



Foraging Ranges of Immature African White-Backed (*Gyps africanus*) and Their Use of Protected Areas in Southern Africa

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Abstract

Vultures in the *Gyps* genus are declining globally. Multiple threats related to human activity have caused declines, especially outside protected areas. Addressing such threats requires the estimation of foraging ranges yet such declines are especially acute for widely ranging species such as the African white-backed vulture (*Gyps africanus*). We tracked six immature African white-backed vultures to study their movement patterns, their use of protected areas and the time they spent in the vicinity of protected areas. Their combined foraging ranges extended into six countries in southern Africa (mean (\pm SE) minimum of the vultures travelled more than 900 km from the capture site). All six vultures spent the majority of their time in protected areas; protected areas were very rarely visited whereas protected areas in northern Botswana and Zimbabwe were supplementary feeding sites regularly, with consequent reduced ranging behaviour, suggesting that individuals are making them susceptible to the full range of threats in the region. The standard approach of designating protected areas for protection of such wide-ranging species against threats in the wider landscape.

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Introduction

Vultures in the *Gyps* genus are obligate scavengers and are the main consumers of ungulate carcasses in /

flight, keen eyesight and social foraging behaviour enable them to locate sparsely and unpredictably distributed mammalian competitors [3], [4]. Their dependence upon such a transient and seasonally variable food supply makes the foraging behaviour of vultures as they attempt to secure a meal whenever an opportunity arises [4]. The ability of vultures to scavenge on the tissues of dead ungulates provides important ecosystem services by recycling carcasses, keeping energy flow and the spread of disease [5].

All eight *Gyps* vulture species found globally are currently declining due to multiple threats including habitat loss and emerging threats such as climate change and fatal collisions with wind turbines and electricity cables [6]–[8]. African vultures (including *Gyps africanus*) generally breed after their fourth year [4]) and relatively low reproductive rates make vulture populations vulnerable. Since the 1990s three species of *Gyps* vultures have declined by more than 95% in parts of Asia mainly due to the use of diclofenac on domestic livestock previously treated with the veterinary non-steroidal anti-inflammatory drug (NSAID), diclofenac. This has resulted in changes to scavenger community composition and a consequent increase in the number of vultures that die [7]. African *Gyps* vultures are equally sensitive to the toxic effects of diclofenac and other NSAIDs, and the future [11], [12].

Large declines in vulture populations have been documented in many parts of Africa, especially outside protected areas. African vultures are food shortages caused by improved animal husbandry and over-harvesting of wild ungulates. They consume carcasses laced with poisons intended to kill predators of livestock [4], [13]. For example, in the Masai Mara ecosystem in Kenya over a 30 year period there was a 52% decline in *Gyps* vulture numbers. Foraging over large areas make *Gyps* vultures particularly susceptible to mass poisoning events which tend to

Additional threats to vultures in Africa include fatal collisions and electrocutions with power lines, illegal harvesting of breeding sites, all of which are more prevalent in unprotected areas [7], [16]. Consequently, vulture populations are increasingly restricted to protected areas in different regions of Africa and the importance of protecting them is paramount to their future conservation [7], [13]–[15]. In an effort to provide an uncontaminated source of supplementary food, “vulture restaurants” have been used in southern Africa since the latter half of the twentieth century [17]. Although supplementary feeding schemes [17], the impact of supplementary feeding on vulture foraging ecology

The African white-backed vulture is widespread in sub-Saharan Africa and is often the most numerous vulture in savannah where it nests in trees in loose colonies [4]. They forage in groups and form extensive social foraging parties. They rely upon air currents which they rely upon to become airborne and gain altitude due to their large body size [2], [3]. Carcasses are typical and give rise to voracious feeding activity, with an individual vulture able to fill its crop with meat. The population has been estimated at 270,000 individuals the species has suffered significant declines through over-harvesting and its conservation status from Near Threatened to Endangered on the IUCN Red List [16]. Through re-sightings of individuals it is known that white-backed vultures are known to travel extensively [19], but a greater understanding of their movement patterns is required to assess their susceptibility to different threats [13].

In this study we use GPS telemetry to study the movement patterns of six immature African white-backed vultures. We use widely applied range estimation methods to determine the size, extent and seasonal variation of the vultures' foraging ranges in protected areas and supplementary feeding sites. Although the survival of breeding adult vultures is essential for population tracking immature birds as we expected them to range further and consequently be most exposed to multiple threats during their life [4], [17], [20]. As immature birds can comprise >50% of the population of African white-backed vultures on the total population size, even if adults, and therefore productivity, are relatively unaffected in the short term, the impact of human-induced versus natural mortality is poorly understood. This study therefore provides a first insight into vulture foraging in southern Africa based on continuous GPS tracking data for the first time.

Methods

Vulture captures

Vultures were caught at a supplementary feeding site for mammalian and avian scavengers at Mankwe Wild Camp east of Pilanesberg National Park (25°14'S, 27°05'E) in the North West Province of South Africa (Fig. 1). A vulture

steel frame overlaid with wire mesh and baited with domestic livestock or wild ungulate carcasses was used. Backed vultures were caught and fitted with GPS-GSM tracking units during three separate captures.

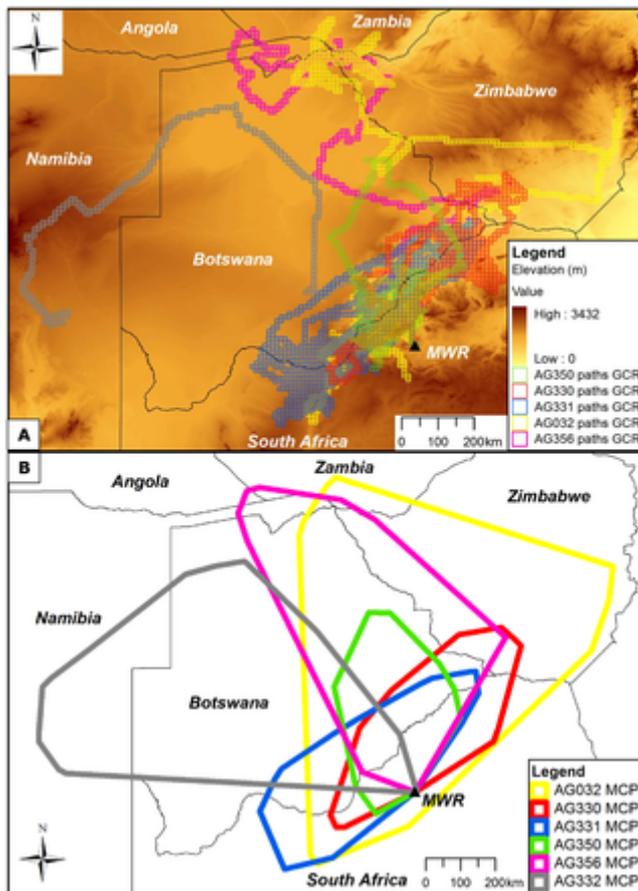


Figure 1. Foraging ranges represented by (A) path GCRs and (B) MCPs for six immature African white-backed vultures. Path GCRs (A) represent 10×10 km grid cells intersected by a continuous line between all consecutive GPS locations of each vulture. MCPs (B) were created by connecting the outermost GPS locations recorded for each vulture. MWR is the Murrelet Water Reserve indicated by a black triangle and “MWR”.

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GPS-GSM tracking units

Hawk105 GPS-GSM tracking units (Africa Wildlife Tracking Ltd., Pretoria, South Africa; www.awt.co.za) were attached to a ribbon backpack-style harness enclosed in flexible plastic tubing to prevent skin abrasions [23]. Each unit was attached to a white-backed vulture [4]) and was encased in hardened epoxy resin for protection and waterproofing. The unit recorded altitude above sea level, speed and direction of travel, date, time and temperature at three times per day: 07:00, 14:00 and 21:00. It also recorded positional dilution of precision (PDOP) value as a measure of the accuracy of each GPS location [24]. The data were transmitted to a database via the GSM network. Whenever a vulture was in an area without GSM coverage, up to 20,000 data points were transmitted when it returned to an area with coverage. It was anticipated that each unit would record and transmit data for up to 100 days. Units were inscribed with a unique four character code were also attached through the patagia of both wings of each vulture after release.

The procedures were approved by the Animal Use and Care Committee of the University of Pretoria (Protocol 000085 NW-09). The capture of vultures and the fitting of tracking units were granted by the Department of Agriculture, Conservation, Environmental and Forestry Affairs, Government, Republic of South Africa (Permit: 000085 NW-09).

Data analysis

For all spatial analyses the GPS locations were projected to the UTM coordinate system (WGS 1984 UTM 2 individual's GPS locations was assessed using Schoener's [25] index of autocorrelation in Home Range To

Distances between consecutive GPS locations were calculated for each vulture. A very conservative estima was obtained by summing the distances between all GPS locations recorded in a 24 hour period (i.e. (07:00 vulture, the total distance travelled, the mean distance between consecutive locations, and the mean and m

Estimates of the foraging ranges traversed by each vulture during their total tracking periods were calculate among techniques [27]. Firstly, foraging ranges were delineated with Minimum Convex Polygons (MCPs) us tendency to overestimate the actual area occupied by an animal by including outlying locations [28], they we tracking studies on *Gyps* vultures (e.g. [20]). Incremental area analysis was carried out in Ranges7 [29] to ir represented by MCPs reached an asymptote during the total tracking period [28]. For each individual, MCPs until all locations were used to produce the MCP for the total tracking period. A foraging range area curve w [28].

Secondly, fixed kernel density estimation (KDE) was used to delineate 95% and 50% contours to represent *ad hoc* bandwidth ($h_{ad\ hoc}$) designed to reduce over-smoothing of the KDE contours [27] was used for KDE i reducing the reference bandwidth (h_{ref}) in increments of 0.05 until the 95% contour became contiguous with etc.; [40], [41]). A 1000×1000 m raster cell size was used for KDE calculations. The Home Range Tools exte analysis.

Thirdly, grid cell range (GCR) estimates [28] were calculated using Hawth's Analysis Tools v3.27 [31]. A 10× connecting all consecutive locations for each individual, which represented the shortest assumed path trave the grid cells that were intersected by the path linking the consecutive locations provided an estimate of the [32]. The number of GPS locations in each grid cell was counted and core areas (core GCRs) were identifie than the mean number per cell across the overall range [33]. Path GCR estimates were also calculated for s of days) for each vulture in order to identify any seasonal patterns in ranging behaviour.

Vulture utilisation of officially protected areas was investigated separately for each vulture at the foraging ran shapefile of protected areas in southern Africa was created using data from the 2010 World Database on Pr protected areas [35] and 'national other areas' (i.e. protected areas uncategorized by IUCN) polygons from single polygon shapefile. All areas outside the protected areas polygons were designated as unprotected ar

Ivlev's electivity index [37] was used to evaluate whether protected areas were used by each vulture in prop $A_i)/(U_i + A_i)$, where E_i is the electivity index value, and U_i and A_i are the use and availability of protected are contour occupied by protected areas defined their availability to each vulture. Use of protected areas was de locations that were recorded inside protected areas within the 95% KDE contour. We also calculated the pr protected areas to estimate their use at the core foraging range scale. Ivlev's electivity index ranges from -1 with zero indicating that use of protected areas was proportional to their availability, while positive and nega than expected, respectively.

To estimate use of supplementary feeding sites, the proportion of stationary GPS locations recorded within in southern Africa was calculated separately for each vulture. The supplementary feeding sites were identifi questionnaire surveys between 2000 and 2010 (K. Wolter, unpublished data). Analyses were conducted for month for all vultures.

Results

The six vultures fitted with tracking units were all less than four years of age and all but one were tracked cc was tracked for 101 days before the tracking unit stopped transmitting data. The six tracking units recorded

high mean (\pm SE) accuracy of 2.4 ± 0.02 PDOP ($n = 4,326$ locations).

Foraging ranges and distances travelled

The combined foraging ranges of all six vultures extended across extensive areas of southern Africa (Fig. 1 (\pm SE) of $56,683 \pm 9,210$ km² (Table 1, Fig. 1A). MCPs included large areas that were never visited by the vultures boundaries for three vultures (AG330, AG331 and AG350; Fig. 2A, B), but for the three widest ranging vultures (AG332, AG333, AG334; Fig. 2C, D). Hereafter, unless otherwise stated, foraging range areas presented in the text are from GCR estimation representation of the vultures' actual movements.

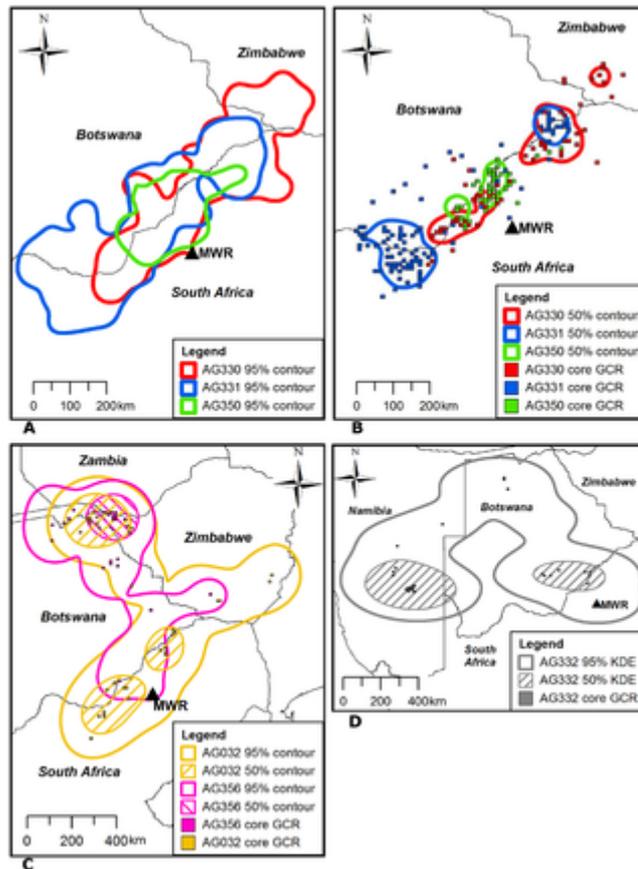


Figure 2. Overall and core foraging ranges for each individual.

95% KDE contours represent overall foraging ranges, 50% KDE contours and core GCRs represent core foraging ranges for AG330, AG331 and AG350; (C) shows the foraging ranges for AG032 and AG356; (D) shows the foraging ranges for AG332. The capture site is indicated by a black triangle and "MWR".

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Vulture ID	Tracking period (days)	Foraging range area estimates (km ²)					Distance estimates (km)				
		GPS locations	100% MCP	95% KDE	50% KDE	Path GCR	Core GCR	Total distance travelled	Mean (± SE) distance between consecutive locations	Maximum distance travelled/day	Mean (± SE) total distance travelled/day
AG356	301	895	149,508	123,861	26,716	19,400	3,700	3,699.03	8.89 ± 0.01	163.00	23.89 ± 2.08
AG331	313	905	176,801	148,014	28,088	30,000	11,400	15,293.89	16.87 ± 0.00	267.00	48.86 ± 2.59
AG330	300	898	126,810	47,110	8,810	40,100	4,200	11,375.71	12.57 ± 0.07	201.00	37.58 ± 2.20
AG355	298	897	202,691	202,613	20,947	19,900	2,000	3,602.76	7.80 ± 0.02	174.00	20.27 ± 1.91
AG332	308	878	386,703	282,793	11,810	79,000	4,300	8,454.76	19.70 ± 1.03	323.00	49.08 ± 2.85
AG333	303	903	430,130	263,083	13,000	30,000	2,700	2,582.17	8.84 ± 0.04	168.00	26.77 ± 1.84

Table 1. Foraging range and distance estimates for six immature African white-backed vultures.
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Foraging range area curves from incremental area analysis reached asymptotes that lasted for at least 50 d pattern of settled periods followed by exploratory movements beyond the existing MCP boundary occurred 1 were asymptotic at the end of their tracking periods, indicating that the tracking periods were sufficient to pr datasets for each of the six vultures were individually significantly autocorrelated, with a mean (± SE) Schoe

The mean (± SE) and maximum speed of all recorded moving (≥ 10 km·h⁻¹) GPS locations was 51.13±0.59 (± SE) distance travelled per day ranged from 22.27±2.13 km for AG356 to 48.86±2.59 km for AG331 (Table day. AG331 travelled the furthest during the total tracking period, moving 15,293 km in 313 days. GPS locat for three vultures. Following its capture, AG332 travelled north through Botswana before proceeding to sout foraging range of 28,400 km² in 101 days (Fig. 2D). AG356 also travelled north immediately after capture, n to the Victoria Falls region (17°55'S, 25°50'E) of Zimbabwe where it remained for a three month period (Fig. south-west Angola, returning to north-east Zimbabwe through northern Botswana. After spending 3.5 month Africa, AG032 travelled north through southern Zimbabwe to north-east Botswana and north-west Zimbabwe travelled over 8,454 km and occupied an overall range of 74,500 km², at one point moving 520 km across th AG356 entered a total of five and six different countries, respectively (Fig. 2C).

The foraging ranges of the remaining three vultures (AG330, AG331 and AG350) extended across the Bots orientated in a south-west to north-east direction from the Vryburg (21°03'S, 29°21'E) region of South Africa south-west Zimbabwe (Fig. 2A). KDE and GCR analyses showed that these three vultures, as well as AG03 South Africa-Botswana border (Fig. 2B).

Monthly path GCR estimates ranged from 600 to 22,200 km² (mean ± SE = 9,878±846 km²; n = 46 months; estimates were recorded in May (Fig. 3). The five vultures that were tracked during both the wet summer (D periods occupied significantly larger average monthly path GCRs during summer months (mean ± SE = 12, (mean ± SE = 8,874±1,720 km²; n = 5 vultures) (Wilcoxon signed-rank test: Z = -2.20, p = 0.043).

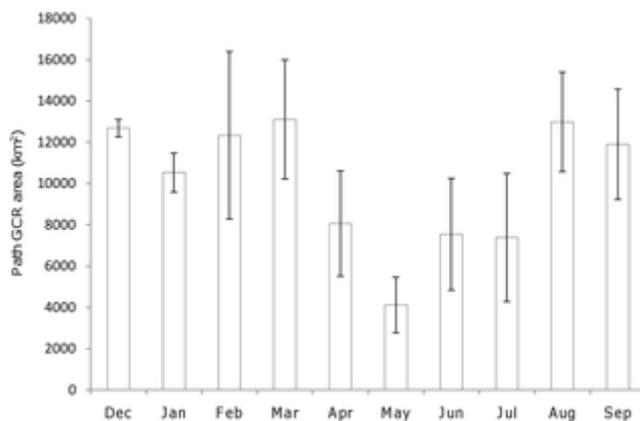


Figure 3. Mean (± SE) path GCR estimates for individual months for six immature African white-b

Due to differences in tracking periods for individuals, estimates were calculated for four vultures for December and September, inclusive.

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Utilisation of protected areas

Protected areas occupied a mean (\pm SE) of $4.33 \pm 1.50\%$ of the 95% KDE contours of the three vultures that the South Africa-Botswana border (AG330, AG331 and AG350), compared to $32.22 \pm 9.75\%$ of the 95% KDE Botswana and Zimbabwe (AG032 and AG356; Table 2). A mean (\pm SE) of $5.21 \pm 0.88\%$ of stationary GPS locations and AG350 were recorded inside protected areas, compared to $35.30 \pm 1.13\%$ for AG356 and AG032 (Table of the 50% KDE contours of AG330, AG331 and AG350, compared to $38.62 \pm 11.63\%$ for AG356 and AG032

Vulture ID	Land use	Availability in 95% KDE (%)	Use at overall foraging range scale (%)	Use at core foraging range scale (%)
AG330	FA	7.20	5.90	4.65
	Non-FA	92.80	94.10	95.35
AG331	FA	2.12	3.97	0.00
	Non-FA	97.88	96.03	100.00
AG350	FA	3.66	4.76	4.82
	Non-FA	96.34	95.24	95.18
AG356	FA	43.97	34.36	50.25
	Non-FA	56.03	65.64	49.75
AG032	FA	22.47	36.43	26.99
	Non-FA	77.53	63.57	73.01
AG032	FA	27.96	8.72	4.66
	Non-FA	72.04	91.28	95.34

The proportion of each vulture's 95% KDE contour occupied by protected areas defined their availability to each vulture. At the overall foraging range scale use of protected areas was defined as the proportion of stationary ($n = 10$ km²) GPS locations within the 95% KDE contour that were recorded inside protected areas. The proportion of each vulture's 50% KDE contours occupied by protected areas defined their use at the core foraging range scale.
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Table 2. Availability and use of protected areas by six immature African white-backed vultures at
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At the overall foraging range scale Ivlev's electivity index values (Fig. S2A) indicated that more stationary GPS locations were expected for three vultures, while fewer than expected were recorded inside protected areas for the other two vultures (Fig. S2B) indicated that protected areas occupied a similar proportion of the 50% KDE contours to the other two. Protected areas were completely avoided in an Ivlev's electivity index value indicating maximum avoidance.

South African protected areas were not visited regularly by any vultures (Fig. 4A), with AG032 never entering any protected areas. Pilanesberg NP ($25^{\circ}14'S$, $27^{\circ}05'E$) and other relatively large conservation areas in the North West Province were visited by any of the vultures, while only two and five stationary locations (both from AG331) were recorded inside Pilanesberg NP ($24^{\circ}24'S$, $27^{\circ}35'E$) respectively. None of the three vultures that spent the majority of their tracking periods inside protected areas.

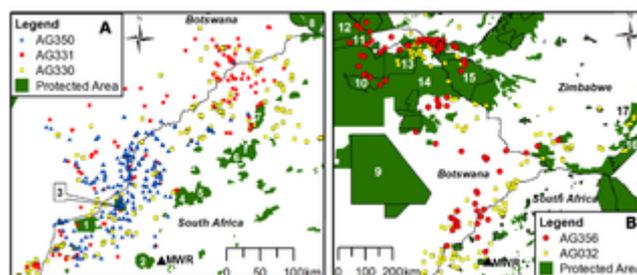


Figure 4. Stationary GPS locations of immature African white-backed vultures in relation to protected areas. (A) shows stationary GPS locations from AG330, AG331 and AG350 in relation to protected areas in the Madikwe GR; 2 = Pilanesberg NP; 3 = Atherstone NR; 4 = Marakele NP; 5 = Welgevonden NR; 6 = La

Tuli conservation area. (B) shows stationary GPS locations from AG356 and AG032 in relation to protected areas: 10 = Moremi GR; 11 = Caprivi GR; 12 = Luiana NP (Angola); 13 = Chobe NP; 14 = Wildlife Management Area = Save Conservancy. Protected area data are from WDPA [32], [33].
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The two vultures that travelled more extensively through southern Africa visited protected areas more regularly. AG330 visited protected areas in Zimbabwe in the Kavango-Zambezi Transfrontier Conservation Area (TFCA), where they spent extended periods (24°43'E) and associated wildlife management areas (WMAs) in northern Botswana, as well as in the Victoria Falls area. AG332 spent an 8 day period passing through the Okavango-Moremi protected area in northern Botswana (19°19'S). Home range estimates were not calculated for AG332 due to its limited tracking period.

Utilisation of supplementary feeding sites

Excluding AG332 which did not visit a supplementary feeding site after leaving the capture site, the proportion of time spent at supplementary feeding sites for each vulture were 1.81% for AG330, 0.84% for AG331, 26.68% for AG350, 22.72% for AG356 and 4 feeding sites each (mean \pm SD = 3.40 \pm 0.89), totalling 8 different sites including the MWR capture site in Zimbabwe, and one was south-east of Gaborone in Botswana. The remaining 5 sites were in the North West Province and were re-visited by any of the vultures fitted with tracking units after they left the capture site.

Two of the vultures spent a relatively large proportion of their time each month in the vicinity of supplementary feeding sites. AG350 spent a relatively large proportion of their time each month in the vicinity of supplementary feeding sites, stationary GPS locations per month being recorded within 1 km of feeding sites for AG350 and AG356, respectively. AG350 visited a privately managed supplementary feeding site approximately 16 km south-east of Gaborone, Botswana (24°43'S, 28°15'E) 24 locations within 1 km of that site. From April until July AG356 regularly utilised a site approximately 16 km south-east of Gaborone with 15.42% of its stationary GPS locations recorded within 1 km of that site. The same vulture was also recorded at several kilometres west of Victoria Falls town at Victoria Falls Safari Lodge (17°54' S, 25°48'E), where it was recorded 15 times. There was a significant negative correlation between the area of monthly path GCRs and the proportion of time spent at supplementary feeding sites ($r_s(24) = -0.674$, $p < 0.001$, $n = 24$ months), indicating that the vultures traverse supplementary feeding sites for longer periods.

Discussion

This study provides the first description of ranging patterns of immature African white-backed vultures tracked in southern Africa. Foraging range estimates varied markedly between methods, emphasising the need to use appropriate methods for such study [27]. As seen previously, MCPs and, to a lesser extent, KDE contours included large areas that were rarely visited by ranging individuals [28], [38]. Path GCRs reduced the inclusion of unvisited areas and produced the most realistic estimates of the vultures' movements. The spatial extent of core GCRs and 50% KDE contours corresponded closely to that of an *ad hoc* method of bandwidth selection and GCR methods should both be considered suitable for the analysis of ranging patterns.

In general, foraging range size among vertebrates is inversely related to resource abundance and spatio-temporal variability. The relatively long distances travelled by the vultures within their range boundaries indicate that the distribution of resources is unpredictable and sparse, as expected [2], [4]. The maximum distances that the vultures travelled in a single day indicate that they are capable of searching for carcasses across a vast daily foraging range and that vultures present at a carcass are likely to have travelled a long distance. Although the large overall foraging ranges recorded during this study were expected because immature *Gyrfalco* vultures are able to disperse widely across southern Africa, possibly to avoid competing with adults for the same resources [1], [4], the long distance movements from the capture site made by three of the vultures during their tracking periods. These results and re-sightings of marked individuals more than 900 km from their natal origin indicate that vultures are able to disperse widely across southern Africa, possibly to avoid competing with adults for the same resources.

Although very few foraging range estimates exist for immature African white-backed vultures, and African vultures in general, a mean home range of 482276 km² for two immature Cape vultures (*G. coprotheres*) (one was a possible *G. coprotheres*) was estimated from satellite tracking data in Namibia [20]. The foraging range estimates in our study are substantially larger than those of vultures in the Western Cape Province of South Africa obtained from landowner questionnaires and radio-tracking [29].

population in the Drakensberg mountains obtained from re-sightings of marked individuals [42]. Comparisons of differences in environmental conditions and foraging ecology of the different study species, and the methods used, provide a much better representation of the vultures' movement patterns [27]. The foraging range estimates are substantially larger than those from similar GPS tracking studies on *Gyps* species in Asia (mean MCP = 24.7 km², MCP = 7419 km² for eight *G. fulvus* [44]), and were therefore some of the largest recorded for any *Gyps* vultures. The speeds of travel correspond to early estimates for *Gyps* vultures in the Serengeti [3], [40].

Although Ivlev's electivity index values indicated that three vultures spent more time inside protected areas in proportion to their availability, only a small proportion (<5%) of stationary GPS locations were recorded inside AG350. The low availability (<4%) of protected areas in the 95% KDE contours of both vultures probably indicates a high degree of positive selection despite use only marginally exceeding availability [34]. The limited amount of protected areas indicates that they were able to locate sufficient carcasses to meet their energy requirements by regularly using protected areas, although the creation of relatively new wildlife reserves such as Pilanesberg National Park and Madikwe Game Reserve benefit vultures in northern South Africa [45], there is an urgent need to implement vulture conservation measures. The ungulate populations inside many of the fenced protected areas in northern South Africa are not as large as those of large carnivores such as lions (*Panthera leo*) rather than other causes of mortality such as malnutrition [46], and the high mortality of ungulates that die from causes other than predation and rarely land at carcasses with large carnivores in attendance [47]. This study could be partially explained by lower food availability and elevated levels of competition in fenced protected areas compared to the much larger protected areas of northern Botswana and Zimbabwe [46].

The geographical distribution of protected areas in northern South Africa might also have reduced their accessibility. Large protected areas within the foraging ranges of the vultures were located in mountainous areas (e.g. the Drakensberg mountains) by all of the tracked vultures (Fig. 4A). As African white-backed vultures favour flat, lowland savannah [4] it is likely that they are located in areas lacking suitable environmental characteristics (e.g. topography) for efficient foraging activities.

More than 34% of stationary GPS locations of the two vultures that travelled more widely through southern Africa were inside protected areas, all of which were outside South Africa. Both vultures spent extended periods in the Madikwe Game Reserve outside South Africa, where ungulate densities are higher than surrounding unprotected land and which supports previous suggestions that vultures regularly use protected areas in Botswana and other African countries [13]–[15], [51], but also show that they spend periods outside protected areas.

The vultures' core foraging ranges (Fig. 2) were located in areas known to be important for African white-backed vultures for the species recorded during ground surveys [4], [52]. The distribution of ungulate carcasses was probably related to the movement patterns of the immature vultures because their principal activity would have been searching for food within a certain distance of a nest site [4], [53]. Farming of wild and domestic ungulate species is common in Botswana, where several of the vultures spent a large proportion of their time [54], [55]. It is likely, therefore, that the use of domestic ungulate species, as previously seen in the study area and elsewhere in South Africa [56], [57]. The high mortality of ungulates recorded during this study might have been caused by higher mortality rates of wild ungulate species during the wet season, forcing vultures to locate carcasses in smaller foraging ranges. Although mortality rates of domestic livestock are generally high, carcasses are more likely to be found and removed by farmers on commercial livestock farms than on more remote farms. Vultures might also be forced to travel further during the wet summer months when increased vegetation can obscure carcasses. It is possible to verify the purpose of the vultures' movements, however, and, as with previous studies that record movements, the underlying causes remain unclear but merit further investigation [20], [43].

Two vultures were regularly recorded in the vicinity of specific supplementary feeding sites that they repeatedly visited. They were able to obtain a large proportion of their food requirements at those sites. *Gyps* vultures frequently use supplementary feeding sites [17], [20], and the provision of supplementary food at fixed locations has been shown to reduce vulture foraging ranges [17]. In this study, with smaller monthly foraging ranges recorded during months when the vultures spent a greater proportion of their time at feeding sites, not all of the vultures were regularly recorded in the vicinity of feeding sites, it is possible that they visited feeding sites more frequently than recorded in this analysis, and so these estimates might be conservative. Further research is required to determine the utility of supplementary feeding sites in Africa, and their potential impacts on vulture foraging ecology and conservation [18].

The small sample size ($n = 6$) and relatively short tracking periods (101 – 313 days) limited by financial and

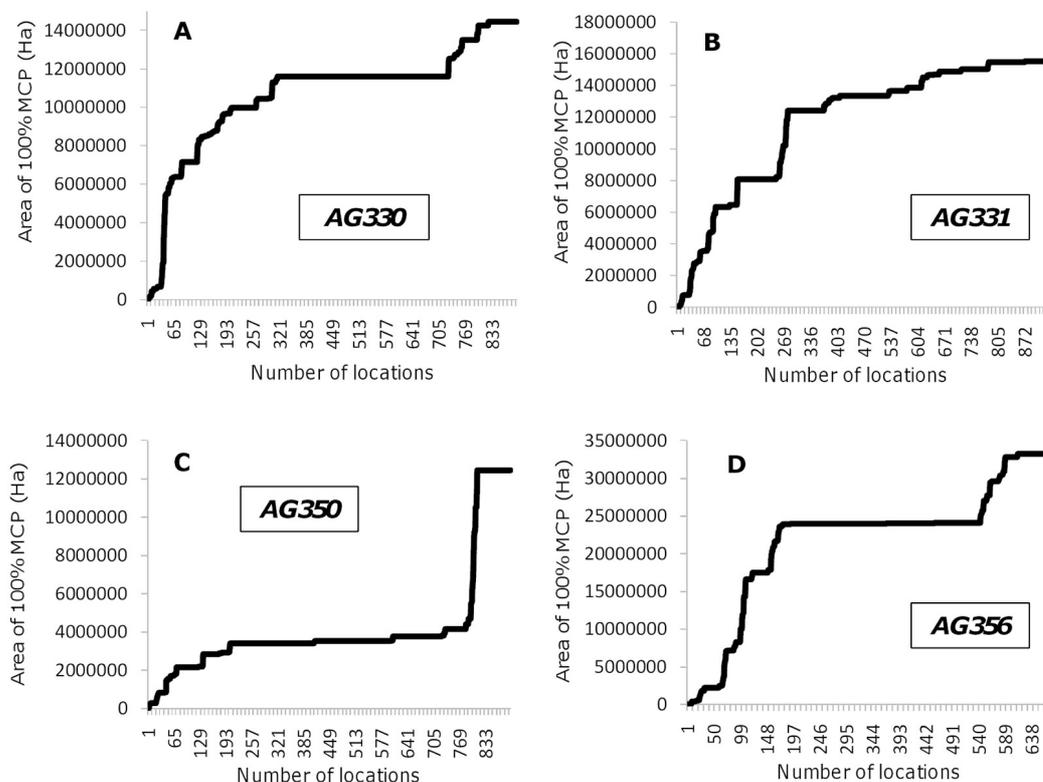
considered with some caution. It was also not logistically feasible to verify the activities of the vultures on their frequent long distance movements. However, despite these limitations the regular sampling intervals and high insight into patterns of space use by immature African white-backed vultures in southern Africa. For conservation investigations into the movement patterns of adult African white-backed vultures as their rates of survival are into the future [17]. It has been estimated that 50% mortality before maturity would lead to only 4.5% adult in at least 22 years to replace themselves [21]. With such long breeding life requirements, even minimal changes entering adulthood could result in population declines.

Conclusions

We have found that immature African white-backed vultures are capable of travelling across the entire region of time outside protected areas. Although based on a small sample size, these findings may have important implications for vultures. If the ranging patterns recorded during this study are repeated across the wider population, then they will be exposed to the full range of threats in southern Africa. Their limited use of protected areas and regular movements outside these areas leaves them susceptible to anthropogenic threats such as poisoning by veterinary NSAIDs or predator control in southern Africa therefore pose a serious threat to vulture populations from all countries in the region, and conservation efforts are required to confront the problem. Our results indicate that monitoring and management of the availability of natural resources is vital for vulture conservation in southern Africa. The findings from this study also demonstrate that GPS tracking is a valuable tool to provide information about vulture movements and land use selection, and as a tool to inform the planning of vulture conservation for adult African white-backed vultures and all other declining vulture species throughout Africa.

Supporting Information

Figure_S1.tif



- International 18: S30–S48. doi: 10.1017/S0959270908000324. Find this article online
7. Ogada DL, Keesing F, Virani MZ (2012) Dropping dead: causes and consequences of vulture popul: of Sciences 1249: 57–71. doi: 10.1111/j.1749-6632.2011.06293.x. Find this article online
 8. Simmons RE, Jenkins AR (2007) Is climate change influencing the decline of Cape and Bearded Vu this article online
 9. Oaks JL, Gilbert M, Virani MZ, Watson RT, Meteyer CU, et al. (2004) Diclofenac residues as the cau 630–633. doi: 10.1038/nature02317. Find this article online
 10. Prakash V, Green RE, Pain DJ, Ranade SP, Saravanan S, et al. (2007) Recent changes in populati Bombay Natural History Society 104: 127–133. Find this article online
 11. Naidoo V, Wolter K, Cromarty D, Diekmann M, Duncan N, et al. (2010) Toxicity of non-steroidal anti-ketoprofen. Biology Letters 6: 339–341. doi: 10.1098/rsbl.2009.0818. Find this article online
 12. Naidoo V, Wolter K, Cuthbert R, Duncan N (2009) Veterinary diclofenac threatens Africa's endanger Pharmacology 53: 205–208. doi: 10.1016/j.yrtp.2009.01.010. Find this article online
 13. Virani MZ, Kendall C, Njoroge P, Thomsett S (2011) Major declines in the abundance of vultures and ecosystem, Kenya. Biological Conservation 144: 746–752. doi: 10.1016/j.biocon.2010.10.024. Find
 14. Herremans M, Herremans-Tonnoeyr D (2000) Land use and the conservation status of raptors in Bc 10.1016/S0006-3207(99)00166-4. Find this article online
 15. Thiollay J-M (2006) Severe decline of large birds in the Northern Sahel of West Africa: a long-term a doi: 10.1017/S0959270906000487. Find this article online
 16. BirdLife International (2013) Species factsheet: *Gyps africanus*. Available: <http://www.birdlife.org>. Ac
 17. Piper SE, Boshoff AF, Scott HA (1999) Modelling survival rates in the Cape Griffon Gyps coprothere Bird Study 46: 230–238. Find this article online
 18. Deygout C, Gault A, Sarrazin F, Bessa-Gomes C (2009) Modeling the impact of feeding stations on 220: 1826–1835. doi: 10.1016/j.ecolmodel.2009.04.030. Find this article online
 19. Oschadleus D (2002) Report on southern African vulture recoveries. Vulture News 46: 16–18. Find 1
 20. Bamford AJ, Diekmann M, Monadjem A, Mendelsohn J (2007) Ranging behaviour of Cape Vultures Namibia. Bird Conservation International 17: 331–339. doi: 10.1017/S0959270907000846. Find this
 21. Brown L, Urban EK, Newman K (1982) The Birds of Africa. London: Academic Press.
 22. Bamford AJ, Monadjem A, Diekmann M, Hardy ICW (2009) Development of non-explosive-based m of Wildlife Research 39: 202–208. doi: 10.3957/056.039.0201. Find this article online
 23. Diekmann M, Scott A, Scott M, Diekmann J (2004) Capture and fitting of satellite- and radio-telemet African white-backed vulture *Gyps africanus* and Lappet-faced vulture *Torgos tracheliotos* in the Wa Find this article online
 24. D'Eon RG, Delparte D (2005) Effects of radio-collar position and orientation on GPS radio-collar per Journal of Applied Ecology 42: 383–388. doi: 10.1111/j.1365-2664.2005.01010.x. Find this article on
 25. Schoener TW (1981) An empirically based estimate of home range. Theoretical Population Biology : this article online
 26. Rodgers AR, Carr AP, Beyer HL, Smith L, Kie JG (2007) Home Range Tools (HRT) for ArcGIS. Vers Northern Forestry Ecosystem Research, Thunder Bay, Ontario, Canada.
 27. Kie JG, Matthiopoulos J, Fieberg J, Powell RA, Cagnacci F, et al. (2010) The home-range concept: : telemetry technology? Philosophical Transactions of the Royal Society B-Biological Sciences 365: 2 online
 28. Harris S, Cresswell WJ, Forde PG, Trehwella WJ, Woollard T, et al. (1990) Home-range analysis usi techniques particularly as applied to the study of mammals. Mammal Review 20: 97–123. doi: 10.11
 29. South AB, Kenward RE, Walls SS (2008) Ranges7: for the analysis of tracking and location data. Or
 30. Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. E online
 31. Beyer HL (2009) Hawth's Analysis Tools for ArcGIS version 3.27 (software). Available: <http://www.sp>
 32. Douglas-Hamilton I, Krink T, Vollrath F (2005) Movements and corridors of African elephants in relat doi: 10.1007/s00114-004-0606-9. Find this article online
 33. Horner MA, Powell RA (1990) Internal structure of home ranges of black bears and analyses of horr 10.2307/1381953. Find this article online

34. Thomas DL, Taylor EJ (2006) Study designs and tests for comparing resource use and availability II 10.2193/0022-541X(2006)70[324:SDATFC]2.0.CO;2. Find this article online
35. IUCN, UNEP (2010) The World Database on Protected Areas (WDPA). UNEP-WCMC. Cambridge, 07/1/2013.
36. IUCN, UNEP (2003) United Nations List of Protected Areas 2003. UNEP-WCMC. Cambridge, UK. [A d-areas.pdf](#). Accessed: 07/1/2013.
37. Ivlev VS (1961) Experimental ecology of the feeding of fishes. New Haven: Yale University Press.
38. Borger L, Franconi N, De Michele G, Gantz A, Meschi F, et al. (2006) Effects of sampling regime on Journal of Animal Ecology 75: 1393–1405. doi: 10.1111/j.1365-2656.2006.01164.x. Find this article c
39. Maher CR, Lott DF (2000) A review of ecological determinants of territoriality within vertebrate speci 10.1674/0003-0031(2000)143[0001:AROEDO]2.0.CO;2. Find this article online
40. Houston DC (1974) Food searching in griffon vultures. East African Wildlife Journal 12: 63–77. doi: .
41. Robertson AS, Boshoff AF (1986) The feeding ecology of cape vultures *Gyps coprotheres* in a stock article online
42. Brown CJ, Piper SE (1988) Status of Cape vultures in the Natal Drakensberg and their cliff site sele 10.1080/00306525.1988.9633714. Find this article online
43. Gilbert M, Watson RT, Ahmed S, Asim M, Johnson JA (2007) Vulture restaurants and their role in re Conservation International 17: 63–77. doi: 10.1017/S0959270906000621. Find this article online
44. Garcia-Ripolles C, Lopez-Lopez P, Urios V (2011) Ranging behaviour of non-breeding Eurasian Griff Ornithologica 46: 127–134. Find this article online
45. Anderson MD (2000) Raptor conservation in the Northern Cape, South Africa. Ostrich 71: 25–32. dc
46. Hayward MW, O'Brien J, Kerley GIH (2007) Carrying capacity of large African predators: Predictions 10.1016/j.biocon.2007.06.018. Find this article online
47. Tambling CJ, Du Toit JT (2005) Modelling wildebeest population dynamics: implications of predation Ecology 42: 431–441. doi: 10.1111/j.1365-2664.2005.01039.x. Find this article online
48. Gusset M, Swarner MJ, Mponwane L, Keletile K, McNutt JW (2009) Human-wildlife conflict in northe wild dog *Lycaon pictus* and other carnivores. Oryx 43: 67–72. doi: 10.1017/S0030605308990475. Fi
49. Parry D, Campbell B (1992) Attitudes of rural communities to animal wildlife and its utilization in Chc Environmental Conservation 19: 245–252. doi: 10.1017/S0376892900031040. Find this article onlin
50. Lindsey PA, Romanach SS, Davies-Mostert HT (2009) The importance of conservancies for enhanc conservation in southern Africa. Journal of Zoology 277: 99–105. doi: 10.1111/j.1469-7998.2008.005
51. Monadjem A, Garcelon DK (2005) Nesting distribution of vultures in relation to land use in Swaziland 10.1007/s10531-004-4358-9. Find this article online
52. Mundy PJ (1997) Whitebacked vulture *Gyps africanus*. In: Harrison JA, Allan DA, Underhill LG, Hen African Birds. Johannesburg: BirdLife South Africa. 160–161.
53. Houston DC (1976) Breeding of white-backed and Ruppell's griffon vultures, *Gyps africanus* and *Gy*
54. St John FAV, Keane AM, Edwards-Jones G, Jones L, Yarnell RW, et al. (2012) Identifying indicators landscapes. Proceedings of the Royal Society B-Biological Sciences 279: 804–812. doi: 10.1098/rsj
55. van der Waal C, Dekker B (2000) Game ranching in the Northern Province of South Africa. South Af article online
56. Murn C, Anderson MD (2008) Activity patterns of African White-backed Vultures *Gyps africanus* in r Ostrich 79: 191–198. doi: 10.2989/OSTRICH.2008.79.2.9.583. Find this article online
57. Benson PC, Plug I, Dobbs JC (2004) An analysis of bones and other materials collected by Cape vl Province, South Africa. Ostrich 75: 118–132. doi: 10.2989/00306520409485423. Find this article onl
58. Cronje HP, Reilly BK, Macfadyen ID (2002) Natural mortality among four common ungulate species 45: 79–86. Find this article online
59. Mapiye C, Chimonyo M, Dzama K (2009) Seasonal dynamics, production potential and efficiency of South Africa. Journal of Arid Environments 73: 529–536. doi: 10.1016/j.jaridenv.2009.01.003. Find tl
60. Schultz P (2007) Does bush encroachment impact foraging success of the critically endangered Nai MSc thesis, University of Cape Town.