

The influence of vulture restaurants on breeding success and nestling body condition of *Gyps* vulture populations across southern Africa.



Photo credit: Charlie Hamilton James

Tapiwa Zimunya

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Rondebosch, 7701, South Africa

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Supervisor: Dr. Robert Thomson

Co-supervisor: Dr. Arjun Amar



FitzPatrick Institute of
African Ornithology



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ABSTRACT

Vulture populations in many parts of the world continue to decline owing to numerous threats, such as lack of adequate food sources, poisoning and collisions with power-lines. Worldwide, supplementary feeding sites (hereafter, vulture restaurants) have been used as a conservation tool aimed at supporting vulture populations. However, in many parts of the world there is little scientific evidence about their effectiveness in aiding vulture populations. Here, I assessed the relationship between chick condition (African White-backed Vultures) and breeding success (Cape Vultures/African White-backed Vultures) in relation to a variety of variables which described levels of access to vulture restaurants. My data suggest the potential of vulture restaurants to increase breeding success in vulture populations. Breeding success generally increased for nests closer to vulture restaurants. There was a significant positive correlation between African White-backed Vulture breeding success and proximity to vulture restaurants ($p < 0.05$), but little evidence to support such a relationship for Cape Vultures ($p > 0.05$). Nestling body condition of African White-backed Vultures was also not influenced by proximity to vulture restaurants ($p > 0.05$). Findings of this study provide motivation on the use of vulture restaurants as a conservation strategy across southern Africa. The current study informs future conservation efforts on the use of vulture restaurants across the region, particularly in countries where a network of vulture restaurants is still being established.

INTRODUCTION

Vultures are specialized obligate scavengers (Ruxton & Houston, 2004) known to play an important role in nutrient cycling, waste removal, and disease control (Prakash *et al.* 2003; Ogada *et al.* 2012b). Despite the ecological importance of vultures and current conservation efforts, African vulture populations continue to collapse and are in danger of extinction (Gilbert *et al.* 2002; Virani *et al.* 2011; Ogada *et al.* 2012a; Krüger *et al.* 2015; Ogada *et al.* 2015; Ogada *et al.* 2016). There are concerns that declining vulture populations will have negative consequences on both ecosystem functioning and human health, similar to the consequences documented in the aftermath of the “Asian vulture crisis” (Oaks *et al.* 2004; Swan *et al.* 2006; Gilbert *et al.* 2007). In south Asia, three *Gyps* vulture species declined by more than 90% within a period of 10 years (Prakash, 1999; Oaks *et al.* 2004), a collapse largely attributed to a single cause: poisoning by the veterinary drug Diclofenac (Gilbert *et al.* 2002; Gilbert *et al.* 2004; Oaks *et al.* 2004; Pain *et al.* 2008). African vultures, in contrast, are facing extinction due to a wide range of threats, including: electrocution, collisions with power-infrastructure, poisoning, and harvesting for cultural beliefs (Ogada *et al.* 2016). This wide range of threats requires diverse conservation strategies to effect change, however, so far little effort has been given to testing the effectiveness of these different strategies.

In Africa, poisoning is regarded as the major threat to vulture populations (Ogada *et al.* 2015). Deliberate and unintentional poisoning has led to 61% of African vulture deaths (Ogada *et al.* 2016), with some countries in Africa labelled as poisoning hotspots e.g. Namibia (Naidoo *et al.* 2016; Santangeli *et al.* 2016). In some cases, deliberate poisoning of vultures is associated with elephant poaching, so called sentinel poisoning, where poachers put poison on carcasses to kill

vultures that may alert park authorities to their illegal activities (Ogada *et al.* 2015). Deliberate poisoning may also occur when vultures are targeted directly for use in belief-based use (Mander *et al.* 2007; McKean & Botha, 2007; McKean *et al.* 2013). In contrast, unintentional poisoning usually stems from human-wildlife conflict that causes farmers to poison carcasses to kill predators such as jackals and lions that prey on their livestock (Ogada *et al.* 2014). A single poisoning incident can cause the deaths of hundreds of vultures (Ogada *et al.* 2012). With the current trend of rapid population decline in these long-lived species, there is a need for integrated, multi-stakeholder and long-term approaches towards vulture conservation (Botha *et al.* 2017).

Globally, providing safe feeding sites is an obvious short-term conservation measure. These vulture restaurants are one of the main conservation strategies used to date, albeit with largely untested effectiveness. Vulture restaurants aim to provide carrion for wild vulture populations that is free from anthropogenic contaminants (i.e. poisons and veterinary drugs, Gilbert *et al.* 2007; Cortés-Avizanda *et al.* 2010; Cortes-Avizanda *et al.* 2016; Hirschauer, 2016), and can serve as a focal point for population monitoring (Mundy *et al.* 1992; Phipps *et al.* 2013; Monadjem *et al.* 2013; Margalida *et al.* 2014). Vulture restaurants were initiated in South Africa in the 1960s, when conservationists believed food scarcity was the major cause of Bearded Vulture declines in the region (Piper, 2004; Ogada *et al.* 2012; Monadjem *et al.* 2013). In the last decades vulture restaurants have spread in South Asia, South-East Asia, and to other African countries (Murn *et al.* 2008). Approximately 200 vulture restaurants are thought to be scattered across the South Africa (Piper, 2004). Within South Africa, the number of vulture restaurants still appears to be increasing as vultures gain attention as a conservation priority (Christiaan

Brink, pers comm). Despite the proliferation of these vulture restaurants, little is known about their effectiveness in benefitting vulture populations across southern Africa.

Previous research suggests that vulture restaurants can have both positive (Oro *et al.* 2006; Margalida *et al.* 2014) and negative effects on vulture populations (Carrete *et al.* 2006; Opperl *et al.* 2016). Their impacts have been investigated in Europe (Gonzalez *et al.* 2006; Margalida 2010; Margalida *et al.* 2017), but scant evidence currently exists for southern African populations. It has been suggested that vulture restaurants may aid in the recolonization of abandoned areas (Mundy *et al.* 1992) and that vulture restaurants have the potential to increase breeding success (Donazar & Fernandez, 1990; Gonzalez *et al.* 2006). In Spain, a study on Griffon Vultures *Gyps fulvus* found breeding colonies almost quadrupled in size following the establishment of vulture restaurants (Donazar & Fernandez, 1990). Therefore, the effectiveness of vulture restaurants in Africa has been assumed based on European population studies and often the gut feelings of vulture conservationists, or simply based on the need to ‘do something’.

The effect of vulture restaurants in an African context remains unstudied except for the study exploring the effects of a single restaurant on a Cape Vulture colony (Schabo *et al.* 2017). This study showed a significant increase in breeding pairs correlating with the establishment of a vulture restaurant but did not find an influence on breeding success of Cape Vultures. However, this was a correlative and un-replicated study and the colony increase could be due to any number of local vulture conservation measures. Hence it is problematic to make conservation decisions based on this weak evidence. Studies on the effects of vulture restaurants in s

outhern Africa have focused on how they influence movement and ranging behaviour of vultures (Bamford *et al.* 2007; Phipps *et al.* 2013; Kane *et al.* 2015; Reid *et al.* 2015; Kane *et al.* 2016)

and some exploring whether vulture restaurants influence abandonment of vulture territories (Krüger *et al.* 2015). However, despite vulture restaurants being present in the environment for almost 50 years, the effects have never been quantified on a national scale.

Despite the proliferation of vulture restaurants, there are also concerns that vulture restaurants might have negative effects on vulture populations (Piper, 2004; Deygout *et al.* 2010; Margalida *et al.* 2013; Oro *et al.* 2013). Vulture restaurants may make carrion resources more predictable altering the spatio-temporal predictability of natural food supply (Oro *et al.* 2008). This potentially leads to changes in vulture foraging behaviour (Deygout *et al.* 2010; Margalida *et al.* 2013; Monstarant *et al.* 2013; Kane *et al.* 2015), and competitive interactions (Deygout *et al.* 2009; Oro *et al.* 2013). Additionally, incorrect spatio-temporal placement of vulture restaurants might expose vulture populations to other threats such as powerlines (Piper, 2004). The presence of vulture restaurants also tends to attract other scavengers and predators in an ecosystem (Piper, 2004; Cortes-Avizanda *et al.* 2009; Selva *et al.* 2014; Yarnell *et al.* 2015). If a vulture colony is close to these vulture restaurants there is a possibility that some of these scavengers and predators might prey on vulture chicks and eggs and therefore negatively affecting breeding success (Anderson & Anthony, 2005). Vulture restaurants also pose a threat of poisoning to vulture populations, given that live animals might have been treated with potentially harmful veterinary drugs (Prakash *et al.* 2003; Piper 2004; Oaks *et al.* 2004) or may contain fragments of lead ammunition (Garcia-fenandez *et al.* 2005; Gangoso *et al.* 2009; Naidoo *et al.* 2018).

Uncertainty about the costs and benefits of using vulture restaurants suggests the need for further evidence of its conservation value, particularly as a tool in Africa, where some of the most pressing conservation actions are required. My study aims to explore evidence for the positive or negative effects of vulture restaurants. I use the locations of vulture restaurants across southern

Africa that have been compiled by various non-governmental organisations (NGOs) and explore whether breeding success of African White-backed Vultures (*Gyps africanus*), and Cape Vultures (*Gyps coprotheres*) is improved depending on their exposure to vulture restaurants. Additionally, from biometric data taken during the ringing of African White-backed Vultures chicks, I examine whether chick condition is influenced depending on the nests' exposure to vulture restaurants. My hypothesis was that safe food sources are a limiting factor in the breeding success of vultures in southern Africa. If this was indeed the case, then I would predict that the breeding success of vultures at colonies nearer to vulture restaurants would have better breeding success. Similarly, I hypothesised that chick condition is limited by food abundance, and I would predict that nests nearer to vulture restaurants would produce chicks in better condition

METHODS

1.1 Study area and species

Southern Africa has important breeding populations of Cape and White-backed Vultures. Cape Vultures are listed as endangered and White-backed as critically endangered by the IUCN Red List (Birdlife International, 2017) owing to rapid population declines which are predicted to lead to 90% decline in the next three generations (Ogada *et al.* 2017).

The Cape Vulture is endemic to southern Africa, with the breeding strongholds found in Lesotho and South Africa. It is the larger of the two southern African *Gyps* species. It is a cliff-nesting species and usually occupies breeding colonies year-round. They lay a single egg, with an average incubation period of 57 days. The nestling period usually lasts about 143 days until fledging (Mundy *et al.* 1992).

The African White-backed Vulture is widely distributed in Africa. In southern Africa they are widespread in eastern Namibia, Swaziland, Zimbabwe, northern South Africa, Botswana, and parts of Mozambique (Mundy *et al.* 1992). They nest in loose colonies on top of trees especially *Vachellia* (*Acacia*) species. African White-backed Vultures are known to occupy the same nest site up to 15 years (Mundy *et al.* 1992). They lay a single egg clutch and the nestling period usually lasts about 120 days (Mundy *et al.* 1992).

1.2 Data sources

I collated mainly unpublished data that was sourced and provided by various organisations that have been involved with vulture population monitoring in southern Africa. I used three types of data: 1) data on the number of active and successful nests from monitoring of breeding vulture populations, 2) data on the nestling biometrics from ringing data (weight and wing length) and 3)

data on the location of vulture restaurants. Breeding monitoring databases were provided by Endangered Wildlife Trust (EWT), Ezemvelo KwaZulu Natal Wildlife (KZN Wildlife), Vulture Programme (VulPro) and Vultures Namibia. The data provided by these organisations included colony-level breeding success for Cape Vulture and White-backed Vulture, and nestling body condition for White-backed Vulture only, which was also complemented by additional data from the South African Bird Ringing Unit (SAFRING, University of Cape Town) which collates bird ringing data from throughout the sub-region.

The vulture restaurant database consisted of a combination of existing databases from VulPro, EWT and KZN Wildlife. The VulPro database was last updated in 2012 (VulPro, pers comm), hence the accuracy of the locations of the vulture restaurants, and the current status (active or inactive) remains unknown. However, this database has been used in recent studies evaluating the movement of vultures relative to vulture restaurants (Bamford *et al.* 2007; Phipps *et al.* 2013; Kane *et al.* 2015; Kane *et al.* 2016) and is currently the best database available. For the purposes of my thesis, I assumed that the restaurant location data points were accurate. A national collated database is currently being compiled, updated and verified (C. Brink, unpublished data). For my analyses, I used 199 vulture restaurants across southern Africa that were included in the database (Figure 1). The position of vulture restaurants and colonies/nests (Cape Vultures/White-backed Vultures) as determined by Universal Transverse Mercator UTM coordinates were obtained from various organisations running long-term vulture monitoring projects.

Vulture restaurants are usually either located on farms, within protected areas or at other conservation related locations. Restaurants range from formal to informal where individual farmers put out carcasses at central positions, with a varying degree of predictability within their farms. Carcasses supplied vary viz. domestic cattle, pigs, goats, and wild game animals. In

vulture restaurants with less intensive livestock farming, feeding is usually irregular depending on the availability of mortalities; hence there are variations on the amount and quality of food supplied. In southern Africa the main motivation behind the establishment of these restaurants has not always been for vulture conservation, but often solely for its waste management utility (Christiaan Brink, pers comm).

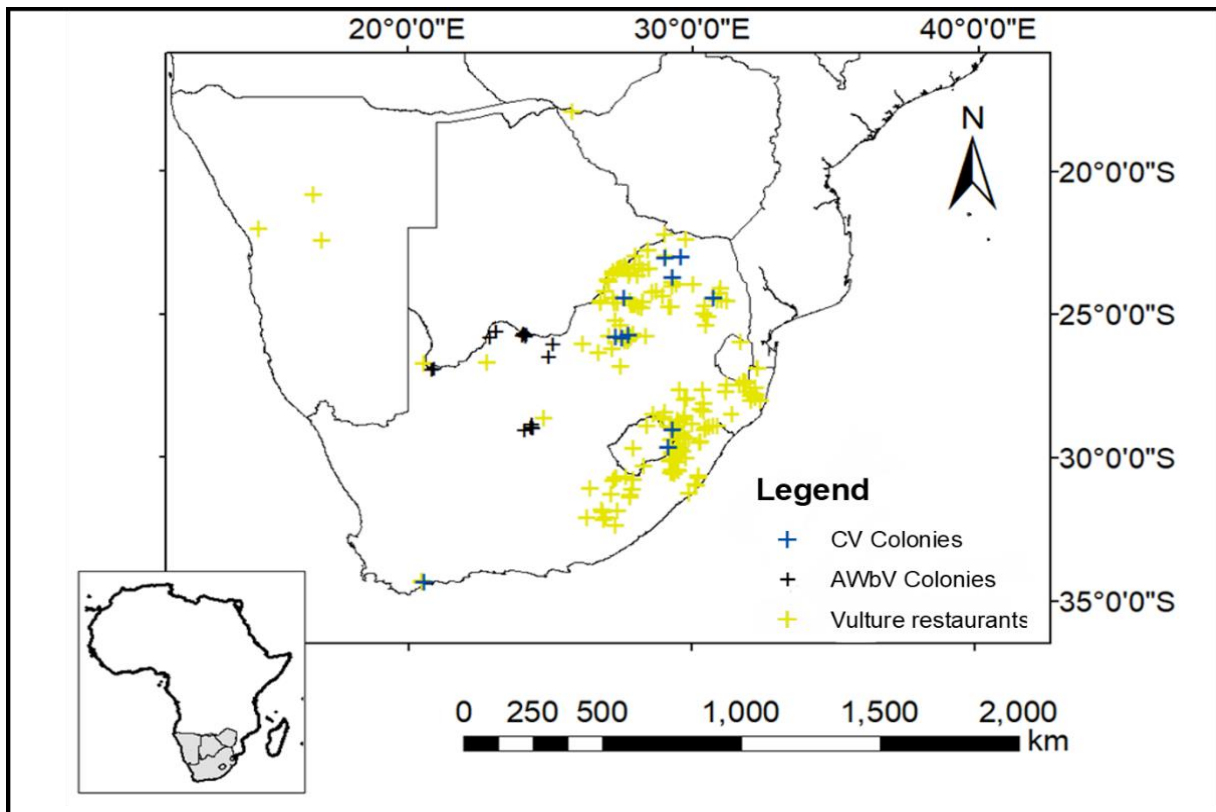


Figure 1: The distribution of vulture restaurants, Cape Vulture, and African White-backed Vulture colonies used in exploring the effect of vulture restaurants on breeding success across southern Africa.

1.3 Monitoring of breeding levels

1.3.1 Cape Vulture Monitoring

Breeding monitoring data was collected following a standardized monitoring protocol developed by the Vulture Study Group (Benson *et al.* 2007). This protocol was formally developed and adopted in 2006 in southern Africa but has been a common methodology already used for similar

species for decades i.e. the Eurasian Griffon *Gyps fulvus* (del Moral, 2009). Colony monitoring was done by scanning the colony from the ground with the aid of telescopes with minimum 60× magnification (see Benson *et al.* 2007 for protocols; Wolter *et al.* 2016). At each breeding site, GPS location, site name and number of breeding pairs was recorded. All nests were referenced using photographs of each cliff face and are numbered to ensure that the same nest on the same ledge is followed within and between years. Observation points varied between 700m and 1600m from the colonies.

Colonies were generally visited at least three times during vulture breeding season across southern Africa. During the first visit (May - June) to colonies, breeding pairs from specific nests were counted. Ledges were counted as containing a breeding pair and breeding attempt, when a pair was seen at a ledge nesting, incubating or copulating. In addition, when a pair was present and displaying behaviour indicating that the ledge was being used as a nest, these ledges were also classed as tenanted and considered a breeding attempt. The colonies were visited again between July and August to confirm the presence of a nestling or an adult incubating for each nest identified as attempting breeding in the first survey. During the final visit from late August to October number of fledglings was counted. Both nestlings and fledglings were confirmed when visually verified. Nestling presence was inferred based on the behaviour of adults (incubating or tenanted nests). Fledgling presence was also identified when a young chick was visually confirmed on the nest. On average, the number of weeks between breeding monitoring visits was 12.56 ± 2.69 (mean \pm SD). All these periods fall within the period of a typical nesting cycle of the vultures, hence it should not be possible that a chick fledged from a nest before the third visit, as this would indicate an empty unsuccessful nest instead of a correctly identified successful nest.

1.3.2 African White-backed vultures monitoring

Aerial and ground surveys were conducted at African White-backed Vulture breeding colonies. Nests were surveyed during the breeding season when most birds were incubating on their nest. Since breeding season varies across regions, the monitoring was conducted twice in April -July and June -September. During the first visit (April-July), specific nests were surveyed, breeding pairs were classified as breeding being attempted where pairs seen nesting, incubating, copulating or when nests were tenanted, i.e. pair present and displaying a behaviour indicating that the nest was being used. During the second visit in June-September, the number of nestlings and fledglings were visually confirmed and counted from the nest identified as attempting breeding in the first survey. Nests were monitored from a helicopter but some were monitored by directly scanning below the nests or at an angled vantage point from the ground using binoculars and 20-60× telescopes.

1.4 Chick body condition

African White-backed Vulture nestlings have been ringed at breeding sites across southern Africa. I extracted historic nestling ringing data provided by SAFRING. Nests were located during aerial / ground surveys, or by opportunistic sightings of the nest. Ringers typically accessed the nest using a ladder, handled and placed the chick in a purpose made bag and lowered down to the ground using a rope (Angus Anthony pers comm). The chick was then weighed, and the right wing length was measured, from the carpus joint to the end of the longest primary feather, flattening the wing and primary feathers in the process following the SAFRING protocol. A metal ring was placed on nestling's right leg, only if the wing length was >125mm (Angus Anthony pers comm). After taking both measurements (mass, wing length) the chick was then placed back in the nest.

1.5 Response variables

To examine the effect of vulture restaurants on vulture populations I used two response variables thus breeding success and nestling body condition as proxies for colony health/success. I make use of these two variables since availability of food affects nestling body condition ultimately determining breeding success or survival during post-fledgling period which consequently affects recruitment to the breeding population (Virani *et al.* 2012). Additionally, nestling body condition might have synergetic carryover effects on the survival of vulture populations (Schwagmeyer & Mock, 2008).

Breeding success

Breeding success was measured as the number of successful nests (defined as nests with confirmed chick/ or that fledged the chick) out of the total number of breeding pairs that initiated a nesting attempt (defined as incubating or a confirmed egg) for each colony following a similar method developed for Eurasian Griffon Vultures (Arroyo *et al.* 1990). However, because some Cape Vulture colonies were monitored only twice in a season, I separated breeding success measures for this species into both mid-season and late-season breeding success. Mid-season breeding success was estimated as number of successful nests in the second visit out of the total number of active nests during the first visit. Late-season breeding success was measured as the number of successful nests during the third visit out of the total number of active nests during the first visit. From all data accumulated for breeding success I excluded colonies that had less than 5 active nests monitored (9 for African White-backed Vultures). Again, from the breeding success data, I excluded data which was accumulated before year 2000 to align colony breeding success data with the known existence of restaurants. Additionally, I eliminated data that was unusable due to clear issues with the monitoring protocol (see Appendix D). I also recorded the

numbers of weeks between each survey, which was later used in the analysis to control for this aspect, which varied between surveys. This could have influenced the estimates of breeding success, with more nests having the opportunity to fail when periods between surveys were longer.

Nestling body condition

Nestling body condition was estimated for each nestling using the mass and wing length of every individual following the Scaled mass index method (Peig & Green, 2009). The method scales each individual body mass to the expected value if all nestlings had the same body size. I divided body mass by wing length to estimate African White-backed Vulture nestling body condition (see formula below). On average, the nestling body condition was 12.51 ± 2.58 (mean \pm SD).

Formula 1:

$$\text{Nestling body condition} = \frac{\text{Body mass (g)}}{\text{Wing length (mm)}}$$

1.6 Proximity Index to vulture restaurants

A proximity index was used to describe the exposure of vulture colonies or nests to vulture restaurants in the landscape. The index calculated the distance from each colony to a vulture restaurant. The coordinates of both vulture restaurants and breeding colonies were entered into ARCGIS-ARCMAP v10.2 (ESRI, Redlands, USA), to assess the proximity of vulture restaurants to breeding sites (Colonies/Nests). For these analyses, colony was considered as the sampling unit. Colony location was clear for tightly packed Cape Vultures cliff colonies, but for looser African White-backed Vultures colonies, all nests were plotted in ArcMap and a central nest

location was chosen to represent the entire colony. At each colony, I created buffer circles with a radius of either 100km or 200km to account for the foraging ranges of vultures (Bamford *et al.* 2007; Phipps *et al.* 2013; Kane *et al.* 2015; Pfeiffer *et al.* 2015). Using ArcView Spatial Analyst 2.a., I calculated the number of vulture restaurants (VR100 & VR200), and distances from each breeding colony to all vulture restaurants within the circles of either 100km or 200km radii. For African White-backed Vulture nestling body condition the sampling unit was at the individual chick level, hence proximity index was calculated for each nest.

1.7 Statistical analysis

Breeding success

To assess the effect of vulture restaurants and breeding success, I fitted generalised linear mixed models (GLMM) using the statistical software R version 3.03 (R-Core Team, 2013) and the ‘lme4’ v.1.0-6 package (Bates *et al.* 2015). I fitted ‘year’ and ‘colony’ as random effects to control for lack of independence of data taken from the same colony over multiple years and from multiple colonies within the same year. I tested for associations by including explanatory variables related to vulture restaurant exposure in my models i.e. number of vulture restaurants within 100km and 200km radius, the vulture restaurant proximity index within 100km and 200km, and distance to the nearest restaurant (see Table 1). For all breeding success models, I also fitted weeks between surveys as a covariate to account for this potential bias. The models for breeding success were fitted using a binomial error structure with a cbind function (successful breeding attempt, failed breeding attempt).

Nestling body condition

To assess the effect of vulture restaurants on nestling body condition, I fitted linear mixed models (LMM) using the statistical software R version 3.03 (R-Core Team, 2013) and the ‘lme4’ v.1.0-6 package (Bates *et al.* 2015). I fitted ‘year’, ‘nestID’ and ‘colony’ as random effects to control for lack of independence of data taken from the same nest over multiple years and from multiple colonies within the same year. I tested for associations by including explanatory variables related to vulture restaurant exposure in my models i.e. number of vulture restaurants within 100km and 200km radius, the vulture restaurant proximity index within 100km and 200km, and distance to the nearest restaurant. I also repeated the analysis, having excluded chicks ringed in Namibia, given the different vulture restaurants’ density and general land-use of Namibia as compared to South Africa (see Appendix C). Table 1 shows the structure of all the models used in my analysis.

Table 1: List of Generalised Linear Mixed Models exploring breeding success (MBS=Mid-season breeding success, LBS=Late-season breeding success, BS=breeding success) & nestling body condition (Cond ALL & Cond) in relation to the proximity to vulture restaurants within 100km (PI100) and 200km (PI200) around breeding colonies/ nests, umber of vulture restaurants within 100km (VR100) and 200km (VR200) and distance to the nearest vulture restaurant (Distance). Weeks represents week differences from first monitoring observation to the next one.

Species	Model	Response Variable	Explanatory Variable	Random Effects	Weight	Distribution
Cape Vultures	M1a	MBS	PI100	Colony + Year	Weeks	Binomial
	M1b	MBS	PI200	Colony + Year	Weeks	Binomial
	M1c	MBS	Distance	Colony + Year	Weeks	Binomial
	M1d	MBS	VR100	Colony + Year	Weeks	Binomial
	M1e	MBS	VR200	Colony + Year	Weeks	Binomial
	M2a	LBS	PI100	Colony + Year	Weeks	Binomial
	M2b	LBS	PI200	Colony + Year	Weeks	Binomial
	M2c	LBS	Distance	Colony + Year	Weeks	Binomial
	M2d	LBS	VR100	Colony + Year	Weeks	Binomial
	M2e	LBS	VR200	Colony + Year	Weeks	Binomial
African White-backed Vultures	M3a	BS	PI100	Colony + Year	Weeks	Binomial
	M3b	BS	PI200	Colony + Year	Weeks	Binomial
	M3c	BS	Distance	Colony + Year	Weeks	Binomial
	M3d	BS	VR100	Colony + Year	Weeks	Binomial
	M3e	BS	VR200	Colony + Year	Weeks	Binomial
	M4a	Cond All	PI100	Colony + Year + NestID		Normal
	M4b	Cond All	PI200	Colony + Year + NestID		Normal
	M4c	Cond All	Distance	Colony + Year + NestID		Normal
	M4d	Cond All	VR100	Colony + Year + NestID		Normal
	M4e	Cond All	VR200	Colony + Year + NestID		Normal
	M5a	Cond	PI100	Colony + Year + NestID		Normal
	M5b	Cond	PI200	Colony + Year + NestID		Normal

M5c	Cond	Distance	Colony + Year + NestID	Normal
M5d	Cond	VR100	Colony + Year + NestID	Normal
M5e	Cond	VR200	Colony + Year + NestID	Normal

RESULTS

I collated data from 11 Cape Vulture breeding colonies. Most colonies had long-term breeding success data except for one colony which was only monitored in one year (Table 2). Kransberg had the highest average number of active nests monitored over a period of 6 years (Table 2, see Appendix A & B). Roberts' farm had the lowest number of active nests (Table 2), and it is now extinct. I collated data from 18 African White-backed Vulture breeding colonies. On average, Schutsekama had the highest number of active nests monitored over a period of 4 years (Table 2).

Table 2: The summary data on Cape vulture and African White-backed Vulture breeding success extracted from various conservation organisations across southern Africa (also see appendix A and B).

Species	Colony	Years	N Mean(Range)
Cape Vultures	Nooitgedacht	2001 – 2017	99 (59 -140)
	Skeerpoort	2001-2017	231 (188-248)
	Roberts' Farm	2001-2011	11(5 -35)
	Manoutsa	2011-2017	550 (434 -644)
	Kransberg	2011-2017	671 (608 -862)
	Soutpansberg	2012-2017	198 (182 -223)
	Mzimkulu/Oribi	2008, 2011 - 2012	37 (22 -49)
	Potberg	2008 - 2009, 2012 - 2013	73 (63 -84)
	Blouberg	2008 - 2009, &2012	589 (433- 851)
	Vulture's retreat	2009	40
	Moletjie	2012 - 2014, 2016 - 2017	14 (5- 20)
African White-backed vultures	Beeswood	2013	5
	Birnamwood	2012 - 2015 & 2017	23 (17 - 29)
	Hurst Park	2014	5
	Kammeldoorn	2015	6
	Khamab	2015 – 2017	11 (7 -19)
	Nottingham	2012 - 2016	14 (8 -21)
	Vergelegen	2013 – 2016	13 (9 - 20)
	Vlakplaas	2012 - 2013, 2015 - 2017	10 (6 - 12)
	Mokala	2011 - 2015 & 2017	34(25 - 50)
	Schutsekama	2014-2017	37(19 - 52)
	Sanddrift	2014, 2016 - 2017	26 (14 - 33)
	Lorraine	2016	29
	Gannahoek	2016 – 2017	22 (20 - 24)

BBF	2017	6
Kalkdam	2017	9
STWld	2017	44
Murray	2017	25
Malopo NR	2012 & 2016	7 (5 - 9)

In southern Africa, total of 1611 African White-backed Vultures were ringed from year 2000 to 2017 (Appendix C). Most of these nestlings were ringed in Namibia (Table 3). A total of 242 chicks were ringed in South Africa. Zimbabwe had the lowest number of individuals ringed within a period of 17 years.

Table 3: Summary data for African white-backed vulture nestling body condition extracted from SAFRING and Vultures Namibia databases. N represents the number of chicks ringed in each province within the last 17years.

Location	N
Limpopo (South Africa)	25
Mpumalanga (South Africa)	2
KwaZulu Natal (South Africa)	28
North West (South Africa)	32
Northern Cape (South Africa)	155
Swaziland	13
Botswana	41
Zimbabwe	2
Namibia	1313

Cape Vulture breeding success

To explore the effect of vulture restaurants on breeding success of Cape Vultures, I ran ten GLMMs (see Table 1). For both mid-season and late-season breeding success measures there was no significant positive relationship between breeding success and any of my measure of vulture restaurant exposure thus, distance to the nearest vulture restaurant, and number of vulture restaurants within each buffer ($p > 0.05$, Table 4). However, I did find a significant negative

relationship between late-season breeding success and number of vulture restaurants within 100km and 200km buffers (Table 4, Figures 2a & 2b).

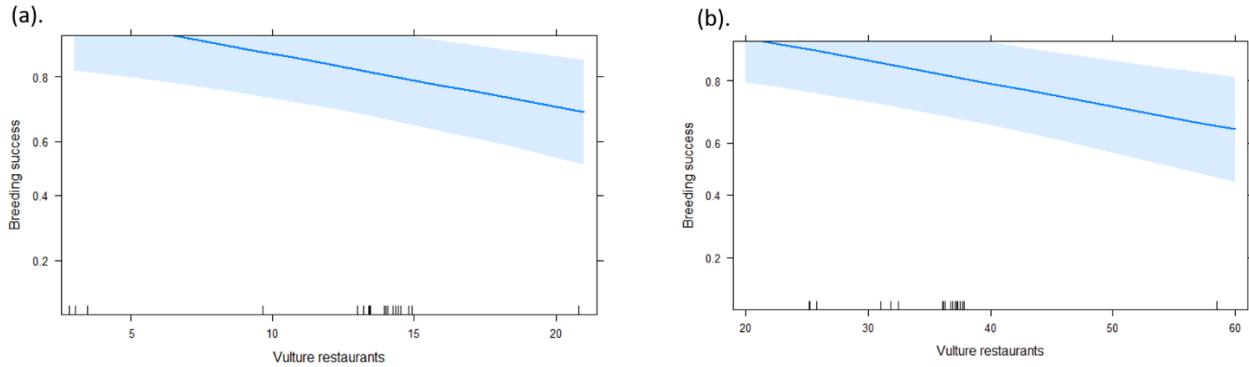


Figure 2: The negative relationship between Cape Vulture late-season breeding success and number of vulture restaurants within 100km (a) and 200km buffer (b) based on the predicted values of GLMMs, 95% Confidence Intervals in shaded blue, black bars on x-axis each represent a restaurant .

African White-backed Vulture breeding success

The effect of vulture restaurants on African White-backed Vultures was explored by running five GLMMs (Table 1). Explanatory variables relating to vulture restaurant availability were significant for four out of the five models (Table 4), in all cases breeding success was higher for colonies with greatest access to vulture restaurants. There was a strong positive relationship between breeding success and proximity to vulture restaurants (Table 4, Figure 3). African White-backed Vulture breeding success was also significantly explained by the distance to the nearest vulture restaurant. Breeding success was increased at colonies that were closer to the nearest vulture restaurant (Table 2, Figure 4). The number of vulture restaurants within 100km also showed a strong positive relationship with breeding success of African White-backed Vultures (Table 2, Figure 5).

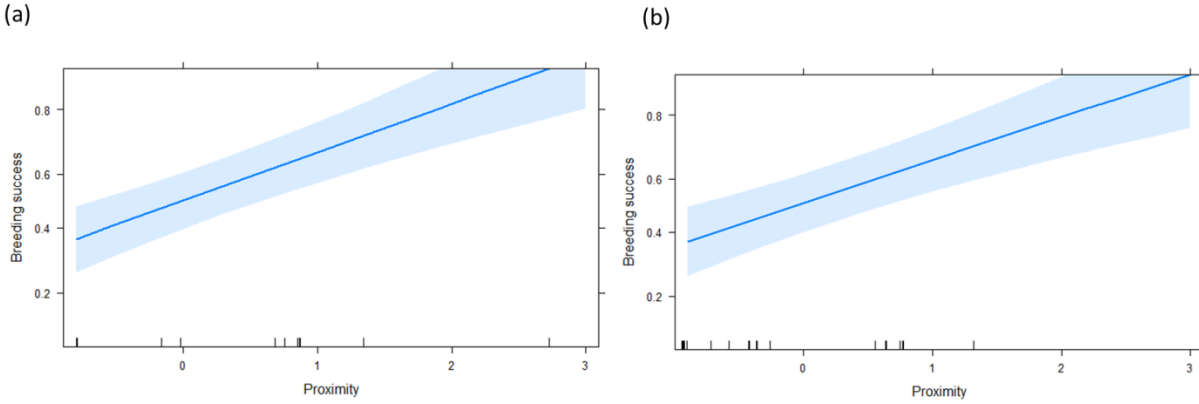


Figure 3: The relationship between African White-backed Vulture breeding success and proximity to a vulture restaurant within a) 100km (PI100) and b) 200km buffer (PI200) as predicted by GLMMs at 95% Confidence Intervals (shaded blue). Black bars on the x-axis represent each restaurant.

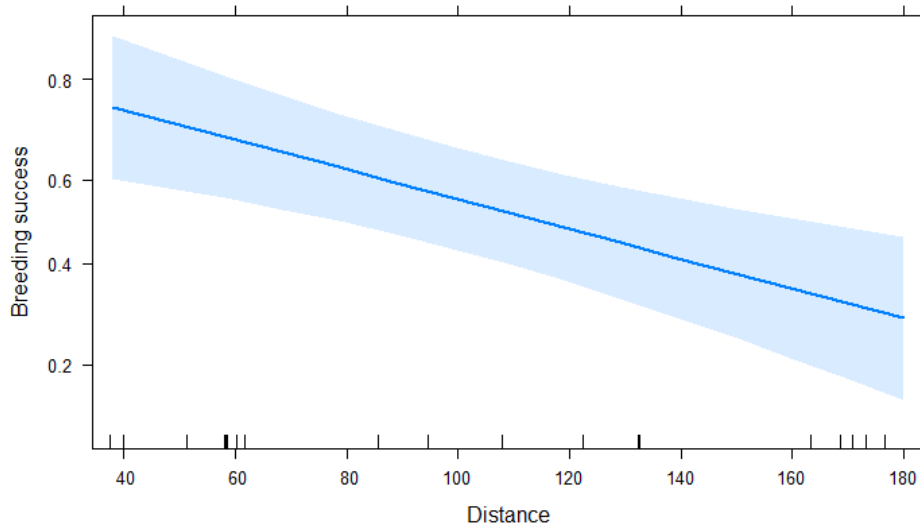


Figure 4: The relationship between African White-backed Vulture breeding success and distance to the nearest vulture restaurant based on the predicted values of GLMMs at 95% Confidence Intervals. Small black bars on the x-axis represent each restaurant.

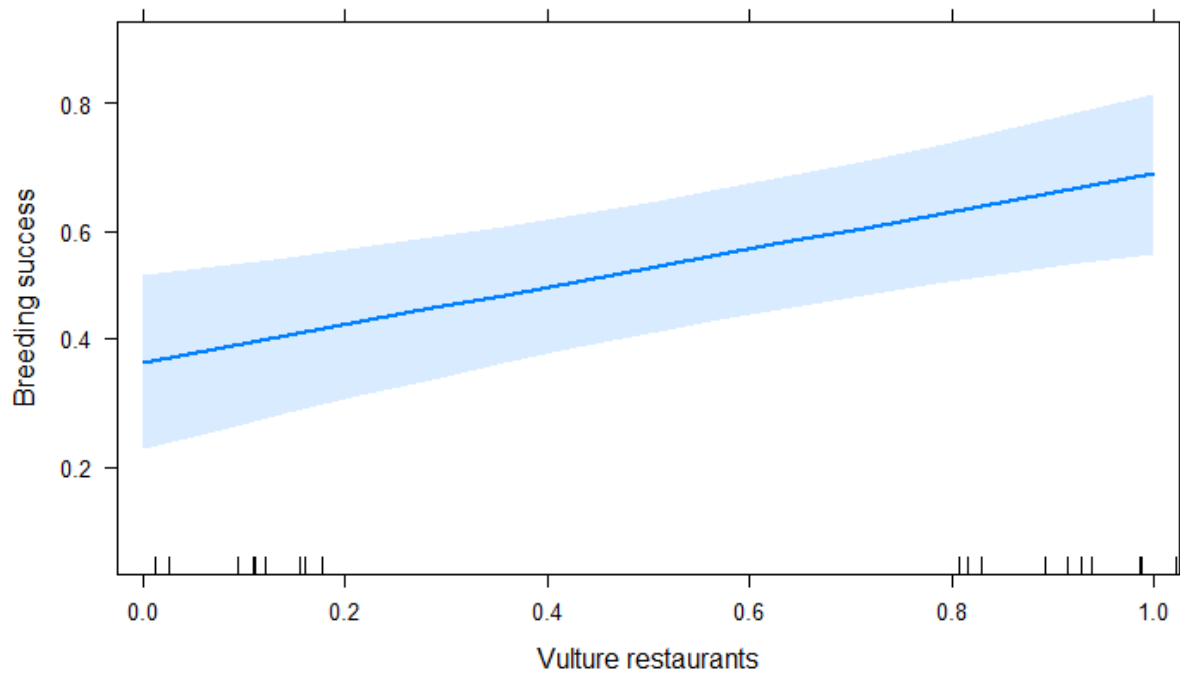


Figure 5: The relationship between African White-backed Vulture breeding success and number of vulture restaurants within a 100km buffer based on the predicted values of GLMMs, 95% Confidence Intervals shaded in blue. Small black bars on the axis represent each restaurant.

African White-backed Vulture nestling body condition

There was no relationship between vulture restaurants (proximity, and distance to the nearest vulture restaurant) with overall nestling body condition of African White-backed Vultures across southern Africa (Table 4). However, there was a negative relationship between nestling body condition and number of vulture restaurants within 100km buffer (Figure 6a. Table 4), and a strong negative relationship was noted for 200km buffer (Figure 6b. Table 4), thus nestling body condition was lower at nests that had a lot of vulture restaurants around them. A similar trend was also noted after removing chicks measured in Namibia (Figure 7a & b, Table 4).

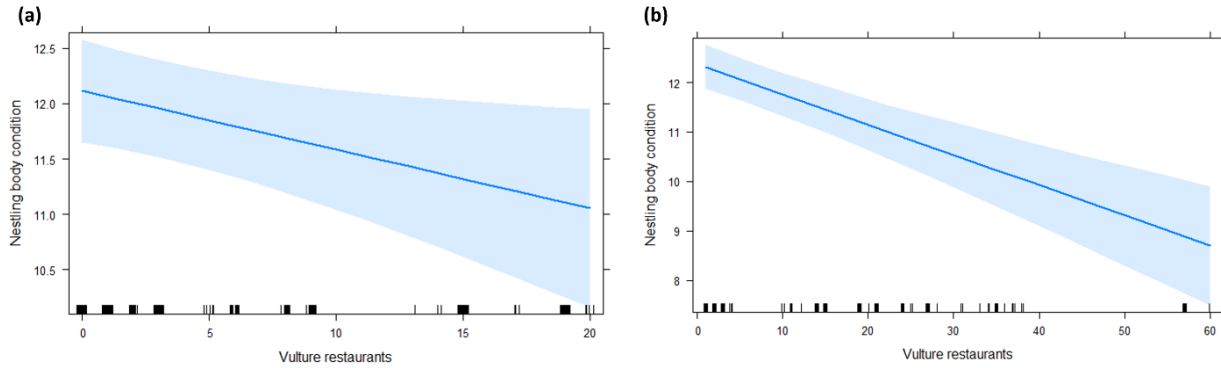


Figure 6: The relationship between African White-backed Vulture overall nestling body condition and number of vulture restaurants within a) 100km and b) 200km buffer based on the predicted values of GLMMs, 95% Confidence Intervals shaded in blue. Small black bars on the axis represent each restaurant.

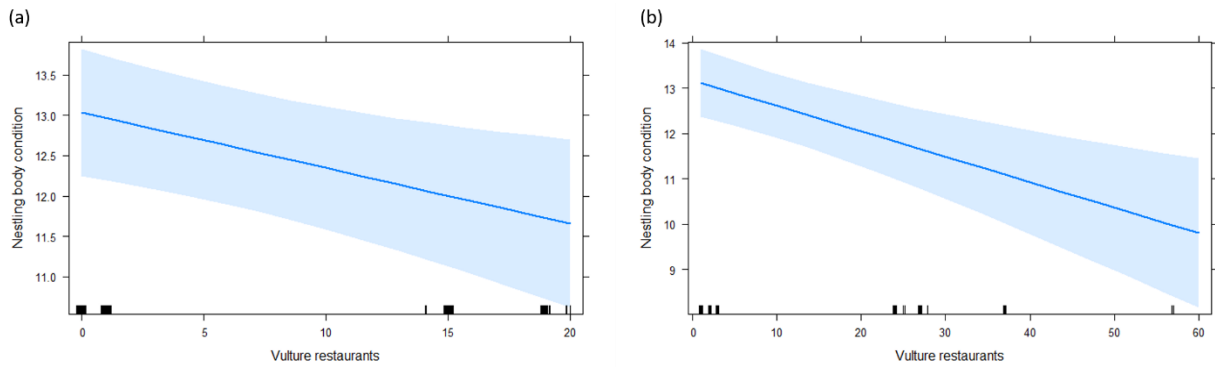


Figure 7: The relationship between African White-backed Vulture nestling body condition (nestlings from Namibia removed) and number of vulture restaurants within a) 100km and b) 200km buffer based on the predicted values of GLMMs, 95% Confidence Intervals shaded in blue. Small black bars on the axis represent each restaurant.

Table 4: Results of Generalised linear mixed models (GLMMs) investigating the effects of vulture restaurants on breeding success and nestling body condition of vultures. Df = degrees of freedom, Res df = residual degrees of freedom, χ^2 = chi square. For each response variable, proximity 100km (PI100), proximity 200km (PI200), distance, vulture restaurants 100km (VR100) and vulture restaurants 200km (VR200) were included. MBS=Mid-season breeding success, LBS=Late-season breeding success, BS=breeding success. Nestling body condition with all data is represented by Condi All & Cond represents nestling body condition with chicks from Namibia excluded. Positive response is represented by + and – for negative response.

Species	Model	Response Variable	Explanatory Variable	Df	Res df	χ^2 Test statistic	P value	Direction of response
Cape Vultures	M1a	MBS	PI100	1	46	0.229	0.632	
	M1b	MBS	PI200	1	46	0.512	0.474	
	M1c	MBS	Distance	1	46	0.966	0.326	
	M1d	MBS	VR100	1	46	1.648	0.199	
	M1e	MBS	VR200	1	46	1.196	0.274	
	M2a	LBS	PI100	1	15	0.192	0.661	
	M2b	LBS	PI200	1	15	0.223	0.636	
	M2c	LBS	Distance	1	15	1.513	0.218	
	M2d	LBS	VR100	1	15	9.704	0.002	-
	M2e	LBS	VR200	1	15	12.524	<0.001	-
African White-backed Vultures	M3a	BS	PI100	1	43	33.719	<0.001	+
	M3b	BS	PI200	1	43	26.273	<0.001	+
	M3c	BS	Distance	1	43	12.905	<0.001	-
	M3d	BS	VR100	1	43	12.555	<0.001	+
	M3e	BS	VR200	1	43	0.983	0.322	
	M4a	Condi All	PI100	1		0.927	0.336	
	M4b	Condi All	PI200	1		0.945	0.331	
	M4c	Condi All	Distance	1		1.951	0.163	
	M4d	Condi All	VR100	1		4.623	0.031	-
	M4e	Condi All	VR200	1		31.412	<0.001	-
	M5a	Cond	PI100	1		0.755	0.385	
	M5b	Cond	PI200	1		0.760	0.384	
	M5c	Cond	Distance	1		0.470	0.493	
	M5d	Cond	VR100	1		6.506	0.012	-
	M5e	Cond	VR200	1		14.183	<0.001	-

DISCUSSION

Overall, my study found strikingly different results between the two study species. For Cape Vultures, I found no positive association between breeding success and any measure of availability of vulture restaurants. In fact, for two of the measures (numbers of vulture restaurants within 100km and 200km) there was a significant negative association between breeding success and availability of vulture restaurants. In contrast, for African White-backed Vultures I found a strong signal for improved breeding success in relation to availability of vulture restaurants. This association was significant for all variables, except for the number of restaurants within the largest buffer radius (200km). However, even for African White-backed Vultures, my results show a negative relationship found for nestling body condition and the numbers of vulture restaurants within my buffer circles.

Effect of vulture restaurants on Cape Vulture breeding success.

Breeding success at Cape Vulture colonies was not influenced by the proximity to vulture restaurants, and my predictions were not met. Thus, my results did not support my hypothesis that the breeding success of this species is limited by food availability. They are also similar to Schabo *et al.* (2017), who also found no influence of the amount of food provided annually at a nearby restaurant of annual breeding success of Cape Vultures at one colony. However, their study did suggest larger amounts of supplementary food were associated with more breeding pairs during the initial stages of breeding. This indicates that vulture restaurants can be used as a successful conservation tool, as feeding during nest-building stage has the potential to increase number of breeding pairs and the latter increases the number of chicks produce per year (Schabo *et al.* 2017). The results of my study are also generally consistent with those of Oppel *et al.* 2016, which also did not detect a positive signal on the effect of vulture restaurants on Egyptian

Vulture breeding success. They are also consistent with Krüger *et al.* (2015), who found that proximity to vulture restaurants did not influence territorial abandonment in Bearded Vultures in Southern Africa. However, Krüger *et al.* (2015) did not look at the effect of vulture restaurants on Bearded Vulture breeding success.

For Cape Vultures it therefore appears that variables other than availability of vulture restaurants may be more important in influencing their breeding success. These variables might include factors such as distance to other land use types, such as human settlement and protected areas, weather conditions, none of which were considered in my analyses. In theory failing to control for these variables in my analysis might also have masked my ability to detect a positive effect of vulture restaurants on breeding success, for example the positive effect of vulture restaurants might only become apparent once the overall abundance of other food (e.g. livestock or game in protected areas) is controlled for. Thus, for future analysis it might be useful to control for these variables first before testing whether there is an effect of vulture restaurants. However, not controlling for these other variables is likely to explain why I detected a negative relationship between two of my measures of vulture restaurant availability and Cape Vulture breeding success.

One potential explanation is that vulture colonies near a vulture restaurant might be exposed to predation pressure and competition for food resources at feeding sites (Anderson and Anthony 2005; Selva *et al.* 2014; Yarnell *et al.* 2015; Oppel *et al.* 2016). Consequently, higher food availability at vulture restaurants can potentially attract more carrion-eating birds for instance crows or ravens, eagles, which can potentially prey on vulture eggs and chicks (Anderson & Anthony, 2005; Schabo *et al.* 2017). Such a situation could therefore potentially attenuate

breeding success at colonies near a high number of vulture restaurants. In addition, the effect of human disturbance on breeding success could also contribute to my results. This has been proven to influence breeding success and nest attendance of two vulture species in Europe (Arroyo & Razin, 2006; Zuberogoitia *et al.* 2008).

A decrease in breeding success as number of vulture restaurants increases as shown in this study suggests that in some cases, vulture restaurants lead to overabundance of carrion resources. This is likely to lead to overcrowding of populations which leads to unusual mating systems for instance polyandrous trios and the latter resulting in decreased breeding success as shown for Pyrenean Bearded Vultures by Carrete *et al.* (2006). Additionally, vulture restaurants appear to have initiated more nests as found by Schabo *et al.* 2017, this is probably due to the stable and abundant food source provided at some vulture restaurants which leads to breeding recruitment of young birds earlier than usual. This might cause an increased number of breeding pairs, but younger birds are more likely to fail, and this could cause the perceived response of lower overall breeding success near restaurants.

My Cape Vulture results focus on only one demographic parameter, breeding success, and it might be that it does increase breeding condition of pre-laying birds (Schabo *et al.* 2017) and 1st year survival. A study on survival rates of Cape Vultures by Piper *et al.* (1999) showed that first year survival was higher for birds that were provided with supplementary feeding. Given this evidence vulture restaurants might well still be a good conservation tool. The next step and arguably the most important test would be to explore whether restaurants influence local population trends and that once the restaurants database has been updated it would be a good future research project.

Effect of vulture restaurants on African white-backed Vulture breeding success.

Breeding success of African White-backed Vultures was found to be positively affected by the proximity to a vulture restaurant. These results therefore support my hypothesis that food is a limiting factor in the breeding success of White-backed Vultures in southern Africa. My prediction that vultures at colonies with greater access to vulture restaurants would have better breeding success was met. Thus, these results suggest that, at least for this species, vulture restaurants have the potential to enhance populations across southern Africa. These results are thus in keeping with studies from elsewhere which have found that vulture restaurants have the potential to increase breeding success in raptor populations (Donazar & Fernandez, 1990; Gonzalez *et al.* 2006).

My findings also suggest that there is potential for recolonization of abandoned colonies or establishment of new colonies near vulture restaurants as more carrion becomes available for African White-backed Vultures. This leads to increased breeding pairs and the latter increases the overall breeding success.

Effect of vulture restaurants on African White-backed Vulture nestling body condition.

I found a strong negative relationship between vulture restaurants and African White-backed Vulture nestling body condition. My results contradict my predictions that vulture restaurants increase nestling body condition of vultures. My findings also contrast with those of Opper *et al.* (2016) who found an increase in nestling body condition at feeding locations. Nestling body condition of vultures, as with other raptors, is typically affected by the quantity and quality of food that parents are likely to provide their chicks (Newton, 1998). The foraging success of parents has therefore been found to have a positive effect on nestling condition, hence proximity to vulture restaurants has the potential to benefit chicks as foraging success of parents improves

(Santangeli *et al.* 2012). Perhaps however, nestlings raised near vulture restaurants are exposed to more lead, antibiotics or other contaminants, which will ultimately reduce their nestling body condition.

Although African White-backed Vultures are known to nest in loose clusters, there is a high possibility of density dependent factors playing a role on nestling body condition. There is high risk of spread of diseases as species breed in groups which might explain why I noticed a decrease in nestling body condition as number of vulture restaurants increased. This suggests that breeding success will increase as individuals get more carrion from a wide range of vulture restaurants in the vicinity to breeding colonies, but however chicks will have a poor body condition as they might be affected by diseases or heavy metals such as lead. Additionally, it should be acknowledged that there might be other factors affecting nestling body condition other than proximity to vulture restaurants, which I never included in my analyses. Thus, the negative effect of vulture restaurants might be an artefact for another variable that is confounded with vulture restaurants.

Data Issues

My findings should be used with caution as there is high variability in how the data was collected by different organisations which might have caused bias on my analyses. This is the only database currently available and for my analysis I eliminated large amounts of unusable data due to issues with the protocol. However, even in the data that we use, relatively minor differences between groups in how the data is collected or indeed how breeding is interpreted can result in issues. Therefore, I recommend development of a standardized monitoring protocol that can be used by all vulture conservation organisations across southern Africa. More

specifically there is need for a coordinated effort in saving vulture populations across southern Africa.

The vulture restaurant database lacks spatio-temporal information on vulture restaurants across southern Africa. Although other studies have used the available vulture database as is, the spatial information of the database has not been validated and updated. Thus, more of the so-called “vulture restaurants” might no longer be restaurants and some may have inaccurate coordinates. All this might have also caused inaccuracies in my analyses. In addition, less is known on the quality and quantity of food supplied at vulture restaurants, hence it makes it difficult to provide detailed evidence on the effect of vulture restaurants. This might have caused over- or under-estimation of real numbers of vulture restaurants.

Conclusion and recommendations

The current study provided good scientific evidence on the effect of vulture restaurants of Cape and African White-backed Vultures in southern Africa. My findings suggest vulture restaurants benefits African White-backed Vultures than Cape Vultures in southern Africa. However, there is need for further assessment to validate some of the assumptions made in the current study and broaden the scope of the study by including other variables that were not included in the analyses. Specifically, there is need for a validated and updated database with correct spatio-temporal distribution of vulture restaurants and confirm whether these restaurants are still active or have discontinued. Thus, current study suggests there is need for future research with an updated layer of vulture restaurants and test the signal of the effect of vulture restaurants on vulture populations across southern Africa. I also recommend a detailed comparison of food sources in different land use types for instance, protected areas, and assess if there is no overlap

on the effects of vulture restaurants on breeding colonies. This could also be validated by making use of tagged individuals.

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APPENDICES

1. Cape Vulture summary data

Appendix A: Table shows the long-term summary data used in exploring the effect of vulture restaurants on breeding success of Cape Vultures. 1st= first breeding monitoring survey, 2nd =second breeding monitoring survey, 3rd = third breeding monitoring survey. ✓ represents if the breeding monitoring survey was conducted and * indicates the breeding survey was not conducted. N represents the total number of nests monitored every year per each breeding colony.

Colony	Location		Province	Year	1 st	2 nd	3 rd	N				
	Latitude	Longitude										
Nooitgedacht	S 25° 51' 7.92"	E 27° 32' 50.24"	North West	2001	✓	✓	*	59				
				2002	✓	✓	*	74				
				2003	✓	✓	*	64				
				2006	✓	✓	*	100				
				2007	✓	✓	✓	88				
				2008	✓	✓	✓	118				
				2009	✓	*	✓	113				
				2010	✓	✓	✓	125				
				2011	✓	✓	✓	93				
				2012	✓	✓	✓	73				
				2013	✓	✓	✓	116				
				2014	✓	✓	✓	97				
				2015	✓	✓	✓	100				
				2016	✓	✓	*	140				
				2017	✓	✓	✓	120				
				Skeerpoort	S 25° 44' 48.12"	E 27° 45' 56.34"	North West	2001	✓	✓	*	200
								2002	✓	✓	*	194
2003	✓	✓	*					188				
2006	✓	✓	*					257				
2007	✓	✓	✓					275				
2008	✓	✓	✓					277				
2009	✓	*	✓					235				
2010	✓	✓	✓					221				
2011	✓	✓	✓					199				
2012	✓	✓	✓					197				
2013	✓	✓	✓					209				
2014	✓	✓	✓					221				
2015	✓	✓	✓					248				
2016	✓	✓	*					250				
2017	✓	✓	✓					289				
Roberts' Farm	S 25° 49' 58.08"	E 27° 18' 27.07"	North West					2011	✓	✓	✓	5
								2010	✓	✓	✓	9

				2009	✓	*	✓	7
				2008	✓	✓	✓	7
				2007	✓	✓	*	6
				2006	✓	✓	*	5
				2003	✓	✓	*	14
				2002	✓	✓	*	15
				2001	✓	✓	*	35
Manoutsa	S 24° 27' 48.24"	E 30° 45' 16.59"	Limpopo	2011	✓	✓	*	539
				2012	✓	✓	✓	434
				2013	✓	✓	*	471
				2014	✓	✓	*	563
				2015	✓	✓	*	579
				2016	✓	✓	*	621
				2017	✓	✓	*	644
Kransberg	S 24° 28' 20.64"	E 27° 36' 11.44"	Limpopo	2011	✓	✓	*	628
				2012	✓	✓	✓	661
				2013	✓	✓	*	608
				2014	✓	✓	*	632
				2015	✓	✓	*	614
				2016	✓	✓	*	862
				2017	✓	✓	*	690
Soutpansberg	S 23° 1' 7.32"	E 29° 35' 15.25"	Limpopo	2012	✓	✓	✓	182
				2013	✓	✓	*	189
				2014	✓	*	✓	187
				2015	✓	✓	*	196
				2016	✓	✓	*	213
				2017	✓	*	✓	223
Mzimkulu/Oribi	S 29° 40' 42.24"	E 29° 10' 29.64"	KwaZulu Natal	2008	✓	✓	*	22
				2011	✓	✓	*	39
				2012	✓	✓	*	49
Potberg	S 34° 22' 41.16"	E 20° 33' 37.83"	Western Cape	2008	✓	✓	*	75
				2009	✓	✓	*	63
				2012	✓	✓	*	69
				2013	✓	✓	*	84
Blouberg	S 23° 2' 38.4"	E 29° 3' 27.36"	Limpopo	2008	✓	✓	*	483
				2009	✓	✓	*	433
				2012	✓	✓	*	851
Vulture's retreat	S 29° 3' 47.16"	E 29° 18' 37.26"	KwaZulu Natal	2009	✓	✓	*	40
Moletjie	S 23° 44' 38.76"	E 29° 19' 24.06"	Limpopo	2012	✓	✓	✓	20
				2014	✓	*	✓	16

2013	✓	✓	*	14
2016	✓	*	✓	15
2017	✓	*	✓	5

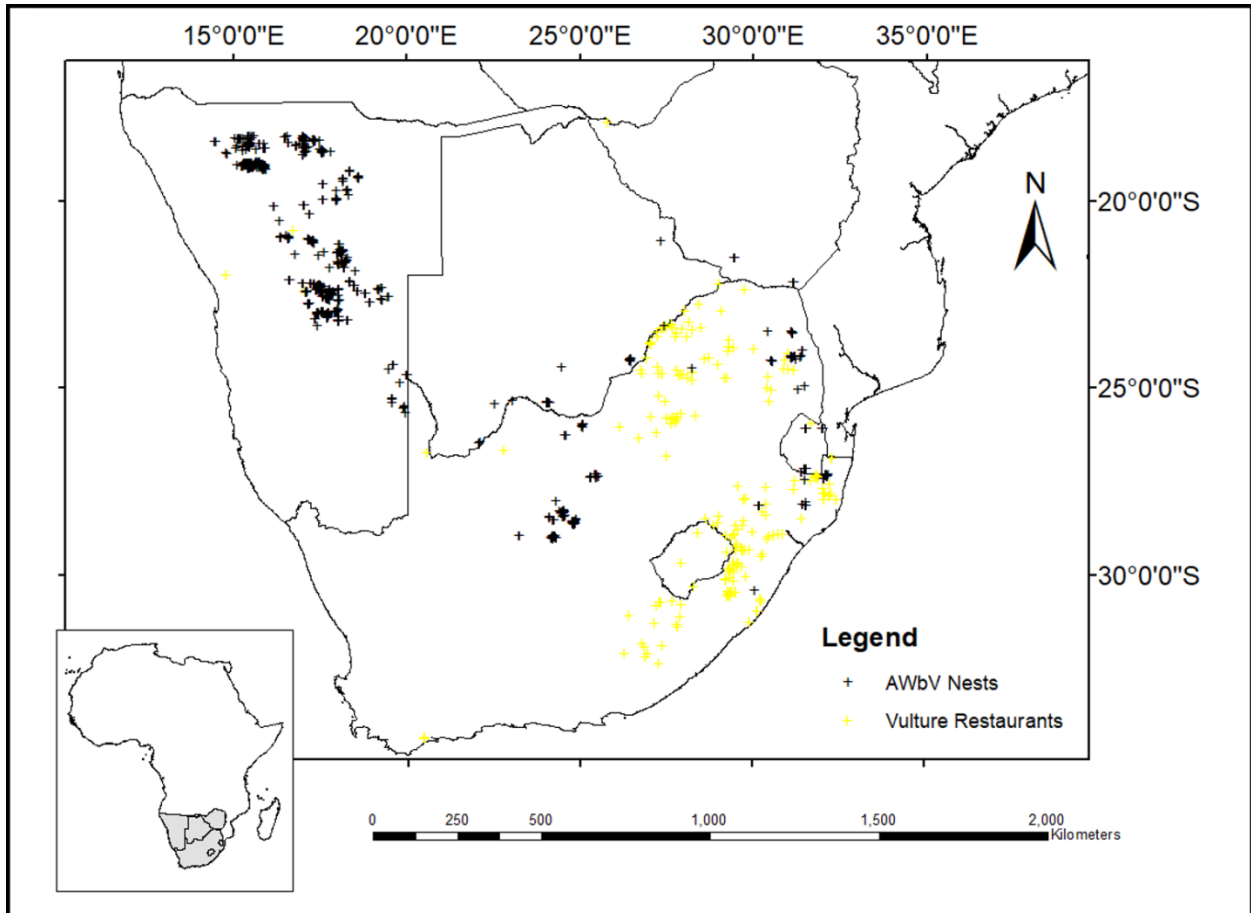
2. African White-backed Vulture summary data

Appendix B: The long-term summary data used in exploring the effect of vulture restaurants on breeding success of African White-backed Vultures. N represents the total number of nests monitored every year per each breeding colony.

Colony	Location		Province	Year	N
	Latitude	Longitude			
Beeswood	S 25° 43' 6.24"	E 24° 4' 48.612"	North West	2013	5
Birnamwood	S 25° 49' 15.996"	E 24° 8' 27.096"	North West	2012	17
				2013	34
				2014	29
				2015	27
				2017	9
Hurst Park	S 25° 47' 2.004"	E 24° 2' 41.892"	North West	2014	5
Kammeldoorn	S 25° 45' 59.004"	E 24° 9' 7.488"	North West	2015	6
Khamab	S 25° 38' 23.1"	E 23° 5' 17.088"	North West	2015	8
				2016	7
				2017	19
Nottingham	S 26° 6' 39.096"	E 25° 6' 10.692"	North West	2012	8
				2013	16
				2014	13
				2015	21
				2016	12
Vergelegen	S 25° 45' 27.108"	E 24° 11' 14.784"	North West	2013	9
				2014	14
				2015	20
				2016	9
Vlakplaas	S 26° 31' 44.112"	E 24° 57' 37.116"	North West	2012	6
				2013	10
				2015	12
				2016	12
				2017	8
Mokala	S 29° 1' 19.668"	E 24° 21' 44.352"	North Cape	2011	25

				2012	31
				2013	34
				2014	30
				2015	35
				2017	50
Schutsekama	S 29° 1' 48.72"	E 24° 23' 58.92"	Nothern Cape	2014	47
				2015	52
				2016	28
				2017	19
Sanddrift	S 28° 59' 56.148"	E 24° 22' 1.92"	Nothern Cape	2014	14
				2016	33
				2017	30
Lorraine	S 29° 0' 14.904"	E 24° 19' 39.072"	Nothern Cape	2016	29
	S 28° 58' 59.16"	E 24° 21' 0.108"		Nothern Cape	2016
Gannahoek					2017
	BBF	S 29° 5' 7.764"	E 24° 6' 14.796"	Nothern Cape	2017
S 28° 53' 8.988"		E 24° 21' 50.94"	Nothern Cape		2017
Kalkdam	S 26° 59' 43.692"	E 20° 50' 16.692"		Nothern Cape	2017
STWld	S 26° 55' 50.808"	E 20° 55' 21.216"	Nothern Cape	2017	25
Murray	S 25° 51' 45.9"	E 22° 53' 16.008"	Nothern Cape	2017	25
Malopo NR			North- West	2012	9
				2016	5

Appendix C: The distribution of vulture restaurants, and African White-backed Vulture nests used in exploring the effect of vulture restaurants on nestling body condition across southern Africa.



Appendix D: Cape Vulture and African White-backed Vulture colonies that were eliminated from the analysis due to unclear protocol.

Species	Site	Year	Active Nests Mean (Range)
Cape Vultures	Mannyelanong	2014	62
African White-backed Vultures	Hluhluwe-Imfolozi Park	2013 -2017	189 (2-225)
	uMkhuze Game Reserve	2013 -2017	38.2 (8-89)
	Pongola Game Reserve	2013 -2016	24 (20 -34)
	Phongolo Nature Reserve	2013 -2017	13 (3 - 20)
	Olifants	2017	36
	Boikarabelo	2017	48
	Thula-Thula Game Reserve	2013 -2017	38 (24 -43)