, T. Skartsi, M. Velevski, et al. 2016a. Assessing the effectiveness of intensive conservation actions: Does guarding and feeding increase productivity and survival of Egyptian Vultures in the Balkans? *Biological Conservation* 198: 157–164. doi:10.1016/j.biocon.2016.04.002.

Oppel, S., V. Dobrev, V. Arkumarev, V. Saravia, A. Bounas, E. Kret, T. Skartsi, M. Velevski, et al. 2016b. Should we trust beliefs or data when assessing conservation interventions? A reply to Stoynov 2016. *Biological Conservation* 204: 149–150. doi:10.1016/j.biocon.2016.10.031.

Oro, D., A. Margalida, M. Carrete, R. Heredia, and J. A. Donázar. 2008. Testing the Goodness of Supplementary Feeding to Enhance Population Viability in an Endangered Vulture. *PLoS ONE* 3: e4084. doi:10.1371/journal.pone.0004084.

Osbaldiston, R., and J. P. Schott. 2012. Environmental sustainability and behavioral science: Meta-analysis of proenvironmental behavior experiments. *Environment and Behavior* 44: 257–299. doi:10.1177/0013916511402673.

Pain, D. J., a a Cunningham, P. F. Donald, J. W. Duckworth, D. C. Houston, T. Katzner, J. Parry-Jones, C. Poole, et al. 2003. Causes and Effects of Temporospatial Declines of Gyps Vultures in Asia. *Conservation Biology* 17: 661–671. doi:10.1046/j.1523-1739.2003.01740.x.

Pérez Urdiales, M., A.O. Lansink, and A. Wall. 2016. Eco-efficiency among dairy farmers: The importance of socio-economic characteristics and farmer attitudes. *Environmental and Resource Economics* 64: 559–574. https://doi.org/10.1007/s10640-015-9885-1.

Pearson, M., and M. Husby. 2021. Supplementary feeding improves breeding performance in Eurasian Eagle Owl (Bubo bubo). *Ornis Fennica* 98: 46–58.

Pennycuick, C. J. 1972. Soaring Behaviour and Performance of Some East African Birds, Observed From a Motor-Glider. *Ibis* 114: 178–218. doi:10.1111/j.1474-919X.1972.tb02603.x.

Perrins, C. M. 1970. The Timing of Birds‘ Breeding Seasons. *Ibis* 112: 242–255. doi:10.1111/j.1474-919X.1970.tb00096.x.

Pfeiffer, M. B., J. A. Venter, and C. T. Downs. 2015a. Foraging range and habitat use by Cape vulture *Gyps coprotheres* from the msikaba colony, Eastern Cape Province, South Africa. *Koedoe* 57: 1–11. doi:10.4102/koedoe.v57i1.1240.

Pfeiffer, M. B., J. A. Venter, and C. T. Downs. 2015b. Identifying anthropogenic threats to Cape Vultures *Gyps coprotheres* using community perceptions in communal farmland, Eastern Cape Province, South Africa. *Bird Conservation International* 25: 353–365. doi:10.1017/S0959270914000148.

Pikula, J., P. Hajkova, H. Bandouchova, I. Bednarova, V. Adam, M. Beklova, J. Kral, K. Ondracek, et al. 2013. Lead toxicosis of captive vultures: Case description and responses to chelation therapy. *BMC Veterinary Research* 9: 11. doi:10.1186/1746-6148-9-11.

Pimm, S. L., C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C. M. Roberts, et al. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344. doi:10.1126/science.1246752.

Piper, S. E. 2004a. Vulture Restaurants-Conflict in the midst of Plenty. In *Proceedings of the 6th World Conference on Birds of Prey and Owls*, ed. R. . Chancellor and B.-U. Meyburg, 341–349. Budapest: WWGBP and MME.

Piper, S. E. 2004b. Vulture Restaurants. In *The Vultures of Southern Africa – Quo Vadis?. Proceedings of a workshop on vulture research and conservation in southern Africa*, ed. A. F. Monadjem, A., Anderson, M.D., Piper, S.E. and Boshoff, 220–227. Johannesburg: Birds of Prey Working Group.

Pitarch, A., C. Gil, and G. Blanco. 2017. Oral mycoses in avian scavengers exposed to antibiotics from livestock farming. *Science of the Total Environment* 605–606: 139–146. doi:10.1016/j.scitotenv.2017.06.144.

Plaza, P. I., and S. A. Lambertucci. 2018. More massive but potentially less healthy: black vultures feeding in rubbish dumps differed in clinical and biochemical parameters with wild feeding birds. *PeerJ* 6: e4645. doi:10.7717/peerj.4645.

Plaza, P., G. Blanco, and S. A. Lambertucci. 2020. Implications of bacterial, viral, and mycotic microorganisms in vultures for wildlife conservation, ecosystem services and public health. *Ibis* 162: 1109-1124. doi:10.1111/ibi.12865.

Pokras, M., and M. R. Kneeland. 2008. Understanding Lead Uptake and Effects across

Species Lines: A Conservation Medicine Based Approach. In *Ingestion ofLead from Spent Ammunition: Implications for Wild- life and Humans*, ed. R. T. Watson, M. Fuller, M. Pokras, and G. Hunt, 7–22. Boise: The Peregrine Fund. doi:10.4080/ilsa.2009.0101.

Potschin, M. B., and R. H. Haines-Young. 2011. Ecosystem services: Exploring a geographical perspective. *Progress in Physical Geography* 35: 575–594. doi:10.1177/0309133311423172.

Prakash, V., D. J. D. J. Pain, A. A. a. Cunningham, P. F. F. Donald, N. Prakash, A. Verma, R. Gargi, S. Sivakumar, et al. 2003. Catastrophic collapse of indian white-backed *Gyps bengalensis* and long-billed *Gyps indicus* vulture populations. *Biological Conservation* 109: 381–390. doi:10.1016/S0006-3207(02)00164-7.

Prakash, V., R. Green, D. Pain, S. Ranade, S. Saravanan, N. Prakash, R. Venkitachalam, R. Cuthber, et al. 2007. Recent Changes in Populations of Resident *Gyps* Vultures in India. *The journal of the Bombay Natural History Society.* 104: 127–133.

Prum, O. R., J. S. Berv, A. Dornburg, D. J. Field, J. P. Townsend, E. M. Lemmon, and A. R. Lemmon. 2015. A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature **526**: 569–573. https://doi.org/10.1038/nature15697*

Pullin, A. S., T. M. Knight, D. A. Stone, and K. Charman. 2004. Do conservation managers use scientific evidence to support their decision-making? *Biological Conservation* 119: 245–252. doi:10.1016/j.biocon.2003.11.007.

QGIS. 2019. QGIS Geographic Information System. Open Source Geospatial Foundation Project.

.

R Core Team. 2019. R: A Language and Environment for Statistical Computing. Vienna, Austria, Austria: R Foundation for Statistical Computing.

Radostits, O. M., C. C. Gay, K. W. Hinchcliff, and P. D. Constable. 2007. *Veterinary Medicine: A Textbook of the Diseases of Cattle, Horses, Sheep, Pigs and Goats*. 10th ed. London: Saunders.

Reading, R. P., J. Bradley, P. Hancock, R. Garbett, M. Selebatso, and G. Maude. 2019. Home-range size and movement patterns of Hooded Vultures Necrosyrtes monachus in southern Africa. *Ostrich* 90: 73–77. doi:10.2989/00306525.2018.1537314.

Redpath, S. M., J. Young, A. Evely, W. M. Adams, W. J. Sutherland, A. Whitehouse, A. Amar, R. A. Lambert, et al. 2013. Understanding and managing conservation conflicts. *Trends in Ecology and Evolution* 28: 100–109. doi:10.1016/j.tree.2012.08.021.

Reid, T., S. Krüger, P. D. Whitfield, and A. Amar. 2015. Using Spatial analysis of bearded vulture movement in southern Africa to inform wind turbine placement. *Journal of Applied Ecology* 52: 881–892. doi:10.1111/1365-2664.12468.

Robb, G. N., R. A. McDonald, D. E. Chamberlain, and S. Bearhop. 2008a. Food for thought: Supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecology and the Environment* 6: 476–484. doi:10.1890/060152.

Robb, G. N., R. A. McDonald, D. E. Chamberlain, S. J. Reynolds, T. J. E. Harrison, and S. Bearhop. 2008b. Winter feeding of birds increases productivity in the subsequent breeding season. *Biology Letters* 4: 220–223. doi:10.1098/rsbl.2007.0622.

Robertson, A.S. (1984). Aspects of the population dynamics of Cape vultures in the Cape Province. *Ostrich* 55: 196-206.

Rooney, E., N. Reid, and W. I. Montgomery. 2015. Supplementary feeding increases Common Buzzard Buteo buteo productivity but only in poor-quality habitat. *Ibis* 157: 181–185. doi:10.1111/ibi.12218.

Rowcliffe, J. M., E. De Merode, and G. Cowlishaw. 2004. Do wildlife laws work? Species protection and the application of a prey choice model to poaching decisions. *Proceedings of the Royal Society B: Biological Sciences* 271: 2631–2636. doi:10.1098/rspb.2004.2915.

Ruffino, L., P. Salo, E. Koivisto, P. B. Banks, and E. Korpimäki. 2014. Reproductive responses of birds to experimental food supplementation: a meta-analysis. *Frontiers in Zoology* 11: 80. doi:10.1186/preaccept-1035746911122745.

Rushworth, I., and S. Krüger. 2014. Wind farms threaten southern Africa's cliff-nesting vultures. *Ostrich* 85: 13–23. doi:10.2989/00306525.2014.913211.

Rust, N. A., J. Tzanopoulos, T. Humle, and D. C. MacMillan. 2016. Why Has Human–Carnivore Conflict Not Been Resolved in Namibia? *Society and Natural Resources* 29: 1079–1094. doi:10.1080/08941920.2016.1150544.

Rust, N. A., K. M. Whitehouse-Tedd, and D. C. MacMillan. 2013. Perceived efficacy of livestock-guarding dogs in South Africa: Implications for cheetah conservation. *Wildlife Society Bulletin* 37: 690–697. doi:10.1002/wsb.352.

Rutherford, C., D. Costa, R. Mercieca-Bebber, H. Rice, L. Gabb, and M. King. 2016. Mode of administration does not cause bias in patient-reported outcome results: a meta-analysis. *Quality of Life Research* 25: 559–574. doi:10.1007/s11136-015-1110-8.

Ruxton, G. D., and D. C. Houston. 2002. Modelling the energy budget of a colonial bird of prey, the Ruppell's gri¡on vulture, and consequences for its breeding ecology. *African*

Journal of Ecology 40: 260–266.

Ruxton, G. D., and D. C. Houston. 2004. Obligate vertebrate scavengers must be large soaring fliers. *Journal of Theoretical Biology* 228: 431–436. doi:10.1016/j.jtbi.2004.02.005.

SABAP2. 2007. Southern African Bird Atlas Project 2.

Sæther, B. E., and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81: 642–653. doi:10.1890/0012-9658(2000)081[0642:alhvac]2.0.co;2.

Sahlsten, J., N. Bunnefeld, J. Månsson, G. Ericsson, R. Bergström, and H. Dettki. 2010. Can supplementary feeding be used to redistribute moose Alces alces? *Wildlife Biology* 16: 85–92. doi:10.2981/08-085.

Santangeli, A., and W. J. Sutherland. 2017. The Financial Return from Measuring Impact. *Conservation Letters* 10: 354–360. doi:10.1111/conl.12284.

Santangeli, A., B. Arroyo, L. V. Dicks, I. Herzon, A. S. Kukkala, W. J. Sutherland, and A. Moilanen. 2016a. Voluntary non-monetary approaches for implementing conservation. *Biological Conservation* 197: 209-214. doi:10.1016/j.biocon.2016.03.013.

Santangeli, A., H. Lehtoranta, and T. Laaksonen. 2012. Successful voluntary conservation of raptor nests under intensive forestry pressure in a boreal landscape. *Animal Conservation* 15: 571–578. doi:10.1111/j.1469-1795.2012.00551.x.

Santangeli, A., M. Girardello, E. Buechley, A. Botha, E. Di Minin, and A. Moilanen. 2019. Priority areas for conservation of Old World vultures. *Conservation Biology* 33: 1056–1065. doi:10.1111/cobi.13282.

Santangeli, A., V. Arkumarev, N. Rust, and M. Girardello. 2016b. Understanding, quantifying and mapping the use of poison by commercial farmers in Namibia - Implications for scavengers' conservation and ecosystem health. *Biological Conservation* 204: 205–211. doi:10.1016/j.biocon.2016.10.018.

Schabo, D. G., S. Heuner, M. V Neethling, S. Rösner, R. Uys, and N. Farwig. 2017. Long-term data indicates that supplementary food enhances the number of breeding pairs in a Cape Vulture *Gyps coprotheres* colony. *Bird Conservation International* 27: 140–152. doi:10.1017/S0959270915000350.

Schmidt, K. T., and H. Hoi. 2002. Supplemental feeding reduces natural selection in juvenile red deer. *Ecography* 25: 265–272. doi:10.1034/j.1600-0587.2002.250302.x.

Scholtz, M. M. 2010. *Beef Breeding in South Africa*. 2nd ed. Pretoria: Agticultural Research Council.

Sekercioğlu, C. H., G. C. Daily, and P. R. Ehrlich. 2004. Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences of the United States of America* 101: 18042–18047. doi:10.1073/pnas.0408049101.

Selva, N., and M. A. Fortuna. 2007. The nested structure of a scavenger community. *Proceedings of the Royal Society B: Biological Sciences* 274: 1101–1108. doi:10.1098/rspb.2006.0232.

Semeniuk, C. A. D., and K. D. Rothley. 2008. Costs of group-living for a normally solitary forager: Effects of provisioning tourism on southern stingrays Dasyatis americana. *Marine Ecology Progress Series* 357: 271–282. doi:10.3354/meps07299.

Sheridan, R., A. . Ferreira, and L. . Hoffman. 2003. Production efficiency of South African Mutton Merino lambs and Boer goat kids receiving either a low or a high energy feedlot diet. *Small Ruminant Research* 50: 75–82. doi:10.1016/S0921-4488(03)00109-3.

Shultz, S., H. S. Baral, S. Charman, A. A. Cunningham, D. Das, G. R. Ghalsasi, M. S. Goudar, R. E. Green, et al. 2004. Diclofenac poisoning is widespread in declining vulture populations across the Indian subcontinent. *Proceedings of the Royal Society B: Biological Sciences* 271: S458–S460. doi:10.1098/rsbl.2004.0223.

Sinclair, A. R. E., J. M. Fryxell, and G. Caughley. 2006. *Wildlife Ecology, Conservation, and Management*. 2nd ed. Oxford: Blackwell Publishing Ltd.

Snyman, M. A. 2014a. *South African sheep breeds: Dohne Merino sheep*. Grootfontein Agricultural Development Institute, Middelburg.

Snyman, M. A. 2014b. *South African sheep breeds: Dormer sheep*. Grootfontein Agricultural Development Institute, Middelburg.

Snyman, M. A. 2014c. *South African sheep breeds: Dorper sheep*. Grootfontein Agricultural Development Institute, Middelburg.

Snyman, M. A. 2014d. *South African sheep breeds: Merino sheep*. Grootfontein Agricultural Development Institute, Middelburg.

Snyman, M. A. 2014e. *South African sheep breeds: SA Mutton Merino sheep*. Grootfontein Agricultural Development Institute, Middelburg.

Sorensen, A., F. M. van Beest, and R. K. Brook. 2014. Impacts of wildlife baiting and supplemental feeding on infectious disease transmission risk: A synthesis of knowledge. *Preventive Veterinary Medicine* 113: 356-363. doi:10.1016/j.prevetmed.2013.11.010

Soulé, M. E. 1985. What Is Conservation Biology? *BioScience*. Vol. 35. doi:10.2307/1310054.

Spiegel, O., W. M. Getz, and R. Nathan. 2013. Factors Influencing Foraging Search

Efficiency: Why Do Scarce Lappet-Faced Vultures Outperform Ubiquitous White-Backed Vultures? *The American Naturalist* 181: 102–115. doi:10.1086/670009.

Steffen, W., P. J. Crutzen, and J. Mcneill. 2008. The Anthropocene : Are Humans Now Overwhelming the Great Forces of Nature The Anthropocene : Are Humans Now Overwhelming the Great Forces of Nature ? *Ambio* 36: 614–621. doi:10.1579/0044-7447(2007)36.

Stevens, A., and R. Milne. 1997. The effectiveness revolution and public health. In *Progress in Public Health*, ed. G. Scally, 197–224. Royal Society of Medicine Press.

Steyaert, S. M. J. G., J. Kindberg, K. Jerina, M. Krofel, M. Stergar, J. E. Swenson, and A. Zedrosser. 2014. Behavioral correlates of supplementary feeding of wildlife: Can general conclusions be drawn? *Basic and Applied Ecology* 15: 669–676. doi:10.1016/j.baae.2014.10.002.

Stoynov, E. 2016. A reply to Oppel et al. concerning "Assessing the effectiveness of intensive conservation actions: Does guarding and feeding increase productivity and survival of Egyptian Vultures in the Balkans?". *Biological Conservation* 204: 151-152. doi:10.1016/j.biocon.2016.04.002.

Stuart, C., and M. Stuart. 2015. *Stuart's field guide to mammals of southern Africa: Including Angola, Zambia and Malawi*. Cape Town, South Africa: Struik Publishers.

Sutherland, W. J., A. S. Pullin, P. M. Dolman, and T. M. Knight. 2004. The need for evidence-based conservation. *Trends in Ecology and Evolution* 19: 305–308. doi:10.1016/j.tree.2004.03.018.

Swanepoel, M., A. J. Leslie, M. Van der Rijst, and L. C. Hoffman. 2016. Physical and chemical characteristics of warthog (Phacochoerus africanus) meat. *African journal of Wildlife Research* 46: 103–120. doi:10.3957/056.046.0103.

Swarup, D., R. C. Patra, V. Prakash, R. Cuthbert, D. Das, P. Avari, D. J. Pain, R. E. Green, et al. 2007. Safety of meloxicam to critically endangered Gyps vultures and other scavenging birds in India. *Animal Conservation* 10: 192–198. doi:10.1111/j.1469-1795.2006.00086.x.

Taylor M., Peacock F. and Wanless R.M. 2015. Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. BirdLife South Africa, University of Cape Town and South African National Biodiversity Institute, Johannesburg, South Africa.

United Nations. 2019. How certain are the United Nations global population projections? *Population Facts* 2019: 1–4.

van de Geissen, J. 2019. SAHGCA's position on the use of lead core bullets and lead shot while hunting. South Africa: SA Hunters and Game Conservation Association.

van den Heever, L., H. Smit-Robinson, V. Naidoo, and A. E. McKechnie. 2019. Blood and bone lead levels in South Africa's Gyps vultures: Risk to nest-bound chicks and comparison with other avian taxa. *Science of the Total Environment* 669: 471–480. doi:10.1016/j.scitotenv.2019.03.123.

van den Heever, L., L. J. Thompson, W. W. Bowerman, H. Smit-Robinson, L. J. Shaffer, R. M. Harrell, and M. A. Ottinger. 2021. Reviewing the role of vultures at the human–wildlife–livestock disease interface: An African perspective. *Journal of Raptor Research* 55: 000–000.

van der Ploeg, J., M. Cauilan-Cureg, M. van Weerd, and W. T. De Groot. 2011. Assessing the effectiveness of environmental education: mobilizing public support for Philippine crocodile conservation. *Conservation Letters* 4: 313–323. doi:10.1111/j.1755-263X.2011.00181.x.

van Franeker, J. A., and P. J. Bell. 1988. Plastic ingestion by petrels breeding in Antarctica. *Marine Pollution Bulletin* 19: 672–674. doi:10.1016/0025-326X(88)90388-8.

van Niekerk, H. N. 2010. The cost of predation on small livestock in South Africa by medium-sized predators. *M.Sc. Agric. Thesis: University of the Free State*. University of the Free State.

van Zyl, L., and A. V. Ferreira. 2004. Physical and chemical carcass composition of springbok (Antidorcas marsupialis), blesbok (Damaliscus dorcas phillipsi) and impala (Aepyceros melampus). *Small Ruminant Research* 53: 103–109. doi:10.1016/j.smallrumres.2003.08.017.

Virgili, R., M. Degni, C. Schivazappa, V. Faeti, E. Poletti, G. Marchetto, M. T. Pacchioli, and A. Mordenti. 2003. Effect of age at slaughter on carcass traits and meat quality of Italian heavy pigs1. *Journal of Animal Science* 81: 2448–2456. doi:10.2527/2003.81102448x.

Vlachos, C. G., D. E. Bakaloudis, and G. J. Holloway. 1999. Population trends of Black Vulture Aegypius monachus in Dadia Forest, north-eastern Greece following the establishment of a feeding station. *Bird Conservation International* 9: 113–118. doi:10.1017/S0959270900002239.

Von La Chevallerie, M. 1970. Meat production from wild ungulates. *Proceedings of the South African Society of Animal Production* 9: 73–87.

Ward, J. M., and P. L. Kennedy. 1996. Effects of supplemental food on size and survival of juvenile Northern Goshawks. *The Auk* 113: 200–208.

Warriss, P. D., S. N. Brown, T. P. Rolph, and S. C. Kestin. 1990. Interactions between the beta-adrenergic agonist salbutamol and genotype on meat quality in pigs. *Journal of Animal Science* 68: 3669. doi:10.2527/1990.68113669x.

Wells, D., and R. C. Krecek. 2001. Socioeconomic, health and management aspects of working donkeys in Moretele 1, North West Province, South Africa. *Journal of the South African Veterinary Association-Tydskrif Van Die Suid-Afrikaanse Veterinere Vereniging* 72: 37–43. doi:10.4102/jsava.v72i1.607.

Williams, N. P., J. Renell, A. Botha, J. Andevski, C. Bowden, M. Gudka, and R. Safford. 2017. Multi-species Action Plan to Conserve African-Eurasian Vultures: 1–195.

Wittmer, H. U., L. M. Elbroch, and A. J. Marshall. 2013. Good intentions gone wrong: Did conservation management threaten Endangered huemul deer Hippocamelus bisulcus in the future Patagonia National Park? *Oryx* 47: 393–402. doi:10.1017/S0030605312000531.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses? *Ecology* 89: 621–634. doi:10.1890/07-0175.1.

Yarnell, R. W., W. L. Phipps, S. Dell, L. M. MacTavish, and D. M. Scott. 2015. Evidence that vulture restaurants increase the local abundance of mammalian carnivores in South Africa. *African Journal of Ecology* 53: 287–294. doi:10.1111/aje.12178.