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

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

3 Adam Kane, Ara Monadjem, H.K. Ortwin Aschenborn, Keith Bildstein, André Botha, Claire

4 Bracebridge, Evan R. Buechley, Ralph Buij, John P. Davies, Maria Diekmann, Colleen T. Downs, Nina

5 Farwig, Toby Galligan, Gregory Kaltenecker, Chris Kelly, Ryno Kemp, Holger Kolberg, Monique L.

6 MacKenzie, John Mendelsohn, Msafiri Mgumba, Ran Nathan, Aaron Nicholas, Darcy Ogada, Morgan

7 B. Pfeiffer, W. Louis Phipps, Matteuns D. Pretorius, Sascha Rösner, Dana G. Schabo, Gabriel Lita

8 Shatumbu, Orr Spiegel, Lindy J. Thompson, Jan A. Venter, Munir Virani, Kerri Wolter, Corinne

9 Kendall*

10 **Author Affiliations**

11 Adam Kane, School of Biology and Environmental Science and Earth Institute, O'Brien Science Centre

12 West, University College Dublin, Belfield, Dublin 4, Dublin, Ireland. ORCID: https://orcid.org/0000-

13 0002-2830-5338

14 Ara Monadjem, Department of Biological Sciences, University of Eswatini, Private Bag 4, Kwaluseni,

15 Eswatini *AND* Mammal Research Institute, Department of Zoology and Entomology, University of

16 Pretoria, Private Bag 20, Hatfield 0028, Pretoria, South Africa. ORCID: https://orcid.org/0000-0003-

17 1906-4023

18 H.K. Ortwin Aschenborn, University of Namibia, School of Veterinary Medicine, Neudamm

19 Keith Bildstein, Hawk Mountain Sanctuary, 410 Summer Valley Rd. Orwigsburg, PA 17961

20 André Botha, Vultures for Africa Programme, Endangered Wildlife Trust, 27 and 28 Austin Road, Glen

21 Austin AH, Midrand, 1685, South Africa. ORCID: https://orcid.org/0000-0003-1077-1215

22 Claire Bracebridge, Department of Conservation, Education and Science, North Carolina Zoo, 4401

23 Zoo Parkway, Asheboro, NC, 27205

24   Evan R. Buechley, Smithsonian Migratory Bird Center, PO Box 37012, MRC 5503, Washington, DC

25   20013-7012, USA AND HawkWatch International, 2240 South 900 East, Salt Lake City, UT 84106, USA

26   Ralph Buij, Wageningen University and Research, Droevendaalsesteeg 3A, 6708 PB Wageningen, The

27   Netherlands AND The Peregrine Fund - World Center for Birds of Prey, 5668 West Flying Hawk Lane,

28   Boise, ID 83709, USA

29   John P. Davies, https://orcid.org/0000-0003-0252-7650 Birds of Prey Programme, Endangered

30   Wildlife Trust, 27 and 28 Austin Road, Glen Austin AH, Midrand, 1685, South Africa.

31   Maria Diekmann, Rare & Endangered Species Trust, P.O. Box 275, Outjo, Namibia 9000

32   Colleen T. Downs, Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-

33   Natal, Private Bag X01, Scottsville, Pietermaritzburg, 3209, South Africa

34   Nina Farwig, Conservation Ecology, Department of Biology, Philipps-Universität Marburg, Karl-von-

35   Frisch-Straße 8, 35043 Marburg

36   Toby Galligan, Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire SG19 2DL,

37   UK

38   Gregory Kaltenecker, Intermountain Bird Observatory, Boise State University, 1910 University Drive,

39   Boise, Idaho, USA

40   Chris Kelly, Wildlife ACT Fund Trust, Cape Town, Gardens, 8001, South Africa

41   Ryno Kemp, VulPro NPO, PO Box 285 Skeerpoort South Africa 0232, ORCID: https://orcid.org/0000-

42   0002-5339-8783

43   Holger Kolberg, Directorate Scientific Services, Ministry of Environment, Forestry and Tourism,

44   Windhoek, Namibia

45   Monique MacKenzie, Centre for Research into Ecological and Environmental Modelling (CREEM),

46   School of Mathematics and Statistics, University of St Andrews, Scotland.

47   John Mendelsohn Ongava Research Centre, Outjo District, Namibia

48   Msafiri Mgumba, Wildlife Conservation Society, Ruaha-Katavi Landscape Program, Tanzania

49   Ran Nathan, Movement Ecology Laboratory, Department of Ecology, Evolution and Behavior,

50   Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem, Israel

51   http://orcid.org/0000-0002-5733-6715

52   Aaron Nicholas, Wildlife Conservation Society, Ruaha-Katavi Landscape Program, Tanzania

53   Darcy Ogada, The Peregrine Fund, 5668 West Flying Hawk Lane, Boise, Idaho USA

54   Morgan B. Pfeiffer, United States Department of Agriculture, Animal and Plant Health Inspection

55   Service, Wildlife Services, National Wildlife Research Center, Ohio Field Station, Sandusky, OH United

56   States. ORCID: https://orcid.org/0000-0002-1079-5295 AND School of Natural Resource

57   Management, George Campus, Nelson Mandela University, George, South Africa

58   W. Louis Phipps, Vulture Conservation Foundation, Wuhrstrasse 12, CH-8003 Zurich, Switzerland

59   Mattheuns Pretorius, Wildlife and Energy Programme, Endangered Wildlife Trust, 27 and 28 Austin

60   Road, Glen Austin AH, Midrand, 1685, South Africa. ORCHID: https://orcid.org/0000-0001-9010-7597

61   Sascha Rösner, Conservation Ecology, Department of Biology, Philipps-Universität Marburg, Karl-

62   von-Frisch-Straße 8, 35043 Marburg AND pixeldiversity GmbH, Kirchweg 2, 35043 Marburg,

63   Germany. ORCID: https://orcid.org/0000-0002-6766-1546

64   Dana G. Schabo, Conservation Ecology, Department of Biology, Philipps-Universität Marburg, Karl-

65   von-Frisch-Straße 8, 35043 Marburg

66   Mr Gabriel Lita Shatumbu, Ministry of Environment Forestry and Tourism, AirWing, Namibia

67   Orr Spiegel, School of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel.

68   ORICD: https://orcid.org/0000-0001-8941-3175

69   Lindy J. Thompson, Birds of Prey Programme, Endangered Wildlife Trust, 27 and 28 Austin Road,

70   Glen Austin AH, Midrand, 1685, South Africa AND Centre for Functional Biodiversity, School of Life

71   Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, 3209, South Africa. ORCID:

72   https://orcid.org/0000-0001-9847-2003.

73   Jan A Venter, School of Natural Resource Management, George Campus, Nelson Mandela University,

74   George, South Africa AND REHABS International Research Laboratory, CNRS-Université Lyon 1-

75   Nelson Mandela University, George, South Africa

76   Munir Virani, The Peregrine Fund, 5668 West Flying Hawk Lane, Boise, Idaho USA, 83709

77   Kerri Wolter, VulPro NPO, PO Box 285 Skeerpoort South Africa 0232, ORCID: https://orcid.org/0000-

78   0002-9291-8622

79   Corinne Kendall*, Conservation, Education and Science, North Carolina Zoo, 4401 Zoo Parkway,

80   Asheboro, NC, 27205, North Carolina State University, Raleigh NC 27695

81   *Corresponding author - Corinne.Kendall@nczoo.org; +1-713-826-5443

82

83   **Acknowledgements**

156

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 km^2 would be needed to protect the entire range of an adult African White-

18   backed vulture and areas of more than 75,000 km^2 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 km^2 (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 (Pennycuick

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-randing 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 Pennycuick 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 abbatoirs 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

5

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-variates. 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 km^2, 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 km^2 for Cape vultures). Breeding adults had smaller home ranges than immature

258   birds (with an average estimate of 9,168 km^2 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 km^2 vs 12,456 km^2) (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 km^2 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   (Pennycuick 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 (Pennycuick 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 km^2 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 km^2, 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 km^2

422   would be needed to protect the entire range of an adult African White-backed vulture and areas of

423   more than 75,000 km^2 for wider-ranging Rüppell's vultures, and this does not consider the exceedingly

424   large average range of 172,450 km^2 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 km^2 and 340,033

490　km^2 versus 13,247 km^2 and 51,788km^2 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 minimial 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 km^2.

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.

531 **References**

532 Alarcón PA, Lambertucci SA. 2018. A three-decade review of telemetry studies on vultures and condors.
533   Movement ecology **6**:13.
534 Attwell RIG. 1963. Some observations on feeding habits, behavior, and inter-relationships of Northern
535   Rhodesian vultures. Ostrich **34**:235-247.
536 Bamford AJ, Diekmann M, Monadjem A, Mendelsohn J. 2007. Ranging behaviour of Cape Vultures Gyps
537   coprotheres from an endangered population in Namibia. Bird Conservation International
538   **17**:331-339.
539 Bamford AJ, Monadjem A, Hardy ICW. 2009a. An effect of vegetation structure on carcass exploitation
540   by vultures in an African savanna. Ostrich **80**:135-137.
541 Bamford AJ, Monadjem A, Hardy ICW. 2009b. Nesting habitat preference of the African White-backed
542   Vulture *Gyps africanus* and the effects of anthropogenic disturbance. Ibis **151**:51-62.
543 Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. . Journal
544   of Statistical Software **67**:1-48.

545   Bose M, Duriez O, Sarrazin F. 2012. Intra-specific competition in foraging Griffon Vultures Gyps fulvus: 1.
546   Dynamics of group feeding. Bird Study **59**:182-192.
547   Boshoff A, Barkhuysen A, Brown G, Michael M. 2009. Evidence of partial migratory behaviour by the
548   Cape Griffon Gyps coprotheres. Ostrich **80**:129-133.
549   Boshoff AF, Minnie JC, Tambling CJ, Michael MD. The impact of power line-related mortality on the Cape
550   Vulture Gyps coprotheres in a part of its range, with an emphasis on electrocution. Bird
551   Conservation International **21**:311-327.
552   Botha A, Andevski J, Bowden C, Gudka M, Safford R, Tavares J, Williams N. 2017. Multi-species action
553   plan to conserve African-Eurasian vultures. CMS raptors MOU technical publication:1-164.
554   Bracis C, Bildstein KL, Mueller T. 2018. Revisitation analysis uncovers spatio-temporal patterns in animal
555   movement data. Ecography **41**:1801-1811.
556   Brink CW, Santangeli A, Amar A, Wolter K, Tate G, Krüger S, Tucker AS, Thomson RL. 2020. Quantifying
557   the spatial distribution and trends of supplementary feeding sites in South Africa and their
558   potential contribution to vulture energetic requirements. Animal Conservation **23**:491-501.
559   Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M,
560   Bolker BM. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated
561   generalized linear mixed modeling. The R journal **9**:378-400.
562   Buechley ER, et al. 2021. Priority areas for vulture conservation in the Horn of Africa largely fall outside
563   the protected area network. Bird Conservation International:1-18.
564   Buechley ER, Sekercioglu CH. 2016. The avian scavenger crisis: Looming extinctions, trophic cascades,
565   and loss of critical ecosystem functions. Biological Conservation **198**:220-228.
566   Calenge C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and
567   habitat use by animals. Ecological Modelling **197**:516-519.
568   Cazalis V, Princé K, Mihoub JB, Kelly J, Butchart SHM, Rodrigues ASL. 2020. Effectiveness of protected
569   areas in conserving tropical forest birds. Nature Communications **11**:4461.
570   Douma JC, Weedon JT. 2019. Analysing continuous proportions in ecology and evolution: A practical
571   introduction to beta and Dirichlet regression. Methods in Ecology and Evolution **10**:1412-1430.
572   Durant SM. 1998. Competition refuges and coexistence: an example from Serengeti carnivores. Journal
573   of Animal Ecology **67**:370-386.
574   Duriez O, Kato A, Tromp C, Dell'Omo G, Vyssotski AL, Sarrazin F, Ropert-Coudert Y. 2014. How Cheap Is
575   Soaring Flight in Raptors? A Preliminary Investigation in Freely-Flying Vultures. Plos One **9**.
576   Ferrer M, Morandini V, Baguena G, Newton I. 2018. Reintroducing endangered raptors: A case study of
577   supplementary feeding and removal of nestlings from wild populations. Journal of Applied
578   Ecology **55**:1360-1367.
579   Fischer JW, Walter WD, Avery ML. 2013. Brownian Bridge Movement Models to Characterize Birds'
580   Home Ranges: Modelos de Movimiento de Puente Browniano Para Caracterizar el Rango de
581   Hogar de las Aves. The Condor **115**:298-305.
582   Fleming CH, Fagan WF, Mueller T, Olson KA, Leimgruber P, Calabrese JM. 2015. Rigorous home range
583   estimation with movement data: a new autocorrelated kernel density estimator. Ecology
584   **96**:1182-1188.
585   Galligan TH, Bhusal KP, Paudel K, Chapagain D, Joshi AB, Chaudhary IP, Chaudhary A, Baral HS, Cuthbert
586   RJ, Green RE. 2020. Partial recovery of Critically Endangered Gyps vulture populations in Nepal.
587   Bird Conservation International **30**:87-102.
588   Geldmann J, Barnes M, Coad L, Craigie ID, Hockings M, Burgess ND. 2013. Effectiveness of terrestrial
589   protected areas in reducing habitat loss and population declines. Biological Conservation
590   **161**:230-238.
591   Gilbert M, Watson RT, Ahmed S, Asim M, Johnson JA. 2007. Vulture restaurants and their role in
592   reducing diclofenac exposure in Asian vultures. Bird Conservation International **17**:63-77.

593 Guido JM, Alarcón PAE, Donázar JA, Hiraldo F, Lambertucci SA. 2019. The use of biosphere reserves by a
594   wide-ranging avian scavenger indicates its significant potential for conservation. Environmental
595   Conservation **47**:22-29.
596 Guixé D, Arroyo B. 2011. Appropriateness of Special Protection Areas for wide-ranging species: the
597   importance of scale and protecting foraging, not just nesting habitats. Animal Conservation
598   **14**:391-399.
599 Gutiérrez-Cánovas C, Moleón M, Mateo-Tomás P, Olea PP, Sebastián-González E, Sánchez-Zapata JA.
600   2020. Large home range scavengers support higher rates of carcass removal.
601   bioRxiv:2020.2002.2007.938415.
602 Harel R, Duriez O, Spiegel O, Fluhr J, Horvitz N, Getz WM, Bouten W, Sarrazin F, Hatzofe O, Nathan R.
603   2016. Decision-making by a soaring bird: time, energy and risk considerations at different spatio-
604   temporal scales. Philosophical Transactions of the Royal Society B: Biological Sciences
605   **371**:20150397.
606 Hirschauer MT, Wolter K, Green RE, Galligan T. 2017. Immature Cape Vulture Gyps coprotheres breaks
607   species range record. Biodiversity Observations **8**:1-4.
608 Houston CS, McLoughlin PD, Mandel JT, Bechard MJ, Stoffel MJ, Barber DR, Bildstein KL. 2011. Breeding
609   Home Ranges of Migratory Turkey Vultures Near Their Northern Limit. The Wilson Journal of
610   Ornithology **123**:472-478.
611 Houston DC. 1974a. Food searching behavior in Griffon vultures. East African Wildlife Journal **12**:63-77.
612 Houston DC. 1974b. The role of griffon vultures *Gyps africanus* and *Gyps rueppellii* as scavengers.
613   Journal of Zoology, London **172**:35-46.
614 Houston DC. 1975. Ecological isolation of African scavenging birds. Ardea **63**:55-64.
615 Houston DC. 1976. Breeding of White-Backed and Ruppells Griffon Vultures, Gyps-Africanus and Gyps-
616   Rueppellii. Ibis **118**:14-40.
617 Houston DC. 1979. The adaptations of scavengers. Pages 263-286 in Sinclair ARE, and Griffiths MN,
618   editors. Serengeti, dynamics of an ecosystem. University of Chicago Press, Chicago.
619 Jobson B, Wolter K, Jordan L, Monadjem A, Rowcliffe JM. 2020. Home range and habitat selection of
620   captive-bred and rehabilitated cape vultures Gyps coprotheres in southern Africa. Oryx:1-6.
621 Kane A, Kendall CJ. 2017. Understanding how mammalian scavengers use information from avian
622   scavengers: cue from above. Journal of Animal Ecology **86**:837-846.
623 Kane A, Wolter K, Neser W, Kotze A, Naidoo V, Monadjem A. 2016. Home range and habitat selection of
624   Cape Vultures Gyps coprotheres in relation to supplementary feeding. Bird Study:1-8.
625 Kendall C. 2013. Alternative strategies in avian scavengers: how subordinate species foil the despotic
626   distribution. Behavioral Ecology and Sociobiology **67**:383-393.
627 Kendall C, Virani M. 2012. Assessing mortality of african vultures using wing tags and GSM-GPS
628   transmitters. Journal of Raptor Research **46**:135-140.
629 Kendall C, Virani M, Kirui P, Thomsett S, Githiru M. 2012. Mechanisms of coexistence in vultures:
630   Understanding the patterns of vulture abundance at carcasses in Masai Mara National Reserve,
631   Kenya. Condor **114**:523-531.
632 Kendall CJ. 2014. The early bird gets the carcass: Temporal segregation and its effects on foraging
633   success in avian scavengers. The Auk **131**:12-19.
634 Kendall CJ, Rubenstein DI, Slater PL, Monadjem A. 2018. An assessment of tree availability as a possible
635   cause of population declines in scavenging raptors. Journal of Avian Biology **49**.
636 Kendall CJ, Virani MZ, Hopcraft JGC, Bildstein KL, Rubenstein DI. 2014. African Vultures Don't Follow
637   Migratory Herds: Scavenger Habitat Use Is Not Mediated by Prey Abundance. PLoS ONE
638   **9**:e83470.
639 Kirk DA, Houston DC. 1995. Social-Dominance in Migrant and Resident Turkey Vultures at Carcasses -
640   Evidence for a Despotic Distribution. Behavioral Ecology and Sociobiology **36**:323-332.

641 Kolowski JM, Holekamp KE. 2006. Spatial, temporal, and physical characteristics of livestock
642   depredations by large carnivores along a Kenyan reserve border. Biological Conservation
643   **128**:529-541.
644 Komen J, Brown CJ. 1993. Food-Requirements and the Timing of Breeding of a Cape-Vulture Colony.
645   Ostrich **64**:86-92.
646 Konig C. 1983. Interspecific and intraspecific competition for food among Old World vultures. Pages 153-
647   171 in Wilbur SR, and Jackson AL, editors. Vulture Biology and Management. University of
648   California Press, Berkeley and Los Angelos.
649 Kranstauber B, Kays R, LaPoint SD, Wikelski M, Safi K. 2012. A dynamic Brownian bridge movement
650   model to estimate utilization distributions for heterogeneous animal movement. Journal of
651   Animal Ecology **81**:738-746.
652 Kranstauber B, Smolla M, Scharf AK. 2020. move: visualizing and analyzing animal track data. R package
653   version 4.0.4. **https://CRAN.R-project.org/package=move**.
654 Kruuk H. 1967. Competition for food between vultures in East Africa. Ardea **55**:171-193.
655 Leepile LBL, Maude G, Hancock P, Reading RP, Bridges B, Hartley R, Amar A. 2020. Changes in nesting
656   numbers and breeding success of African White-backed Vulture Gyps africanus in north-central
657   Botswana. Bird Conservation International:1-18.
658 Lenth R, Singmann H, Love J, Buerkner P, Herve M. 2020. Emmeans: estimated marginal means, aka
659   least-squares means. R Package Vers 1.5.2-1. **https://CRAN.R-project.org/package=emmeans**.
660 Lindsey PA, et al. 2017. The performance of African protected areas for lions and their prey. Biological
661   Conservation **209**:137-149.
662 López-López P, García-Ripollés C, Urios V. 2014. Food predictability determines space use of endangered
663   vultures: implications for management of supplementary feeding. Ecological Applications
664   **24**:938-949.
665 Margalida A, Pérez-García JM, Moreno-Opo R. 2017. European policies on livestock carcasses
666   management did not modify the foraging behavior of a threatened vulture. Ecological Indicators
667   **80**:66-73.
668 Markandya A, Taylor T, Longo A, Murty MN, Murty S, Dhavala K. 2008. Counting the cost of vulture
669   decline - An appraisal of the human health and other benefits of vultures in India. Ecological
670   Economics **67**:194-204.
671 Martens FR, Pfeiffer MB, Downs CT, Venter JA. 2018. Post-fledging movement and spatial ecology of the
672   endangered Cape Vulture (Gyps coprotheres). Journal of Ornithology **159**:913-922.
673 McPherson SC, Brown M, Downs CT. 2019. Home Range of a Large Forest Eagle in a Suburban
674   Landscape: Crowned Eagles (*Stephanoaetus coronatus*) in the Durban Metropolitan Open
675   Space System, South Africa. Journal of Raptor Research **53**:180-188, 189.
676 Mduma SAR, Sinclair ARE, Hilborn R. 1999. Food regulates the Serengeti wildebeest: a 40-year record.
677   Journal of Animal Ecology **68**:1101-1122.
678 Monadjem A, Botha A, Murn C. 2013. Survival of the African white-backed vulture Gyps africanus in
679   north-eastern South Africa. African Journal of Ecology **51**:87-93.
680 Monadjem A, Garcelon DK. 2005. Nesting distribution of vultures in relation to land use in Swaziland.
681   Biodiversity and Conservation **14**:2079-2093.
682 Monadjem A, Kane A, Botha A, Kelly C, Murn C. 2018. Spatially explicit poisoning risk affects survival
683   rates of an obligate scavenger. Scientific Reports **8**:4364.
684 Monadjem A, Wolter K, Neser W, Kane A. 2014. Effect of rehabilitation on survival rates of endangered
685   Cape vultures. Animal Conservation **17**:52-60.
686 Monsarrat S, Benhamou S, Sarrazin F, Bessa-Gomes C, Bouten W, Duriez O. 2013. How Predictability of
687   Feeding Patches Affects Home Range and Foraging Habitat Selection in Avian Social Scavengers?
688   Plos One **8**.

689   Morán-López R, Sánchez Guzmán JM, Borrego EC, Sánchez AV. 2006. Nest-site selection of endangered
690   cinereous vulture (Aegypius monachus) populations affected by anthropogenic disturbance:
691   present and future conservation implications. Animal Conservation **9**:29-37.
692   Moreno-Opo R, Trujillano A, Margalida A. 2020. Larger size and older age confer competitive advantage:
693   dominance hierarchy within European vulture guild. Scientific Reports **10**:2430.
694   Mukherjee A, Galligan T, Prakash V, Paudel K, Khan U, Prakash S, Ranade S, Shastri K, Dave R, Donald P.
695   2014. Vulture Safe Zones to save Gyps Vultures in South Asia. Mistnet **15**:4-21.
696   Mundy PJ, Butchart D, Ledger JA, Piper SE 1992. The Vultures of Africa. Acorn books and Russel
697   Friedman books, Randburg, South Africa.
698   Murn C, Botha A. 2017. A clear and present danger: impacts of poisoning on a vulture population and
699   the effect of poison response activities. Oryx:1-7.
700   Murn C, Holloway GJ. 2014. Breeding biology of the White-headed Vulture Trigonoceps occipitalis in
701   Kruger National Park, South Africa. Ostrich **85**:125-130.
702   Newton I, McGrady MJ, Oli MK. 2016. A review of survival estimates for raptors and owls. Ibis **158**:227-
703   248.
704   Ogada D, Botha A, Shaw P. 2015. Ivory poachers and poison: drivers of Africa's declining vulture
705   populations. Oryx:1-4.
706   Ogada D, et al. 2016. Another Continental Vulture Crisis: Africa's Vultures Collapsing toward Extinction.
707   Conservation Letters **9**:89-97.
708   Ogada DL. 2014. The power of poison: pesticide poisoning of Africa's wildlife. Pages 1-20 in Ostfeld RS,
709   and Power AG, editors. Year in Ecology and Conservation Biology.
710   Ogada DL, Torchin ME, Kinnaird MF, Ezenwa VO. 2012. Effects of Vulture Declines on Facultative
711   Scavengers and Potential Implications for Mammalian Disease Transmission. Conservation
712   Biology **26**:453-460.
713   Ogutu JO, Piepho HP, Dublin HT, Bhola N, Reid RS. 2008. Rainfall influences on ungulate population
714   abundance in the Mara-Serengeti ecosystem. Journal of Animal Ecology **77**:814-829.
715   Palm EC, Newman SH, Prosser DJ, Xiao X, Ze L, Batbayar N, Balachandran S, Takekawa JY. 2015. Mapping
716   migratory flyways in Asia using dynamic Brownian bridge movement models. Movement Ecology
717   **3**:3.
718   Pebesma E. 2018. Simple Features for R: Standardized Support for Spatial Vector Data. The R Journal 10
719   **1**:439-446.
720   Peery MZ. 2000. Factors Affecting Interspecies Variation in Home-range Size of Raptors. The Auk
721   **117**:511-517.
722   Pennycuick CJ. 1972. Soaring behavior and performance of some East African birds, observed from a
723   motor-glider Ibis **114**:178-218.
724   Pennycuick CJ. 1979. Energy costs of locomotion and the concept of "foraging radius" in Sinclair ARE,
725   and Arcese P, editors. Serengeti II: dynamics, management, and conservation of an ecosystem.
726   University of Chicago Press, Chicago.
727   Pfeiffer MB, Venter JA, Downs CT. 2014. Identifying human generated threats to Cape Vultures (*Gyps
728   coprotheres*) using community perceptions in communal farmland, Eastern Cape Province, South
729   Africa. Bird Conservation International **25**:353-365.
730   Pfeiffer MB, Venter JA, Downs CT. 2015. Foraging range and habitat use by Cape Vulture Gyps
731   coprotheres from the Msikaba colony, Eastern Cape province, South Africa. Koedoe **57**.
732   Phipps WL, Willis SG, Wolter K, Naidoo V. 2013a. Foraging Ranges of Immature African White-backed
733   Vultures (*Gyps africanus*) and Their Use of Protected Areas in Southern Africa. PlosOne **8**.
734   Phipps WL, Wolter K, Michael MD, MacTavish LM, Yarnell RW. 2013b. Do power lines and protected
735   areas present a catch-22 situation for cape vultures (Gyps coprotheres)? PLoS One **8**.

736 Piper SE, * Mundy, P.J.**, amp, Vernon CJ. 1989. An ageing guide for the Cape Vulture. Madoqua
737   **1989**:105-110.
738 Riggio J, Jacobson AP, Hijmans RJ, Caro T. 2019. How effective are the protected areas of East Africa?
739   Global Ecology and Conservation **17**:e00573.
740 Robertson AS, Boshoff AF. 1986. The feeding ecology of cape vultures Gyps coprotheres in a stock-
741   farming area. Biological Conservation **35**:63-86.
742 Rolando A. 2002. On the ecology of home range in birds. Revue d Ecologie **57**:53-73.
743 Runge CA, Watson JEM, Butchart SHM, Hanson JO, Possingham HP, Fuller RA. 2015. Protected areas and
744   global conservation of migratory birds. Science **350**:1255.
745 Ruxton GD, Houston DC. 2002. Modelling the energy budget of a colonial bird of prey, the Ruppell's
746   griffon vulture, and consequences for its breeding ecology. African Journal of Ecology **40**:260-
747   266.
748 Ruxton GD, Houston DC. 2004. Obligate vertebrate scavengers must be large soaring fliers. Journal of
749   Theoretical Biology **228**:431-436.
750 Santangeli A, Girardello M, Buechley E, Botha A, Minin ED, Moilanen A. 2019. Priority areas for
751   conservation of Old World vultures. Conservation Biology **33**:1056-1065.
752 Schabo DG, Heuner S, Neethling MV, RÖSner S, Uys R, Farwig N. 2016. Long-term data indicates that
753   supplementary food enhances the number of breeding pairs in a Cape Vulture Gyps coprotheres
754   colony. Bird Conservation International **27**:140-152.
755 Scott TK. 2020. Movements of white-headed and white-backed vultures. Boise State University.
756 Sebastián-González E, et al. 2019. Scavenging in the Anthropocene: Human impact drives vertebrate
757   scavenger species richness at a global scale. Global Change Biology **0**:1-13.
758 Sebastián-González E, et al. 2020. Network structure of vertebrate scavenger assemblages at the global
759   scale: drivers and ecosystem functioning implications. Ecography.
760 Shimada T, Jones R, Limpus C, Hamann M. 2012. Improving data retention and home range estimates by
761   data-driven screening. Marine Ecology Progress Series **457**:171-180.
762 Shobrak MY. 2014. Satellite tracking of the Lappet-faced Vulture Torgos tracheliotos in Saudi Arabia.
763   Jordan Journal of Natural History **1**:131-141.
764 Signer J, Fieberg J, Avgar T. 2019. Animal movement tools (amt): R package for managing tracking data
765   and conducting habitat selection analyses. Ecology and Evolution **9**:880-890.
766 Spiegel O, Getz WM, Nathan R. 2013. Factors Influencing Foraging Search Efficiency: Why Do Scarce
767   Lappet-Faced Vultures Outperform Ubiquitous White-Backed Vultures? American Naturalist
768   **181**:E102-E115.
769 Spiegel O, Harel R, Centeno-Cuadros A, Hatzofe O, Getz WM, Nathan R. 2015. Moving beyond Curve
770   Fitting: Using Complementary Data to Assess Alternative Explanations for Long Movements of
771   Three Vulture Species. American Naturalist **185**:E44-E54.
772 Steyn P. 1980. Breeding and food of the Bateleur in Zimbabwe (Rhodesia). Ostrich **51**:168-178.
773 Team RC 2020. R: A language and environment for statistical computing. R Foundation for Statistical
774   Computing, Vienna, Austria.
775 Thompson LJ, et al. 2020. Variation in monthly sizes of home-ranges of Hooded Vultures
776   Necrosyrtes monachus in western, eastern and southern Africa. Ibis **162**:1324-1338.
777 Thompson LJ, et al. 2021. Assessing African vultures as (i) avian biomonitors and (ii) umbrella species for
778   all African vultures. Frontiers in Conservation Science:81.
779 UNEP-WCMC, IUCN. 2016. Protected Planet Report 2016. UNEP-WCMC and IUCN, Cambridge UK and
780   Gland, Switzerland.
781 van Eeden R, Whitfield DP, Botha A, Amar A. 2017. Ranging behaviour and habitat preferences of the
782   Martial Eagle: Implications for the conservation of a declining apex predator. PLOS ONE
783   **12**:e0173956.

784 Virani M, Kirui P, Monadjem A, Thomsett S, Githiru M. 2010. Nesting status of African White-backed
785   Vultures Gyps africanus in the Masai Mara National Reserve, Kenya. Ostrich **81**:205-209.
786 Virani M, Monadjem A, Thomsett S, Kendall C. 2012. Seasonal variation in breeding Rüppell's Vultures
787   (*Gyps rueppellii*) at Kwenia, southern Kenya with implications for conservation. Bird
788   Conservation International **22**:260-269.
789 Virani MZ, Kendall C, Njoroge P, Thomsett S. 2011. Major declines in the abundance of vultures and
790   other scavenging raptors in and around the Masai Mara ecosystem, Kenya. Biological
791   Conservation **144**:746-752.
792 Walter WD, Onorato DP, Fischer JW. 2015. Is there a single best estimator? Selection of home range
793   estimators using area-under-the-curve. Movement Ecology **3**:10.
794 Wegmann M, Santini L, Leutner B, Safi K, Rocchini D, Bevanda M, Latifi H, Dech S, Rondinini C. 2014. Role
795   of African protected areas in maintaining connectivity for large mammals. Philosophical
796   Transactions of the Royal Society B: Biological Sciences **369**:20130193.
797 Whoriskey K, Auger-Méthé M, Albertsen CM, Whoriskey FG, Binder TR, Krueger CC, Mills Flemming J.
798   2017. A hidden Markov movement model for rapidly identifying behavioral states from animal
799   tracks. Ecol Evol **7**:2112-2121.
800 Wood SN 2017. Generalized additive models: an introduction with R. CRC press.
801 Woodroffe R, Ginsberg JR. 1998. Edge Effects and the Extinction of Populations Inside Protected Areas.
802   Science **280**:2126.
803 Zuberogoitia I, Zabala J, Martinez JA, Martinez JE, Azkona A. 2008. Effect of human activities on Egyptian
804   vulture breeding success. Animal Conservation **11**:313-320.

805

806

Figures and Tables

808
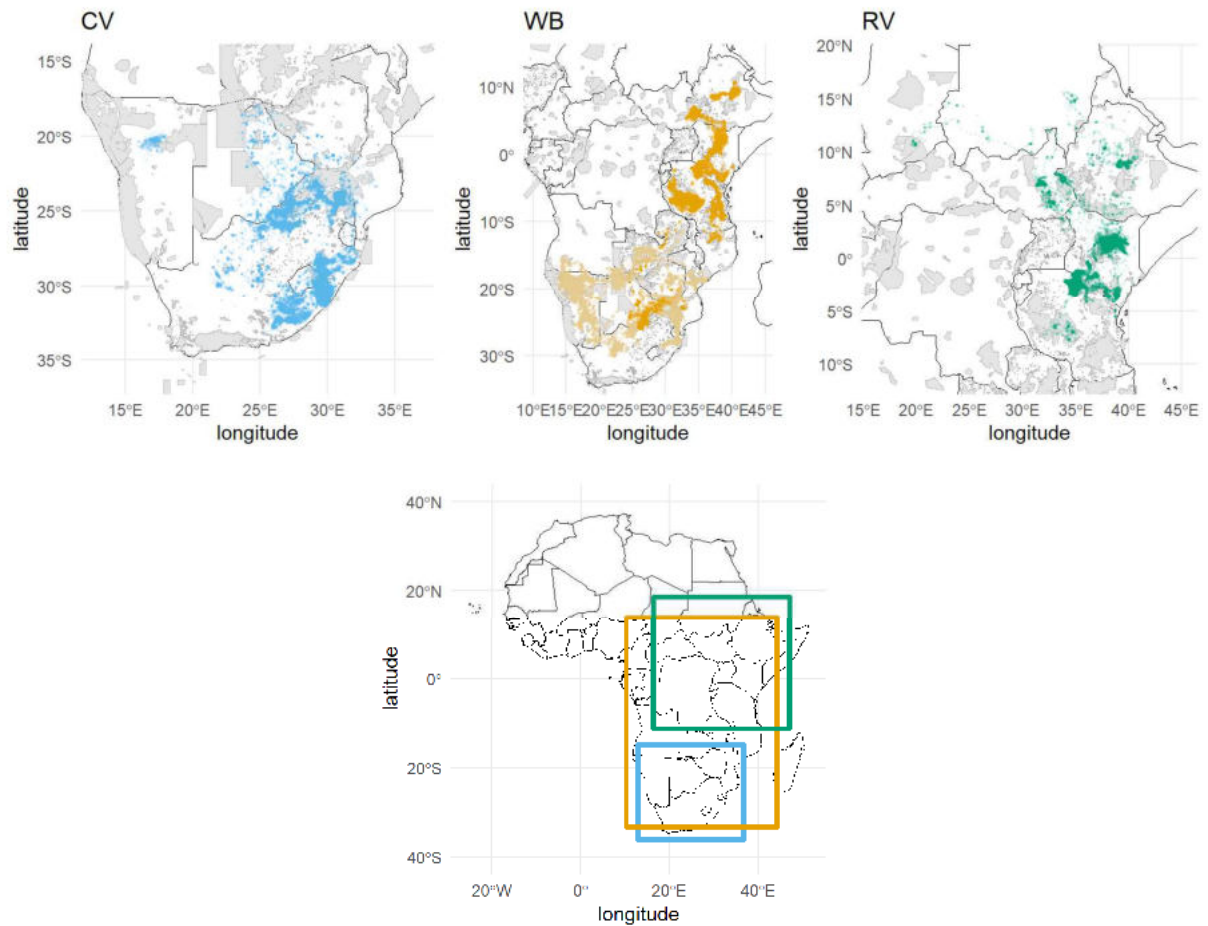
Figure 1 - Distribution of tracks of the three species used in the analysis. CV = Cape vultures; WB =

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/

813

814
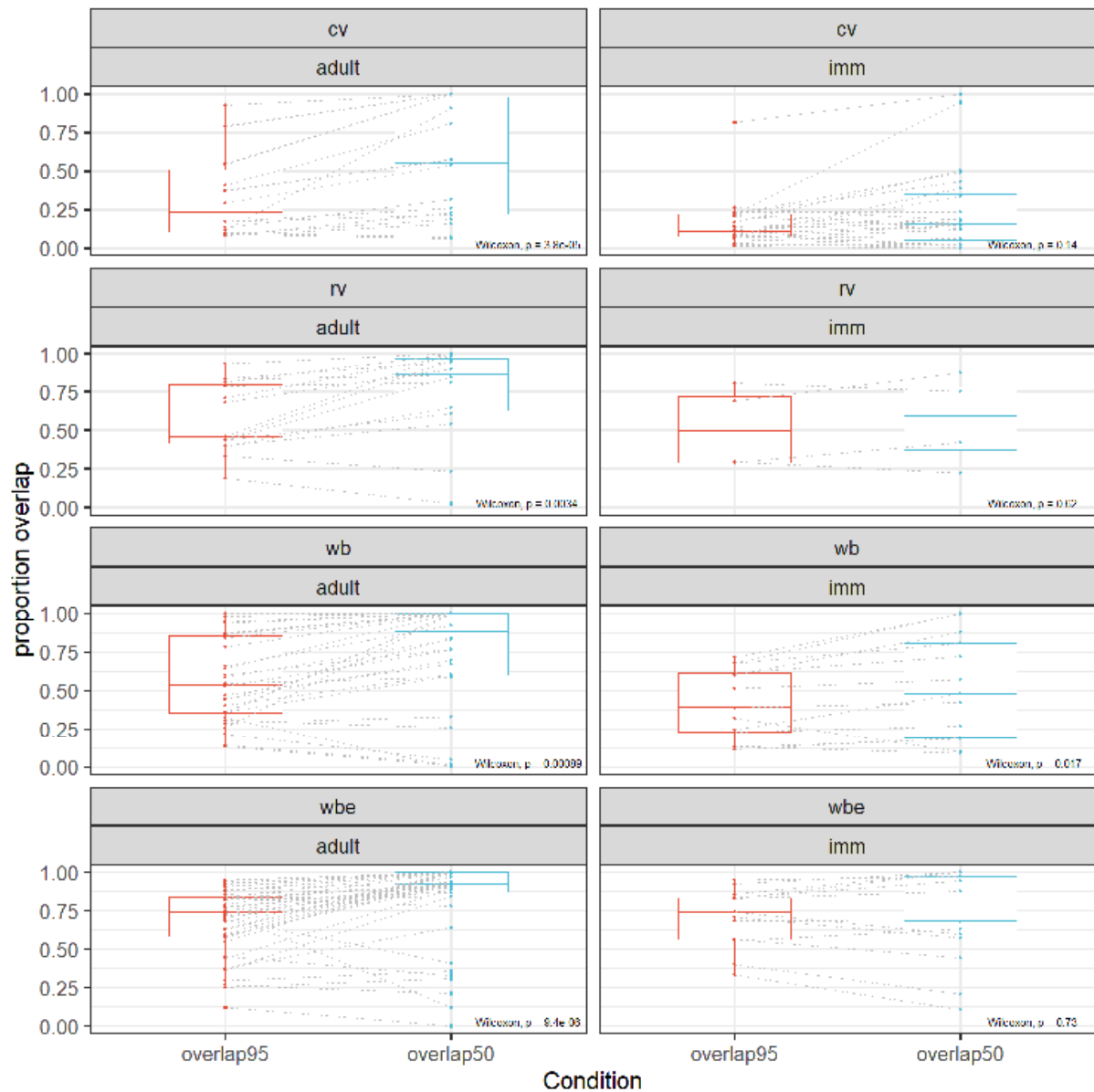
Figure 2 - Comparison of proportion of overlap of Brownian bridges with protected areas at 95% and 50% contours. Dashed lines connect the same bird. Means are compared using a Wilcoxon Rank Sum test. Abbreviations: cv = Cape vulture, rv = Rüppell's vulture, wb = White-backed vulture (southern population), wbe = White-backed vulture (eastern population), imm = immature.

819

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 km^2**

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

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 – -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

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	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

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	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

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	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		

857
858

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