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RESEARCH ARTICLE

Anthropogenic activities influence the abandonment of Bearded Vulture (*Gypaetus barbatus*) territories in southern Africa

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ABSTRACT

Developing an effective conservation strategy for a critically endangered species relies on identifying the most pressing threats to the species. One approach to elucidate these threats for a long-lived animal with high territorial fidelity is to identify factors associated with territorial abandonment. The Bearded Vulture (*Gypaetus barbatus*) has declined dramatically in southern Africa over the past few decades, with nearly 50% of known territories being abandoned. In this study we examine the evidence for 3 hypotheses: that territorial abandonment was associated with (1) human impact, (2) food availability, or (3) climate change, or a combination of these. Model selection was used to determine the relative importance of 7 covariates within the home range of an adult pair, an area of 10 km radius (314 km^2) around each nest. Our analyses provided strongest support for the human impact hypothesis, with abandonment more likely in territories with more power lines and higher densities of human settlements. Additionally, within Lesotho, southern Africa, there was some support for the food shortage hypothesis, with territories more likely to have remained occupied where they had a greater number of feeding sites within close proximity. Our data provided no support for the hypothesis that climate change may be driving abandonment through a direct impact of elevation or nest site aspect. Our results are in accordance with the main causes of mortality: poisoning and power line collisions. We suggest that conservation measures should focus on limiting the development of further human settlements and power lines within 10 km of occupied territories, applying mitigation measures to existing power lines and increasing law enforcement and education in areas still occupied by the species.

Keywords: human impact, food availability, climate change, population decline, conservation, poisoning, power line collisions

Las actividades antropogénicas influyen en el abandono de territorios de *Gypaetus barbatus* en el sur de África

RESUMEN

El desarrollo de estrategias de conservación efectivas para una especie en peligro crítico de extinción se basa en la identificación de las amenazas más urgentes para la especie. Una aproximación para elucidar tales amenazas en un animal de larga vida con alta fidelidad al territorio es identificar los factores asociados con el abandono de su territorio. Las poblaciones de *Gypaetus barbatus* han disminuido dramáticamente en el sur de África en las décadas pasadas y cerca del 50% de los territorios conocidos han sido abandonados. En este estudio examinamos la evidencia a favor de tres hipótesis que establecen que el abandono del territorio se asocia con (1) impacto humano, (2) disponibilidad de alimento o (3) cambio climático, o con una combinación de estos factores. Usamos selección de modelos para determinar la importancia relativa de siete co-variables dentro del ámbito de hogar de una pareja de adultos, un área de 10 km de radio (314 km^2) alrededor de cada nido. Nuestros análisis proveen fuerte sustento para la hipótesis del impacto humano: el abandono fue más probable en territorios con más líneas eléctricas y mayor densidad de asentamientos humanos. Además, en Lesoto hubo algo de sustento para la hipótesis de escasez de alimento: los territorios presentaron mayor probabilidad de permanecer ocupados cuando tenían un gran número de sitios de alimentación en sus proximidades. Nuestros datos no proveen sustento para la hipótesis de que el cambio climático podría estar causando el abandono a través de un impacto directo de la elevación o el aspecto de los sitios de anidación. Nuestros resultados concuerdan con las principales causas de mortalidad: el envenenamiento y la colisión con líneas de energía. Sugerimos que las medidas de conservación se deberían enfocar en limitar el desarrollo de más asentamientos humanos y líneas de energía en un radio de 10 km alrededor de los territorios ocupados, aplicando medidas mitigantes para las líneas eléctricas existentes e incrementando el cumplimiento de la ley y la educación en las áreas que aún son ocupadas por esta especie.

Palabras clave: cambio climático, colisiones con líneas de energía, conservación, declive poblacional, disponibilidad de alimento, envenenamiento, impacto humano

FIGURE 1. Bearded Vulture (*Gypaetus barbatus*). Photo by S. C. Krúger

INTRODUCTION

Unprecedented numbers of animal and plant species face extinction as a result of anthropogenic actions, climate change, and/or invasive alien species (DeSalle and Amato 2004, Heller and Zavaleta 2009). Anthropogenic actions have been responsible for the loss of habitat and the decline in individual populations of many species in the past few decades (Butchart et al. 2010, Convention on Biological Diversity 2010), and global climate change is predicted to cause species extinctions and distributional shifts in the next few decades (Midgley et al. 2001, Erasmus et al. 2002, Thomas et al. 2004).

The scavenger guild is threatened around the globe (Hoffmann et al. 2010), with avian scavengers having the highest percentage of threatened species of any avian functional group (Sekercioglu et al. 2004). Vultures in particular have experienced large population declines worldwide as a result of loss of suitable breeding and foraging habitat and poisoning (Green et al. 2004, Oaks et al. 2004, Ogada et al. 2012). The Bearded Vulture (*Gypaetus barbatus*; Figure 1) is also showing declines throughout much of its range (Mingozzi and Estève 1997, Margalida et al. 2008, Birdlife International 2012). Within southern Africa, where the breeding population has declined in both numbers (32–51%) and range (27%) over the past 5 decades (Krüger et al. 2014), the species was recently up-listed to Critically Endangered (Krüger in press). The southern African population is restricted to the Maloti-Drakensberg mountains of South Africa and Lesotho, Africa (Brown 1997, Krüger et al. 2014), where pairs occupy a territory containing one or more nests on high cliffs generally >1,800 m a.s.l. (Brown 1988, Heredia 1991).

There is an urgent need to identify the factors responsible for the decline of this population. To address this issue, we used Caughley's (1994) declining population paradigm, postulating a series of plausible hypotheses and then testing which factors associated with these hypotheses were most closely linked to the abandonment of breeding territories. Similar approaches have been successful in elucidating important factors constraining other bird populations (e.g., Buchanan et al. 2003, Lewis et al. 2007, Amar et al. 2011). In this study we explore the evidence for the following 3 a priori hypotheses: (1) territorial abandonment has been caused by anthropogenic activity, with abandonment occurring in areas with greater exposure to human impact; (2) territorial abandonment is the result of food shortages, with territories being abandoned in areas with insufficient food; and (3) territorial abandonment is being driven by climate change with abandonment occurring at nest locations most affected by climate change.

The theoretical basis for hypothesis 1 has considerable support. Global vulture declines and declines in Bearded Vulture populations have largely been attributed to human impacts, namely human persecution for traditional medicine, food, ceremonies, and other purposes (Maphisa 1997, Xirouchakis et al. 2001, Mander et al. 2007, Thiollay 2007); indirect poisoning through poison baiting of carnivores (Brown 1991) and use of veterinary drugs (Green et al. 2004, Oaks et al. 2004); collisions with power lines (Krüger et al. 2006); or a combination of these factors (Margalida et al. 2008, Ogada et al. 2012).

The historical declines of the southern African Bearded Vulture population have also been attributed to anthropogenic factors (Siegfried et al. 1976, Brown 1991, Mundy et al. 1992), but the mechanisms for the more recent declines are not well understood. The past few decades have seen a large increase in the human population and associated developments, such as energy infrastructure, within the region (Kalipeni 1994, Energy Sector Policy of the AfDB group 2012), which may be driving the abandonment of territories through the continued exposure of the Bearded Vulture population to unnatural mortality factors. To explore this first hypothesis, we examined whether abandonment was associated with 3 factors: (i) density of human settlements within territories because we predicted that persecution levels might be highest in areas within relatively close proximity to human settlements; (ii) abundance of power lines because of their documented impact on other vulture and large raptor populations through collisions and electrocutions (Lehman et al. 2007, Smallie and Virani 2010, Boshoff et al. 2011); and (iii) the amount of area within a territory that is under formal protection because we expected that territories in protected areas would be insulated and shielded to a greater degree from all anthropogenic threats.

The alternative hypothesis 2 for abandonment, decreased food availability caused by habitat loss and change in land use, has been previously considered as a potential mechanism for the wider historical decline of the species in southern Africa (Siegfried et al. 1976, Mundy et al. 1992), although Brown (1991) did not believe it to be an important driving factor for the local declines witnessed more recently. Food availability is known to affect nest site selection and breeding success of Bearded Vulture populations in Europe (Donázar et al. 1993, Gavashelishivili and McGrady 2006, Margalida et al. 2007). The Bearded Vulture is an obligate scavenger requiring carrion of primarily medium-sized ungulates (Hiraldo et al. 1979, Brown 1997). Livestock graze throughout the species' foraging range and are scavenged from communal grazing lands in Lesotho or commercial livestock farms in South Africa, whereas wild ungulates are scavenged predominantly from protected areas. Related to our food shortage hypothesis, we also investigated whether the presence of more predictable food resources, in the form of supplementary feeding sites, influences territory occupancy because many other vulture populations have been found to be heavily reliant on supplementary feeding (Piper 2005, Deygout et al. 2009, Cortés-Avizanda et al. 2010, Phipps et al. 2013). Although livestock and wild ungulate density is an indirect measure of food availability, we used this as a surrogate for the availability of carrion and predicted that if food supply influences territorial occupancy then it would be positively related to the number of ungulates and the presence of supplementary feeding sites in the landscape.

Hypothesis 3 relates to climate change because Bearded Vultures live in cold, high-elevation climates in a continent that is rapidly warming. The Bearded Vulture is considered particularly vulnerable to the impacts of climate change because it is a long-lived, territorial species and occurs at a low density with low reproductive rates within a restricted distribution range (Simmons et al. 2004). Africa is predicted to be the continent where changes in climate will be most extreme (Hulme 1996, Kruger and Sekele 2012, IPCC 2014), and Lesotho in particular is showing rapid warming (Mokotjomela et al. 2010). Although climate change will occur across a broad landscape scale, not all territories would be equally exposed to negative effects. Because the species is limited to higher elevations, it is vulnerable because it lacks escape options (Thomas et al. 2004), and Colahan and Esterhuizen (1997) and Simmons and Jenkins (2007) noted that many Bearded and Cape Vulture (*Gyps coprotheres*) nest sites in the lower elevation regions were abandoned, whereas higher elevation sites were still occupied. These changes have occurred since the 1950s, and increased temperatures have been tracked in that interval (IPCC 2007).

Nests are built in potholes/small caves or on ledges with overhangs (Hiraldo et al. 1979), and nest entrances generally face cooler aspects (e.g., south in southern Africa) that offer the best shelter against sun, wind, and precipitation (Brown 1988, Gavashelishivili and McGrady 2006). Chaudhry (2007) found that individual Cape Vultures nesting on cliffs that experienced higher temperatures and longer sunlight exposures (northerly aspects) showed significantly higher heat-stress than birds on cliffs with lower temperatures and less exposure to sunlight (southerly aspects). Nest site elevation and aspect were therefore considered as surrogates for temperature to investigate whether climate change is a driver of territorial abandonment because nest sites at lower elevations and those with entrances facing north would experience the highest temperatures.

This study explored the evidence for these 3 hypotheses by examining which covariates (linked to the different hypotheses) are most closely associated with territorial abandonment and comparing these results with known causes of mortality within the study area (S. C. Krüger personal observation). Finally, we recommend conservation actions to reduce the impact of the main drivers of territorial abandonment.

METHODS

Study Area

The Bearded Vulture territories located by Krüger et al. (2014) in southern Africa during 2000–2012 ($n = 190$) formed the baseline of this study. During their 13-year survey period, Krüger et al. (2014) determined the current occupancy status of all known breeding territories occupied since the 1960s, the earliest records of nest site locations within the breeding distribution range in the Maloti-Drakensberg mountains (Brown 1992), as well as any additional territories discovered during the survey period. Krüger et al. (2014) classified 109 territories as currently occupied and 81 as abandoned at some stage during the 5 decade period (1960–2012) based on repeated visits to each territory during 2000–2012 (Figure 2).

The location of the nest site within each territory was plotted using ArcGIS v.10.0 (ESRI, Redlands, USA). Where a pair had alternative nest sites on the territorial cliff, the location of the most frequently used site was plotted (Krüger et al. 2014). Around each nest site we created a buffer with a 10 km radius (314 km^2; Figure 2). These circles were based on the average 90% kernel density home range estimates for adults (286 km^2, 9.5 km radius; Krüger et al. 2015) and aimed to encapsulate the overall home range of a territorial pair, which was supported by the circles encompassing 92% (86–96%, $n = 6$) of all GPS fixes

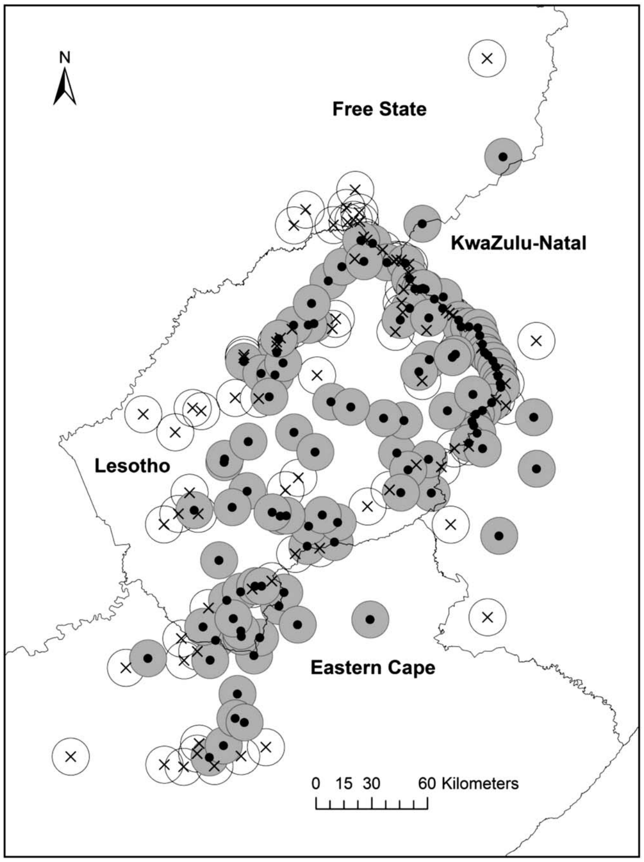

FIGURE 2. The location of breeding territories of the Bearded Vulture in southern Africa with occupied territories (•) surrounded by shaded 10 km radius buffers and abandoned (x) territories surrounded by open 10 km radius buffers.

obtained from satellite tagged adults (S. C. Krüger personal observation). Although many of these buffer circles overlapped, they are broadly representative of foraging territories because the species is known not to be exclusive, exhibiting little intraspecific competition (Brown 1990, Margalida et al. 2003). Information for our covariates relating to human impact, food availability, and climate change (detailed below) were quantified within these circles for the period 2000–2012.

Extraction of covariates within each territory

Seven covariates representing the 3 a priori hypotheses were used to describe the environment within a 10 km radius around each of 190 nest sites (Table 1). Information on environmental variables was calculated in ArcGIS and the Geospatial Modelling Environment (GME; Beyer 2012).

Three covariates were used to examine the *Human Impact* hypothesis: (i) settlements: the density of human settlements measured as the total number of buildings within each territory; (ii) power lines: the density of power lines measured as the total length (in km) of low (11 kV), medium (22 kV), and high voltage (132 kV) power lines within each territory; and (iii) protected areas: the area (km^2) under formal protection within each territory. If human impacts were influencing territorial abandonment, we predicted that territories with higher human densities, more infrastructure, and less protection, would more likely be abandoned.

Two covariates were used to examine the *Food Availability* hypothesis: (i) predictable food resource (feeding sites) and (ii) unpredictable food resource (ungulate numbers). For the predictable food resource (i), a proximity index was calculated using the sum of reciprocals of the squared distance to each feeding site within a 76 km radius of the nest. This distance was chosen based on the average maximum distance an adult would fly to a supplementary feeding site (S. C. Krüger personal observation); therefore, this method incorporates both the abundance and the availability of these food resources within each territory. We predicted that if food shortage is a driver for abandonment, then those territories with a higher proximity index (i.e. those with more feeding sites closer to the nest) would be less likely to be abandoned.

For the unpredictable food resource (ii), food availability was estimated as the total number of ungulates within each territory, calculated based on the type of land use surrounding each nest and the density of ungulates predicted to be in each habitat type. Numbers of ungulates were inferred from statistics available for livestock densities per district in Lesotho (Lehohla 2002, Dzimba and Matooane 2005) and per province in South Africa (2012 Agricultural statistics, Directorate: Statistics and Economic Analysis of the Department of Agriculture, Forestry and Fisheries) and from game count data available for wild ungulates in protected areas (Ezemvelo KwaZulu-Natal Wildlife, South African National Parks, Free State Economic Development, Tourism and Environmental Affairs). Ungulate numbers were then calculated based on the proportion of open vegetation (global land cover data 2009) and protected areas in each district/province (Ezemvelo KwaZulu-Natal Wildlife database) for livestock and wild ungulates respectively. To account for the transhumance of livestock in Lesotho, numbers in the highland regions in Lesotho were halved because livestock were only present in a given area for half the year. A positive relationship between the numbers of ungulates and availability of carcasses was assumed (i.e. more ungulates implies more carcasses available). If food shortages were important in driving territorial abandonment we predicted that territories with an overall higher number of ungulates would be less likely to be abandoned.

Two covariates were used to examine evidence that *Climate Change* may have influenced territorial abandon-

TABLE 1. Variables used to characterize the area within a 10 km radius around the nest site representing the territory of a Bearded Vulture in southern Africa.

Variable	Measure	Data Source
Human Impact		
Settlements	Total number of buildings	South Africa: Eskom 2013 Lesotho: Maloti Drakensberg Transfrontier Project 2006
Power lines	Total distance (km) of 11 kV, 22 kV, and 132 kV power lines	South Africa: Eskom 2012 Lesotho: Lesotho Electricity Corporation, 2013
Protected areas	Total area (in km^2) under formal protection	Maloti Drakensberg Transfrontier Project Database
Food Availability		
Feeding sites	Proximity index calculated based on supplementary feeding sites within a 76 km radius from the nest; $\sum(1/d^2)$, where d = the distance to the feeding site in km	Endangered Wildlife Trust and Ezemvelo KwaZulu-Natal Wildlife Vulture Restaurant Database 2013
Ungulate numbers	Total available biomass (number) of ungulates (livestock and wild ungulates)	Lehohla 2002, Dzimba and Matooane 2005, 2012 Agricultural statistics,[1] Ezemvelo KwaZulu-Natal Wildlife, South African National Parks, Free State Economic Development, Tourism and Environmental Affairs
Climate Change		
Nest aspect	Aspect (4 cardinal directions) of the nest entrance	Field survey data
Nest elevation	Elevation (m) of the nest cliff	1:50,000 topographical maps, GPS readings

[1] Directorate: Statistics and Economic Analysis of the Department of Agriculture, Forestry and Fisheries

ment: (i) aspect and (ii) elevation. Aspect (i) is the direction of the nest entrance, recorded as one of 4 cardinal directions based on field survey data. If climate change is an important factor influencing territorial abandonment, we predicted that nests facing north (i.e. with greatest exposure to the sun) would be most affected and therefore have a higher probability of being abandoned. Elevation (ii) of the nest cliff (1,500–3,000 m) was determined from field survey data or estimated from 1:50,000 topographical maps. We predicted that if climate change is influencing abandonment, then territories with nest sites at lower elevations, where temperatures would be higher, would be most likely to be abandoned. Although ideally temperature change per se would also have been considered as a covariate, detailed climate data were not available at the nest-site scale.

Statistical Analyses

We used Generalized Linear Models (GLiM; binomial error structure and a logit link function) in R v.3.0.1 (R Core Team 2013) to explore associations between the occupancy status (occupied = 1, abandoned = 0) of each territory and the 7 covariates described earlier. Occupancy status was the response variable in the model with all the covariates fitted as main effects in the model, and we looked at all possible combinations of these main effects. We ran models for all breeding territories in southern Africa and then separately for breeding territories in Lesotho ($n = 92$) and South Africa ($n = 98$).

We used model selection using Akaike's Information Criterion (AIC) and multi-model inference with the MuMIn v.1.9.13 package (Barton 2013) to determine which covariates were associated with territorial abandonment. We ranked models using their corrected AIC_c values and derived the Akaike weight of each model (w_i), estimated according to Burnham and Anderson (2002). Model suitability was assessed using AIC ranks and model weights (Whittingham et al. 2006, Lukacs et al. 2007), where the models with the lowest AIC_c value and highest weight were more important relative to others. We determined the change in AIC_c relative to the optimal model (Δ_i), classified top models to be those with $\Delta_i < 2$, and considered all models with $\Delta_i < 4$ as plausible models. We assessed the relative importance of our different covariates by summing the w_i of each model in which the variable appeared for all plausible models ($\Delta_i < 4$). We also used this model subset to generate parameter estimates and their 95% confidence limits through model averaging.

As a cross-validation of our models, we computed the Receiver Operating Characteristic (ROC) curve using the package pROC v.1.7.2 (Robin et al. 2011) to assesses the performance and summarize the overall appropriateness of the model (Nemes and Hartel 2010). The area under the curve (AUC) is a good numerical index (Hanley and

TABLE 2. Results from the 21 plausible models (those with $\Delta_i < 4$) testing for associations between territorial abandonment ($n = 135$ nests) and nest elevation, density of human settlements and power lines, percentage of protected areas, feeding site proximity, and the number of ungulates within a 10 km radius around each nest site. Models are ranked from most to least supported based on Akaike's Information Criterion (AIC_c) values. *K* is the number of parameters, Δ_i is the change in AIC_c relative to the top model, w_i is the AIC_c weight, and Dev is the deviance.

Model description	*K*	Δ_i	w_i	Dev
Power lines + Settlements	3	0.00*	0.15	158.80
Power lines + Settlements + Feeding sites	4	0.87	0.10	157.54
Power lines + Settlements + Protected areas	4	1.04	0.09	157.72
Power lines + Settlements + Ungulates	4	1.58	0.07	158.26
Power lines + Feeding sites	3	1.73	0.06	160.53
Power lines + Settlements + Elevation	4	1.74	0.06	158.41
Power lines	2	1.86	0.06	162.75
Power lines + Settlements + Elevation + Protected areas	5	2.51	0.04	157.02
Power lines + Settlements + Elevation + Feeding sites	5	2.72	0.04	157.24
Power lines + Settlements + Feeding sites + Protected areas	5	2.78	0.04	157.29
Power lines + Protected areas	3	2.97	0.03	161.76
Power lines + Settlements + Feeding sites + Ungulates	5	2.98	0.03	157.49
Power lines + Settlements + Ungulates + Elevation	5	3.16	0.03	157.68
Power lines + Settlements + Protected areas + Ungulates	5	3.19	0.03	157.71
Power lines + Settlements + Aspect	6	3.36	0.03	155.69
Power lines + Ungulates	3	3.43	0.03	162.22
Power lines + Elevation	3	3.43	0.03	162.23
Power lines + Elevation + Feeding sites	4	3.46	0.03	160.13
Power lines + Feeding sites + Protected areas	4	3.81	0.02	160.49
Power lines + Feeding sites + Ungulates	4	3.86	0.02	160.53
Power lines + Settlements + Protected areas + Aspect	7	3.91	0.02	154.00
Null model	1	11.55	0.00	174.50

*The top model had an AIC_c value of 164.98

McNeil 1982) and was thus used to summarize the ROC curve and to measure the performance of the model. Models with an AUC value >0.5 have information about the response variable and possess a certain predictive power. Models with AUC values 0.5–0.7 have low accuracy, 0.70–0.90 have moderate accuracy, and >0.9 have high accuracy (Streiner and Cairney 2007); therefore, the higher the AUC value, the better the fit of the model. Low AUC values, however, do not necessarily indicate a poor model; rather they suggest that factors other than the predictor variables may also be influencing the response variable (Nemes and Hartel 2010).

RESULTS

Data on nest site aspect were only available for 71% of the territories ($n = 89$ occupied and $n = 46$ abandoned). An initial analysis with this smaller sample size revealed that aspect did not feature in any of the top 7 models (i.e those with $\Delta_i < 2$) and only featured in models 15 and 21 of the 21 plausible models (i.e. those with $\Delta_i < 4$; Table 2). Aspect also had by far the lowest relative importance value (Table 3). We therefore excluded aspect from further analyses, allowing a more comprehensive analysis using data from all 190 territories that had complete information for the other covariates.

Influence of environmental variables on territorial abandonment

Our models found strong support for an influence of power lines and settlements on territorial abandonment. All 11 plausible models (Table 4) included the influence of power lines, and 3 of the top 4 models ($\Delta_i < 2$) included settlements. Power lines and settlements had the highest relative importance score (1 and 0.60, respectively). For power lines, the confidence limits of the model-averaged parameter estimate did not overlap zero, and there was marginal overlap with zero for settlements' confidence intervals (Table 5). Two other terms featured in our 4 top models: the percentage of area protected within a territory and the proximity to feeding sites (Table 4). Each of these 2 variables occurred only in 1 of the top 4 models, however, and each had a low relative importance value (Table 5). Furthermore, the confidence limits of the model average parameter estimates for both variables overlapped zero.

Power line density and settlement density were more than twice as high within abandoned territories compared to occupied territories (Figure 3). The relationship between territory occupancy and both power lines and settlements was negative, with the probability of occupancy decreasing with an increase in the density of power lines (Figure 4A) and settlements (Figure 4B). The model-averaged parameter estimates from the best model subsets predicted a

TABLE 3. Model parameter estimates for each variable measured within a 10 km radius around the nest averaged across the 21 plausible models ($\Delta_i < 4$), with the 95% confidence limits of the estimate and the relative importance of each term within those models.

Variable	Parameter estimate	Confidence limits 2.50%	Confidence limits 97.50%	Relative importance
Intercept	1.012000	−0.685145	2.709267	
Power lines	−0.027320	−0.046956	−0.007685	1.00
Settlements	−0.000369	−0.000771	0.000032	0.72
Feeding sites	−15.460000	−53.202860	22.285290	0.34
Protected areas	−0.002352	−0.007899	0.003195	0.27
Elevation	0.000341	−0.000650	0.001333	0.23
Ungulate numbers	0.00000003	−0.00000013	0.00000020	0.21
Aspect N	−0.027750	−1.217802	1.162293	0.05
Aspect S	−0.018830	−1.174604	1.136939	0.05
Aspect W	−2.048000	−4.617748	0.522139	0.05

5.6% increase in the probability of abandonment for each additional 10 km of power line and an increase of 3.3% for each additional 500 settlements.

Although we found little support for elevation or ungulate numbers influencing occupancy, with neither of these variables featuring in any of our top models (Table 4), abandoned territories occurred on average at lower elevations than occupied territories (Figure 3).

Analyzing Lesotho and South African territories separately, our models suggested that the variables associated with abandonment in each country were similar to those in the 2 countries combined. South Africa showed a similar result to the overall models, with the most support for power lines and settlements. Power lines were present in all 5 top models and all but one of the 18 plausible models, and settlements were present in all but one of the top models (Table 6A). Both variables had high relative importance scores of 0.98 and 0.74, respectively (Table 7A). In Lesotho, 9 top models ($\Delta_i < 2$) were identified. Once again, power lines and settlements received the most support, featuring in 7 and 6 of the top 9 models, respectively (Table 6B). In addition, feeding sites also featured in 6 of the top 9 models. For Lesotho, all 3 of these factors (power lines, settlements, and feeding sites) had similar relative importance scores (0.67–0.72; Table 7B). As before, power line and settlement density were negatively related to occupancy, whereas feeding sites were positively related (Table 7B) with a higher feeding site proximity index at occupied sites.

Our overall model had an AUC value of 0.69, and the models for South Africa and Lesotho had AUC values of 0.70 and 0.68, respectively, thus classifying them as poor to moderate fit or low to medium accuracy (Streiner and Cairney 2007).

TABLE 4. Results from the 11 plausible models (those with $\Delta_i < 4$) testing for associations between territorial abandonment and nest elevation, density of human settlements and power lines, percentage of protected areas, feeding site proximity, and the number of ungulates within a 10 km radius around each nest site ($n = 190$ nests; 109 occupied and 81 abandoned). Models are ranked from most to least supported based on Akaike's Information Criterion (AIC_c) values. K is the number of parameters, Δ_i is the change in AIC_c relative to the top model, w_i is the AIC_c weight, and Dev is the deviance.

Model description	K	Δ_i	w_i	Dev
Power lines + Settlements	3	0.00*	0.23	237.26
Power lines	2	0.75	0.16	240.07
Power lines + Settlements + Protected areas	4	1.97	0.09	237.15
Power lines + Settlements + Feeding sites	4	1.98	0.09	237.16
Power lines + Settlements + Ungulates	4	2.06	0.08	237.24
Power lines + Settlements + Elevation	4	2.09	0.08	237.26
Power lines + Feeding sites	3	2.52	0.07	239.78
Power lines + Protected areas	3	2.69	0.06	239.95
Power lines + Ungulates	3	2.80	0.06	240.07
Power lines + Elevation	3	2.81	0.06	240.70
Power lines + Settlements + Ungulates + Protected areas	5	3.77	0.04	236.84
Null model	1	17.88	0.00	259.25

*The top model had an AIC_c value of 243.39

TABLE 5. Model parameter estimates for each variable measured within a 10 km radius around the nest site averaged across the 11 plausible models, with the 95% confidence limits of the estimate and the relative importance of each term within those models.

Variable	Parameter estimate	Confidence limits 2.5%	Confidence limits 97.5%	Relative importance
Intercept	0.794200	−0.093803	1.682162	
Power lines	−0.025280	−0.039733	−0.010835	1.00
Settlements	−0.000298	−0.000669	0.000073	0.60
Protected areas	−0.000967	−0.005683	0.003748	0.18
Ungulate numbers	−0.00000001	−0.00000014	0.00000011	0.17
Feeding sites	−2.351000	−13.819820	9.117642	0.15
Elevation	0.000004	−0.000724	0.000731	0.14

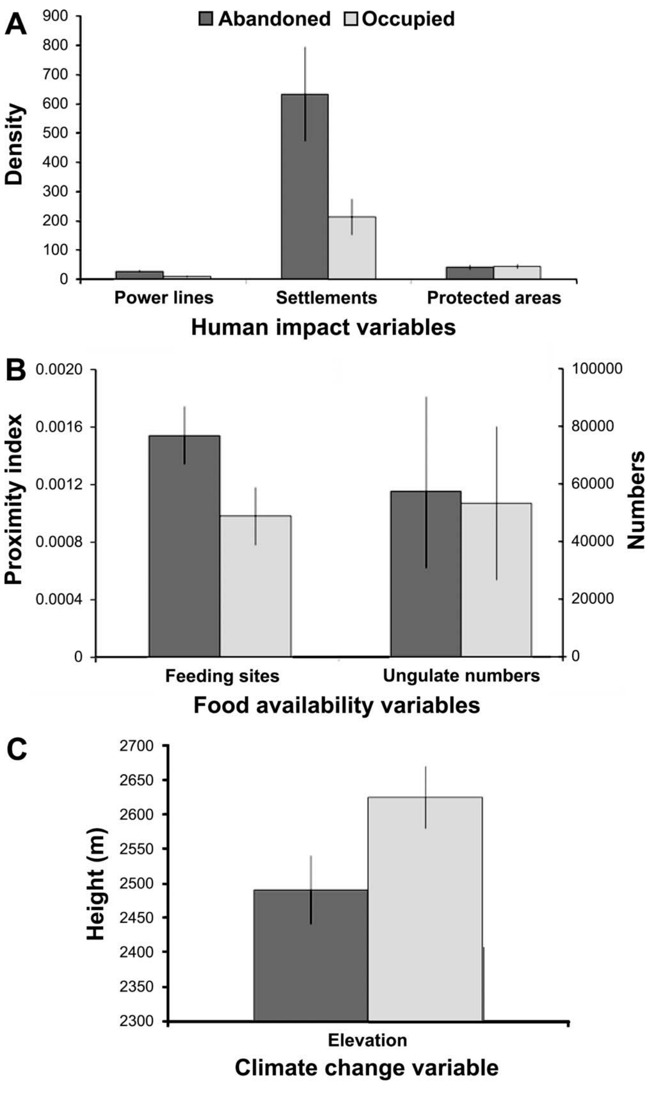

FIGURE 3. Comparison of (**A**) human impact, (**B**) food availability, and (**C**) climate change variables between abandoned and occupied territories indicating that abandoned territories had a higher density of human impacts, a higher feeding site proximity index, and occurred at lower elevations; whereas there was little difference in the percentage of area protected or the number of ungulates within the territory. Values are shown as mean ± SE.

DISCUSSION

Our analyses represent an attempt to empirically assess the evidence for drivers of territorial abandonment of the Bearded Vulture in southern Africa by using variables related to 3 different hypotheses. Our models provide strongest support for the hypothesis that anthropogenic activities are driving territorial abandonment, with a small degree of support for the hypothesis that food shortages are important, and no support for the hypothesis that abandonment has been driven by climate change. The performance of our overall model was similar to the accuracy of the models at a home range scale for Egyptian Vultures (*Neophron percnopterus*; 0.71–0.74) fitted by Mateo-Tomás and Olea (2010). The low to medium accuracy of our models suggests other factors are likely contributing to territorial abandonment. The lack of fit of our models may also be an indication that our indirect measures of food availability and climate change may be too insensitive or were measured during a time period that does not adequately explain the period during which abandonment took place. Ideally we would have used changes in our covariates rather than current measures; however, no such data were readily available. Thus, caution should be applied when interpreting our results, and we stress that our failure to find support for those hypotheses does not rule them out completely as being potentially important factors in the decline of this species.

Across all analyses there was considerable support for an association between nest abandonment and (i) power line density and (ii) human settlements; territories that were abandoned had over twice the density of power lines and human settlements within them than territories that remained occupied. Many of the supported models included both these terms, suggesting that the association between these variables was not simply due to a correlation between these variables, but that both variables were independently associated with abandonment. These patterns were also present from the country-specific analyses, with support for these variables present in both the South African and the Lesotho analyses. This result

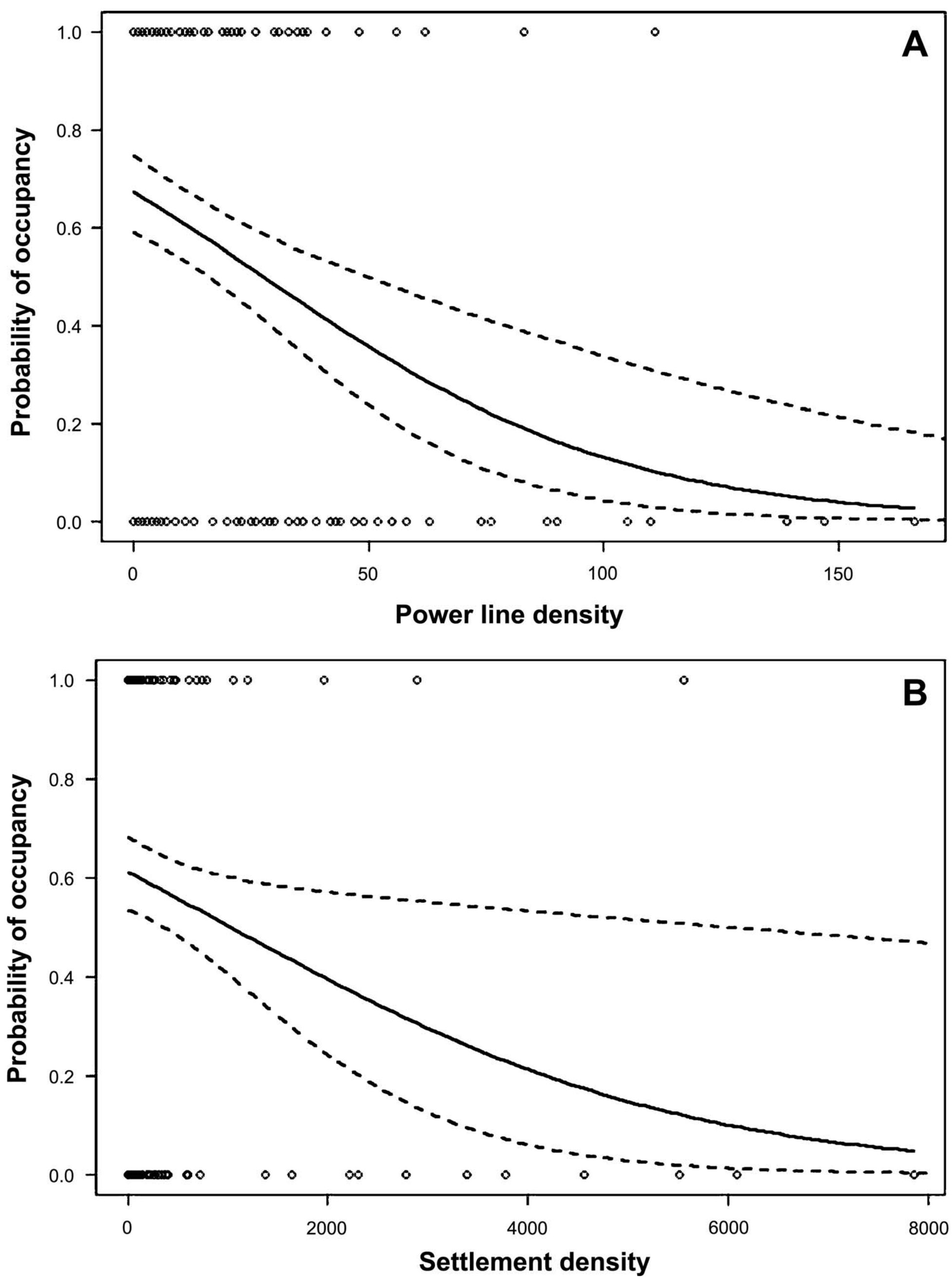

FIGURE 4. The relationship between the probability of territory occupancy (where 0 is abandoned and 1 is occupied) and (**A**) the density of power lines and (**B**) the density of settlements. The solid line is the fitted line from a Binomial Generalized Linear Model with the dashed lines indicating the 95% confidence intervals.

further suggests that these associations were not simply the result of an association in only one location, but a more general pattern occurring across regions.

Krüger et al. (2014) showed that territories in the periphery of the range were more likely to be abandoned than those in the core. We intentionally did not include territory location as a covariate in our models because this variable was correlated with many of our important covariates, and we were interested in the mechanism involved and not merely the spatial pattern of abandonment. Nevertheless, in a post-hoc analysis where we included territory location (core or periphery) as a fixed effect in our model, we found that the territory location variable was not among the top models (those with $\Delta_i < 2$). This finding suggests that the important relationships identified in our models were more important in

TABLE 6. Results from all plausible models (those with $\Delta_i < 4$), testing for associations between territorial abandonment and nest elevation, density of human settlements and power lines, percentage of protected areas, feeding site proximity and the number of ungulates within a 10 km radius around each nest site in; (**A**) South Africa ($n = 98$ nests, 44 occupied and 54 abandoned), and (**B**) Lesotho ($n = 92$ nests, 37 occupied and 55 abandoned). Models are ranked from most to least supported based on Akaike's Information Criterion (AIC_c) values. K is the number of parameters, Δ_i is the change in AIC_c relative to the top model, w_i is the AIC_c weight, and Dev is the deviance.

Model description	K	Δ_i	w_i	Dev
A. South Africa (The optimal model had an AIC_c value of 124.56)				
Power lines + Settlements	3	0.00	0.14	118.31
Power lines + Settlements + Protected areas	4	0.60	0.11	116.73
Power lines + Settlements + Ungulates	4	0.62	0.11	116.75
Power lines	2	1.16	0.08	121.59
Power lines + Settlements + Feeding	4	1.22	0.08	117.35
Power lines + Settlements + Elevation	4	2.06	0.05	118.19
Power lines + Feeding sites	3	2.13	0.05	120.44
Power lines + Settlements + Feeding sites + Ungulates	5	2.31	0.05	116.22
Power lines + Settlements + Feeding sites + Protected areas	5	2.32	0.05	116.24
Power lines + Settlements + Ungulates + Elevation	5	2.44	0.04	116.35
Power lines + Protected areas	3	2.56	0.04	120.87
Power lines + Settlements + Protected areas + Elevation	5	2.57	0.04	116.49
Power lines + Settlements + Protected areas + Ungulates	5	2.78	0.04	116.69
Power lines + Ungulates	3	2.84	0.03	121.15
Power lines + Elevation	3	2.98	0.03	121.29
Power lines + Settlements + Feeding sites + Elevation	5	3.40	0.03	117.31
Power lines + Protected areas + Feeding sites	4	3.96	0.02	120.09
Settlements + Elevation	3	3.97	0.02	122.28
B. Lesotho (The optimal model had an AIC_c value of 120.71)				
Power lines + Settlements + Feeding sites	4	0.00	0.10	112.25
Settlements + Feeding sites	3	0.45	0.08	114.89
Power lines + Settlements	3	0.71	0.07	115.15
Power lines + Feeding sites	3	0.79	0.07	115.23
Power lines + Settlements + Feeding sites + Altitude	5	1.24	0.05	112.17
Power lines + Settlements + Altitude	4	1.33	0.05	115.08
Feeding sites	2	1.74	0.04	118.31
Power lines	2	1.76	0.04	118.34
Power lines + Settlements + Feeding sites + Protected areas	5	1.98	0.04	112.00
Settlements + Feeding sites + Elevation	4	2.05	0.04	114.30
Power lines + Settlements + Feeding sites + Ungulates	5	2.16	0.03	112.17
Power lines + Protected areas + Feeding sites	4	2.19	0.03	114.44
Power lines + Settlements + Protected areas	4	2.38	0.03	114.63
Settlements + Protected areas + Feeding sites	4	2.53	0.03	114.78
Power lines + Protected areas	3	2.55	0.03	116.99
Settlements + Ungulate numbers + Feeding sites	4	2.56	0.03	114.81
Power lines + Settlements + Ungulates	4	2.83	0.02	115.08
Power lines + Ungulates + Feeding sites	4	2.85	0.02	115.10
Power lines + Settlements + Protected areas + Elevation	5	2.85	0.02	112.87
Power lines + Feeding sites + Elevation	4	2.92	0.02	115.17
Power lines + Settlements + Protected areas + Elevation + Feeding sites	6	3.12	0.02	110.84
Settlements	2	3.27	0.02	119.84
Protected areas + Feeding sites	3	3.35	0.02	117.79
Power lines + Settlements + Ungulates + Elevation + Feeding sites	6	3.37	0.02	111.10
Power lines + Settlements + Ungulates + Elevation	5	3.55	0.02	113.56
Power lines + Ungulates	3	3.74	0.02	118.18
Power lines + Elevation	3	3.77	0.02	118.21
Ungulates + Feeding sites	3	3.82	0.01	118.26
Elevation + Feeding sites	3	3.87	0.01	118.31
Null model	1	5.33	0.00	110.78

TABLE 7. Model parameter estimates for each variable measured within a 10 km radius around each nest in (**A**) South Africa ($n = 98$), and (**B**) Lesotho ($n = 92$) averaged across the 18 plausible models ($\Delta_i < 4$) in South Africa and the 29 plausible models ($\Delta_i < 4$) in Lesotho, with the 95% confidence limits of the estimate and the relative importance of each term within those models.

Variable	Parameter estimate	Confidence limits 2.50%	Confidence limits 97.50%	Relative importance
A. South Africa				
Intercept	0.678900	−1.743154	3.101009	
Power lines	−0.026050	−0.046128	−0.005982	0.98
Settlements	−0.000374	−0.000791	0.000042	0.74
Protected areas	−0.003019	−0.010776	0.004739	0.29
Ungulate numbers	0.00000012	−0.000000019	0.00000043	0.26
Feeding sites	−6.317000	−22.310800	9.676210	0.27
Elevation	0.000394	−0.001046	0.001833	0.21
B. Lesotho				
Intercept	1.204000	−1.610974	4.018264	
Power lines	−0.025980	−0.056199	0.004243	0.72
Settlements	−0.012970	−0.027623	0.001675	0.67
Feeding sites	109.900000	−56.771910	276.513500	0.67
Elevation	−0.000510	−0.001720	0.000699	0.27
Protected areas	0.012590	−0.026546	0.051727	0.22
Ungulate numbers	0.00000000	−0.00000022	0.00000022	0.17

explaining abandonment than this simple spatial term and provides further strength for the hypothesis proposed.

Although our results are correlational, support for our anthropogenic activity hypothesis also comes from other lines of evidence. For example, causes of mortality of Bearded Vulture carcasses collected in the study area over a similar time period indicated that death was almost entirely a result of anthropogenic factors, with more than half attributed to indirect and accidental poisoning and persecution, and almost a quarter to power line collisions (S. C. Krüger personal observation). Similarly, non-natural mortalities attributed to illegal poisoning were the main mortality factors in other Bearded Vulture populations (Margalida et al. 2008) and other large raptor populations (Whitfield et al. 2004, Smart et al. 2010, Virani et al. 2010), and collisions with power lines are known to threaten other vulture species in Africa (Smallie and Virani 2010, Boshoff et al. 2011). Impacts related to human disturbance were also found to limit the distribution patterns of Bearded Vulture and other large raptor breeding ranges, densities, and foraging areas (Brown 1988, Herremans and Herremans-Tonnoeyr 2000, Donázar et al. 2002, Bautista et al. 2004, Gavashelishivili and McGrady 2006, Margalida et al. 2007).

There was only limited support for our hypothesis that food shortages could have driven territorial abandonment. In mountainous regions with extensive stock rearing, the livestock death rate is high due to the high incidents of accidents, theft, predation, and poor veterinary care (Newton 1979). This is particularly true for the communal rangelands in Lesotho; therefore, food shortages would not be expected in this country. Food shortages would also not be expected in South Africa because of a number of regularly provisioned supplementary feeding sites in this country. In Lesotho, our country-specific model suggested that feeding sites may play an important role in maintaining territorial occupancy. Because there are very few feeding sites in Lesotho that are regularly provisioned, however, our findings may simply be a result of the location of occupied territories in the mountainous areas close to the South African border where birds have better access to feeding sites. Although our overall results suggest that territorial abandonment is not likely driven by food shortages, territories in Lesotho could benefit from the establishment of supplementary, regularly provisioned feeding sites. Supplementary feeding could also improve productivity and recruitment through non-adult survival, aspects that may be influenced by food shortage and merit further research on their role in the decline of the population.

Our models provide no support for the previously proposed hypothesis that territorial abandonment might be driven by climate change, specifically, increases in temperatures (Colahan and Esterhuizen 1997, Simmons and Jenkins 2007). According to our models, territories with nest sites at lower elevations, and therefore more likely to experience higher temperatures, were not significantly more likely to be abandoned, even though abandoned territories generally occurred at lower elevations than occupied ones. Similarly our models suggest that territories with a hotter nest site aspect (i.e. sites facing north) were also not more likely to be abandoned. Therefore, these results do not suggest that global warming has directly led to territorial abandonment, although this does not necessarily mean that these changes are not influencing other aspects of the species' demography, such as productivity, survival, or timing of breeding. Although we included the most frequently occupied nest site within a territory in our models, we recognize that pairs may have moved to an alternate nest with a cooler aspect within an occupied territory rather than abandoning the territory altogether, thus potentially under-representing the importance of aspect as a driving factor.

Our results lead to the question of whether the continued decline of the species is in response to unnatural mortality factors (as suggested by our analysis), low breeding success/recruitment, or a combination of these. Several studies have found human activities to influence breeding success (Donázar et al. 1993, Margalida et al. 2003, Arroyo and Razin 2006), and breeding pairs are known to prefer more isolated areas with low levels of human activity (Brown 1988). With the expansion of human activities into core breeding areas, we can expect lowered breeding success and ultimately nest abandonment. In addition, there may be a lack of adaptation to the conditions found in the periphery of the range, as shown for harriers (García and Arroyo 2001), which may affect breeding success. We recommend that further studies quantify breeding success and recruitment across a range of human activity levels throughout the species' range.

Based on the identified threats and mechanisms of abandonment, we recommend that conservation management focus on actions that will limit increased human densities and associated developments and influence the attitudes of people living within the territories of breeding pairs. We recommend that mitigation of existing power lines, stricter scrutiny of development proposals, and proactive engagement with developers to influence the placement of structures is essential within the home range of a territorial pair.

For management to be effective, however, both the breeding range (as discussed here) and foraging range of the population must be taken into account (Donázar et al. 1993, Carrete and Donázar 2005). We recommend that the potential threats posed by power lines and human settlements identified in this study be investigated within the foraging range of non-adults to ensure a more holistic approach to the management of the species. Non-adults form a large proportion of the population (Newton 1979, Brown et al. 1982), and conservation measures designed to protect breeding birds may not be sufficient to safeguard the population as a whole (Penteriani et al. 2005, Gonzalez et al. 2006).

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