

1 **Understanding continent-wide variation in vulture ranging behavior to assess feasibility of Vulture**

2 **Safe Zones in Africa: challenges and possibilities**

3 **Keywords:** home range, protected area, scavenger, *Gyps*, Africa, wide-ranging

4 ***Abstract***

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

21

22 ***Introduction***

23 Protected area networks are an important conservation tool (UNEP-WCMC & IUCN 2016) and
24 have been used extensively for conserving various components of biodiversity (Geldmann et al. 2013;
25 Cazalis et al. 2020). Importantly, protected areas can protect against land use conversion and habitat
26 degradation (Riggio et al. 2019). Across Africa, 469 protected areas support populations of 76 species of
27 mammalian carnivores and ungulates (Wegmann et al. 2014). This network of protection is crucial for
28 biodiversity conservation but may be insufficient for the widest ranging species (Woodroffe & Ginsberg
29 1998; Runge et al. 2015). This applies particularly to species that can fly and/or those not well-adapted
30 to human activities or landscapes (Guixé & Arroyo 2011; Lindsey et al. 2017; Guido et al. 2019).

31 As wide-ranging and long-lived species, conserving vultures is challenging (Monadjem et al.
32 2014; Spiegel et al. 2015). The three African breeding resident vulture species of the genus *Gyps* are all
33 threatened with extinction; the African White-backed Vulture *Gyps africanus* and Rüppell's Vulture *Gyps*
34 *rueppelli* are listed as Critically endangered while the Cape vulture *Gyps coprotheres* is listed as
35 Endangered (IUCN Red List 2016). All three species are projected to have declined by more than 90%
36 over three generations (Ogada et al. 2016). In addition, the African White-backed Vulture has recently
37 been suggested as a good umbrella species for conserving all African vultures (Thompson et al. 2021).
38 *Gyps* vultures are known to have extremely large individual home ranges, with some tracked individuals
39 exceeding 2,000,000 km² (Hirschauer et al. 2017), and can spend considerable time outside of protected
40 areas (Bamford et al. 2007; Phipps et al. 2013a; Phipps et al. 2013b), although in certain regions
41 protected areas are used more extensively (Pfeiffer et al. 2015; Martens et al. 2018). Their low-cost
42 soaring flight capability allows them to travel over large distances in a short amount of time (Pennycuik
43 1979; Duriez et al. 2014; Harel et al. 2016). Partially because of their soaring behavior, these obligate
44 scavengers are incredibly efficient at finding carcasses of large mammals (their primary food source)
45 (Spiegel et al. 2013; Kendall et al. 2014). As a result, they are important for mitigating disease spread
46 and structuring scavenger assemblages (Markandya et al. 2008; Ogada et al. 2012; Buechley &

47 Sekercioglu 2016; Kane & Kendall 2017; Sebastián-González et al. 2019; Sebastián-González et al. 2020).
48 However, this same wide-ranging behavior, together with their social feeding, make them highly
49 susceptible to poisoning, which is the primary threat to African-Eurasian vultures (Ogada et al. 2012;
50 Ogada et al. 2016; Murn & Botha 2017). Their wide-ranging behavior also increases the risk of exposure
51 to additional threats, such as electrocution and collision with powerlines and wind farms (Phipps et al.
52 2013b).

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

70 Given the knowledge gap on vulture home range size and the factors that influence it's variation
71 (e.g. age, sex, season), we aim to integrate exiting datasets of tagged vultures to address this gap. In part
72 due to their large body mass, vultures have been popular subjects of wildlife telemetry studies (Alarcón
73 & Lambertucci 2018). To date, there have been a handful of studies assessing ranging behavior in
74 African *Gyps* vultures, but these have been disproportionately focused on Cape vultures and have been
75 conducted at a site-by-site level with limited comparison across countries or regions (Bamford et al.
76 2007; Boshoff et al. 2009; Phipps et al. 2013a; Phipps et al. 2013b; Kendall et al. 2014; Pfeiffer et al.
77 2015; Kane et al. 2016; Martens et al. 2018; Jobson et al. 2020). In addition, these studies have relied on
78 minimum convex polygon (MCP) or traditional kernel-density estimates (KDE), which do not take into
79 account autocorrelation and thus overestimate home range size (Walter et al. 2015). Brownian bridge
80 models, account for variation in temporal lags between sequential locations and thus provide better
81 estimates than traditional KDE, particularly for wide-ranging species (Fischer et al. 2013) and are more
82 appropriate when comparing with environmental covariates, like protected areas (Fleming et al. 2015).
83 A recently introduced home range estimator, the Autocorrelated KDE (AKDE), accounts for
84 autocorrelation, better represents the long-term use of the home range (Fleming et al. 2015) and also
85 performs better than other methods (Noonan et al. 2019) but has not been directly compared with
86 Brownian bridge models.

87 Range size, together with the use of protected areas within their range, are likely to influence
88 mortality risk, given that non-poison related threats tend to be greater outside protected areas (Phipps
89 et al. 2013a; Phipps et al. 2013b; Ogada et al. 2016; Monadjem et al. 2018), although the spatial extent
90 and correlates of the threat of poisoning are less clear (Santangeli et al. 2019). In addition, in existing
91 work, the large variation in individual range size is confounded by small sample sizes and a lack of
92 assessment of breeding status for tracked adults, making it unclear if immature *Gyps* vultures have
93 larger ranges than adults in general or than breeding adults only. There also has been limited

94 comparison between species (Spiegel et al. 2013; Kendall et al. 2014) even though these three species
95 share a similar feeding niche and the mechanisms allowing for their co-occurrence are not yet well
96 understood (Houston 1974b, 1975; Konig 1983; Mundy et al. 1992; Kendall et al. 2012; Kendall 2014).

97 *Gyps* vultures are known to cover large areas as they forage for carrion (Boshoff et al. ;
98 Pennyquick 1979; Phipps et al. 2013a). However, there are important interspecific, age-related,
99 reproductive and geographic covariates that affect their movement ecology and hence have a bearing
100 on their use of protected areas and their conservation (Spiegel et al. 2015). Notably, larger Rüppell's and
101 Cape vultures are cliff-nesting whereas the smaller White-backed vultures are tree-nesting (Mundy et al.
102 1992). This means the latter species can stay closer to productive foraging grounds (Houston 1974b,
103 1976). However, their smaller size means White-backed vultures are competitively subordinate to the
104 cliff-nesters (Attwell 1963; Kruuk 1967). This might compel them to move away from their larger
105 competitors (Kendall 2013; Kendall et al. 2014). A similar dominance hierarchy exists across life stages,
106 with adults generally outcompeting immature conspecifics for food at carcasses (Mundy et al. 1992;
107 Bose et al. 2012; Moreno-Opo et al. 2020). However, breeding adults are tethered to a nest, which
108 means they are far more constrained in their movements during incubation and chick-rearing stages
109 (Houston 1976; Komen & Brown 1993). Finally, there are important broadscale regional differences
110 between southern Africa and east Africa with respect to ungulate densities which form the majority of
111 carrion these species feed on. Southern African vultures rely more heavily on vulture restaurants and
112 highly managed wildlife populations whereas vultures in East Africa can generally utilize higher densities
113 of ungulates, including migratory herds in Mara-Serengeti ecosystem (Kendall et al. 2014; Schabo et al.
114 2016). However, Ethiopia might be considered an outlier for East Africa where scavengers are more
115 likely to use abattoirs and other human-mediated food sources (Buechley et al. 2021).

116 Here we analyzed data from a large telemetry dataset for three *Gyps* vulture species tagged in
117 eight countries over fifteen years (2004 to 2019), to examine how home range size and use of protected

118 areas varies in relation to species, age, breeding status, season, and region. We hypothesize that the
119 larger cliff-nesting Rüppell's and Cape vultures will have larger ranges than the smaller tree-nesting
120 White-backed vulture, due to longer commuting distances from breeding to feeding areas. Even so, we
121 predict that White-backed vultures, which are smaller and subordinate to Cape and Rüppell's vultures
122 when competing at carcasses, will spend greater time outside protected areas (in order to avoid the
123 larger Cape and Rüppell's vultures) (Kruuk 1967; Kendall 2013). In addition, we hypothesize that within
124 species, immature vultures will have a larger range size than non-breeding adults (Mundy et al. 1992;
125 Bose et al. 2012; Spiegel et al. 2015; Moreno-Opo et al. 2020). We also predict that immature birds will
126 spend more time outside of protected areas, possibly to reduce competition at carcasses with more
127 dominant adults, which may relate to the lower survival often found for immature raptors, including
128 vultures (Kirk & Houston 1995; Durant 1998; Kendall 2013; Monadjem et al. 2013; Spiegel et al. 2015;
129 Newton et al. 2016; Monadjem et al. 2018). We predicted that breeding adults would have smaller
130 ranges than non-breeding and immature vultures, particularly during the breeding season, when nesting
131 constrains their movement (Kane et al. 2016). Finally, we predicted that there would be significant
132 regional differences in range size and protected area use between East and Southern African
133 populations of African white-backed vultures (which breeds in both regions), because of significant
134 differences in ungulate densities, particularly in the Mara-Serengeti ecosystem, leading to smaller
135 ranges and greater protected area use in East Africa (Hopcraft et al. 2015).

136 **Methods**

137 *Trapping and Tagging*

138 Methods for trapping and tagging of vultures varied slightly from site to site and in many cases
139 are described elsewhere (Bamford et al. 2007; Phipps et al. 2013a; Phipps et al. 2013b; Spiegel et al.
140 2013; Kendall et al. 2014; Pfeiffer et al. 2015; Spiegel et al. 2015; Kane et al. 2016; Martens et al. 2018).

141 Only wild-caught birds are included in this study. Birds were aged as either adults or immatures based
142 on wing coloration and patterns. This binary classification is justified due to different contributors using
143 different ageing methods. Adult African white-backed vultures are relatively easily discerned by their
144 white back and underwing patterns, which they obtain by the 6th year (Mundy et al. 1992) and birds
145 lacking adult patterns were considered immatures. Adult Cape vultures were determined by pale almost
146 white plumage, yellow eye, and deep blue neck skin (Piper et al. 1989), features which are acquired by
147 the 6th or 7th year (Mundy et al. 1992). Individuals with darker, streaked plumage or with a dark or
148 orange eye were categorized as immatures. For Rüppell's vultures, we identified adults based on yellow
149 eye and yellow bill, which is acquired in the 6th or 7th year (Mundy et al. 1992). We also did not consider
150 a bird to change age class during this study since most birds were tracked for approximately 12 months.

151 *Ethics Statement*

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

154 *Data Analysis*

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

156 *Protected areas*

157 A protected area shapefile was created by merging African country specific shapefiles from
158 <https://www.protectedplanet.net/> into one object using the sf package (Pebesma 2018). Protected
159 Planet includes protected areas of a wide range of statuses from national parks and world heritage sites
160 to game controlled areas and community conservation areas. This dataset thus provides a broad
161 definition for protected areas. The resultant shapefile was projected using the Africa Albers Equal Area
162 Conic projection (ESRI:102022). We made no distinction among the protected areas because 1)

163 ostensibly similar classifications can vary between countries and 2) we wanted to measure *any* potential
164 protection even if not vulture specific.

165 *Tracking data preparation*

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

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

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

184 *Nesting behavior*

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

194 *Home range measurement*

195 Dynamic Brownian Bridge Movement Models were used to measure the home range of each
196 vulture (Kranstauber et al. 2012). This was done for the whole track and by month for each bird. This
197 method uses the time between relocations and accounts for behavioural differences along the track,
198 and is more suitable than traditional KDE to link space use and environmental co-variables. In Brownian
199 bridge, the behavioral differences are measured along a window of track which was set to 31 points with
200 a margin of 11 using the brownian.bridge.dyn function from the move package (Kranstauber et al. 2020).
201 These values approximate to 3-day chunks which should be sufficient to capture seasonal variation in
202 movement and were used to model long distance movement of similarly sampled waterfowl (Palm et al.
203 2015). The location error for each bird was assumed to be 20 m, which is within the horizontal accuracy
204 of most satellite transmitters. The hr_isopleths function from the amt package was used to return the
205 95% and 50% isopleths, i.e. the home range estimate. Minimum convex polygons (MCPs) and kernel
206 density estimates (KDEs) for the tracks were also calculated for comparison with previous studies using
207 the amt package.

208 *Overlap with protected areas*

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

214 *Statistical analysis*

215 *Model 1* explored home range areas as a function of age and population in a generalised
216 additive model (GAM) (Wood 2017). Age was a three-level factor variable consisting of immature birds,
217 breeding adults, and non-breeding adults. Population was a four-level factor variable consisting of Cape
218 vultures (in southern Africa), White-backed vultures in southern Africa, White-backed vultures in eastern
219 Africa, and Rüppell's vulture (in eastern Africa). The southern-eastern split was based on the starting
220 location of each bird with 'eastern' corresponding to those birds captured in Kenya, Tanzania or
221 Ethiopia. This split is further justified by the residence of all tracked eastern White-backed vultures bar
222 one to the east of the continent. The response variable, home range size, was transformed by taking the
223 natural logarithm to achieve normality of model residuals.

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

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

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

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

246 **Results**

247 *Vulture Distributions*

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

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

256 From model 1, non-breeding adults had smaller home ranges than immature birds (Table 6, with
257 an estimate of 36,444 km² for Cape vultures). Breeding adults had smaller home ranges than immature
258 birds (with an average estimate of 9,168 km² for Cape vultures), even more so than the non-breeding
259 adult birds. Study and duration of the track were also both significant. The posthoc test indicated
260 Rüppell's vultures had significantly larger home ranges than the eastern population of African white-
261 backed vultures (Table S3; Figure S1).

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

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

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

274 Analysis of overlap with protected areas at different contour levels showed that, in general, core
275 areas (50% contours) are better protected than the larger home range contours (95%). However, there
276 is a large range of values and three of the eight comparisons show no significant difference – all among

277 the immature birds (Figure 2). Patterns of protected area use by region followed patterns of range
278 overlap with large national parks (Table 10). Overlap for all protected areas larger than 100 km² is
279 provided in supplementary materials.

280 ***Discussion***

281 Our study presents the first comparative analysis of *Gyps* vulture movement ecology in Africa.
282 For three species and across two regions, African *Gyps* vulture consistently had some of the largest
283 home ranges of any terrestrial, non-migratory species in the world, enabled by their energetically
284 efficient soaring flight and required for their use of a dispersed and ephemeral food source, carrion
285 (Pennycuik 1979; Ruxton & Houston 2004). Immature birds consistently used larger areas than adults,
286 even non-breeding birds. *Gyps* vultures had considerably larger home ranges, typically by several orders
287 of magnitude, than other large African eagles (van Eeden et al. 2017; McPherson et al. 2019). Home
288 range size of raptors scales with body size and diet (Peery 2000), which may explain the smaller home
289 ranges of apex African eagles, which typically hunt prey and are territorial (Steyn 1980). In turn, such
290 large ranges may also make vultures some of the most challenging species to conserve and could limit
291 the utility of the concept of VSZ in an African context. Differences among African *Gyps* vultures in both
292 home range size and the use of protected areas has significant implications for their conservation and
293 that of the ecosystem services they provide (Gutiérrez-Cánovas et al. 2020).

294 *Differences in home range size*

295 Contrary to our prediction, the cliff-nesting vulture species (Rüppell's and Cape vultures) did not
296 have consistently larger home range sizes than the tree-nesting species (White-backed vulture).
297 Rüppell's vultures had a larger annual home range than eastern White-backed vultures, but Cape
298 vultures had a smaller monthly home range size than eastern White-backed vultures, with no difference
299 found between southern White-backed vultures and Cape vultures. Although it would be nearly

300 impossible to measure vultures' food supply, we assume that this, together with nest and roost site
301 selection, is a key factor in determining the size of their home ranges (Rolando 2002; Spiegel et al.
302 2015). In southern Kenya, where most of our tracked Rüppell's vultures were tagged, Rüppell's and
303 White-backed vultures follow large ungulate herds present in the Mara-Serengeti ecosystem during the
304 dry season (Houston 1974a), whereas during the wet season the former species shifts to drier regions
305 presumably tracking ungulate mortality (Kendall et al. 2014). Yet, Rüppell's vultures nest well away from
306 the Mara-Serengeti ecosystem whereas White-backed vultures nest within it (Virani et al. 2010; Virani et
307 al. 2012; Kendall et al. 2018), necessitating longer journeys for the former species, and hence larger
308 home ranges (Pennycuik 1972; Houston 1976; Ruxton & Houston 2002). However, Cape vultures, also a
309 cliff-nesting species, had far smaller home ranges than those of Rüppell's vultures, and similar to that of
310 the tree-nesting African White-backed vultures in southern Africa, though larger than the eastern
311 African white-backed vultures. The smaller home ranges of Cape vultures compared with Rüppell's
312 vultures, may be associated with the large number of active vulture restaurants currently within the
313 core of its geographical distribution (Kane et al. 2016; Brink et al. 2020), reducing their need to travel
314 long distances in search of food. However, it is also worth noting that Cape vulture ranging behavior and
315 food sources can vary dramatically between colonies (Phipps et al. 2013b; Pfeiffer et al. 2015; Kane et al.
316 2016; Martens et al. 2018).

317 The home range sizes of immature African *Gyps* vultures presented here are in the same order
318 of magnitude as that of two immature Lappet-faced vultures *Torgos tracheliotus* tracked in Saudi Arabia
319 (Shobrak 2014). However, White-headed vulture *Trigonoceps occipitalis* tracked in central Mozambique
320 had far smaller home ranges, that were typically between 1,000 and 10,000 km² using an autocorrelated
321 KDE (Scott 2020). The fact that *Gyps* vultures have similar home range sizes to the Lappet-faced vulture
322 is not surprising since they share a similar diet of carrion that requires similar foraging techniques,
323 though further study on Lappet-faced vulture is merited for comparison (Spiegel et al. 2013). The

324 smaller home range size of White-headed vultures suggests that they may have a different diet to *Gyps*
325 vultures, possibly with small captured prey playing a larger role than carrion (Mundy et al. 1992).

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

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

346 In our study, home ranges of the Rüppell's vultures were affected by season, with birds using
347 larger areas in the wet season months. Seasonal changes in food availability for scavengers in East Africa

348 have been well-documented and suggest that food is limited in the wet season (Houston 1979; Mduma
349 et al. 1999; Ogutu et al. 2008). This finding is similar to what has been previously reported, which is that
350 East African *Gyps* species follow large ungulate herds present in the Mara-Serengeti ecosystem during
351 the dry season, whereas during the wet season Rüppell's vultures shift to drier regions presumably
352 tracking ungulate mortality (Kendall et al. 2014). Lower food availability driven by rainfall patterns,
353 greater dispersal of ungulates, reduced predation, and reduced mortality rates for migratory herds may
354 thus drive wider ranging behaviors in East African *Gyps* vultures during the wet season. The importance
355 of rainfall seasonality and ungulate mortality is yet to be assessed outside of the Mara-Serengeti
356 ecosystem, and its affect on vulture movements could be a productive field of inquiry, particularly in
357 Ethiopia and Uganda where climate seasonality is strikingly different from southern Kenya. Kane et al.
358 (2016) showed that the home range of immature Cape vultures did not differ with season, but that it
359 was significantly smaller for adults during the dry season, which represents the breeding season for this
360 species (Mundy et al. 1992). However, Kane et al. (2016) did not distinguish between breeding and non-
361 breeding adult birds and thus in their study, breeding may explain the smaller home range size in dry
362 season for adults, which was not found here.

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

366 *Differences in use of protected areas*

367 Contrary to our predictions, Cape vultures, rather than White-backed vultures, showed the
368 lowest amount of overlap with protected areas (Table 4). Cape vultures' home ranges had the least
369 overlap with protected areas, with annual average proportions for adults at 34% and for immatures at
370 16%. This finding contrasts with studies on Cape vultures tagged at the Msikaba colony, which
371 preferentially used protected areas, demonstrating that results may vary by colony (Pfeiffer et al. 2015;

372 Martens et al. 2018). However for this larger dataset of Cape vultures, it suggests that despite the
373 extensive protected area network in southern Africa and smaller home ranges overall, Cape vultures still
374 spend considerable time outside of protected areas (Phipps et al. 2013b). Cape vultures are known to
375 feed extensively on livestock and other domestic species on farmland and several breeding colonies are
376 located outside of protected areas (Robertson & Boshoff 1986; Pfeiffer et al. 2014). Open habitats of
377 importance to Cape vultures may also be more readily represented outside protected areas and bush
378 encroachment may be another important driver of this phenomenon (Bamford et al. 2009a). In addition,
379 preferential use of vulture restaurants, which often occur outside of protected areas, may also explain
380 this pattern, though other studies have shown these don't strongly influence ranging behavior (Kane et
381 al. 2016). Future studies should investigate the birds' behavioral states in these areas to understand the
382 ramifications of this activity altogether. African white-backed vultures in southern Africa and Rüppell's
383 vultures had about half of their range overlap with protected areas (57% and 58% respectively) whereas
384 White-backed vultures in East Africa had the greatest overlap with protected areas, with 70% overlap on
385 average. Even within regions, there were considerable variations and it is important to note that White-
386 backed vultures showed considerable variation in their home range overlap of protected areas in
387 different countries (Table S5). For national parks larger than 10,000 km², the average proportion of the
388 park that overlapped with vulture's 95% contour showed similar regional patterns. A larger proportion
389 of national parks in East Africa tended to be used compared to Southern Africa, suggesting higher
390 suitability, or possibly food availability, within these parks for vultures. However, Ethiopia is an
391 exception to this trend, with relatively low overlap of vulture core areas with protected areas, which has
392 been shown previously (Buechley et al. 2021). However, even for these large parks, average overlap
393 with ranges was less than 40%. This suggests that even where large protected areas are available,
394 vultures may not be heavily using them. There may thus be a mismatch between the needs of vultures
395 and placement of existing national parks. Future studies assessing habitat use would be applicable to

396 explore this pattern and would be better suited to help identify key areas for vultures, as well as
397 prioritize specific protected areas or protected area types (i.e. national park, game reserve,
398 conservancies, etc.) best suited to conserve vultures.

399 As predicted, monthly and annual adult home ranges for breeding individuals overlapped with
400 protected areas more than those of immatures albeit with great variability (Figure 2). In some regions,
401 vultures rely heavily on protected areas for breeding and may avoid human activities when selecting
402 nest sites (Monadjem & Garcelon 2005; Morán-López et al. 2006; Zuberogoitia et al. 2008; Bamford et
403 al. 2009b; Murn & Holloway 2014; Kendall et al. 2018; Leepile et al. 2020), which may in turn lead to less
404 movement outside protected areas for breeding adults. However, there are breeding colonies of both
405 Rüppell's and Cape vulture known outside of protected areas, including some individuals tagged within
406 this study, and thus factors other than breeding behavior, such as food availability and greater energetic
407 needs of breeding birds, may also dictate this greater use of protected areas by breeding individuals. In
408 addition, the monthly home range of non-breeding adults also overlapped more with protected areas
409 than immatures. Adults may be able to use higher quality habitats with greater prey availability, which
410 will tend to overlap with protected areas (Lindsey et al. 2017). Given that vultures are long-lived species
411 and are slow to mature (Mundy et al. 1992), lower risk behavior of adults should have important and
412 positive ramifications for their conservation. However, the extensive use of areas outside of protected
413 areas by immatures potentially exposes them to a greater risk of poisoning and could lead to reduced
414 recruitment in vulture populations, contributing to long-term declines (Phipps et al. 2013a; Monadjem
415 et al. 2018). Accordingly, the conservation of these species will depend on protection not just of
416 breeding birds and breeding areas but also foraging habitats, many of which fall outside of protected
417 areas (Guixé & Arroyo 2011).

418 *Vulture Safe Zones as a Conservation Tool for African Gyps Vultures*

419 For the VSZ concept to be successful in an African context, it will depend on the protection from
420 poisoning and other threats, in sufficiently large areas that incorporate most of vultures' very large
421 ranges, and all of their core foraging area, which will be challenging. At a minimum, areas of 24,000 km²
422 would be needed to protect the entire range of an adult African White-backed vulture and areas of
423 more than 75,000 km² for wider-ranging Rüppell's vultures, and this does not consider the exceedingly
424 large average range of 172,450 km² for immature Rüppell's vultures. As found elsewhere, vultures are
425 likely to require nearly poison-free protection across huge areas to be conserved (Santangeli et al.
426 2019). VSZ would need to be larger than the majority of protected area networks across the African
427 continent. Additionally our results suggest that even where large protected areas do exist, vultures don't
428 heavily use them.

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

437 *Gyps* vultures spend a considerable amount of time outside protected areas, with Cape vultures
438 and immature birds of all three *Gyps* species at greatest risk. Even when 'core areas' are considered
439 (50% contours of the home range estimate) there is still a large proportion of a bird's area left
440 unprotected (Figure 2). In addition, greater use of areas outside of protected areas in the wet season
441 also heightens vultures' risk for poisoning (Kolowski & Holekamp 2006). Further, while threats may be
442 greater outside protected areas, it is known that poisoning still occurs extensively in protected areas in

443 both southern Africa (Monadjem et al. 2018) and East Africa (Virani et al. 2011; Kendall & Virani 2012),
444 particularly where it is motivated by the avoidance of rangers or collection of vulture parts (Ogada et al.
445 2015; Ogada et al. 2016).

446 Given the large ranges of vultures, others have considered the possibility of using vulture
447 restaurants (supplementary feeding) to concentrate or alter foraging behavior (Gilbert et al. 2007;
448 Monsarrat et al. 2013; Kane et al. 2016). Supplementary feeding appears to shape movement for some
449 species or individuals in some areas, but there are mixed results as to how vulture restaurants affect
450 vulture ranging behavior, which suggests this may not be a feasible strategy to contract ranges in many
451 locations (Monsarrat et al. 2013; López-López et al. 2014; Kane et al. 2016; Margalida et al. 2017). In
452 particular, vultures appear to use feeding supplementation most readily when food availability is
453 limited, during breeding, or when weather conditions are poor (Gilbert et al. 2007; Monsarrat et al.
454 2013; Ferrer et al. 2018). These are not necessarily the periods when poisoning is most frequent as
455 would need to be the case to meaningfully prevent poisoning. Despite these limitations, vulture
456 restaurants may be a valuable tool, combined with protected areas, to reduce risk of poisoning if used in
457 periods of high risk. While they are unlikely to eliminate poisoning, the prolonged periods of range
458 reduction or reduced intensity of feeding on carcasses in areas of poisoning of some individuals or
459 species that vulture restaurants may be able create, should benefit vulture conservation. In addition,
460 vulture restaurants have been shown to be valuable where food is limited, and can improve breeding
461 rates and success in these areas, which may be applicable to some areas of Southern and West Africa
462 (Schabo et al. 2016; Ferrer et al. 2018).

463 While working to reduce or eliminate threats to vultures may be easier in protected areas than
464 outside of them, VSZ would have to incorporate reductions in poisoning and other threats both within
465 and outside of protected areas to be successful. Modelling studies suggest that even small amounts of
466 poisoning can have a significant effect on vulture populations (Murn & Botha 2017), but that

467 subpopulation structure may lead to stratified risk even in nearby areas (Monadjem et al. 2018). Thus
468 insights into ranging behavior provided by telemetry studies may be a key tool when considering spatial
469 prioritization of management strategies. Success will only be possible with greater law enforcement and
470 increased anti-poaching efforts inside protected areas along with reduced human-wildlife conflict,
471 targeted persecution of those poisoning, reducing trade in vulture body parts, and mitigation of
472 mortalities associated with electrical infrastructure and wind farms.

473 *Use of Brownian Bridge Home Range Estimates*

474 Home range estimates may vary considerably depending on the tool used. While previous
475 studies have largely relied on traditional Kernel Density Estimates (KDE) or Minimum Convex Polygon
476 (MCP) (Bamford et al. 2007; Phipps et al. 2013a; Phipps et al. 2013b; Kane et al. 2016; Thompson et al.
477 2020) that estimate long-term space use, Brownian bridge estimates occurrence during the sampling
478 period and more effectively account for spatial and temporal autocorrelation inherent in telemetry data
479 (Kranstauber et al. 2012).

480 However, Brownian bridge models have not been directly compared with the autocorrelated
481 kernel density estimation (AKDE) method, which outperformed a variety of traditional home range
482 estimators such as KDE and MCP methods (Noonan et al. 2019). It should be noted that home range
483 estimates obtained through AKDE are typically much larger than KDE or MCP (Noonan et al. 2019), in
484 part because they assume that an animal will move according to the same model even beyond the
485 tracking duration and therefore may also be larger than the Brownian bridge estimates presented here.
486 Particularly for tracks with sufficient duration as included in this study, AKDE may include areas that an
487 animal didn't use during the track and may be unlikely to actually use due to habitat heterogeneity
488 which plays a role in limiting range size and area used. Indeed, a test on a sample of our data illustrated
489 the point with two individuals tracked from Eswatini having AKDE estimates of 78,091 km² and 340,033
490 km² versus 13,247 km² and 51,788km² for the Brownian bridge respectively (this was done with the amt

491 package using 'auto' as the autocorrelation model). Since our Brownian bridge home range estimates
492 already suggest that creating VSZ in Africa will be challenging, due to the large size and minimal overlap
493 with protected areas of their ranges, then such estimates based on AKDE further support our main
494 conclusion. We also found a significant effect of study on our home range estimates, which could relate
495 to differences between individual study populations or to differences in frequency of data collected and
496 how we addressed this in our methods.

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

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

512 *Limitation and Future Directions*

513 A significant caveat of our work is that we have not considered the behavioral state of vultures
514 in relation to habitat use. Future studies investigating whether activity outside of protected areas is

515 primarily travel between protected sites or feeding sites have significant conservation implications,
516 particularly in relation to the risk of encountering poisoning events. New techniques have been
517 developed, allowing for a more sophisticated investigation of behavior from telemetry data and future
518 work applying these to large multi-site datasets such as this one would be valuable (Whoriskey et al.
519 2017).

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

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

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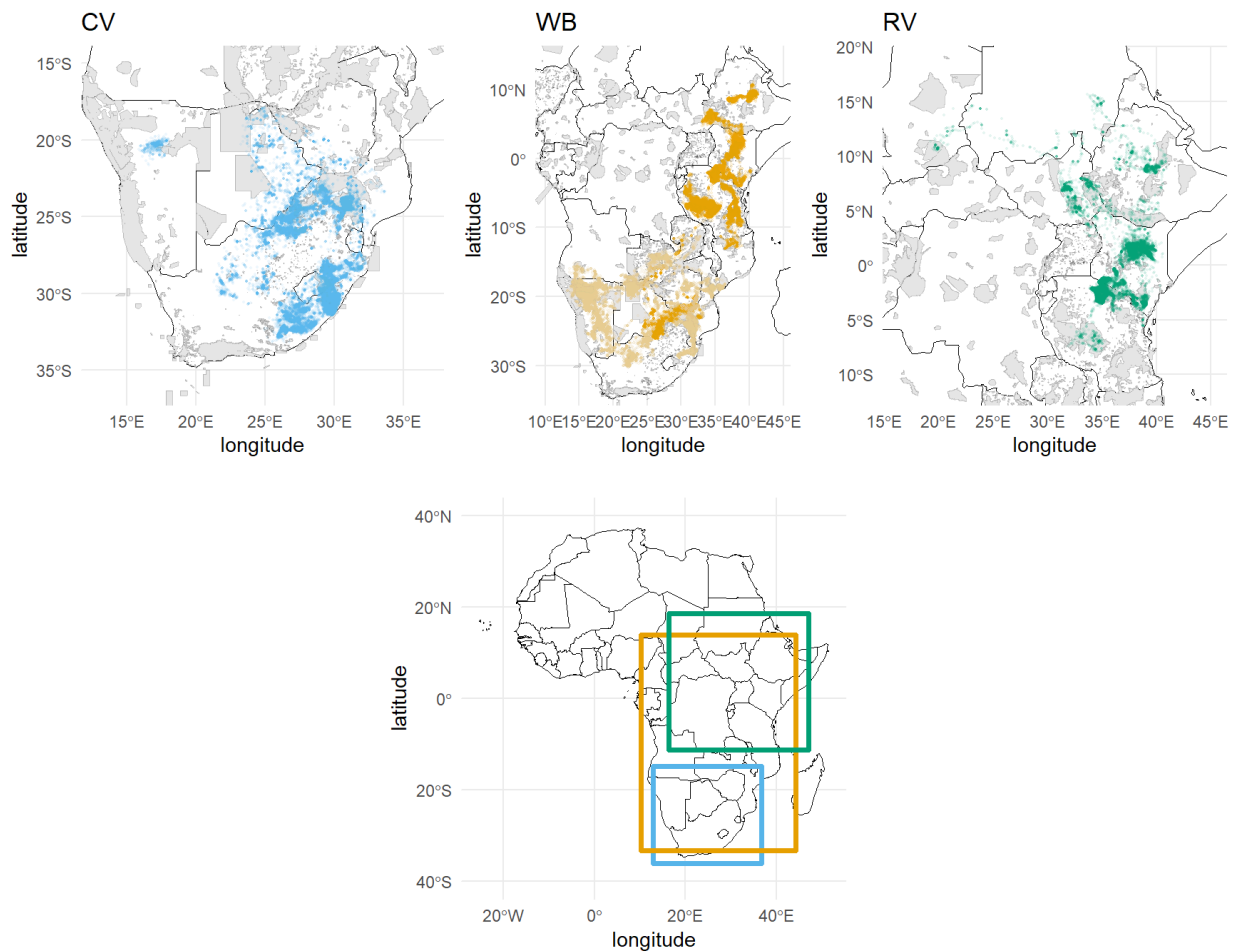
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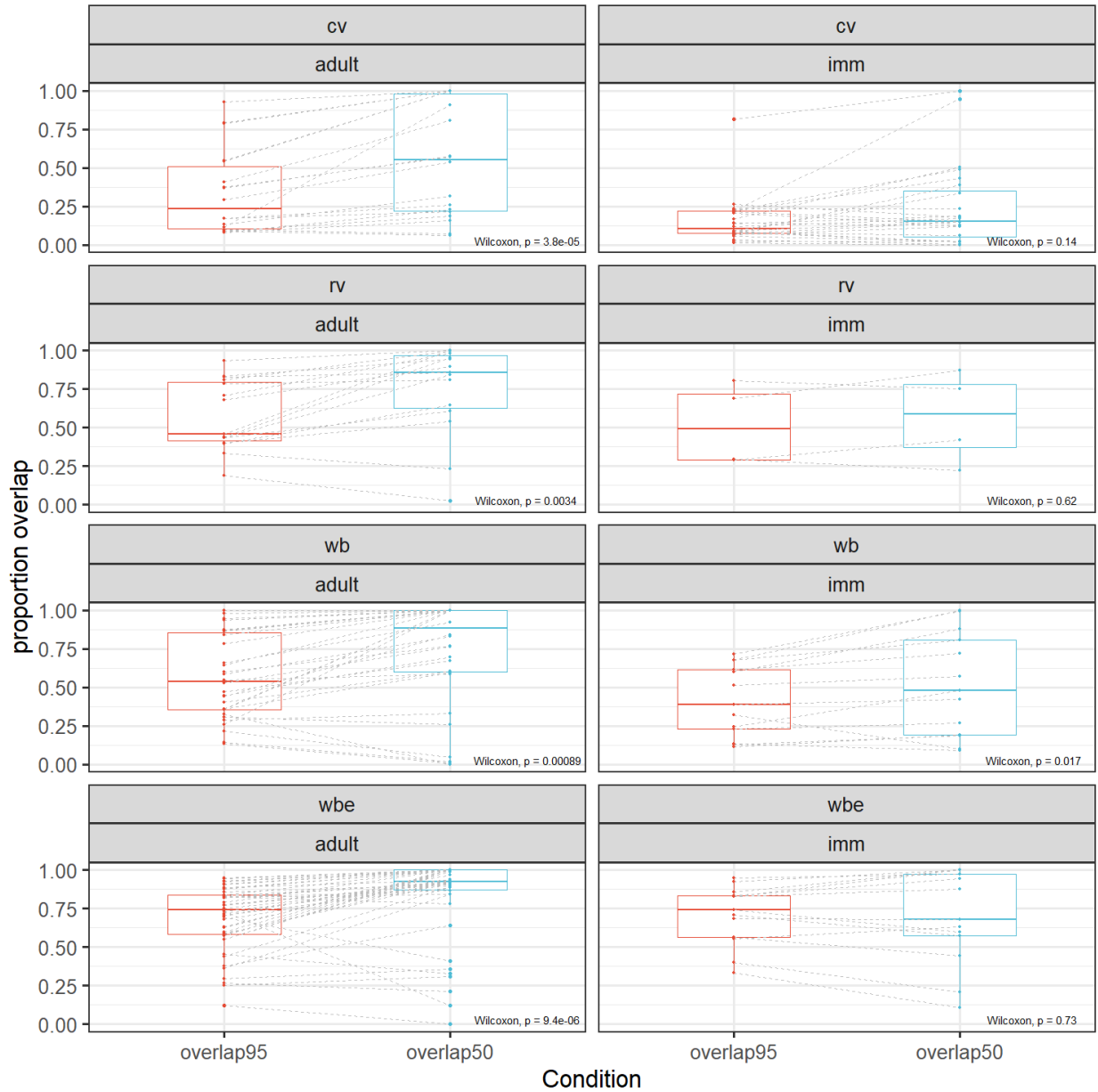
807 **Figures and Tables**



808

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

813



814

815 **Figure 2 - Comparison of proportion of overlap of Brownian bridges with protected areas at 95% and**
 816 **50% contours. Dashed lines connect the same bird. Means are compared using a Wilcoxon Rank Sum**
 817 **test. Abbreviations: cv = Cape vulture, rv = Rüppell's vulture, wb = White-backed vulture (southern**
 818 **population), wbe = White-backed vulture (eastern population), imm = immature.**

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820

821 **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 | |

822

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

827

| species | region | age | count | mean | median | sd | min | max |
|---------|--------|-------|-------|---------|---------|---------|--------|---------|
| cv | south | adult | 18 | 36,145 | 26,220 | 36,464 | 4,270 | 157,828 |
| cv | south | imm | 24 | 74,060 | 47,839 | 68,793 | 1,953 | 245,743 |
| rv | east | adult | 15 | 75,441 | 56,349 | 60,611 | 6,018 | 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 | 3,907 | 113,920 |
| wb | east | imm | 13 | 31,540 | 18,778 | 37,729 | 5,980 | 144,087 |
| wb | south | adult | 30 | 36,186 | 15,978 | 46,505 | 2,371 | 198,900 |
| wb | south | imm | 13 | 96,519 | 88,637 | 80,885 | 5,827 | 295,912 |

828

829

830

831

832

833

834 **Table 3 – Monthly estimate of 95% Brownian Bridge Home Range data for three species of African**
 835 **vulture: Cape (cv); Rüppell’s (rv) and African white-backed (wb). Vultures were tracked in two regions,**
 836 **southern and eastern Africa, and birds were aged as adults or immatures (imm). The total number of**
 837 **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 | 1,021 | 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 | 2,744 | 162,207 |
| rv | east | imm | 29 | 36,023 | 17,312 | 41,572 | 2,855 | 164,411 |
| wb | east | adult | 463 | 12,640 | 8,569 | 13,360 | 700 | 106,227 |
| wb | east | imm | 156 | 11,816 | 9,762 | 7,986 | 1,414 | 38,518 |
| wb | south | adult | 353 | 11,813 | 8,908 | 10,596 | 641 | 61,972 |
| wb | south | imm | 110 | 16,138 | 10,866 | 14,255 | 1,364 | 67,638 |

838

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

| Proportion of 95% BBMM contour covered by PAs | | | | | | |
|---|--------|-------|-------|-------|--------|-------|
| species | region | age | count | 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 |

843

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

| Proportion of 95% BBMM contour covered by PAs | | | | | | |
|---|--------|-------|-------|-------|--------|-------|
| species | region | age | count | 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 |

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

| Predictors | Estimates | CI | p |
|---------------------|-----------|---------------|------------------|
| (Intercept) | 10.50 | 9.95 – 11.05 | <0.001 |
| breeding adults | -1.38 | -1.90 – -0.87 | <0.001 |
| non-breeding adults | -0.40 | -0.77– -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 |

850

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

| Predictors | Estimates | CI | p |
|---------------------|-----------|---------------|------------------|
| (Intercept) | -1.04 | -1.65 – -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 |

853

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

| Predictors | Estimates | CI | p |
|-----------------------------|-----------|---------------|------------------|
| (Intercept) | 9.36 | 8.99-9.73 | <0.001 |
| breeding adults | -0.34 | -0.61 - -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 |

856

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

| Predictors | Estimate | CI | p |
|-----------------------------|----------|---------------|------------------|
| (Intercept) | -1.51 | -2.17 – -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 |

859 **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 |

860