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Using spatial analyses of bearded vulture movements in southern Africa to inform wind turbine placement

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Summary

- 1. Concerns over CO_2 emissions during energy generation and its effect on climate change have led to increases in the use of renewables, such as wind energy. However, there are also serious environmental concerns over this type of energy production due to its impacts on bats and birds.
- 2. In southern Africa, bearded vultures have declined by > 30% during recent decades. They are now regionally critically endangered with only around 100 active pairs remaining. This species is considered vulnerable to collision with wind turbines which are planned within their southern African range.
- 3. In this study, we develop habitat use models using data obtained from 21 bearded vultures of different ages fitted with GPS tags from 2009 to 2013. We further refined these models by incorporating flying heights at risk of collision to predict important areas of use that may conflict with wind turbines.
- 4. Adult and non-adult bearded vultures mostly used areas with high elevations and steep and rugged topography in the core area; adults tended to use areas in relatively close proximity to their nest sites, whereas non-adult birds used areas dispersed over the entire species range and were more likely to fly at risk-height in areas that were less used by adults. Altitudes of fixes of adults and non-adults showed that they spent 55% and 66% of their time, respectively, at heights that placed them at risk of collision.
- 5. Examining the locations of two proposed wind farms in relation to our model of predicted 'at risk' usage suggested poor positioning. Indeed, one of these wind farms was located within the 1% of 'worst' (most heavily used) sites for non-adult bearded vultures suggesting that its current location should be reconsidered to reduce the impact on this vulnerable species.
- **6.** Synthesis and applications. We demonstrate the value of habitat use models for identifying intensively used areas, in order to greatly reduce conflicts with developments such as wind turbines. This tool is operable at the scale of regional and national development plans informed by the habitat use of potentially vulnerable species. Such models should provide important supplementary assessments of site-specific development proposals.

Key-words: collision, conservation management, habitat use model, predicted effect, threat, tracking, wind energy

Introduction

Throughout the world, renewable energy production is a rapidly expanding industry, driven by climate change and political targets for reduced CO₂ emissions, together with increasing energy demands (Lu, McElroy & Kiviluoma 2009; Leung & Yang 2012; Tabassum-Abbasi, Abbasi &

Abbasi 2014). Africa reflects this global trend: central to development goals throughout Africa is the need for greater energy production, particularly for reliable, low CO₂, and affordable-energy supplies. Wind energy can provide such energy, and in many countries across Africa, wind farms are planned or are already under construction (BirdLife International 2013; Nemaxwi 2013). Although wind energy has the advantage of being a relatively established energy source, experience elsewhere has shown that

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inappropriately situated wind farms can have severe environmental consequences, killing many bats and birds, in particular large raptors and vulture species through collision with the turning blades. In some extreme cases, these collisions have led to numerous deaths of vultures and large raptors and may potentially jeopardize the existence of local or regional populations (Hunt *et al.* 1999; Hunt 2002; Drewitt & Langston 2006; Carrete *et al.* 2009; Dahl *et al.* 2012; Martínez-Abrain *et al.* 2012; Bellebaum *et al.* 2013).

The best way to minimize wind farm impacts through collision mortality is to ensure that they are placed away from the nesting, roosting or intensively used foraging areas of these vulnerable species (Madders & Whitfield 2006; Drewitt & Langston 2006). This can be achieved in two ways, each requiring different types of data at different spatial scales. Firstly, ensuring wind farms are not developed in areas where vulnerable species occur. To do this, the distribution of these vulnerable species must be known. This information can then be used to build wind farm sensitivity maps, highlighting the best and the worst locations at a broad scale of where to place wind farms (Bright et al. 2008). Such an exercise has now been successfully completed for South Africa (BirdLife South Africa 2012) and should help in the strategic planning of areas where wind farm developments are likely to be least damaging. The drawback of this approach is that the spatial scale of the data on bird distributions is at a coarser grain than the scale at which individual wind farms are planned. Moreover, such exercises, if based on several species' distributions, may also not provide reliable indices of collision mortality that are later realized in practice (Ferrer et al. 2012).

The second approach operates at a finer scale and aims to ensure that where wind farms and vulnerable species overlap at broad spatial scales (Fielding, Whitfield & McLeod 2006; Tellería 2009), wind turbines are situated in the most appropriate locations, thereby decreasing the risks of collision (Tapia, Domínguez & Rodríguez 2009; Ferrer et al. 2012). To achieve this, data on how a species uses its environment are required. Using such data, predictive models can then be built which should be generalizable across the species' range to identify inappropriate locations for turbine placement (McLeod et al. 2002; Elith & Leathwick 2009; Hijmans et al. 2013).

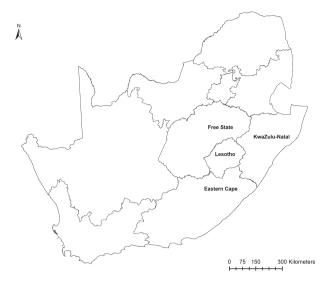
In this study, the second approach has been adopted for a species which has been identified as being vulnerable to the impacts of wind farms, the bearded vulture *Gypaetus barbatus* (Ferguson-Lees & Christie 2001; Barov & Derhé 2011; BirdLife South Africa 2012). This species is classified as *Critically Endangered* in southern Africa (Krüger in press), where the entire population occurs in Lesotho and the surrounding Drakensberg escarpment and mountains in South Africa (Krüger *et al.* 2014). The species is estimated to have declined by between 32 and 51% over the last five decades and currently only 109 occupied territories remain (Krüger *et al.* 2014). However,

the species now faces a new threat in the form of extensive wind farms which are planned for the Lesotho highlands. Currently, there are two active wind farm proposals (42 and 100 turbines) within the Lesotho highlands, and a few others nearby in South Africa, but there are also longer term plans to develop multiple wind farms throughout the Lesotho highland region comprising of up to 4000 turbines in total with a total generating capacity of up to 6000 megawatts (MW) (Jenkins & Allan 2013). Minimizing the impacts of these wind farms on bearded vultures is therefore vital for this species' conservation.

This study aims to use the information obtained from GPS satellite tags attached to bearded vultures to build predictive models of space use (Elith & Leathwick 2009; Hijmans et al. 2013). We construct these models using information on topography, distances to vulture feeding sites and distances to conspecific nest sites, with different models being built for different age classes: first, in two dimensions (landscape models) and then in three dimensions incorporating additional flight height information from the GPS tags. We then apply these models to the entire distribution range of the species to identify which areas of their geographic range are likely to be most frequently used. Finally, we use our three-dimensional model to consider the risk to bearded vultures associated with two proposed wind farms in the Lesotho highland region, as an illustration of the potential of our approach to identify the risk levels for potential turbine placement.

Materials and methods

Within southern Africa, bearded vultures occur over the Lesotho highlands and the Drakensburg escarpment on the north-eastern, eastern and southern border with South Africa and into the Eastern Cape (Fig. 1). All birds studied for this project were captured within this area. This area is characterized by high plateaux and cliffs of basalt and sandstone (Moore & Blenkinsop 2006). All birds were captured between September 2007 and September 2012 (see Tables S1-S3 in Supporting Information) and fitted with GPS satellite transmitters (70 g solar-powered GPS-PTT-100s (Microwave Telemetry Inc., Columbia, MD, USA)). These transmitters provided the location (accurate to within 5-20 m; Krüger, Reid & Amar 2014), the height and the speed of each bird every hour from 05.00 to 20.00 h (SAST), thereby starting and finishing around the hours of sunrise and sunset across the year, respectively. Between September 2007 and December 2012, we obtained a total of 31 bird-years of data from 21 birds, including information on fledglings (n = 3), subadults (n = 12)and adults (n = 6) (Tables S1-S3). Fledglings were classed as birds that had left the nest up to the end of April within their first year (at approximately which time they depart the region of their nest (Krüger, Reid & Amar 2014)). Adults were birds that were known to be breeding. We also used four age classes of non-adult birds (fledgling, juvenile, immature and subadult), which have been used previously to classify non-adult bearded vultures (Brown 1988; Krüger, Reid & Amar 2014). Examination of the distribution of tagged juveniles, immatures and subadults indicated that they inhabited similar areas (Fig. 2b) and so were treated together as one group which from herein we term



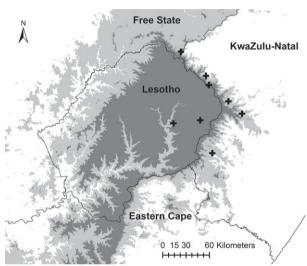


Fig. 1. The Maloti-Drakensberg region in southern Africa, where the darker shades indicate higher altitudes; ■ = >2000 m; 1600–2000 m and $\square = <1600$ m + symbols indicate trap sites.

'non-adults'. Data were sufficiently regular and recorded in enough volume to be assumed to approximate the activity of the birds to which they were attached. Six adult birds were tracked for up to 894 days each (Table S1), eleven non-adult birds were tracked for up to 1243 days (Table S2), and three fledglings were tracked for up to 170 days (Table S3).

HABITAT USE MODELS

We analysed the habitat use of these birds using species distribution modelling (Elith & Leathwick 2009). The species' use of habitats was considered likely to be strongly influenced by distance from nests (Amar & Redpath 2005; Arroyo et al. 2009) and from supplementary feeding sites (hereafter called vulture restaurants) (Anderson & Anthony 2005; Margalida et al. 2010) and by topography (Pennycuick 1972; Donaźar, Hiraldo & Bustamente 1993; McLeod et al. 2002; Hirzel et al. 2004; de Lucas, Ferrer & Janss 2012). Vulture restaurants are locations where land managers or tourism operators put out carcasses to provide a regular source of safe food for vultures, to dispose of carcasses or to attract vultures for tourists. The sites vary in how often (or how regularly) food is provided. Topographic features were taken from a digital elevation model derived from the Shuttle Radar Topography Mission C-Band InSAR 3 arc second (~90-m resolution grid). We used the topographic height at the location of an observation (altitude), plus the standard deviation, skewness and kurtosis over a 5 x 5 grid of these points, giving a grid over 450×450 m. A grid of 270×270 m (i.e. a 3×3 grid of the 90m resolution points) was tested but gave a relatively poorer model fit. Skewness and kurtosis were calculated using the time-Date package in R (R Core Team 2013; Wuertz et al. 2013). Kurtosis was centred around zero (Wuertz et al. 2013). Standard deviation increases when the variation in heights around the observation is large and so relates to the unevenness of the landscape's topography. Skewness and kurtosis are descriptors of the similarity of the shape of surrounding heights to a normal distribution. Skewness is a measure of asymmetry in the distribution of heights around the bird's location and so relates to areas where the frequency of surrounding heights taper in one direction more than in the other. Kurtosis is a measure of how peaked or flat the heights around the observation are relative to a normal

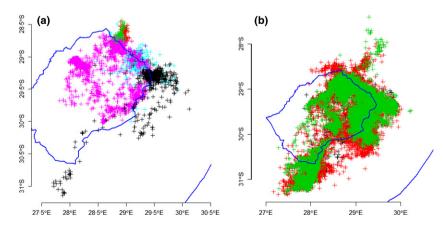


Fig. 2. Locations of points recorded by all tags attached to bearded vultures. South African border represented by blue line; a. adults (each colour represents an individual bird); b. non-adult birds. Different colours represent different non-adult ages (juvenile = red, immature = green and subadult = black).

distribution; a low value of kurtosis indicates a more uniform distribution around the value, and a high value indicates an increasingly narrow peak in distribution with heavy tails.

A significant issue frequently encountered with data on species habitat use or distribution is that often only presence data are obtained (Elith & Leathwick 2009), as is the case with data collected from tracking data. While there are ways to model distribution with only presence data (e.g. bioclim; Elith & Leathwick 2009; Hijmans et al. 2013), greater information can be obtained via background, or pseudo-absence, data. Pseudo-absence data can be generated by selecting points from the area that could have been visited by the observed animals, but were apparently not (Elith & Leathwick 2009; Wakefield et al. 2011). Environmental covariates are then taken at these points and can then be contrasted with the same measurements taken from the fix locations of the tracked animals. Points can be chosen either by modelling the likely range via some distribution where a central place (the nest) is most likely (Wakefield et al. 2011), or by defining an area under which points are likely to occur (Elith & Leathwick 2009). In this study, we took random pseudo-absence points for adults from a circle around their nest to the maximum range that observed data were obtained for that bird, while for subadults, we selected random points from an area between 26-31°E and 27-32°S (encompassing the current range of the species in southern Africa). For modelling, a logistic regression was used, where observed points were given a presence value of one, while pseudo-absence data were given presence values of zero. Three times as many pseudo-absence data points were chosen as observed points in the presented model. This decision was based on Wakefield et al.'s study (2011) and was validated by running the model for the adult presence model with a one-to-one ratio of pseudo-absences and presences. This model's output was very similar to the presented three-to-one ratio model, and so we were confident that our presented model has not altered the position of the allocation threshold (whether a case is predicted to be 0 or 1, when our model was logistic).

In deploying our presence data, we did not mask our habitat use classes by any prior removals as we did not wish to potentially reduce the fit of our models by risking false pseudoabsences if our presence data were unsaturated through inadequate sampling of our study subjects. Despite such precaution, further reassurance on avoiding this risk was given by exploratory analyses revealing that within our study area, there was no habitat class in which bearded vultures were not recorded.

Our initial presence and absence modelling used a generalized additive mixed model (GAMM) to examine the influence of covariates and whether they were linear (Wood 2006). Individuals were treated as random effects. Models derived from GAMMs are more difficult to interpret than those derived from generalized linear mixed models (GLMMs) and are prone to overfitting, therefore their simplification may be advantageous (Randin et al. 2006; Wood 2006). In order to do this, plots of the partial residuals derived from the GAMMs were examined. Where applicable, if coefficients of covariates examined this way could be approximated by a simpler shape such as a straight line or second- or third-order polynomial, these were used in a GLMM. If the shape of their effect appeared not to be biologically important, they were removed. Predictions from these simpler GLMMs were compared to those from the GAMMs, and if results were similar, the GLMM was used in preference. If no simplified model could be found, the initial GAMM was used. GLMMs were used with

individual birds fitted as a random effect. Variance of the random effects for all models was close to zero, so for predictions, the random effects were ignored (and so treated as the mean) (Gelman *et al.* 2003). Once a satisfactory model was identified, this was used to predict the distribution of the birds using the dismo package in R (Hijmans *et al.* 2013). Predictions were made at the scale of the topographic data $(90 \times 90 \text{ m})$.

Model fits were evaluated using area under the receiver curves (AUCs) (Fielding & Bell 1997; Hijmans et al. 2013). AUCs were fitted by dividing the data into five random sections. A model was fitted to four of these (training data), and the fifth was used for predicting distribution (test data). This was then performed five times, repeatedly subsampling for the training and test data sets (Hijmans et al. 2013). Additionally, understanding how useful predictive models are can be best achieved by comparing their predictions to known data that have not been used to create the model (Fielding & Bell 1997; Hijmans et al. 2013). On this basis, a model of adult distribution was created using five randomly chosen adults from the six tracked birds. This model was then used to predict the likely area used by the sixth tracked bird which was then compared visually to the actual locations used by the bird that had not been used in model development. This testing process was also repeated for non-adults.

Once models were developed and validated, they were then applied to the total study area (defined as the square that contained all of the Drakensburg Escarpment/Lesotho Plateau 26–31°E, 27–32°S) to predict areas that would be most used by bearded vultures. This prediction was undertaken using the package dismo from R (Hijmans *et al.* 2013). Distance from all known recently occupied nests (Krüger *et al.* 2014) and vulture restaurants (Ezemvelo KZN Wildlife and Endangered Wildlife Trust unpublished data) were used in these predictive models.

FLYING AT HEIGHTS WITHIN POTENTIAL RANGE OF WIND TURBINES

We modelled areas at heights where bearded vultures would potentially interact with wind turbines - so-called at risk heights. We considered heights of <200 m to be dangerous for encountering turbines. This height was used as this is similar to the height likely to be used for some wind farms in South Africa (Nemaxwi 2013) and although slightly higher than some of the currently planned turbines (100 m; Kneidinger 2011), we considered it prudent to use a higher height to account for the trend of increasing turbine size (Hansen & Hansen 2007). Moreover, Ferrer et al. (2012) indicated that measures of collision mortality may be improved if expectations were based on flight activity heights greater than heights swept by turbine blades. To obtain the height above-ground level (AGL) of the tags used in this study, the altitude of each fix was compared to topographic heights from digital elevation models, and height above-ground level (AGL) was obtained by subtracting the topographic height from the altitude recorded by the tag (height above sea level) (Katzner et al. 2012). Inaccuracies exist in the heights found this way, due to a sum of accuracies of interpolation of the topography data (at the same scale as the measurements), plus that in the GPS heights (Katzner et al. 2012). When the AGL for a location was found to be negative, we compared the altitude to the minimum topographic height over the accuracy of the heights, and used this for calculating the AGL. If the AGL remained negative (ca. 2% of observations), it was not used. AGL height was then modelled

as a logistic regression with the response being '1' to indicate that the location was within 200 m of the ground surface, and '0' to indicate >200 m. This model created a habitat model of the heights used by bearded vultures. This model was tested and validated in the same way as the habitat model using methods from dismo in R (Hijmans et al. 2013). Thus, we explored whether 'at risk' heights were associated with the six variables in Table 2. It is more important to identify areas where the vultures are more likely to occur and to fly at risk-height. To do this, we combined the earlier habitat use model with this height model by using the product of the two. This was then plotted to identify areas of greatest risk to the population.

OVERALL POPULATION DENSITY

Our predictive models provide a probability density across each 90 × 90 m square within the study area for each age class. These models can then be used to estimate the overall spatial use of the area by the population. This is done by first normalizing these probabilities so that the sum of probabilities over the study area adds up to one, with the resultant probability values then multiplied by the estimated overall population size of the different age classes (218 adults and 131 non-adults) (Wakefield et al. 2011; Krüger in press) and then summing across the age classes. The resultant spatial use was then expressed as the estimated number of birds km⁻². We did not estimate the density distribution of fledglings as these were largely dependent on the locations of nests and were considered non-adults after May.

HABITAT USE IN RELATION TO KNOWN WIND FARMS

Two areas have been proposed for the development of wind farms within Lesotho. To explore the application of the model developed here, we divided the study area into a 5.4×5.4 km grid (derived from the 90 × 90 m grid topographic data used in the model, and appropriate to the approximate turbine 'footprints' of the proposed schemes) and calculated the mean probability of birds flying under 200 m AGL within each of these squares throughout the study area. To compare the probability of birds flying at risk-heights in the proposed area to the overall threat throughout the study region, we plotted frequencies of 'at risk' probabilities for all 5.4 × 5.4 km squares throughout the study region and then examined the probabilities for the squares where these wind farms were proposed.

Results

ADULT HABITAT USF

Tagged adult bearded vultures were restricted to areas around the Drakensburg escarpment, especially between Golden Gate Highlands National Park and Maloti Drakensburg Park (Fig. 2a). The simpler GLMM produced very similar results to the original GAMM model and was therefore used in preference (Table 1). Cohen's kappa was reduced slightly between models (0.78 vs. 0.72, respectively) (Fielding & Bell 1997). This model suggested that adult bearded vultures use areas with higher altitudes, with steep slopes and sharp points, and in areas located closer to their nesting site (Table 1). The mean

Table 1. Coefficients of covariates used for predicting distribution of adult bearded vultures from a generalized linear mixed model. Random effect for bird with variance of 1.20E-04

Coefficients	Estimate	SE	Z value	P
Intercept	-6·14E+00	6·35E-02	-96.6	<0.01
Altitude	1.65E-03	1.95E-05	84.3	< 0.01
SD	3·37E-02	3.65E-04	92.4	< 0.01
Skewness ²	9·15E-02	3·54E-02	2.59	< 0.01
Skewness	-5.14E-01	1.85E-02	-27.79	< 0.01
Kurtosis	1.05E-01	2·69E-02	3.89	< 0.01
Distance	-1.78E-02	2·88E-04	-61.8	< 0.01

AUC for this model was calculated as 0.903 (range 0.902-0.904) suggesting a good model fit (Fig. 3a). The model showed steeper sensitivity than specificity (Fig. S1). By applying this model to the entire study area, incorporating all the known occupied breeding sites, the model predicted the greatest habitat use within the Drakensburg Mountains, especially along the border between Lesotho and KwaZulu-Natal, south into Eastern Cape, and in eastern Lesotho (Fig. 4a). Adults were most likely to fly below 200 m over Lesotho, or to the north or south of it (Fig. 4c). Adults were more likely to fly above the riskheight with lower elevation, with distance from the nest and with rugged terrain (Table 2). The mean AUC for this height model was 0.747 (range 0.740-0.751). The model showed steeper sensitivity than specificity (Fig. S2). This suggests the model picked true positives better than it picked true negatives. Combining these models indicated that when present, adult bearded vultures were most likely to be flying low over the escarpment of the Drakensburg Mountains or in eastern Lesotho (Fig. 4e). A total of 55% of positions recorded for adults were within the 'at risk' height.

To further validate the strength and power of our predictive model, a model of adult habitat use was developed using only five of the six adult birds, and predicted habitat use centred on the nest of the known sixth bird was plotted (Fig. 5). This exercise suggests good power to our predictive models with most of the observed locations

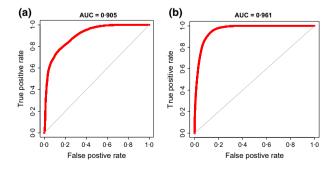


Fig. 3. AUC (area under the receiver curves) for predictive models for the presence of different ages of bearded vultures a. adults; b non-adults

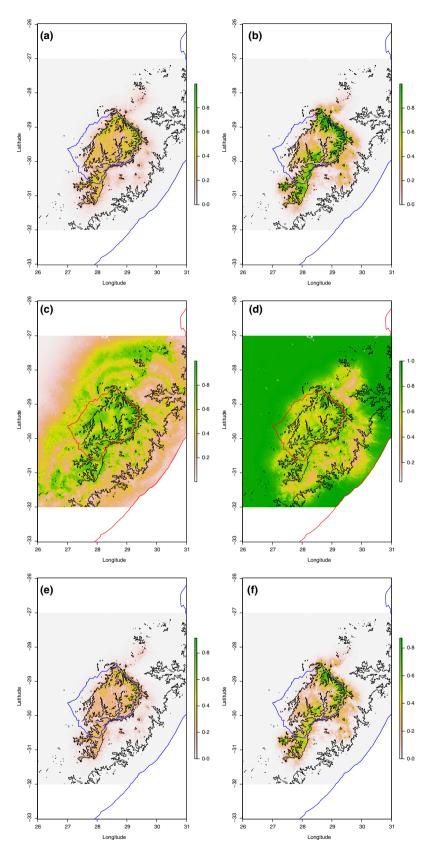


Fig. 4. Predicted distribution of bearded vultures and low flying heights (a, c, e = adults; b, d, f = non-adults). Colour shading proportional to the probability for each 90×90 m square: a and b predicted presence; c and d predicted probability of flying at <200 m; e and f predicted probability of flying in an area at <200 m, given that they are visiting the area. Black lines represent topographic contours (1000, 2000 and 3000 m). South African border represented by blue or red line.

Table 2. Approximate significance of smooth terms used in a model to predict the probability of adult bearded vultures flying below 200 m above-ground level

	Effective d.f.	Chi.sq	P
Restaurant	8.571	307.03	<0.01
Kurtosis	8.575	52.12	< 0.01
Skewness	7.999	119.98	< 0.01
SD	8.627	2036-39	< 0.01
Altitude	7.926	224.71	< 0.01
Distance	5.595	26.87	< 0.01

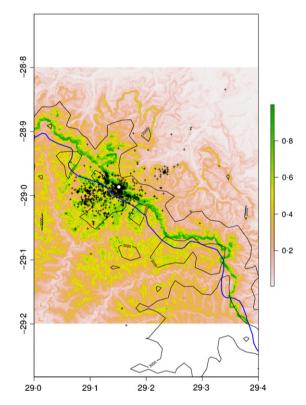


Fig. 5. Predictive model for adult bearded vultures derived from five of the six tagged birds. The actual observed locations for one bird are plotted over this (crosses). Black lines indicate topography (2000 and 3000 m). Nest site represented as white circle.

occurring in areas with a probability >~0.7. Those few fixes which occurred in areas with low probability were mostly in areas that were more distant from the nest.

NON-ADULT HABITAT USE

Non-adult bearded vultures similarly predominantly used areas over the northern and eastern Drakensburg Mountains (Fig. 4b). Again, a GLMM was developed that fitted the data well, with some covariates fitted as polynomials (Table 3). Birds were more likely to use areas at higher altitudes, with steeper slopes and more rugged terrain, and in areas closer to bearded vulture nesting sites and restaurants and were less likely to use areas with skew values close to zero (Table 3). The mean AUC for this

Table 3. Approximate significance of smooth terms used in a model to predict the distribution of non-breeding bearded vultures. Random effect for bird with variance of 1.35E-04

Coefficients	Estimate	SE	Z value	P
Intercept	-8·46E+00	1·71E-01	-49.53	<0.01
Altitude	4·48E-03	1.47E-04	30.40	< 0.01
Altitude ²	-3.94E-07	3·11E-08	-12.69	< 0.01
SD	3.49E-02	7.63E-04	45.70	< 0.01
SD^2	2·82E-05	6·78E-06	4.17	< 0.01
Skewness	-2.44E-01	1-46E-02	-16.70	< 0.01
Skewness ²	5.61E-01	3.59E-02	15.64	< 0.01
Kurtosis	-2.80E-01	2·42E-02	-11.57	< 0.01
Kurtosis ²	-1·25E-02	2.90E-03	-4.30	< 0.01
Restaurant	-8·92E-02	1.09E-03	-81.89	< 0.01
Restaurant ²	4·56E-04	1·13E-05	40.29	< 0.01
Distance	1.05E-01	2.66E-03	39.58	< 0.01
Distance ²	-2·83E-03	7·24E-05	-39.05	<0.01

model was calculated as 0.962 (range 0.960-0.963) (Fig. 3b). The model showed steeper sensitivity than specificity (Fig. S3). While similar to the adult model, the model predicted non-adult habitat use over a much wider area in the north-east, as well as to the south-east and the south-west into the Eastern Cape (Fig. 4b). Non-adult bearded vultures were predicted to fly high over areas to the east of the Drakensburg Mountains (Fig. 4d). They were most likely to fly at 'at risk' heights in areas with relatively flat land with high elevation, and more distant from nests (Table 4); however, they were unlikely to use those areas (Fig. 4f). Generally, non-adults were more likely to fly at 'at risk' heights in areas where adults were less likely to do so. The mean AUC for the height model was 0.692 (range 0.686-0.698). The model showed steeper sensitivity than specificity (Fig. S4). A total of 66% of non-adults heights were within the 'at risk' height.

OVERALL POPULATION DENSITY OF HABITAT USE

Greatest densities of bearded vultures occurred along the Drakensburg Escarpment from the area of Golden Gate Highlands National Park south into the northern part of the Eastern Cape (Fig. 6). Density was also high within areas of eastern Lesotho at altitudes >2000 m (Fig. 6).

LEVEL OF PREDICTED HABITAT USE WITHIN THE PROPOSED WIND FARM SITES

The probability of adults flying at 'at risk' heights within the areas of the two proposed wind farm sites was fairly low (P < 0.4), while the chance of non-breeding birds visiting was high (P > 0.7 at one site) (Fig. 7). A histogram of the estimated probabilities of 'at risk' usage for each 5.4×5.4 km grid within the overall study area showed an approximately exponential shape where most areas had low probability, while the two areas with wind farm proposals were within some of the higher threat areas (Fig. 8). For adults, the two wind farm sites are within

Table 4. Approximate significance of smooth terms used in a model to predict the probability of subadult bearded vultures flying below 200 m above-ground level

Term	Effective d.f.	Chi.sq	P
Restaurant	8-40	318-7	<0.01
Kurtosis	7.69	407.3	< 0.01
Skewness	6.21	193.6	< 0.01
SD	8.60	2605.3	< 0.01
Altitude	7.48	969.9	< 0.01
Distance	8.65	205.6	< 0.01

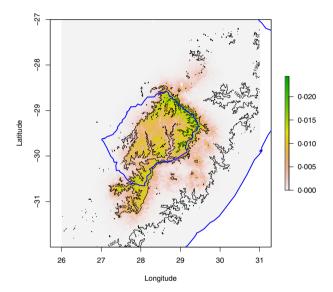


Fig. 6. Estimated density of bearded vultures (adults and subadults) throughout the distribution range in birds $\rm km^{-2}$. The estimate is the sum of the densities of adults and of subadults. Densities for each derived from the models of the probabilities of presence in each square normalized over the total range and accounted for the estimated population. Black lines represent height contours (1000, 2000 and 3000 m). South African border represented by blue line.

the 1% and 3% of most 'at risk' areas, and for subadults, the wind farms are within the 0.5% and 3% of most 'at risk' areas. Thus, these results suggest that the current proposed locations are poorly situated with respect to the overall risk of the area from the perspective of bearded vulture conservation and that many areas exist which have a much lower 'at risk' usage.

Discussion

We aimed to produce predictive models of 'at risk' habitat use by bearded vultures to help inform wind turbine placements within an area that is proposed to be heavily developed by this industry in the coming years. Using data from GPS tracking units, we were able to produce apparently reliable models of habitat use for this species across its entire southern African range, which should hopefully be useful for future developments in avoiding areas of heavy use for potential wind farms. Results, however, suggested that the current proposed areas for wind farms are amongst the worst areas, that is to say the most heavily used areas, by the species and therefore have the potential to cause the most damage to the population through collisions, particularly by non-adult birds.

Bearded vultures in all age categories were predicted to have a higher probability of using areas of high ground with steep ridges and slopes. To some degree, this fits with their previous description as being a bird of high-altitude grasslands and escarpments (Hockey, Dean & Ryan 2005; Krüger et al. 2014). Our models for both adults and subadults emphasize the importance of the proximity of nests, as well as land topography and change in steepness (e.g. cliffs). Vulture restaurants showed limited effects on adults in the models, while non-adults showed an increased chance of occurring within 100 km of restaurants. These areas are similar to those used by bearded vultures in Europe and Asia (Ferguson-Lees & Christie 2001). In addition to factors considered here, the distribution of ungulates has been found to be of some influence, especially for non-adults (Hirzel et al. 2004). We also could not consider the location of ossuaries (areas used by bearded vultures for breaking bones). While Hirzel et al. (2004) speculated that features of ossuaries may have influenced habitat selection of bearded vultures in the Alps, according to Margalida & Bertran (2001), bearded vultures spend relatively little time at ossuaries, and Hirzel et al. (2004) concluded that landscape features promoting wind conditions to facilitate the searching for food were paramount, even while including variables on the distribution of large ungulates. The goodness-of-fit of our models in southern Africa was consistent with this conclusion of the overriding influence of topography on range use, even with less information on food availability. This is encouraging for the wider application of our approach, in terms of what data are needed to inform the siting of potential wind farm developments, across large areas, for other vultures and raptors that fundamentally rely on topographically generated air movement to search for food (see also McLeod et al. 2002).

The fitted models gave a good fit of the distribution of the birds, lowering the residual deviance by 50-65%; however, the models of flying heights were less successful (lowering the deviance by 10-20%). These comparative results are broadly to be expected. Location fixes approximate the time spent, with increasing numbers of records in areas of increasing importance. Fixes were taken hourly with sufficiently few missing compared to total numbers to suggest biases would have been minimal. However, flying height data are somewhat more difficult to collect and model. Inaccuracies in these AGL data can appear due to the summing of errors such as the GPS position and the topographic mapping. This is likely to be of particular concern within the landscape that this population occupies due to the large numbers of cliffs over which they were flying, which can give rise to negative values in

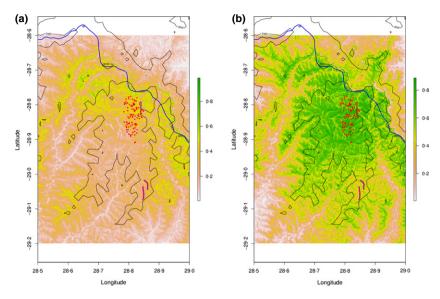


Fig. 7. Probability of birds flying within the danger heights (<200 m) given that they are present within the area (subset plots from Figs 3e and f) in regions of two proposed wind farms in Lesotho. Red dots = site 1; violet dots = site 2; blue line = Lesotho and South Africa border; black lines = land contours. a. adults, b. non-adults.

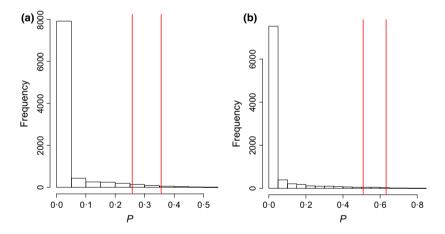


Fig. 8. Frequency plots of probability of birds flying below 200 m (i.e. 'at risk' height) within all 5.4 × 5.4 km blocks (approximately size of a wind farm) from throughout the entire study region. The red lines represent the probability of birds using the area and flying below 200 m for two blocks that have been proposed for wind farms (shown in Fig. 7; in each case, the right line (higher P) is site 1). a. adults, b. non-adults.

AGL height (Katzner et al. 2012). A further concern was as a result of the tags taking a snapshot of flight height once every hour. While these can be presumed to be settling towards being representative with increasing sample size, they are still a small proportion of the actual time. Further to this, there are potentially other variables that have not been measured that may be important in predicting how airspace is used by the birds. Since the birds ride thermals, the time of day is likely to have an important effect upon the AGL measures (Pennycuick 1972; Krüger, Reid & Amar 2014). Wind patterns, as they pass over ridges and through valleys, are also likely to have important effects. However, there are no data collected on this by the tags, and little data on the patterns of wind over South Africa, especially at the time and spatial scales appropriate for making use of these measures within mod-

els (WASA 2013). In spite of these considerations with modelling the AGL, it is noteworthy that broadly the areas that were used by bearded vultures flying below 200 m were similar to those predicted for presence (Fig. 4), indicating that even data from tags that do not collect height data will approximate the areas which are likely to pose the greatest threat from wind farms. This will, however, potentially simplify the identification of areas of importance for this and other vulture species which show similar patterns of vertical space use. Nevertheless, understanding areas where birds are flying at heights that potentially put them into conflict with wind turbines is likely to be useful, even where it is relatively uncertain. However, Ferrer et al. (2012) concluded that expected (pre-turbine construction) estimates of griffon vulture Gyps fulvus collision mortality were more likely to

be closer to observed (post-construction) measures of collision mortality if expectations were based on flight activity heights greater than heights swept by turbine blades.

Improved knowledge of the movements and habitat use of species of concern for conservation has the potential to vastly improve our understanding of their needs and improve management decisions. In this study, we have developed a suite of models of habitat use by bearded vultures to understand how they might interact with wind farms. These models are useful both for describing how bearded vultures' habitat use is distributed and how certain features within their environment are important for influencing this habitat use. Further to this, they can be used for predicting in which areas wind farms are likely to have higher or lower impacts on the vultures. This has the potential to be expedient for planning the future deployment of wind farms and to reduce the need for mitigation following any construction.

Our approach has followed other studies that have used information on the distribution or generic flight activity patterns of individual species to provide a measure of the potential conflict with wind farms (Fielding, Whitfield & McLeod 2006; Tapia, Domínguez & Rodríguez 2009; Tellería 2009; Eichhorn *et al.* 2012; Katzner *et al.* 2012; Miller *et al.* 2014). Similarly, we used our models to examine the chance of bearded vultures visiting two wind farms proposed in Lesotho. Our models indicated that both areas have a high probability of posing a threat to bearded vultures, particularly non-breeding birds. Of 10 000 5×5 km squares in the study area, one of the wind farm proposals was within one of the 1% of squares most likely to be visited by bearded vultures flying below 200 m.

The advantage of our models over previous research is that they provide for estimation of use (and flight activity within the airspace swept by turbine blades) across all cohorts of a population, and at a scale such that it should be possible to identify areas at the scale of tens of metres or more to inform the prospective siting of both wind farms, but also the specific turbines within these farms to minimize their threat to this species. Thus, our models allow for recommendations on wind turbine placement before areas have been chosen, with these recommendations being based on a holistic age-cohort basis and at a scale that has been emphasized as providing the most realistic predictions of potential collision mortality for another vulture species (Carrete *et al.* 2009; Ferrer *et al.* 2012).

Our models potentially have a vital conservation application. The bearded vulture population in southern Africa has been declining from before the introduction of wind turbines (Brown 1991; Krüger *et al.* 2006; Simmons & Jenkins 2007) and has declined by over 30% over the last few decades down to just over 100 active pairs currently (Krüger *et al.* 2014). The species previously had a more extensive distribution and was present in southern and western South Africa, as far south as Cape Town (Piper

2006). Various factors have been blamed for their declines, including habitat destruction and poisoning; one study has suggested that declines were unlikely to be related to food (Brown 1991), while another more recent study has linked anthropogenic factors (powerlines and human settlements) to territorial abandonment (Kruger, Simmons & Amar 2015). Throughout their global range, they are currently threatened by poisoning, persecution by humans and by collisions with power lines (Ogada, Keesing & Virani 2012). Regardless, if wind turbines are constructed in areas where they pose the most threat to vultures, they will likely accelerate this decline (e.g. Martínez-Abrain *et al.* 2012; Bellebaum *et al.* 2013).

In spite of the cautions required in their interpretation, our models are broadly useful for identifying areas that may cause high risk for bearded vultures from wind turbines, and areas that are more suitable for wind farm placement. In this respect, they build on the novel utility of remote satellite tagging in the study of wind farm-bird interactions (Katzner *et al.* 2012). By adding linkage between bird use and predicted collision mortality (e.g. Band, Madders & Whitfield 2007), our models should be further developed to realize their full potential by examining the mortality effects that placement of turbines could potentially have on the population trajectory.

Our approach can be easily replicated for other species with similar data. For example, our study area also supports around 25% of the world's population of Cape vultures Gyps coprotheres. Similar tracking data are currently being gathered from several individuals of this species and should allow a similar exercise to be conducted in the future. Our study illustrates that with the use of satellite tracking data and readily available landscape data, the risks posed by wind farms (current or prospective) can be successfully modelled over large areas for other similar resident 'soaring' vultures and raptors that are considered to be vulnerable to collision with turbine blades (Drewitt & Langston 2006; Ferrer et al. 2012). This is likely because critical features of the habitat selection of such species are topographic features associated with the generation of winds that allow low energetic costs of birds searching for food or other movements (e.g. McLeod et al. 2002; Katzner et al. 2012; de Lucas, Ferrer & Janss 2012). The applied benefits of our approach for the large number of such species are many, especially pertinent when the rapid pace of wind farm development continues to outstrip the capacity for applied research on bird impacts and relevant data availability to keep up.

For example, it is apparent that data on potentially influential variables such as food abundance may be desirable, but not essential to model potential risk (see also de Lucas, Ferrer & Janss 2012). Hence, the probable absence of such data in some parts of the world, notably developing countries, where wind farm development is being increasingly proposed, should not be an obstacle to considering potential impacts, provided that the essential data in our approach have been collected (from satellite tag-

ging a representative sample of birds). In addition, our approach allows greater capacity for assessment of potential adverse effects not only at specific sites (as our study has illustrated directly) but also to inform larger scale strategic environmental assessments on which, even in Europe with a strong legislative framework, there has been criticism of inadequate compliance and thereby threats to important faunal interests (Gove et al. 2013).

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Data accessibility

The data used in this paper can be accessed by applying to data@kznwildife.com or writing to the Data Manager, Ezemvelo KZN Wildlife, PO Box 13053, Cascades 3202, South Africa. A digital copy (GIS layer) of the main habitat use maps is available on request from the above address.

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Supporting Information

Additional Supporting Information may be found in the online version of this article

- Table S1. Dates and number of records for adult bearded vultures.
- **Table S2.** Dates and number of records for bearded vultures aged between fledglings and adults.
- Table S3. Dates and number of records for fledgling bearded
- **Table S4.** Coefficients of covariates used in a model to predict the distribution of fledgling bearded vultures.
- Fig. S1. Sensitivity and specificity of adult presence model.
- Fig. S2. Sensitivity and specificity of adult height model.
- Fig. S3. Sensitivity and specificity of non-adult presence model.
- Fig. S4. Sensitivity and specificity of non-adult height model.
- Fig. S5. Locations of points recorded by fledgling tags attached to bearded vultures.
- **Fig. S6.** AUC curves for predictive models for presence for fledgling bearded vultures.
- **Fig. S7.** Predicted probability of fledgling bearded vultures spending time in areas.