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Potential release sites and strategies for a Bearded Vulture *Gypaetus barbatus* reintroduction in South Africa

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The southern African population of Bearded Vultures *Gypaetus barbatus* has declined rapidly and it is threatened with extinction. In response to this decline and the additional threats of wind farm developments in the core of the species' range, it has been proposed to establish a reintroduced population within their historic South African range as insurance against regional extinction. To facilitate such a reintroduction, we used Maximum Entropy Modelling based on suitable nesting habitat to identify and define five potential reintroduction sites. We then compared the suitability of these sites based on the quantification of various threats and benefits within each site. The two highest-ranking sites were located mostly in the Eastern Cape Province of South Africa. We then compared different release strategies, using a Population Viability Analysis, to determine which approach would be most likely to be successful (defined as >34 individuals after 30 years). These models suggest that establishing a captive breeding programme and releasing captive-bred young would lower failure rates to 25.5–49.8%, compared with the direct releases of wild taken fledglings, without a supporting captive breeding programme (78.3–95.7%). Our models also suggest that even in the presence of high mortality rates at the reintroduction site, such a reintroduction would still be a worthwhile project, because it reduces the probability of extinction of the southern African population by approximately 30% over a 50-year period.

Sites de lâchers potentiels et stratégies pour la réintroduction du gypaète barbu en Afrique du Sud

La population de gypaètes barbus *Gypaetus barbatus* d'Afrique australe a rapidement diminué et est menacée d'extinction. En réponse à ce déclin et aux menaces supplémentaires liées au développement de parcs éoliens au cœur de l'aire de répartition de l'espèce, il a été proposé d'établir une population réintroduite au sein de l'aire de répartition historique de l'espèce en Afrique du Sud comme assurance contre l'extinction régionale. Pour faciliter une telle réintroduction, nous avons utilisé une modélisation de l'entropie maximale basée sur un habitat de nidification approprié pour identifier et définir cinq sites de réintroduction potentiels. Nous avons ensuite comparé l'adéquation de ces sites en nous basant sur la quantification des diverses menaces et des avantages de chaque site. Les deux sites les mieux classés étaient situés pour la plupart dans la province du Cap-Oriental en Afrique du Sud. Nous avons ensuite comparé différentes stratégies de réintroduction, en utilisant une analyse de viabilité de la population, afin de déterminer quelle approche aurait le plus de chances de réussir (définie comme >34 individus après 30 ans). Ces modèles suggèrent que la mise en place d'un programme d'élevage en captivité et le lâcher de jeunes élevés en captivité réduirait les taux d'échec à 25.5–49.8% par rapport aux lâchers directs de jeunes oiseaux capturés dans la nature, sans programme de soutien à l'élevage en captivité (78.3–95.7%). Nos modèles suggèrent également que même en présence de taux de mortalité élevés sur le site de réintroduction, une telle réintroduction serait toujours un projet intéressant, car elle réduit la probabilité d'extinction de la population d'Afrique australe d'environ 30% sur une période de 50 ans.

Keywords: captive breeding, *ex situ* conservation, habitat suitability analysis, population viability analysis, vulture crisis

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Introduction

Vultures are one of the fastest declining avian groups globally (McClure et al. 2018), with 61% of species being at risk of extinction (Ogada et al. 2012). The Bearded Vulture *Gypaetus barbatus* is a large raptor occurring in Africa, Asia and Europe. Although globally it is Near Threatened (BirdLife International 2017), regionally in southern Africa, it

is classified as Critically Endangered. In southern African, the population has a declining trend and a contracting breeding range (Krüger et al. 2014a) with projections predicting the regional extinction within the next 50 years (Krüger 2015). The cause of this decline is similar as for other vultures, in that of 19 recorded mortalities over a

14-year period, 53% were attributed to poisoning and 21% to power line collisions (Krüger 2014). Additionally, a new threat is now emerging for this population, with plans for extensive wind farm developments within its breeding range (Reid et al. 2015; Rushworth and Krüger 2014). A number of proposals have already been submitted and there is a long-term goal of having up to 4 000 turbines in the region (Jenkins and Allan 2013; Reid et al. 2015).

In light of these threats and the continual decline of the southern African population, *ex situ* conservation efforts are now being considered (Krüger 2015). These approaches have proven successful elsewhere for this species. The Alpine population of Bearded Vultures became extinct in the early 1900s, as a result of poisoning and shooting (Mingozzi and Estève 1997), but was restored through releases of captive-bred birds starting in the mid-1980s (Frey 1992). This population is now self-sustaining without the requirement for additional releases (Schaub et al. 2009). Similar projects have been initiated in Andalusia (Spain) and Grands Causses (France), with an aim to restore the species across its former European range (Frey and Llopis 2014).

Inspired by the success of the alpine reintroduction, the current decline, and the emergence of the novel threat of wind farms, conservation practitioners are now considering the reintroduction of Bearded Vultures into parts of their historic South African range. Such a reintroduction would provide an insurance population against the threat of regional extinction of the species.

The International Union for Conservation of Nature (IUCN) advocates for a feasibility analysis when reintroductions are considered (IUCN 2013). This analysis should include an assessment of the availability and suitability of the habitat at proposed reintroduction sites, and modelling to predict the outcome of the project under various scenarios to provide valuable insight for selecting the optimal strategy for release.

In this study, we therefore aim to assess the feasibility of establishing a reintroduced population of Bearded Vultures in South Africa. Firstly, we identify potential areas for a reintroduction based on habitat and climate similarities to known southern African nest sites. Secondly, we assess the most suitable reintroduction sites and release sites within these, based on landscape features, habitat requirements, and the features associated with the most common causes of mortality and territorial abandonment in southern Africa (e.g. powerlines and human settlements) (Krüger et al. 2015). Lastly, we build stochastic population models with different strategies for release and captive breeding to explore the most effective approach to establish an insurance population and, thereby decrease the risk of regional extinction for the species.

Materials and methods

Study sites and species

The Bearded Vulture is a large, non-colonial, cliff nesting raptor that occupies territories at an altitude of >1 800 m and feeds almost exclusively on bone (Brown and Plug 1990; Brown 1998). These birds start breeding at seven years of age and females lay a maximum of two eggs (Bustamante 1996), but only ever fledge one young, because of obligate sibicide (Margalida et al. 2004).

The species breeds in Eurasia and in Africa. In Africa, numbers are declining and only isolated pockets remain. The southern African breeding range has declined by 27% over the past five decades, leaving the species restricted to the Maloti-Drakensberg Mountains of Lesotho and South Africa (Brown 1990; Krüger et al. 2014a). Historically, its range extended across all mountainous areas between Lesotho and Cape Town (Brooke 1984; Figure 1) and it is the suitability of this area that we evaluate for a reintroduction.

Identification of potential reintroduction sites

We identified potentially suitable nesting areas in the Bearded Vulture's historic range using data on the current species distribution (nest site locations between 2000 and 2014) (Krüger et al. 2014a), and a maximum-entropy approach with the environmental niche modelling software MaxEnt (Phillips et al. 2006). We extracted information for the models from digital layers using Geographic Information Systems (GIS) techniques in the ArcMAP 10.2 (ESRI 2013) software. Cliffs were identified by their slopes (>45°) from a 30 m resolution Digital Elevation Model (Wakamiya 2008; Loye et al. 2009). Our MaxEnt model identified cliff areas in the historic range with similar environmental conditions to known nest sites. Building distribution models with current occurrence records, that could represent sub-optimal habitat characteristics, may reduce model projection accuracy (Giovannini et al. 2014). In the absence of records of nest locations within the historic range of the species, recent nest site locations were the only reliable information on suitable nesting conditions.

Environmental variables included in the MaxEnt model were the presence of cliffs, elevation, climate data (WorldClim) (Hijmans et al. 2005) and terrain ruggedness (standard deviation of slope). Elevation and terrain ruggedness had previously been shown to be important in predicting habitat use by this species (Reid et al. 2015). These environmental variables were fitted at a resolution of 898 m × 898 m, which was the resolution of our coarsest layer. We used subsampling with 20 random test points to evaluate model performance and ran the model for 5 000 iterations. We used a low threshold of 1% probability of occurrence to select potential areas for releases. The threshold was set low, as the purpose of this model was simply to exclude areas that were completely unsuitable nesting habitat for Bearded Vultures. Only areas that differed starkly from current nesting sites were therefore excluded. This low threshold consequently compensated for the absence of nesting data in the historic range in the model. If hypothetically current nest sites represent suboptimal habitat, a model with such a low threshold would naturally include optimal nesting sites as well. The model output provided the necessary information (Figure 1) from which we could delimit discrete reintroduction sites.

To delimit these areas for potential reintroduction, cliffs were selected that fell within the areas identified by the model, were 100 km away from the Bearded Vulture's current range and were within the Bearded Vulture's historic range. The maximum-recorded foraging radius

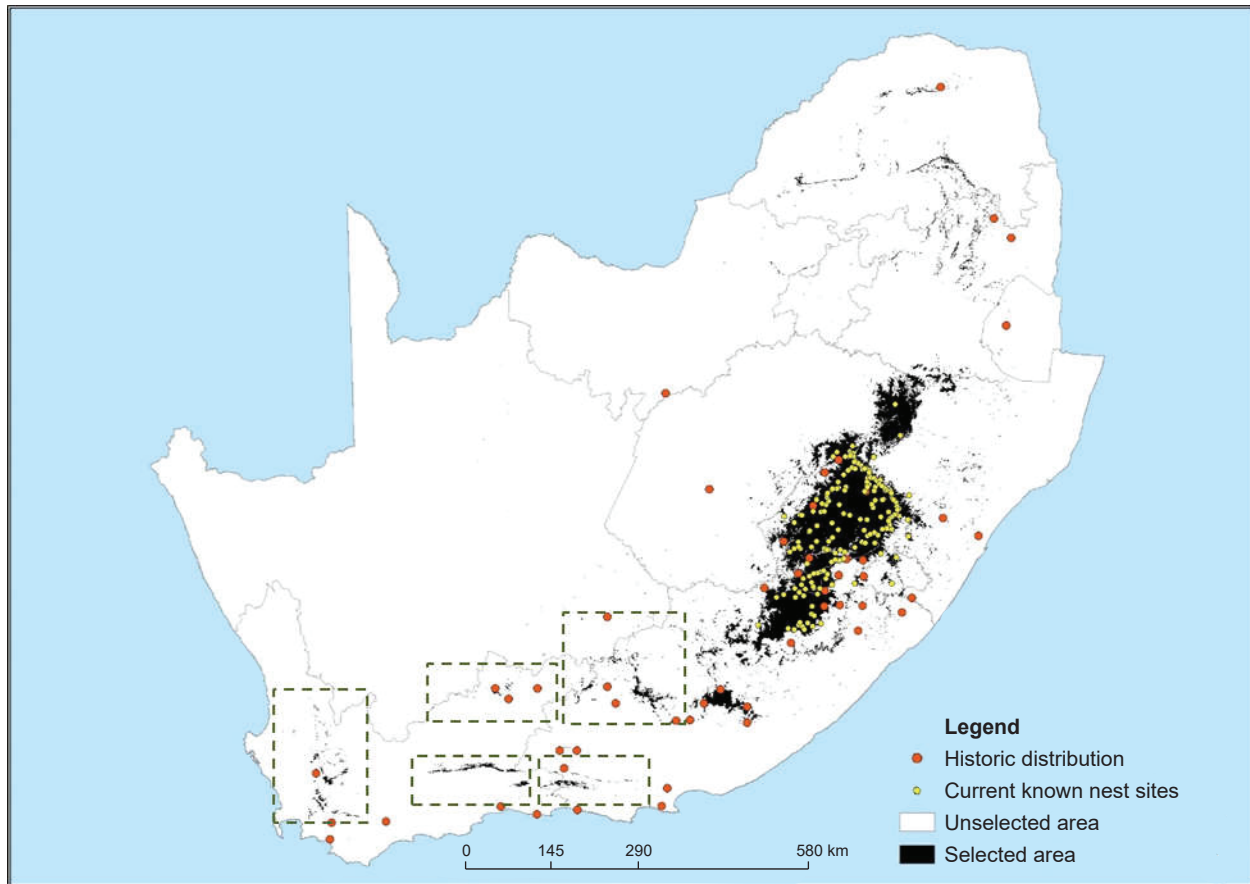


Figure 1: Results from the nest site suitability model (MaxEnt) built with the environmental variables; cliff presence, elevation, climate and terrain ruggedness, and based on known nest sites. Black shading indicates areas with >1% probability of Bearded Vulture nest site occurrence. Squared-off areas indicate areas that were consistently chosen across all models, are more than 100 km away from the current Bearded Vulture range and within the Bearded Vulture's historic range

of non-adult Bearded Vultures is c. 91 km (Krüger et al. 2014b), therefore a 100 km threshold is likely to ensure the establishment of a population separate from the current wild one, which is the expressed management goal. We aggregated the selected cliffs together based on visual observation of natural breaks with a 40 km threshold identified to deliver suitable discrete reintroduction sites encapsulating all relevant cliffs. We then placed a buffer, the size of an adult's home range (c. 10 km radius; Krüger et al. 2014b) around these areas, to include all areas that would be used by breeding adults in our habitat assessment. Unlike other Bearded Vulture populations (Margalida et al. 2008), there is some spatial segregation between age classes in southern Africa. However, the combined foraging range of the more widely ranging non-adults is 65% of the overall range (Krüger et al. 2014b). This suggests that non-adults stay mostly within the total area used by all adults. We therefore assumed that the adult home range size buffer encapsulated the majority of the area that Bearded Vultures, of all age classes, would use. We considered each one of the resulting buffered areas as a potential reintroduction site (see shapes one to five in Figure 2).

Reintroduction site ranking

To identify which potential reintroduction site was most suitable, we compared these sites based on a range of variables corresponding to threats and benefits for Bearded Vultures. These variables were power lines, wind farms, human settlements and unsuitable habitat (negative variables), and livestock and protected areas (positive variables) (see Table 1 for a full description of each variable). Livestock density was used as a proxy for food availability, because no other reliable information was available. We determined the densities or proportions of these variables within each proposed reintroduction site and scaled them by dividing by the total across all sites.

To calculate the number of potential breeding territories in each reintroduction site, we manually assigned nests to cliffs, with a 9 km mean inter-nest distance, based on the known information for the southern African population (Krüger et al. 2014a). This indicated whether sites were of sufficient size to support the nesting requirements of a viable population.

To determine the relative importance of each variable used to compare potential reintroduction sites, we employed an Analytical Hierarchy Process (AHP) (Saaty 1980). This technique is based on the user providing scaled scores,

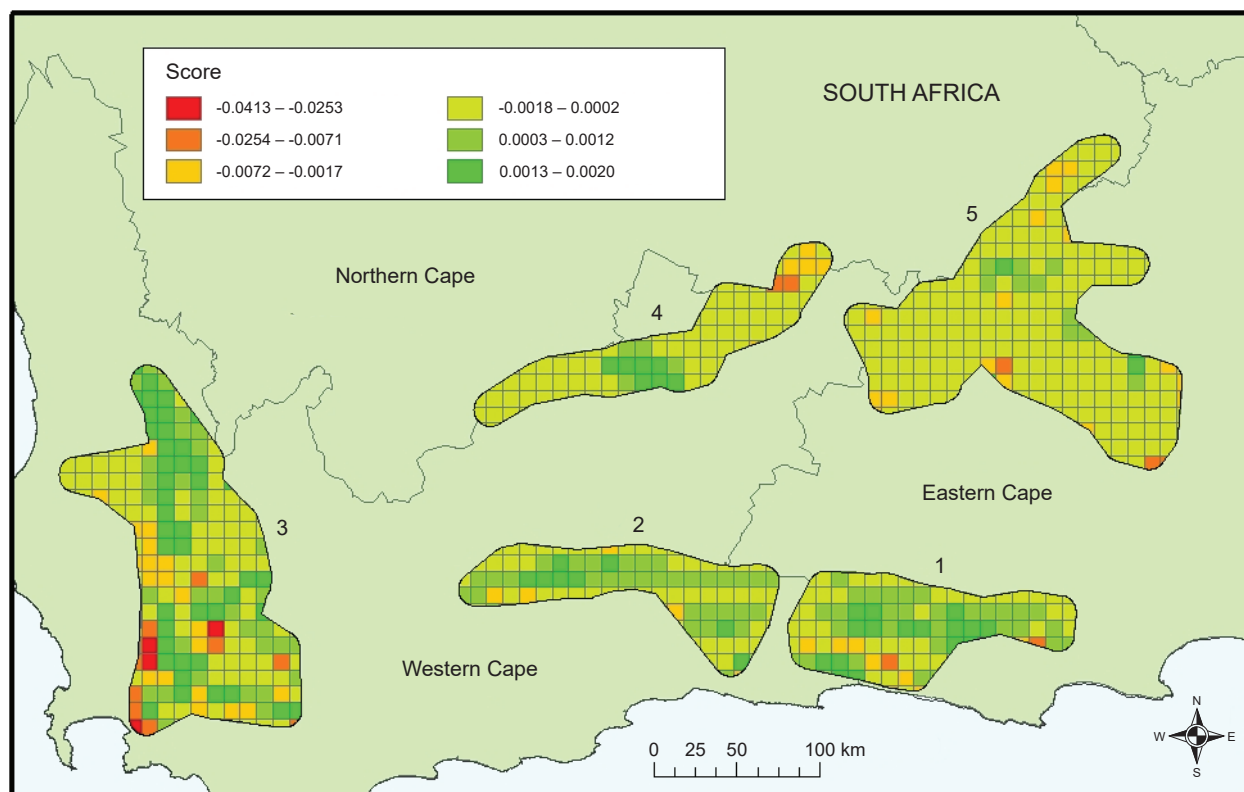


Figure 2: Suitability scores calculated for 10 km × 10 km release site grid cells across all identified potential Bearded Vulture reintroduction sites (1–5). Green sites are the most suitable release sites and red sites are the least suitable

for the relative importance of each variable in relation to all other variables in turn, in a pairwise comparison matrix. Our comparisons were based on the degree to which each variable contributed to the mortality of tracked Bearded Vultures and other individuals found dead in the range (Krüger 2014). From this matrix, relative weightings are calculated. The consistency of the pairwise comparisons is then checked through the calculation of a consistency ratio that has to fall below a threshold of 0.1. We applied our calculated weightings to each variable's corresponding score. We then calculated a total score for each reintroduction site by subtracting the scores of the variables with a negative impact (power lines, wind farms, human settlement and unsuitable habitat) from those with a positive influence (livestock and protected areas). We ranked the reintroduction sites based on these scores. Other reintroduction studies have used a similar process of comparing area attributes to explore potential reintroduction sites (Thatcher et al. 2006; LaRue and Nielsen 2011).

Release site selection

Given the large size of the reintroduction sites, we attempted to narrow down the most suitable locations for actual releases of fledglings (release sites) within each reintroduction site. This could have important consequences, because birds are generally most vulnerable within their first year (Krüger 2014), the age of released birds in other reintroduction projects (Frey 1992). We divided reintroduction

sites into 10 km × 10 km grid cells, each representing a release site, and compared each 10-km² cell using the same process and variables as used for the reintroduction sites. We did not consider livestock density, because the scale at which these data were available (provincial) was too coarse to be meaningful for this assessment.

Population modelling

We used the stochastic population simulation software Vortex 10 (Lacy et al. 2014), to model the outcomes of various management strategies for the proposed reintroduction. Management strategies focussed on alternative ways to reintroduce fledglings produced from eggs taken from the wild. We assumed a single reintroduction site would be used to create a single separate population from the current one. We assumed that removal of eggs would have no effect on the current population, because of the obligate siblicide that occurs in this species (Margalida et al. 2015). Egg removals were limited to a maximum of six nest sites per year, because of logistical and financial constraints. Harvesting was envisioned to continue for five years. We consequently used a conservative estimate of four fledglings available per year over a period of five years (accounting for captive mortalities, infertile eggs) to model the effect of three likely management strategies (Supplementary Figure S1):

- Model 1 (M1): All four fledglings released directly into a single reintroduction site each year.

Table 1: Parameters assessed to determine site suitability for a Bearded Vulture reintroduction

Variable	Rationale	Measure	Data source and/or layer name
Livestock density	This was used as a proxy for food availability.	Number of ungulate livestock (pigs, sheep, cattle and goats) per km ² .	2013 National Livestock Statistics ^a
Power line density	Cause of mortality and territory abandonment (Krüger et al. 2015).	Total distance (km) of 11 kV, 22 kV and 1 322 kV power lines per km ² .	ESKOM 2015.
Proportion wind farms	Wind farms can have severe consequences for raptors who are killed when colliding with turbine blades (Reid et al. 2015).	Proportion of reintroduction site that has wind farm developments, either existing, in process or proposed.	'REEA_OR_2015_Q3'. Department of Environmental Affairs 2015, Republic of South Africa.
Proportion human settlement	Human settlement is assumed to be related to increased instances of poisoning and persecution, which are the main causes of mortality and territory abandonment (Krüger et al. 2015).	Proportion of reintroduction site that is classified as human settlement.	'Dea_cardno_2014_sa_lcov' Department of Environmental Affairs 2015, Republic of South Africa.
Proportion protected area	These areas represent protection from many threats, enforced through regulation and management.	Total area (km ²) under formal protection.	'SAPAD_OR_2014_Q2' Department of Environmental Affairs 2015, Republic of South Africa.
Proportion unsuitable habitat	Unsuitable habitat decreases the amount of habitat available to Bearded Vultures at a given site.	Proportion of reintroduction site considered as habitat that is unusable by Bearded Vultures (thickly vegetated areas, wetlands, waterbodies, urban areas, mines, commercially cultivated fields).	'Dea_cardno_2014_sa_lcov' Department of Environmental Affairs 2015, Republic of South Africa
Number of potential nests	Provides an estimate of the potential number of breeding pairs and therefore whether a viable population can be supported at the site.	Calculated number of nest sites based on the nest site suitability model outputs and 9 km inter-nest distances (Krüger et al. 2014a).	Calculated from extracted cliff sites in the nest site suitability model (see above for explanation).

^a2013 National Livestock Statistics, Directorate: Statistics and Economic Analysis of the Department of Agriculture, Forestry and Fisheries.

- Model 2 (M2): All four fledglings retained to build up a captive population, with birds released into the wild after 10 pairs are breeding in captivity.
- Model 3 (M3): A blended model, with simultaneous and equal supplementation of fledglings to both the captive population and the reintroduced population. Releases from the captive population were specified to commence only after the captive population had reached 10 breeding pairs. We used the demographic rates from the Maloti-Drakensberg population as a baseline in the model. This included a 25.8% mortality for birds in their first year, 22.8% mortality for those between the ages of one and seven and an 8.4% mortality rate for birds older than seven (Krüger 2014) (Supplementary Table S1).

Females in captivity produce their first and last egg at a median of 6.5 years and 31 years, respectively (Bustamante 1996). Although some studies have found small differences in age of first breeding between the sexes (Antor et al. 2007), for simplicity we set the age of sexual maturity to be seven years for both sexes and assumed no sex differences in lifespan. We assumed no sex differences in mortality rates, as was found in previous studies on this species (Bustamante 1996). We assumed a stable age distribution for the Maloti-Drakensberg population and no inbreeding depression was anticipated, because of the constant influx of unrelated birds. The parameter values used in all models are detailed in Supplementary Table S1.

Because it is uncertain what mortality rates the reintroduced population might experience, we modelled various mortality scenarios, differing from the baseline by 10% increments. Demographic rates for the captive breeding simulations were acquired from the captive population in Europe between 1973 and 1993 (Bustamante 1996; Supplementary Table S1). Captive mortality was set at 7.6% for the first year, 1.1% for birds aged one to seven years, and 3.3% for birds over seven years.

Using the success of the alpine reintroduction as a model, we used a conservative aim of establishing at least 10 breeding pairs after 30 years (Schaub et al. 2009). Assuming all adults breed, this equates to at least 20 adults being present in the reintroduced population, which based on the age distribution calculated by Krüger (2014), equates to a total population size of 34 individuals. Accordingly, in order to explore the probability of reintroduction success from the model output, we defined extinction to be fewer than 34 individuals, running the model over 30 years. Therefore, the probability of extinction in the model output is the estimated probability of the reintroduction failing.

We estimated the full capacity of any breeding facility as 10 breeding pairs. Fledgling removal was set to occur when the captive population reached 23 individuals allowing the captive population to stabilise at around 20 individuals after each year's fledgling removal event had occurred (Supplementary Figure S2).

To explore the longer-term viability of the reintroduced population, we selected the best performing management model and re-projected it over a 50-year period, but with supplementation from the captive population stopping after 30 years. Additionally, the model was run at baseline demographic rates in tandem with the current Maloti-Drakensberg population projection, over the same period, to explore the overall value of a reintroduction project if mortality rates remain similar to that currently experienced in the wild (Supplementary Table S1).

Results

Nest site suitability

Maximum Entropy Model outputs consistently highlighted the same areas as suitable. We identified five potential reintroduction sites, situated mostly within the Western and Eastern Cape Provinces of South Africa (Figure 1). The sizes of these areas ranged between approximately 7 100 km² and 18 200 km² (Table 2). The area under the curve (AUC) was used to summarise the Receiver Operating Characteristic (ROC) curve and measure the performance of the model. The model, including all variables, performed well, giving an AUC value of 0.989. Elevation and presence of cliffs had the highest predictive contribution with a 45.7% and 35.1% contribution, respectively. Terrain ruggedness and climate were relatively unimportant.

Potential reintroduction sites

The proportion of human settlements in a site was identified as the variable considered to have the greatest importance in determining the suitability as a reintroduction site and for the specific release sites (Table 3). We identified Site 5 (Figure 2) as the most suitable site for a Bearded Vulture reintroduction (Table 2). This was despite having the lowest percentage of area protected (<5%), and the second highest percentage area of wind farms (Table 2; Supplementary Figures S3 and S4). This is the largest site

and consequently contains the largest number of potential breeding territories (Table 2).

Site 1 ranked second and was the only site that had no wind farms (Table 2; Supplementary Figures S3). This site, however, contained the second highest percentage of unsuitable habitat, as well as the second highest power line density (Table 2; Supplementary Figures S3 and S5). Site 1 was about 56% smaller than Site 5, but was much better protected, with approximately 37% of the site consisting of protected area (Table 2; Supplementary Figure S4).

Suitability of release sites

Suitability scores for the 10 km × 10 km cells within reintroduction sites varied between -0.041 and 0.002 (Figure 2). As a result of the high weighting of protected areas, there was a close association between high scoring cells and the presence of protected areas (Figure 2; Supplementary Figure S4). Within our highest-ranked reintroduction site (Site 5), only three release sites had high suitability scores (Figure 2), each corresponding to a protected area: the Agter Sneeu Berg Nature Reserve, the Mountain Zebra National Park and the Compasberg Protected Environment (Supplementary Figure S4). Site 1 had more widespread high scoring release sites, because of a considerably higher proportion of protected areas (Table 2; Supplementary Figure S4), including the Cape Floral Region Protected Areas and the Garden Route National Park, amongst others.

Reintroduced population trends

Our simulations of captive breeding followed by reintroduction (Model 2) gave the lowest failure probability (25.5–49.8%), followed by our simulations of simultaneous captive breeding and reintroduction (Model 3) (27.6–53.8%). Our simulations of direct and immediate releases (Model 1) gave the highest probability of failure (78.3–95.7%) (Figure 3). The different approaches resulted in different numbers of young being supplemented each year over the

Table 2: Attributes of each identified potential reintroduction site, as well as the calculated suitability score and resulting rank of each reintroduction site (Wind Farms (WF), Protected Area (PA), Power Lines (PL), Human Settlement (HS), Unsuitable Habitat (UH), Livestock Density (LD) and Potential Breeding Territories (PBT)). The highest-ranking reintroduction site is indicated in bold.

Area ID	Site size (km ²)	WF (%)	PA (%)	PL (km km ⁻²)	HS (%)	UH (%)	LD (numbers km ⁻²)	PBT	Score	Rank
1	8 077.84	0	37.41	1.50	0.31	22.69	54.79	27	0.21	2
2	7 278.69	0.15	32.47	1.47	0.10	17.25	29.68	25	0.15	3
3	16 523.52	0.41	40.80	3.94	0.80	30.60	4.92	55	-0.19	5
4	7 083.98	7.39	11.47	1.10	0.02	3.63	32.54	18	0.09	4
5	18 174.73	0.97	4.48	1.31	0.20	7.20	99.71	62	0.36	1

Table 3: Resulting weightings of each parameter calculated from pairwise comparisons, done during an Analytical Hierarchy Process (AHP) and the consistency ratio (CR) of these pairwise comparisons

	Unsuitable habitat	Livestock density	Wind farms	Protected area	Power lines	Human settlement	CR
Reintroduction site weightings	0.038	0.040	0.094	0.094	0.198	0.537	0.061
Release site weightings (10 km)	0.034	N/A	0.065	0.314	0.127	0.460	0.078

30-year period, ranging from less than one per year for Model 1 (0.66 ± 1.52) to nearly four per year for Model 2 (3.7 ± 4.9). The population size of extant populations also varied considerably between the different models; for Model 2 (i.e. the model with the lowest probability of failure) extant populations range was from ~92 to ~161 (Figure 4). Our results therefore suggest that Model 2 and Model 3 are the preferable management strategies. If mortality rates were 40% lower at the reintroduction site, the reintroduced population could theoretically grow larger than the Maloti-Drakensberg population within 30 years (Figure 5).

Our simulations of captive breeding followed by reintroduction (Model 2) built up the captive population to

the threshold for fledgling removal after nine years (9.0 ± 0.9 years), which was on average 4.9 years more rapid than our simulations involving simulations of simultaneous captive breeding and reintroduction (Model 3) (13.9 ± 3.2) (Supplementary Figure S2).

Running our simulations over a long period (i.e. 50 years), resulted in much higher probabilities of failure (range: 50.5%–86.9%). From the simulations of the best strategy (Model 2), there was an 80.5% probability of failure when mortality rates were similar to those currently experienced, with an extant population size between 157 and 251 (Figure 6). However, failure probability fell to ~50.5% when mortality rates were reduced by 40%. Our

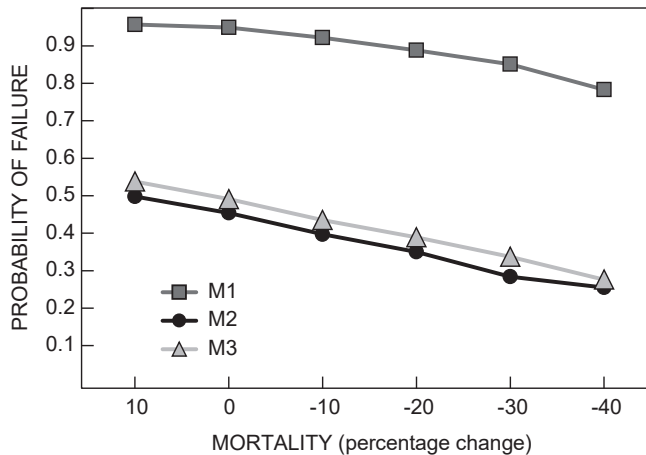


Figure 3: Probability of failure (defined as less than 34 individuals after a 30-year period), in relation to 10% increment changes in baseline mortality rates (0), of a Bearded Vulture reintroduction under three different management models (M1–M3)

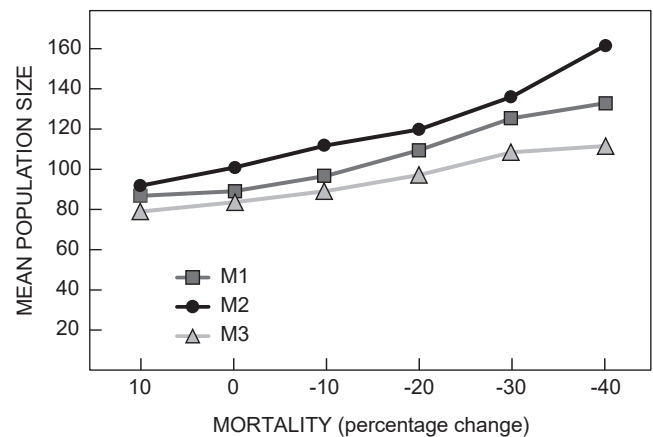


Figure 4: Mean population size after 30 years for a reintroduced Bearded Vulture population in relation to 10% increment changes in the baseline mortality (0) for three different management models (M1–M3)

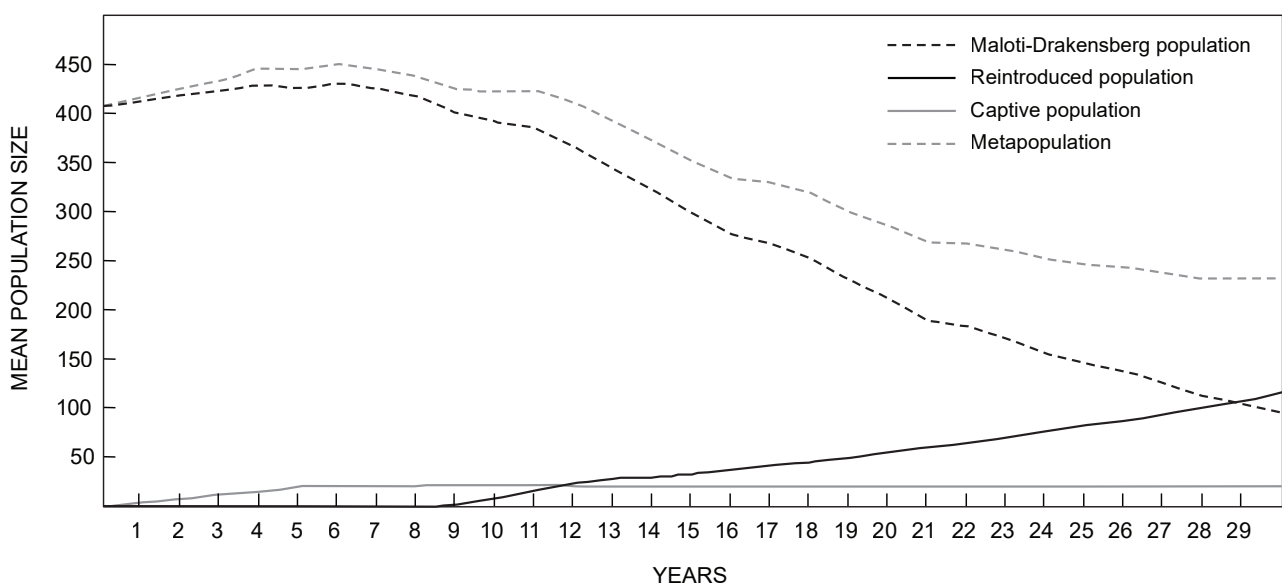


Figure 5: Mean population size of each population per year for all iterations of a Bearded Vulture reintroduction project simulation with the reintroduced population run at a 40% reduction of baseline mortality rates with the Model 2 management scenario (captive breeding followed by a reintroduction) implemented

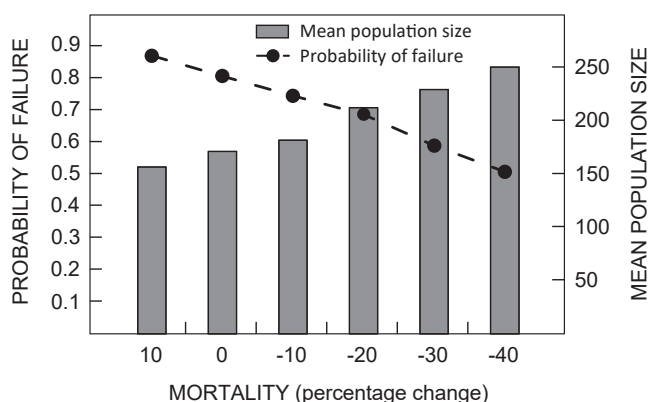


Figure 6: Probability of failure (<34 individuals) of a Bearded Vulture reintroduction and the mean population size after 50 years, across mortality rates varied by 10% increments from baseline demographic parameters for the Model 2 management scenario

simulations also suggested that the current southern African Bearded Vulture population had a very high probability of extinction (one sex remains) over the next 50 years. A reintroduction initiative will lower the probability of this extinction from 92.5% to 62.6%, even when mortality rates of the reintroduced birds were similar to those currently experienced (Figure 7).

Discussion

Reintroduction site selection

According to the IUCN guidelines (IUCN 2013), reintroductions should only be attempted if the original causes of extinction have been addressed. The aim of our study was to identify topographically and climatically suitable areas for reintroduction, where the major causes of mortality for the species were expected to be least severe. Results from this study indicate that there are suitable sites for a potential population reintroduction of Bearded Vultures in South Africa. The two highest-ranked sites for a reintroduction were located mostly within the Eastern Cape Province. The top-ranking reintroduction site (Site 5), was the largest site and contained an estimated 62 potential breeding territories (Table 2).

Poisoning is one of the major threats to Bearded Vultures and farmers commonly use poison for predator control, in the hope of reducing livestock losses (Ogada et al. 2012). Livestock densities in Site 5 were significantly higher, compared with any other site, indicating that intensive farming activities occur in this area. Community engagement and awareness campaigns, as well as strong enforcement of environmental laws, are therefore important for the success of any reintroduction, as well as for addressing the Maloti-Drakensberg population decline (Krüger et al. 2006). The fact that the reintroduction site would be smaller than the current range, and does not traverse political boundaries, means that the management of the population and the enforcement of conservation regulations may be more effective. Furthermore, the novelty of the species in the area and the dedicated monitoring of released individuals

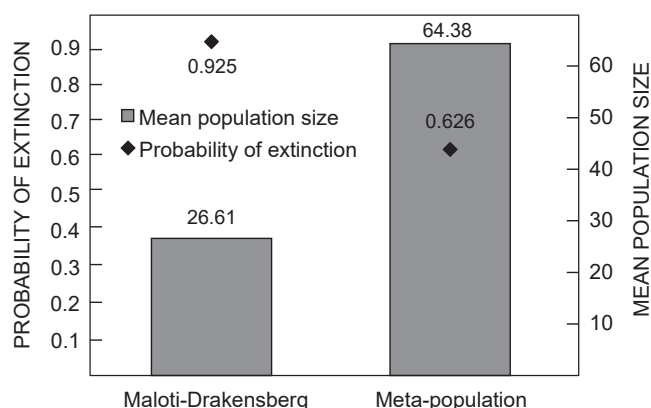


Figure 7: Probability of extinction, defined as one sex remaining, and mean population size after 50 years, for the Maloti-Drakensberg population and the meta-population (Maloti-Drakensberg and reintroduced population combined) using baseline demographic rates and the Model 2 management scenario

(e.g. using Global Positioning System tracking of individuals) should also help discourage unlawful behaviour as perpetrators would be more easily discovered. Management of the reintroduction and mitigation of the threat of poisoning would be easier if the release site was within a protected area. Therefore, the presence of a suitable protected area was considered an important attribute in the identification of specific release sites within reintroduction sites. Within Site 5, the Compasberg Protected Environment seems to be the best-situated high scoring release site (Figure 2). This site should therefore be assessed in more detail to ground truth the suitability of this site prior to a reintroduction. Although Site 3 had the highest percentage of protected area, it also had the highest percentage of unsuitable habitat, human settlements and power line density. Because there is no way of confining vultures within protected areas, these factors are likely to increase mortality rates at this site.

Authorities considering the reintroduction of Bearded Vultures in South Africa should carefully scrutinise the results from this study, and any decisions on which potential reintroduction site to use should be made based on their capacity to mitigate the various threats assessed. Site 4, for example, seemed highly suitable apart from pockets of highly concentrated wind farms and power lines in the north (Supplementary Figures S3 and S6). If vulture movements could be manipulated away from these areas, for example through supplementary feeding and mitigation implemented to increase power line visibility, then the suitability of this site could be greatly improved.

Dispersal between populations

We only considered areas that were at least 100 km away from the current Bearded Vulture range, because the aim of the project was to establish a separate insurance population. Because Site 5 (the top ranked reintroduction site) is the closest site to the current range, reintroduction here has the highest probability of resulting in dispersal to and from the Maloti-Drakensberg population. Bearded Vultures have been known to range up to 869 km (Margalida et al. 2013).

Dispersal between the populations could be both beneficial and disadvantageous and authorities should carefully evaluate the merits of this situation. Inbreeding and the genetic integrity is, for instance, always a concern in small populations and natural movement of individuals between the reintroduced and Maloti-Drakensberg populations would result in increased gene flow between these populations (Alexandre et al. 2007). Choosing a release site that promotes the establishment of a meta-population may therefore be desirable.

Our species distribution model identified large suitable patches between Site 5 and the current Maloti-Drakensberg range (Figure 1). If Site 5 were to be chosen for the reintroduction then the abandoned territories between these sites (Krüger et al. 2015) may be re-occupied, a scenario that is more likely if individuals move between these populations. When deciding which scenario (establishing a meta-population or a separate reintroduced population) is preferable, managers should choose the scenario most likely to ensure the continued persistence of Bearded Vultures at a regional level.

Release strategies

Results from our population models (Model 1) strongly suggest that releasing birds into the wild without supporting releases from a captive population has a very high probability of failure (Figure 3), whereas establishing a captive breeding programme to supplement the reintroduced population (e.g. Models 2 and 3), greatly increased the probability of success of the reintroduction. Probabilities of failure were less than 50% under most mortality scenarios (Figure 3). Although Models 2 and 3 had similar probabilities of failure (<34 individuals), those of Model 2 were consistently slightly lower and had higher extant population sizes (Figures 3 and 4). Model 2 was the only model in which the reintroduced population reached a larger population size than the current Maloti-Drakensberg population within 30 years (Figure 5). Our results consequently indicate that prioritising the building of a captive breeding population is the most efficient management strategy in terms of producing the strongest reintroduced population.

The benefit of management Model 3 is that releases start earlier, in the first year of the reintroduction project, and more gradually than in Model 2. These early releases of smaller numbers of birds could be used to test the suitability of the reintroduction sites. If early releases incur high mortalities, then the reintroduction site can be changed more readily and cheaply, compared with Model 2. Accordingly, an adaptive management programme could be implemented with early releases and mitigation measures (e.g. education or enforcement) being implemented as necessary. If large numbers of birds were released into an inadequate area, then it would be a significant waste of resources, because each released individual represents a large investment (Frey 1998). Evidence, however, shows that the productivity in breeding facilities can differ significantly and deciding which management model to implement may be dependent on the performance of the breeding programme. Additionally, other evidence shows that the breeding success and survival of wild fledged

raptors can be much higher than that of reintroduced raptors (Evans et al. 2009). This therefore also favours the strategy used in Model 3, because wild fledged birds will start appearing and contributing earlier to the reintroduced population with this approach.

High mortality rates, such as those experienced in the Maloti-Drakensberg population, pose a major threat to the proposed reintroduction. Our results nonetheless indicate that a reintroduction project would be a valuable initiative, even if mortality rates at the reintroduction site were similar to those experienced in the wild. Despite the high probability of failure of the reintroduced population 20 years after supplementation has ceased (Figure 6), such an initiative would result in an approximately 30% decrease in the probability of extinction of the species from southern Africa in the next 50 years and a 242% larger population (Figure 7).

Building a captive population may also be considered regardless of any reintroduction. When a species faces extinction, intensive conservation actions, such as captive breeding or supplementary feeding, to sustain the population until environmental conditions return to a favourable state for a self-sustaining population, are justifiable actions (Anderson et al. 2015).

If the reintroduced population is to be viable after a 50-year period, then the mortality rates in the reintroduced site should be at least 40% lower than currently experienced by the Maloti-Drakensberg population (Figure 6). Supplementation from a captive population buys at least 30 years to achieve this mortality reduction, as shown by the relatively low probabilities of extinction after 30 years in simulations where a captive breeding model was used (Figure 3).

The required decrease in mortality may be achieved simply through the release of birds in areas with lower anthropogenic pressures. The next step, therefore, would be to ground truth such pressures in the potential reintroduction sites. Once a site has been selected, the initial priority should be eliminating or reducing such anthropogenic pressures.

Limitations and recommendations for supplementary studies

Although this study has provided insight into potential reintroduction sites, release sites and management strategies, it is not a comprehensive feasibility analysis. Additional research would be required to compare habitat attributes of the potential reintroduction sites with those in the existing Maloti-Drakensberg population. However, the lack of relevant data from Lesotho (where the core of the Bearded Vulture range resides) will make this problematic.

We based our assessment of food availability on coarse data of livestock numbers per province. Information on wild ungulate numbers was unavailable and although they are generally considered to only occur at low densities in these areas, our measure of food availability was incomplete. Reintroduction sites with a high proportion of protected area in particular could have higher food availability than anticipated. However, we did not consider food availability of major importance as supplementary feeding sites might provide suitable food sources, as well as economic benefits to local livestock farmers (Brink et al. 2020). A thorough

assessment of food availability before reintroduction would nonetheless be advisable.

Cost analyses should also be considered in the future, when the specific potential release sites have been chosen. Costs incurred at each site may vary, for example, because of logistical reasons. We did not apply such cost considerations to the different management scenarios. These considerations may also be important in terms of future monitoring, as required by the IUCN (2013).

Before reintroductions begin, there should also be additional investigation of reintroduction sites. Arguably, the most important action would be to acquire some measure of the prevalence of the use of poison at these sites and an assessment of the attitudes of the landowners to Bearded Vultures.

Conclusions

This study has identified five candidate sites for a Bearded Vulture reintroduction and provided a qualitative assessment of each. Additional assessment is, however, required to validate assumptions made in this study and broaden the scope of the parameters analysed. Specifically, an assessment of stakeholder attitudes and the likely prevalence of poisoning is required. In terms of release strategies, it is clear that a captive breeding programme is an important contributing factor for the success of the reintroduction and is a prudent measure, considering the current decline of the Maloti-Drakensberg population. Such a captive breeding programme is currently being established and our study provides a valuable baseline for the consideration of reintroduction sites and release sites.

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