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Population growth rates in northern Cape Vulture *Gyps coprotheres* colonies between 2010 and 2019

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Summary

The 'Endangered' Cape Vulture *Gyps coprotheres* has been monitored across its range for decades through disparate studies varying in geographical scope and length. Yet, no long-term, range-wide survey exists for the species. Coordinated monitoring across the range of the Cape Vulture would be logistically challenging but provide a holistic view of population dynamics in this long-lived species that forages across much of southern Africa. Here, we report breeding pair counts from seven colonies in the Cape Vulture's north-eastern breeding region from 2010 to 2019. We used state-space models to assess population growth across time. Manutsa, Soutpansberg, and Nooitgedacht colonies increased significantly over the study period, with three other colonies having positive estimates of population growth, but 95% credible intervals overlapped zero. The smallest colony at Moletjie is declining toward extirpation; only one breeding pair remained in 2019. Our results suggest the north-eastern population has been stable or increasing since 2010 with our 2019 surveys counting 2,241 breeding pairs across all sites. Indeed, there is an 89% chance that the population across the colonies we monitored increased from 2010 to 2019. Coordinated, range-wide, full-cycle monitoring is needed to thoroughly assess conservation status and efficacy of conservation actions taken for this endangered species.

Keywords: Cape Vulture, *Gyps coprotheres*, population growth rate, state-space models, colony monitoring, breeding pairs

Introduction

Africa is in the midst of a continent-wide vulture crisis. Eight of Africa's nine vulture species are declining at alarming rates (Ogada and Buij 2011, Ogada *et al.* 2015), placing them in danger of extinction with projected population declines between 70% and 97% over their next three generations (Ogada *et al.* 2015). Researchers fear the decline of Africa's vulture populations will negatively affect ecosystems, human health, and national economies as was seen with India's vulture crisis in the late 2000s (Pain *et al.* 2003, Ogada *et al.* 2012b). Although the loss of over

97% of India's vultures was attributed mainly to the use of the veterinary drug diclofenac on cattle (Pain *et al.* 2008), African vultures are facing extinction from numerous threats, the majority of which are directly or indirectly the results of humans (Ogada *et al.* 2015, Buechley and Şekercioğlu 2016, McClure *et al.* 2018). These threats, combined with the species' wide-ranging behaviour, necessitate a multi-organizational and trans-national conservation approach for their management and threat mitigation.

The Cape Vulture *Gyps coprotheres*, a large bodied scavenger endemic to southern Africa, was recently listed as 'Endangered' (BirdLife International 2019) and has been the focus of conservation efforts over several decades. The species' threats are relatively well documented; the reasons for its decline are varied and numerous: lack of safe food (Boshoff and Vernon 1980), human persecution and harvesting for cultural beliefs (McKean *et al.* 2013, Williams *et al.* 2014, Pfeiffer *et al.* 2015a), deliberate and indirect poisoning including large mammal poaching (Ogada *et al.* 2012a, Murn and Botha 2018, Monadjem *et al.* 2018, Margalida *et al.* 2019), power line collisions and electrocutions (van Rooyen 2004, Phipps *et al.* 2013). Now additional pressures are emerging from wind energy developments and climate change (Rushworth and Kruger 2014, Phipps *et al.* 2017).

There is debate regarding the level of the species' decline between studies with variable geographic scope, length of study, and timeframe. Historically, the Cape Vulture population has undergone several contractions and expansions. Recent genetic analysis provides evidence for a bottleneck event (Kleinhans and Willows-Munro 2019) suspected around the year 1900 (Boshoff and Vernon 1980). Another phase of expansion and growth was documented up until the 1970s and 1980s (Boshoff and Vernon 1980, Benson and McClure 2020). The species is currently in another period of range contraction, evidenced by extirpations in Namibia, Zimbabwe, and Eswatini (BirdLife International 2019). Contractions have been witnessed in 'core' range regions, i.e. North West Province, South Africa (Wolter *et al.* 2016), Eastern Cape Province, South Africa (Boshoff *et al.* 2009), and Lesotho / Maloti-Drakensberg Massif (Simmons and Jenkins 2007).

Ogada *et al.'s* (2015) composite indices indicated a 5.1% annual population decline across five countries, contributing to the species being listed as 'Endangered' (BirdLife International 2019). However, recent assessments of several north-eastern colonies suggest the population is stable or increasing, while also documenting local colony extinctions and range contraction within the north-eastern population (Wolter *et al.* 2016). A longitudinal study of a single, large north-eastern colony at Kransberg reported a population increase of 2.65% (± 0.14%) per year since 2003 (Benson and McClure 2020).

Systematically monitoring an entire species across its range is logistically challenging and requires extensive human and financial resources. Benson and McClure (2020) concluded skipping more than two years of surveys reduces confidence in population trend analysis. There is currently no range-wide, continuous survey available for the Cape Vulture. Most published surveys address single colonies or regions spanning various, often relatively short, time periods. This lack of congruity across space and time leaves many questions unanswered, especially regarding the role of movement or immigration between colonies or geographic regions (Benson 2015, Wolter *et al.* 2016, Schabo *et al.* 2017) because Cape Vultures are known to travel over vast distances, especially early in life (Phipps *et al.* 2013, Kane *et al.* 2016, Hirschauer *et al.* 2017).

Recent analysis of genetic diversity across the entire range suggests shallow genetic differences (Kleinhans and Willows-Munro 2019), which is not surprising given that individuals of this species range widely (Kane *et al.* 2016). However, this genetic analysis also provides evidence for regional philopatry, suggesting birds breed in the region of their hatching, highlighting the importance of understanding population trends on a regional level. The entire global Cape Vulture breeding population can be grouped into two core breeding regions (a north-eastern region located above 27°S latitude and a south-eastern region located south of 27°S latitude) with a much smaller south-western region around the Potberg colony (located at 34°S latitude, see Figure 1; Allan 2015, Wolter *et al.* 2016, Kleinhans and Willows-Munro 2019). There is evidence for connectivity between regions, with the south-eastern region, especially the Collywobbles colony in the Eastern Cape Province, South Africa, acting as a source for the other two regions (Kleinhans and Willows-Munro 2019).

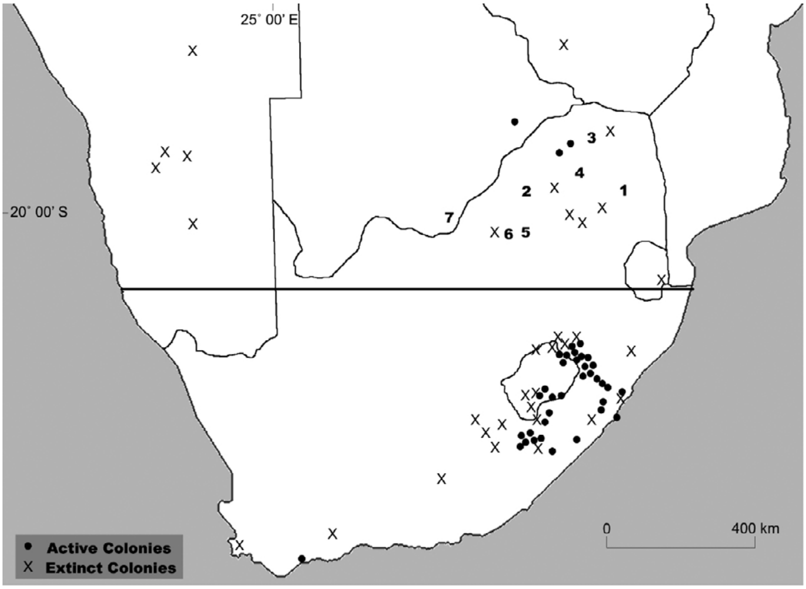

Figure 1. Map of southern Africa showing national boundaries and all known Cape Vulture colonies. North-eastern and south-eastern breeding regions are delineated by a black line at 27°S parallel. Colonies monitored and discussed here are marked with the following numbers: 1, Manutsa; 2, Kransberg; 3, Soutpansberg; 4, Moletjie; 5, Skeerpoort; 6, Nooitgedacht; 7, Mannyelanong.

The goal of this study was to assess population trends of several Cape Vulture colonies in the north-eastern breeding region. Here we report the results of our annual breeding surveys and population growth witnessed across seven colonies in the north-eastern region from 2010 to 2019.

Methods

Breeding surveys between 2010 and 2019 encompassed the north-eastern region (north of 27°S latitude), except for the Blouberg colony in Limpopo Province, South Africa and the Tswapong Hills colony in Botswana. Colonies included in our analysis are Kransberg, Manutsa, Moletjie, Soutpansberg, Nooitgedacht, and Skeerpoort in South Africa, as well as Mannyelanong in Botswana (Figure 1). We were not able to survey all colonies every year due to limited funding and personnel; however, between 2012 and 2019 we monitored six colonies annually (Table 1).

Authors MH, KW, and AH, as well as other trained observers, conducted breeding surveys on behalf of VulPro, a non-profit vulture conservation organization in South Africa. Our survey methods follow the cliff colony monitoring protocols set out by the Vulture Study Group (Cape Vulture breeding monitoring protocols 2018) and are summarised here. A team consisting of the same two observers visited each colony three times per season. Teams worked together to view cliff ledges from the same locations (between 700 m and 1,600 m away from the colony) using two 60 x spotting scopes. All nests were individually identified with alphanumeric codes that remained unchanged across years. These codes were marked on high resolution photograph references of the cliff face. We counted breeding pairs at each established and marked nest and noted new active nests during the first annual visit in May and June. We considered a nest to be an occupied territory containing a breeding pair if we witnessed an adult building a nest, incubating, copulating, or tenanted (i.e. present and displaying behavior suggesting the ledge is being used as a nest; see Franke *et al.* [2017] for terminology). In subsequent visits to each colony, we counted nestlings in

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Table 1. Breeding pair counts for Cape Vulture colonies monitored between 2010-2019.

Site (GPS coordinate)	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
Kransberg (24°28′S, 27°36′E)		628	662	608	632	575	869	691	793	757
Mannyelanong (25°03′S, 25°45′E)					62			81	84	89
Manutsa (24°27′S, 30°45′E)			433	447	563	558	621	644	631	737
Moletjie (23°44′S, 29°19′E)			20	13	16	18	19	5	5	1
Soutpansberg (23°01′S, 29°35′E)			181	168	187	196	213	223	197	225
Nooitgedacht (25°51′S, 27°32′E)	125	93	73	116	97	96	140	120	151	145
Skeerpoort (25°44′S, 27°45′E)	221	223	197	209	222	248	251	290	316	287

July and August and then fledglings in September and October to measure breeding success. Our results from late season surveys and measures of breeding success are not reported here; we focus on breeding pair counts from the first survey only.

We used a state-space model in a Bayesian framework to estimate changes in counts of breeding pairs throughout the study. State-space models can separate observation error from process error and are therefore especially useful for estimating trends in abundance from count data (Kéry and Schaub 2012). Following Benson and McClure (2020), we modified a model from Kéry and Schaub (2012: 127) that was designed to model trends in abundance at a single site to include multiple sites (The Peregrine Fund 2020; Appendix S1 in the online Supplementary Material). The model estimated population dynamics and assumed that abundance was a Markovian process, that is, abundance during a given year was autocorrelated and dependent on abundance during the previous year. The model allowed for false positive detections and false negative detections, and this formulation assumed they are equally probable. We estimated trends at each colony by adding a factor level for each colony in the model for abundance and population growth rate. We then estimated the study-wide trend as the average across all colonies and years. We compared trends using 95% credible intervals, the Bayesian version of frequentist 95% confidence intervals, by calculating the 2.5 and 97.5 percentiles of the posterior distribution for each parameter estimate of population growth rates. We describe populations as having positive population growth when population growth rates were positive numbers and 95% credible intervals excluded zero, and we describe populations as having negative population growth when population growth rates were negative numbers and 95% credible intervals excluded zero.

We implemented models using JAGS (Plummer 2003) and the package 'jagsUI' (Kellner 2016) in R (R Core Team 2017) and used three chains with 300,000 iterations, burn-in of 150,000, adaptation of 20,000, and we thinned one out of every 50 posterior draws resulting in three chains each having 3,000 posterior draws. We used the Gelman-Rubin statistic (Gelman and Rubin 1992) to determine convergence of chains when parameters had an $\widehat{R}$ <1.1. We visually assessed trace plots of each parameter chain to check for convergence. Vague priors were used for all parameters (Kéry and Schaub 2012).

Results

The largest colony we monitored was Kransberg with 757 pairs counted in 2019, followed by Manutsa with 737 pairs. Moletjie, the smallest colony monitored, declined between 2012 and

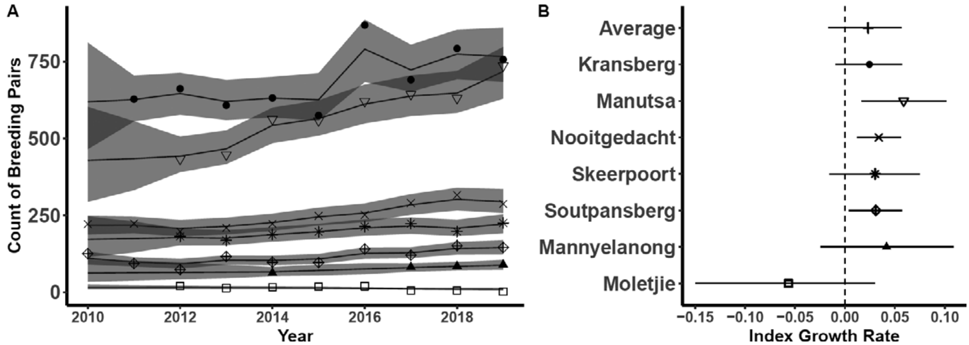

Figure 2. A) Observed (points) and estimated (lines, shaded areas = 95% CRIs) counts of breeding pairs of Cape Vultures at colonies across the northern part of their range. B) Population growth rates for each colony. Points represent average growth rates across all years. Lines represent 95% CRIs. The average represents the mean population growth across all colonies. Note that the point symbols represent the same colonies across both panels (A and B).

Table 2. Mean estimates (and lower and upper bounds of 95% credible intervals) of population growth rates of Cape Vulture colonies monitored between 2010 and 2019.

Site	Mean	Lower	Upper
Soutpansberg	0.031	0.004	0.057
Skeerpoort	0.030	-0.015	0.075
Nooitgedacht	0.034	0.012	0.056
Moletjie	-0.056	-0.150	0.030
Manutsa	0.059	0.017	0.102
Mannyelanong	0.042	-0.025	0.109
Kransberg	0.025	-0.010	0.057
Average	0.023	-0.017	0.057

2019 from 20 pairs to one pair (Figure 2), although the credible interval for the population growth rate overlapped zero. Manutsa, Nooitgedacht, and Soutpansberg colonies show positive population growth rates with credible intervals excluding zero (Figure 2; Table 2). The average across all colonies was positive, but the 95% credible interval overlapped zero (Figure 2). Our analysis suggests an 89% chance that breeding pairs across all colonies monitored have increased since 2010.

Discussion

Collectively, our standardized surveys counted 2,241 breeding pairs in 2019. The Blouberg colony is also in the north-eastern region but was not included in our survey efforts. The most recent breeding pair count from Blouberg is estimated at 1,319 from surveys of occupied nests (J van Wyk pers. comm. September 2019). Including the Blouberg colony count, we estimate the north-eastern population holds approximately 3,560 breeding pairs. However, our total regional estimation must be taken with caution because we are not able to account for variations in survey protocols or effort between our surveys and those at the Blouberg colony.

Based on the most recent global population estimate of 4,700 pairs (Allan 2015), our surveys account for 48% of mature Cape Vultures. Allan (2015) estimated the north-eastern region holds 56% of the Cape Vulture breeding population, or 2,464 breeding pairs, however his account did not include colonies in Botswana. Considering our speculative regional count including the Blouberg colony but excluding our Mannyelanong colony count in Botswana (to directly compare with

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Allan's (2015) estimate), we suggest the north-eastern region holds 3,471 breeding pairs, or 74% of the mature Cape Vulture population. Whether the north-eastern region holds 56% or 74% of the breeding population, it is clear that the region is still the species' stronghold.

The best estimate for the north-eastern population in 1985 was 2,987 active pairs (Benson *et al.* 1990). Our 2019 survey results of 3,560 breeding pairs (including the Blouberg colony survey estimates mentioned above) concludes the north-eastern population has been stable over the last 30 years. The second largest colony in the region at Kransberg was monitored annually across these 35 years, showing a clear decline with subsequent rise starting in 2003 (Benson and McClure 2020). Because continuous, long term studies such as these are rare, it is not clear if this trend was mirrored across all colonies or regions during this timeframe.

Immigration between colonies and regions cannot be ruled out when scrutinizing counts of a single colony or region (Bamford *et al.* 2007, Kane *et al.* 2016, Wolter *et al.* 2016, Schabo *et al.* 2017, Benson and McClure 2020). Natal philopatry, where an animal returns to the site or colony of its hatching to breed, has been suggested but only confirmed in a few ringing studies (Robertson 1983, Hirschauer *et al.* 2016). Recent genetic evidence does not suggest natal philopatry, but regional philopatry, where an individual remains to breed in the region of its hatching (Kleinhans and Willows-Munro 2019). Although genetic evidence suggests the north-eastern population is demographically dependent upon immigration from the south-eastern and south-western regions (south of 27ºS) to our study area, immigration still cannot be ruled out because unfortunately there are no updated holistic accounts of population growth rates from other Cape Vulture populations. KwaZulu-Natal Province held an estimated 196 breeding pairs in 2004, and this population was expected to be declining (Rushworth and Piper 2004), although the most recent account of a single colony at Mzimkhulu showed relatively stable breeding pair counts between 2001 and 2012 (Schabo *et al.* 2017). We are not aware of any recently published data regarding population growth rates from Eastern Cape Province colonies, but Allan (2015) estimated 42% of the global population breeds in the south-eastern region, with an estimated 20% specifically in the Transkei region (Pfeiffer *et al.* 2015b). The Potberg colony in the south-western region, Western Cape Province, South Africa, has been steadily increasing over the study period (K. Shaw pers. comm.).

The Manutsa colony is the third largest in the north-eastern region. Here we document a steady increase in breeding pairs between 2012 and 2019. This colony is unique because it consists of a north aspect cliff face, exposing all nestlings to direct sun and heat. Phipps *et al.* (2017) determined changing global climate will reduce suitable habitat for the species and further shift the 'core' range southward. It has also been predicted that northern colonies surveyed here will show the first signs of abandonment with climate change (Simmons and Jenkins 2007). We speculate that breeding success at the Manutsa colony will be disproportionately affected by increasing temperatures in the future due to its north-aspect cliff face, yet surprisingly our surveys show marked growth of breeding pairs at the colony.

The decline documented at Moletjie contrasts the growth witnessed at other colonies. Moletjie is a unique colony in both its topography and human disturbance. The rock formation which hosts the colony is a large boulder rising out of the ground, relatively small compared to other Cape Vulture colony cliffs. We estimate there is only space available for a maximum of 30 nests on ledges spanning 200 m of the boulder. The colony lies within the 2.3 km^2 Moletjie Nature Reserve under the jurisdiction of Limpopo (Province) Nature Conservation. Human development encroaches directly upon the park boundary less than 1 km from the colony, fences have not been maintained, and livestock frequently graze inside. Wild mammals are not present in the reserve due to excessive poaching. During our 2018 surveys, we witnessed disturbance from community members on top of the boulder. We confirmed with community leaders and reserve managers that cultural rituals involving music are held on top of the boulder on a regular basis including during the breeding season. Although we have no evidence that nestlings or eggs have been harvested, the nest ledges are accessible from above. Community leaders have confirmed a demand for vulture parts in the region and asserted any available vulture would be taken for cultural *muthi* practices (McKean *et al.* 2013, Williams *et al.* 2014, Williams and Whiting 2016). We believe that it is this disturbance and suspected persecution, combined with the reserve's lack of law enforcement personnel and poor infrastructure, that is leading to this colony's extirpation.

Although food shortage has been suggested as a cause for limiting vulture population growth, increasing young vulture mortalities, and decreasing breeding success (Boshoff and Vernon 1980, Piper 1994, Margalida *et al.* 2010, 2011), we do not believe a lack of food is a contributing factor in the Moletjie colony's decline because two active vulture supplemental feeding sites exist at Ibis Farms and Mockford Farms, 16 km and 32 km from the colony, respectively. Recent assessment of active supplemental feeding sites documented 32 such sites in Limpopo Province which collectively provided 1,200 tons of food annually (Brink *et al*. 2020). Brink *et al.* (2020) suggest supplemental feeding sites in South Africa potentially provide enough food to fulfill almost all of the energetic requirements of the current South African adult vulture population. Although these food provisions are not distributed evenly across the country, Brink *et al.*'s (2020) comparisons between provinces show Limpopo Province hosts the second highest number of sites which collectively provide the greatest biomass of food annually.

Cape Vultures face many threats that change in scope and severity based on location. Breeding colonies in the south-eastern region (in Lesotho and the Eastern Cape and KwaZulu-Natal Provinces, South Africa) are threatened by existing and pending wind energy developments (Rushworth and Krüger 2014) as well as electrical infrastructure (Boshoff *et al.* 2011), persecution for cultural beliefs (Pfeiffer *et al.* 2015a), and their body parts are sought after for *muthi* trade (McKean *et al.* 2013). The steady increase in the north-eastern population discussed here is promising, but a holistic assessment of the entire global population is needed to understand if this trend is occurring range wide.

Although our survey efforts suggest the north-eastern breeding region's population appears stable, we also document a severe decline in the Moletjie colony located within the 'core' of the species' range. Piper (1994) predicted that Cape Vulture population declines (at first) may be difficult to detect because of their wide-ranging behaviour. He suggested sub-populations on the periphery of the species' range are more sensitive to extinction, may be the first to show declines, and therefore global population declines will be exhibited as a range contraction (Piper 1994). In fact, his predictions have come to light as we have seen the extirpations of peripheral breeding colonies in Namibia, Zimbabwe, and Eswatini (Parker 1994, Mundy *et al.* 1997, Monadjem and Garcelon 2005, Wolter *et al.* 2014, BirdLife International 2019). The south-eastern breeding region in the 'core' of the species' range has also contracted with breeding colonies only remaining in the eastern half of the Eastern Cape Province, South Africa, the Drakensberg escarpment in Kwa-Zulu Natal Province, South Africa, and the Lesotho highlands (Allan 2015). More recently, Wolter *et al.* (2016) documented the extirpation of the Roberts' Farm colony, located in core of the north-eastern breeding region (Figure 1). It is with this historical and demographic context in mind that we report our survey results.

The north-eastern Cape Vulture population is increasing or stable compared to 30 years ago, despite the decline and perhaps impending extirpation of a small colony within the core of the species' range. Emphasis must be placed on coordinated, systematic monitoring across the species' range and annual cycle to produce accurate population counts. Continued annual monitoring—illuminating breeding success, population dynamics, and elaborating on site-specific threats of each colony—will be critical to continuing pertinent conservation actions for this endemic and imperiled species.

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Supplementary Materials

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S0959270920000465.

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