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Changes in nesting numbers and breeding success of African White-backed Vulture *Gyps africanus* in north-central Botswana

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Summary

African White-backed Vultures were recently uplisted to 'Critically Endangered' by IUCN due to declines across their range. Poisoning is widely accepted as the major reason for these declines. Botswana supports a high number of this species (breeding pairs > c.1,200), but as yet no published information exists on their breeding success in the country. However, mass poisonings within Botswana and neighbouring countries have killed thousands of White-backed Vultures in recent years. We therefore expected that nesting numbers may have declined in this region if these poisoning events killed local breeding birds. We used information from aerial surveys conducted between 2006 and 2017 in Khwai and Linyanti, two important breeding areas for this species in north-central Botswana, to determine if there was any change in nesting numbers and breeding success of White-backed Vultures. Results showed an overall 53.5% decline in nesting numbers, with a greater decline in Linyanti than in Khwai. In both areas, breeding success was significantly lower in 2017 than it was 10 ten years earlier. We recommend that similar repeat surveys are continued to provide greater confidence in the trends of both nesting numbers and breeding performance. Population viability analysis suggested that if the productivity levels detected in 2017 were a true indication of current productivity levels for this population, and if recent high poisoning rates continue, this population could be extirpated from the area in the next 13 years.

Keywords: Raptors, Aerial surveys, African-scavengers, Breeding success, Population declines, Local extinction, Poisoning, PVA

Introduction

Vultures are obligate scavengers and belong to the most threatened avian guild worldwide (Buechley and Şekercioğlu 2016, McClure *et al.* 2018). Within southern Asia, vulture populations completely collapsed in the late 1990s and early 2000s due to the use of veterinary diclofenac, which contaminated 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 status of vultures within Africa (Virani *et al.* 2011, Ogada *et al.* 2015).

Poisoning is considered to be the main cause of the recent declines in vultures witnessed throughout Africa (Ogada *et al.* 2016). Reasons for the use of poisons are varied; they include intentional "sentinel" poisoning by poachers (Ogada *et al.* 2016, Murn and Botha 2018) in which poachers deliberately target vultures to reduce the chance of their position being revealed by circling birds. Poisoning is also used for belief-based reasons (Ogada *et al.* 2012), while secondary poisoning occurs when farmers target carnivores that depredate livestock (Herholdt and Anderson 2006). Additional threats include unintentional lead poisoning from spent ammunition (Naidoo *et al.* 2012, Garbett *et al.* 2018b).

Since 2012, an increase in poaching of large mammals (Chase *et al.* 2016) has likely escalated the incidents of "sentinel poisoning" (Ogada *et al.* 2016). Types of poisons used in these actions, include carbamate (Virani *et al.* 2010) and cyanide (Ogada *et al.* 2016). Due to the rapid decline of some populations, eight of the nine vulture species found in southern Africa were uplisted to higher conservation categories by IUCN (BirdLife International 2018). Four of these vulture species (Hooded *Necrosyrtes monachus*, White-headed *Trigonoceps occipitalis*, Ruppell's *Gyps rueppelli* and African White-backed *Gyps africanus*) are now classified as 'Critically Endangered'. The African White-backed Vulture (Salvadori, 1865) (hereafter White-backed Vulture) is the most numerous vulture in Africa (BirdLife International 2015) and comprises over 90% of the observed mortalities in mass poisoning incidents across southern Africa over the past five years (Endangered Wildlife Trust 2017, Rutina *et al.* 2017). 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 species, including on population monitoring (Thiollay 2006, Virani *et al.* 2011, Ogada *et al.* 2015, Murn and Botha 2018, Garbett *et al.* 2018a), poison loads (Kenny *et al.* 2015, Naidoo *et al.* 2017, Garbett *et al.* 2018b), space use (Phipps *et al.* 2013, Kane *et al.* 2014, 2015), identification of threats (Monadjem *et al.* 2013), and exploration of conservation management approaches (Brown *et al.* 2015, Murn and Botha 2018).

Most trend data for White-backed Vulture populations come from repeat road counts (see Ogada *et al.* 2015, Garbett *et al.* 2018a), with relatively little monitoring of breeding populations being conducted (Murn *et al.* 2002, Monadjem and Garcelon 2005, Doulton and Diekmann 2006, Virani *et al.* 2010). Currently, there are few data published on the breeding success and changes in breeding performance of White-backed Vultures over time (e.g. Santangeli 2018). 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 documented since 1965 (Anthony 2012, 2015, Murn *et al.* 2017).

According to movement records available from various monitoring projects, the White-backed Vulture uses a wide area over the Southern African region (Phipps 2011, Paijmans *et al.* 2017). Breeding sites occur within northern Botswana, including in and near the protected Okavango Delta Ramsar Site. It is thus important to quantify changes in breeding parameters as this information gives a more complete picture of the Southern African meta-population, which is part of the global decline.

Botswana is among the countries with the highest proportion of land devoted to wildlife (World Bank 2018). Over 39% of its land is under some form of protection, 18% being within Protected Areas and another 21% within Wildlife Management Areas (World Database on Protected Areas; https://www.protectedplanet.net). Thus, Botswana is likely to be important for the conservation of vultures in the region.

Within northern Botswana and immediately near its borders, poisoning has killed a minimum of 1,150 White-backed Vultures in at least 18 incidents between 2008 and 2016 (Hancock 2010a, 2010b, Bradley and Maude 2014, Rutina *et al.* 2017). Additionally, it is likely that many more White-backed Vultures were poisoned at other locations that remained undiscovered. In 2013 alone, over 900 White-backed Vultures were killed in just three incidents in northern Botswana and north-western Namibia (Hartman 2013). In spite of high mobility (Phipps 2011, Paijmans *et al.* 2017), vulture breeding areas are restricted by availability of nesting sites, and hence mortality during poisoning events are likely to affect local breeding populations. However, the proportion of regional birds among the total poisoned locally remains unknown. Also unknown is the extent to which these poisoning incidents have resulted in declines of the local breeding population.

Previous monitoring of the region's Important Bird Areas (IBAs) (Hancock *et al.* 2007a, 2007b) revealed that the Khwai and Linyanti areas were two important areas for breeding areas of White-backed Vultures in north-central Botswana. These dispersed areas were monitored through aerial surveys in 2006 and 2007. In 2017, we undertook a comprehensive repeat survey in these two areas. These data provided an opportunity to explore changes from 10 years earlier, specifically over the time period when the use of poison has increased.

The aim of this study was to use the monitoring data of White-backed Vultures in Linyanti and Khwai to explore changes in nesting numbers over the last decade. These data also presented an opportunity to quantify the breeding success of the population and to explore whether it had changed over the same period. In addition, we built population models using 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 compared it with observed trends, as well as likely population trends in the future to explore the population's viability.

Materials and Methods

Study area and species

Our study area lies from 18.0 to 19.5°S, and from 23.5 to 24°E (Figure 1) and encompasses a combined area of 1,000 km^2. We picked the area to explore all known nesting sites and potential nesting sites based on past records defined by presence of nesting trees. Northern Botswana is dominated by Kalahari soils (Tyler and Bishop 1998) 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 m, compared to 10 m elsewhere (Teren 2016). Canopies of such trees provide the nesting sites for White-backed Vultures (Monadjem and Rasmussen 2008). Tree species commonly used for nesting by White-backed Vultures include knobthorn *Acacia nigrescens* (now *Senegalia nigrescens*), fan palm *Hyphaene petersiana*, and raintree *Lonchocarpus capassa* (Muller and Hancock 2007).

The Linyanti area is situated < 50 km west of Chobe National Park, and Khwai is 50 km due south of Linyanti, straddling the border of Moremi Game Reserve. Both areas have similar terrain and similar species of fauna, and the surrounding areas have a low human population. A large diversity of wild ungulates inhabits the study area. The most abundant of these are African savanna elephant *Loxodonta africana*, plains zebra *Equus quagga*, impala *Aepyceros melampus*, red lechwe *Kobus leche*, Cape buffalo *Syncerus caffer*, and blue wildebeest *Chonnachaetes taurinus* (DWNP 2013). There are only two forms of land use in the area, Protected Areas and the partially protected Wildlife Management Areas. This has been the case for several decades. The primary land use in northern Botswana is low-density ecotourism (Maude and Reading 2010, Chase *et al.* 2015).

White-backed Vultures nest on trees in loose clusters along flat plains and within riparian areas (Monadjem and Rasmussen 2008). They build their nests in the crowns or sturdy forks of trees (Mundy 1982). Their large nests can measure 830 mm in diameter and 210 mm in depth and are sparsely lined with dry grass (Houston 1976). Breeding commences in March–April (Piper 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 pair may lay a replacement clutch if failure occurs early enough in the season (Mundy 1982). Incubation lasts approximately 56 days, and the nestling period prior to fledging lasts for 120–125 days (Houston 1976).

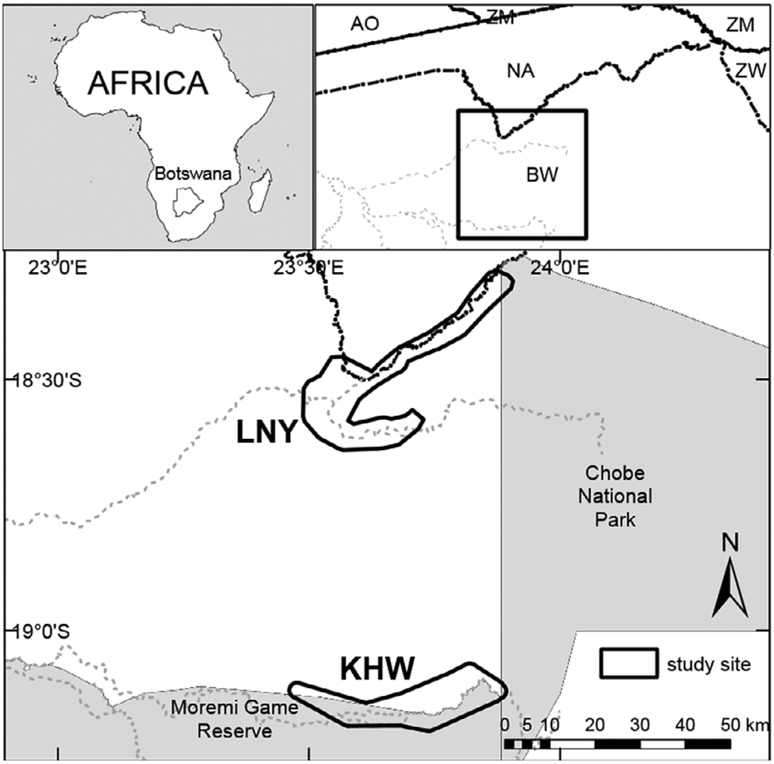

Figure 1. Map of the study area in the north-central Botswana, showing our two study sites (LNY = Linyanti; KHW = Khwai) where two loose colonies of White-backed Vulture were surveyed intermittently between 2006 and 2017. Polygons represent minimum convex polygon of the nest sites, including a 3-km buffer that was the area surveyed. The map in the upper right hand corner shows 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.

Nest monitoring and data collation

Data on the number of active nests and breeding success were obtained through aerial surveys using AirCam fixed-wing light aircraft in 2006–2008, and a Magni-16 gyrocopter in 2006–2008 and in 2017. The number of aerial surveys conducted each year at each area varied from one to three (Table 1). Survey visits were conducted during three time periods:

1) 'Early' survey visits were conducted between 19 June and 03 July, aiming to coincide with the main incubation period. For Linyanti, this survey was used to estimate the number of 'active' nests, to examine population changes; these were the nests that were monitored in subsequent survey visits to estimate breeding success. For Khwai, no historical surveys (2006 or 2007) were conducted during this time. In 2017, nests identified from this survey visit were used to contribute data on the minimum nesting numbers at Khwai.
2) 'Middle' survey visits were conducted between 24 July and 11 August – aiming 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. These were the nests that were monitored in subsequent survey visits to estimate breeding success. For years with 'Early'

Table 1. Survey times relative to timing of various breeding activities for White-backed Vultures (LNY = Linyanti) (KHW = Khwai). Numbers indicate dates of the month in which areas were surveyed. Dates in bold indicate the survey visits that we used to estimate active nests and/or for breeding success. Peak laying season is around 2nd half of May, while peak fledging is in 2nd half of October (Brown *et al.* 2013).

		June	**July**	**July**	**Aug**	**Sept**	**Sept**	**Oct**
survey	laying	incubating		nesting		fledging		
	Early survey visit			*Middle survey visit*		*Late survey visit*		
KHW 2006					**02-05**	03-04		
KHW 2007				**25-26**				
KHW 2016							23-25	
KHW 2017		30	-02		**08-11**			03-05
LNY 2006				24-29				12-16
LNY 2007		**25-26**					14-16	
LNY 2008			**01-03**					
LNY 2017		**19-22**			04-05		26-27	

survey visits, these 'Middle' survey visits helped in monitoring nesting progress and provided additional nests, which contributed to estimates of minimum nesting numbers.

3) 'Late' survey visits were conducted between 03 September and 16 October – aiming to coincide with the main late-nestling stage. These surveys were used to estimate breeding success of the previously identified 'active' nests located during either the 'Early' (Linyanti) or 'Middle' (Khwai) surveys visits. Thus, nests that contained a chick during the 'Late' survey visit and were identified as 'active' during the appropriate previous survey visit of that year, were classified as successful. Again, some additional nests were found during these survey visits, these late breeders contributed to estimates of the minimum nesting numbers of the area but were not used to estimate breeding success or numbers of active nests.

Survey visits to each area used multiple flight routes, each lasting around two hours. Survey routes were selected to explore all past known nesting sites and potential nesting sites. During the first survey years (2006 and 2007), all areas that had potential trees suitable for nesting raptors were surveyed. Isolated nests do occur outside the survey area; however, years of searching showed no evidence that other breeding colonies apart from Linyanti and Khwai exist in north-central Botswana. For each survey year, the first survey visit was the most comprehensive, with subsequent survey visits then targeting known nests, but also sometimes finding new nests along the routes. During these subsequent surveys the pilot flew directly from one known raptor nest to another. 'New' nests or those that had escaped previous detection were opportunistically identified during flying. This included late breeders though not all were necessarily so. Flights took place in early to mid-morning and late afternoon, approximately 09h00–11h00 and 15h00–17h00 depending on suitable weather and flying conditions.

Survey aircraft were flown at a ground speed of approximately 80–130 km per hour averaging approximately 113 km per hour, at a height of 70 m above the nests, providing an effective viewing distance of approximately 500 m on either side. Active monitoring of each nest from the air occurred for just as long as needed to confirm the nesting species and the nest contents, which was typically 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, or at most two flypasts, to identify the current nesting status. During each survey visit (Early, Middle, or Late) each nest was monitored only once. For each nest survey visit the following details were recorded: nest co-ordinates in decimal degrees and tree species (at time of first discovery), 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 prior to the start of laying). When recording data, 'no nest' indicated that despite repeated searches at the location, a nest was no longer present, but also included broken or damaged nests, as well as nests whose host trees had fallen over.

Adults observed sitting low on the nest were assumed to be incubating if observed before 15 July or assumed to be brooding if seen on or after 15 July. A breeding attempt was classified as successful for our estimates of breeding success when a previously identified active nest was still active with a chick during the late survey. Our measure of success based on early survey visits may thus be biased upwards, if other nests initiated late were on average less successful, as is usually the case for at least some raptor species (e.g. Martin *et al.* 2014, Garcia-Heras *et al.* 2016, Murgatroyd *et al.* 2016). Successful nests were those that had a nestling during the late survey visit, but this approach would have incorrectly classified a few nests as successful, but which may have failed after this last survey visit. However, failure during the later nestling stages is relatively rare in large raptors as compared to other stages of the breeding cycle (Newton 1979).

Population modelling

We explored whether we would predict the population to have declined between the mid-2000s and 2017, based on productivity in the mid-2000s and the average levels of poisoning experienced over the last decade. We also explored whether the current population is productive enough to be viable in future, assuming that poisoning either continues at a similar level, or is eliminated. Stochastic models were built using the Vortex population viability software (version 10.2.15.0; Lacy and Pollak 2014). We constructed models using the same basic demographic parameters that Murn and Botha (2018) used for their baseline model for this species, altering only three parameters; population size, reproduction rate, and adding catastrophes (to simulate mortality by mass poisonings) (Table 2).

To calculate the initial population size, we multiplied the nesting females by 1.25 (to include non-breeding adults) and thereafter multiplied the product by 1.3 (to account for immatures), the product of which was then multiplied by 2 to account for males. The carrying capacity was set to six times the past population estimate (2000); whilst probably unrealistic, no reliable site-specific estimate of the carrying capacity exists. However, given that biologists believe that the population was much higher historically, we selected a value that would ensure that carrying capacity did not constrain population growth during the modelling period. Models assumed a closed population, with no immigration or emigration as has been done in similar modelling exercises. Whilst we recognise that for this species this is unrealistic, there was an absence of good data on movements into and out of this population. However, because of this, output from this exercise should of course be treated with caution. We used this basic model to explore four scenarios:

I) The first model predicted the past population growth rate in the absence of mass poisoning, using 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 severity was modelled to affect 15% of the population, with 12% for severity on breeding (as only 80% of adults breed) and had a 0.9 probability of occurring in a year. This severity was derived from the median number of White-backed Vultures killed by poisoning each year over the last 10 years (Table S1 in the online supplementary material), within a 200 x 200 km square laid over the study area. We based this estimate on the assumption that all poisoned individuals originated from the local population and that no local birds were poisoned outside the area. The selection of the catastrophe function (rather than harvesting) allows density-dependence in the mortality as the population size changes. The harvest function would result in a fixed number of birds dying, irrespective of the numbers in the population. Such inflexibility in the model would

Table 2. Parameters used in the population model in program VORTEX for White-backed Vultures in north-central Botswana. The only difference between models, was the initial population and reproductive rates, as well as the inclusion of a catastrophe as described in text.

Parameter	Input value	Source
Scenario settings		
Number of iterations	100	
Number of years	30	
Extinction definition	20 individuals	Murn and Botha (2018)
Number of populations	1	
Inbreeding depression	no	
Reproductive system		
Pair system	Long-term monogamous	Murn and Botha (2018)
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	80±10	
Environmental variation (EV) in % adult females breeding successful/year	61.9 or 36.1	
Mean number of offspring/female/year (± SD)	1	
Mortality rates ± SD		
% mortality from age 0-1 (juveniles)	58±10	Murn and Botha (2018)
% mortality from age 1-2 (sub-adult)	15±3	Murn and Botha (2018)
% mortality from age 2-3 (sub-adult)	10.3±3	Murn and Botha (2018)
% mortality from age 3-4 (sub-adult)	10.9±1	Murn and Botha (2018)
% mortality from age 4-5 (sub-adult)	10.9±1	Murn and Botha (2018)
% mortality from age 5+ (adult)	1.3±0.3	Murn and Botha (2018)
Catastrophe		
Number of types	0 (none) or 1	See text
Frequency	90%	
Severity on Reproduction (proportion of normal)	0.88	
Severity on Survival (proportion of normal)	0.85	
Mate Monopolization		
Mates in breeding pool, %	100	
Initial population structure		
Initial population size	322 or 150	Present study
Stable age structure	yes	
Carrying capacity, individuals	2000	
Emigration	none	See text

have quickly led to a complete collapse in the population. In reality, a combination of harvests and catastrophes probably affects the population, but we felt that the catastrophe function (which denotes both severity and effect) was a more realistic situation than a constant yearly harvest.

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

IV) The fourth model used model III, but imposed the same levels of mortality from poisoning as model II. Differentiating the impact of catastrophes on proportion of population versus proportion of breeding attempts was particularly important for this model.

Data analysis

Nesting numbers: To compare how nesting numbers changed between 2007 and 2017, we used numbers from the survey visits in 2017 that most closely matched the timing of survey visits in 2007. For Khwai, these were the 'Middle' survey visits, and for Linyanti they were the 'Early' survey visits. For completeness, we also produced an estimate of minimum nesting number, with any additionally nests identified from other times also included, but these were not used in any comparison. Some areas in certain years had only one survey visit (Table 1). In 2006, only a partial survey in both areas was undertaken, the data from these survey visits were useful for estimating breeding success (from these sample nests – see below), but because it was not a full survey it was not used to estimate the number of active nests.

Breeding success: Only years with an 'Early' or a 'Middle' survey visit, plus a late survey visit were used to estimate breeding success. We compared previous breeding success to that from the 2017 survey for each area. No repeat survey was conducted in 2007 for Khwai, thus for breeding success estimates and comparisons we used data from the 'Middle' and 'Late' survey visits from the partial survey conducted in 2006 and from the full survey in 2017 (Table 1). We used 'Early' and 'Late' survey visits for 2007 and 2017 to calculate breeding success for Linyanti (Table 1).

Statistical analysis: We tested whether there was a change in breeding success between the survey years for the two sites and whether changes were different between the sites; for this we used a generalised linear model (GLM) with a binomial error structure and a logit link function. Our response variable was the success of each active nest surveyed in each year in each area, given as a binary variable (1 = success, 0 = failure).

In the analysis, we used data for both areas, and fitted period (mid-2000s or 2017), area (Khwai or Linyanti), and the interaction between the two terms as categorical fixed effects in the model. To provide estimates of breeding success (and 95% confidence limits) for each area in each year, and to explore for differences (e.g. between areas, or between years), we used the 'lsmeans' function within the 'lsmeans' package (Lenth 2016). In different years and in the different areas, we used the exact period between the two surveys to estimate how breeding success varied (Table 1), because there was the potential for fewer failures to have occurred when survey visits were closer together. To control for this, we fitted the number of weeks between the paired surveys within a year as a weighted term in the model. We performed statistical analyses using R statistical software (version 3.4.3; R Core Team 2017).

Results

Changes in nesting numbers

We found large declines in the numbers of nests in Linyanti between the mid-2000s and 2017. In 2007, there were 60 active nests in Linyanti during the 'Early' survey visit (Figure 2a), with an additional 13 active nests found in subsequent survey visits in that year, thus there were a minimum of 73 breeding pairs nesting in the area in 2007. This represented a minimum density of 14.9 nests/100 km^2 in an area of 490 km^2. There was only one survey visit in 2008, an 'Early' survey visit (Table 1), which found 48 active nests (cf. 60 nests in 2007). In 2017, we found only 21 active nests during the 'Early' survey visit, with one additional nest found in subsequent survey visits in that year, representing a minimum density of 4.49 nests/100 km^2. In Linyanti, 65% fewer active nests (from the 'Early' survey visits) were thus found in 2017 than in 2007.

In Khwai, numbers remained more stable over time. In 2007, from the single 'Middle' survey visits in Khwai, 35 active nests were found (Figure 2b) with an additional four active nests identified in later surveys visits, giving a minimum of 39 breeding pairs. In 2017, there were 25 active nests

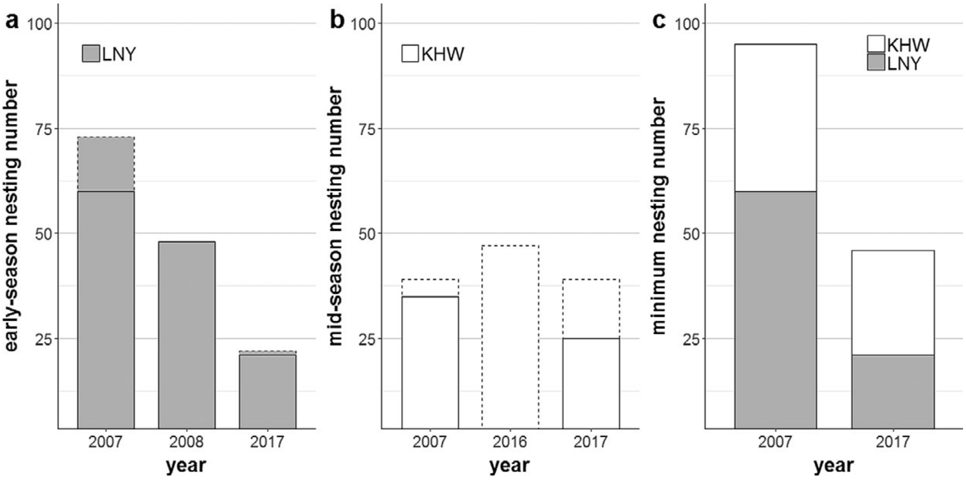

Figure 2. Yearly nesting numbers of White-backed Vultures in north-central Botswana by area (LNY = Linyanti, based on 'Early' survey visits) (KHW = Khwai, based on 'Middle' survey visits). In Figures 'a' and 'b', the solid bars are the numbers found during comparable survey visits. The higher dotted lines represent the minimum number of nests, and therefore include extra nests found active during additional survey visits, but were not used in the comparsion. In Linyanti there was only one (Early) survey visit during 2008, so no additional nests were located. In Khwai there was only one (Late) survey visit during 2016, so no comparable information is available either. Figure C shows the minimum number of nests for both areas combined (using only comparable survey visits between the two years).

during the comparable 'Middle' survey visits, plus an additional 13 active nests found at other times, giving a minimum of 38 active nests. The change in number of active nests in Khwai (during the 'Middle' survey visits) represents a 29% decrease over the last decade. In terms of density, this represents a decline from 14.40 nests/100 km^2 to 10.28 nests/100 km^2 in an area of 243 km^2. In 2016, only a 'Late' survey visit was conducted, which found 47 active nests (Table S2). Combining all the data on active nests from the comparable survey visits and within the two survey areas, we found a 54% decrease in nesting numbers between 2007 and 2017 from 99 active nests to 46 (Figure 2c).

Changes in breeding success

The breeding success estimates for Linyanti and Khwai in the mid-2000s were very similar. For Linyanti, breeding success in 2007 was estimated at 62% (Figure 3a), with 33 successful nests from the 53 monitored nests. For Khwai, breeding success in 2006 was estimated at 60% (Figure 3a), with nine successful nests from 15 monitored nests.

In 2017, the breeding success rates were also very similar between the two areas but had declined considerably compared to the breeding success estimates from the mid-2000s at both sites. In 2017, the breeding success estimate for Linyanti was 37%, with seven successful nests from 19 monitored nests, and was 35% for Khwai, with seven successful nests from 20 monitored nests. The change over 10 years represents a decline of 46.3% for Linyanti and 35.3% in Khwai. Combining all data together, irrespective of area, this represents a decline from an average breeding success of 61.8% ten years ago to 35.8% in 2017 in the study area, a decline of 42.1%.

Our statistical analyses showed a significant difference in breeding success between periods (mid-2000s and 2017) ($\chi^2_{1,138} = 52.175$, $P < 0.001$), but no differences between the areas

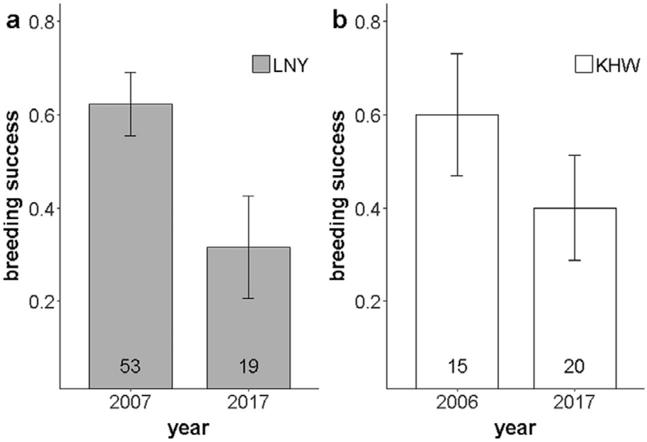

Figure 3. Yearly breeding success of White-backed Vultures in north-central Botswana by area ± 95% CI. The Khwai (KHW) breeding success (bs) was based on numbers found during the 'Middle' survey visits, while the Linyanti (LNY) was based on 'Early' survey visits. The mid-2000s data from KHW were based on the partial survey from 2006, while for Linyanti (LNY) we used the full survey done in 2007. Labels denote sample size of nests used to estimate breeding success. For some nests there were no late survey data, usually because they could not be relocated –and hence variation between label values and those indicated in Figure 2.

($\chi^2_{1,137} = 0.351$, $P = 0.5536$). There was also no interaction between area and period ($\chi^2_{1,136} = 0.083$, $P = 0.7735$), suggesting the decline in breeding success was very similar between the areas. Breeding success was not statistically different between the two areas in both the mid-2000s ($P = 0.9342$) and 2017 ($P = 0.9916$).

Population viability analysis

Our population model I based on previous productivity and in the absence of additional mortality from poisoning predicted that, from a starting population of 322 individuals across the two areas (including sub-adults and non-breeders), we would have expected the population to increase by 2.9% per year. However, model II, which includes additional mortality based on past poisoning levels, predicts that the population would have declined by around 12.8% per year, which over the ten years since the initial survey would represent a decline of 70.8% (Figure 4a).

Model III examined future population growth based on current productivity levels and predicted that, in the absence of poisoning, the population would be largely stable over the next 30 years, declining only by 0.02% per year. However, model IV, which used the current productivity and poisoning levels, predicted that the population would decline by 11.0% per year, with average time to extinction of the population (20 individuals or less) being only 13 years (Figure 4b).

Discussion

Our results indicate that large but spatially variable decreases in nesting numbers of White-backed Vultures have occurred in two important nesting regions in north-central Botswana over the last 10 years. Such a decline was predicted given the prevailing severity of vulture poisoning in the region during this time period (Endangered Wildlife Trust 2017). Although this reflects a decline in

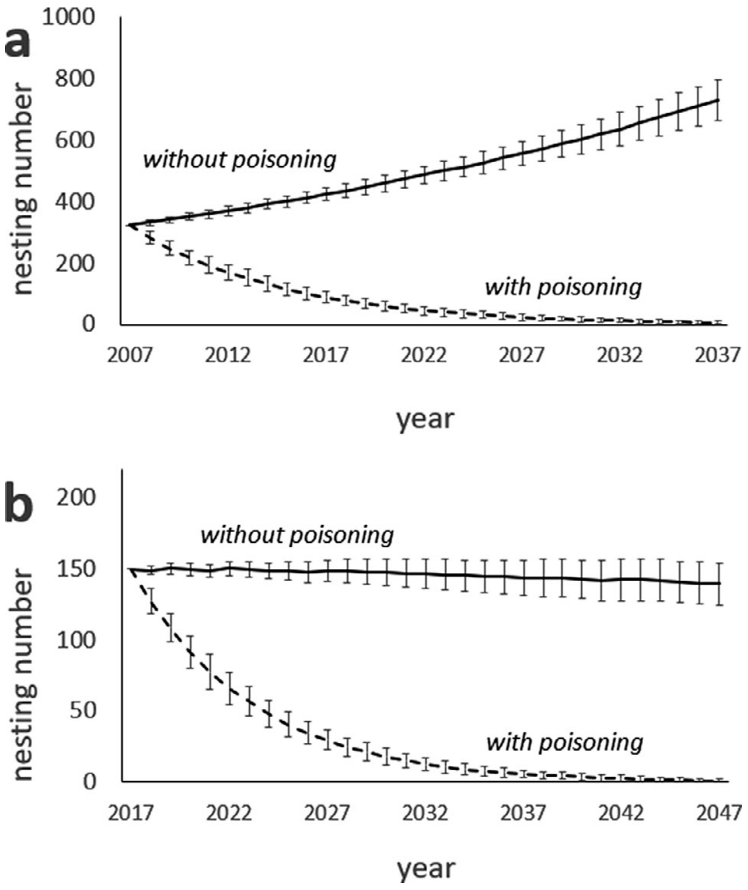

Figure 4. Simulated population projection of White-backed Vultures in north-central Botswana under different demographics (± SD). Figure 'a' represents the projected population under previous productivity levels, the dashed line considers the poisoning rate over the past decade. At 0.62 young per breeding pair per year (ypby) in the absence of mass-poisoning there would be population growth, but a decline with poisoning (of 15% severity, 12% on reproduction) 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 poisoning continues at 15% severity on survival and 12% on reproduction.

this breeding population, it does not necessary reflect similar decline in the overall population of the region. It may simply reflect a local decline as reasons for change may be subject to spatial variation.

The overall decline in nesting numbers in this region of north-central Botswana of 54% over the last 10 years mirrors trends for this species across Africa, but is even more severe than the rate of change in nesting numbers seen in some other areas for the species. For example, a more conservative overall decline of 26% over 13 years was observed in six breeding areas near Kimberley, South Africa, but with variable trends detected among the colonies, with some colonies showing overall increases while other colonies declined or disappeared (Murn *et al.* 2017).

Within our study, there was also a contrast in the trends within our two areas, with the population at Linyanti showing more than double the decline (65%) compared to that at Khwai

(29%). It is important to note that in 2016 the apparent minimum number of nests in Khwai was actually higher than 2007. These contrasting results may reflect differences in exposure to poisoning events, with more severe incidents being concentrated around Linyanti. A total of 1,276 White-backed Vultures killed was recorded in 10 incidents between 2010 and 2016 within 120 km of Linyanti, compared to 900 individuals in 12 incidents over the same period in an area of similar extent surrounding Khwai. However, as noted for the Kimberley area, there is a possibility that the birds had moved between colonies, or that birds from one colony have moved to a new area (Murn *et al.* 2017). Subject to availability of suitable trees, White-backed Vultures may change their nesting areas in response to local conditions and food availability (Howells and Hustler 1984, Anthony 2012, 2015; Murn *et al.* 2017). Spatial variation likely also exists further afield, though very far from our population, the Dronfield colony has been used as an indicator for the Kimberley White-backed Vulture breeding population, this colony increased by over 50% between 1993 and 2014, and by smaller amounts between 2001 and 2014.

Because surveys were not conducted during each survey visit period in each year, comparisons of active nests were made using counts from survey visits conducted during comparable times of the year. Our approach aimed to maximise the comparability of the counts, because comparisons made between nest counts at different times of the year (e.g. 'Early' vs 'Late'), could simply reflect differences in the number of nests that had failed between the nest survey visits. This approach means that any shifts toward later laying would be reflected as a decrease in active nests. However, our middle visits aimed to capture the majority of laying birds based on the average laying dates and, given that most species laying dates are shifting to be earlier, we feel it is unlikely to have played a strong role in influencing our conclusions. We used this approach due to the limited data available. We could only base our data on available historical data and were constrained logistically with how close we could match the surveys due to flying conditions and availability of aircraft. We believe there is merit to using the selected data as a baseline. However, because the resurvey data is based on only one year, future surveys are required to confirm any observed trends.

Our study also found declines in the breeding success of these two populations over the last 10 years. This decline was significant at each area and was strikingly similar in magnitude, with breeding success declining at both sites from around 60% in the mid-2000s to only around 35% in 2017. However, when considering these levels of decline, it is necessary to recognise that our recent estimates are derived from only a single year of monitoring (2017), thus it is not clear whether these levels accurately reflect longer term levels of current productivity or just represent an unusually low breeding success in this one year. In the Kgalagadi Transfrontier Park, RSA, breeding success over a three-year period varied from as low as 8% to a high of 61%, with an average of 47% (Herholdt and Anderson 2006). In Kenya, breeding success over a five-year period varied between 40% and nearly 78%, with an average of 59% (Virani *et al.* 2010). In Tanzania, breeding success over two years was 83% and 91% (Houston 1976). In Dronfield in South Africa, breeding success over 22 years varied between as low as 37% to a high of 79%, with an average of 59% (Anthony 2015). Thus, the level of nesting success seen at our study site 2017 were within the bounds of breeding success of other populations (albeit at the lower end of the spectrum).

If the decline in breeding success does represent a real long-term trend, rather than an unusually poor year for breeding, it is not immediately clear why such a trend may have occurred. One possible explanation could be linked to the increased recent levels of poisoning. 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 (Whitfield *et al.* 2004) that usually have a lower breeding performance in vultures and other raptors (Grubač *et al.* 2014, Murgatroyd *et al.* 2016). Such a situation was found to affect breeding success in Spanish Imperial Eagle *Aquila adalberti*, whereby pairs that include non-adults produced less chicks than adult pairs (Margalida *et al.* 2008).

Monadjem *et al.* (2018) suggested that poisoning incidents would have greatest impacts on adults, since during feeding, they outcompete juveniles. This could result in a preponderance of young birds in the population. A suggestion of this occurring in Botswana was observed by Garbett *et al*. (2018b), where the majority (79%) of White-backed Vultures they trapped were sub-adults. We acknowledge, however, that a possible alternative interpretation of this observation is the increased likelihood of sub-adults being trapped due to inexperience. If, however, the former explanation holds true, then a higher proportion of adult mortalities from poisoning would also account for the decline in nesting numbers, observed in this study.

A variety of other environmental factors could influence breeding performance in this population. These include weather patterns, vegetation cover, fire frequency and severity, and flood levels and patterns, which can differ dramatically between years in the region. We did not specifically collect detailed data on these variables and even with such data, it would not be possible to understand the importance of these of factors with our data, due to the limited number of years of monitoring. However, at a very crude level, we found only small differences in weather variables (maximum temperature, total hot days, and precipitation) between the early and later study years (NASA 'POWER' Global Meteorology, Surface Solar Energy and Climatology Data; https://power.larc.nasa.gov).

Lead (Pb) poisoning may be another explanation for the declines in breeding success. A recent survey in Botswana found that over 30% of nearly 600 White-backed Vulture had elevated lead levels. These elevated levels were associated with areas used for recreational hunting as well as during the hunting season (Garbett *et al.* 2018b). They suggested that the most likely source of this poisoning was from spent lead ammunition from hunting. Elevated lead levels can negatively affect breeding performance in raptors (Gil-Sánchez *et al.* 2018), including effects of adult sub-lethal exposure causing chick death (Pikula *et al.* 2013). Thus, high levels of lead in the local White-backed Vulture population could partially explain the reduced breeding success observed in this population. However, whether levels of lead have changed in vultures in the area between our two survey periods is not known.

Our PVA model suggests that the population was, at least in the past, sufficiently productive and should have been a net source of birds for the regional population. However, after considering the poisoning levels over the past decade, the population was projected to have declined by over 70% over the last decade. This projected value is quite close to the actual observed decline in nesting numbers from our surveys (54%), suggesting that localised poisoning would, in theory, be sufficient to explain the entirety of the observed levels of decline in nesting numbers, without the need to invoke additional factors (e.g. reduced breeding success).

Modelling the current population into the future projected a slight decline under 2017 levels of productivity, even in the absence of poisoning. However, if current poisoning levels continue in the future, models suggest the population faces a high probability of extinction, with average time until extinction estimated at 13 years. Mass poisoning events tend to be sporadic and can easily include over 100 individuals in a single incident (Endangered Wildlife Trust 2017). Additionally, the illicit nature of poisoning events means that the numbers used in our study are likely to be conservative, with many undocumented cases of poisoning also likely. Given that vultures may abandon breeding sites under low density (Allee effect) as suggested by Margalida *et al.* (2012), it may be that local extinction could occur sooner than projected.

Despite the support from our modelling, it remains possible that reasons other than mortality through poisoning could explain the change in nesting numbers observed. However, given that the model based on observed mortality and breeding rates, poisoning remains the most likely explanation. Drowning, power line injuries, electrocutions, and belief-based use have not been recorded as prevalent in the region but could represent underestimated additional threats to the population.

Overall, the population is predicted to fare worse than the projection for the Kruger population, where Murn and Botha (2018) predicted extinction within three generations (55 years). This difference is due to higher productivity, lower frequency of mortality, and greater breeding numbers in Kruger, which are at least double those of the study population. Additionally, our model assumed a closed population, where all the recorded deaths would come from the resident population, which we acknowledge is unlikely, so our prediction must be interpreted with caution. Through replacement of dead adults from the breeding population by other external recruits, the study area may continue to remain a regionally important area for breeding in the wider setting, but may be operating as a sink population (Pulliam 1988). In addition to habitat quality, birds use social information to assess breeding site quality (Mariette and Griffith 2012). In the colonially breeding White-backed Vulture, the historical presence of conspecifics in this region could attract young prospectors in subsequent breeding seasons, thereby providing a buffer in the overall decline of nesting numbers.

Given that the observed changes in nesting numbers may be largely explained by the prevailing poisoning-related mortality, there is an urgent need to ensure implementation of the Multi-species Action Plan (Botha *et al.* 2017) in this region. Through monitoring and eradication of poison use, or provision of safe food, survival might be enhanced (Kane *et al.* 2015), offsetting the decline rate. It is also vital that the population receive continued monitoring to understand whether the declines and the change in breeding productivity indicated by this study are a true reflection of the population trends.

Supplementary Materials

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S0959270920000179.

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