

Understanding continent-wide variation in vulture ranging behavior to assess feasibility of Vulture Safe Zones in Africa: Challenges and possibilities

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Abstract

Protected areas are intended as tools in reducing threats to wildlife and preserving habitat for their long-term population persistence. Studies on ranging behavior provide insight into the utility of protected areas. Vultures are one of the fastest declining groups of birds globally and are popular subjects for telemetry studies, but continent-wide studies are lacking. To address how vultures use space and identify the areas and location of possible vulture safe zones, we assess home range size and their overlap with protected areas by species, age, breeding status, season, and region using a large continent-wide telemetry datasets that includes 163 individuals of three species of threatened *Gyps* vulture. Immature vultures of all three species had larger home ranges and used a greater area outside of protected areas than breeding and non-breeding adults. Cape vultures had the smallest home range sizes and the lowest level of overlap with protected areas. Rüppell's vultures had larger home range sizes in the wet season, when poisoning may increase due to human-carnivore conflict. Overall, our study suggests challenges for the creation of Vulture Safe Zones to protect African vultures. At a minimum, areas of 24,000 km² would be needed to protect the entire range of an adult African White-backed vulture and areas of more than 75,000 km² for wider-ranging Rüppell's vultures. Vulture Safe Zones in Africa would generally need to be larger than existing protected areas, which would require widespread conservation activities outside of protected areas to be successful.

Keywords: Home range; Protected area; Scavenger; *Gyps*; Africa; Wide-ranging

1. Introduction

Protected area networks are an important conservation tool (UNEP-WCMC and IUCN, 2016) and have been used extensively for conserving various components of biodiversity (Geldmann et al., 2013; Cazalis et al., 2020). Importantly, protected areas can protect against land use conversion and habitat degradation (Riggio et al., 2019). Across Africa, 469 protected areas support populations of 76 species of mammalian carnivores and ungulates (Wegmann et al., 2014). This network of protection is crucial for biodiversity conservation but may be insufficient for the widest ranging species (Woodroffe and Ginsberg, 1998; Runge et al., 2015). This applies particularly to species that can fly and/or those not well-adapted to human activities or landscapes (Guixé and Arroyo, 2011; Lindsey et al., 2017; Guido et al., 2019).

As wide-ranging and long-lived species, conserving vultures is challenging (Monadjem et al., 2014; Spiegel et al., 2015). The three African breeding resident vulture species of the genus *Gyps* are all threatened with extinction; the African White-backed Vulture *Gyps africanus* and Rüppell's Vulture *Gyps rueppelli* are listed as Critically Endangered while the Cape

vulture *Gyps coprotheres* is listed as Vulnerable (IUCN Red List 2021). All three species are projected to have declined by more than 90% over three generations (Ogada et al., 2016). In addition, the African White-backed Vulture has recently been suggested as a good umbrella species for conserving all African vultures (Thompson et al., 2021). *Gyps* vultures are known to have extremely large individual home ranges, with some tracked individuals exceeding 2,000,000 km² (Hirschauer et al., 2017), and can spend considerable time outside of protected areas (Bamford et al., 2007; Phipps et al., 2013a; Phipps et al., 2013b), although in certain regions protected areas are used more extensively (Pfeiffer et al., 2015; Martens et al., 2018). Their low-cost soaring flight capability allows them to travel over large distances in a short amount of time (Pennycuik, 1979; Duriez et al., 2014; Harel et al., 2016). Partially because of their soaring behavior, these obligate scavengers are incredibly efficient at finding carcasses of large mammals (their primary food source) (Spiegel et al., 2013; Kendall et al., 2014). As a result, they are important for mitigating disease spread and structuring scavenger assemblages (Markandya et al., 2008; Ogada et al., 2012; Buechley and Sekercioglu, 2016; Kane and Kendall, 2017; Sebastián-González et al., 2019; Sebastián-González et al., 2020). However, this same wide-ranging behavior, together with their social feeding, make them highly susceptible to poisoning, which is the primary threat to African-Eurasian vultures (Ogada et al., 2012; Ogada et al., 2016; Murn and Botha, 2017). Their wide-ranging behavior also increases the risk of exposure to additional threats, such as electrocution and collision with powerlines and wind farms (Phipps et al., 2013b).

Vulture Safe Zones (VSZ) (Mukherjee et al., 2014), areas where concerted efforts are made to reduce all threats to vultures, have been proposed as a conservation tool for the protection of vultures in Africa (Botha et al., 2017; Guido et al., 2019). In its original formulation, which is used to protect Asian vultures, VSZ were defined as an extensive area (typically in the same order of magnitude as the foraging range of vultures) free of non-steroidal, anti-inflammatory drugs (NSAIDs). VSZ have been an effective strategy for vulture conservation in Southeast Asia where diclofenac bans across large areas are operable because this type of poisoning is unintentional (Galligan et al., 2020). Yet, it remains to be seen if VSZ would be feasible in Sub-Saharan Africa where safe zones would need to be free of pesticide-based poisoning, which is widely targeted at large mammalian carnivores and, in some cases, intentionally at vultures as well (Ogada et al., 2012; Ogada, 2014; Ogada et al., 2016; Murn and Botha, 2017; Monadjem et al., 2018). This poisoning would need to be mitigated over several suitably large, but as yet unquantified areas, to cover the core foraging ranges of *Gyps* vultures (Botha et al., 2017). Of course, additional thought will need to be given to the role of local communities, park staff, and interactions across reserve and national boundaries (Mukherjee et al., 2014) that might require a unique approach in Africa given the variety of land uses. Understanding variation in home range size and protected area use among three *Gyps* vulture species and across age, breeding status, season, and region will provide valuable insight into the potential feasibility of VSZ concept in Africa.

Given the knowledge gap on vulture home range size and the factors that influence its variation (e.g. age, sex, season), we aim to integrate existing datasets of tagged vultures to address this gap. In part due to their large body mass, vultures have been popular subjects of wildlife telemetry studies (Alarcón and Lambertucci, 2018). To date, there have been a handful of studies assessing ranging behavior in African *Gyps* vultures, but these have been disproportionately focused on Cape vultures and have been conducted at a site-by-site level

with limited comparison across countries or regions (Bamford et al., 2007; Boshoff et al., 2009; Phipps et al., 2013a; Phipps et al., 2013b; Kendall et al., 2014; Pfeiffer et al., 2015; Kane et al., 2016; Martens et al., 2018; Jobson et al., 2020). In addition, these studies have relied on minimum convex polygon (MCP) or traditional kernel-density estimates (KDE), which do not take into account autocorrelation and thus overestimate home range size (Walter et al., 2015). Brownian bridge models, account for variation in temporal lags between sequential locations and thus provide better estimates than traditional KDE, particularly for wide-ranging species (Fischer et al., 2013) and are more appropriate when comparing with environmental covariates, like protected areas (Fleming et al., 2015). A recently introduced home range estimator, the Autocorrelated KDE (AKDE), accounts for autocorrelation, better represents the long-term use of the home range (Fleming et al., 2015) and also performs better than other methods (Noonan et al., 2019) but has not been directly compared with Brownian bridge models.

Range size, together with the use of protected areas within their range, are likely to influence mortality risk, given that non-poison related threats tend to be greater outside protected areas (Phipps et al., 2013a; Phipps et al., 2013b; Ogada et al., 2016; Monadjem et al., 2018), although the spatial extent and correlates of the threat of poisoning are less clear (Santangeli et al., 2019). In addition, in existing work, the large variation in individual range size is confounded by small sample sizes and a lack of assessment of breeding status for tracked adults, making it unclear if immature *Gyps* vultures have larger ranges than adults in general or than breeding adults only. There also has been limited comparison between species (Spiegel et al., 2013; Kendall et al., 2014) even though these three species share a similar feeding niche and the mechanisms allowing for their co-occurrence are not yet well understood (Houston, 1974b, Houston, 1975; Konig, 1983; Mundy et al., 1992; Kendall et al., 2012; Kendall, 2014).

Gyps vultures are known to cover large areas as they forage for carrion (Boshoff et al., 2011; Pennycuik, 1979; Phipps et al., 2013a). However, there are important interspecific, age-related, reproductive and geographic covariates that affect their movement ecology and hence have a bearing on their use of protected areas and their conservation (Spiegel et al., 2015). Notably, larger Rüppell's and Cape vultures are cliff-nesting whereas the smaller White-backed vultures are tree-nesting (Mundy et al., 1992). This means the latter species can stay closer to productive foraging grounds (Houston, 1974b, Houston, 1976). However, their smaller size means White-backed vultures are competitively subordinate to the cliff-nesters (Attwell, 1963; Kruuk, 1967). This might compel them to move away from their larger competitors (Kendall, 2013; Kendall et al., 2014). A similar dominance hierarchy exists across life stages, with adults generally outcompeting immature conspecifics for food at carcasses (Mundy et al., 1992; Bose et al., 2012; Moreno-Opo et al., 2020). However, breeding adults are tethered to a nest, which means they are far more constrained in their movements during incubation and chick-rearing stages (Houston, 1976; Komen and Brown, 1993). Finally, there are important broadscale regional differences between southern Africa and east Africa with respect to ungulate densities which form the majority of carrion these species feed on. Southern African vultures rely more heavily on vulture restaurants and highly managed wildlife populations whereas vultures in East Africa can generally utilize higher densities of ungulates, including migratory herds in Mara-Serengeti ecosystem (Kendall et al., 2014; Schabo et al., 2016). However, Ethiopia might be considered an outlier

for East Africa where scavengers are more likely to use abattoirs and other human-mediated food sources (Buechley, 2021).

Here we analyzed data from a large telemetry dataset for three *Gyps* vulture species tagged in eight countries over fifteen years (2004 to 2019), to examine how home range size and use of protected areas varies in relation to species, age, breeding status, season, and region. We hypothesize that the larger cliff-nesting Rüppell's and Cape vultures will have larger ranges than the smaller tree-nesting White-backed vulture, due to longer commuting distances from breeding to feeding areas. Even so, we predict that White-backed vultures, which are smaller and subordinate to Cape and Rüppell's vultures when competing at carcasses, will spend greater time outside protected areas (in order to avoid the larger Cape and Rüppell's vultures) (Kruuk, 1967; Kendall, 2013). In addition, we hypothesize that within species, immature vultures will have a larger range size than non-breeding adults (Mundy et al., 1992; Bose et al., 2012; Spiegel et al., 2015; Moreno-Opo et al., 2020). We also predict that immature birds will spend more time outside of protected areas, possibly to reduce competition at carcasses with more dominant adults, which may relate to the lower survival often found for immature raptors, including vultures (Kirk and Houston, 1995; Durant, 1998; Kendall, 2013; Monadjem et al., 2013; Spiegel et al., 2015; Newton et al., 2016; Monadjem et al., 2018). We predicted that breeding adults would have smaller ranges than non-breeding and immature vultures, particularly during the breeding season, when nesting constrains their movement (Kane et al., 2016). Finally, we predicted that there would be significant regional differences in range size and protected area use between east and southern African populations of African white-backed vultures (which breeds in both regions), because of significant differences in ungulate densities, particularly in the Mara-Serengeti ecosystem, leading to smaller ranges and greater protected area use in East Africa.

2. Methods

2.1. Trapping and tagging

Methods for trapping and tagging of vultures varied slightly from site to site and in many cases are described elsewhere (Bamford et al., 2007; Phipps et al., 2013a; Phipps et al., 2013b; Spiegel et al., 2013; Kendall et al., 2014; Pfeiffer et al., 2015; Spiegel et al., 2015; Kane et al., 2016; Martens et al., 2018). Only wild-caught birds are included in this study. Birds were aged as either adults or immatures based on wing coloration and patterns. This binary classification is justified due to different contributors using different ageing methods. Adult African white-backed vultures are relatively easily discerned by their white back and underwing patterns, which they obtain by the 6th year (Mundy et al., 1992) and birds lacking adult patterns were considered immatures. Adult Cape vultures were determined by pale almost white plumage, yellow eye, and deep blue neck skin (Piper et al., 1989), features which are acquired by the 6th or 7th year (Mundy et al., 1992). Individuals with darker, streaked plumage or with a dark or orange eye were categorized as immatures. For Rüppell's vultures, we identified adults based on yellow eye and yellow bill, which is acquired in the 6th or 7th year (Mundy et al., 1992). We also did not consider a bird to change age class during this study since most birds were tracked for approximately 12 months.

2.2. Ethics statement

All studies were consistent with country and university or institutional policies related to the study of animal subject in their relevant sites.

2.2.1. Data analysis

Analyses were performed using R version 4.0.3 (Team RC, 2020).

2.2.2. Protected areas

A protected area shapefile was created by merging African country specific shapefiles from <https://www.protectedplanet.net/> into one object using the *sf* package (Pebesma, 2018). Protected Planet includes protected areas of a wide range of statuses from national parks and world heritage sites to game controlled areas and community conservation areas. This dataset thus provides a broad definition for protected areas. The resultant shapefile was projected using the Africa Albers Equal Area Conic projection (ESRI: 102022). We made no distinction among the protected areas because 1) ostensibly similar classifications can vary between countries and 2) we wanted to measure *any* potential protection even if not vulture specific.

2.2.3. Tracking data preparation

All GPS tracking data were cleaned by removing NAs, duplicates, and then applying a speed filter to remove points with speed over 100 km/h using the *SDLfilter* package (Shimada et al., 2012). All time zones were set to UTC and nocturnal points were removed using the *time_of_day* function from the *amt* package (Signer et al., 2019); this was done to reduce the influence of the roost site on home range analyses (since barring disturbance, the birds are confined to a single location from at least sunset to sunrise) and because some tracks were only recorded diurnally. The tracks were projected using the Africa Albers Equal Area Conic projection (ESRI: 102022). 15 different datasets were combined for this yearly analysis and 16 for the monthly analysis (Supplementary material Tables S6 & S7). These are referred to as 'study' in the analyses that follow.

Because different birds had GPS units collecting data at different temporal resolutions (from every minute to every seven hours), tracks that recorded more frequently than once per hour were resampled to a one-hour rate using the *adehabitatLT* package (Calenge, 2006). This subsampling reduces variation in sampling intervals and avoids high autocorrelation among points. Tracks with large gaps (e.g. due to a temporary unit failure) were split before applying the *redistraj* function and then stitched back together to avoid adding interpolated points over large periods — what constituted a large gap was dependent on the study (mean maximum gap was just under eight days).

To examine variation in home range size, each track was also split into monthly groups. Only tracks that had at least 28 days per month were included to ensure an unbiased comparison.

2.2.4. Nesting behavior

To identify whether adult birds were breeding, the number of revisitations to an area were measured on a monthly basis using the *recurse* package (Bracis et al., 2018). This is done along the length of the track. A 50 m radius was used to define an area around each point so that the time spent at a location could be measured. The maximum value in days for this was calculated for each month for all adult birds. A small proportion of the vultures (11 individuals) were known to be breeding, so this was used to set a lower threshold for the time a breeder spent at a nest, by taking the 1st quartile of the maximum time a known breeding bird spent in one area (threshold = 11.4 days). A bird that had two consecutive months that exceeded the threshold was designated as a breeding adult. We did not define breeding season as these can vary by species and region (Mundy et al., 1992).

2.2.5. Home range measurement

Dynamic Brownian Bridge Movement Models were used to measure the home range of each vulture (Kranstauber et al., 2012). This was done for the whole track and by month for each bird. This method uses the time between relocations and accounts for behavioral differences along the track, and is more suitable than traditional KDE to link space use and environmental co-variables. In Brownian bridge, the behavioral differences are measured along a window of track which was set to 31 points with a margin of 11 using the *brownian.bridge.dyn* function from the *move* package (Kranstauber et al., 2020). These values approximate to 3-day chunks which should be sufficient to capture seasonal variation in movement and were used to model long distance movement of similarly sampled waterfowl (Palm et al., 2015). The location error for each bird was assumed to be 20 m, which is within the horizontal accuracy of most satellite transmitters. The *hr_isopleths* function from the *amt* package was used to return the 95% and 50% isopleths, i.e. the home range estimate. Minimum convex polygons (MCPs) and kernel density estimates (KDEs) for the tracks were also calculated for comparison with previous studies using the *amt* package.

2.2.6. Overlap with protected areas

The proportions of the home ranges for each bird's total home range and the monthly home ranges that overlapped with the protected area shapefile were then measured using functions from the *sf* package. This was done for both the 95% and 50% contours of the Brownian bridge models. For parks larger than 10,000 km², we also calculated the average proportion of the national park that overlapped with bird's 95% contour across individuals that used a given park.

2.3. Statistical analysis

Model 1 explored home range areas as a function of age and population in a generalized additive model (GAM) (Wood, 2017). Age was a three-level factor variable consisting of immature birds, breeding adults, and non-breeding adults. Population was a four-level factor variable consisting of Cape vultures (in southern Africa), White-backed vultures in southern Africa, White-backed vultures in eastern Africa, and Rüppell's vulture (in eastern Africa). The southern-eastern split was based on the starting location of each bird with 'eastern' corresponding to those birds captured in Kenya, Tanzania or Ethiopia. This split is further

justified by the residence of all tracked eastern White-backed vultures bar one to the east of the continent. The response variable, home range size, was transformed by taking the natural logarithm to achieve normality of model residuals.

Model 2 explored the overlap of the proportion of home ranges within protected areas as a function of age and population using a GAM. A Beta distribution was used with a logit link function because the response variable (proportion overlap with protected area) was a continuous proportion. Because the Beta distribution only has a support of (0,1) the response variable was rescaled following Douma and Weedon (2019). For both model 1 and 2, only tracks with at least two months of data were used and duration of the track for each bird was fit as a smooth function and 'study' (see Table S5) was included as a random effect using the basis spline for random effect.

Model 3 explored monthly home range areas as a function of age, population, and climatic season in a mixed effects model using the lmer function from the lme4 package (Bates et al., 2015). Season was a two-level factor variable with wet and dry seasons which differed depending on the region the bird was trapped in (Ethiopia, eastern Africa, southern Africa). The southern Africa dry season was set as April to October, eastern Africa dry season as June to September and Ethiopian dry season as October to May. Population and season were modelled using an interaction and individually as fixed effects. The response variable was the natural log of home range size.

Model 4 explored the overlap of the proportion of monthly home ranges within protected areas as a function of age, population, and climatic season using the glmmTMB function (Brooks et al., 2017). Population and season were modelled using an interaction. A Beta distribution was chosen as the error distribution with a logit link function. Here dispersion of the fixed effects was also modelled. For both models 3 and 4, because multiple monthly home ranges came from the same individual, bird ID was used as a random effect nested within study; month was also specified as a random effect.

To investigate pairwise differences between the four populations for the yearly data the emmeans function from the emmeans package was used (Lenth et al., 2020).

3. Results

3.1. Vulture distributions

Vultures tracked in this study ranged widely, regularly moving beyond the borders of the countries they were trapped in (Fig. 1 and Table 1). Table 2, Table 3, Table 4, Table 5 show the summary statistics of home range size and overlap with protected areas for the total track and on a monthly basis. Home range sizes from the Brownian bridge estimate strongly correlate with the traditional KDE and MCP estimates (Tables S1 & S2). Birds were tracked for an average of 398 days (range 70–1447 days).

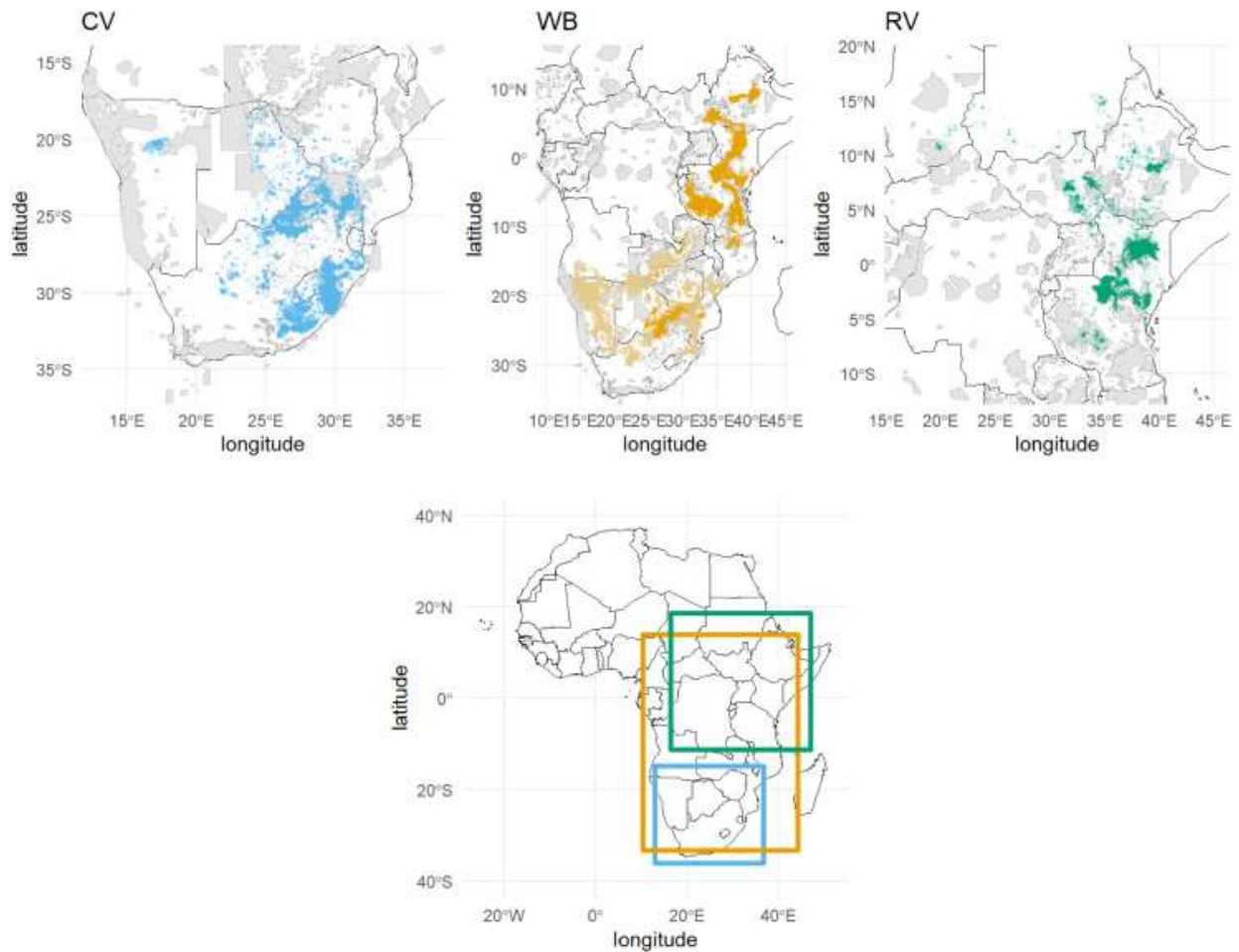


Fig. 1. Distribution of tracks of the three species used in the analysis. CV = Cape vultures; WB = White-backed vultures; RV = Rüppell's vultures. Light orange represents the southern population of White-backed vultures, and dark orange the eastern population. Protected areas are shown in grey and are taken from <https://www.protectedplanet.net/>.

Table 1. Countries traversed by each of the three species. Asterisks represent trapping locations.

Country	Cape vulture	White-backed vulture	Rüppell's vulture
Angola		X	
Botswana	X	X	
Chad			X
DRC		X	
Eswatini	X	X*	
Ethiopia		X*	X*
Kenya		X*	X*
Lesotho	X		
Mozambique	X	X*	
Namibia	X*	X*	
South Sudan		X	X
South Africa	X*	X*	
Sudan			X
Tanzania		X*	X
Uganda			X
Zambia		X*	
Zimbabwe	X	X	

Table 2. 95% Brownian Bridge Home Range estimates for three species of African vulture: Cape (cv); Rüppell's (Table 2rv) and African white-backed (wb). Vultures were tracked in two regions, southern and eastern Africa, and birds were aged as adults or immatures (imm). The total number of birds (count) used for each analysis is also provided. Units are in km².

Species	Region	Age	Count	Mean	Median	sd	Min	Max
cv	South	Adult	18	36,145	26,220	36,464	4270	157,828
cv	South	Imm	24	74,060	47,839	68,793	1953	245,743
rv	East	Adult	15	75,441	56,349	60,611	6018	202,662
rv	East	Imm	4	172,450	169,825	171,850	19,439	330,711
wb	East	Adult	46	23,649	15,261	22,457	3907	113,920
wb	East	Imm	13	31,540	18,778	37,729	5980	144,087
wb	South	Adult	30	36,186	15,978	46,505	2371	198,900
wb	South	Imm	13	96,519	88,637	80,885	5827	295,912

Table 3. Monthly estimate of 95% Brownian Bridge Home Range data for three species of African vulture: Cape (cv); Rüppell's (rv) and African white-backed (wb). Vultures were tracked in two regions, southern and eastern Africa, and birds were aged as adults or immatures (imm). The total number of bird months (count) used for each analysis is also provided. Units are in km².

Species	Region	Age	Count	Mean	Median	sd	Min	Max
cv	South	Adult	278	12,950	10,253	10,005	1021	80,238
cv	South	Imm	320	16,800	11,310	16,162	535	104,417
rv	East	Adult	100	36,189	23,555	33,916	2744	162,207
rv	East	Imm	29	36,023	17,312	41,572	2855	164,411
wb	East	Adult	463	12,640	8569	13,360	700	106,227
wb	East	Imm	156	11,816	9762	7986	1414	38,518
wb	South	Adult	353	11,813	8908	10,596	641	61,972
wb	South	Imm	110	16,138	10,866	14,255	1364	67,638

Table 4. The proportion of overlap of 95% Brownian Bridge areas with protected areas for three species of African vulture: Cape (cv); Rüppell's (rv) and African white-backed (wb). Vultures were tracked in two regions, southern and eastern Africa, and birds were aged as adults or immatures (imm). The total number of birds (count) used for each analysis is also provided.

Species	Region	Age	Count	Proportion of 95% BBMM contour covered by PAs		
				Mean	Median	sd
cv	South	Adult	18	0.337	0.233	0.277
cv	South	Imm	24	0.155	0.105	0.16
rv	East	Adult	15	0.577	0.457	0.228
rv	East	Imm	4	0.518	0.49	0.268
wb	East	Adult	46	0.694	0.742	0.21
wb	East	Imm	13	0.708	0.742	0.194
wb	South	Adult	30	0.571	0.537	0.277
wb	South	Imm	13	0.413	0.388	0.231

Table 5. Monthly proportion of overlap of 95% Brownian Bridge areas with protected areas for three species of African vulture: Cape (cv); Rüppell's (rv) and African white-backed (wb). Vultures were tracked in two regions, southern and eastern Africa, and birds were aged as adults or immatures (imm). The total number of bird months (count) used for each analysis is also provided.

Species	Region	Age	Count	Proportion of 95% BBMM contour covered by PAs		
				Mean	Median	sd
cv	South	Adult	278	0.302	0.164	0.306
cv	South	Imm	320	0.14	0.072	0.174
rv	East	Adult	100	0.54	0.549	0.271
rv	East	Imm	29	0.493	0.491	0.285
wb	East	Adult	463	0.734	0.78	0.214
wb	East	Imm	156	0.642	0.696	0.219
wb	South	Adult	353	0.606	0.663	0.325
wb	South	Imm	110	0.412	0.293	0.321

Note that for all models that follow reference level corresponds to immature Cape vultures. Models 1 and 2 were based on 163 birds (42 Cape Vultures, 19 Rüppell's Vultures, and 102 African white-backed Vultures). The models based on monthly home ranges had 1809 bird-months of data.

From model 1, non-breeding adults had smaller home ranges than immature birds (Table 6, with an estimate of 36,444 km² for Cape vultures). Breeding adults had smaller home ranges than immature birds (with an average estimate of 9168 km² for Cape vultures), even more so than the non-breeding adult birds. Study and duration of the track were also both significant. The posthoc test indicated Rüppell's vultures had significantly larger home ranges than the eastern population of African white-backed vultures (Table S3; Fig. S1).

Table 6. Output from analysis on model 1. Significant values ($p < 0.05$) are in bold. Values are on the log scale.

Predictors	Estimates	CI	p
(Intercept)	10.50	9.95–11.05	<0.001
Breeding adults	-1.38	-1.90 to -0.87	<0.001
Non-breeding adults	-0.40	-0.77 to -0.04	0.030
Population [rv]	0.71	-0.11–1.54	0.091
Population [wb]	0.24	-0.32–0.80	0.406
Population [wbe]	-0.26	-0.99–0.48	0.491
Smooth terms			
Duration			<0.002
Study			<0.001

From model 2, breeding adult home ranges overlapped significantly more with protected areas than immature birds, and all had more protected area overlap than Cape vultures (Table 7). There was also a significant effect of 'study' as a random effect. The posthoc test indicated that Cape vultures had significantly less of their home range fall within protected areas than either of the White-backed vulture populations (Table S4; Fig. S1).

Table 7. Output from analysis on model 2. Significant values ($p < 0.05$) are in bold. Values are on the log odds scale.

Predictors	Estimates	CI	<i>p</i>
(Intercept)	-1.04	-1.65 to -0.43	0.001
Breeding adults	0.85	0.36–1.34	0.001
Non-breeding adults	0.16	-0.19–0.50	0.378
Population [rv]	1.16	0.24–2.08	0.013
Population [wb]	0.77	0.21–1.32	0.007
Population [wbe]	1.25	0.40–2.10	0.004
Smooth terms			
Duration			0.425
Study			<0.001

From model 3, breeding adults had a significantly smaller monthly home range than immature birds. There was a significant interaction between Rüppell's vultures and season such that their home ranges were larger during the wet season (18,033 km² vs 12,456 km²) (Table 8).

Table 8. Output from analysis on model 3. Significant values ($p < 0.05$) are in bold. Values are on the log scale.

Predictors	Estimates	CI	<i>p</i>
(Intercept)	9.36	8.99–9.73	<0.001
Breeding adults	-0.34	-0.61 to -0.07	0.012
Non-breeding adults	-0.11	-0.35–0.12	0.341
Population [rv]	0.41	-0.20–1.03	0.190
Population [wb]	0.03	-0.35–0.41	0.874
Population [wbe]	-0.25	-0.78–0.27	0.345
Seasonwet	-0.07	-0.19–0.04	0.206
Population[rv] * seasonwet	0.44	0.14–0.75	0.004
Population[wb] * seasonwet	-0.11	-0.27–0.06	0.206
Population[wbe] * seasonwet	0.14	-0.01–0.30	0.074
Random effects			
Bird:study	0.30		
Study	0.15		
Month	0.001		

From model 4, monthly home ranges of non-breeding and breeding adults had significantly greater overlap with protected areas than immature birds (Table 9). For monthly home ranges, both populations of African white-backed vultures had significantly greater overlap with protected areas than Cape vultures.

Table 9. Output from analysis on model 4. Significant values ($p < 0.05$) are in bold. Values are on the log odds scale.

Predictors	Estimate	CI	<i>p</i>
(Intercept)	-1.51	-2.17 to -0.86	<0.001
Breeding adults	0.71	0.28–1.14	0.001
Non-breeding adults	0.72	0.31–1.12	0.001
Population [rv]	0.98	-0.08–2.05	0.07
Population [wb]	1.06	0.37–1.75	0.003
Population [wbe]	1.84	0.93–2.76	<0.001
Seasonwet	-0.08	-0.29–0.14	0.488
Population[rv] * seasonwet	0.17	-0.28–0.62	0.458
Population[wb] * seasonwet	0.12	-0.14–0.37	0.366
Population[wbe] * seasonwet	-0.12	-0.32–0.09	0.27
Random effects			
Bird:study	0.99		
Study	0.44		
Month	0.01		

Analysis of overlap with protected areas at different contour levels showed that, in general, core areas (50% contours) are better protected than the larger home range contours (95%). However, there is a large range of values and three of the eight comparisons show no significant difference — all among the immature birds (Fig. 2). Patterns of protected area use by region followed patterns of range overlap within large national parks (greater than 10,000 km²) (Table 10).

Table 10. Average overlap of national park with vulture 95% range going from northeast to south.

National parks	Country	Average overlap
Boma	South Sudan	0.73
Loelle	South Sudan	0.38
Borena	Ethiopia	0.21
Arsi Mountains	Ethiopia	0.09
Tsavo East	Kenya	0.43
Serengeti	Tanzania	0.52
Ruaha	Tanzania	0.54
Kafue	Zambia	0.59
Luengue-Luiana	Angola	0.40
Etosha	Namibia	0.42
Chobe	Botswana	0.45
Hwange	Zimbabwe	0.19
Limpopo	Mozambique	0.32
Kruger	South Africa	0.33
Gemsbok	South Africa	0.20

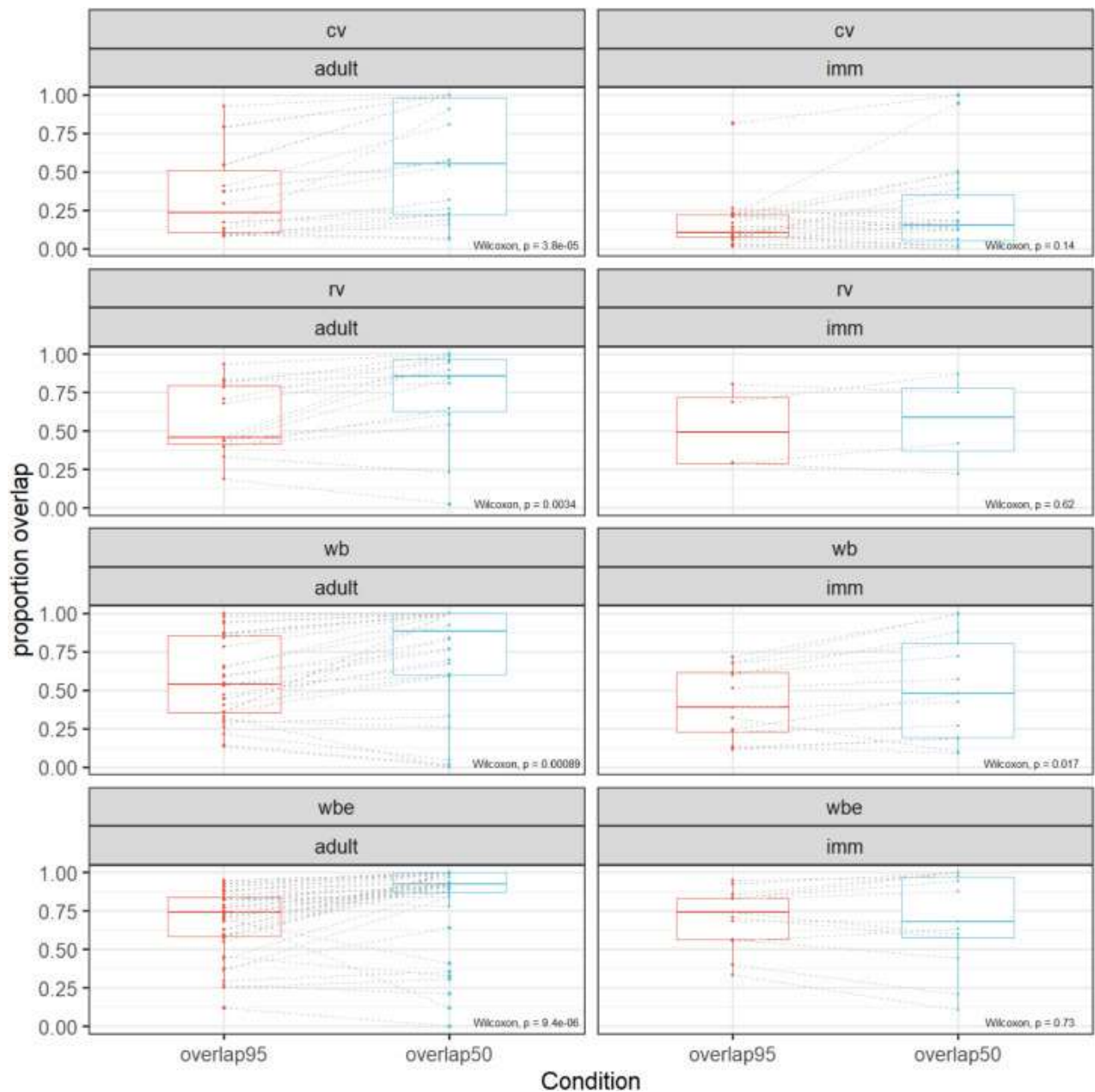


Fig. 2. Comparison of proportion of overlap of Brownian bridges with protected areas at 95% and 50% contours. Dashed lines connect the same bird. Means are compared using a Wilcoxon Rank Sum test. Abbreviations: cv = Cape vulture, rv = Rüppell's vulture, wb = White-backed vulture (southern population), wbe = White-backed vulture (eastern population), imm = immature.

4. Discussion

Our study presents the first comparative analysis of *Gyps* vulture movement ecology in Africa. For three species and across two regions, African *Gyps* vulture consistently had some of the largest home ranges of any terrestrial, non-migratory species in the world, enabled by their energetically efficient soaring flight and required for their use of a dispersed and ephemeral food source, carrion (Pennycuick, 1979; Ruxton and Houston, 2004). Immature birds consistently used larger areas than adults, even non-breeding birds. *Gyps* vultures had

considerably larger home ranges, typically by several orders of magnitude, than other large African eagles (van Eeden et al., 2017; McPherson et al., 2019). Home range size of raptors scales with body size and diet (Peery, 2000), which may explain the smaller home ranges of apex African eagles, which are typically smaller than vultures, hunt prey, and are territorial (Steyn, 1980). In turn, such large ranges may also make vultures some of the most challenging species to conserve and could limit the utility of VSZs in an African context. Differences among African *Gyps* vultures in both home range size and the use of protected areas has significant implications for their conservation and that of the ecosystem services they provide (Gutiérrez-Cánovas et al., 2020).

4.1.1. Differences in home range size

Contrary to our prediction, the cliff-nesting vulture species (Rüppell's and Cape vultures) did not have consistently larger home range sizes than the tree-nesting species (White-backed vulture). Rüppell's vultures had a larger annual home range than eastern White-backed vultures, but Cape vultures had a smaller monthly home range size than eastern White-backed vultures, with no difference found between southern White-backed vultures and Cape vultures. Although it would be nearly impossible to measure differences in vultures' food supply at this scale, we assume that this, together with nest and roost site selection, is a key factor in determining the size of their home ranges (Rolando, 2002; Spiegel et al., 2015). In southern Kenya, where most of our tracked Rüppell's vultures were tagged, Rüppell's and White-backed vultures follow large ungulate herds present in the Mara-Serengeti ecosystem during the dry season (Houston, 1974a), whereas during the wet season the former species shifts to drier regions presumably tracking ungulate mortality (Kendall et al., 2014). Yet, Rüppell's vultures nest well away from the Mara-Serengeti ecosystem whereas White-backed vultures nest within it (Virani et al., 2010; Virani et al., 2012; Kendall et al., 2018), necessitating longer journeys for the former species, and hence larger home ranges (Pennycuick, 1972; Houston, 1976; Ruxton and Houston, 2002). However, Cape vultures, also a cliff-nesting species, had far smaller home ranges than those of Rüppell's vultures, and similar to that of the tree-nesting African White-backed vultures in southern Africa, though larger than the eastern African white-backed vultures. The smaller home ranges of Cape vultures compared with Rüppell's vultures, may be associated with the large number of active vulture restaurants currently within the core of its geographical distribution (Kane et al., 2016; Brink et al., 2020), reducing their need to travel long distances in search of food. However, it is also worth noting that Cape vulture ranging behavior and food sources can vary dramatically between colonies (Phipps et al., 2013b; Pfeiffer et al., 2015; Kane et al., 2016; Martens et al., 2018).

The home range sizes of immature African *Gyps* vultures presented here are in the same order of magnitude as that of two immature Lappet-faced vultures *Torgos tracheliotus* tracked in Saudi Arabia (Shobrak, 2014). However, White-headed vulture *Trigonoceps occipitalis* tracked in central Mozambique had far smaller home ranges, that were typically between 1000 and 10,000 km² using an autocorrelated KDE (Scott, 2020). The fact that *Gyps* vultures have similar home range sizes to the Lappet-faced vulture is not surprising since they share a similar diet of carrion that requires similar foraging techniques, though further study on Lappet-faced vulture is merited for comparison (Spiegel et al., 2013). The smaller home range size of White-headed vultures suggests that they may have a different diet to

Gyps vultures, possibly with small captured prey playing a larger role than carrion (Mundy et al., 1992).

Following our predictions, and similar to findings for Hooded vultures across Africa (Thompson et al., 2020), for all three *Gyps* species, immature birds had much larger annual and monthly home ranges than adult birds. With immature bird's ranges typically at least twice as large as adults, except for African White-backed vultures in East Africa where the difference was 1.5-fold, similar to what has been found previously for Cape and White-backed vultures in southern Africa (Bamford et al., 2007; Phipps et al., 2013a). In addition, we found that breeding adults had smaller annual and monthly home ranges than non-breeding adults, which is to be expected, as these birds are constrained by their use of a fixed nesting site for up to six months of the year (Houston, 1976; Komen and Brown, 1993).

Importantly, non-breeding adults consistently had smaller ranges, for both annual and monthly assessments, than immature birds. By controlling for the effect of breeding status among adults, we were able to assess if there were other drivers for larger range size in immature vultures. Consistently smaller home ranges found for non-breeding adults versus immatures demonstrates that the smaller ranges are due not just to breeding activity itself. Instead these findings suggest that immature birds may widen their foraging area, and thus total range, perhaps in response to foraging competition with adults, or as part of dispersal (Mundy et al., 1992; Bose et al., 2012; Spiegel et al., 2015; Moreno-Opo et al., 2020). Bush encroachment may further exacerbate this competition as it can limit areas where birds are able to land and successfully forage (Bamford et al., 2009a). While some of the non-breeding adults in this study could have had failed breeding attempts that may have reduced ranging behavior, it would be unlikely that the monthly home range estimates would also be smaller overall if this was the case (since failed nesters are more likely to have failed earlier in the breeding period than later).

In our study, home ranges of the Rüppell's vultures were affected by season, with birds using larger areas in the wet season months. Seasonal changes in food availability for scavengers in East Africa have been well-documented and suggest that food is limited in the wet season (Houston, 1979; Mduma et al., 1999; Ogutu et al., 2008). This finding is similar to what has been previously reported, which is that east African *Gyps* species follow large ungulate herds present in the Mara-Serengeti ecosystem during the dry season, whereas during the wet season Rüppell's vultures shift to drier regions presumably tracking non-migratory ungulate mortality (Kendall et al., 2014). Lower food availability driven by rainfall patterns, greater dispersal of ungulates, reduced predation, and reduced mortality rates for migratory herds may thus drive wider ranging behaviors in east African *Gyps* vultures during the wet season. The importance of rainfall seasonality and ungulate mortality is yet to be assessed outside of the Mara-Serengeti ecosystem, and its effect on vulture movements could be a productive field of inquiry, particularly in Ethiopia and Uganda where climate seasonality is strikingly different from southern Kenya. Kane et al. (2016) showed that the home range of immature Cape vultures did not differ with season, but that it was significantly smaller for adults during the dry season, which represents the breeding season for this species (Mundy et al., 1992). However, Kane et al. (2016) did not distinguish between breeding and non-breeding adult birds and thus in their study, breeding may explain the smaller home range size in dry season for adults, which was not found here.

We did not see significant differences in ranging behavior related to regions. In general, variation within a region and species may be greater than between region or species, though regional variation in ranging has been found for the migratory Turkey vulture (Houston et al., 2011).

4.1.2. Differences in use of protected areas

Contrary to our predictions, Cape vultures, rather than White-backed vultures, showed the lowest amount of overlap with protected areas (Table 4). Cape vultures' home ranges had the least overlap with protected areas, with annual average proportions for adults at 34% and for immatures at 16%. This finding contrasts with studies on Cape vultures tagged at the Msikaba colony, which preferentially used protected areas, demonstrating that results may vary by colony (Pfeiffer et al., 2015; Martens et al., 2018). However for this larger dataset of Cape vultures, it suggests that despite the extensive protected area network in southern Africa and smaller home ranges overall, Cape vultures still spend considerable time outside of protected areas (Phipps et al., 2013b). Cape vultures are known to feed extensively on livestock and other domestic species on farmland and several breeding colonies are located outside of protected areas (Robertson and Boshoff, 1986; Pfeiffer et al., 2014). Open habitats of importance to Cape vultures may also be more readily represented outside protected areas and bush encroachment may be another important driver of this phenomenon (Bamford et al., 2009a). In addition, preferential use of vulture restaurants, which often occur outside of protected areas, may also explain this pattern, though other studies have shown these don't strongly influence ranging behavior (Kane et al., 2016). Future studies should investigate the birds' behavioral states in these areas to understand the ramifications of this activity altogether. African white-backed vultures in southern Africa and Rüppell's vultures had about half of their range overlap with protected areas (57% and 58% respectively) whereas White-backed vultures in East Africa had the greatest overlap with protected areas, with 70% overlap on average. Even within regions, there were considerable variations and it is important to note that White-backed vultures showed considerable variation in their home range overlap of protected areas in different countries (Table S5). For national parks larger than 10,000 km², the average proportion of the park that overlapped with vulture's 95% contour showed similar regional patterns. A larger proportion of national parks in East Africa tended to be used compared to Southern Africa, suggesting higher suitability, or possibly food availability, within these parks for vultures. However, Ethiopia is an exception to this trend, with relatively low overlap of vulture core areas with protected areas, which has been shown previously (Buechley, 2021). However, even for these large parks, average overlap with ranges was less than 40%. This suggests that even where large protected areas are available, vultures may not be heavily using them. There may thus be a mismatch between the needs of vultures and placement of existing national parks. Future studies assessing habitat use would be applicable to explore this pattern and would be better suited to help identify key areas for vultures, as well as prioritize specific protected areas or protected area types (i.e. national park, game reserve, conservancies, etc.) best suited to conserve vultures.

As predicted, monthly and annual adult home ranges for breeding individuals overlapped with protected areas more than those of immatures albeit with great variability (Fig. 2). In some regions, vultures rely heavily on protected areas for breeding and may avoid human

activities when selecting nest sites (Monadjem and Garcelon, 2005; Morán-López et al., 2006; Zuberogoitia et al., 2008; Bamford et al., 2009b; Murn and Holloway, 2014; Kendall et al., 2018; Leepile et al., 2020), which may in turn lead to less movement outside protected areas for breeding adults. However, there are breeding colonies of both Rüppell's and Cape vulture known outside of protected areas, including some individuals tagged within this study, and thus factors other than breeding behavior, such as food availability and greater energetic needs of breeding birds, may also dictate this greater use of protected areas by breeding individuals. In addition, the monthly home range of non-breeding adults also overlapped more with protected areas than immatures. Adults may be able to use higher quality habitats with greater prey availability, which will tend to overlap with protected areas (Lindsey et al., 2017). Given that vultures are long-lived species and are slow to mature (Mundy et al., 1992), lower risk behavior of adults should have important and positive ramifications for their conservation. However, the extensive use of areas outside of protected areas by immatures potentially exposes them to a greater risk of poisoning and could lead to reduced recruitment in vulture populations, contributing to long-term declines (Phipps et al., 2013a; Monadjem et al., 2018). Accordingly, the conservation of these species will depend on protection not just of breeding birds and breeding areas but also foraging habitats, many of which fall outside of protected areas (Guixé and Arroyo, 2011).

4.1.3. Vulture Safe Zones as a conservation tool for African *Gyps* vultures

For the VSZ concept to be successful in an African context, it will depend on the protection from poisoning and other threats, in sufficiently large areas that incorporate most of vultures' very large ranges, and all of their core foraging area, which will be challenging. At a minimum, areas of 24,000 km² would be needed to protect the entire range of an adult African White-backed vulture and areas of more than 75,000 km² for wider-ranging Rüppell's vultures, and this does not consider the exceedingly large average range of 172,450 km² for immature Rüppell's vultures. As found elsewhere, vultures are likely to require nearly poison-free protection across huge areas to be conserved (Santangeli et al., 2019). VSZ would need to be larger than the majority of protected area networks across the African continent. Additionally our results suggest that even where large protected areas do exist, vultures don't heavily use them.

A lack of regional differences in home range size suggests that the size of VSZ could be similar in southern and eastern Africa, though the establishment of the size of vulture core foraging areas will be needed to determine the adequate size required for VSZ, if poisoning and other threats are to be mitigated. For VSZ to effectively eliminate threats to vultures, they may be most applicable to African white-backed vultures in eastern Africa (particularly feasible for southern Tanzania and the Mara-Serengeti ecosystem) where a significant proportion of both adult and immature birds spend their time within already protected areas and where ranges are smaller overall and particularly for breeding adults.

Gyps vultures spend a considerable amount of time outside protected areas, with Cape vultures and immature birds of all three *Gyps* species at greatest risk. Even when 'core areas' are considered (50% contours of the home range estimate) there is still a large proportion of a bird's area left unprotected (Fig. 2). In addition, greater use of areas outside of protected areas in the wet season also heightens vultures' risk for poisoning (Kolowski and Holekamp,

2006). Further, while threats may be greater outside protected areas, it is known that poisoning still occurs extensively in protected areas in both southern Africa (Monadjem et al., 2018) and eastern Africa (Virani et al., 2011; Kendall and Virani, 2012), particularly where it is motivated by the avoidance of rangers or collection of vulture parts (Ogada et al., 2015; Ogada et al., 2016).

Given the large ranges of vultures, others have considered the possibility of using vulture restaurants (supplementary feeding) to concentrate or alter foraging behavior (Gilbert et al., 2007; Monsarrat et al., 2013; Kane et al., 2016). Supplementary feeding appears to shape movement for some species or individuals in some areas, but there are mixed results as to how vulture restaurants affect vulture ranging behavior, which suggests this may not be a feasible strategy to contract ranges in many locations (Monsarrat et al., 2013; López-López et al., 2014; Kane et al., 2016; Margalida et al., 2017). In particular, vultures appear to use feeding supplementation most readily when food availability is limited, during breeding, or when weather conditions are poor (Gilbert et al., 2007; Monsarrat et al., 2013; Ferrer et al., 2018). These are not necessarily the periods when poisoning is most frequent as would need to be the case to meaningfully prevent poisoning. Despite these limitations, vulture restaurants may be a valuable tool, combined with protected areas, to reduce risk of poisoning if used in periods of high risk. While they are unlikely to eliminate poisoning, the prolonged periods of range reduction or reduced intensity of feeding on carcasses in areas of poisoning of some individuals or species that vulture restaurants may be able create, should benefit vulture conservation. In addition, vulture restaurants have been shown to be valuable where food is limited, and can improve breeding rates and success in these areas, which may be applicable to some areas of southern and western Africa (Schabo et al., 2016; Ferrer et al., 2018).

While working to reduce or eliminate threats to vultures may be easier in protected areas than outside of them, VSZ would have to incorporate reductions in poisoning and other threats both within and outside of protected areas to be successful. Modelling studies suggest that even small amounts of poisoning can have a significant effect on vulture populations (Murn and Botha, 2017), but that subpopulation structure may lead to stratified risk even in nearby areas (Monadjem et al., 2018). Thus insights into ranging behavior provided by telemetry studies may be a key tool when considering spatial prioritization of management strategies. Success will only be possible with greater law enforcement and increased anti-poaching efforts inside protected areas along with reduced human-wildlife conflict, targeted persecution of those poisoning, reducing trade in vulture body parts, and mitigation of mortalities associated with electrical infrastructure and wind farms.

4.1.4. Use of Brownian bridge home range estimates

Home range estimates may vary considerably depending on the tool used. While previous studies have largely relied on traditional Kernel Density Estimates (KDE) or Minimum Convex Polygon (MCP) (Bamford et al., 2007; Phipps et al., 2013a; Phipps et al., 2013b; Kane et al., 2016; Thompson et al., 2020) that estimate long-term space use, Brownian bridge estimates occurrence during the sampling period and more effectively account for spatial and temporal autocorrelation inherent in telemetry data (Kranstauber et al., 2012).

However, Brownian bridge models have not been directly compared with the autocorrelated kernel density estimation (AKDE) method, which outperformed a variety of traditional home range estimators such as KDE and MCP methods (Noonan et al., 2019). It should be noted that home range estimates obtained through AKDE are typically much larger than KDE or MCP (Noonan et al., 2019), in part because they assume that an animal will move according to the same model even beyond the tracking duration and therefore may also be larger than the Brownian bridge estimates presented here. Particularly for tracks with sufficient duration as included in this study, AKDE may include areas that an animal didn't use during the track and may be unlikely to actually use due to habitat heterogeneity which plays a role in limiting range size and area used. Indeed, a test on a sample of our data illustrated the point with two individuals tracked from Eswatini having AKDE estimates of 78,091 km² and 340,033 km² versus 13,247 km² and 51,788 km² for the Brownian bridge respectively (this was done with the amt package using 'auto' as the autocorrelation model). Since our Brownian bridge home range estimates already suggest that creating VSZ in Africa will be challenging, due to the large size and minimal overlap with protected areas of their ranges, then such estimates based on AKDE, which will be larger, would only further support our main conclusion. We also found a significant effect of study on our home range estimates, which could relate to differences between individual study populations or to differences in frequency of data collected and how we addressed this in our methods.

This study represents the first reported home range estimates from satellite-telemetry for Rüppell's vultures, which had the largest annual home range sizes of the three African *Gyps* species, regardless of whether this was estimated using Brownian bridge, KDE, or MCP, roughly twice the size of the home ranges of the other two species (Fig. S2). The same trend was true for monthly Brownian bridge home range sizes, which were on average three times smaller than the annual home ranges. In general, the Brownian bridge estimates were substantially smaller than either of the other two estimates.

Our home range estimates for adult Cape vultures are larger than those previously published for adults of this species from the Eastern Cape province of South Africa (Pfeiffer et al., 2015), which had average breeding and non-breeding minimum convex polygon ranges of between 14,000 and 17,000 km². However, Kane et al. (2016) reported slightly larger home ranges for adult Cape vultures than our estimates. This is not surprising, since our estimates presented here combined these two datasets along with several others. There are few comparable estimates of the home range of African white-backed vultures, however, a small dataset of six immature birds tracked in South Africa had slightly larger minimum convex polygon estimates than ours (Phipps et al., 2013a).

4.1.5. Limitation and future directions

A significant caveat of our work is that we have not considered the behavioral state of vultures in relation to habitat use. Future studies investigating whether activity outside of protected areas is primarily travel between protected sites or feeding sites have significant conservation implications, particularly in relation to the risk of encountering poisoning events. New techniques have been developed, allowing for a more sophisticated investigation of behavior from telemetry data and future work applying these to large multi-site datasets such as this one would be valuable (Whoriskey et al., 2017).

The location of trapping could potentially influence subsequent space use (i.e. within or outside of a protected area) and it is worth noting that most birds tracked here were trapped within or near protected areas. Another limitation of our work is the use of Protected Planet maps for consideration of protected areas. Protected areas can vary considerably in terms of their level of protection based on status, location, and size and further consideration of these differences will aid in efforts to create meaningful VSZs.

Finally, while our study represents significant compilation of the movement of 163 individuals from 16 different study sites, it also demonstrates the gaps in existing telemetry studies for African vultures. In particular, West Africa remains largely understudied as well as Uganda, Malawi, and Angola. In several cases, these areas represent general knowledge gaps for vulture conservation, but could represent important populations that merit future study.

CRedit authorship contribution statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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