Habitat selection of adult Bearded Vultures *Gypaetus barbatus* in southern Africa: implications for conservation

Mohammad Imthiaz Zulfur Ali Sheik Abbass

Supervised by Ass. Prof. Arjun Amar, Dr Megan Murgatroyd, Dr Sonja Krüger

DST/NRF Centre of Excellence at the

Percy FitzPatrick Institute of African Ornithology

Department of Biological Science

University of Cape Town

Rondebosch 7701

South Africa

Email: sa.imthiaz@gmail.com

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PLAGIARISM DECLARATION

I know the meaning of plagiarism and declare that all of the work in the dissertation (or thesis), save for that which is properly acknowledged, is my own.

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Contents

Acknowledgments 1
Abstract 2
1. Introduction 3
1.1 Habitat selection: application for conservation 3
1.2 Declining vulture population 4
1.3 Causes of vulture decline in Africa 4
1.4 Southern Africa's Bearded Vultures 5
1.5 Aims, hypothesis and objectives 6
2. Methodology 7
2.1 Study area 7
2.2 GPS tracking 8
2.3 Raster processing 8
2.4 Statistical analysis of habitat selection 9
3. Results 12
3.1 Habitat selection – percentage of built-up areas 12
3.2 Habitat selection – distance to built-up areas 13
4. Discussion 15
4.1 Habitat selection 15
4.2 Caveats 16
4.3 Conservation implications 17
4.4 Recommendations for future research 18
5. Conclusion 18
6. References 19
Appendices 26

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Abstract

The Bearded Vulture, *Gypaetus barbatus*, was previously distributed across southern and western South Africa, as far south as Cape Town. Today, the entire population in southern Africa is restricted to the Lesotho highlands and the Drakensberg escarpment and nearby mountains in South Africa, where the population continues to decline. Research has shown that territorial abandonment is apparently associated with the density of human settlements within 10km of a territory. This pattern was assumed to be linked to the increased risk of unnatural mortalities in areas with higher human presence. However, habitat use and habitat selection, especially whether the species actively avoids human settlements has not yet been explored and could contribute to this pattern. In this study, we used data from nine adult Bearded Vultures fitted with Global Positioning System (GPS) satellite tags to determine which habitat is being selected. We modelled habitat selection in relation to various topographic and habitat variables, including information on built-up areas (i.e., areas with a high density of buildings). We predicted that birds would select areas of grassland and avoid areas with high building density and adjoining areas. We found that Bearded Vultures selected areas closer to their nest sites and supplementary feeding sites, with steeper slopes, and highly rugged terrain. In terms of habitat, they selected areas with grassland and avoided areas with forest, while cropland was neither selected nor avoided. As predicted Bearded Vultures avoided built-up areas and their vicinity. These results suggest that the Bearded Vulture may be sensitive to the negative impacts of a changing landscape in its distribution range. These results can help conservation managers in guiding development (e.g., human settlement expansion and afforestation) and protecting priority habitats (e.g., grassland) within the breeding range of adult Bearded Vultures.

Keywords: Land cover, vulture, habitat selection, conservation management, telemetry

1. Introduction

Presently, most animal species inhabit novel landscapes combining native habitats with human altered habitats (Hobbs et al. 2006). As human populations and their associated threats continue to grow, conservation efforts need to expand from protecting native habitat remnants to include the management of land with varying degrees of transformation (Daily et al. 2001; Norris 2008). To better manage these multi-use landscapes, we first need to understand how changes in landscape influence habitat selection of threatened species. Fretwell and Lucas' (1969) theory on Ideal Free Distribution (IFD) helped in the development in habitat selection research. The theory assumes individuals 1) distribute themselves so as to optimise their fitness, 2) can select freely habitats where fitness (e.g., reproduction) is highest, and 3) fitness will decline with increasing population density (Fletcher & Fortin 2018). The theory was later extended to include non-ideal behaviour, despotic and pre-emptive behaviour preventing "free" settlement, Allee effects, species interaction and predation risk, social behaviour and stochasticity (Fletcher & Fortin 2018). Many theoretical developments in interpreting space use and resource selection across landscapes emerge from the IFD extension. Theory suggests that high-quality habitats will be selected, used more consistently over space and time, and may be selected more rapidly and by dominant and experienced individuals (e.g., older or larger individuals) (McLoughlin et al. 2010). However, there are cases where rapid changes in the landscape can lead to selection of poor-quality habitat instead of better alternatives; this is known as an ecological trap (Hale & Swearer 2016; Vlaschenko et al. 2019). Consequently, species presence in novel habitats could be due to maladaptive processes, making the species more vulnerable to further landscape change.

1.1 Habitat selection: application for conservation

Before establishing the habitat selection pattern for any species, we need to understand variation in their home range. Typically, home range size will vary, based on environmental conditions (e.g. resource abundance), individual traits (e.g. age, sex), and population density (Fletcher & Fortin 2018). Johnson (1980) classified habitat selection into four levels each operating at different spatiotemporal scales; 1) selection of the geographical range of a species, 2) selection of home range of an individual or group, 3) use of habitat patches within the home range, and 4) selection of specific resources within the habitat patches. The increasing availability of GPS telemetry data has made it easier to understand how species use the habitat within their home ranges, thereby improving conservation effectiveness (Katzner & Arlettaz 2020). For example, modelling the flight heights and ranging behaviour of GPS tagged raptors allowed researchers to make recommendations on wind farm placements so as to minimise the likelihood of collisions with turbines (Reid et al. 2015; Murgatroyd et al. 2021). Another study used GPS tags and land cover layers, to look at how the rewilding process in the Mediterranean landscapes influenced Griffon Vulture (*Gyps fulvus*) habitat selection (Martin-Díaz et al. 2020). Understanding how species persist in a constantly changing landscape is important in establishing patterns of habitat selection and in identifying important habitat-related features which may be potential limiting factors for range

expansion and persistence (Boggie et al. 2018). This allows managers to know where and how to focus conservation efforts on different spatial scales.

1.2 Declining vulture population

Scavengers play a key role in the landscape by providing ecosystem services such as removal of carcasses, controlling disease spread, and helping nutrient recycling (Prakash et al. 2005). Vultures represent the only known vertebrate obligate scavengers (Ruxton & Houston 2004), and yet, are one of the fastest declining groups of birds (Buechley & Sekercioglu 2016; McClure et al. 2019). The decline of vultures is particularly worrying, given the important ecosystem services they provide. Vultures can break down large quantities of animal carcasses (e.g. deceased animals, roadkill, and culled animals), maintaining nutrient recycling in the ecosystem and also regulating the spread of disease and the populations of facultative scavengers (Peisley et al. 2017). Studies have shown that vultures provide an efficient and cost-effective carcass disposal service. For example, Indian vultures before their decline, were estimated to provide carcass disposal services valued at US$ 34 billion per annum helping to reduce the food supply available for feral dogs thereby reducing the cases of rabies in the human population (Markandya et al. 2008). Vultures also provide cultural, spiritual, and recreational services. For example, Becker et al (2005) have estimated that the annual benefit generated from viewing Griffon Vultures (*Gyps fulvus*) at Gamla Nature Reserve in Israel was around US$1 million per annum, and that 85% of the visitors went to the park for the vultures. Many have suggested there is an African Vulture Crisis (Krüger et al. 2014a), and a recent study by Ogada et al. (2016) showed that eight of the 11 African vulture species have declined by an average of 62%. Currently, four species of vulture are classified as Critically Endangered, and three as Endangered (Sarasola et al. 2018).

1.3 Causes of vulture decline in Africa

The principal causes of vulture declines in Africa are poisoning and human persecution (Ogada et al. 2016). However, the rate of decline and causes of poisoning vary across the continent. The life-history traits of vultures (foraging behaviour and long-lived) make them prone to bioaccumulation of toxic substances thus affecting their reproductive success, behaviour, immune response, and physiology (Gangoso et al. 2009). Unintentional poisoning can occur in many ways. For example, to combat livestock loss, farmers put out poisoned baits to kill predators (e.g., lions, hyenas, and jackals), and when vultures consume those carcasses, they die from unintentional poisoning (Safford et al. 2019). Another major unintentional threat is lead poisoning, through ingestion of carcasses that contain lead-based bullets or pellets (Naidoo et al. 2017; Garbett et al. 2018). For example: in a tracking study involving 20 Bearded Vultures in South Africa, eight out of ten that died from poisoning during the study exhibited high levels of lead, specifically in the bones suggesting a long-term exposure to lead (Krüger 2014). However, the deliberate persecution of vultures is also increasing (Ogada et al. 2012). For example,

poachers intentionally poison vultures to disguise their location/activities or vultures are killed to obtain parts for belief based use (Ogada et al. 2012; McKean et al. 2013).

Land use change and climate change are among the major factors contributing to species extinction, and vultures are not excluded (Botha et al. 2017). Anthropogenic land conversion (habitat loss, degradation, and fragmentation) is suspected of having contributed to the declining vulture populations (Safford et al. 2019). Africa is amongst those regions showing the most rapid anthropogenic land conversion (Thuiller et al. 2006; Botha et al. 2017). The negative impacts of infrastructures associated with anthropogenic land conversion such as power lines and wind farms on vultures, through collisions and electrocutions, have been widely documented (Rushworth and Krüger 2014; Ogada et al. 2016). The behaviour and distribution of vultures are strongly correlated with the availability of carrion (Phipps et al. 2013; Dodge et al. 2014). Anthropogenic land conversion and declining wild ungulate numbers have led to a change in abundance, mortality, and distribution of carrion as well as its visibility and accessibility in space and time (Spiegel et al. 2013; Kendall et al. 2014; Kitina Nyamasyo & Odiara Kihima 2014; Kane & Kendall 2017). Even though the impacts of land use change on vultures have been widely acknowledged, there is still a lack of research on this topic, especially in Africa. In southern Africa land use varies considerably and changes in land use, such as the intensification of agriculture, expansion of cultivation, urbanisation, mining expansion, desertification, afforestation, and bush encroachment (by both indigenous and alien vegetation), are widespread. There is a need to determine which of these land use are more important for the persistence of African vultures (Botha et al. 2017). For example, Pfeiffer et al. (2015) showed the importance of subsistence farmland as a foraging habitat for Cape Vultures (*Gyps coprotheres*), thus allowing managers to better focus their conservation effort.

1.4 Southern Africa's Bearded Vultures

The Bearded Vulture (*Gypaetus barbatus*) is a large non-colonial, cliff-nesting scavenger; the breeding pairs can have one or more nests in their territories and they nest at high altitudes generally, 1,800 m above sea level (Brown 1989; García et al. 2009). Their diet consists predominantly of bones from the carcasses of wild and domestic ungulates (Margalida et al. 2009). They are distributed in the high mountainous areas of Africa, Europe, and Asia, and forage extensively over the surrounding areas. However, Bearded Vulture populations have been declining throughout their range, with the exception of Europe, where the population has increased as a result of an intensive reintroduction effort (Margalida et al. 2008; Acharya et al. 2010; Krüger et al. 2014b). In Africa, isolated populations remain in the Ethiopian highlands, and in southern Africa. In southern Africa, between the 1960 and 2010s, the Bearded Vulture breeding range has contracted by 27% and the breeding population range has declined by between 32 and 51%; currently, only 109 occupied territories remain (Krüger et al. 2014a, 2014b). Today, the entire population in southern Africa is restricted to the Lesotho highlands and the Drakensberg escarpment and associated/nearby mountains in South Africa. The primary threats are unintentional poisoning (poison baits and lead) and collisions with energy infrastructure while

secondary threats include habitat disturbance and degradation (Botha et al. 2017). Consequently, the southern African population has been classified regionally as Critically Endangered, due to the declining trend and the ongoing threats faced by the population (Krüger 2015).

To prioritise actions for Bearded Vulture protection, information on their habitat use is required. Establishing patterns of habitat use, for any species requires knowledge on their distribution, variation in resource availability, and identification of important habitat-related features and potential limiting factors. Previous studies have described the species home range, which show considerable variation between age groups (Krüger et al. 2014b; Krüger and Amar 2017). An average adult home range is 286 km^2, which is 1% the size of the average foraging ranges of non-adults (10 540 –25 985 km^2); when breeding their home range is even smaller (95 km^2) (Krüger et al. 2014b). However, range size and use between sexes does not differ across any age classes (Krüger et al. 2014b). Thus, each age class experiences different degrees of exposure to threats. Reid et al. (2015) found that distance to nest, supplementary feeding site, and topographical variables influenced habitat selection of Bearded Vultures. A study by Krüger et al. (2015) showed that nest abandonment by Bearded Vultures was associated with increasing anthropogenic activities (settlement and power line density) and those territories with feeding sites in close proximity were more likely to remain occupied. However, to date no research has explored space use and selection for this species based on habitat type in Africa. Therefore, detailed information on the spatial habitat selection by Bearded Vultures will facilitate understanding of their resource requirements and predict the impacts of changing land uses

1.5 Aims, hypothesis and objectives

This study aimed to use data obtained from GPS tagged adult Bearded Vultures to determine their habitat selection pattern. The specific objectives were to: 1) identify the different habitat types selected and avoided by the Bearded Vulture in their current distribution range, which corresponds to the third orders of selection, following the definition of Johnson (1980), and 2) investigate the impact of human settlement on the space use of the Bearded Vulture in their current distribution range. We hypothesise that certain habitat types will be selected over others. For instance, open habitat types such as grassland (e.g., commercial livestock farms, communal grazing lands) are predicted to be selected as they have the greatest visibility, accessibility, and possible abundance of food, whereas forests and plantations are predicted to be avoided due to low ungulate numbers and poor visibility of carcasses. Areas with high densities of human settlements are also predicted to be avoided due to lower food availability and higher levels of disturbance. Vultures are also expected to preferentially use areas further away from these urbanised areas.

2. Methodology

2.1 Study area

The Bearded Vultures were tagged in the Maloti-Drakensberg region of southern Africa. The area encompasses the lowlands, highlands and Maloti Mountains of Lesotho and the Drakensberg mountain range of the Free State, KwaZulu-Natal, and Eastern Cape provinces of South Africa between 28˚00'00"–32˚00'00" S and 27˚00'00"–30˚00'00" E (Fig. 1). The entire population of Bearded Vultures is restricted to our study area (Krüger et al. 2014b). The topography in the area varies greatly, with several peaks and plateaus, cliffs of basalt and sandstone, deep valleys, and intervening spurs; with an average altitude of 2 200 m above sea level (1 280–3 500 m) (Krüger et al. 2014b). The study area consists of various types of land uses, including commercial and subsistence cropping, commercial and subsistence livestock grazing, protected areas, afforestation, settlement, and mining (Zunckel 2007). A large portion of the international boundary between Lesotho and South Africa comprises the Maloti-Drakensberg Park World Heritage Site, an inland protected area totalling 2428 km^2.

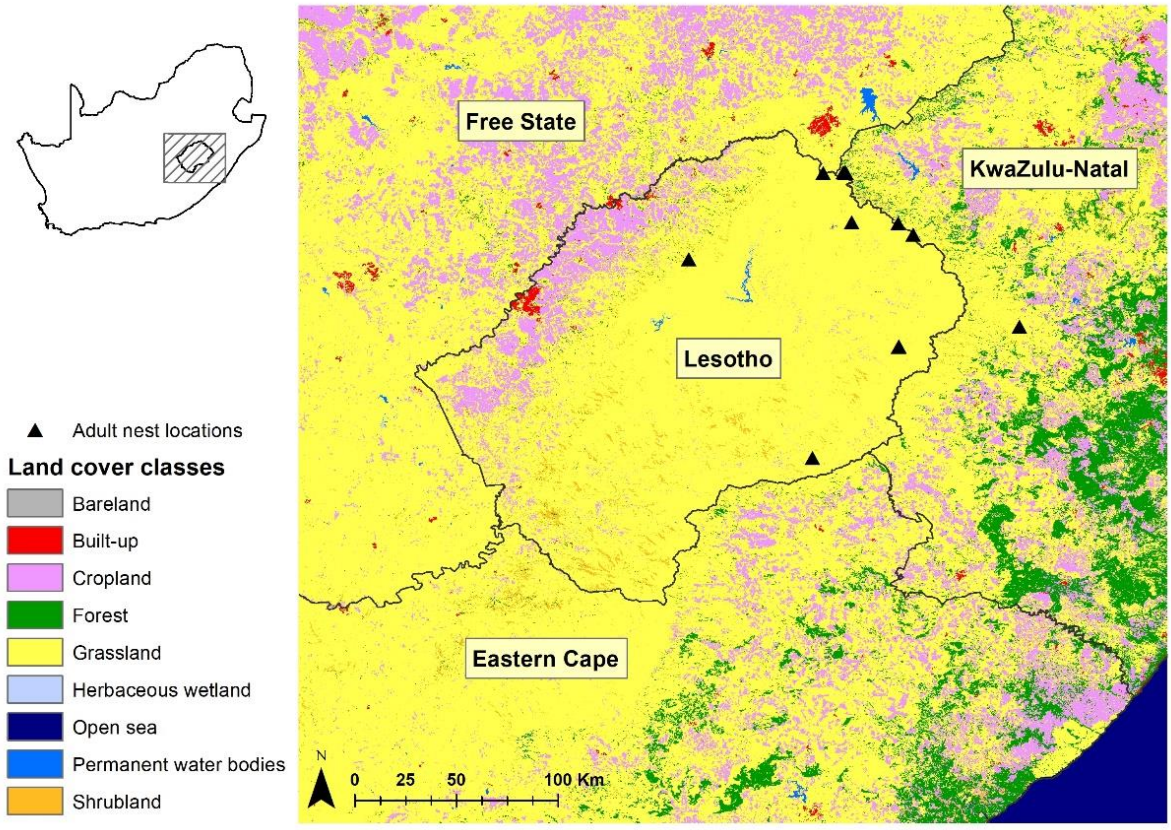

Figure 1. Map of the study area in southern Africa showing land cover and nest site locations (▲) for the nine adult Bearded Vulture used in this study. The land cover is from the Copernicus Global Land Service – Land Cover V3.0 (100m resolution). Map created using ArcGIS v10.3.

2.2 GPS tracking

All adult Bearded Vultures were fitted with GPS satellite transmitters (70 g solar-powered GPS-PTT-100s (Microwave Telemetry Inc., Columbia, MD, USA)). The transmitter provided the location (accurate to within 5 – 20 m, Krüger et al. 2014b), height, and the speed of each bird every hour from 05:00 to 20:00 h (SAST). For the study, we filtered the data at two levels: 1) selected the data spanning the years 2013 to 2017 and, 2) we selected only adult Bearded Vultures, these included birds caught as adults and birds that became adults during the period (n = 9).

2.3 Raster processing

Since the distribution of the Bearded Vulture spans both Lesotho and South Africa we required land cover layer data covering both countries to be able to explore habitat selection. Unfortunately, we only had access to the high-resolution National Land Cover data for South Africa (NLC30) (30 m resolution). Therefore, to have consistent information for both countries, we evaluated three global land cover layers available: 1) European Space Agency Climate Change Initiative Land Cover 300 m resolution (ESA CCI-LC300), overall global accuracy 71.1%, 2) Copernicus Global Land Service – Land Cover V3.0 with 100 m resolution (CGLS-LC100), overall global accuracy 80.6% and, 3) Global land with 30 m resolution (GL30), overall global accuracy 75.82%. To be certain that the accuracy applies for our study area, we compared the mapping accuracy for each land cover type with the NLC30 which was assumed to be a true representation of land cover types. The classification systems of GL30, ESA CCI-LC300, CGLS-LC100 and NLC were converted to be consistent across layers (Appendix 1). The NLC30 was resampled by majority (i.e., resample a cell according to the most frequently occurring value) to match the coarser scale layers respectively for comparison; for example, if five of the pixels in one target aggregation unit (3 x 3 pixel in total) in NLC30 were grassland while the other four were forest, then the unit would be classified as grassland in the aggregation map. Once the layers were processed, 1500 random points were generated, and land cover classes under each point were extracted for comparison with the NLC30 using a confusion matrix (Appendix 1). Overall, the CGLS-LC100 had the highest similarity to the NLC30 (62.4%), followed by GL30 (59.07%) and the ESA CCI-LC300 (53.2%). We, therefore, selected the 2015 CGLS-LC100 layer for the analysis. All the land cover processing was carried out using ArcGIS v10.3 (ESRI, Redlands, USA).

In terms of class-specific accuracy, forest and grassland had the highest accuracy. The class accuracy of cropland, built-up areas, and water were moderate while wetland and shrubland had the lowest class accuracy (Appendix 2A & 2B). Also, shrubland was often confused with the forest and grassland classes. Taking these into consideration, we aggregated the 23 global land-cover types (hereafter called habitat types) into four categories to reduce the complexity of the layer and our analyses. The final categories were “Cropland” (composed of class 40), “Forest” (composed of class 11, 112, 113, 114, 115, 116, 121, 122, 123, 124, 125, 126), “Grassland” (composed of class 20, 30) and “others” (composed of class 50,

60, 80, 90, 200) (Appendix 2C). To answer our research question on the impact of human settlement density, we used a High-Resolution Settlement Layer; which maps buildings with a spatial resolution of approximately 30 m (Tiecke et al. 2017). Due to its high resolution, the layer contains a high proportion of isolated single pixels and a single building (e.g., farm buildings) could easily be represented by up to sixteen pixels (Appendix 3B). This made it difficult to distinguish avoidance from low and high human settlement density. To circumvent this issue, we aggregated the layer to 210 m resolution with each pixel value representing the percentage of pixel classified as building according to the initial finer resolution layer. The, values could range from 0-100% and represent the density of human settlement; hereafter called 'built-up'. Additionally, because we already know that Bearded Vulture habitat use is influenced by topography, we extracted topographical variables such as slope, elevation, roughness, and a vector ruggedness measure using the 30 m resolution Digital Elevation Model layer.

2.4 Statistical analysis of habitat selection

To determine the habitat selection of adult Bearded Vultures, we firstly determined the approximate area of the home range for each bird, by calculating the 99th percentile of the normal maximum ranging distance from the nest site of that bird. Fixes outside of this ranging distance were excluded. We then generated random pseudo-absence points within a buffer circle with a radius equal to the maximum ranging distance around each individual nest, with respect to tracking fixes in ratio of three-to-one, similar to Reid et al. (2015). Based on previous studies (Hirzel et al. 2004; Reid et al. 2015; Margalida et al. 2016), we chose a primary set of nine explanatory variables to characterise each presence and pseudoabsence points: these include elevation (m), slope (degree), topography ruggedness index, vector ruggedness measure, roughness, percentage of built-up cover (%), distance to the nest (km), and nearest supplementary feeding sites (km). To avoid co-linearity, we calculated the Pearson correlation among all pairs of candidate variables (Appendix 4) and removed one of the variables if they were strongly correlated ($r \geq 0.6$). The variables slope, topography ruggedness index, and roughness were highly correlated. We decided to retain slope, because Reid et al. (2015) showed that it played an important role in habitat selection by Bearded Vultures. We used generalised linear mixed models (GLMM) from the "lme4" R-package (Bates et al. 2020), to evaluate the presence/absence of Bearded Vultures (vulture points = 1; pseudo-absence points = 0; binomial response with a logit function). We scaled all the explanatory variables as they all had different units, to improve model convergence and provide meaningful comparison of effect sizes. To account for repeated fixes from the same bird, we included individual bird identity as a random factor.

Our first model looked at selection of percentage of built-up area, explanatory variables entered in the GLMM included elevation (m), slope (degrees), vector ruggedness measure, distance to nest (km), distance to nearest supplementary feeding site (km), and percentage of built-up area (%) (see Table 1). We used the result from the first model to assess the percentage of built-up areas within a 210 m resolution pixel at which the probability of use by the Bearded Vultures declined by 50%. Consequently, we created a new layer by filtering out all the pixels with ≤ 50% probability of use by the Bearded Vultures and then calculated distance to the nearest built-up area for each presence/pseudoabsence location. For modelling habitat selection, we repeated the previous model, but this time included distance to the nearest built-up areas (instead of the percentage of built-up area); and included another variable: describing habitat types at four levels (see Table 2). For both models, using the 'dredge' function from the "MuMIn" R-package (Barton & Barton 2020) we compared all possible variable combinations, then selected model with the lowest corrected Akaike Information Criteria (AICc). We further tested for multicollinearity among variables in the best model by examining the Variance Inflation Factor (VIF) using the "car" R-package (Fox & Weisberg 2019). To assess the models' performance, we used the receiver operator curves (ROC) using the R-package "pROC" (Robin et al. 2011); it evaluates the trade-off of the model in making a true positive prediction (sensitivity) versus a false prediction (specificity). Then we calculated area under curve (AUC) to determine the model performance; theoretically an accurate model will have AUC ≥ 0.9, whereas a poor model will have AUC < 0.7 (Swets 1988). All statistical procedures were performed in R version 4.0.3 (R Core Team 2020), and figures were produced using the "effects" R-package (Fox & Weisberg 2019).

Table 1. All candidate variables entered in the initial model for built-up area selection.

Variables	Description
Elevation	Altitude of fixes/pseudo absence points above sea level (m).
Slope	Steepness of the cliffs (in degrees).
Vector ruggedness measure	Measure of terrain ruggedness as the variation in three-dimensional orientation of grid cells within a neighbourhood.
Distance to nest	Linear distance to nest (km).
Distance to feeding site	Linear distance to nearest Supplementary feeding site (km).
Built-up area	Building percentage (%) in a 210m resolution layer.

Table 2. All candidate variables entered in the initial model for habitat selection.

Variables	Description
Elevation	Altitude of fixes/pseudo absence points above sea level (m)
Slope	Steepness of the cliffs (in degrees)
Vector ruggedness measure	Measure of terrain ruggedness as the variation in three-dimensional orientation of grid cells within a neighbourhood
Distance to nest	Linear distance to nest (km)
Distance to feeding site	Linear distance to nearest feeding site (km)
Distance to Built-up area	Linear distance to nearest built-up area (km)
Land cover	**Grassland:** Plants without persistent stem or shoots above ground and lacking definite firm structure. With varying degree of tree and shrub cover **Forest:** Mixture of open and closed forest with tree canopy >15%. The trees can be evergreen and deciduous. **Cropland**: Lands covered with temporary crops followed by harvest and a bare soil period. **Other:** Land cover classes making less than 2% of the study area. These include bare land, wetland, water bodies and urban areas.

3. Results

We obtained a total of 65 427 GPS locations from nine adult Bearded Vultures from 2013 to 2017. Within the entire area used by our tracked Bearded Vultures, 55.9% of the fixes fell in Lesotho and 44.1 % in South Africa. The combined population home range of the studied vultures was, 12 6739 km^2. Within the area exploited by these tracked vultures, grassland accounted for 70% of the total area, followed by cropland (19.5%), forest (9.3%), and other (1.2%).

3.1 Habitat selection – percentage of built-up areas

Our top model incorporated all the variables and suggested that Bearded Vultures responded to the topographic features of elevation, ruggedness and slope, the distance from the nest, the distance from a supplementary feeding site, and percentage of built-up area (Appendix 5). The model also indicated that Bearded Vultures' use declined with an increasing percentage of built-up area. The probability of use decreases by 50% for area with > 27.1 % of built-up cover. The probability of an area being used by a Bearded Vulture within its home range increased closer to its nest site and closer to supplementary feeding sites; use decreased by 50% at 12.2 km from the nest site and by 50% at 14.1 km from a supplementary feeding site. The use of an area increased with the steepness of slope and with greater terrain ruggedness (see Table 3). The AUC for this model was 0.950, indicating a very good model fit.

Table 3. GLMM results showing the fixed effects (scaled) estimates for all the variables in the best model exploring habitat selection by the Bearded Vultures. The model included, percentage built-up area, distance to nest, distance to nearest supplementary feeding site, slope, elevation, and vector ruggedness measure.

Model: Built-up area selection	Estimate	SE	CI (2.5%)	CI (97.5%)	z value	Pr(>|z|)
Intercept	-3.78	0.48	-4.71	-2.84	-7.92	< 0.001
Elevation	0.65	0.01	0.63	0.68	56.23	< 0.001
Slope	0.69	0.01	0.67	0.71	79.41	< 0.001
Vector ruggedness measure	0.54	0.01	0.53	0.56	64.78	< 0.001
Distance from nest	-5.59	0.05	-5.69	-5.49	-115.56	< 0.001
Distance from supplementary feeding site	-1.48	0.03	-1.54	-1.42	-46.78	< 0.001
Percentage built-up cover	-0.13	0.02	-0.16	-0.09	-7.42	< 0.001

3.2 Habitat selection – distance to built-up areas

Our most parsimonious model showed the same relationship with topography (excluding elevation), distance from nest, distance to nearest supplementary feeding site as with our previous analysis; additionally, the variables distance to built-up area and habitat types were also important (Appendix 6). Bearded Vultures selected grassland areas and avoided areas of forest as confirmed by pairwise comparisons (Fig. 2). Cropland was neither selected nor avoided but was used in proportion to its availability (Fig. 2). The probability of an area being used by a Bearded Vulture within its home range increased closer to its nest site and closer to feeding sites; when controlling for habitat type as in this model, use decreased by 50% at 13.1 km from the nest site and by 50% at 21.2 km from a supplementary feeding site. The use of an area increased with the steepness of slope and with greater terrain ruggedness (see Table 4). The probability of use of an area by Bearded Vultures increased further away from a built-up area; the use of an area increased by 50% at 5.1 km from a built-up area. The AUC for this model was 0.949, indicating a very good model fit.

Table 4. GLMM results showing the fixed effects (scaled) estimates for all the variables in the best model exploring habitat selection by the Bearded Vultures. The model included, Land cover classes (four level), distance to nest, distance to nearest supplementary feeding site, distance to nearest built-up area, slope, and vector ruggedness measure.

Model: Habitat type selection	Estimate	SE	CI (2.5%)	CI (97.5%)	z value	Pr(>|z|)
Intercept	-4.32	0.47	-5.25	-3.4	-9.19	< 0.001
Distance from nest	-6.36	0.05	-6.46	-6.27	-131.01	< 0.001
Distance from supplementary feeding site	-1.02	0.03	-1.08	-0.98	-33.5	< 0.001
Slope	0.72	0.01	0.7	0.74	84.1	< 0.001
Vector ruggedness measure	0.58	0.01	0.56	0.59	69.52	< 0.001
Land cover: Forest	-0.62	0.09	-0.79	-0.44	-7.12	< 0.001
Land cover: Grassland	0.57	0.07	0.44	0.7	8.32	< 0.001
Land cover: Others	0.04	0.17	-0.29	0.38	0.25	0.8
Distance from built-up areas	0.09	0.01	0.07	0.1	9.18	< 0.001

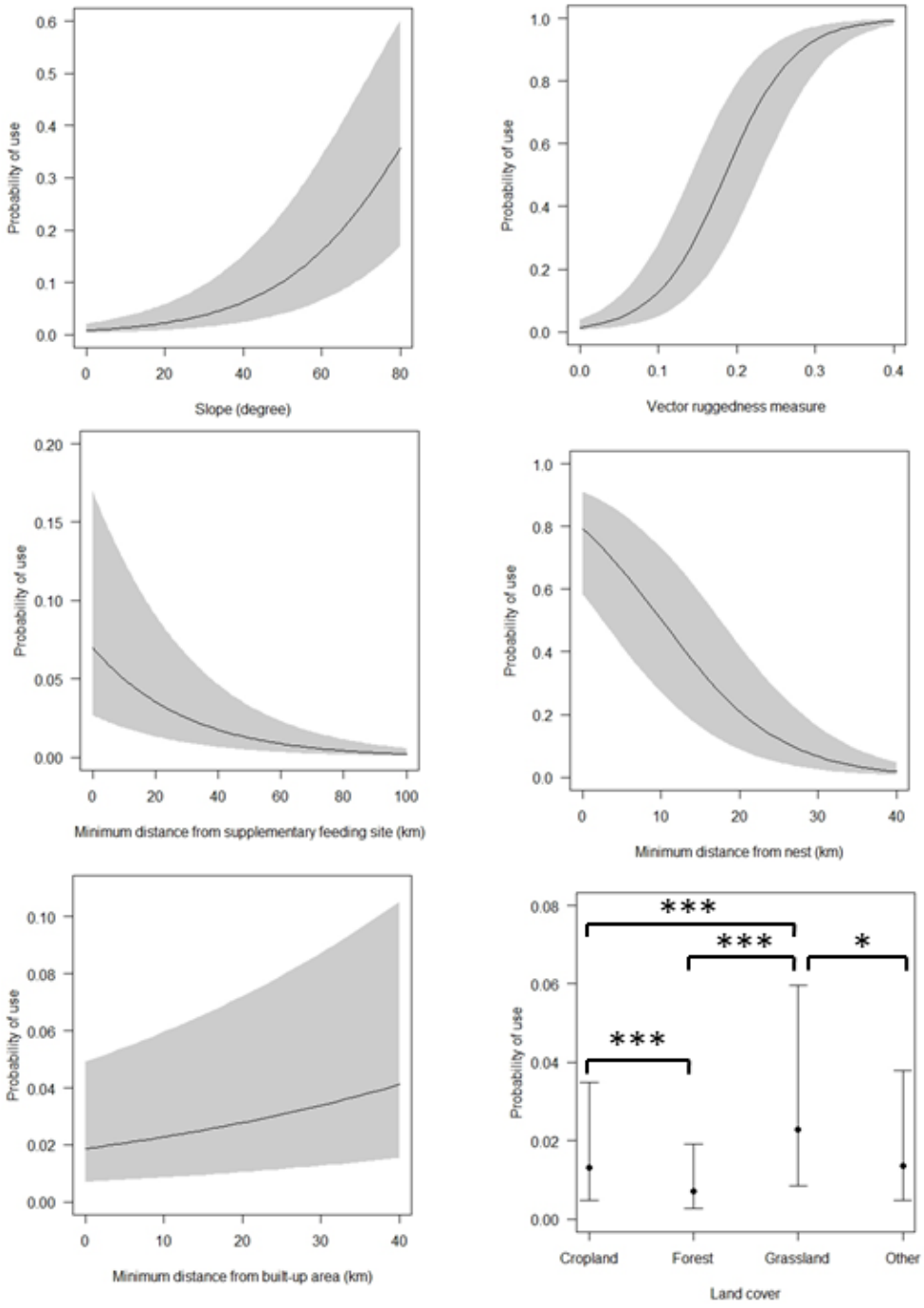

Figure 2. GLMM predictive fixed-effect plots showing the modelled habitat utilisation of Bearded Vultures according to several habitat features: topographic slope, vector ruggedness measure (vrm), distance from nest, distance from supplementary feeding site, distance from built-up area and land cover. Solid line shows predicted relationship, with 95% confidence limits captured within grey shaded areas. The bottom right panel shows the predicted probability of habitat types (four level), with 95% confidence limits represented by vertical lines. * $p < 0.01$; *** $p < 0.0001$ indicating significance of pairwise differences in lsmeans.

4. Discussion

4.1 Habitat selection

Our results, in accordance with past studies, indicated that the species typically selected areas with steeper slopes, more rugged terrain, as well as areas closer to the nest and those closer to supplementary feeding sites (Reid et al. 2015). After controlling for these important variables, we found that forest areas were avoided whereas grassland was selected. Most importantly, from the perspective of this study, we also found that Bearded Vultures avoided areas with a high percentage of built-up cover or areas close to these.

The habitat selection of Bearded Vultures in this study supports their description as a species of high-altitude grasslands and escarpments (Krüger et al. 2015; Reid et al. 2015). The landscape features selected by the species also promote wind conditions that facilitate orographic lift, which increases energy efficiency and reduces wing loading during flight while foraging (Hirzel et al. 2004; Murgatroyd et al. 2018). Given the fact that the species is territorial and a central place forager, our study showed, unsurprisingly, that vultures were more likely to use areas closer to their nest than those further away (Houston & McNamara 1985; Reid et al. 2015). Our study also showed that adult Bearded Vultures selected areas closer to feeding sites. Interestingly, in Europe, supplementary feeding sites did not seem to play such an important role in space used by Bearded Vultures (Margalida et al. 2016). Margalida et al. (2016), suggested that adult Bearded Vultures in the Pyrenees are more experienced in exploiting unpredictable higher-quality prey more efficiently than sub-adult vultures. There could be two possible reasons why our results differ from theirs; 1) there are not enough wild high-quality ungulate carcasses in southern Africa to be exploited by Bearded Vultures (Moleón et al. 2020), and 2) Bearded Vultures may have developed a dependency on supplementary feeding sites for their food supply (Brink et al. 2020b).

The foraging behaviour of adult Bearded Vultures will be linked to habitat choice, functional responses and the trade-offs between food seeking and safety, and net energy gain (Stephens 2008; Margalida et al. 2016). Given that Bearded Vultures rely on vision to locate carrion, it is not surprising that forested habitats are avoided. Afforested areas also harbour fewer ungulates (Armstrong et al. 1998). The same pattern was observed for Bearded Vultures in the Italian alps where they avoided forested habitats (Bogliani et al. 2011). These results also suggest that Bearded Vultures may be susceptible to the increasing spread of invasive alien plants, and the extent of bush encroachment in southern Africa (O'Connor et al. 2014). Bush encroachment in the foraging range of the Bearded Vulture, could lead to a decrease in the visibility and accessibility of carrion. Such an impact has already been reported in species such as the Cape Vulture (Bamford et al. 2007). On the other hand, the communal rangeland in Lesotho and its extensive stock rearing practices coupled with livestock deaths, might be providing the appropriate habitat for foraging (Krüger et al. 2015), thus explaining the preferential use of grassland.

Studies showed that Griffon Vultures (Martin-Díaz et al. 2020) and Egyptian Vultures (*Neophron percnopterus*) (Buechley et al. 2018), also selected grassland. This indicates the importance of open grassland habitat for vultures relying on visual cues in locating carrions.

Most importantly, to address the aims of this study, we found that Bearded Vultures actively avoided areas with a high percentage of built-up cover and their vicinity. There could be two reasons for this' behaviour; firstly, these areas may have a lower density of carrion. Secondly, urbanization is often associated with habitat alteration, infrastructure development (e.g., power lines and roads), and noise pollution. Encountering this human disturbance when previously foraging may have taught the species to avoid those areas. The avoidance of urbanized area was also documented by Pfeiffer et al. (2015) for Cape Vulture in South Africa. In concordance with Krüger et al. (2015), which linked territorial abandonment by Bearded Vultures to human settlements density; our findings suggest that together with additional mortalities (e.g. poisoning or collisions with power lines), reduction in the quality of the foraging habitat may also be contributing to increased territorial abandonment. Interestingly, a study in El Salvador by Campbell (2014) showed that Turkey (*Cathartes aura*) and Black (*Coragyps atratus*) Vultures were frequently found in densely populated areas; showing their adaptive capacity to the changing environment. Similarly, Hooded Vultures (*Necrosyrtes monachus*) were frequently detected in area of high human density in Guinea-Bissau (Henriques et al. 2018). This contrast indicates that Bearded Vultures may be more sensitive to high human settlement density and may have a lower adaptive capacity.

4.2 Caveats

Although our model has potential conservation applications, caution must still be applied in its interpretation. For example, the model shows avoidance of forest cover but, in the land cover layer used for this study, there is no distinction between planted forest and indigenous forest, and there are known errors in correctly identifying shrublands. Most of the Afromontane forest and shrubland occurs in the Maloti-Drakensberg Transfrontier Park, where they are patchily distributed on a small scale and harbour a diversity of wild ungulates. The movement of wild ungulates from Afromontane forest or shrubland to open grassland could result in potential carcasses appearing in an unpredictable way in space and time, either by natural death, predation, or poaching. In this case, the diversity of natural habitat will facilitate the availability of carcasses for the scavenger guild (Selva & Fortuna 2007). On the other hand, plantations are monocultures, and thus, are less likely to contain a high density and diversity of wild ungulates, which could lead to a decrease in the availability and accessibility of carrions. Forestry plantations are also likely to be more extensive and contiguous than natural forested areas, which will further decrease their value as foraging locations for this species. Therefore, an increase in forest cover through commercial plantation or bush encroachment may lead to a reduction of foraging habitat, while existing patches of indigenous forest are not to be interpreted in the same way. Also, even though cropland was not identified as a particularly important variable in the model, it does not necessarily

mean that it has no impact on Bearded Vultures. It should also be noted that the layer used in our analysis tended to underestimate cropland, and hence, could have masked its effect on habitat selection.

4.3 Conservation implications

With increasing anthropogenic threats outside protected areas, animals are forced to either coexist in a human altered landscape or perish. Thus, there is an increasing need for conservation intervention outside protected areas to reduce the risk of non-natural mortalities, but also potentially to increase the quality of foraging habitat. The findings of this study emphasise that increases in afforestation and human settlement expansion within the distributional range of Bearded Vultures will reduce available foraging habitat. Loss of foraging area may, in turn, result in reduced food availability and/or may force birds to forage over greater distances to find sufficient food, thereby increasing energetic costs and bringing them into contact with additional mortality risk factors such as power lines, wind turbines and poisons. Further increases in adult mortality of Bearded Vultures should be avoided at all costs (Rushworth & Krüger 2014). Future collision risk models should incorporate land cover information in addition to topographic, nest site and feeding site information (Rushworth & Krüger 2014; Reid et al. 2015). Development projects such as wind farms may be better placed within existing large contiguous areas of afforestation or around densely settled areas, both of which are avoided by Bearded Vultures.

Based on the observed avoidance of afforested areas, conservation managers should consider the impact of commercial plantations, expansion of alien invasive trees, such as those in the Pinus, Acacia, and Eucalyptus genera (Ezemvelo KZN Wildlife & MTEC, 2016), all of which could lead to a reduction in foraging habitat of Bearded Vultures. It is therefore important to control the extent of afforestation, invasive alien trees and bush encroachment within the range of breeding adult Bearded Vultures. Government-funded invasive alien plant control programmes, and enforcement actions relating to the spread of listed alien plants, should be prioritised within the adult Bearded Vulture range. Conservationists, landowners, and land use planners need to work together to ensure an appropriate balance of land covers and land uses are retained within the breeding range of Bearded Vultures. To compensate for the loss of foraging habitat, it may be necessary to establish supplementary feeding sites in active breeding ranges with higher proportions of afforestation and/or settlement, or where the expansion of such is anticipated. Likewise, to achieve the population restoration objectives (Department of Environmental Affairs, 2014), the establishment of feeding sites within abandoned territories with high proportions of afforestation and/or human settlement may be necessary. The results could also be used to better guide the selection of potential reintroduction sites (Brink et al. 2020a). Finally, the approach used in this study can be easily replicated for other species and also for different age classes of Bearded Vulture using similar tracking data.

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4.4 Recommendations for future research

Although this study has provided an insight into the types of habitats selected by adult Bearded Vultures, additional research would be required to understand habitat selection at a finer scale and for different age classes. However, the lack of a fine-scale land cover layer for Lesotho (where the core of the Bearded Vulture range lies) is problematic. For example, we used a land cover layer of 100m resolution which did not distinguish accurately between all the land cover classes present, at least when compared with the NLC of South Africa (Appendix 2A). These errors limit the resolution and accuracy of our habitat selection analysis. A first step would be to create accurate fine-scale land cover layers for Lesotho. Secondly, age-related habitat selection patterns for a species like the Bearded Vulture that explores vast areas during its sub-adult years and becomes more and more territorial when becoming sexually mature (Margalida et al. 2016) could also be explored in the future. Thirdly, it would be interesting to investigate seasonal requirements, given that food availability and vegetation cover might fluctuate with season (Arkumarev et al. 2021). With the spread of invasive alien trees, understanding their effects on habitat selection by vultures or any other species will be crucial for future management intervention. Understanding to what extent Bearded Vultures are dependent on supplementary feeding sites would be important in helping to maintain the current range or when expanding the species range (e.g., the creation of vulture restaurants in re-introduction sites) (Schabo et al. 2017). Using fine-scale NLC30 layer from 1990 to 2018 one could quantify levels of land use change in the past distribution range of Bearded Vultures, with a focus on human development, and investigate whether there is a threshold level above which territories area abandoned.

5. Conclusion

In today's constantly changing landscape, Bearded Vultures are increasingly exposed to anthropogenic threats. Understanding their pattern of habitat selection is crucial for their conservation. This study provides the first description of Bearded Vulture habitat selection in southern Africa, using data from birds tracked with GPS tags. In summary, we found that the birds selected grassland areas and avoided forest and built-up areas and their vicinity. The major limitation of this study remains the availability of fine-scale land cover data for Lesotho. Therefore, some caution is required when interpreting the results. Nevertheless, conservation measures based on these findings may help minimise the impacts of land use change within the adult Bearded Vultures' breeding range. We hope that in near future this analysis will be repeated using finer scale land cover data once available for the full range of the species.

6. References

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Appendices

Appendix 1. Detailed classification systems of the three datasets (GL30, CGLS-LC100, ESA CCI-LC300) and the target conversion land cover classification (NLC).

Target type	**Conversion type**		
NLC	**GL 30**	**CGLS-LC 100**	**ESA CCI-LC 300**
No Data	No Data	No Data	No Data
Barren land	Barren land	Bare/Sparse vegetation	Bare area and sparse vegetation
Built-up	Impervious	Urban	Urban
Cultivated	Cropland	Cropland	Rainfed cropland, Irrigated cropland, Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%), Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (< 50%)
Forest	Forest	Closed forest evergreen needle leaf, Closed forest deciduous needle leaf, Closed forest evergreen broad leaf, Closed forest deciduous broad leaf, Closed forest mixed and unknown, Open forest evergreen needle leaf, Open forest deciduous needle leaf, Open forest evergreen broad leaf, Open forest deciduous broad leaf, Open forest mixed and unknown	Tree cover, broadleaved, evergreen, closed to open (>15%), Tree cover, broadleaved, deciduous, closed to open (> 15%), Tree cover, needle leaved, evergreen, closed to open (> 15%), Tree cover, needle leaved, deciduous, closed to open (> 15%), Tree cover, mixed leaf type (broadleaved and needle leaved), Mosaic tree and shrub (>50%) / herbaceous cover (< 50%), Tree cover, flooded, fresh or brackish water.
Grassland	Grassland	Herbaceous vegetation	Mosaic herbaceous cover (>50%) / tree and shrub (<50%), Grassland
Shrubland	Shrubland	Shrubs	Shrubland
Waterbodies	Water	Permanent water bodies	Water
Wetland	Wetland	Herbaceous vegetation	Shrub or herbaceous cover, flooded, fresh-saline or brackish water, Tree cover, flooded, saline water

Appendix 2A. Confusion matrix result for CGLS-LC100, ESA CCI-LC300 and GLC30. User accuracy (UA) and Producer accuracy (PA). The land classes in horizontal rows represent the reference data (NLC30) and the ones in vertical columns represent the predicted land classes.

		Reference									
Layer	**Class Value**	**BL**	**BP**	**CL**	**FR**	**GR**	**SR**	**WA**	**WE**	**Total**	**UA (%)**
ESA CCI-LC 300	**Barren land (BL)**	**0**	0	0	0	1	0	0	0	1	0.00
	Built-up (BP)	0	**7**	1	3	3	0	0	1	15	46.67
	Cropland (CL)	8	36	**214**	27	109	0	0	2	396	54.04
	Forest (FR)	4	14	11	**87**	51	0	0	3	170	51.18
	Grassland (GR)	22	17	134	30	**484**	2	2	9	700	69.14
	Shrubland (SR)	4	7	18	44	131	**4**	4	0	212	1.89
	Waterbodies (WA)	0	0	0	1	1	0	**2**	0	4	50.00
	Wetland (WE)	0	0	0	2	0	0	0	**0**	2	0.00
	Total	38	81	378	194	780	6	8	15	**1500**	0.00
	PA (%)	0.00	8.64	56.61	44.85	62.05	66.67	25.00	0.00	0.00	**53.20**

		Reference									
Layer	**Class Value**	**BL**	**BP**	**CL**	**FR**	**GR**	**SR**	**WA**	**WE**	**Total**	**UA (%)**
CGLS-LC 100	**Barren land (BL)**	**0**	0	0	0	0	0	0	0	0	0.00
	Built-up (BP)	0	**21**	1	0	2	1	0	1	26	80.77
	Cropland (CL)	3	30	**178**	17	63	1	0	5	297	59.93
	Forest (FR)	0	4	20	**112**	21	0	0	2	159	70.44
	Grassland (GR)	27	50	179	87	**621**	9	4	14	991	62.66
	Shrubland (SR)	0	0	2	8	6	**0**	1	0	17	0.00
	Waterbodies (WA)	0	0	0	0	1	0	**3**	0	4	75.00
	Wetland (WE)	0	0	1	0	2	0	2	**1**	6	16.67
	Total	30	105	381	224	716	11	10	23	**1500**	0.00
	PA (%)	0.00	20.00	46.72	50.00	86.73	0.00	30.00	4.35	0.00	**62.40**

Layer	Class Value	Reference									
		BL	**BP**	**CL**	**FR**	**GR**	**SR**	**WA**	**WE**	**Total**	**UA (%)**
GL30	**Barren land (BL)**	**0**	0	0	0	0	0	0	0	0	0.00
	Built-up (BP)	0	**25**	1	1	3	0	1	0	31	80.65
	Cropland (CL)	4	20	**234**	29	87	1	0	3	378	61.90
	Forest (FR)	0	4	10	**93**	32	1	2	2	144	64.58
	Grassland (GR)	21	21	125	71	**520**	1	4	8	771	67.44
	Shrubland (SR)	8	4	26	22	97	**6**	1	1	165	3.64
	Waterbodies (WA)	0	0	0	0	2	0	**8**	0	10	80.00
	Wetland (WE)	0	0	0	0	0	0	0	**0**	0	0.00
	Total	33	75	396	216	741	9	16	14	**1500**	0.00
	PA (%)	0.00	33.33	59.09	43.06	70.18	66.67	50.00	0.00	0.00	**59.07**

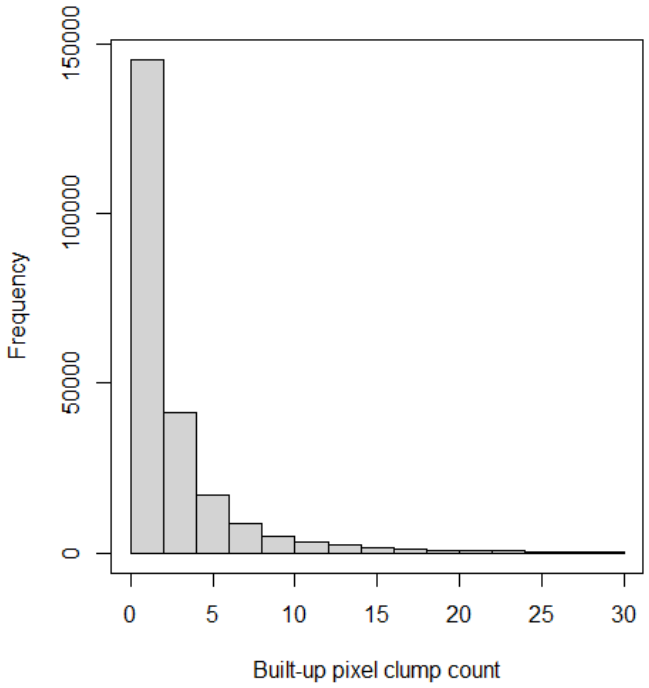
Appendix 2B. Overall mapping accuracy of the three land cover layers used in this study. The accuracies for the specific land cover types are the mean of the producer's and user's accuracy. Where OA = Overall accuracy; Cl = Cropland; Fr = Forest; Gr = Grassland; SR = Shrubland; WE = Wetland; WA = Water.

	Accuracy (%)								
	OA	**BL**	**BP**	**CL**	**FR**	**GR**	**SR**	**WA**	**WE**
CGLS-LC 100m	62.4	0	50.39	53.33	60.22	74.69	0	52.5	10.51
GL 30m	59.07	0	56.99	60.99	53.82	68.81	35.16	65	0
ESA CCI-LC 300m	53.2	0	27.66	55.33	48.02	65.59	34.28	37.5	0

Appendix 2C. Detailed classification systems of Landcover classes CGLS-LC100* and the final land cover classification used in this study.

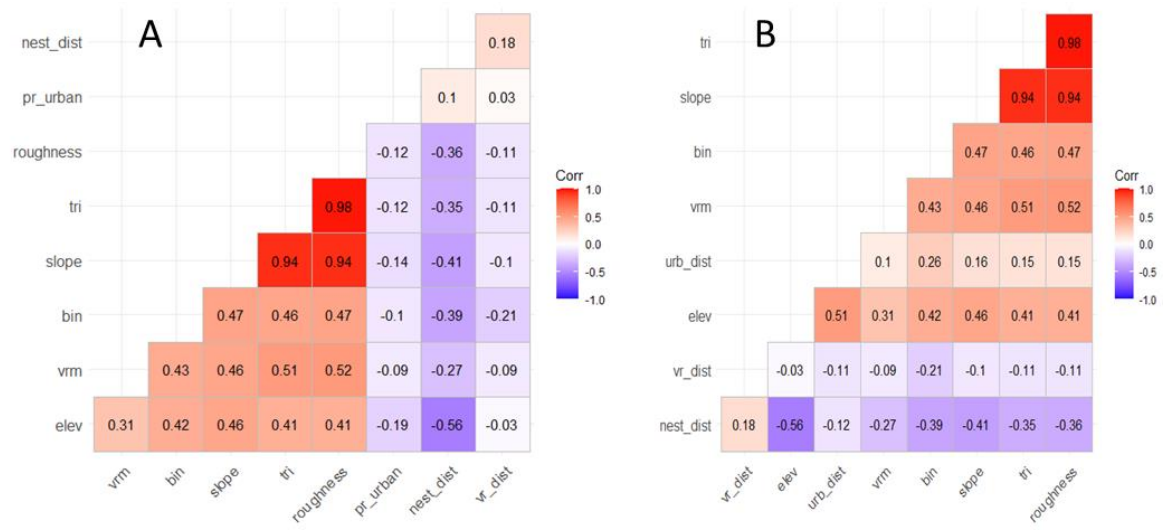
Map code	Land cover class CGLS-LC 100	Final classification
0	No input data available	No data
111	Closed forest, evergreen needle leaf	Forest
113	Closed forest, deciduous needle leaf	
112	Closed forest, evergreen, broad leaf	
114	Closed forest, deciduous broad leaf	
115	Closed forest, mixed	
116	Closed forest, unknown	
121	Open forest, evergreen needle leaf	
123	Open forest, deciduous needle leaf	
122	Open forest, evergreen broad leaf	
124	Open forest, deciduous broad leaf	
125	Open forest, mixed	
126	Open forest, unknown	
20	Shrubs	Grassland
30	Herbaceous vegetation	
40	Cultivated and managed vegetation/agriculture (cropland)	Cropland
90	Herbaceous wetland	Other
100	Moss and lichen	
60	Bare / sparse vegetation	
50	Urban / built up	
80	Permanent water bodies	
200	Open sea	

* Copernicus Global Land Service – Land Cover V3.0 100m resolution (2015)



Appendix 3A. The frequency distribution of built-up pixels in the distribution range of the Bearded Vulture in southern Africa. The figure shows a high frequency of one to five pixels representing built-up areas.

Appendix 3B. Randomly selected smallholding and high-density built-up areas represented by the HRSL layer where the yellow dots are the centre point of urbanized pixels/cells. We can see isolated structures such as (A, B and C) can be easily represented by one to fifteen pixels. (D) shows a densely built-up area. These images were extracted from Google earth pro version 7.3 (15th February 2021).



Appendix 4. Multi-collinearity result among the predictor variables prior to the final habitat selection models. Plot A shows multi-collinearity for habitat selection model – percentage of built-up area. Plot B shows multi-collinearity for habitat selection model – distance from built-up area. Elevation (elev); terrain ruggedness index (tri); terrain roughness (roughness); terrain slope (slope); fixes and pseudo-absence points (bin); vector ruggedness measure (vrm); distance to nearest supplementary feeding site (vr_dist); minimum distance from nest (nest_dist); percentage urban areas (pr_urban); distance to nearest built-up area (urb_dist).

Appendix 5. Akaike Information Criteria (AICc) and associated statistics for the top five Generalized linear mixed models for the habitat selection by Bearded Vultures in relation to distance from nest (nest_dist), distance to nearest supplementary feeding site (vr_dist), percentage of built-up cover (pr_urb), elevation (elev), slope and vector ruggedness measure (vrm).

Model	df	AICc	ΔAIC	W*i*
pr_urb + elev + slope + vrm + nest_dist + vr_dist	8	131192.8	0	1
elev + slope + vrm + nest_dist + vr_dist	7	131260.2	67.36	0
pr_urb + elev + slope + vrm + nest_dist	7	133426.8	2234.02	0
elev + slope + vrm + nest_dist	6	133496.7	2303.94	0
pr_urb + slope + vrm + nest_dist + vr_dist	7	134477.7	3284.87	0

Appendix 6. Akaike Information Criteria (AICc) and associated statistics for the top five Generalized linear mixed models for the habitat selection by Bearded Vulture in relation to habitat types (land_cover), distance from nest (nest_dist), distance to nearest supplementary feeding site (vr_dist), distance to nearest built-up area (urb_dist), slope and vector ruggedness measure (vrm).

Model	df	AICc	ΔAIC	W*i*
land_cover + nest_dist + vr_dist + urb_dist + slope + vrm	10	133982.5	0	1
land_cover + nest_dist + vr_dist + slope + vrm	9	134064.4	81.88	0
nest_dist + vr_dist + urb_dist + slope + vrm	7	134585.2	602.63	0
nest_dist + vr_dist + slope + vrm	6	134710.8	728.23	0
land_cover + nest_dist + slope + vrm	9	135118	1135.49	0