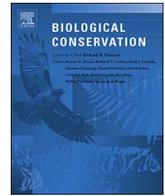




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Due South: A first assessment of the potential impacts of climate change on Cape vulture occurrence



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ABSTRACT

Multiple anthropogenic threats have caused vulture populations to decline globally, with serious ecological and socio-economic implications. The Cape vulture (*Gyps coprotheres*) has declined throughout its range in southern Africa, recently being listed as extinct as a breeding species in Namibia. It has been suggested that climate change might have contributed to the decline of Cape vultures in northern parts of the range. To provide a first assessment of the potential impacts of climate change on the occurrence of Cape vultures, a presence-only environmental niche modelling method (Maxent) was used to predict the spatial occurrence patterns of wild vultures fitted with GPS tracking units in northern Namibia and northern South Africa, under current and future climatic conditions. The models showed high predictive power ($AUC > 0.868 \pm 0.006$), with precipitation seasonality identified as the most important variable for predicting Cape vulture presence. Of the area estimated to be suitable for Cape vultures under current conditions, 28–55% was predicted to become unsuitable under future climate conditions, with a pole-ward shift in the mean centre of the range of 151–333 km and significant range loss from the former breeding range in north-central Namibia and the core breeding range in northern South Africa. The total area of suitable range was predicted to increase in the future due to modelled expansions into grassland and cropland areas where the species has been absent historically. The coverage of suitable areas by protected areas was predicted to decrease from 5.8–7.9% to 2.8–3.8%, suggesting that private land will become increasingly important for Cape vulture conservation.

1. Introduction

African vulture populations are declining across the continent due to multiple anthropogenic threats such as poisoning (Ogada et al., 2015a), collisions and electrocutions on the expanding power line network (Boshoff et al., 2011) and food shortages due to depleted wild ungulate populations and improved livestock husbandry (Mundy et al., 1992; Krueger et al., 2015; Ogada et al., 2015b). The potential consequences of continuing declines are likely to be far reaching due to the essential ecosystem services that vultures provide (e.g. nutrient recycling; limiting the development and spread of disease (Moleon et al., 2014; Morales-Reyes et al., 2015; Buechley and Şekercioğlu, 2016)). However, despite an increasing number of remote tracking

studies on African vulture species (Phipps et al., 2013a; Spiegel et al., 2013; Kendall et al., 2014; Krueger et al., 2014) to our knowledge there has been no attempt to investigate what drives their spatial distribution using tracking data and multivariate modelling methods.

Successful efforts to plan and implement conservation strategies in key areas are often reliant on the ability to describe the ecological niche and map the spatial distribution of threatened species to inform their management, ecosystem restoration, reintroduction programs and population viability analysis (Elith et al., 2011; Razgour et al., 2011; Guillera-Arroita et al., 2015). Environmental niche modelling (ENM) methods estimate the relationship between species presence records at sites and the environmental characteristics of those sites, and are widely used in conservation biology and ecology (Elith et al., 2011;

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Porfirio et al., 2014). Increasingly Global Positioning System (GPS) tracking data provide the species presence records necessary for ENM analyses (Hebblewhite and Haydon, 2010) for conservation themed studies on terrestrial (Swanepoel et al., 2013; Van Gils et al., 2014) and avian species (Jiguet et al., 2011; Gschweng et al., 2012; Liminana et al., 2014). Maxent (Phillips et al., 2006) is a common and favoured method for ENM analysis using tracking data because it does not require true absence data and has been shown repeatedly to outperform other presence-only modelling techniques (Hernandez et al., 2006; Elith and Leathwick, 2009). Examples of its successful application with avian tracking data include predicting the extent of suitable wintering habitats for pallid (*Circus macrourus*) and Montagu's (*Circus pygargus*) harriers in sub-Saharan Africa (Liminana et al., 2012; Liminana et al., 2014), and the response of Eleonora's falcons (*Falco eleonora*) to environmental change (Gschweng et al., 2012).

The Cape vulture (*Gyps coprotheres*) is endemic to southern Africa and is listed as Endangered on the IUCN Red List due to recently estimated population declines of –92% over three generations (48 years), at a median annual rate of –5.1% (Taylor et al., 2014; Ogada et al., 2015b; Simmons et al., 2015). It is a gregarious cliff-nesting species with a global population estimated at 8000–10,000 individuals (circa 4000 breeding pairs) (BirdLife International, 2016). The largest remaining breeding colonies are located in the north-eastern provinces of South Africa with smaller, more dispersed colonies in the Maloti-Drakensberg mountains of Lesotho and south-east South Africa (Rushworth and Kruger, 2014; Wolter et al., 2016). An isolated breeding colony located on the cliffs of the Waterberg Plateau Park in north-central Namibia that numbered 500 Cape vultures in 1940 was reduced to as few as 13 individuals in 1985 (Brown, 1985) and the species has recently been classified as extinct as a breeding species in the country (Simmons et al., 2015). The declines have been mainly attributed to the widespread use of poisons for killing predators in the region and the loss of foraging habitat due to shrub encroachment (Brown, 1985; Mundy et al., 1992; Bamford et al., 2007; Schumann et al., 2008; Bamford et al., 2009; Santangeli et al., 2016).

It has also been suggested that climate change may have played a role in the extinction of Cape vulture colonies in the north of their range since the 1950s due to the increasing temperatures and changing rainfall patterns recorded in the region (Simmons and Jenkins, 2007; IPCC, 2014). Southern Africa, and Namibia in particular, is predicted to experience particularly significant changes to climatic conditions (e.g. rising temperatures and altered rainfall patterns (Conway et al., 2015; van Wilgen et al., 2016)) which are expected to drive pole-wards range shifts and loss of climatically suitable conditions for many species from different taxa (Simmons et al., 2004; Thuiller et al., 2006b; Midgley and Thuiller, 2011; Garcia et al., 2012). There is evidence that rainfall patterns influence vulture breeding success (Bridgeford and Bridgeford, 2003; Virani et al., 2012); breeding Cape vultures suffer increased levels of heat stress in higher temperatures and longer sunlight exposures (Chaudhry, 2007); Cape vulture nest sites at higher elevations are more likely to be occupied and breeding success is higher when they are more sheltered from extreme weather conditions (Pfeiffer et al., 2017); and increased temperatures and carbon dioxide levels enhance woody vegetation cover (Midgley and Bond, 2015), inhibiting the visual foraging of vultures by obscuring carcasses (Schultz, 2007; Bamford et al., 2009). Simmons and Jenkins (2007) therefore propose that climate change may work in concert with other factors to push Cape vultures away from their northernmost colonies in a southwards direction, and further work is required to investigate the potential impacts of climate change on Cape vulture occurrence (Krueger et al., 2015).

In this study we use Maxent modelling to provide a first description of the spatial niche characteristics for Cape vultures and identify some of the environmental factors driving their occurrence. The presence locations were derived from GPS tracking data from wild-caught vultures from northern South Africa (Phipps et al., 2013b) and from

some of the last remaining Cape vultures in Namibia (Bamford et al., 2007). We investigate the potential influence of climate change on the extent of areas predicted to be currently suitable by projecting the models onto future bioclimatic conditions. We compare results from models using only data from South African-tagged vultures with models from data from all vultures to assess whether conditions in north-central Namibia are predicted to be suitable for Cape vultures under current and future climate scenarios. We also evaluate the coverage provided by protected areas under current and future conditions as species turnover in protected areas is expected to be high in the region (Hole et al., 2009). The intention of this study is to provide a first description of the spatial niche of a sample of Cape vultures from the core breeding range of the species and to test whether vulture occurrence patterns might be influenced by global climate change.

2. Methods

2.1. Modelling method and study area

The presence-only method Maxent (Phillips et al., 2006) was used to model the environmental niche of the Cape vulture as it does not require true absence data (Elith et al., 2011) and has been used previously with avian tracking data obtained from a small number of individuals (Gschweng et al., 2012; Liminana et al., 2012; Liminana et al., 2014). The geographical area used for environmental niche modelling was delineated by the borders of South Africa, Lesotho, Swaziland, Zimbabwe, Botswana and Namibia, and corresponds with the historical distribution of the Cape vulture (Mundy et al., 1992; BirdLife International, 2016).

2.2. GPS tracking and presence data

Presence locations were derived from two studies that fitted GPS tracking units to wild-caught Cape vultures using walk-in cage traps (Bamford et al., 2007; Phipps et al., 2013b). The first capture site was located on a private livestock and game farm in the Waterberg region of north east Namibia (20°15'54"S, 17°03'53"E) while the second was 1180 km to the south-east on a private wildlife reserve in the North West Province of South Africa (25°13'S, 27°18'E). Vultures captured in Namibia were fitted with solar-powered Argos/GPS PTT-100 tracking units made by Microwave Telemetry Inc. (Columbia, Maryland) programmed to record GPS locations every hour from 06:00 to 21:00 CAT (Bamford et al., 2007). The vultures captured in South Africa were fitted with battery-powered Hawk105 GPS-GSM tracking units programmed to record GPS locations up to four times per day at 07:00, 11:00, 13:00 and 15:00 CAT (Phipps et al., 2013b). Tracking units were fitted to vultures with Teflon® ribbon backpack-style harnesses and GPS locations were accurate to within 10 m. Data were derived from a total of five adult and four immature Cape vultures tagged in South Africa and five adults tagged in Namibia. The nine South African tagged vultures were tracked from 2009 to 2011 for 31–558 days (median tracking period = 300 days; median number of GPS locations = 922, range = 84–1860), and the five vultures from Namibia were tracked from 2004 to 2009 for 57–1656 days (median tracking period = 1231 days; median number of GPS locations = 15,447, range = 654–19,400).

Spatial preparation of GPS location and environmental variable data was performed in SDMtoolbox v1.1b (Brown, 2014) in ArcMap (ESRI, 2014) with all data projected to the Africa Albers Equal Area Conic coordinate system. Only stationary (< 10 kmh⁻¹) GPS locations were selected to more accurately represent actual use of a given area. Additional details on further filtration of the GPS locations to reduce spatial autocorrelation and the influence of tracking period disparity are provided in the “Presence data” section of the Appendices.

Two datasets of presence locations were generated for modelling purposes. The first dataset consisted of 1437 presence locations from

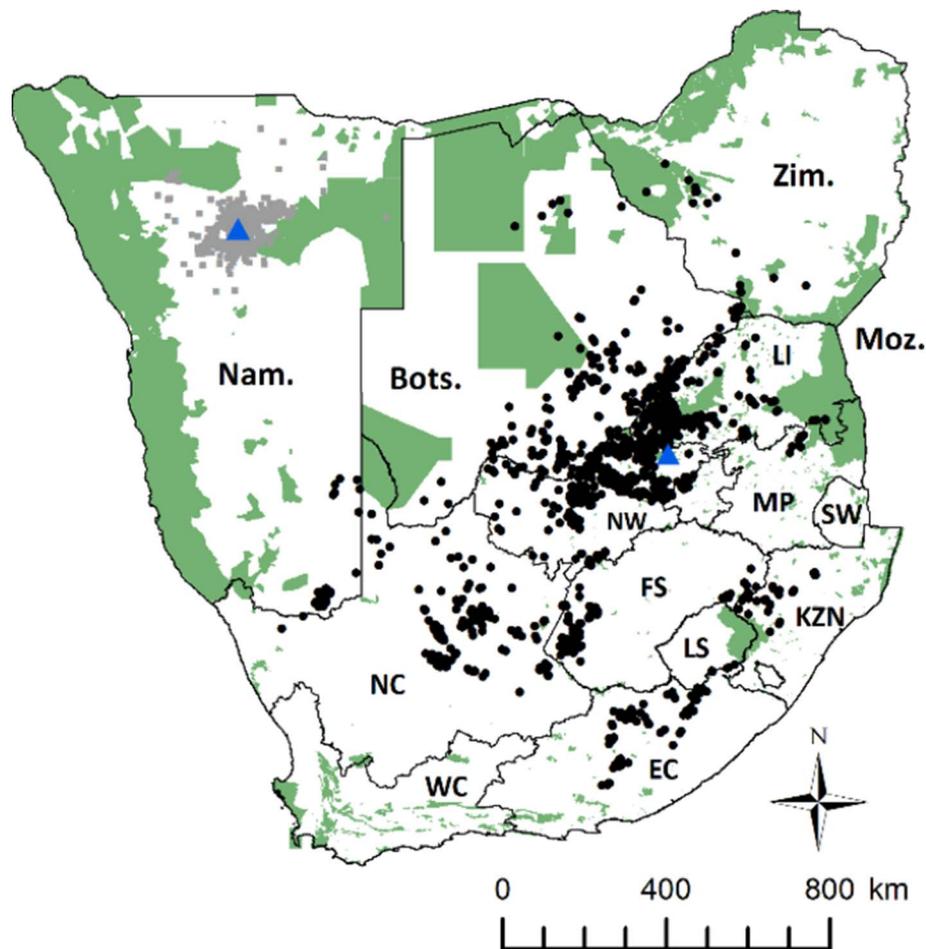


Fig. 1. Presence locations used for Maxent modelling from GPS tracking data from Cape vultures tagged in South Africa (black circles) and Namibia (dark grey squares). Capture sites are indicated by blue triangles and protected areas are shown by filled green polygons (IUCN and UNEP-WCMC 2015). Letters indicate abbreviated country names and provinces of South Africa (NC = Northern Cape; WC = Western Cape; EC = Eastern Cape; KZN = KwaZulu-Natal; MP = Mpumalanga; NW = North West; LI = Limpopo; LS = Lesotho; SW = Swaziland; Nam. = Namibia; Bots. = Botswana; Zim. = Zimbabwe; Moz. = Mozambique). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the nine South African tagged individuals only. The second included an additional 686 presence locations from the five Namibian vultures, bringing the total to 2123 locations for all 14 vultures (Fig. 1). This was done to compare results based on data from only South African tagged birds (i.e. captured in the “core” of the species’ breeding range (Mundy et al., 1992; BirdLife International, 2016)) to those that included presence locations from Namibia where the species formerly bred but is now considered extinct as a breeding species (Brown, 1985; Simmons et al., 2015). This provided an indication of the suitability of environmental conditions in northern Namibia compared to the rest of the study area and whether or not the region was predicted to be negatively affected by climate change compared to more southern areas.

Capture and tagging procedures were approved by the ethical review committee of the School of Animal, Rural and Environmental Science, Nottingham Trent University, and permits were granted by the Department of Agriculture, Conservation, Environment and Rural Development, North West Provincial Government, Republic of South Africa (Permit: 000085 NW-09) and the Namibian Ministry of Environment and Tourism (Permit: 1578/2004–2005). All procedures were carried out by South African Bird Ringing Unit permit holders.

2.3. Environmental variables

Only environmental variables with a pairwise Pearson’s correlation coefficient of < 0.7 (assessed using SDMtoolbox v1.1b (Brown, 2014)) were included in the modelling process to reduce multi-collinearity

effects (Phillips and Dudik, 2008). Environmental variables were subsequently selected based on prior knowledge of their ecological relevance to Cape vultures and their contribution to preliminary models in an effort to achieve parsimony to reduce the risk of over-fitting (Anderson and Gonzalez, 2011; Van Gils et al., 2014). The models included a total of 14 environmental variables (Table 1, Table A1) at a spatial resolution of 30 arc-seconds (approximately 1 km^2 at the equator). Further information on the selection of environment variables can be found in the “Environmental data” section in the Appendices.

For projections to future climatic conditions the current Bioclim variables were replaced with the corresponding Bioclim variables for the year 2050 from the WorldClim database from the HadGEM-AO model under emissions scenario RCP 8.5 which is a “worst case” scenario that predicts increasing greenhouse gas emissions and a likely global mean temperature increase of $1.4\text{--}2.6^\circ\text{C}$ between 2046 and 2065 (Riahi et al., 2007).

2.4. Environmental niche modelling procedure

Models were run using default settings in Maxent version 3.3.3 (Phillips et al., 2006) apart from the maximum number of iterations which was set at 5000 to achieve algorithm convergence (Elith et al., 2011; Kassara et al., 2013). Ten replicate models were run each using repeated random subsampling of 75% of the presence locations to train the model with the remaining 25% used to evaluate its predictive performance (i.e. test dataset). Results are presented as the mean and

Table 1
 Mean (± SE), minimum and maximum values for environmental variables in raster cells modelled to be suitable under current and future (2050) climatic conditions using two presence location datasets from Cape vultures fitted with GPS tracking units in South Africa only ($n = 9$; Model_SA) and combined with data from Namibia ($n = 5$; Model_NamSA). Median and mode values are given for categorical variables. The mean (± SE) and range of values of the logistic probability of presence for each area of modelled suitability are also provided. The number of grid cells predicted to be suitable by each model are given in parentheses after the model name.

Variable*	Model_SA current ($n = 593,816$)			Model_SA 2050 ($n = 766,707$)			Model_NamSA current ($n = 633,576$)			Model_NamSA 2050 ($n = 650,658$)		
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
bio_1 (°C)	17.88 ± 0.0029	5.80	22.30	19.98 ± 0.0026	7.50	24.40	18.41 ± 0.0026	6.40	22.20	16.06 ± 0.0022	5.60	21.50
bio_2 (°C)	15.69 ± 0.0013	7.30	19.00	16.10 ± 0.0014	9.90	19.20	15.90 ± 0.0011	11.50	18.90	15.66 ± 0.0013	10.40	18.10
bio_3 (%/10)	5.38 ± 0.0004	4.40	6.40	5.44 ± 0.0003	4.60	6.30	5.48 ± 0.0005	4.40	7.30	5.32 ± 0.0004	4.40	7.30
bio_6 (°C)	1.61 ± 0.0025	-5.90	6.90	3.48 ± 0.0019	-3.00	9.80	2.21 ± 0.0027	-5.90	9.90	0.03 ± 0.0020	-5.90	9.80
bio_12 (mm)	499.49 ± 0.2286	81	1605	495.44 ± 0.2316	77	1218	480.50 ± 0.1938	103	1489	534.90 ± 0.2408	105	1489
bio_15 (%)	72.74 ± 0.0123	35	105	73.88 ± 0.0121	34	98	78.51 ± 0.0187	29	134	66.23 ± 0.0130	20	136
bio_19 (mm)	21.58 ± 0.0199	2	326	24.09 ± 0.0172	3	333	17.47 ± 0.0163	0	235	29.12 ± 0.0157	0	233
Alt (m asl)	1222.61 ± 0.3567	517	3084	1346.14 ± 0.3225	596	3308	1248.70 ± 0.3199	519	2946	1420.00 ± 0.3349	389	3143
ndvi_aug (NDVI*1000)	103.91 ± 0.0189	10	245	100.67 ± 0.0169	10	255	101.56 ± 0.0157	10	185	101.06 ± 0.0165	10	223
slope_perc (%)	2.23 ± 0.0049	0	52.01	2.38 ± 0.0042	0	52.01	1.75 ± 0.0039	0	52.55	2.59 ± 0.0047	0	52.55
FAOcattle05 (cattle·km ⁻¹)	10.53 ± 0.0152	0	121.94	11.74 ± 0.0165	0	468.60	9.34 ± 0.0141	0	468.60	13.31 ± 0.0234	0	468.60
Probability of presence	0.48 ± 0.0001	0.31	0.89	0.55 ± 0.0002	0.31	0.93	0.46 ± 0.0001	0.31	0.88	0.59 ± 0.0002	0.31	0.97
Categorical variables	Median (Mode)			Median (Mode)			Median (Mode)			Median (Mode)		
rum_prod_system	2 (2)			4 (2)			2 (2)			4 (2)		
GLC2000	14 (14)			14 (14)			14 (14)			14 (14)		
WWF_ecoregion_ID	31009 (31309)			31009 (31009)			31009 (31309)			31009 (31009)		

*bio_1 = annual mean temperature; bio_2 = mean diurnal temperature range; bio_3 = isothermality (% / 10); bio_6 = minimum temperature of the coldest week; bio_12 = annual precipitation; bio_15 = precipitation seasonality (% - coefficient of variation); bio_19 = precipitation of the coldest quarter; Alt = elevation above sea level; ndvi_aug = NDVI in August (NDVI*1000); slope_perc = slope percent rise; FAOcattle05 = FAO cattle density; rum_prod_sys = FAO ruminant production systems (2 = Livestock-only systems in arid areas; 4 = Livestock-only systems in temperate areas or tropical highlands); GLC2000 = Global Land Cover from the year 2000 (14 = Open grassland with sparse shrubs); WWF_ecoregion_ID = WWF ecoregion (31,009 = Highveld grasslands; 31,309 = Kalahari xeric savannah). Refer to 'Environmental Data' in Appendices.

standard deviations of the ten replicate models. The area under the curve (AUC) of the receiver operating characteristic (ROC) and regularized training gain were used to evaluate model performance (Elith and Graham, 2009; Elith et al., 2011; Gormley et al., 2011). Variable importance was assessed using two heuristic tests (percent contribution and permutation importance) and the jackknife procedure in Maxent (Phillips et al., 2006; Elith et al., 2011; Gschweng et al., 2012). Further explanation is provided in the “Environmental niche modelling” section of the Appendices.

2.5. Assessment of environmental suitability and impact of climate change

The logistic output from the Maxent model was used to display the spatial predictions of the probability of Cape vulture presence across the study area with values ranging from 0 to 1 (Phillips and Dudik, 2008). To classify the model predictions into areas of binary suitability (1) and unsuitability (0) the mean (0.31) of the maximum training sensitivity plus specificity logistic threshold (*MaxTSS*) for the model with only South African tagged vulture presences (*MaxTSS* = 0.28) and the model with both presence datasets (*MaxTSS* = 0.33) was used. The *MaxTSS* threshold is independent of prevalence of presence locations and is recommended for use with presence only data as an objective method of binary suitability threshold selection (Jiguet et al., 2011; Liu et al., 2013). Binary maps of suitability were created using this method for both current and future (for the year 2050) climatic conditions for the two different presence datasets on which the models were based (i.e. *Model_SA* = presence locations from South African tagged vultures; *Model_NamSA* = presence locations from both South African and Namibian tagged vultures). Subsequently the areas predicted to be unsuitable and suitable were compared for each model separately under the current and future environmental conditions (Fig. 2). This was done in ArcMap to produce a raster dataset with areas predicted to be unsuitable in both current and future conditions; suitable under current but not future environmental conditions (range contraction); unsuitable under current conditions but suitable under future conditions (range expansion); and suitable under both current and future conditions (stable range). The distance between the mean centres of the extent of the suitable areas under current and future conditions was calculated in

ArcMap to quantify the directional range shift from current to future conditions.

2.6. Evaluation of protected area coverage

To assess the level of protection afforded to areas predicted as suitable for Cape vultures based on the binary suitability maps, the number of suitable raster cells located within nationally and internationally designated protected areas in the 2015 World Database on Protected Areas (IUCN and UNEP-WCMC 2015) were counted for current and future models in ArcMap (Swanepoel et al., 2013; Liminana et al., 2014).

3. Results

3.1. Environmental niche model description and variable importance

The model constructed with the presence locations only from the South African tagged birds (*Model_SA*) and the model constructed with presence locations from South African and Namibian tagged birds (*Model_NamSA*) showed good predictive power based on mean AUC values of the 10 replicate runs (*Model_SA* AUC = 0.886 ± 0.009 ; *Model_NamSA* AUC = 0.868 ± 0.006). The regularized training gain was lower for *Model_NamSA* (0.906 ± 0.009) compared to *Model_SA* (1.084 ± 0.009).

Model_SA classed 15.08% of the study area ($460,801 \text{ km}^2$) as suitable for Cape vultures under current environmental conditions, while *Model_NamSA* classed 16.09% ($491,655 \text{ km}^2$) of the area as suitable. Both models delineated an almost continuous area of suitability associated with the distribution of the bushveld savannah and dry Highveld grassland bioregions (Fig. 2; Fig. A1), extending into the upper Karoo in the south-west and the uKhahlamba-Drakensberg mountains in the south-east (Rutherford et al., 2006). An extensive area of central-east South Africa characterised by mesic Highveld grassland and cropland was modelled to be unsuitable under current conditions, dividing suitable areas in the north and south (Fig. 2). *Model_NamSA* also predicted environmental suitability in an isolated area in north-central Namibia extending up to 300 km south and east of

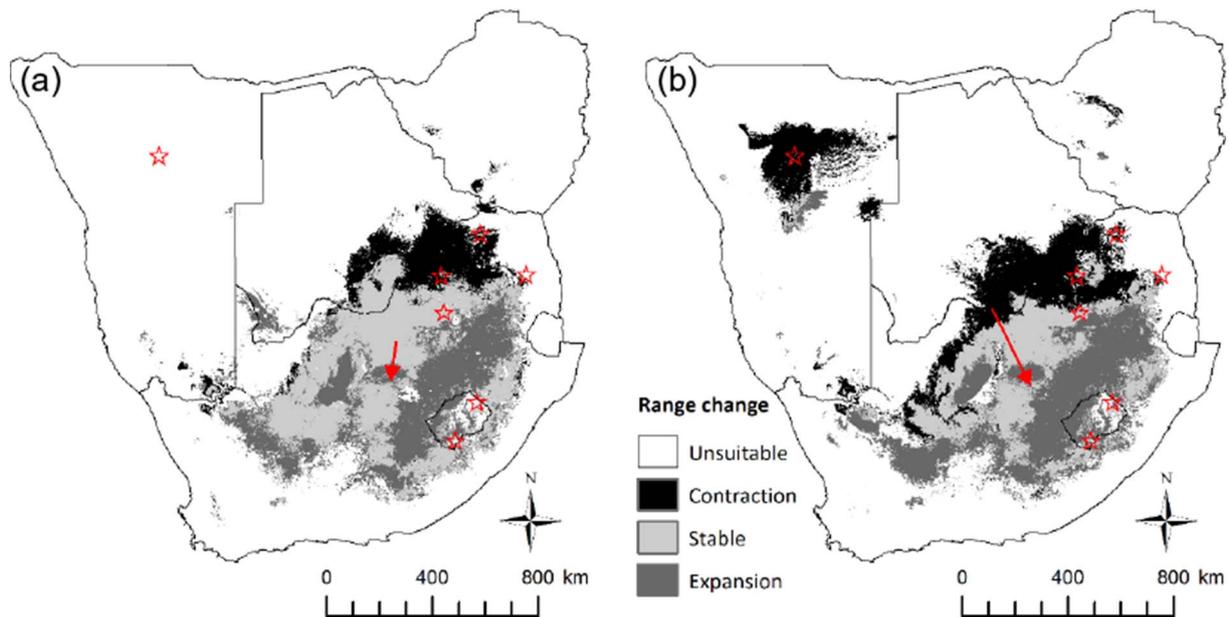


Fig. 2. Areas predicted by Maxent models to be unsuitable in both current and future (2050) climatic conditions (unsuitable); suitable in both (stable); suitable in current but not future conditions (range contraction); and suitable in future but not current conditions (range expansion) for (a) *Model_SA* which was modelled with presence locations from South African tagged vultures only and (b) *Model_NamSA* which was modelled with all presence locations. The red arrows show to scale the projected movement of the mean centre of the suitable area under current conditions to the mean centre under future conditions. Red stars indicate some of the main Cape vulture colonies. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the former breeding colony in the Waterberg Mountains (Fig. 2b).

Bioclimatic variables were the most influential to model predictions according to the heuristic tests of variable importance (Fig. A2). Precipitation seasonality (*Bio_15*) contributed $29.88 \pm 2.14\%$ ($35.98 \pm 2.72\%$ permutation importance) to Model_SA and five bioclimatic variables (*Bio_2*, 12, 6, 3 and 1 in descending order) collectively contributed 73.70% to Model_NamSA (Fig. A2). The four variables that contributed the most to Model_SA (*Bio_15*, 6, 12 and 19 in descending order) collectively contributed 70.44% to the model. Elevation (*alt*) was also a relatively important variable with a permutation importance of 20.99% for Model_NamSA and 10.08% for Model_SA. The jackknife tests identified precipitation seasonality as the most important variable for both models, followed by precipitation of the coldest quarter (July–September; *Bio_19*), minimum temperature of the coldest week (*Bio_6*) and WWF ecoregion ID for Model_SA (Fig. A2). WWF ecoregion ID was also identified as an important variable for Model_NamSA, followed by elevation, minimum temperature of the coldest week and NDVI in August (Fig. A2).

The average environmental variable values for raster cells predicted to be suitable for Cape vultures were similar for Model_SA and Model_NamSA (Table 1). The elevational range of cells predicted to be suitable for Cape vulture occurrence under current conditions was 517–3084 m-asl, with a mean elevation of 1223 m-asl for Model_SA and 1249 m-asl for Model_NamSA. For all models, cells predicted to be suitable for Cape vulture occurrence tended to consist, on average (median and mode), of “livestock-only ruminant production systems in arid areas” with mean (\pm SE) cattle densities from 9.34 ± 0.014 cattle-km⁻¹ (Model_NamSA current) to 13.31 ± 0.023 cattle-km⁻¹ (Model_NamSA 2050), in areas of “open grassland with sparse shrubs” land-cover in the Highveld grasslands or Kalahari xeric savannah ecoregions (Table 1).

3.2. Projected extent of future environmental suitability

Of the 460,801 km² predicted by Model_SA to be suitable for Cape vultures under current conditions, 28% was predicted to become unsuitable in 2050 with a pole-ward shift of 151 km of the mean centre of the suitable area (Fig. 2a). However, under future conditions the overall suitable area was predicted to increase from 15% to 19% (594,965 km²) of the study area, of which 44% (264,070 km²) extended into areas predicted to be unsuitable in current conditions (Fig. 2a). For Model_NamSA a greater degree of current suitable range loss was predicted, with 55% of the 491,655 km² current suitable range predicted to become unsuitable in 2050, with a pole-ward shift of 333 km of the mean centre of the suitable area (Fig. 2b). Of the area predicted to be suitable in 2050 (503,911 km²), 56% (284,669 km²) was classed as unsuitable in current conditions, resulting in a relatively small (2.70%) increase in suitable area compared to current conditions (491,655 km²; Fig. 2b) Both models predicted that the largest area of range contraction would be in northern South Africa and south-east Botswana (Fig. 2). Almost the whole area in north-central Namibia modelled to be suitable under current conditions by Model_NamSA was predicted to become unsuitable under climatic conditions in 2050 (Fig. 2b; Fig. A1). The mean elevation for areas modelled as suitable increased by 123 m and 171 m for Model_SA and Model_NamSA, respectively (Table 1).

3.3. Protected area coverage under current and projected suitability

Of the area predicted by Model_SA to be suitable for Cape vultures, 5.85% (26,961 km²) and 3.79% (22,560 km²) was covered by protected areas under current and future conditions, respectively. The protected areas covering > 1000 km² of suitable area under current conditions were the Waterberg Biosphere Reserve (BR) in Limpopo Province, South Africa, the Drakensberg World Heritage Site (WHS), and the Central Kalahari Game Reserve (GR) in south-east Botswana. Under

future conditions only the Kalahari-Gemsbok National Park (NP) and the Drakensberg WHS covered > 1000 km². For Model_NamSA, 7.91% (38,874 km²) and 2.77% (13,963 km²) of the modelled suitable area was covered by protected areas under current and future conditions, respectively. Several conservancies in north-central Namibia, the Waterberg BR, and the Central Kalahari GR covered > 1000 km² of suitable area under current conditions, while only the Drakensberg WHS and the Waterberg BR covered > 1000 km² of suitable area under future conditions.

4. Discussion

This study provides a first description of the environmental characteristics of the spatial niche occupied by the Cape vulture using a presence-only ENM method based on GPS tracking locations from vultures caught from the wild in north-central Namibia and north-central South Africa. As with previous ENM studies on raptor species the most important variables determining the limits of predicted suitability were bioclimatic variables, with precipitation seasonality (i.e. variation in monthly precipitation totals across the course of the year (Table A1)) consistently identified as one of the most influential variables (Gschweng et al., 2012; Liminana et al., 2012). The areas predicted to be suitable for Cape vultures by both models broadly corresponded with the known current and historical distribution of the species, with a core range in the dry Highveld and bushveld of South Africa and a secondary region of suitability in the more mountainous south-east of the country, mainly along the Maloti-Drakensberg escarpment (Mundy et al., 1992; BirdLife International, 2016). The area of suitability also extended beyond the current western boundary of the recognised species distribution range, which has been linked to the relatively recent construction of power lines in an area otherwise devoid of suitable roost sites (Phipps et al., 2013b).

A first estimate of the potential impact of climate change on the distribution of suitable areas for Cape vultures predicted a pole-ward shift in suitable conditions away from their core breeding and foraging range in northern South Africa, which conforms with projected patterns of bird species' responses to climate change in the region (Simmons et al., 2004; Hole et al., 2009). The model that included the presence locations from the vultures tagged in Namibia predicted that the majority of an isolated area of suitable conditions around the former breeding colony in the Waterberg region would become unsuitable under future (2050) climatic conditions. Coverage by protected areas of the currently suitable area for Cape vultures was small (5.85–7.91%) compared to their coverage more widely across southern Africa (circa 23% of total land area, excluding Mozambique (IUCN and UNEP-WCMC 2015)), and was predicted to decrease to < 4% under future conditions.

4.1. Influence of environmental variables on predicted probability of presence

Overall, bioclimatic variables, and precipitation seasonality in particular, were the most influential in both models, which is consistent with previous studies that used GPS tracking data to model the ecological niche of raptors (Gschweng et al., 2012; Liminana et al., 2012). Vegetation production is dependent on climatic conditions and precipitation patterns in determining forage abundance and quality, and subsequently nutrition-related mortality rates for ungulates (Boone et al., 2006; Ogutu et al., 2008; Chamaille-Jammes and Fritz, 2009). Vulture movement patterns have been shown to be closely associated with seasonal ungulate mortality rates driven by seasonal changes in vegetation productivity indicated by changes in NDVI, with tracked vultures preferring to forage in areas with higher ungulate mortality during the dry season in the Masai Mara, Kenya (Kendall et al., 2014). NDVI in August was identified as the most important variable in the preliminary model which included only the twelve monthly NDVI

variables, as well as for both models including all variables. August is one of the coldest and driest months in southern Africa and mortality of both wild and domestic ungulates can be relatively high during that due to nutritional stress (Owen-Smith et al., 2005; Mapiye et al., 2009). It is likely, therefore, that the models reflect the influence of seasonal vegetation production on ungulate carrion availability, a main driver of vulture occurrence (Kendall et al., 2014). Correspondingly, the probability of Cape vulture presence was highest in areas characterised by relatively cold, dry winters, which would result in seasonal periods of low grass productivity and potentially higher ungulate mortality rates (Owen-Smith, 2008). Together with the availability of cliff nesting sites, this partially explains why the core breeding and foraging ranges are located in the northern provinces of South Africa which are characterised by distinct wet summer (October–April) and dry winter (May–September) seasons (Benson et al., 1990; Mundy et al., 1992; Borello and Borello, 2002), as Cape vultures, like other *Gyps* species, time their breeding seasons with the highest availability of ungulate carrion in the dry season (Houston, 1974b; Piper et al., 1999; Virani et al., 2010; Virani et al., 2012). This is consistent with previous studies that found an inverse relationship between vulture breeding success and rainfall in the previous year mediated through reduced ungulate carrion availability (Bridgeford and Bridgeford, 2003; Virani et al., 2012).

As large soaring fliers, Cape vultures are reliant on suitable climatic conditions, strong air currents and thermals to cover large distances to locate their naturally ephemeral food source; and high rainfall and adverse weather conditions limit their ability to do so (Pennycuik, 1972; Lambertucci and Ruggiero, 2013; Harel et al., 2016). The influence of local climatic factors such as temperature range and precipitation in determining the occurrence of large soaring birds has been shown for the Andean condor (*Vultur gryphus*), which should, according to a modelling study, prefer roost sites on climatically stable cliffs in areas of low rainfall (Lambertucci and Ruggiero, 2013). The importance of isothermality (a measure of diurnal and annual temperature ranges) in both models (Bio_3; Fig. A3f) and the higher probabilities of occurrence in areas with moderate seasonal rainfall, are consistent with this and possibly reflect the influence of meteorological variables on the local flying conditions for Cape vultures (Shepard and Lambertucci, 2013; Harel et al., 2016).

African vultures locate carcasses by sight alone (Houston, 1974a) and it has been shown that high tree densities reduce their ability to locate and land at carcasses, decreasing their foraging efficiency (Schultz, 2007; Bamford et al., 2009). Higher probabilities of Cape vulture presence were predicted in habitats characterised by relatively low tree density and more open habitats (e.g. Highveld grassland and southern African bushveld; Table 1 (Olson et al., 2001)). These results correspond with previous descriptions of suitable Cape vulture habitat (Mundy et al., 1992) and support suggestions that they avoid heavily wooded areas and might be susceptible to the increasing rate and extent of bush encroachment in southern Africa (Schultz, 2007; Bamford et al., 2009).

Although variables related to land use and farming practices were not identified as particularly important variables for either model, relatively high probabilities of presence were predicted in livestock-only systems compared to more arable-dominated landscapes (Fig. A4b). Average cattle densities of approximately 10–20 cattle km⁻² were favoured and predicted presence declined thereafter (Fig. A4c). This supports suggestions that ungulate mortality rather than abundance is a main driver of vulture presence (Kendall et al., 2014), particularly as more intensive farming systems remove carcasses more frequently, reducing food availability for vultures (Murn and Anderson, 2008; Margalida et al., 2014). These patterns are also consistent with observations that Cape vultures often utilise commercial farmland in addition to more extensive systems to exploit all sources of available carrion, including domestic livestock, as well as wild ungulates (Benson et al., 2004; Murn and Anderson, 2008; Phipps et al., 2013b; Pfeiffer

et al. 2015). Consequently, food availability is likely to remain the primary factor in determining vulture occurrence patterns, and it is possible that growing numbers of supplementary feeding sites in southern Africa will influence vulture movement patterns (Phipps et al., 2013a) and assist them to adapt to fluctuating ungulate mortality patterns caused by the changing climate (Cortés-Avizanda et al., 2016).

4.2. Projected influence of climate change

The pole-ward shifts and increase in mean elevation of areas modelled as suitable for Cape vultures in 2050 correspond with previous studies that have predicted similar responses to changing climatic conditions in bird species in southern Africa (Simmons et al., 2004; Hole et al., 2009; Willis et al., 2009; BirdLife International and Durham University 2015). Although the model that used presence locations from Namibian vultures predicted an area of suitability in the north-central region of the country (Fig. 2b and A1c), the model that only used presence locations from South African vultures predicted a very low probability of presence in the same area (Fig. 2a and A1a). This indicates that bioclimatic conditions are very different in north-central Namibia compared to the majority of the modelled suitable area in South Africa and Botswana (Williams et al., 2007). Under future conditions the area modelled to be suitable in north-central Namibia was predicted to contract 170 km south from its current location around the former breeding cliffs of the Waterberg Plateau (Fig. 2b). This is consistent with previous studies that predict that northern Namibia is likely to be particularly vulnerable to the effects of climate change as current climatic conditions shift pole-wards or even disappear, causing high rates of range loss for a high number of species from different taxa (Thuiller et al., 2006a; Thuiller et al., 2006b; Williams et al., 2007; Garcia et al., 2012). Significant range loss was also predicted by both models in the current core breeding range of Cape vultures in northern South Africa and south-east Botswana (Fig. 2), areas which are predicted to undergo high levels of bird and mammal species turnover and range loss driven by climate change (Thuiller et al., 2006a; Hole et al., 2009). These modelled patterns of range contraction support the suggestion that the northernmost Cape vulture breeding colonies could be at risk of becoming climatically unsuitable for the species, and that climate change might have already played a role in the extinction of the only breeding colony in northern Namibia (Simmons and Jenkins, 2007). Correspondingly, recent surveys indicate that while several peripheral, northern colonies have been abandoned, the core breeding population in the Magaliesberg mountains remains stable (Wolter et al., 2016). An increase in supplementary carrion at vulture feeding sites in that area might have led to higher local survival rates and recruitment from more peripheral colonies (Wolter et al., 2016), potentially mitigating any adverse impacts of climate change. The influence and interaction of these factors requires further investigation, however.

In contrast to the loss of suitable areas in the north of the modelled range, an increase in overall extent of suitable area was predicted by both models, largely due to a southwards range expansion into mesic Highveld grasslands and croplands in central-east South Africa (Fig. 2). This region is considered to be outside the historical distribution of the Cape vulture due to the relatively long distances from major breeding colonies; a prevalence of unsuitable habitat transformed by intensive agriculture; and the decline of wild ungulate populations (Mundy et al., 1992; Mucina et al., 2003; Boshoff and Kerley, 2015). Therefore, although large-bodied species that exhibit evidence of nomadic-like movements, such as *Gyps* vultures (Phipps et al., 2013a; Phipps et al., 2013b), are expected to be more capable of dispersing in response to climate change (Simmons et al., 2004; Dodge et al., 2014), any predicted range expansions should be considered with caution, particularly as factors such as dispersal capability and land use change were not accounted for (Guisan and Thuiller, 2005). Even so, fluctuating carrion availability regularly forces vultures to shift their movement

patterns (Kendall et al., 2014), and they even forage beyond their historical distribution by perching on newly constructed pylons in areas previously devoid of natural perches (Phipps et al., 2013b), indicating that they might show a degree of plasticity in their movement patterns in response to future climate change (Simmons et al., 2004; Dodge et al., 2014).

4.3. The current and future role of protected areas

Protected areas cover 9% of South Africa's land surface, with the largest reserves concentrated in the east and a network of small, isolated protected areas across the majority of the country (Fig. 1 (IUCN and UNEP-WCMC 2015)). This pattern is reflected in the limited coverage by protected areas (< 8%) of the modelled suitable Cape vulture range under current climatic conditions. This provides further evidence that vultures in southern Africa are likely to spend a significant amount of time foraging beyond the boundaries of protected areas, exposing them to multiple threats across the region (Herremans and Herremans-Tonnoeyr, 2000; Murn and Anderson, 2008; Phipps et al., 2013b).

Under future climate conditions the models predicted a decrease in the suitable area covered by protected areas to < 4% for both models. The largest losses of protected area coverage were predicted in the core breeding range of the Cape vulture in the North West and Limpopo Provinces of South Africa (e.g. the Waterberg Biosphere Reserve), and in northern Namibia (Fig. 2). In contrast, protected areas in the south of the range, such as the Maloti-Drakensberg mountain reserves, were predicted to retain or even gain areas predicted to be suitable in the future. Two of the largest remaining Cape vulture colonies are located within protected areas adjacent to or part of the Waterberg Biosphere Reserve (Kransberg in Marakale National Park, and Blouberg in Polokwane Nature Reserve (Mundy et al., 1992; BirdLife International, 2016)) and were predicted to become unsuitable in the future by both models (Fig. 2). Although breeding season monitoring indicates that the populations of both colonies are currently stable (Benson, 2015; Wolter et al., 2016), the predictions from this study that Cape vulture colonies in the north of the range are potentially at greater risk from the effects of climate change than those in the south, and that the Maloti-Drakensberg mountains could play an increasingly important role for breeding vultures in the future, support previous concerns and calls for additional research (Simmons and Jenkins, 2007).

4.4. Conservation implications and limitations

The modelling methods used in this study can only provide an approximation of the potential effects of climate change on the distribution of environmentally suitable conditions for Cape vultures and cannot provide definitive information about the underlying mechanisms driving those effects (Thuiller et al., 2008; Elith et al., 2011). Neither can they predict exactly how vultures will respond to climate change in real circumstances (Porfirio et al., 2014). Moreover, the future climate data used in this study (a “worst case” scenario) are derived from modelling methods that vary in accuracy regionally, with some variables performing better than others (Braconnot et al., 2012; Waltari et al., 2014), particularly in southern Africa where high levels of seasonal variance are expected (Winsemius et al., 2014). Even so the findings from this study provide the first evidence to support suggestions that the northern bounds of the Cape vulture range are potentially vulnerable to the effects of climate change (Simmons and Jenkins, 2007). Given that higher temperatures and longer sunlight exposures have been shown to cause higher heat-stress on nesting Cape vultures (Chaudhry, 2007) and cliff-nesting seabirds (Oswald and Arnold, 2012), and rainfall patterns influence breeding success in other African vultures (Bridgeford and Bridgeford, 2003; Virani et al., 2012), it is possible that warming temperatures and changing precipitation patterns (IPCC, 2014) have already affected the breeding distribution of

Cape vultures by contributing to the extinction of the Waterberg Plateau breeding colony in north-central Namibia (Simmons and Jenkins, 2007; Krueger et al., 2015). Further evidence is provided by a recent study which showed that Cape vulture nest site occupancy increased with elevation and breeding success was higher at more sheltered nest sites, with climatic conditions suggested as a possible driver (Pfeiffer et al., 2017). It is unlikely, however, that climate change is solely responsible for the observed declines in Cape vultures in Namibia or elsewhere across their range, and the severe impacts of widespread poisoning (Ogada et al., 2012; Ogada, 2014; Santangeli et al., 2016), fatal interactions with power lines (Boshoff et al., 2011), habitat degradation (Bamford et al., 2009), food shortages (Krueger et al., 2015) and other factors, are widely recognised. Our findings do, however, provide a first indication that climate change might pose an additional direct threat to vultures and indirectly through climate-driven changes in vegetation (Thuiller et al., 2006; Chamaille-Jammes and Fritz, 2009) and mammal distributions (Thuiller et al., 2006a) reducing the availability of carrion and suitable foraging habitat.

It remains unknown exactly how Cape vultures will respond to future climate change in real terms and further related research is required (Simmons and Jenkins, 2007; Krueger et al., 2015), particularly as this study involves a relatively small sample of individuals. However, if southern areas such as the Maloti-Drakensberg mountains do become more important for Cape vultures in the future, then additional conservation measures to prevent or mitigate the impacts of proposed wind farms (Rushworth and Kruger, 2014), power lines (Boshoff et al., 2011) and ongoing poisonings (Krueger et al., 2015) will be essential in these areas. In addition, the limited coverage by protected areas illustrates that it will be essential to direct vulture conservation measures to private lands, as acknowledged for other carnivore species (Lindsey et al., 2004; St John et al., 2012; Swanepoel et al., 2013). From a global perspective, the findings from this study provide a first indication that changing climatic conditions should be considered when planning to mitigate worldwide vulture population declines.

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Appendix B. Supplementary data

Supplementary data associated with this article can be found in the online version at doi: <http://dx.doi.org/10.1016/j.biocon.2017.03.028>. These data include the Google map of the most important areas described in this article.

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