Changes in nesting numbers and breeding success of African White-backed Vultures in northern Botswana

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This project is my own work.

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Contents

Abstract

African White-backed Vultures have recently been uplisted to Critically Endangered by the IUCN due to declines across their range mainly linked to high levels of poisoning. Botswana likely supports significant numbers of this species, but as yet there is no published information on their population trends or their breeding success in this country. However, in recent years within Botswana and neighbouring countries there have been multiple incidents of mass poisonings, which have resulted in the deaths of thousands of White-backed Vultures. I therefore expected that nesting numbers of this species may have declined in this region, with potential additional negative impacts to breeding success. I used information from aerial surveys conducted between 2006 and 2017 in Khwai and Linyanti, two of the most important breeding areas for this species in northern Botswana to examine changes in nesting numbers and breeding success. The results showed a 53.5% decline in nesting numbers from these colonies, from 99 pairs in 2007 to 46 in 2017; with a greater decline in Linyanti than in Khwai. In both areas breeding success was significantly lower in 2017 than it was ten years ago. Current breeding success rates were generally lower than for other populations in South Africa. A population viability analysis suggested that if the productivity levels detected in 2017 were a true indication of current levels of productivity for this population, and if recent poisoning rates continue, this population has a high probability of extinction in the next 5 to 13 years.

Introduction

Vultures are among the most threatened avian guild worldwide (Buechley & Şekercioğlu 2016). Within southern Asia, vulture populations completely collapsed in the late 1990s and early 2000s due to the use of veterinary diclofenac, which contaminates livestock carcasses and is lethal to vultures (Green et al. 2004; Oaks et al. 2004). More recently, considerable concern has been raised about the conservation of vultures within Africa (Virani et al. 2011; Ogada et al. 2015).

Threats to African vulture populations include reduced availability of food (Bamford et al. 2009; Kane et al. 2014), nesting-site loss (Monadjem & Garcelon 2005), and collisions and electrocution (Anderson 1995). However, poisoning has caused the majority of the decline witnessed throughout Africa (Ogada et al. 2016). Reasons for poisoning are varied, including unintentional lead poisoning from spent ammunition (Garbett et al. in press; Naidoo et al. 2012; Kenny et al. 2015), intentional sentinel poisoning by poachers (Ogada et al. 2016; Murn & Botha 2017), targeted poisoning for belief-based use (Ogada et al. 2012), accidental exposure to veterinary drugs (Basson 1987; Naidoo et al. 2018), and accidental poisoning when farmers target “problem animals,” such as carnivores that depredate livestock (Herholdt & Anderson 2006).

Since 2012, an increase in poaching of large mammals (Chase et al. 2016) has escalated the incidents of sentinel poisoning, whereby poachers deliberately target vultures (Ogada et al. 2016) due to the fear of vultures being used to detect poaching scenes. The types of poisons include carbamate (Virani et al. 2010; McNutt & Bradley 2016), aldicarb, carbofuran and cyanide (Ogada et al. 2016).

Due to the rapid rate of decline in some populations, seven of the eight vulture species found in Southern Africa have now been uplisted to higher conservation categories by the International Union for Conservation of Nature (IUCN) (Birdlife International 2018). Three of these (Hooded, *Necrosyrtes monachus*; White-headed, *Trigonoceps occipitalis*; and African White-backed Vulture, *Gyps africanus*) are now classified as Critically Endangered. The African White-backed Vulture (Salvadori, 1865) (hereafter White-backed Vulture) is the most widespread vulture in Africa and as such represents over 90% of the recorded mass-mortalities in poisoning incidents in several Southern African countries over the past five years (Endangered Wildlife Trust 2017; Rutina et al. 2017). Higher losses of White-backed Vultures relate to the species’ higher abundance and aggressive feeding behaviour (Anderson

2004; Bamford et al. 2009). Notable declines of this species have been recorded in west and east Africa (Thiollay 2007; Virani et al. 2011). Several studies have been conducted on the White-backed Vulture in Southern Africa that inform the conservation status of this species. Such work includes population monitoring (Thiollay 2006; Virani et al. 2011; Ogada et al. 2015; Murn & Botha 2017), as well as studies on poisoning loads (Kenny et al. 2015; Naidoo et al. 2017, 2018), space use (Phipps et al. 2013; Kane et al. 2014, 2015), the identification of threats (Monadjem et al. 2013), and the exploration of conservation management approaches (Murn & Botha 2017).

The majority of the trend data for White-backed Vultures comes from road counts (see Ogada et al. 2015), with relatively little breeding colony monitoring being conducted (Murn et al. 2002; Monadjem & Garcelon 2005; Doulton & Diekmann 2006; Virani et al. 2010). However, to understand the conservation status of this species going forward, it is important to establish current demographic rates, including patterns of breeding success. Currently, there is little data published on the breeding success of this species. The one key exception to this is the long term monitoring of the population at Dronfield farm in Kimberley, Republic of South Africa (RSA), which has been monitored since 1972 (Angus 2012a; Murn et al. 2017). In a study of six colonies between 2001 and 2014, nesting numbers were found to have declined in 4 while in 2 colonies there were increases.

Botswana is among the countries with the greatest proportion of areas in the world that are devoted to wildlife (World Bank 2018). Over 39% of its land base is under some form of protection – 18% within protected areas and another 21% within Wildlife Management Areas (Tyler & Bishop 1998), Because of this, Botswana is likely to be very important in the conservation of vultures in the region. However, almost no published information exists on the population trends of any vulture species within the country (Ogada et al. 2015).

Within northern Botswana and immediately near its borders, poisoning has killed a minimum of 1150 White-backed Vultures in at least 18 incidents between 2008 and 2016 (Hancock 2010a, 2010b; Bradley & Maude 2014; McNutt & Bradley 2014; Rutina et al. 2017). Many more White-backed Vultures were likely poisoned at non-discovered locations. In 2013 alone, over 900 individuals belonging to this species were killed in just three incidents (Hartman 2013; McNutt & Bradley 2014, 2016) in northern Botswana and north-western Namibia. This makes this area a hotspot for vulture mortality due to poisoning. However, because vultures can undertake huge cross country movements (Phipps 2011; Paijmans et al. 2017), there is uncertainty on whether the poisoned birds were local birds or were part of the wider regional population. We also have no information on whether these poisoning incidents have resulted in localised population level declines. Poisoning is likely to also have indirect effects on population such as reduced social location resulting from reduced numbers (Deygout et al. 2010). It is important to understand how these factors, may have influenced this species population size in the region, and how poisoning may have impacted other vital rates (e.g., reproduction), and to understand how robust the local population in the face of such impacts.

Previous monitoring of the region's Important Bird Areas (IBAs) (Hancock et al. 2007a, 2007b) revealed that Khwai, Linyanti and Makgadikgadi areas of northern Botswana were the three most important areas for breeding colonies of White-backed Vultures. Lesoma Valley has also been recognised as an important breeding site for these species in the region (Hancock 2010b). Three widely dispersed colonies of Khwai, Linyanti and Makgadikgadi were monitored through aerial surveys in 2006/07. At Khwai and Linyanti, monitoring was subsequently conducted intermittently thereafter. In 2017, a comprehensive aerial survey was undertaken at these two colonies. These data provided an opportunity to explore changes from ten years ago, specifically over the time period when poisoning has become more severe.

The aim of this study was to use monitoring data of White-backed Vultures in Linyanti and Khwai colonies to explore changes in nesting numbers and breeding success over a ten-year period. In addition, I collated data from other monitored populations in Southern Africa to compare past and current breeding success within northern Botswana with the breeding success of other populations within the region. Lastly, I used information on the current population size, past and current productivity, and poisoning levels in the region to estimate the predicted population trend over the last 10 years and to compare it with the observed trends, as well as the likely population trends in the future to explore the viability of this population.

Method

Study area

Northern Botswana is dominated by Kalahari soils (Tyler & Bishop 1998; Sianga & Fynn 2017) inundated by perennial and seasonal rivers (Hancock et al. 2007b; Chase et al. 2015). It is close to these rivers that tall trees grow to heights that exceed 20 meters compared to ten meters elsewhere (Teren 2016). Canopies of such trees provide the nesting sites for White-backed Vultures (Kemp & Kemp 1975). Species used for nesting include Palm tree (*Hyphaene petersiana*), knobthorn (*Acacia nigrescens*), and raintree (*Lonchocarpus capassa*) (Muller & Hancock 2007).

My study area lies from 18.0 to 19.5 °S, and from 23.5 to 24 °E (fig 1) and encompasses a combined area of around 1,000 km^2. The Linyanti area is situated <50 km west of Chobe National Park, and Khwai is 50 km due south of Linyanti on the fringes of the Okavango Delta. Both areas have similar terrain and biodiversity. The surrounding areas have a very low human population and are primarily devoted to nature conservation. The primary land use in northern Botswana is low density ecotourism (Maude & Reading 2010; Chase et al. 2015).

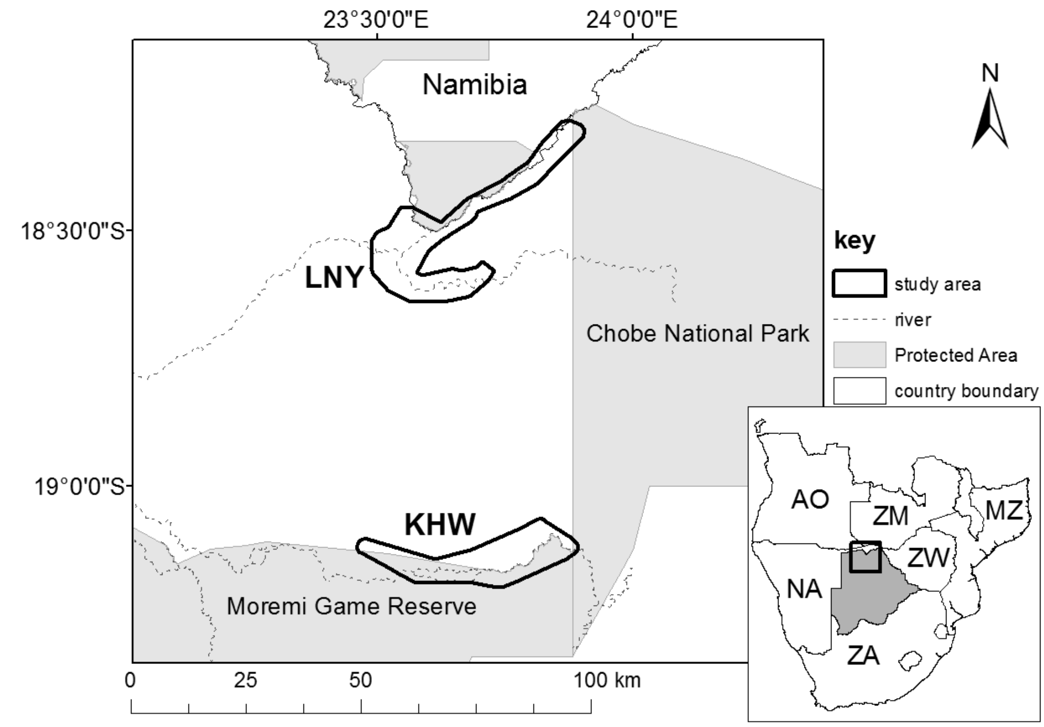

Figure 1. Map of the study area within northern Botswana, showing my two study sites (LNY = Linyanti; KHW = Khwai) where two loose colonies of White-backed Vulture were surveyed intermittently between 2006 and 2017. The map in the lower right hand corner shows Southern Africa and the location of the inset map. The breeding sites straddle Protected Area and Wildlife Management Areas that are partially-protected areas where non-consumptive wildlife utilization is the main land use type.

Study species

White-backed Vultures nest on trees in aggregated clusters along flat plains and within riparian areas (Tarboton 2001). They build their nests in the crowns or sturdy forks of trees

(Mundy 1982). Nests can measure 830 mm in diameter and 210 mm in thickness and are sparsely lined with dry grass (Houston 1976).

Breeding commences in March/April (Hockey et al. 2005). Egg laying peaks in May, but can range between April and June (Mundy 1982). White-backed Vultures are a single brooding species and lay a single egg. A replacement clutch may often be laid if failure occurs early enough in the season (Mundy 1982). Incubation lasts around 56 days, and nestling period prior to fledging is 120-125 days (Houston 1976).

Nest monitoring and data collation

Data on the number of active nests and breeding success were obtained through aerial surveys using a Magni-16 gyrocopter. In 2006 and 2007 an AirCam fixed-wing light aircraft was also used during surveys. The number of aerial surveys conducted each year at each colony varied from one to three (see table 2). Surveys were conducted at three time periods:

1) 'Early' surveys were conducted between 19 June and 15 July – this aimed to coincide with the main incubation period. For Linyanti, this survey was used to estimate the number of 'active' nests, to examine population changes, and these were the nests that were surveyed in subsequent visits to estimate breeding success. For Khwai, no historical surveys (2006 or 2007) were conducted during this time. In 2017, nest identified from this visit were used to contribute data on the minimum nesting numbers at Khwai.
2) 'Middle' surveys were conducted between 24 July and 09 August – this aimed to coincide with the late incubation period/early nestling stage. For Khwai, this was the survey used to estimate the number of 'active' nests, to examine population changes, and these were the nests that were surveyed in subsequent visits to estimate breeding success. For years with 'early' surveys, these 'middle' surveys helped to monitoring nesting progress and provided additional nests, which contributed to estimates of minimum nesting numbers.
3) 'Late' surveys were conducted between 04 September and 03 October – this aimed to coincide with the main late-nestling / early-fledgling stage. These surveys were used to estimate breeding success of the previously identified 'active' nests located during either the 'early' or 'middle' surveys. Thus, nests which had a chick during the 'late' survey and had been identified as 'active' during the appropriate previous survey of that year, were classified as successful. Again some additional

nests were also found during these surveys, these contributed to estimates of the minimum nesting numbers of the colony, but were not used to estimate breeding success or numbers of active nests.

For aerial surveys, each colony was stratified and surveyed through different flying routes each lasting around two hours. During the first surveys, every area that had potential trees suitable for nesting raptors was examined for raptor nests (including White-backed Vultures). For each survey year, the first visit was the most comprehensive coverage, and with subsequent surveys then targeted known nests, but also picked up new nests along the routes. During subsequent surveys the pilot flew directly from one known nest to another. ‘New’ nests or those that had escaped previous detection were opportunistically identified during flying. Flights took place in early to mid-morning and late afternoon, approximately 0900-1100 and 1500-1700hrs depending on suitable weather and flying conditions.

Aircraft were flown at approximately 60-80 $km \cdot h^{-1}$ ground speed, at a height of 70 m above the nests, providing an effective viewing distance of approximately 500m on either side. Active monitoring of each nest from the air occurred for just as long as it took to confirm the nesting species and the nests’ contents, which was on average less than 30 seconds. At this point nest site location was also recorded using a hand held Global Positioning System (GPS) device.

Monitoring was usually restricted to one fly-past; however, if the nesting status was still not clear, a second pass was made. In just a few cases, several fly-pasts were necessary to either locate the nest, or clarify the content. During each survey (early, mid, or late) each nest was visited only once. The details recorded were: nest co-ordinates in decimal degrees (for new nests), tree species, date, name of observers, and content (no nest = when the nest had disappeared, empty, egg, chick, or incubating/brooding adult). Active nests were defined as those with an egg, chick, or incubating/brooding adult in the nest (or adult perched close to the nest). When recording data, ‘no nest’ indicated that despite repeated searches at the location, a nest had disappeared. For purposes of analysis ‘no nest’ also included: broken or damaged nests, as well as nests whose host trees has fallen over.

Adults observed in an incubating position were assumed to be incubating if this was observed before 9th of August. Thus any birds sitting tight after 9th of August was assumed to be brooding. From mid-August many chicks may have already hatched. In this case chick referred to any young from a hatchling to a fledgling. A breeding attempt was classified as successful and used in the estimate of breeding success, when an active nest (identified during either the early or middle survey, depending on the specific colony and year) was still active with a chick during the late survey. Thus my measure of success based on early visits (as the first visit) may be biased upwards, if other late initiated nests were on average less successful, as is usually the case for raptor species (eg Martin et al. 2014; Garcia-Heras et al. 2016; Murgatroyd et al. 2016); or may be biased downwards for success measures based on middle visits (as the first visit). Nests that had a nestling during the late visit were assumed to be successful, but this would have included a few nests that may have failed after this last visit, although as a general rule failure during the later nestling stages is relatively rare in large raptors as compared to other stages of the breeding cycle (Newton 1979).

Additional data on breeding success for this species was obtained from several other South African colonies. Data were obtained from the Endangered Wildlife Trust (EWT) for colonies in Northern-Cape, North-West) and Ezemvelo KwaZulu-Natal Wildlife (EKZN) (for colonies in Kwazulu-Natal). Data were only used from colonies that were collected in a manner similar to the data collected in northern Botswana. These were either aerial or ground surveys that included at least two visits. In the same manner as the Botswana surveys, only nests active during the earlier visit were used to estimate breeding success. For my analysis, I used only colonies with a minimum of 10 nests monitored in any one year.

For some of the KZN surveys, nests were not allocated a unique identifier that allowed specific nests to be tracked between different nest surveys within the same year. To address this issue, data between surveys conducted in August and in October were matched using a proximity table in ArcGIS (version 10.2.0.3348 Environmental Systems Research Institute 2011). A buffer was used to select only those nests from the October shapefiles that were within 200 m of an August site. Thereafter the 'Generate Nearest Table' tool was used to predict a match in October of each nest that was monitored in August. Only one late-visit nest was used per match using minimum Euclidian distance. Colonies whose nests were matched this way were HIP (Hluhluwe-Imfolozi Park), MKH (uMkhuze Game Reserve), PNR (Phongolo Nature Reserve), PGR (Pongola Game Reserve and PPS), and THL (Thula Thula Private Game Reserve). In these 5 colonies, a total of 370 nests across three years were matched using this procedure.

Additionally, I ranked findings of the present study to literature values of White-backed Vulture breeding success. I searched primary and grey literature for reported values of breeding success, making sure to quote breeding success values that had been calculated in a similar manner to that used in this study. Only colonies for which breeding success estimates were based on ten or more nests were used for this comparison.

Table 1. Survey times relative to timing of various breeding activities for White-backed Vultures. Solid borders around the grey boxes indicate the visits that were used to estimate active nests and breeding success. Peak laying season is around mid-late May, while peak fledging is mid-late October (Brown et al. 2013). Surveys were scheduled for June/July; while the late-season surveys occurred in late-September/early October, targeting chicks just before they fledged. Numbers indicate dates of the month on which colonies were surveyed.

	June	**July**	**Aug**	**Sept**	**Oct**	**Nov**
survey	laying	incubating	nesting		fledging	
	early-visit		*mid-season visit*	*late-visit*		
KHW 2006			02-05	03-04		
KHW 2007		25-26				
KHW 2017		30 - 02	08-11		03-05	
LNY 2007	25-26			14-16		
LNY 2008		01-03				
LNY 2017	19-22		04-05	26-27		

Population modelling

I aimed to explore whether the population would have declined (and to what extent) between the mid-2000s and 2017, based on past productive and poisoning levels, and whether the population will produce enough young to be sustainable on a longer term basis with, or without, the documented levels of poisoning currently occurring. Models were built using the VORTEX population viability software (version 10.2.15.0 Lacy & Pollak 2014). Stochastic models were constructed using the same basic parameters as Murn and Botha (2017) used for their baseline model for this species, altering only three parameters; population size, reproduction rate, and adding catastrophes (to simulate offtake by mass poisonings). Population size was calculated from number of breeding pairs (in each period – e.g. mid-2000s or 2017), multiplied by 1.25 to include nonbreeding individuals, multiplied by 1.3 to account for juveniles and immatures, and multiplied by 2 to include males. This was in line with (Murn et al. 2017) who assumed that only 0.8 of adults breed year to year, added 0.33 for nonbreeding immatures, and assumed equal sex ratio. The carrying capacity was set to three times the population estimate. This value of 3 was arbitrarily selected as other authors multiplied their population sizes by between 2.5 and 4 (Velevski et al. 2014; Murn & Botha 2017).

Populations were assumed to be closed for these models, with no immigration or emigration. I used this model to explore five scenarios:

I) The first model was used to predict the past population growth rate in the absence of mass poisoning, using the breeding success of the population during the mid-2000s from the previous surveys.

II) The second model used model I, but imposed additional mortality from poisoning, this was implemented as a catastrophe function. The catastrophe was modelled to affect 20% of the frequency, and had a 0.9 probability of occurring in a year. This was derived from the median count of White-backed Vultures killed by poisoning within an arbitrarily selected 200 x 200 km grid laid over the study area each year over the last ten years (appendix A). I assumed that all poisoned individuals originated from the local population and that no local birds were poisoned outside the grid.

III) My third model, explored the population growth rate using the current levels of breeding success for 2017 (with no additional poisoning mortality).

IV) My fourth model, used model III, but imposed the same levels of mortality from poisoning as model II.

V) My fifth model, used model III, but imposed a severity of 34% at 90% frequency, which considered that at the same level of poisoning severity would be increased in a reduced initial population.

Data analysis

Nesting numbers

To compare how nesting numbers had changed between the 2007 and 2017, I used the visits in 2017 which most closely matched the timing of visits in 2007. For Khwai, this was the mid-season visit, and for Linyanti it was the early-season visit. The area surveyed in Khwai in 2017 was expanded out to include a larger area than that surveyed in 2007, thus comparison was confined to the original study area that was surveyed in 2007. To produce an estimate of minimum nesting-number, nests identified from visits from other times were included, this was used for any comparison but is estimate for interest's sake. In 2008, there was only a single (as opposed to repeat) survey for Linyanti, as well as the 2016 which only had a late visit at Khwai. Since each colony was visited three times in 2017, counts from the additional visits that were not used to estimate active nests contributed to the estimate of minimum nesting number.

Breeding success

I compared breeding success from 2006/07 to that from the 2017 survey. Data from the 2006 sample survey was useful in determining breeding success, but it was not a full survey and was therefore not used to examine changes in numbers of active nests. No repeat survey was conducted in 2007 for Khwai, thus for breeding success estimates and comparisons I used breeding success for 2006. Early visits for 2007 and 2017 were used to calculate breeding success for Linyanti, while for Khwai the mid-season visits were used as the reference point for both breeding success estimates (2006 and 2017).

Statistical analysis

All analysis were conducted using R statistical software (version 3.4.3 R Core Team 2017). I tested whether there was a change in breeding success between the survey years for each site; for this I used a generalised linear model (GLM) with a binomial error structure and a logit link function. In the analysis, I used data for both colonies, and fitted period (mid 2000s or 2017), colony (Khwai or Linyanti) and the interaction between the two terms as the categorical fixed effects in the model. To explore for individual differences (e.g. between colonies, or between years), I used the pairwise comparison function the lsmeans package (Lenth 2016), which was also used to generate breeding success estimates by years, and their 95% confidence limits. In different years the number of weeks between the early and late surveys varied (Table 1), and therefore less failures may have occurred when visits were closer together. To control for this issue, I fitted the number of weeks between surveys (within a year) as a weighted term in the model. My sampling unit used in the analysis was the success of each active nest surveyed in each year, given as a binary variable (1=success, 0=failure).

I also compared breeding success in Botswana in the different periods (past = 2007 and/or 2006; present = 2017) with the breeding success found from other colonies in different regions of South Africa. For this wider-region comparison I used a generalised linear mixed model (GLMM), with colony as a random variable to compare at the broader regional level (Botswana past or present, Kwa-Zulu Natal, Northern-Cape, and North-West). I used the lsmeans function (Lenth 2016) to perform pairwise comparisons between regions, and to generate regional estimates of breeding success and their associated 95% confidence limits. For this regional comparison, breeding success of nests in Khwai inside the 2017 expanded study area were also included in the analysis.

Results

Changes in nesting numbers

There were 60 active nests in Linyanti during the early 2007 visit (Figure 2a). There were an additional 13 nests that were active during the later visits, which had been either inactive during the early visit or had not been found. Thus, there were a minimum of 73 breeding pairs nesting in the area in 2007. There was only one visit in 2008, an early visit in late June. This found 48 active nests (*cf.* 60 nests in 2007). In 2017 only 21 active nests were found during the early visit, and one additional nest in later visits. This represents 65% fewer active nests (from the early visits) in 2017 than there were in 2007 (Figure 2a).

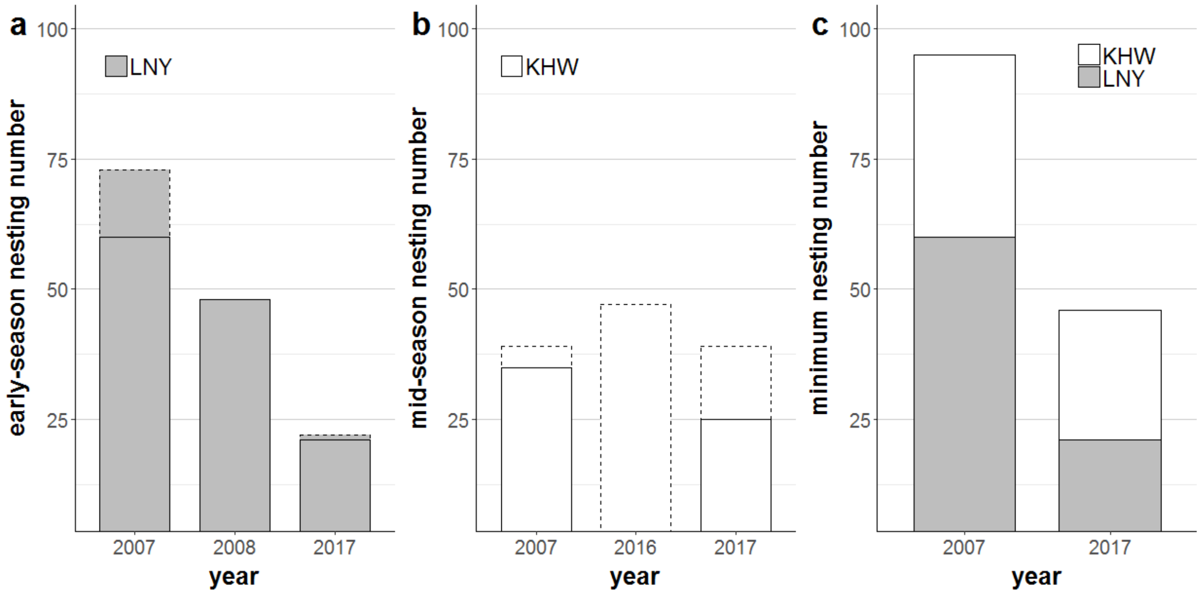

Figure 2. Yearly nesting numbers by colony (LNY = Linyanti, based on early-season survey) (KHW = Khwai, based on mid-season survey). In Figures 'a' and 'b', the main bars are the numbers found during the comparable visits and therefore for years with multiple nest visits. The higher dotted lines in Figures 'a' and 'b' represent the minimum number of nests, and therefore include extra nests that may have been found active during the non-comparable surveys. In Linyanti there was only one (early) visit during 2008, so no additional minimum information is available. In Khwai there was only one (late) visit during 2016, so no comparable information is available either. Figure C shows the minimum number of nests for both colonies combined (using only comparable visits between the two years).

In Khwai there was only one survey (a mid-season visit in late July) in 2007. From this visit, 35 active nests were found (fig 2b), with an additional 4 found outside normal visits. Thus, there was a minimum of 39 breeding pairs. In 2017, there were three visits. From the same core study area, there were 25 active nests during the comparable mid-season visit, plus an additional 13 active nests found at other times. Thus, in this core area there was a minimum of 38 active nests. The change in number of active nests in Khwai (during the mid-season visits) represents a 28.6% decrease over the last decade. In 2016, only a late visit was conducted, which found 47 active nests. Thus also the direct comparison suggested a small decline, the minimum numbers of nests during the last 10 years have remained very similar.

Combining all the data on active nests from the comparable visits and within the comparable study areas, there was a 53.53% decrease between 2007 and 2017 from 99 active nests to 46 (fig 2c).

Table 2. Number of active nests across survey years in northern Botswana. (LNY = Linyanti) (KHW = Khwai). In Linyanti, corresponding nesting were a third of what they had been in 2007, and they had a slightly less rate of decline for Khwai. All comparisons were done over the same area. Values quoted here include nests that could not be relocated during later surveys, hence the difference from values used for breeding success.

site	**2006***		**2007**			**2008**	**2016**	**2017**		
	mid	late	early	mid	late	early	late	early	mid	late
LNY	30	27	60		42	48		21	12	7
KHW	17	15		35			47	32	25	35
Total	47	42						53	37	42

*only cursory sample surveys were done in 2006

Changes in breeding success

For Linyanti, the breeding success was 62% in 2007 (fig 4a), with 33 successful nests from the 53 monitored nests (based on early visit). For Khwai in 2006, the breeding success from 15 nests was at 60% (fig 4b) (based on mid visit). The breeding success rates for similar surveys in Linyanti and Khwai in 2017 were 33.3% and 35.8%, respectively. No repeat visit was done for Khwai in 2007 nor in Linyanti in 2008, so breeding success for these colonies in those years was not estimated. The change over ten years thus represents a decline of 46.3% for Linyanti and 35.3% in Khwai. In overall, this represents a decline from an average breeding success of 61.8% ten years ago to 35.2% in 2017. My analysis, showed there was a significant difference in breeding success between periods (mid-2000s and 2017) (Table 3), but no differences between the colonies (Table 3), there was also no interaction between colony and period, suggesting the decline in breeding success had been very similar between the colonies Breeding success was not statistically different between the two colonies in both the mid-2000s (p=0.9342) and 2017 (p=0.9916).

Table 3. Results of generalised linear model of breeding success in Botswana between years and colonies. There was no statistical difference between the breeding success rates between colonies, while breeding success was significantly different between the two study periods ($p < 0.001$).

model	response	variable	df	X^2	*p*-value
glm	breeding success	period (mid 2000s/2017)	1,138	52.175	< 0.001
		colony	1,137	0.351	0.5536
		period*colony interaction	1,136	0.083	0.7735

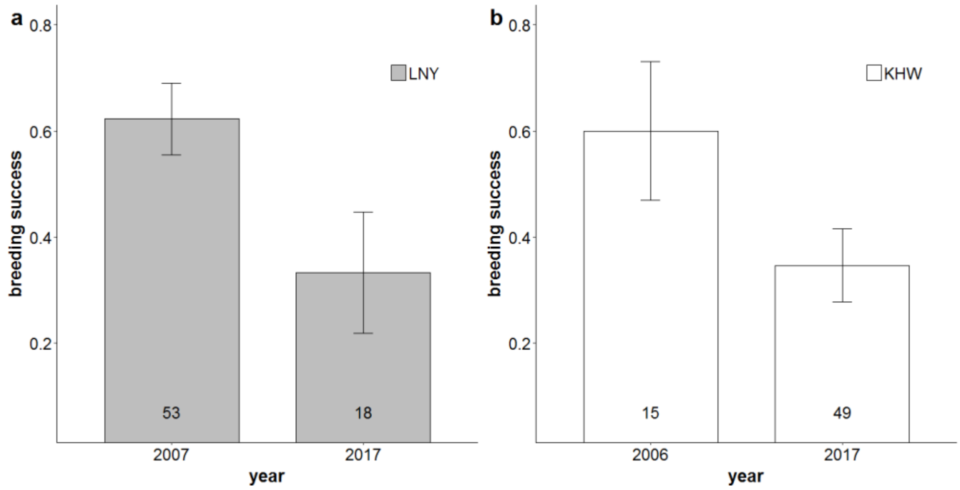

Figure 3. Yearly breeding success by colony ± 95%CI. The Khwai (KHW) breeding success (bs) was based on mid-season numbers, while the Linyanti (LNY) was based on early-season nesting numbers. The old data from Khwai is based on the partial survey from 2006, while for LNY I used the full survey done in 2007. Labels denote number of nests used to calculate bs. For some nests there was no late survey data, usually because they could not be relocated –and hence variation between label values and values indicated in figure 2.

Breeding success for other regions in South Africa in the 2010s were higher than those found in Botswana in 2017 (table 4). The only exception was colonies in the North-Western Province which were similar to those of Botswana in 2017, and which have been below 0.50 for the past three years. Breeding success in Botswana in the mid-2000s was lower, but more comparable to these other South African colonies (Figure 5).

Table 4. Summary of breeding performance across survey years; 2006-2017. Breeding success (bs), and total on which breeding success was calculated (n). (LNY = Linyanti) (KHW = Khwai) and (MKG = Makgadikgadi). Values also include those from regions in Republic of South Africa (RSA) (KZN = Kwazulu Natal) (NC = Northern Cape) (NW = North West). Figures for KHW 2017 include nests outside core study area. For RSA sites no data was available before 2013.

	KHW		**LNY**		**MKG**		**KZN**		**NC**		**NW**	
year	bs	n	bs	n	bs	n	bs	n	bs	n	bs	n
2006	0.60	15										
2007			0.62	53	0.95	38						
2013							0.78	244			0.49	35
2014							0.87	31			0.48	42
2015							0.89	18	1	16	0.29	70
2016									0.85	82		
2017	0.36	49	0.33	18			0.87	15	0.78	81		

Data source: (McCulloch et al. 2007), Endangered Wildlife Trust, Ezemvelo KZN Wildlife

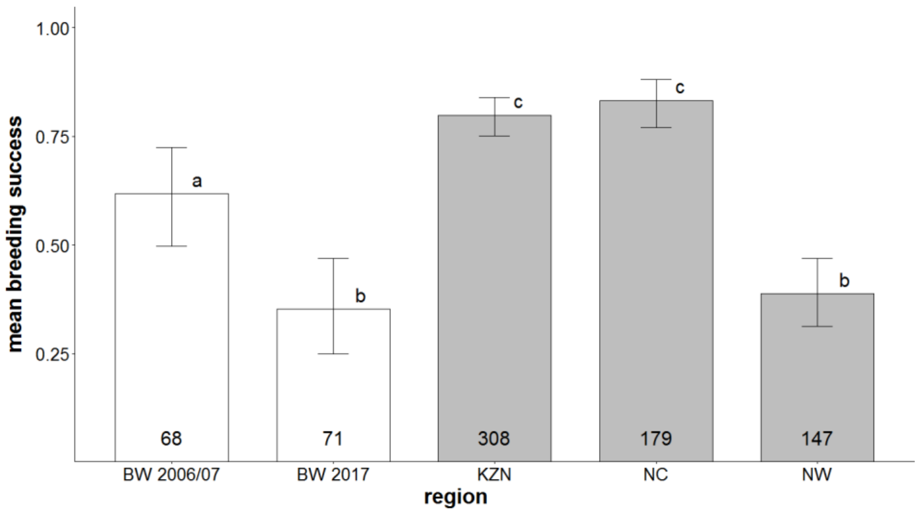

Figure 4. Breeding success estimates per region over several years, ± 95%CI (generated from the lsmeans from the GLMM, with colony fitted as a random term). Grey bars indicate regions from Republic of South Africa (RSA) where KZN = Kwazulu Natal, NC = Northern Cape, and NW = North West. Letters indicate similarity between estimates. Inner labels indicate the number of nests used to calculate breeding success. Breeding success from KZN and NC was higher than past and present BW, while NW was lower than past BW but similar to present BW.

Table 5. Results of pairwise comparisons of lsmeans of breeding success between regions and survey years. 'BW past' denotes Botswana in 2006/07, while 'BW present' denotes Botswana in 2017. When controlling for colony, a comparison to South African regions, shows Kwazulu-Natal (KZN) and Northern-Cape (NC) to fare better than Botswana, while North-West (NW) is similar to recent productivity. Comparison was confined to colonies with at least 10 nests.

Compared regions	**odds.ratio**	**SE**	**df**	**z.ratio**	**p.value**
BW past – KZN	0.40713	0.116913	NA	-3.129	0.0151*
BW past - NC	0.325245	0.104035	NA	-3.511	0.0041**
BW past - NW	2.550607	0.769104	NA	3.105	0.0163*
BW present - KZN	0.136974	0.039207	NA	-6.945	<.0001***
BW present - NC	0.109425	0.034911	NA	-6.935	<.0001***
BW present - NW	0.858124	0.258	NA	-0.509	0.9865

Table 6. Literature values of breeding success of White-backed Vulture. n denotes number of nests used to calculate breeding success (bs). Sorted by bs in descending order to underscore the rank of the present study (in bold).

Country, colony	Year	bs	n	Source
BW, Makgadikgadi	2007	95.4	38	McCulloch et al. 2007
RSA, Timbavati-Klaserie	1977	86.0	36	Tarboton & Allan 1984
RSA, Dronfield	1993	79.0		Angus 2012a*
RSA, Dronfield	2014	69.0	99	Koen 2014
RSA, Kruger NP	1968	64.2	56	Kemp & Kemp 1975
SW, Mlawula NR	2000	62.0	26	Monadjem 2001
BW, Linyanti	**2007**	**62.0**	**53**	***Present Study (historical)***
RSA, Kgalagadi TP	1988	60.9	23	Herholdt & Anderson 2006
BW, Khwai	**2006**	**60.1**	**15**	***Present Study (historical)***
SW, Mlawula NR	2003	59.0	24	Monadjem et al. 2004; Monadjem & Garcelon 2005
RSA, Kruger NP	1967	58.3	12	Kemp & Kemp 1975
RSA, Kimberley & ZIM, GNP	1976	52.6	95	Mundy 1982
RSA, Kgalagadi TP	1989	52.0	25	Herholdt & Anderson 2006
ZW, GonareZhou NP	1973	51.2	41	Mundy 1982
RSA, Dronfield	2013	49.4	79	Angus 2013
ZW, GonareZhou NP	1974	42.7	75	Mundy 1982
SW, Mlawula NR	2002	40.0	18	Monadjem 2001
RSA, Dronfield	2002	37.0		Angus 2012a*
BW, Khwai	**2017**	**35.8**	**49**	***Present Study (latest)***
BW, Linyanti	**2017**	**33.3**	**18**	***Present Study (latest)***
RSA, Dronfield	2012	33.0	75	Angus 2012a
RSA, Dronfield	2010	25.0	95	Angus 2012b
ZW, Hwange NP	1971-82	18.0	540	Howells & Hustler 1983*
RSA, Kgalagadi TP	1990	8.3	12	Herholdt & Anderson 2006

∗procedure for calculating bs couldn't be confirmed

Population viability analysis

Population viability analyses predicated that, based on previous productivity and in the absence of additional poisoning, the population would grow by, on average, 2.89% per year. However, with the additional mortality based on past poisoning levels, the population was expected to decline by around 12.8% per year, which over the ten years since the initial survey would represent a decline of 70.8% (fig 6a).

The viability models examining future population growth based on current productivity levels suggest that, in the absence of poisoning, the population would decrease marginally over the next 30 years, but only by 0.02% per year. However, with the current levels of productivity and poisoning, the population would decline by an annual rate of 15.0% (due to lower initial population size), with average time to extinction of the population being only 13 years (fig 6b). If severity is calculated relative to the 2017 population, the severity increases to 34%, which has a time to extinction of five years (fig 6b).

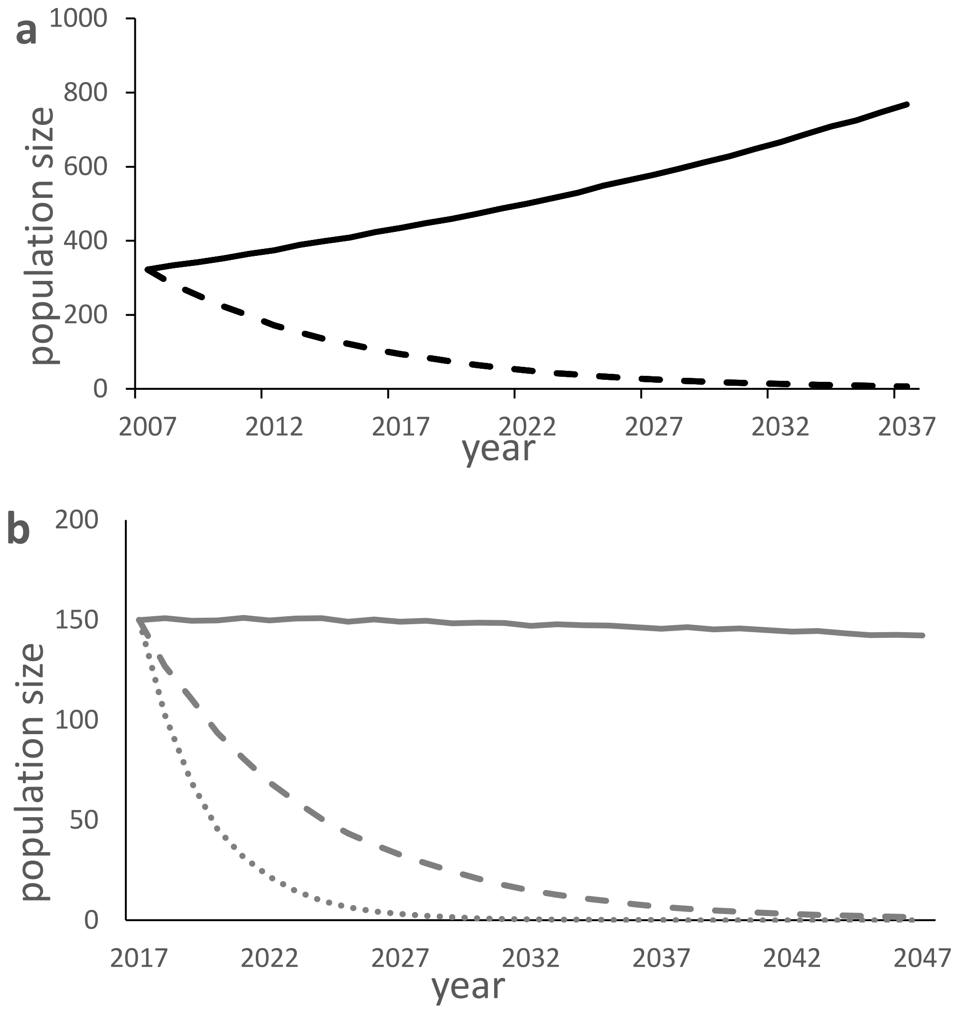

Figure 5. Simulated population projection under different demographics. Figure 'a' represents the projected population under previous productivity levels, the dashed line considers the poisoning rate over the past decade. At 0.62 young per breeding pair per year (ypby) in the absence of mass-poisoning there would be population growth, but a decline with poisoning with 100% possibility of extinction in 30 years. Under current productivity level 'b' of 0.36 ypby, the population is projected to marginally decline in the absence of poisoning, and be extinct in 13 years if current rates of poisoning continue. The dotted line indicates the population trajectory at a severity of 34% at the same probability of occurrence (0.9).

Discussion

My findings suggest a long-term decrease in nesting numbers of African White-backed Vultures in the study area. I observed a decline of 53.5% in nesting pairs over the last decade over the entire study area, with the decline in Linyanti being double of that of Khwai. A decline was predicted given the prevailing severity of vulture poisoning in the region (Endangered Wildlife Trust 2017).

The decline in nesting numbers in northern Botswana are more severe than many of the findings from elsewhere in the region. For example, a more conservative decline of 26% over 13 years was observed in breeding colonies near Kimberley RSA (Murn & Botha 2017), whilst other populations in Dronfield and Secretarius colonies in South Africa were found to have increased nesting numbers over 15 years since 2001 (Murn et al. 2017). In Kenya a decline of 52% in the overall population was observed over 27 years from repeat road transect (Virani et al. 2011). It took only a third of that time to achieve a similar decline in my study population. However, within West Africa a decline of 97% over 35 years was found outside protected areas (Thiollay 2007).

Within my broad study area, there was also a contrast in the trends of the two colonies, with a far larger decline recorded in Linyanti than at Khwai. These contrasting trends may reflect differences in exposure to poisoning events, with more severe incidents being concentrated around Linyanti. A total of 1276 White-backed Vultures were killed in ten incidents between 2010 and 2016 within 120 km of Linyanti, compared to 900 in 12 incidents within the same area surrounding Khwai. Recorded declines may however be an underestimate due to the buffering effect of migration between colonies throughout Southern Africa.

Similar to changes in nesting numbers, there were declines in breeding success over the same period. This change was significant at each colony and similar in magnitude. However, it should be recognised that because my recent survey only comes from a single year (2017) it is not clear whether these levels accurately reflect current levels of productivity or just represent an unusually low breeding success in this one year. If, however, this year's breeding success accurately represents the current decline, a pertinent question would be – why has breeding success declined in this region? One possible explanation could link to the increased levels of poisoning lately. If poisoning has killed older, more experienced individuals, which tend to display higher breeding performance, there may have been an increase in the proportion of younger less experienced individuals which usually have a lower breeding performance (Grubač et al. 2014). Such a situation has been found to have affect breeding success in Spanish Imperial Eagle (*Aquila adalberti*) (Margalida et al. 2008). During a 21-year study adult pairs produced more chicks than mixed adult/non-adult pairs, which in turn produced more chicks than non-adult pairs (Margalida et al. 2008). Alternatively, juvenile-biased mortality may have occurred at poisoning sites. Indeed, from another study which trapped vultures at carcases in the region, the majority of trapped birds were young birds (Garbett et al. in press). If this scenario is indicative of poisoning scenes as well, which seems likely, then the result of this would be that older animals may remain in the breeding pool, resulting in reduced breeding success due to senescence (Murgatroyd et al. in review).

I found that, with the exception of RSA's North-West province, breeding success was lower in my study population than in other populations in the region. The current breeding success also ranked within the lowest twenty-percentile of previously recorded values. Food supply is the most common factor that can influence breeding success of raptors in the absence of persecution (Newton 1979). Food supplementation was correlated with enhanced breeding success in White-backed Vultures (Zimunya 2018). Within a buffer of 200 km, breeding success in this species was directly correlated to proximity to vulture restaurants (Zimunya 2018). This intervention would have to be implemented with caution, however, as it might have unintended effects such as it might lead to change in foraging behaviour of vultures (Deygout et al. 2010; Kane et al. 2015) as well as that of other mammalian scavengers (Monadjem et al. 2004).

I collected no direct high-resolution data on weather condition or food availability, and thus am unable to make inferences on their influence on breeding success. However, to the best of my knowledge, no large environmental changes occurred between the two survey periods (flood, vegetation cover, fire frequency and severity, annual temperature and precipitation). It would be ideal to establish through follow up surveys in subsequent years whether breeding numbers and this reduced breeding rate reflect a longer term change, rather than interannual variation.

Mate loss can also contribute to reduced productivity or breeding success depending on when it occurs relative to the breeding season. Additionally, sub-lethal effects of poisoning may reduce individual health of either the chick (Mee et al. 2007) or the adult. In incidents where poisoning occurs regularly, sublethal exposure can increase the toxicity of susequent sublethal poison exposure or alternative threats (Cramp 1963). Hence reduced productivity can result from not only death but also from secondary effect or sublethal impacts.

Lead (Pb) poisoning may represent another explanation for declines in breeding success. A recent survey found that over 30% of 477 White-backed Vulture in Botswana have Pb exposure (Kenny et al. 2015), and a more comprehensive survey building on that result found that higher blood Pb levels were associated with hunting areas as well as during the hunting season (Garbett et al. in press). This study suggested that the most likely source of this poisoning was from spent Pb ammunition from both legal and illegal hunting (Garbett et al. in review). Pb negatively affects breeding performance in raptors (Gil-Sánchez et al. 2018), in the Cinereous Vulture (*Aegypius monachus*), a chick from an egg produced by an adult with lead toxicosis died even after artificial incubation (Pikula et al. 2013). Thus high levels of Pb in the White-backed Vultures could in theory be reducing breeding success in this population. Although whether levels of Pb have changed in vultures in the area is not known.

My PVA model suggests that the population was, at least in the past, sufficiently productive and should have been a net export of birds into the regional population. However, after considering the poisoning levels of the past decade, the population was projected to have declined by 70.8%. This projected value is therefore within a few percentages of the decline observed from my surveys, suggesting that localised poisoning is sufficient to entirely explain the levels of decline in nesting numbers witnessed.

Modelling of the past population led to local extinction in 29 years if poisoning and productivity levels remained constant. Modelling the current population showed a projected decline under present levels of productivity, even in the absence of poisoning. However, given current poisoning levels, the populations faces a 100% probability of extinction in 13 years. This extinction estimate is based on a severity of 15% at 0.9 probability of occurence per year, whereas in reality this is an optimistic scenario. Given the large population decline (thus increased severity), if past poisoning levels continue, this population could completely disappear within the next 5 years. Mass poisoning levels tend to be sporadic and can easily escalate to over 100 individuals in one incident (McNutt & Bradley 2014, 2016). Additionally, the elicit nature of poisoning events means that the numbers used in our study are conservative. Given that vultures may abandon breeding sites under low density (Allee effect) as suggested by Margalida et al. (2012), in reality extinction might occur sooner than projected.

Overall, the study population has demonstrated sensitivity over the last decade despite high productivity in the past. The estimate based on past productivity compares well with the Zululand population’s decline over 26 years (McKean & Botha 2007; McKean et al. 2013). It however fares worse than the projection for the Kruger population (Murn & Botha 2017) projection of three generations (55 years), but only due to higher productivity, lower frequency of offtake, and greater breeding numbers in Kruger which are double those of the study population. Additionally, the model assumed that this would be a closed population, where all the recorded deaths would be from the resident population, which is unlikely. My model also assumed constancy of other breeding parameters, which is will likely be a best case scenario.

Given that the observed changes in nesting numbers can be largely explained by the prevailing poisoning-related mortality, there is an urgent need to ensure implementation of UNEP/CMS Resolution 10.26 (Convention on Migratory Species 2011) in this region. Through monitoring and eradication of poison use – or provision of safe food, survival can be enhanced, which would offset the decline rate. Finally, the continued monitoring of these breeding colonies would enhance to refine the model and hopefully inform the evation of the eminent extinction.

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Appendix

Table A1. Poisoning incidents between 2007 and 2017 within a 400 x 400 km grid (18.0°S, 23.5°E to 19.5°S, 24°E) on which African White-backed Vulture mortality estimates were based. Yearly mean = 151.8 and yearly median = 51.

latitude	longitude	count	year	source
-19.8922	23.05745	50	2008	Endangered Wildlife Trust 2017
-19.7207	23.05465	52	2009	DWNP 2009 [1]
-17.906	24.774	15	2010	Endangered Wildlife Trust 2017
-18.6419	23.9892	200	2012	Endangered Wildlife Trust 2017
-19.7207	23.05465	11	2013	Endangered Wildlife Trust 2017
-18.7858	22.3962	35	2013	Endangered Wildlife Trust 2017
-17.842	22.751	600	2013	Endangered Wildlife Trust 2017
-18.2171	23.19047	260	2013	McNutt & Bradley 2014
-19.8212	22.76581	24	2014	Endangered Wildlife Trust 2017
-18.1534	24.5034	1	2014	Endangered Wildlife Trust 2017
-18.623	23.03183	85	2014	Bradley & Maude 2014
-18.1675	24.26582	34	2015	Endangered Wildlife Trust 2017
-19.6815	23.70573	46	2016	Endangered Wildlife Trust 2017
-19.8085	23.44389	103	2016	McNutt & Bradley 2016
-18.228	21.644	2	2017	Endangered Wildlife Trust 2017

[1]Department of Wildlife and National Parks (Botswana)

Table A2. Parameters used in the population model in program Vortex. The only difference between models, was the intial population and reproductive rates, as well as the inclusion of a catastrophe as decribed in text.

Parameter	Input value	Source
Scenario settings		
Number of iterations	100	
Number of years	30	
Extinction definition	20 individuals	Murn and Botha (2017)
Number of populations	1	
Inbreeding depression	no	
Reproductive system		
Pair system	Long-term monogamous	Murn and Botha (2017)
Age at first breeding, years (female)	5	Mundy et al. (1992)
Age at first breeding, years (male)	5	Mundy et al. (1992)
Maximum age of reproduction	45	
Maximum number of broods/year	1	
Maximum number of progeny/year	1	Mundy (1982)
Sex ratio at birth (m/f)	50/50	
Density dependent reproduction	no	
Reproductive rates		
% adult females breeding successful/year[1]	80±10	
EV in% adult females breeding	61.9,36.1	
Mean number of offspring/female/year[1] (±	1	
Mortality rates ± SD		
% mortality from age 0-1 (juveniles)	58±10	Murn and Botha (2017)
% mortality from age 1-2 (sub-adult)	15±3	Murn and Botha (2017)
% mortality from age 2-3 (sub-adult)	10.3±3	Murn and Botha (2017)
% mortality from age 3-4 (sub-adult)	10.9±1	Murn and Botha (2017)
% mortality from age 4-5 (sub-adult)	10.9±1	Murn and Botha (2017)
% mortality from age 4-5 (adult)	1.3±0.3	Murn and Botha (2017)
Catastrophe		
Number of types	0,1	See text
Frequency	90%	
Severity on Reproduction (proportion of	0.85	
Severity on Survival (proportion of normal)	0.85	
Mate Monopolization		
Mates in breeding pool, %	100	
Initial population structure		
Initial population size	322,150	Present study
Stable age structure	yes	
Carrying capacity	1300	
Emigration	none	See text