Exploring the use of GPS-tracking to investigate the diet of African vultures

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Abstract

Vultures are highly mobile scavengers that cover vast distances on their daily foraging trips. Vultures display specific spatial and behavioral patterns when feeding on carcasses, and these behaviors are potentially identifiable in the tracks of geographical positioning system (GPS)-tagged birds. Thus, by applying algorithms to classify their movements it may be possible to create a carcass detection system using these spatial signatures. In this study I applied this approach to explore its efficiency in detecting carcasses and describing the diet of 12 GPS-tagged vultures in Botswana. I tracked five resident vulture species in Botswana using GPS-trackers, these were: Cape Vulture (*Gyps coprotheres* n=2), Hooded Vulture (*Necrosyrtes monachus* n=2), Lappet faced Vulture (*Torgos tracheliotos* n=2), African White-backed Vulture (*Gyps africanus* n=4) and the White-headed Vulture (*Trigonoceps occipitalis* n=2). I attempted to search as many as possible of the feeding sites identified by the algorithms between January and June 2022. These potential feeding events were ground-truthed to confirm carcass presence. At each investigated site, any carcass found was identified down to species level. The ground-truthed sites constituted 22% (n=109) of all potential feeding sites identified within the study time frame (n=494). Carcasses were recorded at 62% (n=67) of these investigated sites. Carcasses associated with feeding events from all vulture species were located, except for Hooded Vultures. For this species only one site was checked, with no carcass found. At vulture feeding sites, carcasses from a total of ten taxa were identified. These were mainly wild ungulates (84%) with livestock making up a far lower proportion (16%) comprising of cattle (*Bos taurus*) and donkey (*Equus asinus*). Elephant (*Loxodanta africana*) was the most frequently identified taxon in the carcasses (31%; n=21) and was found at feeding sites of all four vulture species. Although sample sizes were relatively small for each species, it appeared that livestock was recorded only at Lappet-faced and White-backed Vulture investigated sites. Furthermore, Cape and White-headed Vultures had wildlife mostly giraffe and elephant at their investigated sites.

Potential feeding events were ground-truthed on average 8 ± 8.35 days after the initial identification of the feeding event. The likelihood of detecting a carcass at these sites declined significantly with the amount of time lapsed from initial identification. The intercept of this

relationship suggested that at the time of initial identification there was an 85% chance of detecting a carcass. Vegetation biomass at the sites, and the vulture species involved, had no influence on the likelihood of detecting a carcass.

My study, on the application of GPS-tracking to understand the diet of a sample of African vultures in Botswana suggests that this technique is a useful approach but requires substantial resources in terms of personnel to investigate the identified feeding events as soon as these events are triggered, to derive a sufficient sample size to characterize the diets of these different vulture species.

Acknowledgements

“Without whose help the project would not have materialized”

Firstly, I would like to thank God for making it all happen like this. This have been a mystery revealed to me. Now I can say that I see it.

I then would like to thank my supervisors, Associate Professor Arjun Amar, Dr Gareth Tate and Dr Glyn Maude for their patience and guidance in various parts of my dissertation and field work. This have been a grateful time working under your supervision.

Would also like to thank the Botswana Wild Bird Trust for their belief in me and financial support throughout my studies. I am grateful of all the support you offered and would like to share that I can confidently articulate conservation issues better and with ease. I foresee our relations going far.

It gives me pleasure to also thank the Government of Botswana through the Department of Wildlife and National Parks as they granted me a “sabbatical leave”, thus allowing me to further my studies. Because of your support, I am now a robust “Conservation Biologist” ready to contribute to the environmental management body of knowledge and influence conservation decision making in Botswana.

My family and friends have been that pillar of strength through this endeavour. I would like to thank them for all their efforts which they invested in me, especially when I was down. To my wife and kids, “I love you all and dedicate this piece of writing to you”. To a classmate and a special friend “Ricardo Guta”, who passed away few days before our graduation day, I will always cherish the short time we had together.

To all those I didn’t mention by name, especially the different organizations and individuals who assisted during ground truthing of sites, I would like to let you know that I wouldn’t have made it without you. Therefore, I salute you.

Introduction

Various measures have been proposed to reduce current biodiversity loss (Turner et al., 2007; Wilson et al., 2006). These, nevertheless, have achieved minimal positive results in recent years (Butchart et al., 2010), with populations of many wildlife species still declining rapidly (Dirzo et al., 2014; WWF, 2020). Studies show that larger species tend to be more at risk of extinction than smaller species, as they appear less resilient to environmental changes (Cardillo et al., 2000; Ripple et al., 2017). Losing such keystone species from the environment can have far reaching and cascading affects (Cunningham et al., 2018; Estes et al., 2011).

Raptors are amongst those animal species which are declining most rapidly. McClure et al., (2018), assessed the trends of all raptors species, and found that Old World Vultures were showing declines in their conservation status at a far higher rate than other bird species. These declines are a cause for concern, as vultures play a pivotal role in the environment, offering an important ecosystem service by feeding on carrion and waste, likely reducing the spread of disease associated with these carcasses (Gangoso et al., 2013) and shaping the community of facultative scavengers (Kane et al., 2014; Buechley and Şekercioğlu 2016; Selva and Fortuna 2007; Morales-Reyes et al., 2017).

In Africa, vulture populations are declining rapidly, with some populations declining as much as 95% over the last 20 years (Krüger et al., 2014; Leepile et al., 2020; Ogada et al., 2016; Virani et al., 2011) . Their decline has been attributed to multiple factors, principally intentional and unintentional poisoning (Monadjem et al., 2018; Murn and Botha 2018; Loveridge et al., 2019; Ogada, Botha, and Shaw 2016, Leepile 2020) as well as electrocution and collisions with powerlines (Jenkins et al., 2010; McKean et al., 2018; Roxburgh and McDougall, 2012). Given this decline, it's important to understand the resource requirements for different vulture species to help with their conservation. Understanding how specific vulture species utilize available habitat and resources, may help develop and inform guided mitigative measures to curb the ongoing species declines (Bergman et al., 2006; Bridge et al., 2013; Fraser et al., 2018; Katzner and Arlettaz, 2020). More specifically, it is important to understand the habitat (eg. nesting habitats, foraging habitats) and food resource requirements for vultures.

Because of their population declines, vultures have more recently had a higher number of studies conducted on them (Koenig, 2006). Much of this research has been focused on habitat use (Kane et al., 2014; Kane et al., 2016), movement patterns and breeding success (Alarcón and Lambertucci, 2018; Goikantswemang et al., 2021; Pfeifer et al., 2015; Reading et al., 2019a). Although there have been some studies on their foraging ecology and movement patterns, these have been mainly focusing on supplementary feeding stations and individuals in captivity (Cortés-Avizanda et al., 2016; Jobson et al., 2021; Sahu et al., 2010) or on the relationships and interactions between different species at feeding sites (Kendall et al., 2012). However, there have been relatively few studies exploring vulture food resource requirements in the wild. This may be due to the difficulty in studying this topic. For example, Kane et al., (2015) explored abundance of vulture food provided by wild ungulates and highlighted the potential importance of supplementary feeding stations for some populations. Other studies have investigated food brought back to the nest, for example, Margalida et al., (2009) studied the diet of Bearded Vultures (*Gypaetus barbatus*) from observations made at the nest. Unlike other vultures, these species carry prey remains to the nest with their feet and bill and do not feed their young by regurgitation (Brown· and Plug, 1990; Margallda and Bertran, 2000). Cabrera García et al., (2020) and Karimov and Guliyev, (2017) investigated the diet of vultures through prey remains at the nest. However, for species which regurgitate food to their young, more conventional methods of studying diet are challenging (Tauler-Ametller et al., 2018).

Arkumarev et al., (2020) overcame these difficulties by studying the diet of Eurasian Griffon Vulture (*Gyps fulvus*) using geographic positioning system (GPS) backpack trackers in Bulgaria and Greece to identify feeding locations and quantify their diet. Their study identified 13 taxa in the diet of the study species. Livestock was recorded as representing majority of their diet, with predation by mammals (Grey Wolves *Canis lupus*, Golden Jackals *Canis aureus*, or Feral Dogs *Canis lupus familiaris*) identified as the main cause of mortality of their prey (Arkumarev et al., 2020). Understanding the relative importance of domestic versus wild ungulates in vulture diet is particularly important for African vulture conservation, not least because it can reveal the route by which toxic chemicals may become available or exposed to vultures. If domestic animals are more important food sources, then veterinary drugs will be important to regulate. Whereas if wild ungulates form majority of vulture diets, then other pollutants and pressures may be more relevant, for example, lead (Pb) ammunition from wild ungulates that have been shot by hunters (Avery and Watson, 2009; Hankook, 2010; Bradley and Maude, 2014; Kruger and Amar, 2018; Garbett et al., 2018). Further, if prey is killed naturally through predation, this would stress the importance of the healthy predator populations in a system. In another study, Arkumarev et al., (2021), used this same approach to explore the reliance of vultures on supplementary food vs wild food. They found that wild food was far more important to this population, but that the importance varied seasonally between the breeding and non-breeding season. These studies suggest that the use of GPS tracking may be a useful method with which to explore food requirements of vultures.

In this study, I explore the application of GPS-tracking technology to investigate the diet of several vulture species in Botswana. I assess the feasibility of using tracking information to study the diet of vultures in an African context, which may be very different to the situation in Europe (Arkumarev et al., 2020, 2021), given the differing diversity of potential prey, habitat and scavengers. I used data from five vulture species which were GPS tagged. These were the Cape Vulture (*Gyps coprotheres*), Hooded Vulture (*Necrosyrtes monachus*), Lappet-faced Vulture (*Torgos tracheliotos*), African White-backed Vulture (*Gyps africanus*) (hereafter referred to as White-backed Vulture) and White-headed Vulture (*Trigonoceps occipitalis*). Locations categorized as a potential feeding site from the movement behavior were then ground-truthed. I explored whether the likelihood of detecting a carcass at a potential vulture feeding site varied based on the time between initial identification of a feeding event and ground-truthing that site, the plant biomass (NDVI) at the investigated site and the species of vulture involved.

I hypothesized that the likelihood of finding a carcass at ground-truthed sites may be influenced by i) the time elapsed between initial identification and when it is checked, ii) the lushness of the vegetation at a site, and iii) the species of vulture that identified the site. I predicted that the likelihood of finding a carcass would decreases with increasing time lapsed between initial identification of a potential feeding event and ground-truthing the site. I furthermore predicted that carcasses at lusher vegetation (i.e. higher NDVI) may be less detectable during ground truthing. I also predicted that the likelihood of finding a carcass might differ between different vulture species if the size and types of carcasses that they feed on differed.

Methods

Study area

Botswana lies between 18° to 26° South and 20° to 28° East, it is a landlocked country bordering with Namibia on the west, Zambia on the north, Zimbabwe on the east and South Africa to the south. It is a semi desert area with an average annual precipitation ranging from 200 to 500mm (MENT, 2019). The southwestern part of the country is the driest, often receiving only ca. 100mm of rainfall per year (Nkemelang et al., 2018). Botswana has hot and wet summers with cold and dry winters. Rainfalls mainly between November to April.

The land tenure system in Botswana is broadly split between state, communal and freehold land (Figure 1). State land covers mainly the protected areas such as the game reserves, national parks and the wildlife management areas (WMA) which act as buffer zones between protected areas and the communal land. Communal land is used by the local communities as range lands to rear livestock, other agricultural projects and as well as for home steads. The freehold land is mostly found along the eastern part of the country which are mainly privately owned game and cattle ranches, and surrounding the Ghantsi township in the western part of the country.

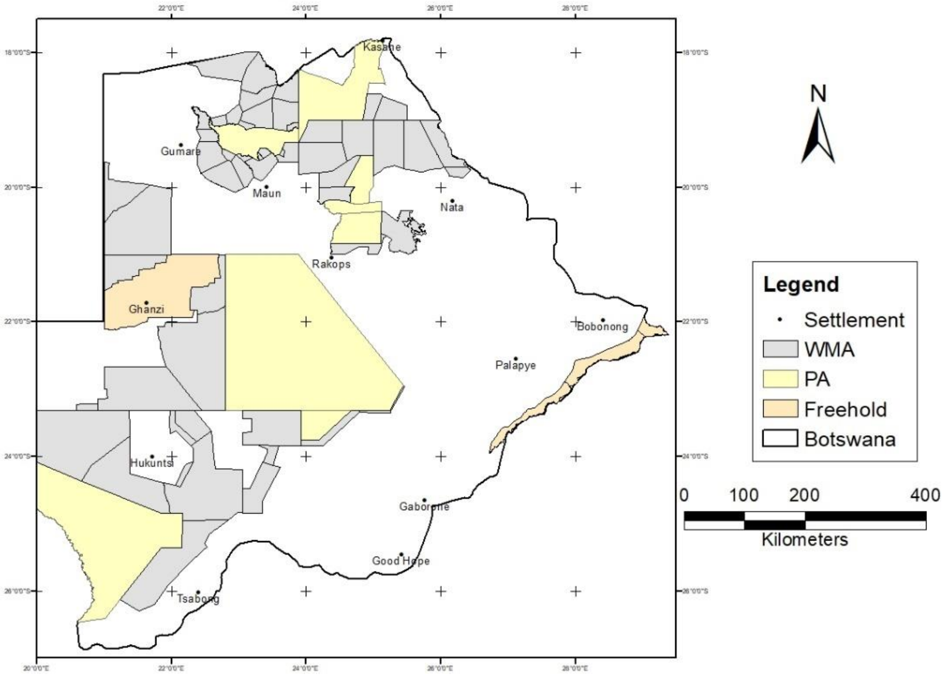

Figure 1: A map of Botswana showing the different land tenure systems and some major settlements used as communal rangelands.

Study species

There are five breeding resident vulture species which occur in Botswana all of which were tracked as part of this study. These are the Cape vulture, Hooded Vulture, Lappet-faced Vulture, White-backed Vulture, and the White-headed Vulture (Borello and Borello, 2002; Davies and Virani, 2013; Garbett, 2018; Reading et al., 2019b). All the species are threatened by extinction. The Global conservation status of these species are as follows: Cape Vulture (Vulnerable), Lappet-faced Vulture (Endangered), Hooded Vulture (Critically Endangered), White-backed Vulture (Critically Endangered) and the White-headed Vulture (Critically Endangered) (Birdlife International, 2021a, 2021b, 2021c, 2021d, 2017). The Botswana Wildlife Conservation and National Parks Act of 1992 also recognizes all these species as globally threatened and advocates for their protection (MENT, 1992).

Bird capturing and GPS tagging

The sample vulture individuals for this study were captured and GPS tagged by a non-governmental organization called Raptors Botswana. They trapped the birds across Botswana between 2020 and 2022 at locations specified in Figure 2(a). To capture some individuals, they used the noose strings set around small bait sites (Bloom et al., 2007) or carcasses whilst to capture other individuals, they used a compressed-air canon net (Netblaster, WCS NetBlaster™, Wildlife Control Supplies, East Granby, CT 06026, USA) installed near a fresh carcass (Bamford et al., 2009; Garbett et al., 2018). They fitted the birds with either 48g solar-powered Iridium GPS/Satellite tracking units (Solar Bird Flight Tracker, Intricode Solutions, Cape Town, South Africa), or 70g GPS PTT-100 tags (Microwave Telemetry Inc., Maryland, USA) using a backpack harness made from 8mm Teflon ribbon (Bally Ribbon Mills, Bally, PA, USA) as per the IUCN Vulture Specialist Group Guidelines. The GPS backpack trackers weight ranged between 2.6-3.8% of the average weight of targeted vulture species, this falls within the ethically approved weight for loggers (i.e. <5% of the species total weight; Wilson and McMahon, 2006). The tracking units were recording GPS fixes on hourly basis and were accurate to within 1-15m.

Tracking data processing

The GPS tracking data was collected from 27 April 2020 to 30 June 2022. The GPS units were set to deposit tracking data once a day on MoveBank (www.movebank.org). All GPS tracking data processing was done in R (R Core Team, 2022). There were some preliminary processing which was done to standardize the data for all birds, firstly ensuring that only hourly fixes (GPS tracking locations) were used. Extreme outlier locations were removed, which for example required the bird to travel more than 150Km between two fixes. Distance between points was calculated using the *distm* function in the package "geosphere" (Hijmans, 2021).

Activity Clusters: Determining and classifying potential feeding events and other activity.

After a full year of tracking data was collected, the most recent tracking data was imported from MoveBank into R weekly, the data was then subset into 0-7-day, 8-14-day, 15-31-day, 32-180-day and >181-day time interval windows starting from the current day of each data download. For activity detection and classification, I only used tracking data from positions recorded between dawn and dusk and only those fixes that corresponded to stationary vultures. To calculate dawn and dusk times the *crepuscule* function in the package "maptools" (Bivand and Lewin-Koh, 2022) was used. To identify periods in which the vultures were stationary, I analyzed the instantaneous speed readings provided by the GPS units. For tracking units that were not able to record speed readings, I used GPS points that were <15m apart, coupled with a change in altitude (Δ altitude) of 0≤ 5m, filtering for birds that were holding a stable elevation between fixes. Using the most recent 0-7-day window data subset, I looked for clustering in movement data using the *hclust* function in the package "stats" (R Core Team, 2022) and a 500 m distance threshold. The function categorizes clusters using the differences in objects being clustered. To begin with, each of the objects will have its own cluster, then the algorithm will repeat the sequence of operation ascertaining that two most similar clusters are joined together. This process will continue until all clusters joins together to be one cluster. Depending on the clustering method used, the Lance-Williams dissimilarity update formula was used to recalculate the distances between clusters at each stage.

To verify that all possible clusters were identified, a parallel cluster identification analysis was run to calculate recursions by passing all GPS tracked individuals through the activity cluster polygons using the *getRecursions* function in the “recurse” package; and using a K-Means clustering method to cluster the coordinates of the top 20% of locations by number of revisits for all birds combined. This can be useful for finding locations that are important across the population (i.e., watering holes, feeding sites, or foraging areas) versus to a single individual (Bracis et al., 2018). Differences in clustering techniques were

determined by mapping all cluster outputs and visually examining for disparities. Differences in clustering techniques were minimal for this study and application and thus only used the *hclust* method.

Once activity clusters were established for the 0–7-day subset, then the centroids for each cluster were calculated using the *gCentroid* function in “rgeos” and computed 500 m circle buffers around the centroids to capture all points of the cluster. The circular buffers were then converted to multi-part polygons using the *st_cast* function in “sf” (Pebesma, 2018). I then calculated revisitation metrics and residence time (i.e number of revisits, entry and exit time, time inside the cluster, as well as species and number of birds present in the cluster) of these circular activity cluster polygons using the *getRecursionsInPolygon* function (Bracis et al., 2018). I then repeated the analysis for all other subset time windows, until the full length of the tracking data was passed through all activity cluster polygons. For this study, I used the revisitation combinations to activity clusters over the respective time windows to classify or predict the type of activity occurring at each cluster (see Table 1).

Using this approach, over the duration of this project, weekly activity clusters were identified and most importantly for this study, potential feeding sites. These were used for the field-based (ground-truthing) phase of the project.

Table 1: Potential revisitation combinations used to classify vulture activity clusters produced by GPS tracked vultures across Botswana. Of importance in my study was if a location was revisited within 7 days (and not again) or was revisited within 7 days and again between 8-14 days – that cluster of points was classified as a potential feeding site.

Revisitation					
Present in 0–7-day cluster	Present in 8-14-day cluster	Present in 15–31-day cluster	Present in 32–180-day cluster	Present in 181–365-day cluster	Predicted activity in activity cluster
1	0	0	0	0	**Feeding detected**
1	1	0	0	0	**Feeding detected**
1	1	1	0	0	Roost/Water/Supplementary Feeding site
1	1	1	1	0	Roost/Water/Supplementary Feeding site
1	1	1	1	1	Breeding site
1	0	1	0	0	Roost/Water/Supplementary Feeding site
1	0	0	1	0	Roost/Water/Supplementary Feeding site
1	0	0	0	1	Roost/Water/Supplementary Feeding site
1	0	0	1	1	Roost/Water/Supplementary Feeding site
1	0	1	1	1	Roost/Water/Supplementary Feeding site
1	1	0	1	0	Roost/Water/Supplementary Feeding site
1	1	1	0	1	Roost/Water/Supplementary Feeding site
1	0	1	0	1	Roost/Water/Supplementary Feeding site

Ground truthing potential feeding events sites

From January to June 2022, I aimed to ground-truth and verify as many potential feeding sites as possible. Each potential feeding site was examined on foot or from a light aircraft, where search and identification of any carcass remains at the locality was conducted. Searches were conducted within a radius of 100m from the potential feeding site location. Where possible the carcass species and cause for its death were recorded (e.g., poaching, lion kill, legal trophy hunting). Known supplementary feeding site locations were excluded from these searches and were identified using a different algorithm. Observers from three different groups were recruited to undertake the ground-truthing, these included teams from 1) tourism service operators (LODGES) e.g., nearby lodges, 2) workers from non-governmental organizations (NGO) e.g., Raptors Botswana staff, and 3) workers from the Department of Wildlife and National Parks (DWNP). The length of time elapsed between the initial identification of a potential feeding site (from the tracking data) and ground truthing was recorded.

Ground-truthed sites data mapping

I developed four maps, these were (1) a map showing locations of where the vultures were captured and GPS-tagged, (2) a map showing the location of where a carcass and no carcass was recorded, (3) a map showing location of where each vulture species might have been feeding at and (4) a map showing location of where each carcass species was recorded during site investigations. To develop the maps, I sourced Botswana data layers on districts, protected areas, wildlife management areas, major roads, and major settlements from MLMWSS, 2010; UNEP-WCMC and IUCN, 2022. The data layers were overlaid with ground truthed site locations in ArcMap 10.8.1 (ESRI, 2020). The investigated sites were grouped according to layers which overlaid with them. Findings at all investigated potential feeding sites were recorded. Carcasses found were recorded to species level. See Figure 2 below.

Estimation of vegetation biomass status at vulture feeding sites

To explore whether the probability of finding a carcass at a potential feeding site differed depending on the vegetation structure, I extracted information on the normalized difference vegetation index (NDVI) from each potential feeding site. The NDVI measures the greenness, which relates to the density of vegetation or biomass, in a specific area. This measure is achieved through the variation between visible and near-infrared reflectivity of vegetation (Lee et al., 2020). I extracted the NDVI from the raster file images acquired from Earth Explorer United States Geological survey government agency website. The images used were from Landsat 8 Operational Land Imager and Thermal Infrared Collection 2 Level-2 Science Products. The images had a 30 m-resolution. Data scenes were retrieved for time frame between March to June 2022, the time frame largely corresponds with when the ground truthing was undertaken. No image with cloud cover of more than 20% was used in deducing the NDVI. I retrieved band 4 (red) and band 5 (near Infrared), then processed them to facilitate extraction of the NDVI values from the single band product.

Data were added to and processed in ArcMap 10.8.1 (ESRI, 2020). Using the raster calculator under the spatial analyst tool map algebra, I estimated the NDVI for each land parcel within the sampled tile using formula:

$$\mathbf{NDVI} = \frac{\mathbf{B5-B4}}{\mathbf{B4+B5}}$$

From the output single layer band product, I extracted the indices values for all the potential feeding sites that were ground truthed. This was done using the extract multiple values to points spatial analyst tool. Each value was deduced from the layer which overlapped with respective GPS fixes (potential feeding coordinates point). Where a point occurred on two tiles which overlapped, the highest NDVI score was used as it represented the best vegetation health status at that point in time. These were used as the output measure of the vegetation greenness at each potential feeding site and were used in the analysis.

Data analysis

I was interested in exploring whether the probability of finding a carcass at a potential feeding site was influenced by 1) the time elapsed between the initial identification of a potential feeding site to the time it was ground truthed, 2) the vegetation biomass at the site and 3) the species of vulture for which the site was identified. I undertook a Generalized Linear Model (GLM), fitted with a binomial distribution with a logit link function with the response variable being a binary term of either finding (1) or not finding (0) a carcass at a ground truthed site and the three variables above included as explanatory fixed effect variables. I performed a backward stepwise selection procedure with the three terms (time elapsed, NDVI, and vulture species), where I removed the least significant term in sequence until only terms that were significant at the $P<0.1$ remained. Analyses of data collated was performed in R version 4.1.2 (R Core Team, 2022).

Results

Potential feeding sites that could be checked came from 12 individual GPS tagged vultures (although 16 vultures were tagged, all of which were used in the development of the algorithm, some had stopped sending GPS fixes prior to the ground truthing work which occurred from January to June 2022). Potential feeding sites visited came from only 8 individuals, with sites for 4 individuals not being investigated (see Table 2), because they were too remote with poor access roads and lacking potential site investigators. A total of 494 potential feeding sites were identified during the study period, of which 22% (n=109) were visited. One hundred sites were ground-truthed on foot, whilst nine sites were visited using a light aircraft. Other non-visited sites comprised of 78%, these were not visited because I was not able to find anyone to visit them, as they largely were too remote. Tourism service operators visited the highest proportion of sites (47%, n=51) followed by non-governmental organizations (38%, n=41), and then by staff from the Department of Wildlife and National Parks (15%, n=17)

White-headed Vultures had the most visits to potential feeding, which came from two birds (44 sites, 40% of sites), followed by White-backed Vultures, also from two birds (37 sites, 34% of sites), then Lappet-faced Vultures, whose sites came from only one bird (23 sites, 21% of sites) (Table 2). Only four sites were ground truthed for two Cape Vultures (4% of sites) and only one site from one Hooded Vultures (1 % of sites) (Table 2).

Table 2: Summary of the numbers and species of 12 tagged vultures used to ground truth and investigate diet, giving the number of sites investigated per individual bird, and the total number of carcasses recorded for each vulture species. Carcasses included all prey species recorded at visited vulture feeding sites.

Vulture Species	No. of individuals tagged	No. of Sites Investigated*	No. of carcasses found
Cape Vulture	2	1, 3	1
Hooded Vulture	2	1, 0	0
Lappet-faced Vulture	2	23, 0	14
White-backed Vulture	4	7, 30, 0, 0	24
White-headed Vulture	2	34, 10	28
Total	12	109	67

*Individuals separated by comma

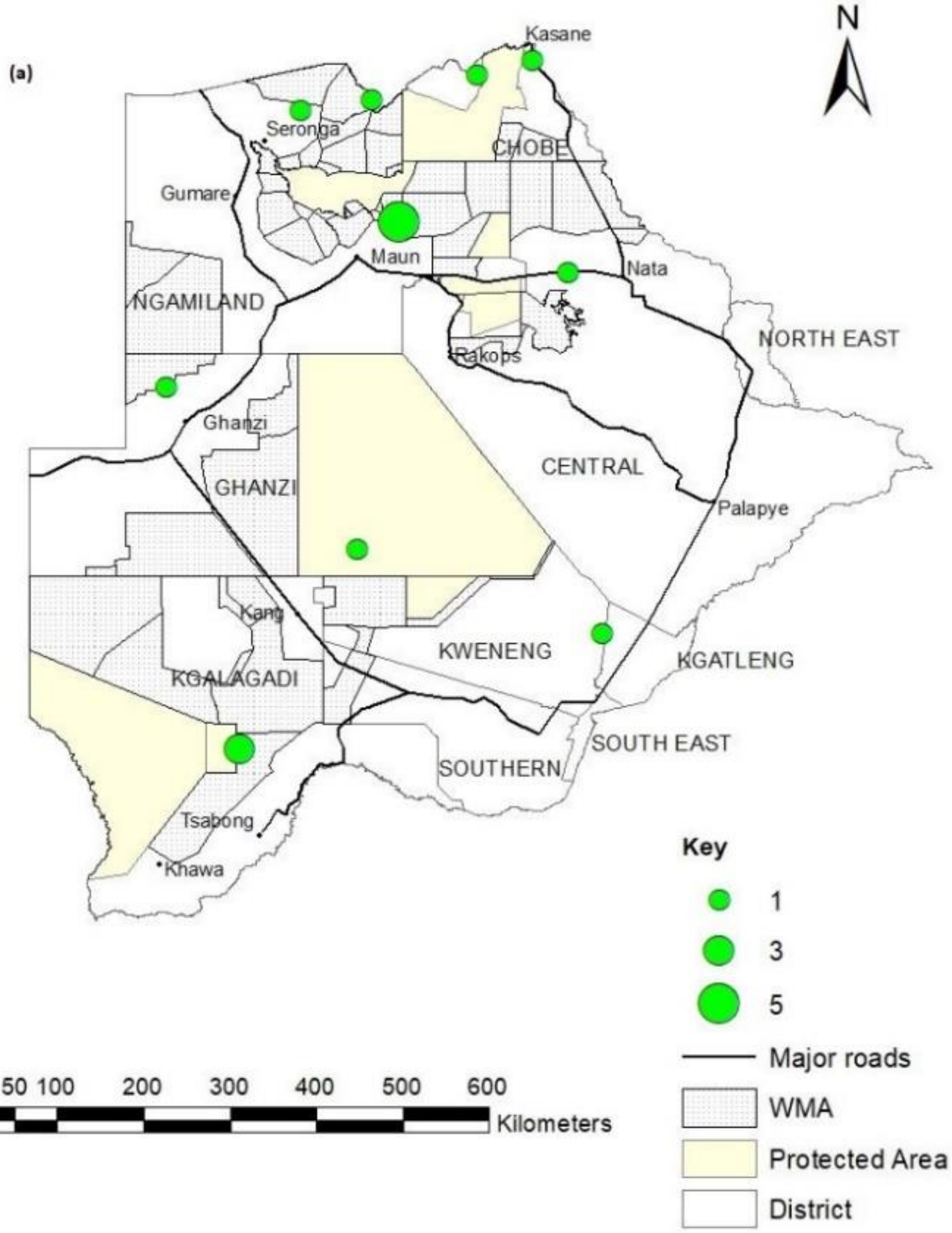

Figure 2(a): Maps of Botswana showing locations of the trapping and tagging sites for the 16 vultures, size of the point reflects the number of individuals tagged at that site. Map also show protected areas, the main districts, and some of the major roads within Botswana.

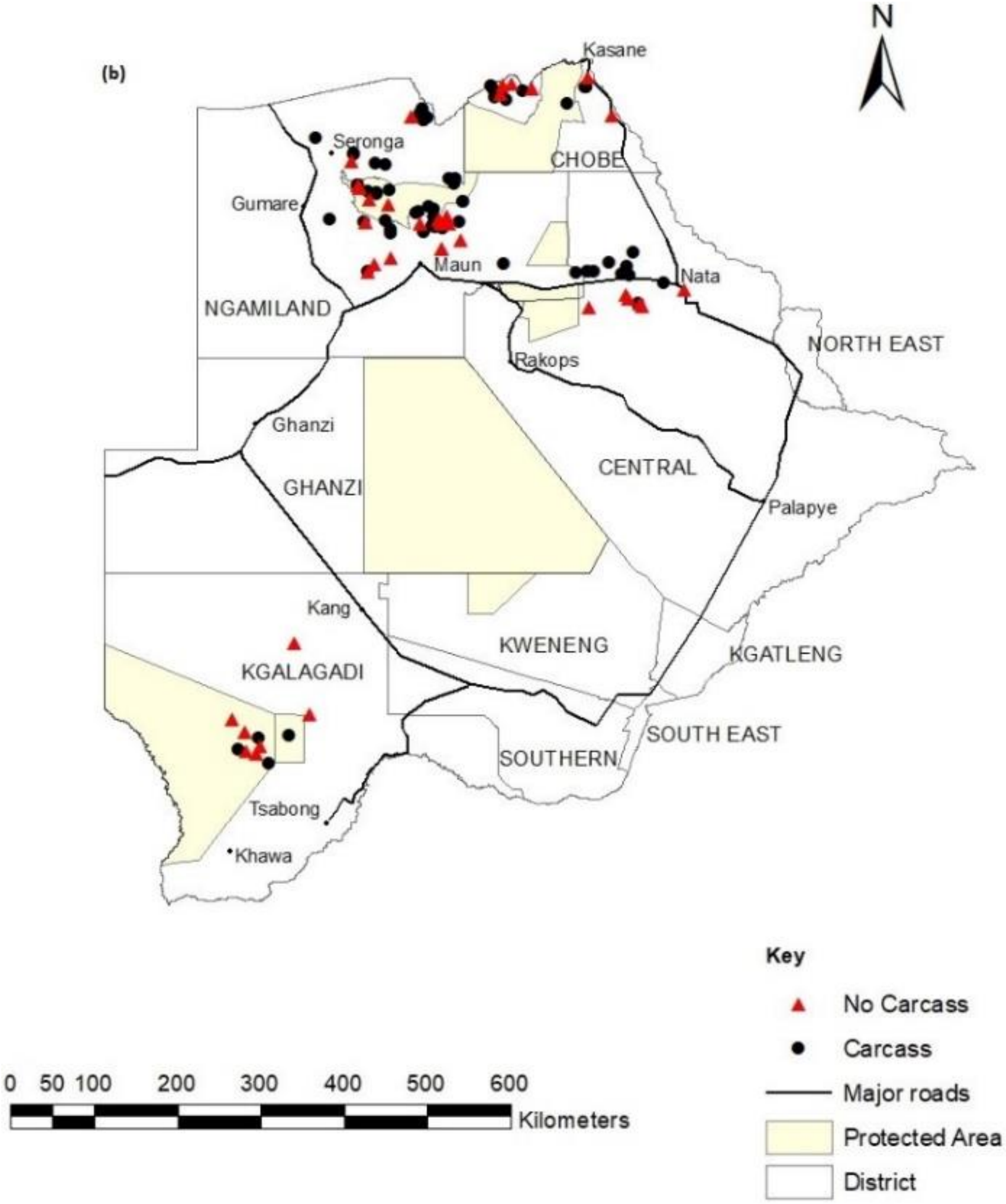

Figure 2(b): Maps of Botswana showing the ground truthed sites categorized according to whether i) a carcass was found or ii) no carcass was found. Map also show protected areas, the main districts, and some of the major roads within Botswana.

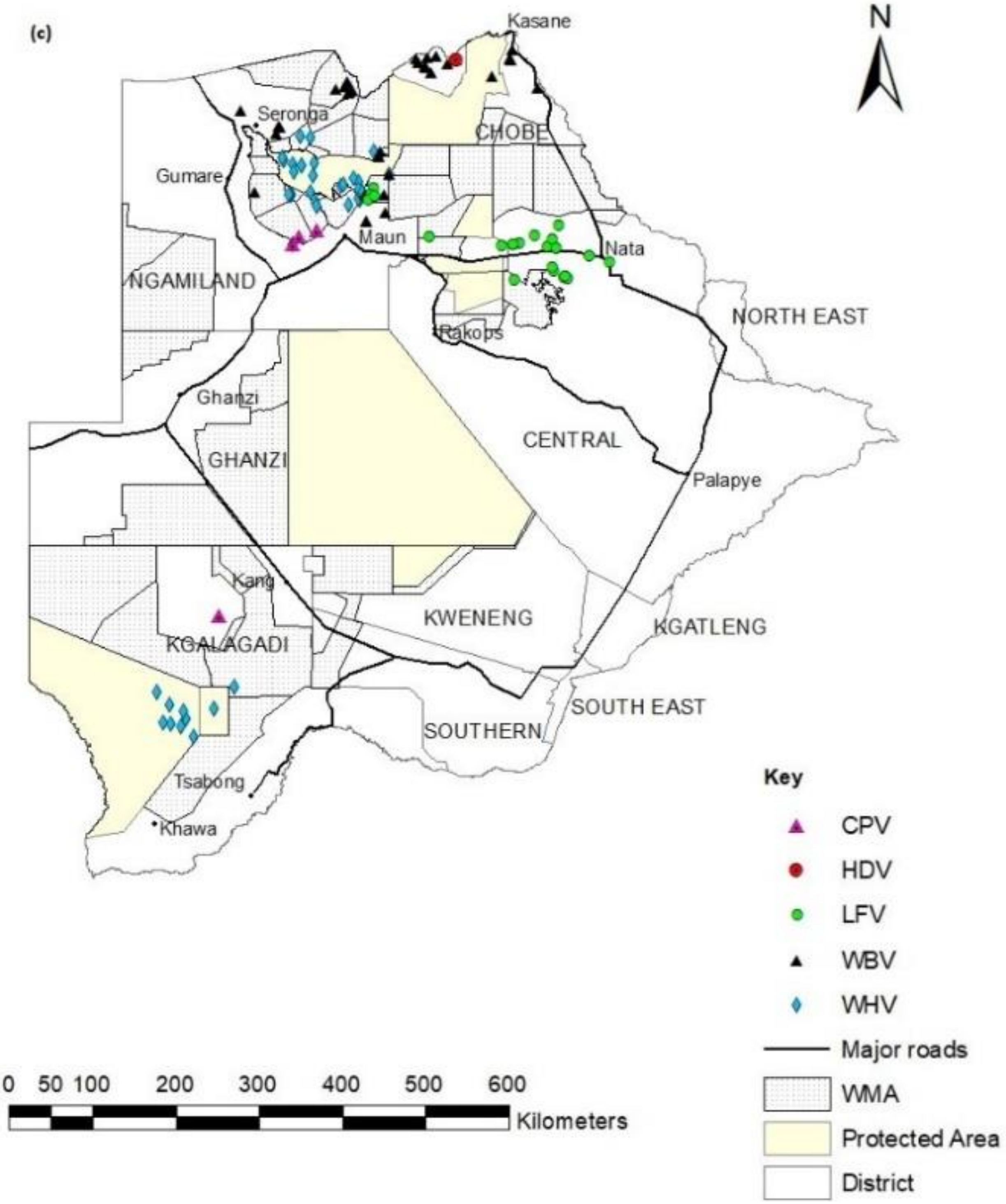

Figure 2(c): Maps of Botswana showing potential feeding events sites which were ground truthed for each vulture species. Map also show protected areas, the main districts, and some of the major roads within Botswana.

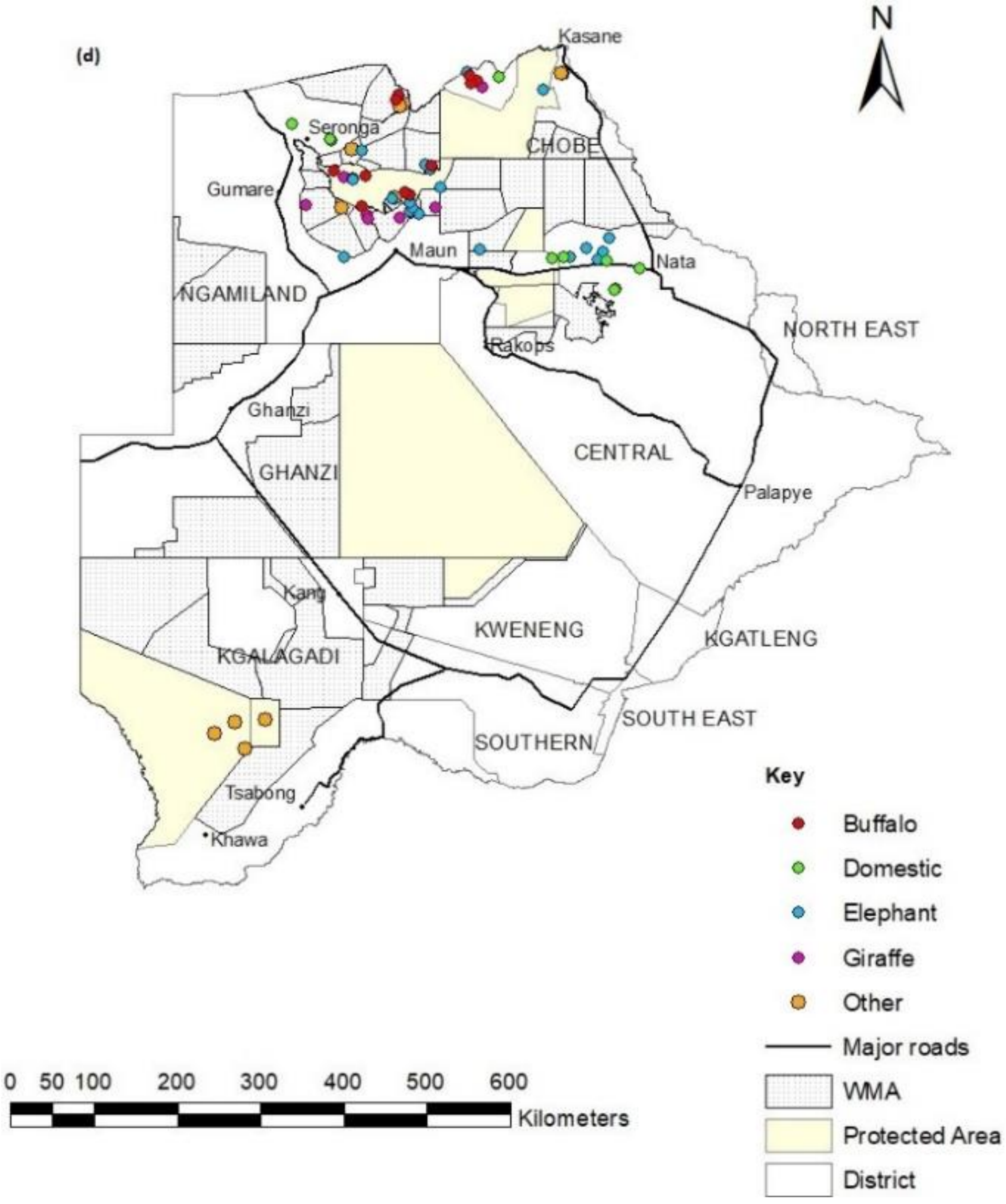

Figure 2(d): Maps of Botswana showing the ground truthed sites where ≥ 9 carcasses for each taxon were recorded. Domestic livestock constituted of cow and donkey. Other species consisted of eland, gemsbok, Impala, kudu and red lechwe. Map also show protected areas, the main districts, and some of the major roads within Botswana.

From the 109 ground truthed potential feeding sites, I found carcasses at 67 (62%). The ground truthed sites grouped into two clusters located in northern and southwestern Botswana (Figure 2(b)), with the majority (90%, n=98) in the northern cluster. For vulture species with more than 20 ground truthed sites, I explored the types of land where these sites were located (WMA, communal land, protected areas). For both Lappet-faced Vultures and White-backed Vultures most sites were in communal land, with 74% and 62% in this land type, respectively. In contrast, for White-headed Vultures most were in protected areas (54%) or WMA's (43%) with far less sites in communal areas (1%) (Figure 2(c)). Figure 3 reports on the relationship of finding a carcass with the significant term which was time elapsed from initial recording of potential feeding site to ground truthing it. The probability of finding a carcass at a potential feeding site reduced with an increase in the number of days that had elapsed between the initial identification of a site and when ground truthing occurred ($\chi^2_{1,107}$ = 22.285, P = 0.001) (Figure 3).

Based on the intercept of this relationship, it suggests that at day zero (when sites were originally identified) there was around about an 85% chance of finding a carcass at a potential feeding site. In contrast to this time period relationship, I found no evidence that either the vegetation biomass at a feeding site ($\chi^2_{1,108}$ = 0.006, P = 0.938), nor species of vulture involved ($\chi^2_{4,103}$ = 3.652, P = 0.455) influenced the probability of finding a carcass at potential feeding sites.

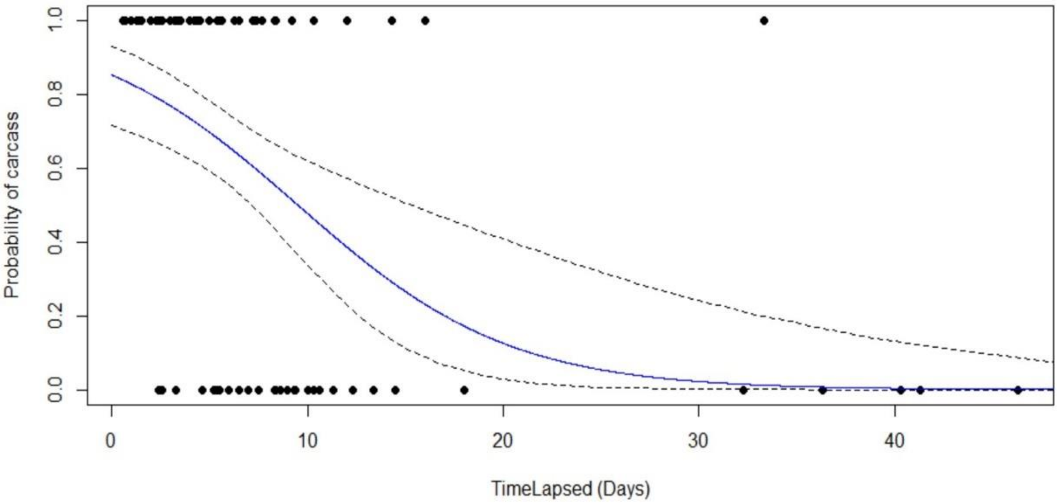

Figure 3: Shows the relationship between time lapsed to ground truthing a potential feeding site on probability of finding a carcass at investigated feeding sites. The blue line is the prediction of the relationship, the dashed line above it is the upper confidence while the dashed line below it is the lower confidence limits. The dots are the occurrence records on whether a carcass was recorded or not at each investigated site.

Table 3: Causes of death for the prey items identified at ground truthed sites, and the main type of investigator of the different causes. Carnivores recorded were Lion (*Panthera leo*), Spotted Hyena (*Crocuta crocuta*) and African Wild Dog (*Lycaon pictus*). The amount of prey contribution towards the investigated vulture species is also specified.

Cause of death	No. of investigated sites	Recorded carcasses	Contribution to Vulture diet (%)	Main site investigator (% visited)
Carnivores	27	Buffalo*, eland, gemsbok, giraffe*, livestock, red lechwe	LFV (7), WBV (45), WHV (48)	LODGES (70)
Natural	5	Elephant, giraffe	LFV (20), WBV (20), WHV (60)	LODGES (60)
Professional hunter	6	Elephant*	LFV (100)	DWNP (100)
Unknown	29	Buffalo, livestock*, elephant*, gemsbok, giraffe, Impala, kudu, red lechwe	CPV (4), LFV (17), WBV (38), WHV (41)	LODGES (48)
Total	67	N/A	N/A	N/A

*Had ≥ 5 carcasses recorded

I found ten different taxa across the 67 carcasses located at the ground truthed sites, (Table 3 and Figure 4). Majority of the carcasses were wild animals (84%, n=56), rather than domestic livestock (16%, n=11). Livestock comprised of cows (*Bos taurus*) (82% of livestock, 13% of all carcasses, n=9) and donkeys (*Equus asinus*) (18% of livestock, 3% of all carcasses, n=2). The most important wild prey species was Elephant (*Loxodanta africana*) (31% of all carcasses, n=21), Buffalo (*Syncerus caffer*) (21%, n=14), and Giraffe (*Giraffa camelopardalis*) (13%, n=9). Elephant featured in the diet of all species but seem to be particularly important for the Lappet-faced Vulture, where they made up 50% of all carcasses (Fig.3). Domestic livestock only featured in Lappet-faced and White-backed vultures and did not feature in the diet of White-headed vultures. Buffalo featured only in White-headed (21% of their diet) and White-backed vultures (30% of their diet) and not at all in the diet of Lappet-faced Vultures (Figure 4).

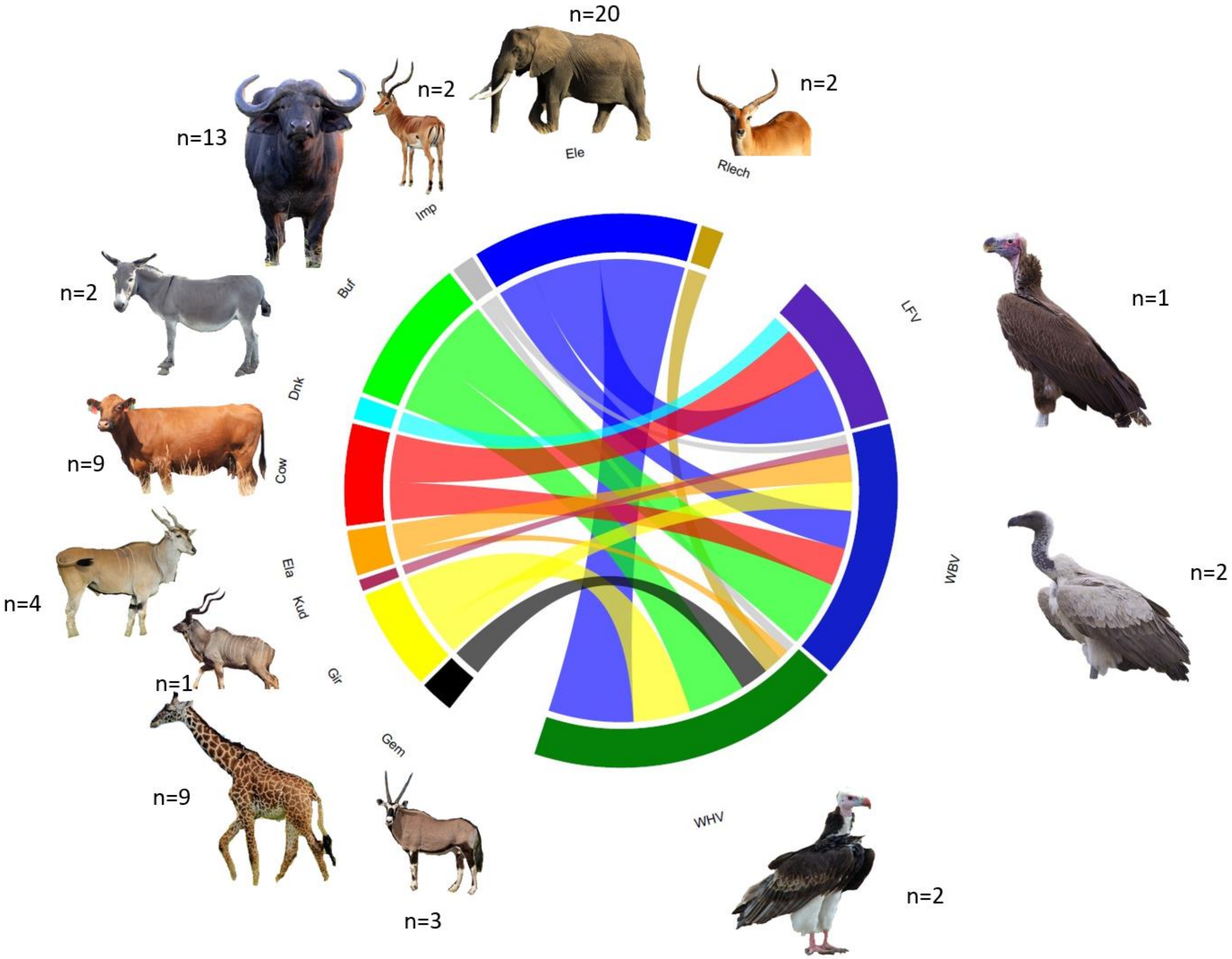

Figure 4: Chord diagram showing the distribution of the carcass taxa between the different species of vulture, for vulture species where more than 10 carcasses were detected at ground truthed sites. Lappet-faced Vulture (LFV), White-backed Vulture (WBV) and White-headed Vulture (WHV). Buffalo (Buf), Cow(cow), Donkey (Dnk), Eland (Ela), Elephant (Ele), Giraffe (Gir), Gemsbok (Gem), Impala (Imp), Kudu (Kud) and Red lechwe (Rlech).

Discussion

From all ground-truthed locations, I managed to confirm a carcass at approximately 62% of the sites. This is lower than the percentage found by Arkumarev et al., (2020), using a similar approach for Griffon Vultures in Bulgaria. They found carcasses in 92% of their searches. However, their searches occurred within one to six days after initial reporting of a feeding event and also made use of sniffer dogs, whereas for my study searches were conducted on average eight days after initial feeding events, with some sites visited after forty-six days. However, at the time of the initial feeding event, my model (from the intercept) suggested an 85% probability of finding a carcass, which is more similar to the estimates of Arkumarev et al., (2020). Importantly, these findings suggests that the algorithm I used was useful at distinguishing movements related to feeding, rather than other non-feeding events, with an estimate of only around 15% false positive. I do not, however, as yet know the potential rates of false negatives (i.e., feeding sites that were not identified).

Initially, a total of 16 vultures were GPS tagged however, I only used data from 12 active individuals during the active ground truthing period. This yielded nearly 500 potential feeding sites during the 6-month period, which equates to around 7 feeding clusters per individual per month. From these 500 sites, I was able to ground truth just over 100. Because of the vast distances between feeding sites detected in this study, I relied on a network of nearby people to ground-truth the sites. Most sites were investigated by staff from lodges, with nearly half of all ground truthed sites checked by tourism service operators, and fewer sites checked by staff from NGOs or DWNP. It is worth noting that, this approach did therefore inevitably bias the sites that were checked to protected areas or other more natural sites (where most lodges operate), rather than farmland. Although I did not explore it within this study, it would be possible to examine the level of this bias but comparing the land use associated with potential feeding sites against those that were ground truthed.

The DWNP staff mainly reported on carcasses at sites, where they had escorted professional wildlife trophy hunters at specific wildlife concessionaire areas. These were through the government authorized trophy hunting season quota (DWNP, 2021). DWNP staff visited the least number of sites due to their administrative offices being located further away from the reported feeding sites, as compared to other site investigators.

The importance of visiting the potential feeding sites soon after initial identification was highlighted by my finding that as the time to visit a site increased, the probability of finding a carcass decreased. This is not a surprising result given that scavengers would have more opportunities to clear up a site, and thus less likely to find a carcass there. The nature of this relationship showed that the likelihood of finding a carcass decreased by 50% after 10 days, and after 20 days, there was less than 20% chances of finding a carcass. Hence for future work, it may be advantageous to only visit site after a limited period has elapsed (e.g., within 10 days) to increase the efficiency of the method.

Despite my initial prediction, it appeared that the difference between areas with higher NDVI (thicker vegetation) compared to those with lower NDVI (less vegetation) at the ground-truthed sites did not influence the likelihood of finding a carcass at a site. This might have been because of the small sample size of sites which was managed to be ground truthed. Also, most of the investigated sampled sites (more than 70%) were in northern Botswana especially in the Okavango delta and the Chobe district, which mainly have woodland vegetation cover. Furthermore, there was no significant difference in the probability of positively detecting a carcass at potential feeding sites depending on the vulture species involved.

There is less information on the relative importance of wild animals vs livestock in the diet of different African vulture species. Understanding their diet is important to address some of the threats that may be associated with their food sources. For example, indirect poisoning through specific veterinary drugs uses especially on livestock (Anderson, Piper, and Swan 2005; Risebrough 2004). Therefore, this study was interested in addressing the data paucity in vulture diet within Botswana. Nevertheless, its crucial to acknowledge that given the small number of individuals involved, I can’t conclude that these data are necessarily representative of the diet for each species.

In this study, I found out that there were 10 taxa of carcass species which the vultures were feeding on, and these were mainly wild ungulates. Arkumarev et al., (2020) study found a total of 13 taxa in the diet of the Griffon Vulture. Importantly they found that livestock was the main food source for the species, with around 87% of the diet being livestock. This was in direct contrast to my study, where I found that 84% of the diet was wild animals. These differences might occur for several reasons. For example, most of the vulture species were feeding mainly in protected and wildlife management areas while in the Arkumarev et al.,

(2020) study, the vulture feeding sites were mostly in livestock dense areas where they mainly practiced extensive livestock grazing. This links to the findings of Moleón et al., (2020) which compared foraging of vultures in Africa (South Africa) with those in Europe (Spain) and showed that South African vultures tended not to leave protected areas, whereas Spanish vultures foraged extensively outside of protected areas. They speculated that this was due to the abundance of fallen livestock outside of protected areas in Spain, whereas this was not the case in South Africa. Nevertheless, it’s worth noting that there are some studies which have shown that African vultures tends to also feed in areas other than protected areas (Bamford et al., 2007; Phipps et al., 2013). However, for this study, most sites which were ground truthed were in or near protected areas.

Another major difference between my study and that of Arkumarev et al., (2020) is the number and proportion of feeding locations that were checked. Over the course of my study, I only was able to investigate 22% (n=109) of all potential feeding sites, whereas of Arkumarev et al., (2020) managed to ground truth 43% (n=305) of their potential feeding sites. Perhaps given the more limited infrastructure in African as compared with Europe this is not particularly surprising. However, if this technique is to be adopted more widely in Africa this is an important consideration, along with ensuring that the samples are not geographically biased (as mentioned before).

I collected data mainly in rainy season, so there might have been some feeding behavior evident in other seasons which were not investigated. The White-backed, White-headed and the Hooded vultures were breeding during a reasonable portion of this study, hence likely travelling shorter distances than in non-breeding season (BirdLife International, 2022; Leepile et al., 2020; Murn and Holloway, 2014a). It would also be interesting to continue this study in the non-breeding season to allow comparisons in diet between the breeding and non-breeding season. For example, Arkumarev et al., (2020) found significant differences in the seasonal diet in their study, with the contribution of smaller livestock varying between seasons, and it would be very interesting to explore whether the importance of livestock varied in the vultures between breeding and non-breeding season.

Notwithstanding many of the limitations (e.g., small number of individuals sampled, geographic bias, seasonal bias) of this study, I was able to gain some important insights into the potential food requirements of vultures in Botswana. The White-headed Vultures had most of their feeding sites within protected areas. This supports findings from other studies which also shows that the species tends to confine itself to wildlife protected areas (Monadjem and Garcelon, 2005; Murn and Holloway, 2014b; Murn et al., 2016; Scott, 2020). This pattern was also reflected in their diet, with no cases of domestic livestock present in their diet, with buffalo, elephant and giraffe contributing most of their diet. The other sampled vulture species had most of their feeding sites recorded within the wildlife management and communal areas. Likewise, I found that Lappet-faced and White-backed vultures had cow and donkey remains at their feeding sites. Making livestock a more important source of food for these species. This emphasizes that for conservation of these vulture species, regulating veterinary drugs, such as diclofenac will be important, given its known toxicity to vultures (Cuthbert et al., 2014; Naidoo et al., 2018, 2009; Yasmeen et al., 2022). However, with wild ungulates accounting for over 80% of the carcasses that vultures were feeding on, key considerations in vulture conservation in Botswana should include motivating for implementation of strategies which reduces poisoning of vultures especially through wildlife carcasses. This includes advocating for banning of lead ammunition which have been used in wildlife trophy hunting (Garbett et al., 2018). However, it is also acknowledged that only a relatively small number of carcasses need to be contaminated with veterinary drugs for this to impact the population, so any consumption of livestock suggests that these could still pose a threat (Green et al. 2004)

For the known causes of death of the prey items, more prey individuals were confirmed to be killed by carnivores. These cases were mainly in protected and wildlife management areas and identified by tourism operators. This, therefore, may be due to higher numbers of carnivores in protected and wildlife management areas when compared to other landuse areas. There are 43% (n=29) cases of unknown causes of death of the prey items recorded. Poaching incidents were unlikely to be responsible for large number of these cases, since at all confirmed carcasses, there were no signs of illegal activities. However, this might be because of the presence of anti-poaching officers operating within areas where most carcasses were found. Indeed, many of the potential feeding sites which could not be investigated, were in more remote areas and could not be visited due to poor access roads and lack of nearby people to assist in the ground-truthing, and those areas could be where poaching might be occurring. With these insights, I therefore recommend further research to better understand vulture feeding ecology. This could be through expanding the project to other parts of Africa, increasing number of individuals tagged and study in other seasons to draw more comprehensive conclusions.

Conclusion

The use of GPS tracking tools in monitoring the diet of vultures within Africa has considerable potential. Within Europe it has been used successfully (Arkumarev et al., (2020, 2021) , and here, I show for the first time that it also has considerable potential to be used to study the diet of vultures in Africa. This is particularly important because it is widely recognized that we are currently facing an African Vulture Crisis (Krüger et al., 2014; Ogada et al., 2016). Thus, a better understanding of the diet composition of vultures in different areas of Africa will help organizations better implement the Vulture Multi-species Action Plan (Botha et al., 2017; Pritchard, 2020) which will be crucial for the survival of these important and iconic African species.

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Appendix

Table A1: Landcover images where band 4 and band 5 were extracted and processed for estimation of NDVI at specific points within each processed layer. These were the only layers which overlapped with the ground truthed sites. Location path and rows identified using Worldwide Reference System for data from Landsat 8 operational Land imager and Thermal Infrared collection 2 Level 2. The data was sourced from Earth Explorer United States Geological survey government agency website.

General location/region	Path	Row
Kasane	173	073
Sowa – Gweta	173	074
Letlhakane – Sowa	173	075
Eastern part of Kgalagadi	173	077
Western part of Chobe	174	073
South part of Okavango Delta	174	074
Central part of Kgalagadi	174	077
North part of Okavango Delta	175	073
Western part of Okavango Delta	175	074
Western part of Kgalagadi	175	077