MOVEMENTS OF WHITE-HEADED AND WHITE-BACKED VULTURES

by

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The following individuals read and discussed the thesis submitted by student Teague K. Scott, and they evaluated their presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

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The final reading approval of the thesis was granted by Jay D. Carlisle, Ph.D., Chair of the Supervisory Committee. The thesis was approved by the Graduate College.

DEDICATION

I dedicate this work to all the wonderful Mozambicans with whom I had the pleasure to laugh, dance, feast on carapau and xima, and share the endless beauty of Gorongosa National Park.

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ABSTRACT

Vultures are the only obligate vertebrate scavengers, and as such provide crucial services as keystone species and support the health and function of ecosystems in which they live. African vultures are a diverse group, with nine species found throughout Sub-Saharan Africa, many with overlapping distributions. Unfortunately, African vultures are faced with numerous threats throughout their range that have led to significant population declines, some greater than 90%, in only three generations. Four of these species are currently listed as critically endangered, and three as endangered.

Despite the significant perils faced by African vultures, there are still significant knowledge gaps and, until recently, very little was known about vultures in Mozambique, a large country that falls within the distribution of six of these species. Our research in Gorongosa National Park, Mozambique, focused on movement data collected from 10 White-backed Vultures (*Gyps africanus*) and 12 White-headed Vultures (*Trigonoceps occipitalis*), one of Africa's rarest vulture species.

We first focused on estimating White-headed Vulture monthly home ranges and core ranges with continuous-time movement models. We assessed the relationship between ranging behavior and extrinsic (environmental characteristics) and intrinsic (individual characteristics) predictor variables using Bayesian generalized linear mixed effects models. We also explored the degree of White-headed Vulture home range and core range overlap with Gorongosa National Park and its buffer zone. We found that breeding individuals had smaller home ranges and could maintain these into the non-breeding season or abandon them. These small breeding and non-breeding home ranges were representative of central place foraging and averaged 239 km^2 and 131 km^2, respectively, 80-90% smaller than the average 1180 km^2 non-breeding, non-central place foraging home range. Home ranges of birds that used resources outside of the park and its buffer zone were approximately 2.5 times larger than of birds that stayed within park boundaries, suggesting an increase in search effort required to locate less abundant resources. Excursions outside of the park and its buffer zone were rare. Only 15 of the 149 monthly home ranges suggested that birds used resources outside the park; the remaining 134 monthly home ranges fell within 10 km of the edge of the park buffer zone.

Additionally, we explored differences in White-headed Vulture and White-backed Vulture movement characteristics. We used Bayesian generalized linear models to determine the effect of species as a predictor for flight altitude, flight speed, onset of movement on two scales (>100 m and >1000 m), and onset of flight at altitude, and the effect of species and hour predictors on hourly activity levels. We found that White-headed Vultures flew at lower altitudes and slower speeds, and initiated movement and flight at altitude earlier than White-backed Vultures. All of these findings correspond with flight less reliant on strong thermals and suggest that the White-headed Vulture is more likely a *pioneer* than *follower*.

These findings expand on our understanding of both space use by White-headed Vultures and their place within the avian scavenging guild. They also demonstrate the critical importance of protected areas for the survival of the White-headed, and probably other, African Vultures.

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LIST OF ABBREVIATIONS

ctmm	Continuous-time movement model
AKDE	Autocorrelated kernel density estimator
AICc	Corrected Aikake Information Criterion
WH	White-headed Vulture
WB	White-backed Vulture
HR	Home range
CR	Core range
AD	Adult
SA/Subad.	Subadult
JUV/Juv.	Juvenile
B	Breeding
NC	Non-breeding/central place
NN	Non-breeding/non-central place
NDVI	Normalized difference vegetation index
AGL	Above ground level
SE	Standard error
CI	Credible interval
IUCN	International Union for Conservation of Nature

CHAPTER ONE: HOME RANGE AND USE OF PROTECTED AREAS BY WHITE-HEADED VULTURES *TRIGONOCEPS OCCIPITALIS*

Abstract

The White-headed Vulture *Trigonoceps occipitalis* is an uncommon, critically endangered African vulture species, and many aspects of its basic ecology are still unknown. An understanding of ranging behavior has the potential to shape conservation planning that effectively takes important ecological processes into account. We used continuous-time movement models to estimate the size of 149 monthly home ranges and core ranges for 12 White-headed Vultures tracked in and around Gorongosa National Park, Sofala province, Mozambique. We then explored covariates that influenced ranging behavior and reliance on the protected area. White-headed Vulture home ranges averaged 1261 km^2 per month (SE ± 137.2; n = 149 bird-months) and ranged from 10.8 km^2 to 10179 km^2. Breeding and non-breeding individuals that foraged around a central place had home ranges that were 80-90% smaller than those of non-breeding, non-central place foraging individuals. Home ranges that suggested vultures used space outside of the national park buffer zone were 2.5 times larger than those constrained to the park buffer zone. The majority of tracked individuals had monthly home ranges >90% contained by the Gorongosa National Park boundary, and 134 of the 149 fell within 10 km of the park buffer zone. We show there is large variation in ranging behavior that is dependent on breeding status and use of a central place. These data imply that protected areas are vital to the longevity of the species.

Introduction

The White-headed Vulture *Trigonoceps occipitalis* is one of Africa's rarest vulture species. The species' global population has declined by 60% to 97% over recent decades (Ogada et al., 2016), and a recent estimate suggests only 5,500 individuals remain (Murn & Botha, 2016). This population trajectory led, in 2015, to the rapid up-listing of the species by the International Union for Conservation of Nature (IUCN) from vulnerable to critically endangered (BirdLife International, 2017). Although seven of Africa's nine resident vulture species are facing a similar trend (Ogada et al., 2016), this apparent decline in the White-headed Vulture population is particularly concerning due to our extremely limited understanding of the species' life history, habitat requirements, movements, and threats (Botha et al., 2017; Murn & Botha, 2016; Murn et al., 2016). Whereas poisoning is considered the largest threat to African vultures throughout their distribution (Ogada et al., 2016), specific drivers of this observed decline of White-headed Vultures are still unclear.

The White-headed Vulture is a solitary species and adults are thought to be territorial. These traits do not support high population densities (Mundy, Butchart, Ledger, & Piper, 1992; Murn & Holloway, 2016). The species' current distribution appears largely limited to protected areas (Herremans & Herremans-Tonnoeyr, 2000; Hustler & Howells, 1988; Monadjem, 2004; Murn et al., 2016; Virani, Kendall, Njoroge, & Thomsett, 2010), and the species exists at densities thought to be well below potential carrying capacity outside of protected areas (Herremans & Herremans-Tonnoeyr, 2000). Given their imperiled status, we need greater knowledge of foundational aspects of White-headed Vulture ecology, such as their movements and space use relative to biotic and abiotic conditions. This knowledge would further our understanding of space requirements and use of protected areas.

Animal movements can be influenced by age, sex, or breeding status and can reflect aspects of ecology such as foraging method, diet, and territoriality (Demšar et al., 2015; Krüger, Reid, & Amar, 2014; Margalida, Pérez-García, Afonso, & Moreno-Opo, 2016). Resource availability and distribution can vary throughout the year, leading to variations in the size and spatial distribution of an individual's movements (McLoughlin & Ferguson, 2000). An animal's home range can be a useful proxy for exploring these variations (McLoughlin & Ferguson, 2000; Mitchell & Powell, 2004); an understanding of home range and the movements that shape it can guide better conservation action for this species.

Whereas there has been increased focus on the White-headed Vulture in recent years, its movements remain largely unknown (Murn & Holloway, 2014). It is difficult to target conservation efforts and place value on certain protected areas as strongholds for the species without an understanding of its movement ecology and spatial requirements. Here we estimate home ranges of White-headed Vultures in central Mozambique from tracking data obtained via satellite telemetry. First, we explore extrinsic (environmental characteristics) and intrinsic (individual characteristics) variables that might affect the size of the White-headed Vulture home range. We observed that location data from some bird-months was representative of central place foraging, where an individual's movements appeared centered around a hub of activity. We hypothesized that the apparent difference in range sizes between vultures that foraged around a central place and those that did not could be facilitated by a shift in foraging method or diet. Second, we investigate the extent to which White-headed Vultures are constrained to Gorongosa National Park – the main protected area in the region. We predicted that individuals would maintain home ranges within the park, and that significant shifts in home range size or spatial distribution would be associated with forays across park boundaries.

Methods

Study Area

Gorongosa National Park (Gorongosa) is located at the southern end of the Rift Valley in central Mozambique (Figure 1.1). The core area of Gorongosa encompasses 3,788 km^2 of diverse landscape and vegetation types, the most salient being the Rift Valley dominated by Acacia-Combretum savannah (Stalmans & Beilfuss, 2008). Gorongosa is part of the greater Gorongosa Ecosystem, which also contains the Marromeu Complex to the East.

The Mozambican Civil War (1977-1992) and subsequent years of unrest led to a >90% decline in wildlife biomass density in Gorongosa by the early 21st century (Stalmans, Massad, Peel, Tarnita, & Pringle, 2019). Gorongosa has undergone a significant recovery since restoration efforts were initiated in 2004, but while biomass density has rebounded to ~95% of pre-war estimates, species composition has seen a major shift (Stalmans et al., 2019). Today, waterbuck (*Kobus ellipsiprymnus*) are the most abundant of eight ungulate species counted during aerial surveys in the park; while they constituted approximately 4% of pre-war biomass density, the species currently makes up 74% of total wildlife biomass density (Stalmans et al., 2019). Other species are recovering at varying rates and levels of success. The predator guild is still recovering with hyena (*Crocuta crocuta*), leopard (*Panthera pardus*), and jackal (*Canis aureus*) having been recorded only occasionally since restoration efforts began and lion (*Panthera leo*) populations steadily growing from a very small population only 15 years ago (Bouley, Poulos, Branco, & Carter, 2018; Stalmans et al., 2019).

Gorongosa is Mozambique's flagship National Park and sees significant law enforcement and anti-poaching efforts. A 5,402 km^2 buffer zone surrounds the core area and contains a population of ~200,000 people residing in rural settlements (Bouley et al., 2018; Pringle, 2017; Stalmans et al., 2019). The Marromeu Complex lies 25 km to the east of Gorongosa (Figure 1.1) and comprises a 11,270 km^2 mosaic of two forestry reserves, four privately-leased hunting concessions, commercial agricultural land, community land, and the Marromeu Reserve (Beilfuss, Bento, Haldane, Ribaue, & ..., 2010). The Marromeu Complex is recognized by the Ramsar Convention as a Wetland of International Importance (Pritchard, Bamba, & Rilla, 2009), but its broad range of land management types lends varied levels of protection to the species that exist within its boundaries (Beilfuss et al., 2010). Outside Gorongosa and the Marromeu Complex wildlife densities decline significantly, limiting food resource biomass for vultures (Stalmans et al., 2019).

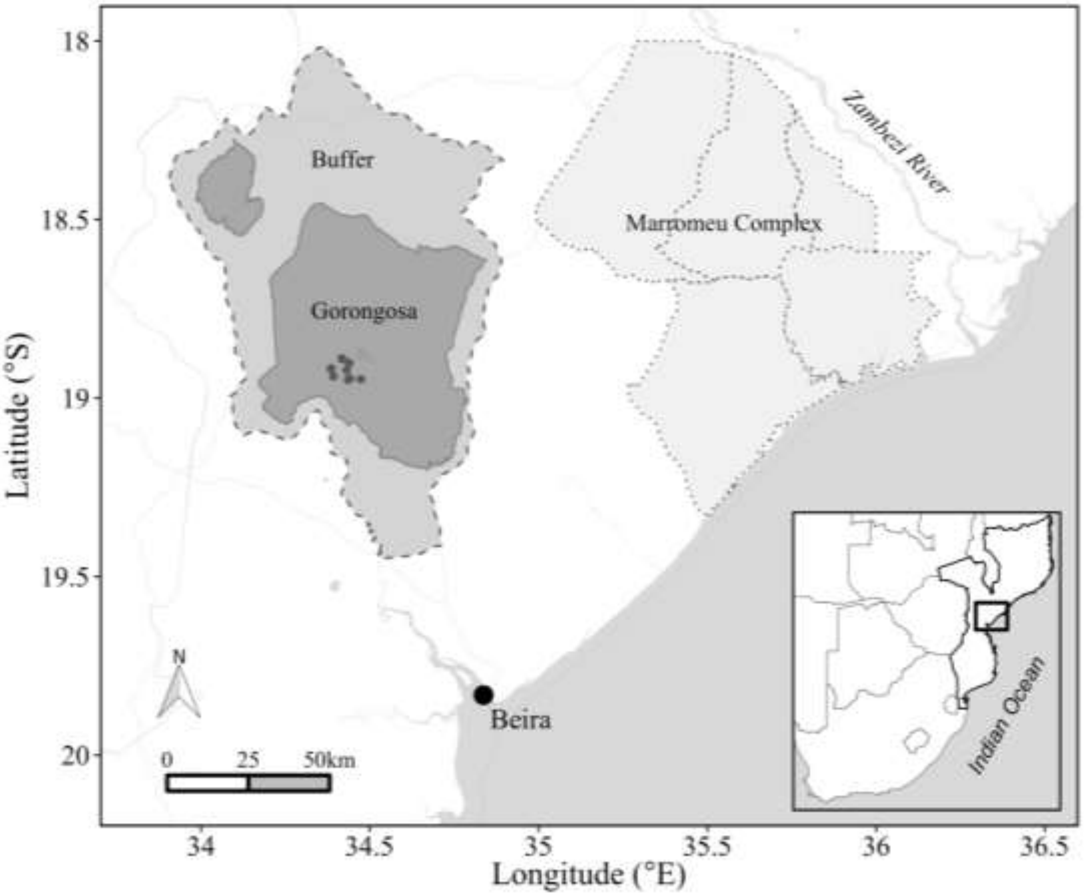

Figure 1.1 The ~3,800 km2 Gorongosa National Park (dark gray, solid line) is encompassed by the ~5,400 km2 buffer zone (gray, dashed line). To the east, the Marromeu Complex (light gray, dotted lines) consists of four large "coutadas" (hunting concessions), the Marromeu Reserve, and a mosaic of other land use types. We captured and tagged White-headed Vultures at locations within the core road network (gray points). Inset map shows Mozambique (bold borders) and the study area map bounding box.

<u>Vulture Movement Data Collection</u>

We trapped and tagged White-headed Vultures within Gorongosa during field work in May and June of 2016 - 2018. Trapping locations were restricted to suitable sites along the road network located in the southern portion of the national park (Figure 1.1). We trapped White-headed Vultures using noose-lines arranged around goat meat or ground beef. We aged and sexed White-headed Vultures using plumage characteristics: adult plumage is readily distinguished from that of immatures, and adults can be sexed by their sexually dimorphic plumage (Mundy et al., 1992). We fitted each bird with a solar-powered 70 g Argos/GPS satellite transmitter (PTT-100, Microwave Telemetry, Inc., Columbia, MD) using a backpack-style harness made of 8mm Teflon ribbon (Bally Ribbon Mills, Bally, PA). We programmed transmitters to collect GPS location data hourly from 0400 to 1900 hours Central Africa Time. We collected morphometric data and looked for the presence of a brood patch on both sexes when trapping to determine whether or not a bird was breeding (Mundy et al., 1992; Murn & Holloway, 2014).

Inspection of the movement data allowed us to identify potential nest locations. We ground-truthed these locations in 2017 and 2018 to determine whether or not individuals were breeding. Because of logistical and financial constraints, we could not assess breeding activity via field observation in 2019. For that year, we used information from prior years (known nest locations and patterns of space use associated with them) to characterize nesting behavior.

Processing Vulture Movement Data

We downloaded data for each bird from Movebank (Wikelski & Kays, 2019) and cleaned them in R version 3.5.2 (R Core Team, 2018) prior to analysis following the steps outlined below. We used data collected between 1 July 2016 and 31 October 2019. We created monthly subsets of locations for each individual and filtered out months with < 25 days of data to ensure consistent comparison of home range estimates across time and individuals. We chose to explore range use on a monthly scale to better understand variation across the annual cycle. We classified bird-months by age (adult, subadult, and juvenile) and a combination of breeding status and whether or not locations appeared distributed around a central place (breeding, non-breeding central place, non-breeding non-central place). We defined breeding individuals as those that made near daily visitation to nests within the breeding season (June-early November). We defined an individual as non-breeding either during months outside of the breeding season (December-May) or when it did not frequent a nest during the breeding season. We considered that a non-breeding individual could be caring for dependent young outside of the breeding season.

We visually inspected raw location data to determine whether movements from each bird-month reflected central place foraging behavior. If locations from a month were distributed around one primary patch, we classified the month as having a central place. If locations from a month were distributed around multiple patches, we classified the month as not having a central place. Breeding individuals always utilized a central place and we observed that non-breeding individuals could either be associated with a central place or not, regardless of season.

Home Range Estimation

We estimated monthly home range size using the autocorrelated kernel density estimator (AKDE) in R package *ctmm* (Fleming & Calabrese, 2019; R Core Team, 2018). Following the *ctmm* workflow outlined by Calabrese et al. (2016), we defined a distribution of minimum speeds that would support displacement between subsequent locations and then we removed locations associated with outlier speeds. We defined outliers as those that were greater than 30 m/s. White-headed Vultures are capable of flying at speeds greater than 30 m/s, but we would not expect them to sustain such speeds over extended distances. We then estimated measurement error using five days' worth of locations collected by a transmitter that remained in a static location after falling off a bird and added the estimate to our GPS data to ensure a more accurate home range estimation.

We plotted error-corrected monthly location data as variograms, which are plots of semi-variance in position as a function of the range of time lags in a dataset, and visually inspected these for autocorrelation structure (Fleming et al., 2014). We determined whether individuals exhibited range-residency, non-uniform use of space and use of a restricted range through time (Martinez-Garcia, Fleming, Seppelt, Fagan, & Calabrese, 2020), by the presence of an asymptote in variograms, a prerequisite for home range analysis following *ctmm* methods. This trait is reflective of a constant variance at longer time lags that is associated with discrete space use.

We fit continuous-time movement models using maximum likelihood estimation for each bird-month. These models account for different types of autocorrelation present in the data (Calabrese, Fleming, & Gurarie, 2016). The independent identically distributed (IID) model assumes that there is no autocorrelation structure in the data; the Brownian motion (BM) model assumes regular diffusion without autocorrelation in velocity (directional persistence) or space use (range-residency); the Ornstein-Uhlenbeck (OU) model accounts for range-residency without directional persistence; the integrated Ornstein-Uhlenbeck (IOU) model accounts for directional persistence without range-residency; the Ornstein-Uhlenbeck Foraging (OUF) model accounts for both range-residency and directional persistence. We selected best-fit models using AICc and used these best-fit models to estimate monthly home range (95%) and monthly core range (50%) AKDEs along with 95% confidence intervals for each bird-month.

Preliminary analysis indicated that three individuals had more than one distinct area of range-residency per month. This use of multiple areas of range-residency within one month led to variograms without asymptotes (Figure 1.2) and artificially increased AKDE estimates. In cases where birds did not have only one distinct area of range residency, we segmented the location data for these months and repeated the *ctmm* workflow outlined in the methods to create multiple within-month AKDEs (Figure 1.2) (Calabrese et al., 2016). We then averaged these to produce a single monthly AKDE estimate.

Home Range and Core Range NDVI

We quantified average Normalized Difference Vegetation Index (NDVI) for each monthly home and core range using Sentinel-2 imagery (Drusch et al., 2012). We consider NDVI as a proxy for potential available carrion biomass. An increase in NDVI reflects an increase in vegetation productivity (Pettorelli et al., 2005), which implies greater forage availability and quality. Following Kendall et al. (2014), we expect that ungulate mortality rates unrelated to predation decline under these conditions leading to less predictable food resources for vultures and therefore larger home ranges. We obtained imagery collected over the course of the study period, masked clouds, created a composite image with an appended NDVI band for each month, and reduced monthly composite images to corresponding monthly home range and core range polygons. We averaged NDVI values within each polygon and exported data for further analysis in program R. We processed NDVI data using Google Earth Engine (Gorelick, Hancher, Ilyushchenko, Thau, & Moore, 2017).

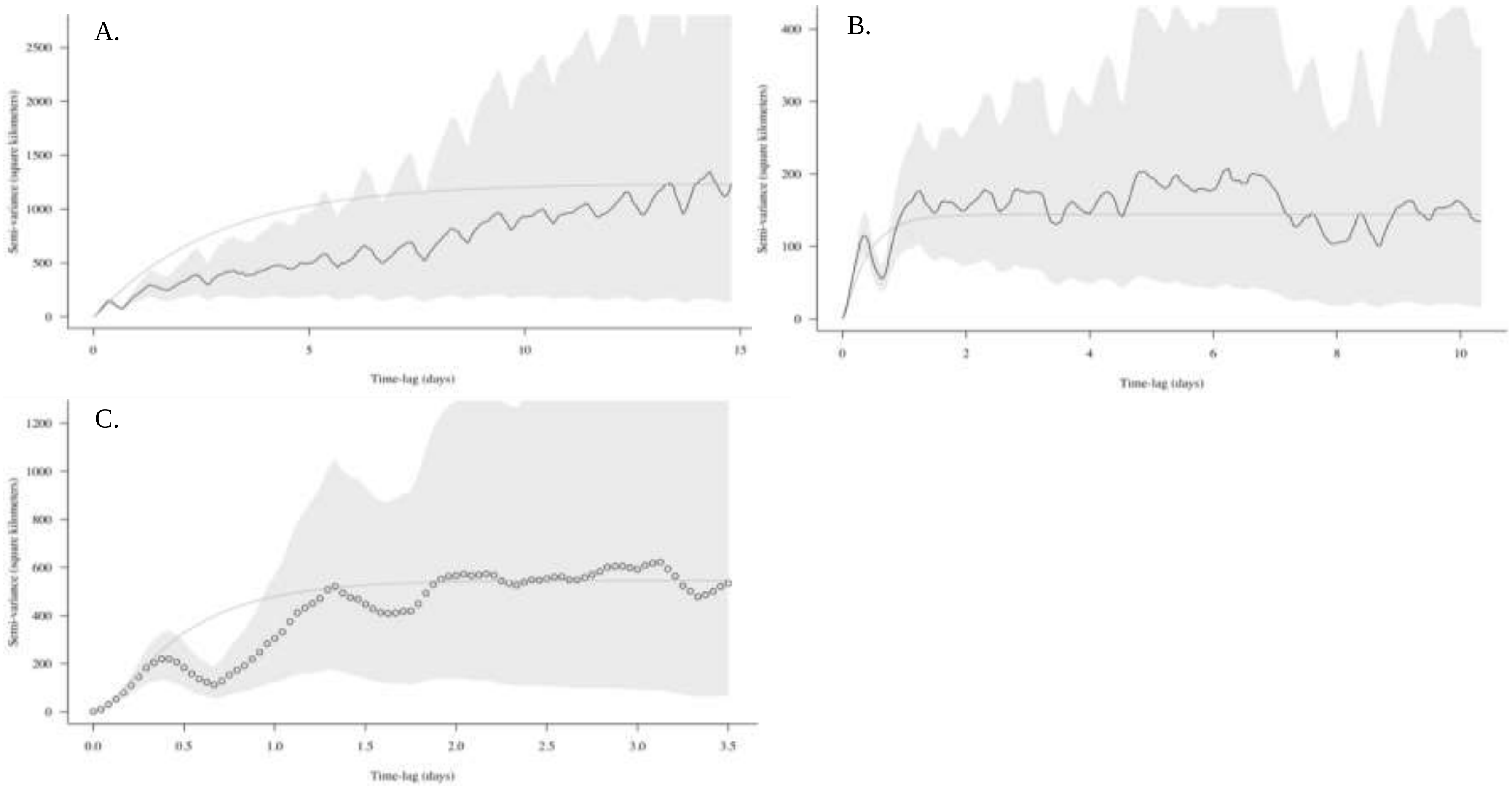

Figure 1.2 Variograms comparing lack of range-residency and range-residency in the same White-headed Vulture bird-month. Individual WH37_17 utilized two geographically distinct areas, in Gorongosa National Park and the Marromeu Complex, in October 2017. Plot A shows this bird-month with continually increasing semi-variance (black line with gray 95% CI) caused by a lack of single area range-residency. Plots B and C show the same bird-month segmented into two separate areas of range-residency. The best-fit model line is plotted in dark gray.

Assessing Home Range and Core Range Variation

To assess variation in home range and core range size, we fit Bayesian gamma-distributed generalized linear mixed models to determine the effect on ranging behavior (home and core range size) of extrinsic temporal and seasonal predictor variables (month represented by Julian day; year; NDVI), intrinsic predictor variables (breeding/central place status; age), and a use of protected area predictor (whether or not a home range AKDE was constrained to the park buffer zone). We included individual as a random-intercept to account for repeated range estimates from the same bird. Month and NDVI parameters were centered around their respective means to ensure that continuous variables were similarly distributed.

We estimated parameter coefficients using Bayesian Markov chain Monte Carlo (MCMC) sampling with 4 chains for 2000 iterations each with a 1000 iteration burn-in period (Goodrich, Gabry, Ali, & Brilleman, 2018). We used weakly informative priors for all parameters. We assessed model and parameter convergence using the posterior predictive distribution and the Gelman-Rubin statistic, respectively, and ensured that minimum effective sample size requirements were met (Gelman & Donald, 1992). If the 95% posterior uncertainty intervals did not overlap 0, we considered the parameter to have an important effect on ranging behavior (i.e., Chanthorn et al. 2013). We present marginal effects and their 95% uncertainty interval for each important parameter. We performed all modelling with packages *rstanarm* and *stan* in program R (Carpenter et al., 2017; Goodrich et al., 2018).

Degree of Overlap with Protected Area

To answer our second research question, how much does the White-headed Vulture rely on a protected area, we quantified the percent of each monthly home range and core range AKDE that was contained by either (A) Gorongosa National Park only, or (B) both the park and its buffer zone. We report the average percent overlap of both home range and core range and these boundaries as well as the range of observed percent overlap. Through this process we also aimed to identify where individuals were traveling outside of the park and its buffer. We used the *Overlap analysis* tool in QGIS (QGIS.org, 2020) to quantify the percent overlap of home range and core range AKDEs with the boundaries of interest.

Results

Home Range and Core Range Size

We analyzed data from 12 White-headed Vultures, 8 adults and 4 immatures, tracked for durations of three to 39 months (Appendix A.1). Over the course of the study period (July 2016 – October 2019), we collected 77,972 GPS locations, of which 74,613 met our criteria for inclusion in home range analysis. We estimated home ranges and core ranges for a total of 149 bird-months (Appendix A.2).

All 149 bird-months, including those that were segmented to account for multiple within-month ranges, exhibited range-residency, as evidenced by asymptotes in variograms. The OU anisotropic continuous-time movement model was the top performing model for 132 bird-months (confirming range-residency). The remaining 17 bird-months were fit to other range-residency models with parameters representing autocorrelation in position or velocity (Table A.2).

Monthly home range size for White-headed Vultures in Gorongosa National Park averaged 1261 km^2 (SE ± 137.2; n = 149 bird-months) and ranged from 10.8 km^2 to 10179 km^2 (Figure 1.3). Monthly core range size averaged 271.3 km^2 (± 29.9; 149 bird-month) and ranged from 1.2 km^2 to 2092 km^2. Non-breeding, non-central place birds exhibited monthly home ranges averaging 2319 km^2 (± 425; n = 9 birds), breeding birds 163 km^2 (± 86; n = 5 birds), and non-breeding, central place birds 243 km^2 (± 154; n = 5 birds; Table 1.1; Figure 1.4).

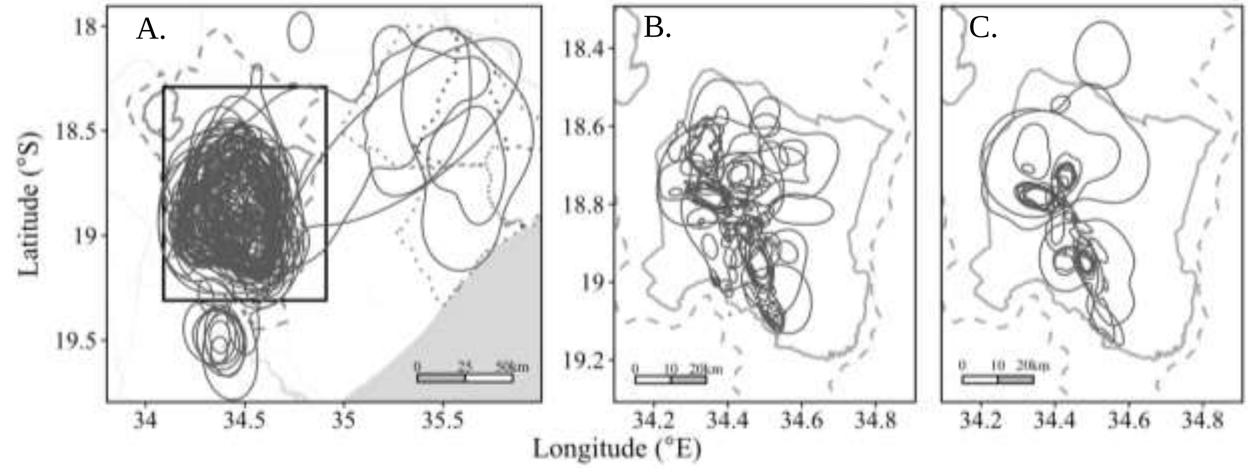

Figure 1.3 All 149 White-headed Vulture (A) Non-breeding non-central place, (B) breeding, and (C) non-breeding central place monthly home ranges overlaid on Gorongosa National Park (solid), park buffer zone (dashed), and Marromeu Complex (dotted) borders. The black rectangle in map A defines the bounding box for (B) breeding and (C) non-breeding central place home range maps.

Table 1.1 Summary of White-headed Vulture home range (HR) and core range (CR) AKDE estimates grouped by breeding status. Global means and standard errors for both home range and core range estimates are presented along with ranges for each AKDE metric. Sample size for each group is the number of individuals. Breeding: B; Non-breeding central place: NC; Non-breeding non-central place: NN.

Breeding Status	n	Mean HR km^2 (±SE)	HR Range	Mean CR km^2 (±SE)	CR Range
B	5	163 (±86)	18-500	17 (±9)	3-52
NC	5	243 (±154)	39-847	39 (±26)	6-141
NN	9	2319 (±425)	169-5101	476 (±68)	41-812

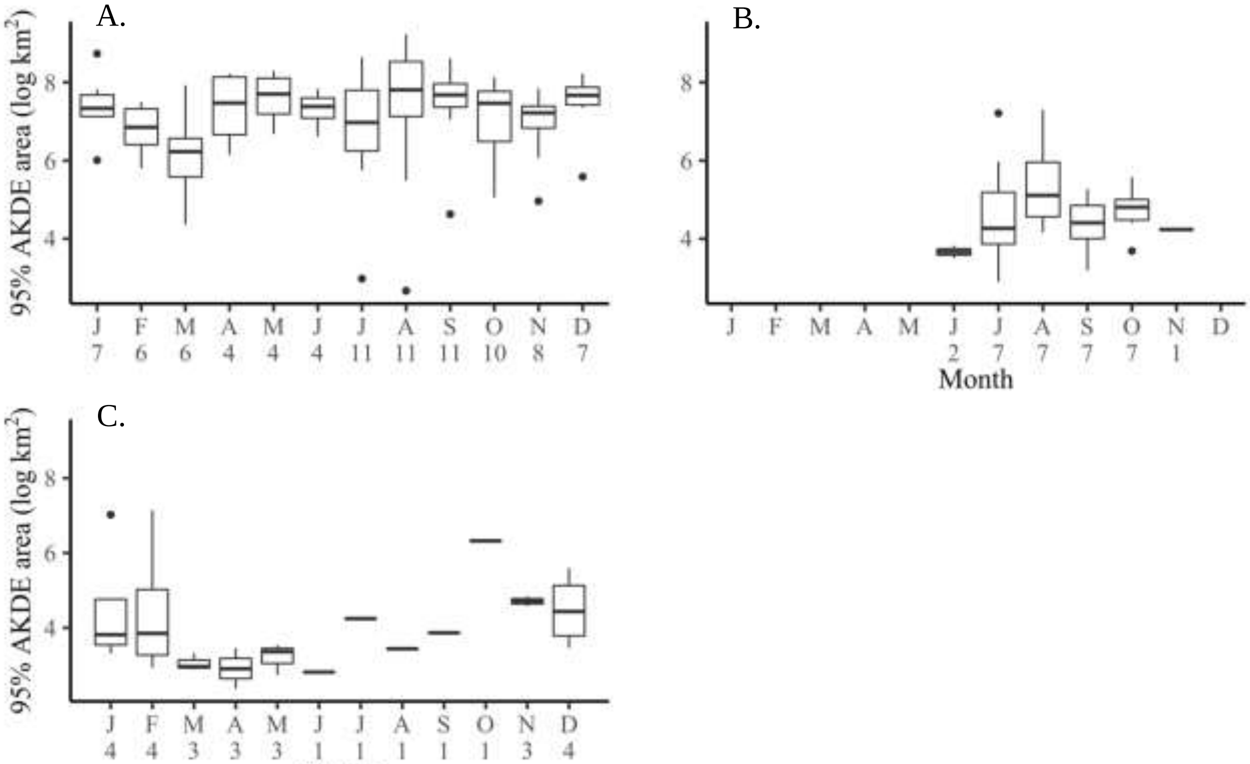

Figure 1.4 White-headed Vulture monthly home range size for (A.) non-breeding non-central place, (B.) breeding, and (C.) non-breeding central place individuals. We estimated monthly home range size using the 95% AKDE. The number of home range estimates for each month is noted on the x-axis.

Assessing Home Range and Core Range Variation

We found that non-breeding birds that were not central place foragers had larger home ranges and core ranges than did breeders and non-breeders that were central-place foragers. The posterior prediction for the average non-breeding bird that was not a central place forager with monthly home ranges contained within the park was 1180 km^2 (95% credible interval (CI) 248-5918). The posterior prediction for a breeding bird with monthly home ranges contained within the park averaged 239 km^2 (95% CI 49-1313). Non-breeding birds that were central place foragers and had monthly home ranges within the park averaged 131 km^2 (95% CI 28-653. Breeding and non-breeding birds that were central place foragers had monthly core ranges 11% (95% CI 4-33) and 8% (95% CI 3-20) of the size of non-breeding birds that were not central place foragers, respectively (Figure 1.5).

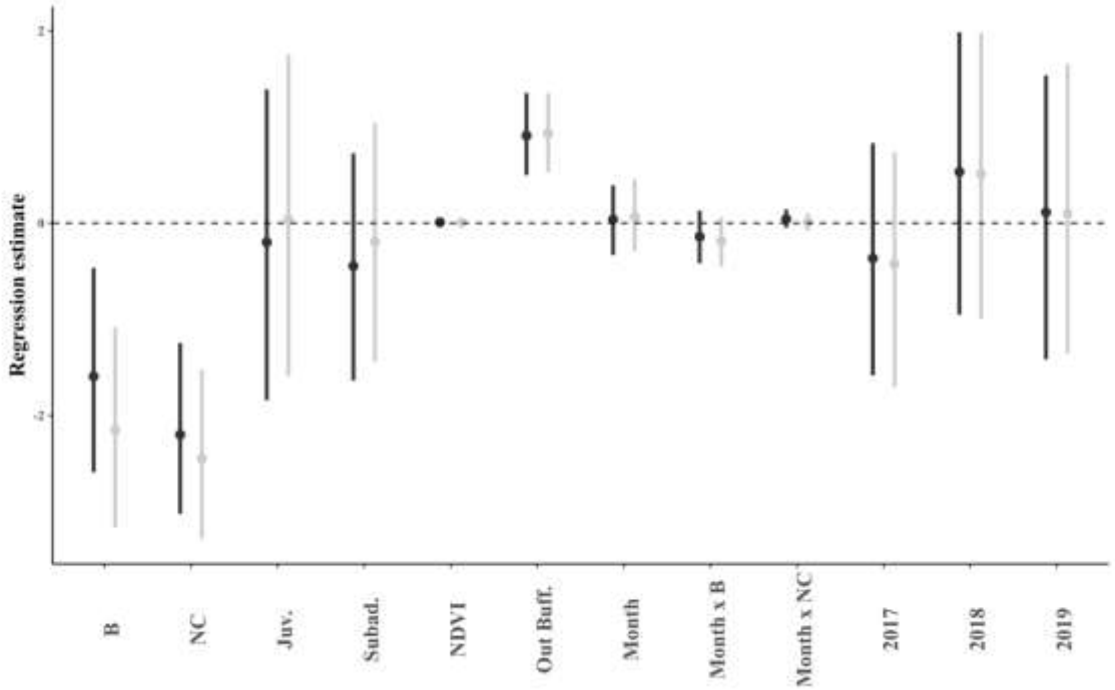

Figure 1.5 Coefficient estimates for models predicting White-headed Vulture home range (black) and core range (gray) size. Points represent coefficient mean effects and bars the 95% credible intervals. Coefficients with 95% credible intervals not overlapping zero were considered important. Important predictors for both models included breeding status/central place use and foraging range extent. Breeding: B; Non-breeding central place: NC; outside buffer zone: Out Buff.

Birds that left the park generally used more space than birds that stayed within the park. Home ranges extending beyond outside the park buffer zone were approximately 2.5 times larger than home ranges contained within the park buffer zone (95% CI 1.64-3.85). We found that the average 1180 km^2 home range of a non-breeding bird that was not a central place forager and remained within the park grew to approximately 2931 km^2 (95% CI 634-14733) when it included space use outside of the park boundary. Likewise, the average 223 km^2 non-breeding non-central place core range also grew by a factor of 2.5 to approximately 573 km^2 (95% CI 115-2888) when associated home ranges extended outside of the park buffer zone (Figure 1.5).

Average home range and core range NDVI was 0.379 and 0.361 and ranged from 0.131-0.626 and 0.0904-0.641, respectively. We found that home range and core range NDVI values were least in the months of September and October, and greatest in January (Figure 1.6). We did not find that NDVI, age, month, or year had an effect on home range or core range size (Figure 1.5).

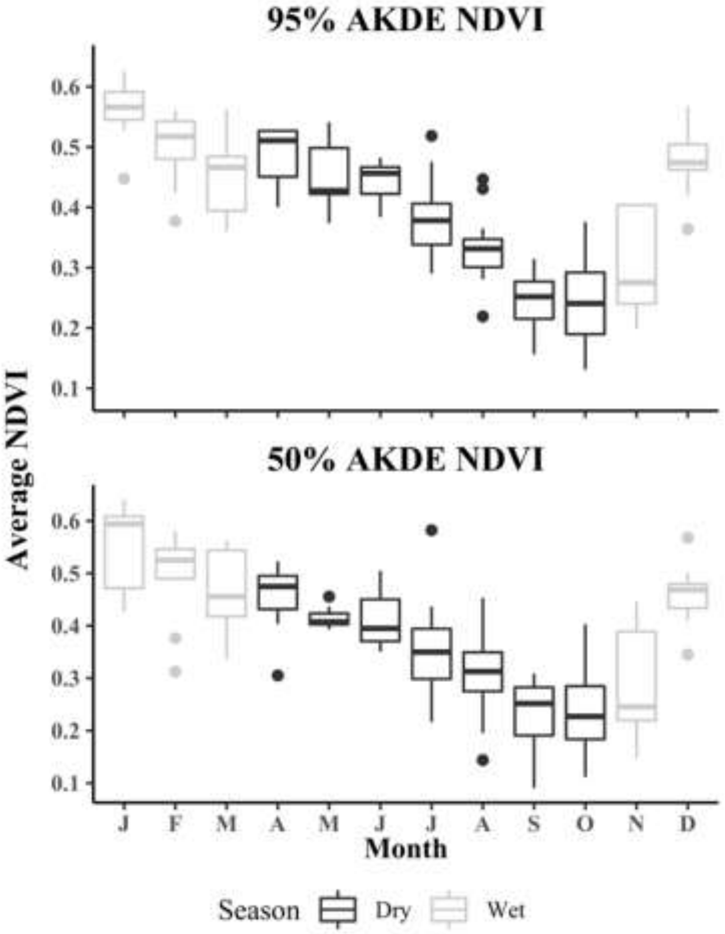

Figure 1.6 Monthly White-headed Vulture (A) home range and (B) core range NDVI. Observed NDVI ranged from 0.131 to 0.626 with lowest home range and core range NDVI values occurring in the months of October and September, respectively, and highest NDVI values in January.

Two individuals exhibited noticeably different movement behavior than others in their age/breeding status categories, and this was evident in the random effect estimates for both home range and core range models. These individuals had smaller than average monthly home ranges than the population level estimates (Figure 1.7). An adult female had consistently smaller monthly home ranges than any other breeding or non-breeding central-place individual and a subadult of unknown sex foraged exclusively at a single spot – a waterbird colony.

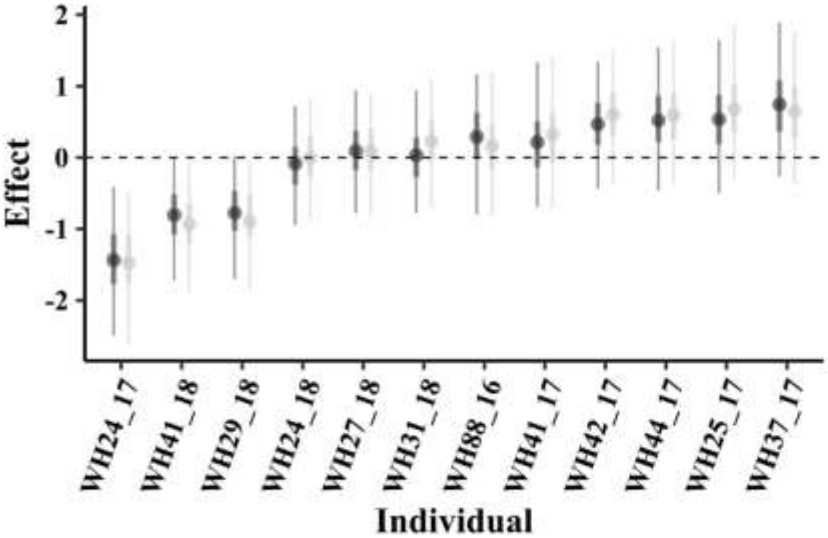

Figure 1.7 Individual-level White-headed Vulture variation from the population-level mean. Point estimates and their 95% uncertainty intervals show the effect of individual in both home range (dark) and core range (light) models. Individual effects with 95% uncertainty intervals overlapping zero (dotted line) are not considered important.

Degree of Overlap with Protected Area:

Although only 4 of 12 birds had all monthly home ranges >90% within park boundaries, all monthly home ranges of 7 of 12 birds were >90% within the park buffer zone. Similarly, 46% of all monthly home ranges fell entirely within the park boundary and 71% of all monthly home ranges fell entirely within the park and its buffer zone (Table 1.2).

Table 1.2 White-headed Vulture monthly home range (HR) and core range (CR) overlap estimates with the Gorongosa National Park boundary. We present average overlap estimates with standard errors and the range exhibited by each individual.

INDIVIDUAL	AVERAGE % HR/PARK OVERLAP (±SE)	% HR/PARK OVERLAP (RANGE)	AVERAGE % CR/PARK OVERLAP (±SE)	% CR/PARK OVERLAP (RANGE)
WH88_16	90 (±2)	49-100	99 (±1)	86-100
WH24_17	100 (±0)	100-100	100 (±0)	100-100
WH25_17	88 (±4)	77-97	100 (±0)	100-100
WH37_17	53 (±22)	29-98	54 (±25)	13-100
WH41_17	67 (±9)	51-94	89 (±6)	73-100
WH42_17	94 (±4)	70-100	100 (±0)	100-100
WH44_17	67 (±17)	0-99	71 (±18)	0-100
WH27_18	100 (±0)	100-100	100 (±0)	100-100
WH29_18	100 (±0)	99-100	100 (±0)	100-100
WH31_18	88 (±5)	28-100	96 (±3)	52-100
WH41_18	100 (±0)	100-100	100 (±0)	100-100
WH24_18	95 (±3)	80-100	96 (±2)	84-100

Nine individuals exhibited core ranges at least 90% contained within the buffer zone; five birds had core ranges entirely within the park boundary. 83% (123 of 149) of monthly core ranges fell completely within the park boundary, and 93% (139 of 149) within the park and its buffer zone. Only two individuals exhibited core ranges that extended outside of the park buffer zone. Both these birds spent time within the Marromeu Complex.

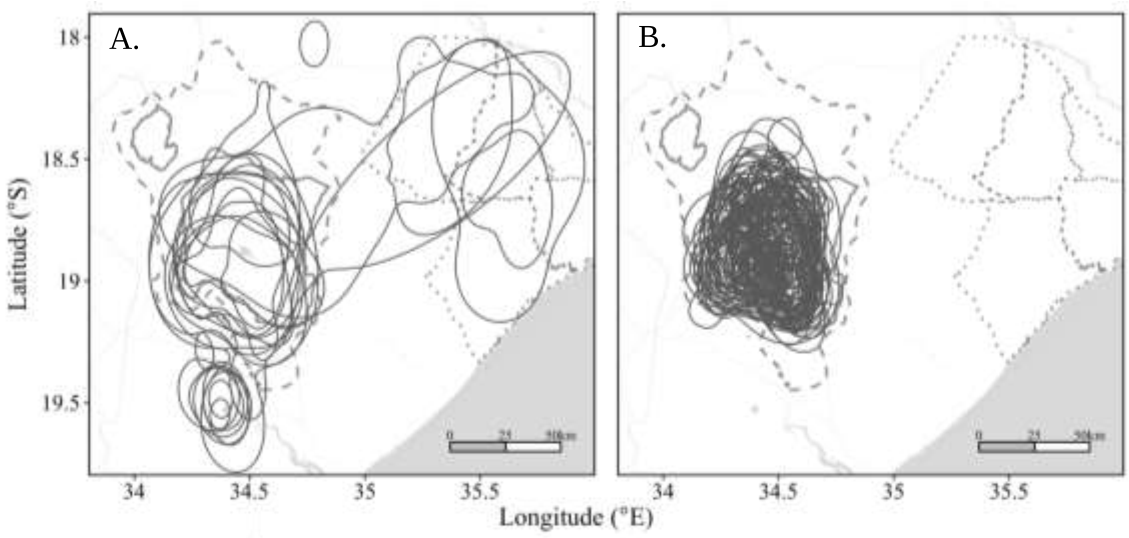

Figure 1.8 (A) Six of the twelve tagged White-headed Vultures utilized resources outside of Gorongosa National Park and its buffer zone in 15 of 149 bird-months. Three individuals moved between the park and the Marromeu. Two individuals foraged within an area of concentrated cattle bomas. One moved outside of the park to utilize locations in an area without any discernable resources. (B) 134 of 149 White-headed Vulture bird-months from 7 individuals were almost entirely contained by Gorongosa National Park and its buffer zone.

Movements outside of the buffer zone were made by six individuals in 15 of the 149 monthly home ranges to utilize resources at three distant locations (Figure 1.8). Five of these individuals utilized two known resources: two traveled to an area with a high concentration of cattle corrals approximately 38-48 km south of the park boundary and three made movements between the park and Marromeu Complex. The sixth individual utilized an area without any discernable concentrated or anthropogenic resources approximately 25 km northeast of the buffer zone.

The remaining 134 monthly home ranges that did not involve use of distant resources correlated with the park and its buffer zone (Figure 1.8). Of these 134 home ranges, 28 included small proportions just outside the buffer zone boundary; none were more than 10 km from the boundary.

Discussion

Our results suggest that the local White-headed Vulture population is strongly tied to Gorongosa National Park and its buffer zone, and that movements outside of the protected area are associated with foraging opportunities provided by predictable food resources. Both home range size and core range size responded to breeding status and use of a central place. Breeding and non-breeding individuals that utilized a central place had home ranges 10-24% of the size of non-breeding individuals that did not utilize a central place. Home range sizes also grew by a factor of 2.5 when they included resource use outside of the park buffer zone.

Many vulture species are capable of making large movements, either migratory or nomadic (Beuchley et al., 2017; Bittel, 2018; Phipps, Willis, Wolter, & Naidoo, 2013), and so can utilize a multitude of spatially discrete home ranges through time. The relative lack of movement to areas outside of the greater Gorongosa and Marromeu Complex landscape suggests that the White-headed Vulture is far more dependent on habitat quality or characteristics supported by or only within a protected area with a few exceptions (Herremans & Herremans-Tonnoeyr, 2000; Hustler & Howells, 1988; Murn et al., 2016). This is further supported by the fact that the majority (134 of 149) of White-headed Vulture monthly home ranges correlated with the boundary of the park and its buffer zone (Figure 1.8B). Although we do not understand the underlying causes, our findings correspond with the observation that White-headed Vultures appear largely confined to protected areas.

Our model showed that both home range and core range size are most affected by the combination of breeding status and use of a central place. The White-headed

Vulture's capacity to constrict its space use in such a dramatic way suggests that the species is potentially territorial during certain life-stages and is capable of utilizing food resources within a localized area, a finding that supports and quantifies previous observations (Hustler & Howells, 1988; Mundy et al., 1992). Our observations of breeding adults maintaining small monthly home ranges into the next breeding season is also in line with previous observations of site fidelity (Murn & Holloway, 2014). While we could not confirm whether breeding attempts were successful, this continued constricted range use outside of the breeding season could be associated with an extended post-fledging dependence period (Mundy et al., 1992; Murn & Holloway, 2014; Pennycuick, 1976).

The difference in home range size between birds that used a central place and those that did not is interesting for a number of reasons. First, many vulture species require a large foraging range to adequately exploit spatiotemporally ephemeral resources (Kane, Jackson, Monadjem, Colomer, & Margalida, 2015; Kane et al., 2016; Rivers et al., 2014). Some of these species have been shown to modify foraging behavior during the breeding season by decreasing foraging trip frequency while still doing so over large areas (Spiegel, Harel, Getz, & Nathan, 2013); we did not observe this behavior in this study. Second, smaller home ranges might be correlated with spatiotemporal predictability of food resources (Maher & Lott, 2000). Following central place foraging theory, home range size should increase with less predictable food or lower quality resources, and vice versa (Ford, 1983; Mitchell & Powell, 2004). White-headed Vultures have been observed hunting and preying upon small mammals and reptiles (Mundy et al., 1992; Murn, 2014). Though we didn't have the opportunity to witness that here, we suggest that this observed predatory behavior could be more strongly associated with individuals utilizing a central place. Finally, we would typically expect to find that individuals not associated with nests would range more widely. We found that non-breeding central place individuals had slightly smaller home ranges than breeding individuals. We suggest that this may be reflective of an extensive post-fledging dependence period (Murn, 2013; Murn & Holloway, 2014), during which a smaller home range is maintained while caring for a fledged juvenile bird. A home range might be smaller during this stage because of the decreased mobility of the juvenile bird.

Quantifying the effect of ranging behavior outside of the park buffer zone on home range and core range size provides a means of understanding how these birds use the landscape outside of protected areas. The fact that home range size increases greatly with foraging ranges outside of the buffer zone suggests that resources outside of these protected areas are extremely limited (Stalmans et al., 2019). Habitat loss and land use change has the potential to shape resource availability, and in turn species distribution; this affects different species in different ways. For example, White-backed Vultures *Gyps africanus* exhibit the potential to cope with limited resources by adopting a nomadic lifestyle that can span entire landscapes, countries, and even portions of continents (Phipps et al., 2013). The need to further define variables that limit White-headed Vulture movement is critical.

White-headed Vultures with either large or small home ranges could be subject to stressors related to resource availability. Resource availability could shape the demographics of a population if this observed difference in range size is facilitated by foraging method and diet. Assuming predatory behavior is more strongly associated with individuals using a central place, an ecosystem might not support a sustainable breeding population if there are not sufficient densities of suitable prey species. An ecosystem or habitat with a greater abundance of large-bodied “prey” species that generate carcasses across the landscape might favor a population of nonbreeders, whereas an ecosystem supporting diversity in species size might more effectively support a breeding population. We expect that resource availability would also have a quantifiable effect on home range size and breeding success regardless of foraging method. We stress the need to investigate White-headed Vulture diet in an attempt to understand whether the species does in fact modify foraging strategy and to explore how resource diversity and availability influence breeding home range size and breeding success. We cannot be sure that a given population is sustainable without an understanding of the underlying variables that facilitate these shifts in range size.

Our study relied on small sample sizes of subadult and juvenile individuals. We suggest that future investigations of White-headed Vulture movements seek to better understand how immature home ranges change as these individuals age. One of the most important questions related to long-term sustainability of the greater metapopulation is whether, and to what extent, White-headed Vultures disperse between regional populations. Our results suggest that there is limited to no movement outside of these localized populations, but continued monitoring is required to understand both whether this pattern holds locally and throughout the species’ greater range.

CHAPTER TWO: COMPARING MOVEMENT PATERNS OF WHITE-HEADED VULTURES *TRIGONOCEPS OCCIPITALIS* AND WHITE-BACKED VULTURES *GYPS AFRICANUS* IN GORONGOSA NATIONAL PARK, MOZAMBIQUE

Abstract

There is significant overlap in the distribution of the 9 vulture species found throughout Sub-Saharan Africa. Niche-partitioning and ecological interactions between these species have long been a point of interest for researchers studying these important birds. Many studies have focused on observations in the field, but movement data provides us with another means of quantifying differences in African vultures. We focused on 4 trajectory characteristics to explore differences in movement ecology of White-headed Vulture and White-backed Vulture. We found that White-headed Vultures flew at lower altitudes and slower speeds, and initiated movement and high-altitude flight earlier in the day than White-backed Vultures. These findings suggest White-headed Vulture flight behavior requires less intense thermal uplift and support the hypothesis that the White-headed is likely a more efficient searcher, making it a *pioneer* in the African avian scavenger guild.

Introduction

Scavengers perform critical ecosystem services and are integral to the maintenance of healthy ecosystem functions. Vultures, the only obligate vertebrate scavengers on the planet (Buechley & Sekercioglu, 2016), play a significant role in this important guild throughout the various ecosystems in which they occur (Houston, 1986). They are extremely efficient and effective in providing services that slow and eradicate the spread of disease (Devault et al., 2016; Ogada, Torchin, Kinnaird, & Ezenwa, 2012), which benefits not only wild systems but also those in which humans are included (Moleón et al., 2014).

African vultures are in peril, and populations of some species have undergone declines greater than 90% in three generations (Ogada et al., 2016). These rapid declines have warranted the listing of four of the nine African species as critically endangered and three as endangered (BirdLife International, 2017). Unfortunately, there are large gaps in our ecological understanding of these species and we are racing to learn how to effectively conserve them.

There can be considerable overlap in the ranges of African vulture species; for example, there are seven breeding vulture species found in Ethiopia and six in Mozambique (Mundy et al., 1992). While these species all share a similar ecological role and can be considered as competing for similar resources, they likely coexist through niche-partitioning (Kendall, 2013; Kendall, Virani, Kirui, Thomsett, & Githiru, 2012; Spiegel, Getz, & Nathan, 2013). Researchers have long sought to disentangle methods of niche-partitioning among vultures, and many have focused on morphological characteristics that define feeding behavior (Hertel, 1994; Kruuk, 1967; Moreno-Opo, Trujillano, Arredondo, González, & Margalida, 2015) and consider body size or group size as means of exerting dominance over competitors (Kendall et al., 2012). Other studies have investigated the temporal segregation of food resource use, often in the context of *searcher* and *scrounger* game theory, referring to relative search efficiency and reliance on social information transmitted through the sky network (Cortés-Avizanda, Jovani, Donázar, & Grimm, 2014; Kane & Kendall, 2017; Spiegel, et al., 2013). We consider White-headed and White-backed Vultures in the context of this theory and classify species as either *pioneer* or *follower*. The sky network refers to the transmission of social information through the sky as individuals cue in to behavior of conspecifics and other species. Movement data collected from multiple species within the same system allow us to gain insight into these processes.

The White-backed Vulture *Gyps africanus* is the most abundant and wide-ranging of the sub-Saharan African vultures and is relatively well studied (Bamford, Monadjem, & Hardy, 2009; Murn & Botha, 2017; Phipps et al., 2013). We know that the White-backed Vulture is an obligate scavenger that competes for resources with and feeds among large groups of conspecifics (Mundy et al., 1992). They are considered one of the *followers* in the avian scavenger group, relying on other species that serve as *pioneers* that are more effective at searching for and locating carrion (Kruuk, 1967). Thus, this species most often arrives at carcasses after other avian scavengers (Kruuk, 1967). White-backed Vultures often cover large distances in the effort to locate food resources that are spatially and temporally ephemeral (Ruxton & Houston, 2004).

While there is comparatively little known about the much less numerous White-headed Vulture *Trigonoceps occipitalis*, the species appears to fill a slightly different niche (Monadjem, 2004). Field observations suggest that, in addition to scavenging, this species also preys on small mammals and reptiles (Murn, 2014), and is typically observed singly or in small numbers when at carcasses (Mundy et al., 1992; Murn, 2013; Murn & Holloway, 2014). Portugal et al. (2017) found White-headed Vulture visual characteristics align more closely with those of diurnal hunting raptors than obligate scavengers, with binocular vision better suited for a *pioneer*. Where present, the White-headed Vulture is often one of the first vultures to arrive at carrion despite the significantly lower densities in which it occurs (Kruuk, 1967; Mundy et al., 1992). Movement data show that, unlike White-backed Vultures, adult White-headed Vultures can maintain a small territory throughout the breeding season and into the nonbreeding season, showing they are capable of foraging successfully within a relatively small area (Chapter 1).

In our urgency to further understand these imperiled species, we need to continue exploring how each species' ecology supports its coexistence with other vulture species that share similar resources. A deeper understanding of the ecology of these species could inform a conservation model that works for all or most. Whereas Pennycuick (1972), Kruuk (1967), and Mundy et al. (1992) all note differences in African vulture flight characteristics, relatively few contemporary studies have considered empirical measures of ranging behavior as derived from movement data.

Here we use movement data derived from satellite transmitters to compare basic aspects of White-headed and White-backed Vulture movements by exploring trajectory characteristics. We focus on 4 trajectory characteristics – average flight altitudes and speeds, daily onset of activity, and distribution of hourly activity – and explore these by subdividing movement data into daily trajectories. We expected that White-headed Vultures would generally move at slower speeds and lower altitudes and initiate activity earlier in the day than White-backed Vultures, reflecting higher search efficiency and ability to use weaker thermals because of their lower wing loading (Mundy et al., 1992; Pennycuick, 1972). We also expected that the distribution of White-headed Vulture hourly activity levels would remain relatively uniform throughout the day, also reflective of a foraging method less reliant on thermals. Conversely, we expected that White-backed Vultures, reliant on other species to locate carcasses and strong thermals for efficient soaring flight, would fly at greater speeds and higher altitudes, initiate activity later, and that the distribution of hourly activity levels would be centered around a peak from late morning through early afternoon during the onset of optimal soaring flight conditions (Avery et al., 2011).

Methods

Study Area

Gorongosa National Park (Gorongosa) is located at the southern end of the Rift Valley in central Mozambique (Figure 2.1). The core area of Gorongosa encompasses 3,788 km^2 of diverse landscape and vegetation types, the most salient being the Rift Valley dominated by *Acacia-Combretum* savannah (Stalmans & Beilfuss, 2008).

The Mozambican Civil War (1977-1992) and subsequent years of unrest led to a >90% decline in wildlife biomass density in Gorongosa by the early 21st century (Stalmans et al., 2019). Gorongosa has undergone a significant recovery since restoration efforts were initiated in 2004, but while wildlife biomass density has rebounded to approximately 95% of pre-war estimates, species composition has seen a major shift (. Whereas, waterbuck (*Kobus ellipsiprymnus*) constituted approximately 4% of pre-war large-herbivore biomass, the species currently makes up an astounding 74% of large-herbivore biomass in the park (Stalmans et al., 2019). Today, waterbuck are the most abundant of eight ungulate species counted during aerial surveys in the park. Other species are recovering at varying rates. The predator guild is still recovering with hyena (*Crocuta crocuta*), leopard (*Panthera pardus*), and jackal (*Canis aureus*) having been recorded only occasionally since restoration efforts began and lion (*Panthera leo*) populations steadily growing from a very small population only 15 years ago (Bouley et al., 2018; Stalmans et al., 2019).

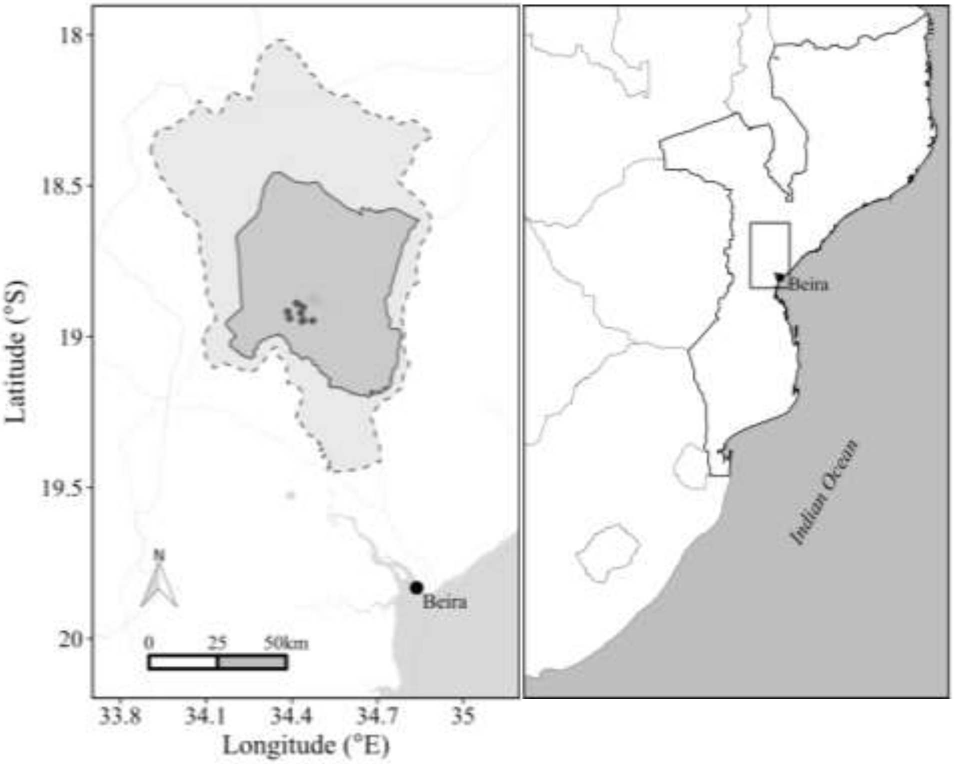

Figure 2.1 (A) The ~3,800 km2 Gorongosa National Park (dark gray, solid line) is encompassed by the ~5,400 km2 buffer zone (light gray, dashed line). We captured and tagged White-backed and White-headed Vultures at locations within the core road network (dark gray points). (B) Mozambique (bold borders) and bounding box (gray) for plot (A).

Gorongosa is Mozambique's flagship National Park and sees significant law enforcement and anti-poaching efforts. A 5,402 km^2 buffer zone surrounds the core area and contains a population of roughly 200,000 people residing in rural settlements (Bouley et al., 2018; Pringle, 2017; Stalmans et al., 2019). Outside Gorongosa's boundaries, wildlife densities decline significantly, limiting food resource biomass for vultures (Stalmans et al., 2019).

Satellite Transmitter Deployment

We trapped and tagged 12 White-headed Vultures and 9 White-backed Vultures within Gorongosa during field work in May and June of 2016 - 2018. Trapping locations were restricted to easily accessible sites along the road network located in the southern portion of the national park (Figure 2.1). We trapped vultures using noose-lines arranged around bait items consisting of either goat meat or ground beef. We fitted each bird with a solar-powered 70 g Argos/GPS satellite transmitter (PTT-100, Microwave Telemetry, Inc., Columbia, MD) using a backpack-style harness made of 8mm Teflon ribbon (Bally Ribbon Mills, Bally, PA). We programmed transmitters to collect GPS location, altitude above sea level, and instantaneous speed data hourly from 0400 to 1900 Central Africa Time. Data were collected on or very close to the hour.

Processing Vulture Movement Data

We associated each location with the ground elevation above sea level at that point on the ASTER ASTGTM2 Global 30-m digital elevation model (NASA/METI/AIST/Japan Spacesystems, 2009) using the env-DATA annotation service in Movebank (Wikelski & Kays, 2019) and downloaded the data for manipulation and analysis in program R (R Core Team, 2018). We excluded any 2D fixes without height or altitude data from analysis. We created a trajectory for each day's locations by defining start and end times to each trajectory as 0400 and 1900, respectively, using R package *adehabitatLT* (Calenge, 2015). Whereas White-backed Vultures frequently utilized resources outside of Gorongosa, White-headed Vulture movements were largely constrained to the protected area (Chapter 1). Daily trajectories with locations outside of the park could be initiated either inside the park or outside the park. Because we wanted to compare onset of activity and flight characteristics under similar environmental conditions and within shared habitat, we clipped location data to the extent of Gorongosa by filtering out any daily trajectories not entirely contained by the park boundary using R package *sf* (Pebesma, 2018). We removed any trajectories with fewer than 16 daily locations (the maximum number of possible locations collected during the pre-programmed hours) to ensure we were not considering days with large gaps that might skew results.

Trajectory characteristics

Altitude Correction and Classification

We corrected raw altitude data recorded at each GPS location to obtain height above ground level (AGL) following established methods (Poessel, Duerr, Hall, Braham, & Katzner, 2018). First, we obtained geoid undulation values using the 2008 Earth Gravitational Model (Pavlis, Holmes, Kenyon, & Factor, 2012) and subtracted these from the raw altitude data to obtain altitude above sea level. We then subtracted the digital elevation model from the corrected altitude data to obtain altitude above ground level for each GPS location. Some negative altitudes above ground level are to be expected due to error associated with GPS and elevation data (Poessel et al., 2018). We filtered out extreme negative altitudes following a thresholding method (Katzner et al. 2012, Poessel et al. 2018). We removed locations with associated altitudes less than -60 m AGL, the sum of GPS error (c. 18 m), digital elevation model error (10 – 25 m), and the digital elevation model interpolation error equal to the resolution of the data (30m). We assumed minimal digital elevation model error because of the relatively homogenous topography of Gorongosa National Park.

Speed Classification

By plotting the distributions of instantaneous speeds as recorded by the GPS, we determined that speed data for both White-headed Vulture and White-backed Vulture fit bimodal distributions, with lower modes centered around approximately 1 m/s and upper modes centered around approximately 18 m/s and 20 m/s, respectively (Figure 2.2). We decided the bimodal distribution was reflective of speeds that either could or could not sustain prolonged flight. We chose 5 m/s and 2.5 m/s as the thresholds for White-headed Vultures and White-backed Vultures, respectively, by locating the antimode of these bimodal distributions. While these thresholds are below Pennycuick's (1972) estimates of a 9 m/s minimum gliding speed and 13 m/s optimal glide ratio for White-backed Vultures, we wanted to ensure inclusion of lower horizontal speeds associated with sinking motion, flapping flight, or initiation of flight. We classified locations with speeds above the threshold as flighted and below it as grounded (or perched). Some of the locations classified as grounded were associated with altitudes greater than 100 m. Given the altitudinal error of ±60 m (outlined above), and the maximum tree height in Gorongosa, approximately 30 – 40 m AGL (Tinley, 1977), we reclassified these locations as flighted to account for the potential for little to no horizontal speed during thermaling behavior. Mundy et al. (1992) estimated the average rate of climb in thermals for vultures as 3 m/s, and Akos et al. (2010) estimated that rate of climb associated with weak thermals could be as little as 0.4 m/s. The instantaneous horizonal speed associated with a slow rate of climb is likely below the level of accuracy of our satellite transmitters.

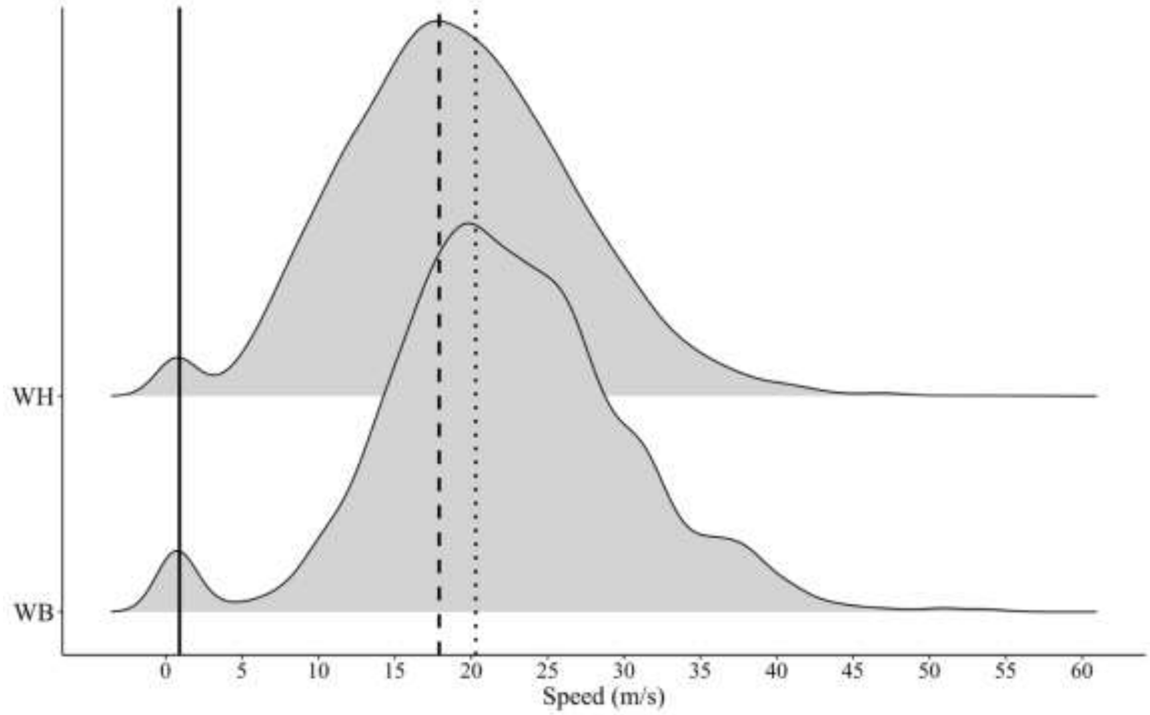

Figure 2.2 Bimodal distributions of observed instantaneous speeds for White-headed Vultures (WH) and White-backed Vultures (WB). Lower modes for both species were approximately 1 m/s (solid line) and upper modes were approximately 18 (dashed line) and 20 m/s (dotted line), for White-headed Vulture and White-backed Vultures, respectively.

Day Period

We classified locations as either night or day by determining sunrise and sunset times for each daily trajectory using R package *maptools* (Bivand & Lewin-Koh, 2019). Sunrise times fell between 0551 and 0615 hours, and sunset times between 1716 and 1735 hours. Daylight hours were defined as 0600-1800 hours. We classified night locations that were also classified as perched as roost locations and night locations also classified as flighted were visually checked; we would not expect to see high-altitude soaring behavior during the hours between sunset and sunrise.

Onset of Movement and Flight at Altitude

We considered the hour of first location of each day associated with step lengths (Euclidian distance of between locations at times *t* and *t+1*) of either 100 m (hereafter "short-distance movements") or 1 km (hereafter, "long-distance movements") as the onset of daily movement on two scales. We considered the hour of first location of each day associated with an altitude greater than 100 m AGL (hereafter "high-altitude flight") as the onset of flight behavior.

Proportion of Hourly Activity

Given the coarse sampling interval of our data, we relied on two lines of evidence to identify periods of activity. These were (1) step lengths greater than 100 m and (2) whether a location was associated with flight. We then determined the level of activity within each daylight hour from 0600-1800 (13 possible locations during this time span) by grouping observations by hour and calculating the proportion of locations that were classified as active within each hour. We followed this process for each individual to obtain an estimate of activity level for each daylight hour.

Data Analysis

We fit a series of Bayesian generalized linear models for our two study species, White-headed Vulture and White-backed Vulture. We used gamma distributed models to determine the effect of species as a predictor for differences in the means of flight altitudes and speeds; we used Poisson distributed models to determine the effect of species as a predictor for differences in the timing of onset of short and long-distance movements, and high-altitude flight; and we used a beta distributed model to determine the effect of species and hour (cubic) predictors on timing of peak activity levels and proportion of locations classified as active. We only considered location data classified as flighted for models comparing vulture flight speeds and altitudes.

We estimated parameter coefficients using Bayesian Markov chain Monte Carlo (MCMC) sampling with 4 chains for 2,000 iterations each with a 1,000 iteration burn-in period (Goodrich et al., 2018). We used weakly informative priors for all parameters. We assessed model and parameter convergence using the posterior predictive distribution and the Gelman-Rubin statistic, respectively, and ensured minimum effective sample size requirements were met. We considered there was a difference in the two species' trajectory characteristics if the 95% posterior credible interval for the species predictor did not overlap 0 (Gelman & Donald, 1992). We performed all modelling with packages *brms* and *stan* in program R (Carpenter et al., 2017; Goodrich et al., 2018).

Results

We used a total of 91,784 locations to create 5,568 daily trajectories that included space use both inside and outside of the Gorongosa boundary. These daily trajectories included 1,500 from White-backed Vultures and 4,068 from White-headed Vultures. We removed daily trajectories that included space use outside of Gorongosa, resulting in 4,910 daily trajectories entirely contained within the Gorongosa boundary, 1,082 (72% of the species total) from 9 White-backed Vultures and 3,828 (95% of the species total) from 12 White-headed Vultures (Figure 2.3; Table B.1).

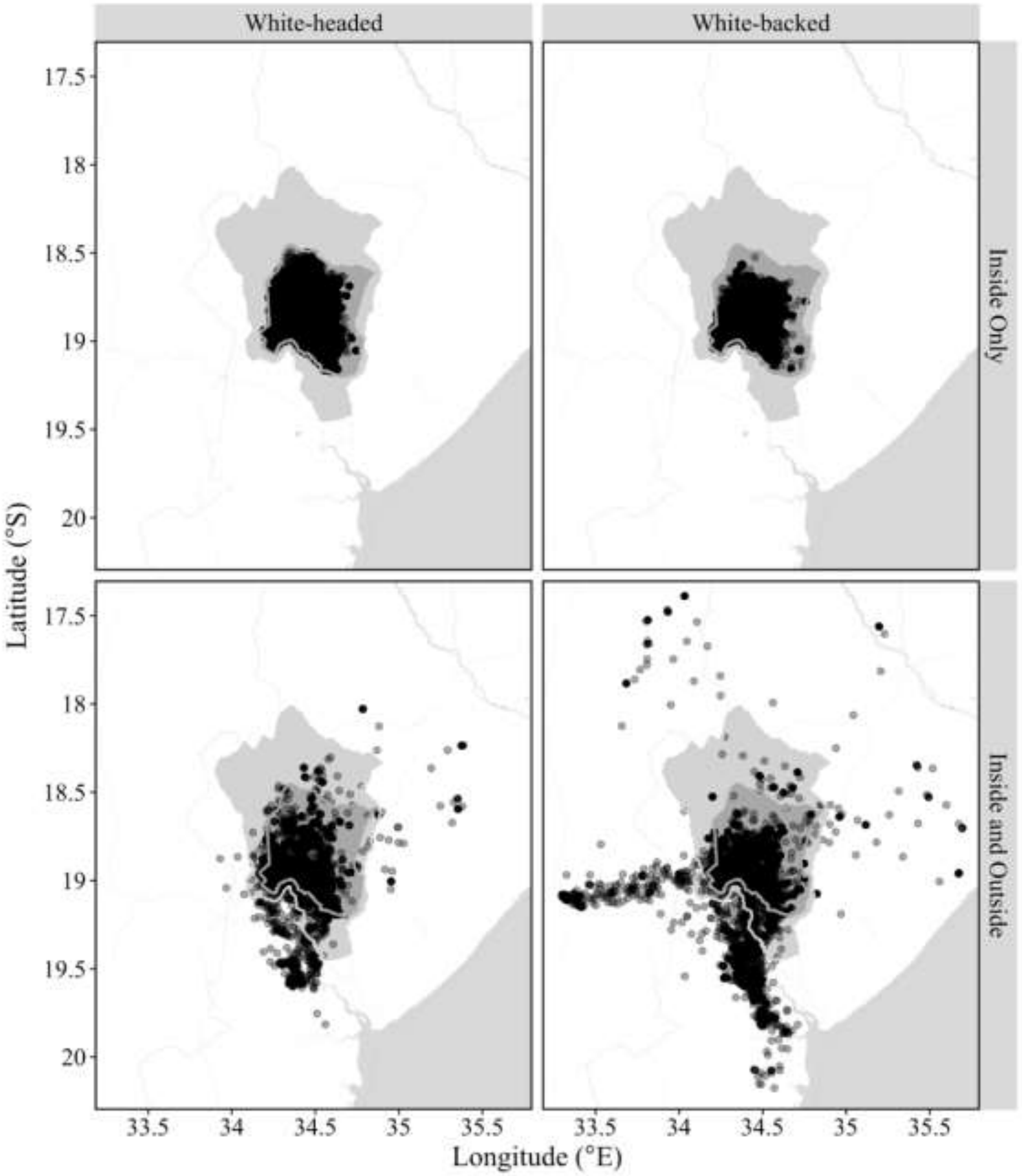

Figure 2.3 Locations from White-headed Vulture (left) and White-backed Vulture (right) daily trajectories involving use of Gorongosa National Park, Mozambique. The upper plots show daily trajectories completely within Gorongosa boundaries. The lower plots show daily trajectories involving space use both inside and outside of the park boundaries (bottom). White-backed Vultures daily trajectories (right) included substantial use of outside resources, whereas White-headed Vulture daily trajectories (left) were largely confined to Gorongosa.

Approximately 10% of the total number of locations were associated with negative altitudes, with a minimum of -59.7 m AGL (Figure 2.4). We analyzed trajectory characteristics during daylight hours using 50,741 (74%) of the total number of locations from daily trajectories limited to Gorongosa. On average, 50% (SD: 0.1) of each individual's locations during daylight hours were classified as active.

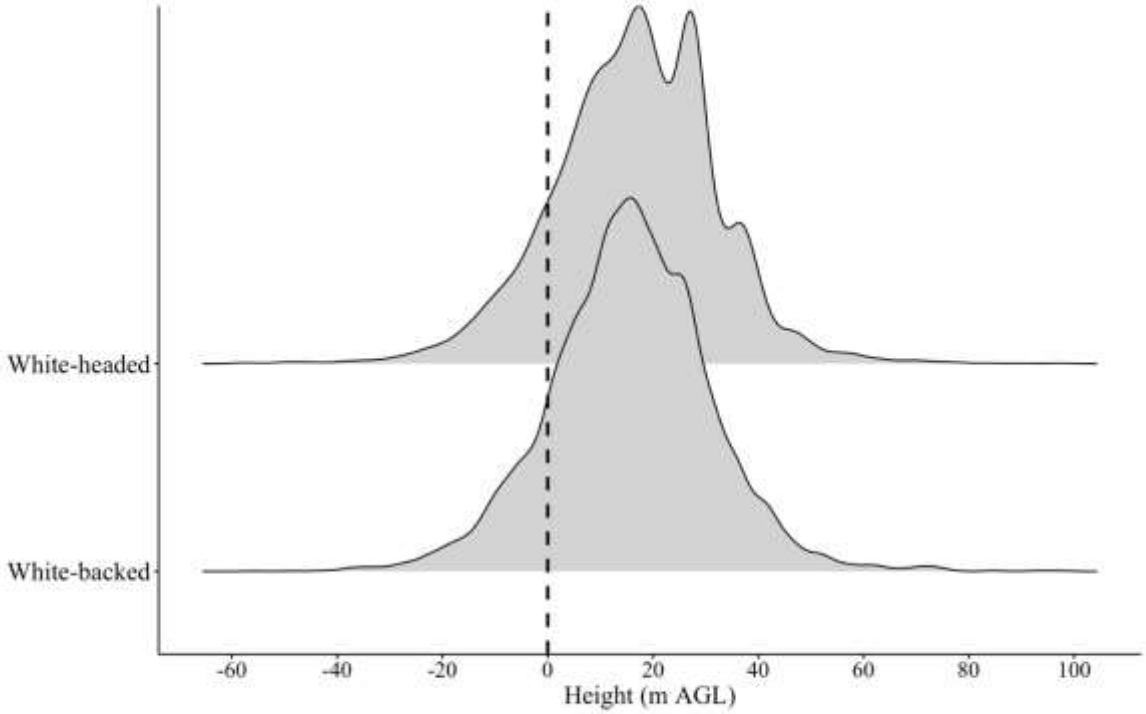

Figure 2.4 Density distributions of empirical height data less than 100 m AGL for White-headed (top) and White-backed Vultures (bottom) in Gorongosa National Park, Mozambique. The distributions for both species were centered around a mean of approximately 17 m AGL. Approximately 10% of all recorded heights fell below 0 (dashed line) after removal of heights below the -60 m threshold.

Trajectory Characteristics

White-headed Vultures flew at lower altitudes than did White-backed Vultures (315 vs. 380 m AGL). Ninety-eight percent of White-headed Vulture and 75% of White-backed Vulture flight altitudes were below 1,000 m AGL, and we found flight altitudes up to 2,859 and 2,477 m AGL, respectively. Both species flew at altitudes within a similar range; 95% of White-headed Vulture flight altitudes fell between 24 m and 997 m

AGL, and 95% of White-backed Vulture flight altitudes fell between 27 and 1,126 m AGL (Figure 2.5).

On average, White-headed Vultures flew slower than White-backed Vultures (14 vs. 23 m/s). Again, we found a large amount of overlap in the overall range of instantaneous flight speeds; ninety-five percent of the time White-headed Vultures flew at speeds between 5 and 32 m/s, whereas White-backed Vultures flew at speeds between 10 and 40 m/s (Figure 2.6). We found a maximum flight speed of 58 m/s for White-headed Vultures and 75 m/s for White-backed Vultures

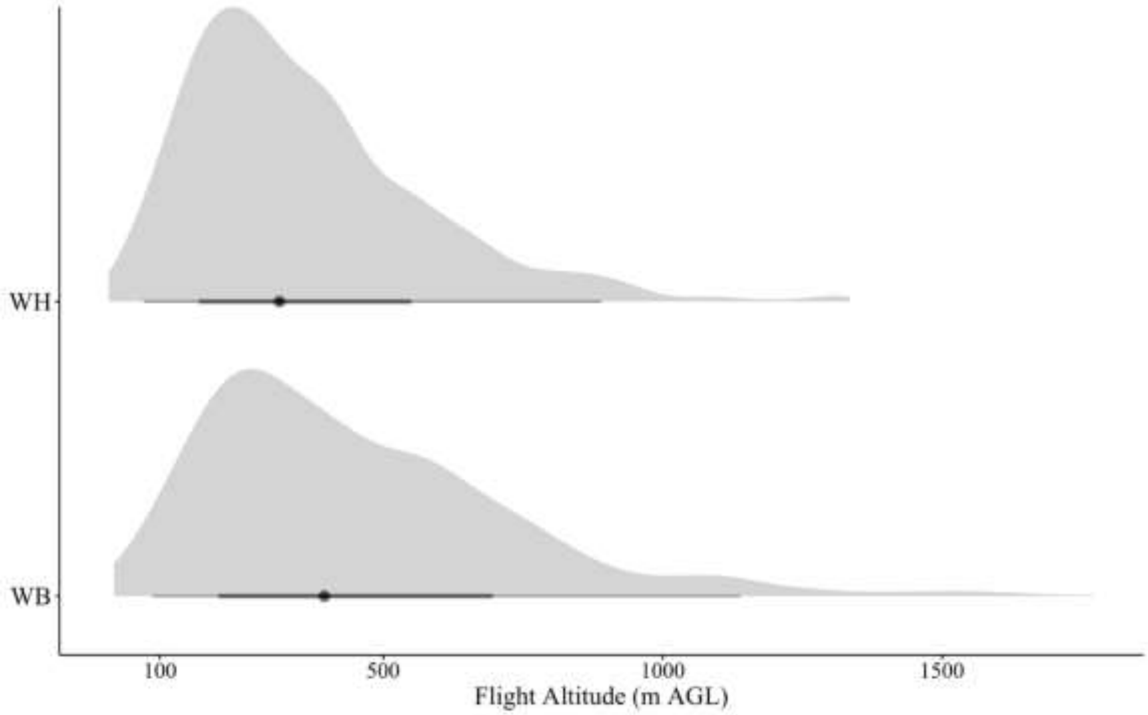

Figure 2.5 Posterior distributions and mean point estimates with 50% (thick bar) and 95% (thin bar) credibility intervals for White-headed Vulture (WH) and White-backed Vulture (WB) flight altitude in Gorongosa National Park, Mozambique.

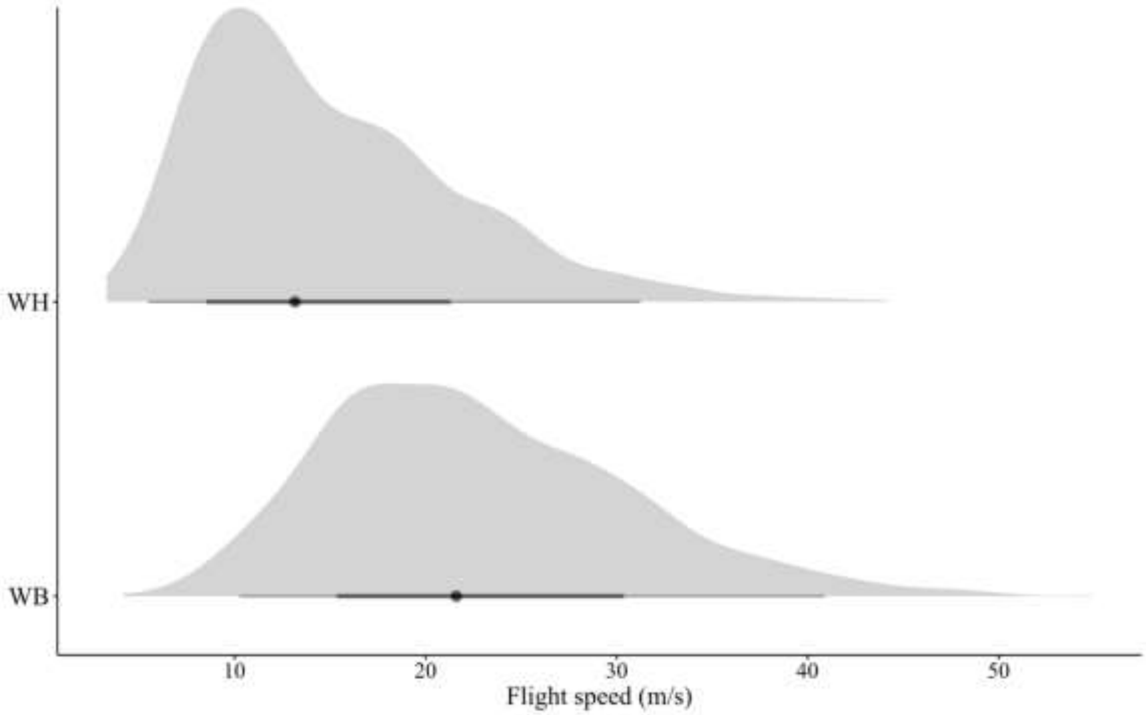

Figure 2.6 Posterior distributions and mean point estimates with 50% (thick bar) and 95% (thin bar) credibility intervals for White-headed Vulture (WH) and White-backed Vulture (WB) flight speed in Gorongosa National Park, Mozambique.

White-headed Vultures initiated short-distance movements earlier than White-backed Vultures (0700 vs. 0800 hours; Figure 2.7). White-headed Vultures also initiated long-distance movements earlier than White-backed Vultures (0830 vs. 0900 hours; Figure 2.7). Just as White-headed Vultures were less reliant on development of flight conditions to initiate daily movement, they also initiated high-altitude flight earlier than White-backed Vultures (1030 vs. 1100 hours; Figure 2.8).

We found a minimal difference in timing of peak activity for White-headed Vultures and White-backed Vultures – both species were most active in the 1100 hour. We also found a minimal difference in the proportion of active locations within the 1100 hour – 73% and 68% for White-headed Vultures and White-backed Vultures, respectively (Figure 2.9).

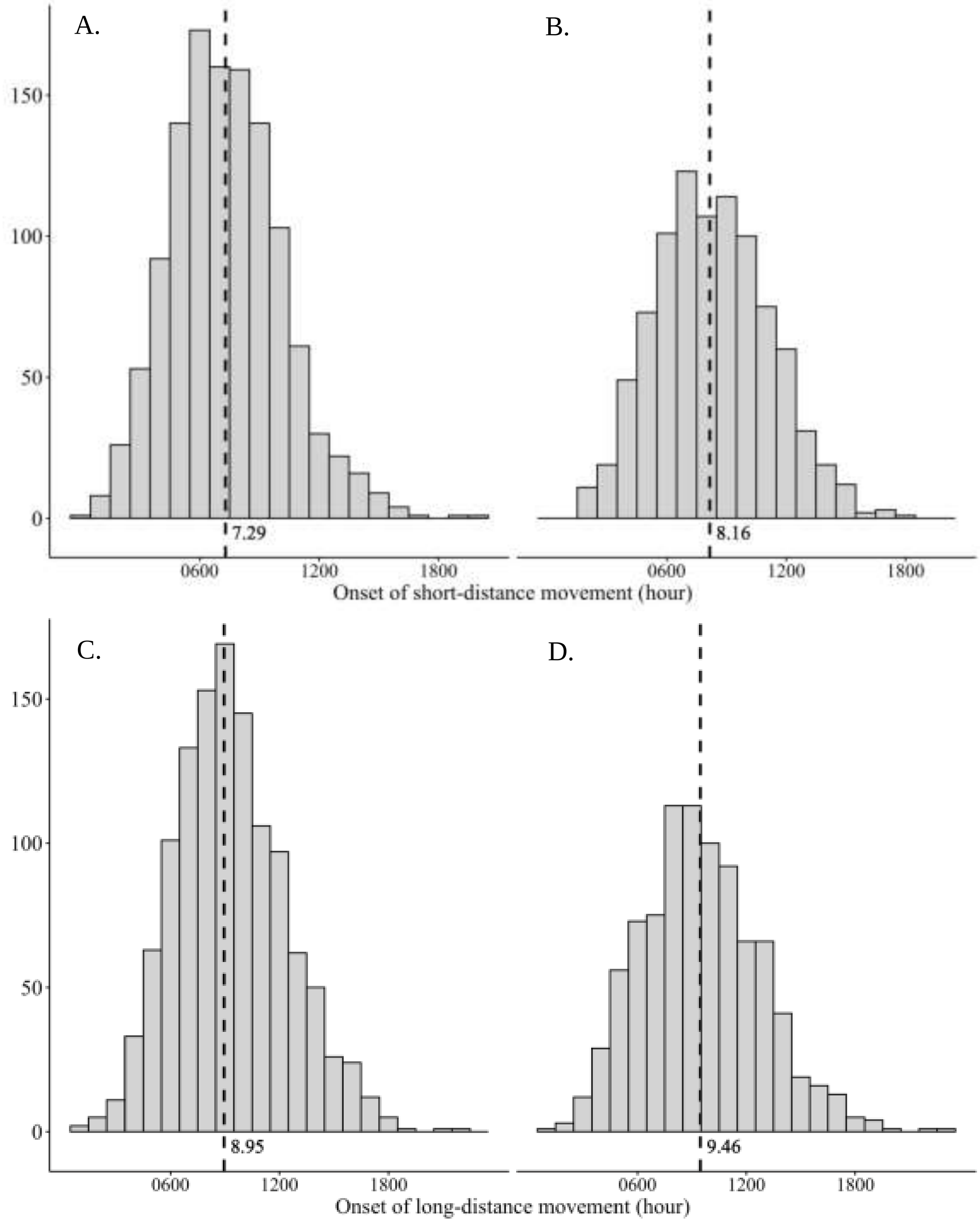

Figure 2.7 Histograms of posterior predictions for the hour for onset of short-distance and long-distance movement (step length >100 m and >1000 m, respectively) for (A & C) White-headed Vultures and (B & D) White-backed Vultures in Gorongosa National Park, Mozambique. Model predicted averages are noted below each histogram.

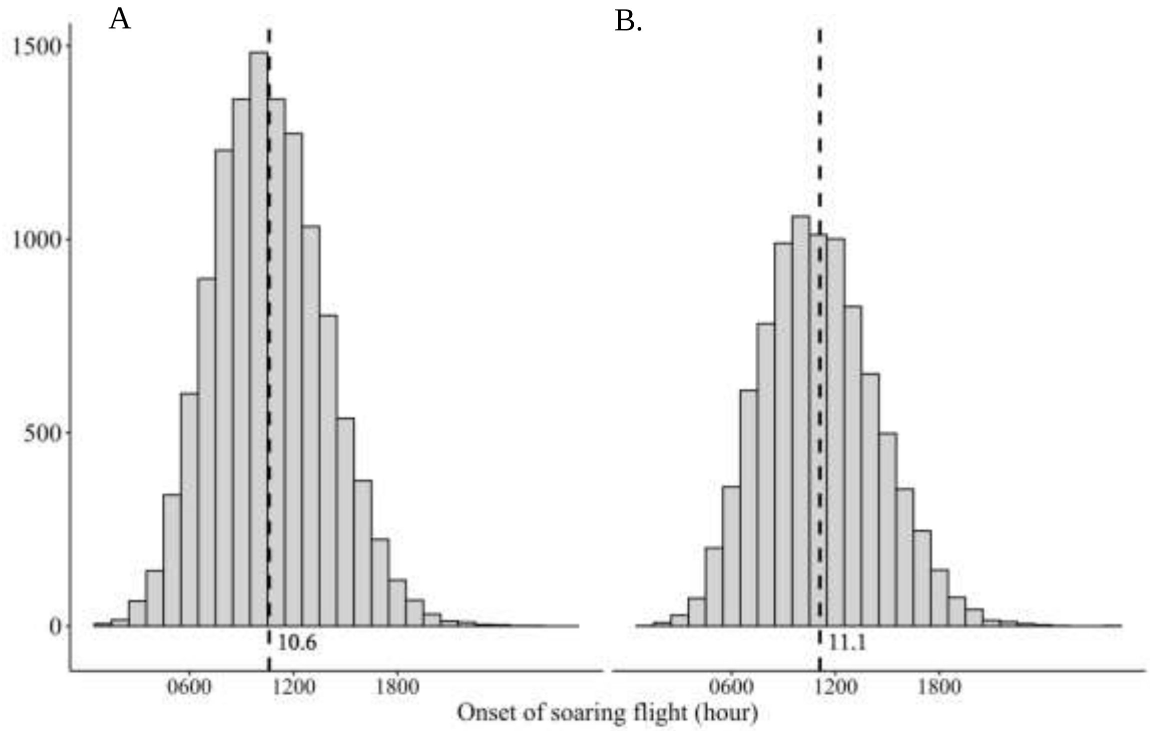

Figure 2.8 Histograms of posterior predictions for the hour of onset of soaring behavior for (A) White-headed Vultures and (B) White-backed Vultures in Gorongosa National Park, Mozambique. The onset of soaring behavior was centered around a mean (dashed line) of approximately 1030 and 1100 hours for White-headed and White-backed Vultures, respectively. Model predicted averages are noted below each histogram.

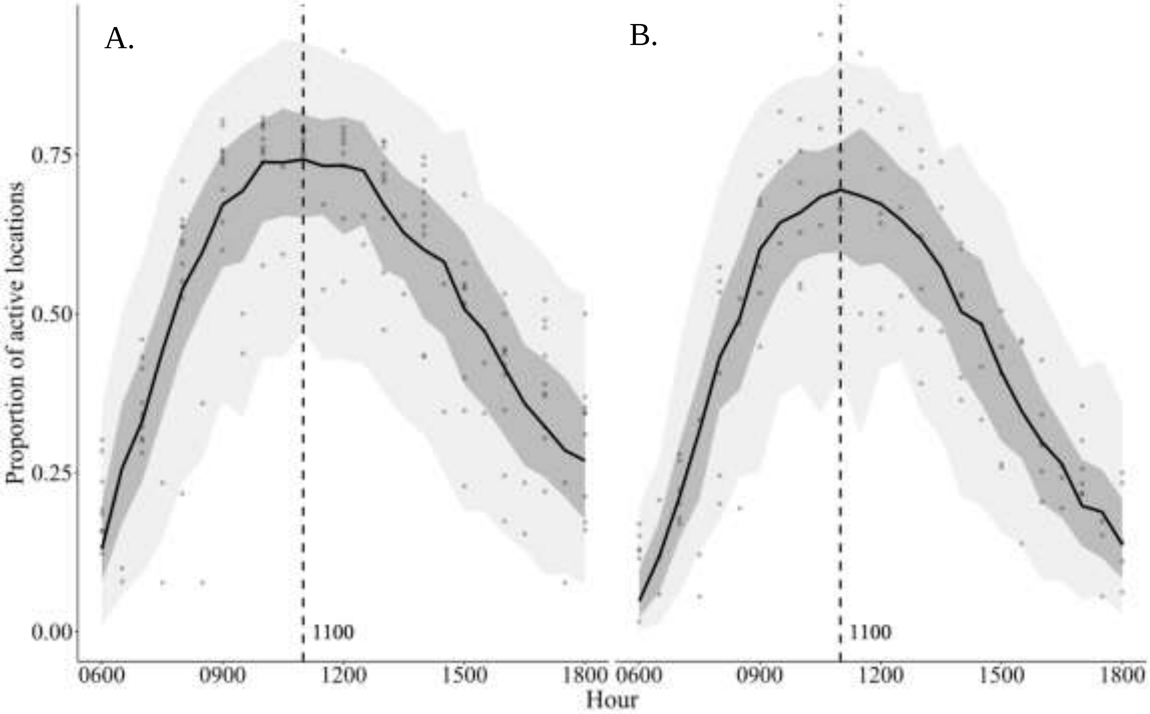

Figure 2.9 Posterior predictive fit curves for the proportion of active locations by hour for White-headed Vultures (A) and White-backed Vultures (B) in Gorongosa National Park, Mozambique. Observed proportions of activity for each hour are shown with overlaid points. Peak activity was observed in the 1100 hour (dashed line).

Discussion

Kane & Kendall (2017) found White-backed Vultures and White-headed Vultures in the Masai Mara, Kenya, arrived at experimental carcasses at the same median arrival order, third, along with the Lappet-faced Vulture (*Torgos tracheliotos*) and Hooded Vulture (*Necrosyrtes monachus*), following the Tawny Eagle and Bateleur (*Terathopius ecaudatus*). Their study was carried out in an ecosystem with a healthy Tawny Eagle population – this is not the case in Gorongosa. We believe that whereas a species like the Tawny Eagle serves as the primary *pioneer* in a system like the Masai Mara, the White-headed Vulture might play a significant part in Gorongosa where Tawny Eagles are currently rare to nonexistent. Our field observations of vulture arrival times at carcasses in Gorongosa support this – White-headed Vultures were typically the first vulture species to arrive at carcasses, often preceded by the Bateleur, and followed by one of the other resident vulture species (T. Scott, pers. obs.).

Our model predictions for flight altitude largely mirrored the empirical data but were more conservative when considering maximum flight altitude. The highest recorded vulture flight altitude of approximately 11,000 meters AGL (Laybourne, 1974) is likely an extreme outlier, and both our model and empirical data suggest the estimate of a typical maximum thermaling altitude of 800 m AGL for White-backed Vultures by both Pennycuick (1972) and Mundy et al. (1992) is low. Whereas only 5% of predicted White-headed Vultures flight altitudes were greater than 800 m, we found that 32% of White-headed flight altitudes were above this previous estimate of maximum thermaling altitude. We found vultures do occasionally fly at altitudes higher than 1,000 m AGL, including extremes greater than 2,000 m AGL.

Our findings for flight speed are slightly greater than but support previous estimates for the White-backed Vulture by Pennycuick (1972) and Mundy et al. (1992). Pennycuick (1972) estimated a median speed of approximately 18 m/s, 5 m/s slower than both our model predicted median and empirical median. The higher speeds predicted by our model are similar to the 33 and 39 m/s diving speeds mentioned by Mundy et al. (1992), but both the model and our empirical data support the potential for higher flight speeds by both species, with outliers greater than 50 m/s.

The earlier onset of movement and flight at altitude for White-headed Vultures is likely largely attributed to their lower wing loading, allowing them to move throughout their home ranges with less reliance on thermals. An earlier onset of movement also supports the notion that White-headed Vultures could play the role of primary *pioneer*. That being said, the two species' distributions of hourly activity level largely overlap, suggesting that both species take advantage of similar conditions during hours of peak activity. The coarse sampling interval of our data and significant amount of error associated with our 3D data potentially masks much of the lower flight altitudes we expected to find with White-headed Vultures. It would be valuable to build on these findings with higher resolution tracking data.

Both species exhibited a peak in activity around the expected onset of suitable thermaling conditions. Generally, the hourly activity level of White-headed Vultures was slightly higher and dropped off at a slower rate over the course of the day than that of White-backed Vultures. This suggests that White-headed Vultures are more consistently active over the course of the day, perhaps reflective of a foraging method more reliant on smaller prey items. Conversely, White-backed Vulture hourly activity levels had a well-defined peak possibly associated with foraging behavior that quickly drops off after discovery of carrion. Again, tracking data with a higher resolution sampling interval or integration of additional data collected via biologgers (i.e., acceleration and heart rate) could vastly increase our understanding of behaviors associated with varied levels of activity over the course of the day.

Finally, though we had a significantly larger sample of daily trajectories for White-headed Vultures, 4,068 of 5,568 (73%), we found a much lower number of instances in which they ventured outside of Gorongosa to utilize resources. This finding furthers our understanding of the importance of protected areas to the survival and well-being of this imperiled species.

The fact that White-headed Vultures fly at lower altitudes and speeds, and initiate activity earlier, coupled with our recent findings of intensive range-residency (Chapter 1) imply that the White-headed Vulture fills a similar niche among African vultures as the Lappet-faced Vulture. Spiegel et al. (2013a) suggest that the Lappet-faced Vulture, a *pioneer* demonstrating heightened search efficiency, plays an important role in sustaining the fitness of White-backed Vultures, and note that the species is at greater risk of local extinction due to low occurrence densities.

Our findings suggest White-headed Vultures use a foraging method capable of exploiting a wider range of food resources through increased vigilance and a higher intensity search over a smaller area. These support the hypothesis that the White-headed Vulture is more likely a *pioneer* than a *follower* (Houston, 1975). As we strive to conserve these and other species at risk of extinction, we need to continue building on our knowledge of intraspecific ecological relationships; with so much overlap in species occurrence, this is particularly important for African vultures. Conservation decisions shape the many protected areas crucial to the longevity of these species, and to be effective these decisions need to take species interactions into account.

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APPENDIX A

Home range Supplemental Information

A.1 Summary of tag durations and intrinsic classifiers for the 12 White-headed Vultures included in this study. We tagged and tracked all birds in Gorongosa National Park, Mozambique, in the 2016-17, 2017-18, and 2018-19 field seasons. Start and end dates are identified by month and year. Some individuals transitioned between multiple age and breeding status categories as data collection progressed. Breeding/central place status is summarized by year. We could not assign sex to juvenile and younger subadult birds by plumage aspect. Breeding: B; Non-breeding central place: NC; Non-breeding non-central place: NN.

					BREEDING/CENTRAL PLACE STATUS				
BIRD	**START**	**END**	**DURATION (MONTHS)**	**AGE**	**2016**	**2017**	**2018**	**2019**	**SEX**
WH88_16	2016-07	2019-10	40	Juv., Subad.	NN	NN	NN	NN	Unk.
WH24_17	2017-07	2018-03	9	Juv., Subad.	--	NN	NN	--	Unk.
WH25_17	2017-07	2017-11	5	Subad.	--	NN	--	--	M
WH37_17	2017-07	2017-09	3	Adult	--	NN	--	--	M
WH41_17	2017-07	2017-10	4	Adult	--	NN	--	--	F
WH42_17	2017-07	2018-03	9	Adult	--	B	NC;NN	--	F

A.1 Continued

BIRD	START	END	DURATION (MONTHS)	AGE	BREEDING TERRITORIAL STATUS 2016	2017	2018	2019	SEX
WH44_17	2017-07	2018-01	7	Subad.	--	NN	N	--	Unk.
WH27_18	2018-07	2019-10	16	Adult	--	--	B;NC	NC	M
WH29_18	2018-07	2019-10	16	Adult	--	--	B;NC	NC	M
WH31_18	2018-07	2019-10	16	Adult	--	--	NN	NN	M
WH41_18	2018-07	2019-10	16	Adult	--	--	B;NC	NC	F
WH24_18	2018-07	2019-02	8	Adult	--	--	B;NC	NC;NN	M

A.2 Empirical AKDE model results for all 149 White-headed Vulture bird-months with associated model covariate values. Within-individual bird-months are distinguished by table shading. 132 bird-months AKDE were fit to the Ornstein-Uhlenbeck (OU) continuous-time movement model. The remaining 17 bird-months, noted by an asterisk, were fit to variations of the OU movement model that include parameters accounting for autocorrelation in velocity, tracks of short duration, and oscillatory movement across a range. Breeding: B; Non-breeding central place: NC; Non-breeding non-central place: NN; juvenile: JUV; subadult: SA; adult: AD.

BIRD	95% AKDE (km^2) (95% CI)	50% AKDE (km^2) (50% CI)	MO	YEAR	BR STATUS	Age	NDVI (95% AKDE)	NDVI (50% AKDE)	95% AKDE/Park overlap (%) (50% AKDE)
WH24_17	19.7 (12-29.3)	3 (1.8-22.7)	07	2017	N	JUV	0.33	0.41	100 (100)
WH24_17	14.5 (12.3-16.8)	1.2 (1-15.2)	08	2017	N	SA	0.36	0.38	100 (100)
WH24_17	102.5 (81.3-126)	24.2 (19.2-110.2)	09	2017	N	SA	0.26	0.29	100 (100)
WH24_17	156.9 (110.6-211.1)	37.5 (26.5-174.2)	10	2017	N	SA	0.17	0.18	100 (100)
WH24_17	143.4 (78.9-226.8)	30.2 (16.6-169)	11	2017	N	SA	0.4	0.45	100 (100)
WH24_17	266.9 (192-354)	61 (43.9-294.9)	12	2017	N	SA	0.46	0.5	100 (100)
WH24_17	407.3 (299-532)	98.7 (72.5-447.4)	01	2018	N	SA	0.45	0.48	100 (100)
WH24_17	330.7 (195.1-501.5)	88.9 (52.5-383.7)	02	2018	N	SA	0.38	0.31	100 (100)
WH24_17	78.4 (42.2-125.7)	20.4 (11-92.9)	03	2018	N	SA	0.36	0.46	100 (100)

A.2 Continued

BIRD	95% AKDE (km^2) (95% CI)	50% AKDE (km^2) (50% CI)	MO	YEAR	BR STATUS	Age	NDVI (95% AKDE)	NDVI (50% AKDE)	95% AKDE/Park overlap (%) (50% AKDE)
WH24_18	18.2 (16.4-20.2)	2.6 (2.3-18.9)	07	2018	B	AD	0.39	0.33	100 (100)
WH24_18	31.3 (27.6-35.1)	6.5 (5.8-32.5)	08	2018	NC	AD	0.3	0.27	100 (100)
WH24_18	47.9 (42-54.1)	10.4 (9.1-49.9)	09	2018	NC	AD	0.25	0.25	100 (100)
WH24_18	558.4 (430.1-703)	74.5 (57.4-605.4)	10	2018	NN	AD	0.28	0.25	100 (100)
WH24_18	1236.5 (946.4-1564.8)	281.5 (215.4-1343.1)	11	2018	NN	AD	0.24	0.24	99 (100)
WH24_18 *	2143.8 (1547.7-2835.6)	569.8 (411.4-2365.9)	12	2018	NN	AD	0.47	0.42	91.2 (93.6)
WH24_18 *	2486.9 (1875.3-3183.4)	570.8 (430.4-2712.3)	01	2019	NN	AD	0.59	0.61	87.7 (93.9)
WH24_18	1802.2 (1268.9-2427.4)	359.9 (253.4-2002)	02	2019	NN	AD	0.54	0.58	80 (83.5)
WH25_17	3123.4 (1341.7-5644.8)	892.3 (383.3-3871.9)	07	2017	NN	sa	0.36	0.29	76.5 (100)
WH25_17	3234.3 (1655.6-5332.7)	867.2 (443.9-3871.7)	08	2017	NN	sa	0.28	0.27	81 (99.8)

A.2 Continued

BIRD	95% AKDE (km^2) (95% CI)	50% AKDE (km^2) (50% CI)	MO	YEAR	BR STATUS	Age	NDVI (95% AKDE)	NDVI (50% AKDE)	95% AKDE/Park overlap (%) (50% AKDE)
WH25_17	2518.9 (1305.2-4124.8)	621.2 (321.9-3007.5)	09	2017	NN	sa	0.24	0.22	96.6 (100)
WH25_17	1841.3 (1057.2-2839.3)	559.1 (321-2149.6)	10	2017	NN	sa	0.15	0.13	88.3 (100)
WH25_17	435.6 (197.7-765.8)	121.9 (55.4-534.3)	11	2017	NN	sa	0.41	0.4	97.3 (100)
WH27_18	1355.2 (974.1-1798.2)	179.1 (128.7-1497.2)	07	2018	B	AD	0.37	0.35	99.9 (100)
WH27_18	1485 (1138.7-1876.6)	151.9 (116.5-1612.2)	08	2018	B	AD	0.35	0.32	99.6 (100)
WH27_18	24.1 (21.8-26.5)	4.4 (4-24.9)	09	2018	B	AD	0.22	0.14	100 (100)
WH27_18	82.1 (73.6-91.1)	9.7 (8.7-85.2)	10	2018	B	AD	0.24	0.21	100 (100)
WH27_18	111.1 (94-129.7)	15.5 (13.1-117.3)	11	2018	NC	AD	0.23	0.23	100 (100)
WH27_18	32 (28.6-35.6)	5.2 (4.7-33.2)	12	2018	NC	AD	0.47	0.45	100 (100)
WH27_18	37.4 (32.7-42.5)	6.3 (5.5-39.1)	01	2019	NC	AD	0.6	0.64	100 (100)
WH27_18	29.7 (26-33.6)	5.6 (4.9-31)	02	2019	NC	AD	0.56	0.54	100 (100)

A.2 Continued

BIRD	95% AKDE (km^2) (95% CI)	50% AKDE (km^2) (50% CI)	MO	YEAR	BR STATUS	Age	NDVI (95% AKDE)	NDVI (50% AKDE)	95% AKDE/Park overlap (%) (50% AKDE)
WH27_18 *	18 (16.5-19.6)	2.6 (2.4-18.5)	03	2019	NC	AD	0.48	0.42	100 (100)
WH27_18	18.3 (16.4-20.4)	3.2 (2.9-19)	04	2019	NC	AD	0.53	0.52	100 (100)
WH27_18	28.9 (25.9-32.1)	4.8 (4.3-30)	05	2019	NC	AD	0.48	0.46	100 (100)
WH27_18	33.2 (29.6-37)	4.5 (4-34.5)	06	2019	B	AD	0.45	0.41	100 (100)
WH27_18	394.3 (324.4-470.9)	26.1 (21.5-419.5)	07	2019	B	AD	0.4	0.38	100 (100)
WH27_18	690 (565.4-826.8)	53.7 (44-735)	08	2019	B	AD	0.3	0.28	99.9 (100)
WH27_18	171.3 (145.1-199.7)	13.5 (11.4-180.7)	09	2019	B	AD	0.17	0.18	100 (100)
WH27_18	265.6 (226.7-307.6)	23.5 (20-279.6)	10	2019	B	AD	0.24	0.24	100 (100)
WH29_18	56.5 (48.7-64.8)	10.8 (9.3-59.3)	07	2018	B	AD	0.38	0.39	100 (100)
WH29_18	165.8 (142.5-190.9)	10 (8.6-174.2)	08	2018	B	AD	0.35	0.32	98.7 (100)
WH29_18	95.5 (82.7-109.1)	6.3 (5.5-100)	09	2018	B	AD	0.31	0.28	100 (100)
WH29_18	40 (36.4-43.8)	3.4 (3.1-41.3)	10	2018	B	AD	0.31	0.29	99.1 (100)

A.2 Continued

BIRD	95% AKDE (km^2) (95% CI)	50% AKDE (km^2) (50% CI)	MO	YEAR	BR STATUS	Age	NDVI (95% AKDE)	NDVI (50% AKDE)	95% AKDE/Park overlap (%) (50% AKDE)
WH29_18	127 (109.9-145.2)	10.9 (9.5-133)	11	2018	NC	AD	0.3	0.25	99.9 (100)
WH29_18	270.5 (228.4-316)	20.6 (17.4-285.6)	12	2018	NC	AD	0.42	0.48	100 (100)
WH29_18	27.6 (23.6-32)	5.4 (4.6-29.1)	01	2019	NC	AD	0.56	0.59	100 (100)
WH29_18	18.8 (16.4-21.3)	4.5 (3.9-19.6)	02	2019	NC	AD	0.53	0.55	100 (100)
WH29_18	19.5 (17.1-22)	4.1 (3.6-20.3)	03	2019	NC	AD	0.47	0.54	100 (100)
WH29_18	10.8 (9.6-12.1)	2.8 (2.5-11.2)	04	2019	NC	AD	0.42	0.49	100 (100)
WH29_18	15.4 (13.6-17.4)	4 (3.5-16.1)	05	2019	NC	AD	0.37	0.41	100 (100)
WH29_18	16.8 (14.7-18.9)	3.5 (3.1-17.5)	06	2019	NC	AD	0.38	0.39	100 (100)
WH29_18	70 (56.6-84.8)	10.3 (8.3-74.8)	07	2019	NC	AD	0.38	0.38	100 (100)
WH29_18	217 (176.8-261.2)	18.6 (15.2-231.5)	08	2019	B	AD	0.31	0.31	99.6 (100)
WH29_18	68.4 (56.9-80.9)	7.1 (5.9-72.5)	09	2019	B	AD	0.28	0.26	100 (100)

A.2 Continued

BIRD	95% AKDE (km^2) (95% CI)	50% AKDE (km^2) (50% CI)	MO	YEAR	BR STATUS	Age	NDVI (95% AKDE)	NDVI (50% AKDE)	95% AKDE/Park overlap (%) (50% AKDE)
WH29_18	143.5 (114.4-175.8)	13.5 (10.8-154.1)	10	2019	B	AD	0.38	0.4	99 (100)
WH31_18 *	2556.3 (1745.8-3518.9)	622 (424.8-2862.2)	07	2018	NN	AD	0.39	0.36	88 (97.3)
WH31_18 *	10179.4 (8146.7-12435.2)	2092.3 (1674.5-10918.1)	08	2018	NN	AD	0.43	0.42	27.5 (52.2)
WH31_18	2756 (1606.7-4210.4)	716.6 (417.8-3206.3)	09	2018	NN	AD	0.27	0.28	80.9 (94.8)
WH31_18	2384.9 (1499-3473.3)	591 (371.4-2726)	10	2018	NN	AD	0.26	0.31	94 (100)
WH31_18	2553.6 (1334.7-4161.4)	688.9 (360.1-3043.4)	11	2018	NN	AD	0.25	0.22	94.6 (100)
WH31_18	3743.6 (2334.9-5479.5)	771.5 (481.2-4286.9)	12	2018	NN	AD	0.5	0.46	73.9 (97.2)
WH31_18	1887.1 (1262.1-2635.8)	531.8 (355.6-2124.2)	01	2019	NN	AD	0.57	0.55	100 (100)

A.2 Continued

BIRD	**95% AKDE (km^2) (95% CI)**	**50% AKDE (km^2) (50% CI)**	**MO**	**YEAR**	**BR STATUS**	**Age**	**NDVI (95% AKDE)**	**NDVI (50% AKDE)**	**95% AKDE/Park overlap (%) (50% AKDE)**
WH31_18	1720.2 (1193.3-2341.8)	426.9 (296.1-1918.3)	02	2019	NN	AD	0.54	0.52	99.1 (100)
WH31_18	428.1 (312.2-562)	59.4 (43.3-471.1)	03	2019	NN	AD	0.39	0.43	100 (100)
WH31_18	466.8 (334.7-620.7)	93 (66.7-516.1)	04	2019	NN	AD	0.4	0.46	100 (100)
WH31_18	793.7 (549.8-1081.7)	123.4 (85.5-885.5)	05	2019	NN	AD	0.42	0.44	96.4 (100)
WH31_18	746.9 (506.5-1033.3)	127.5 (86.4-837.8)	06	2019	NN	AD	0.47	0.49	91 (100)
WH31_18	352.5 (277.9-435.9)	71.7 (56.5-379.8)	07	2019	NN	AD	0.48	0.44	98.5 (100)
WH31_18	2459.6 (1557.4-3564.5)	734 (464.8-2806.2)	08	2019	NN	AD	0.34	0.33	79.8 (96.9)
WH31_18	2094.3 (1231.4-3182.7)	591.6 (347.8-2431.8)	09	2019	NN	AD	0.22	0.21	88.3 (99.9)
WH31_18	2324.2 (1596.4-3186.5)	578.8 (397.6-2598.5)	10	2019	NN	AD	0.3	0.24	96.3 (100)

A.2 Continued

BIRD	95% AKDE (km^2) (95% CI)	50% AKDE (km^2) (50% CI)	MO	YEAR	BR STATUS	Age	NDVI (95% AKDE)	NDVI (50% AKDE)	95% AKDE/Park overlap (%) (50% AKDE)
WH37_17 *	757.9 (551-997.2)	94.9 (69-834.8)	07	2017	NN	AD	0.52	0.58	97.8 (100)
WH37_17 *	9057 (5945.9-12812.4)	1677.8 (1101.5-10242.4)	08	2017	NN	AD	0.45	0.45	29.1 (48.9)
WH37_17 *	5488.4 (4348.3-6759.2)	662 (524.5-5903.7)	09	2017	NN	AD	0.3	0.31	32.8 (13)
WH41_17 *	2331.6 (1396.5-3502.4)	442.1 (264.8-2695.6)	07	2017	NN	AD	0.41	0.32	64.1 (92.4)
WH41_17	3695.6 (2233.1-5520.6)	745.7 (450.6-4263.9)	08	2017	NN	AD	0.34	0.31	50.5 (72.5)
WH41_17	3009.2 (1963.2-4275)	636.4 (415.2-3408.3)	09	2017	NN	AD	0.28	0.3	59.5 (89.2)
WH41_17	521.2 (390.5-670.6)	97.6 (73.1-569.5)	10	2017	NN	AD	0.21	0.22	93.5 (100)
WH41_18	81.3 (73.3-89.7)	5.8 (5.2-84.1)	07	2018	B	AD	0.33	0.23	100 (100)
WH41_18	96.2 (87.4-105.4)	7.8 (7.1-99.3)	08	2018	B	AD	0.29	0.2	100 (100)

A.2 Continued

BIRD	95% AKDE (km^2) (95% CI)	50% AKDE (km^2) (50% CI)	MO	YEAR	BR STATUS	Age	NDVI (95% AKDE)	NDVI (50% AKDE)	95% AKDE/Park overlap (%) (50% AKDE)
WH41_18	82.1 (75-89.6)	4.5 (4.1-84.6)	09	2018	B	AD	0.21	0.13	100 (100)
WH41_18	122.6 (111-134.8)	10.7 (9.7-126.7)	10	2018	B	AD	0.22	0.14	100 (100)
WH41_18	97.2 (87.3-107.6)	12.9 (11.6-100.6)	11	2018	NC	AD	0.2	0.15	100 (100)
WH41_18	49.3 (44.6-54.2)	7.8 (7.1-50.9)	12	2018	NC	AD	0.51	0.47	100 (100)
WH41_18	55.5 (50.1-61.1)	7.6 (6.9-57.3)	01	2019	NC	AD	0.63	0.61	100 (100)
WH41_18	74.9 (66.4-84)	8.9 (7.9-77.9)	02	2019	NC	AD	0.56	0.57	100 (100)
WH41_18	27.6 (25.1-30.2)	4.4 (4-28.4)	03	2019	NC	AD	0.54	0.56	100 (100)
WH41_18	31.8 (28.8-35)	6.2 (5.6-32.9)	04	2019	NC	AD	0.53	0.5	100 (100)
WH41_18	34.5 (31.4-37.7)	6.1 (5.6-35.6)	05	2019	NC	AD	0.43	0.41	100 (100)
WH41_18	45.9 (41.4-50.5)	6.9 (6.3-47.4)	06	2019	B	AD	0.4	0.35	100 (100)
WH41_18	40.3 (36.7-44)	2.4 (2.2-41.5)	07	2019	B	AD	0.35	0.3	100 (100)

A.2 Continued

BIRD	95% AKDE (km^2) (95% CI)	50% AKDE (km^2) (50% CI)	MO	YEAR	BR STATUS	Age	NDVI (95% AKDE)	NDVI (50% AKDE)	95% AKDE/Park overlap (%) (50% AKDE)
WH41_18	64.6 (58.5-71)	5.3 (4.8-66.7)	08	2019	B	AD	0.29	0.2	100 (100)
WH41_18	44.1 (39.7-48.7)	4.1 (3.7-45.7)	09	2019	B	AD	0.16	0.09	100 (100)
WH41_18	154.7 (138.6-171.7)	12.2 (11-160.4)	10	2019	B	AD	0.24	0.21	100 (100)
WH42_17	71.3 (64-79.1)	11.6 (10.4-73.9)	07	2017	B	AD	0.29	0.22	100 (100)
WH42_17	95.8 (86.5-105.6)	10.2 (9.3-99.1)	08	2017	B	AD	0.22	0.14	100 (100)
WH42_17	195.9 (173.9-219.2)	19.4 (17.2-203.7)	09	2017	B	AD	0.19	0.15	98.6 (100)
WH42_17	94.8 (85-105.1)	8 (7.2-98.2)	10	2017	B	AD	0.13	0.11	100 (100)
WH42_17	69.2 (60.5-78.5)	11.3 (9.8-72.3)	11	2017	B	AD	0.4	0.44	100 (100)
WH42_17	145.1 (117.6-175.4)	29 (23.5-155)	12	2017	NC	AD	0.57	0.57	100 (100)
WH42_17 *	1122.7 (797.8-1502.3)	123.2 (87.5-1244.2)	01	2018	NC	AD	0.59	0.61	78.1 (100)
WH42_17	1272.8 (779.3-1885.3)	272 (166.6-1463.9)	02	2018	NC	AD	0.48	0.53	95.8 (100)

A.2 Continued

BIRD	95% AKDE (km^2) (95% CI)	50% AKDE (km^2) (50% CI)	MO	YEAR	BR STATUS	Age	NDVI (95% AKDE)	NDVI (50% AKDE)	95% AKDE/Park overlap (%) (50% AKDE)
WH42_17 *	2772.2 (1750-4025.8)	430.2 (271.6-3165.3)	03	2018	NN	AD	0.56	0.56	70.1 (100)
WH44_17	314.5 (241.7-396.8)	68.4 (52.6-341.2)	07	2017	NN	SA	0.33	0.26	96.4 (100)
WH44_17	240.8 (180.3-309.9)	54.4 (40.7-263.1)	08	2017	NN	SA	0.33	0.31	99 (100)
WH44_17	1155.7 (669.9-1771.9)	215.4 (124.8-1346.3)	09	2017	NN	SA	0.29	0.29	83.8 (99)
WH44_17	2550.3 (1157.4-4484)	716.4 (325.1-3128.3)	10	2017	NN	SA	0.18	0.18	93.9 (100)
WH44_17	1835.3 (1009.3-2904.2)	434.3 (238.9-2163.4)	11	2017	NN	SA	0.41	0.36	95.8 (100)
WH44_17	1799.4 (1066.3-2721.1)	475.9 (282-2085.5)	12	2017	NN	SA	0.46	0.47	0 (0)
WH44_17	6208.5 (2522.2-11526.1)	1499.8 (609.3-7776.4)	01	2018	NN	SA	0.57	0.6	0 (0)
WH88_16	1088.1 (821.8-1391.2)	224.2 (169.3-1186.2)	07	2016	NN	JUV	0.37	0.3	99.4 (100)

A.2 Continued

BIRD	95% AKDE (km^2) (95% CI)	50% AKDE (km^2) (50% CI)	MO	YEAR	BR STATUS	Age	NDVI (95% AKDE)	NDVI (50% AKDE)	95% AKDE/Park overlap (%) (50% AKDE)
WH88_16	1094.6 (842.6-1379.1)	260.5 (200.5-1187)	08	2016	NN	JUV	0.31	0.35	91.6 (100)
WH88_16 *	2078.8 (1559.9-2671.1)	541.2 (406.1-2270.3)	09	2016	NN	JUV	0.19	0.2	88.8 (100)
WH88_16	1663.5 (1186-2220.5)	380 (270.9-1841.9)	10	2016	NN	JUV	0.24	0.26	94.5 (100)
WH88_16	1556.3 (1066.2-2137.6)	414.1 (283.7-1741.2)	11	2016	NN	JUV	0.25	0.18	99.1 (100)
WH88_16	2279 (1701.6-2939.4)	556.5 (415.5-2492.3)	12	2016	NN	JUV	0.36	0.35	87.5 (99.8)
WH88_16	1278.7 (923.6-1690.6)	322.9 (233.2-1411)	01	2017	NN	JUV	0.53	0.43	100 (100)
WH88_16	859.9 (621.3-1136.7)	165.8 (119.8-948.8)	02	2017	NN	JUV	0.5	0.49	100 (100)
WH88_16	227.2 (172.1-289.7)	34.1 (25.8-247.4)	03	2017	NN	JUV	0.48	0.52	100 (100)

A.2 Continued

BIRD	95% AKDE (km^2) (95% CI)	50% AKDE (km^2) (50% CI)	MO	YEAR	BR STATUS	Age	NDVI (95% AKDE)	NDVI (50% AKDE)	95% AKDE/Park overlap (%) (50% AKDE)
WH88_16 *	930.8 (694.3-1201.5)	161.7 (120.6-1018.3)	04	2017	NN	JUV	0.53	0.48	100 (100)
WH88_16	1579.4 (936.7-2387.3)	327 (193.9-1830.2)	05	2017	NN	JUV	0.54	0.4	93.4 (100)
WH88_16	1399.2 (911.1-1990.4)	226.8 (147.7-1585.5)	06	2017	NN	JUV	0.46	0.35	99.2 (100)
WH88_16	1068.4 (715-1491.8)	212 (141.9-1202.5)	07	2017	NN	JUV	0.33	0.32	98.6 (100)
WH88_16	1422.6 (993.3-1927.7)	291.3 (203.4-1583.8)	08	2017	NN	SA	0.32	0.3	87.1 (100)
WH88_16	1205.9 (895.8-1561.5)	162.5 (120.7-1320.7)	09	2017	NN	SA	0.28	0.28	98.7 (100)
WH88_16	1313.5 (808-1939.9)	326.9 (201.1-1509.1)	10	2017	NN	SA	0.18	0.18	89.8 (98.3)
WH88_16 *	1195.6 (798.7-1671.2)	291.9 (195-1346.2)	11	2017	NN	SA	0.41	0.39	94.6 (100)

A.2 Continued

BIRD	95% AKDE (km^2) (95% CI)	50% AKDE (km^2) (50% CI)	MO	YEAR	BR STATUS	Age	NDVI (95% AKDE)	NDVI (50% AKDE)	95% AKDE/Park overlap (%) (50% AKDE)
WH88_16	1557.2 (1097.9-2095.4)	312.3 (220.2-1729.2)	12	2017	NN	SA	0.52	0.47	96 (100)
WH88_16	1535 (1177.8-1938.8)	379.8 (291.4-1666.1)	01	2018	NN	SA	0.54	0.44	98.5 (100)
WH88_16	1039.8 (636.1-1541.1)	214 (130.9-1196.2)	02	2018	NN	SA	0.42	0.38	98.5 (100)
WH88_16	601.8 (460.2-762)	95.1 (72.7-653.8)	03	2018	NN	SA	0.46	0.41	100 (100)
WH88_16 *	3713.2 (2632.5-4976.9)	620.8 (440.1-4117.5)	04	2018	NN	SA	0.51	0.4	67.3 (100)
WH88_16 *	4006.7 (2556.2-5777.8)	612.1 (390.5-4563)	05	2018	NN	SA	0.52	0.41	65.2 (100)
WH88_16	1847.3 (1333.8-2443.2)	241 (174-2038.6)	06	2018	NN	SA	0.48	0.39	86.3 (100)
WH88_16	767.9 (516.7-1068.1)	196.8 (132.4-863.1)	07	2018	NN	SA	0.41	0.39	98 (100)

A.2 Continued

BIRD	95% AKDE (km^2) (95% CI)	50% AKDE (km^2) (50% CI)	MO	YEAR	BR STATUS	Age	NDVI (95% AKDE)	NDVI (50% AKDE)	95% AKDE/Park overlap (%) (50% AKDE)
WH88_16	2221.8 (1485.1-3104.6)	488.4 (326.5-2501.4)	08	2018	NN	SA	0.37	0.38	83.8 (100)
WH88_16	2164.6 (1431.4-3046.9)	592.2 (391.6-2443.4)	09	2018	NN	SA	0.26	0.26	97.7 (100)
WH88_16	170.5 (140-203.9)	21.6 (17.7-181.5)	10	2018	NN	SA	0.32	0.34	100 (100)
WH88_16	1512 (1039.1-2072.2)	381.5 (262.2-1690.2)	11	2018	NN	SA	0.24	0.2	95.8 (100)
WH88_16	3043.3 (2133.2-4112.6)	850 (595.8-3384.7)	12	2018	NN	SA	0.5	0.41	83.6 (100)
WH88_16 *	1217.7 (911.7-1567.2)	244.6 (183.2-1330.7)	01	2019	NN	SA	0.55	0.47	99.7 (100)
WH88_16	539.5 (382.6-722.9)	144.5 (102.5-598.1)	02	2019	NN	SA	0.49	0.5	100 (100)
WH88_16	751 (372.4-1260)	179.7 (89.1-904.9)	03	2019	NN	SA	0.37	0.34	100 (100)
WH88_16	3332.1 (2186.6-4714.9)	700 (459.4-3768.5)	04	2019	NN	SA	0.48	0.31	83.7 (100)

A.2 Continued

BIRD	95% AKDE (km^2) (95% CI)	50% AKDE (km^2) (50% CI)	MO	YEAR	BR STATUS	Age	NDVI (95% AKDE)	NDVI (50% AKDE)	95% AKDE/Park overlap (%) (50% AKDE)
WH88_16 *	3100.6 (2333.6-3975)	637.1 (479.5-3383.5)	05	2019	NN	SA	0.43	0.39	60.6 (86.1)
WH88_16 *	2538.7 (1820.8-3374.1)	478.4 (343.1-2806.6)	06	2019	NN	SA	0.46	0.51	80.7 (86.9)
WH88_16 *	5655.9 (4007.3-7584)	1283.3 (909.2-6272.7)	07	2019	NN	SA	0.43	0.42	55 (97.4)
WH88_16	6972.4 (4217.5-10408.5)	1554.3 (940.2-8042.4)	08	2019	NN	SA	0.33	0.35	49.3 (99.2)
WH88_16	3422.8 (2194.9-4919.2)	986.6 (632.6-3893.3)	10	2019	NN	SA	0.3	0.29	86.1 (100)
WH88_16	3451.2 (2314.6-4811.3)	688.2 (461.5-3882.1)	09	2019	NN	SA	0.22	0.22	80.8 (100)

A.3 Summary of White-headed Vulture home range (HR) and core range (CR) AKDE estimates for each individual. Averages and standard errors for both home range and core range estimates are presented along with ranges for each AKDE metric.

INDIVIDUAL	N (MONTHS)	MEAN HR (±SE)	HR RANGE	MEAN CR (±SE)	CR RANGE
WH24_17	9	169 (±46)	15-407	41 (±12)	1-99
WH24_18	8	1041 (±359)	18-2487	235 (±87)	3-571
WH25_17	5	2231 (±513)	436-3234	612 (±139)	122-892
WH27_18	16	299 (±119)	18-1485	32 (±14)	3-179
WH29_18	16	86 (±20)	11-271	9 (±1)	3-21
WH31_18	16	2341 (±579)	352-10179	551 (±122)	59-2092
WH37_17	3	5101 (±2404)	758-9057	812 (±463)	95-1678
WH41_17	4	2389 (±682)	521-3696	481 (±142)	98-746
WH41_18	16	69 (±10)	28-155	7 (±1)	2-13
WH42_17	9	649 (±309)	69-2772	102 (±50)	8-430
WH44_17	7	2015 (±767)	241-6209	495 (±190)	54-1500
WH88_16	40	1935 (±223)	171-6972	420 (±51)	22-1554

APPENDIX B

Movement Patterns Supplemental Information

B.1 Summary of number of daily trajectories included in analyses and tracking start and end dates for individual White-headed Vultures (WH) and White-backed Vultures (WB) from Gorongosa National Park, Mozambique.

SP	ID	DAILY TRAJECTORY COUNT	START DATE	END DATE
WH	WH88_16	805	2016-07-01	2020-04-10
WH	WH25_17	64	2017-07-01	2017-12-04
WH	WH37_17	23	2017-07-01	2017-08-18
WH	WH41_17	26	2017-07-01	2017-10-27
WH	WH42_17	178	2017-07-01	2018-04-12
WH	WH44_17	40	2017-07-02	2017-11-27
WH	WH24_17	118	2017-07-03	2018-04-16
WH	WH24_18	143	2018-07-01	2019-03-14
WH	WH29_18	415	2018-07-01	2020-04-07
WH	WH41_18	420	2018-07-01	2020-01-02
WH	WH27_18	580	2018-07-02	2020-04-08
WH	WH31_18	502	2018-07-02	2020-04-07
WB	WB43_16	36	2016-07-01	2016-10-14
WB	WB40_16	78	2016-07-03	2017-02-02
WB	WB32_16	143	2016-07-08	2018-07-27
WB	WB36_16	103	2016-07-12	2017-08-11
WB	WB90_16	33	2016-07-15	2016-11-02
WB	WB30_18	165	2018-07-02	2019-12-22
WB	WB36_18	24	2018-07-09	2018-10-04
WB	WB39_18	187	2018-09-01	2020-02-18
WB	WB40_18	107	2019-09-10	2020-03-21