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Identifying priority locations to protect a wide-ranging endangered species☆

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ABSTRACT

1. Medium and large scavengers often move long distances to locate sufficient foraging areas, often including buffer zones of protected areas, putting them at considerable risk from geographically dispersed threats.

2. Vultures are declining worldwide with poisoning being the greatest threat in Africa. Using a novel capture-recapture model applied to carcasses found by 51 GPS tracked vultures, we estimated the exposure, threat, and risk of poisoning to vultures in southern Tanzania. Exposure to poisoning was defined as the areas that vultures use and where carcasses are likely to be found by a given individual. We used a human footprint map as a proxy for threat, identifying locations where poisoning was possible. Risk of poisoning was determined as areas with an overlap of exposure and threat.

3. We found that locations with the greatest risk of poisoning were within 20 km of protected areas. Although most high-risk areas we identified fell within this buffer, our risk assessment method identified additional hot-spots including some high-risk areas that fell outside nearby buffers.

4. We found that our risk assessment allowed us to identify more localised, high-risk areas that cover a much smaller total area. This gives more precise insight into where conservation management should be prioritised and limited resources should be focused.

1. Introduction

Protected areas are considered key areas for conservation and vital habitat for the species that inhabit them (Oldekop et al., 2016; Kiffner et al., 2013; Watson et al., 2013). Large land conservation networks may also include areas with less strict regulation intended to buffer national parks such as game reserves and wildlife management areas, which may be managed for combined community and conservation objectives (Watson et al., 2013). Effectiveness of protected areas can vary and can

be related to their size and human activity in neighbouring areas such as cattle-grazing and firewood collection (Kiffner et al., 2013). Buffer areas aim to reduce human edge effects by allowing regulated and sustainable wildlife and land use around protected areas (Watson et al., 2013). However, necessary buffer size and management may be hard to establish, and large buffer areas can be impossible for law enforcement to patrol adequately (Watson et al., 2013). Conflict with humans in border areas is the major cause of mortality for many species and can create population sinks (Santangeli et al., 2019; Broekhuis et al., 2017;

Woodroffe and Ginsberg, 1998). Wide-ranging species are most likely to disappear from small reserves with high edge areas (Woodroffe and Ginsberg, 1998). Edge effects influence even wide-ranging species that have high quality habitat available and the means to travel between them without encountering or using lower quality or 'risky' areas (Carneiro et al., 2020; Henriques et al., 2018; Broekhuis et al., 2017; Santangeli et al., 2017; Pomeroy et al., 2015; Phipps et al., 2013; Woodroffe and Ginsberg, 1998). Thus, understanding how wide-ranging species use border areas is of high conservation concern.

Human-wildlife conflict is one of the major conservation challenges toward the sustainable management and conservation of biodiversity worldwide, specifically for carnivores and scavengers. In East Africa, poisoning is strongly linked to human-wildlife conflict which tends to occur in the boundaries of protected areas, where humans with livestock and carnivores meet (Santangeli et al., 2019; Broekhuis et al., 2017; Kolowski and Holekamp, 2006). Here poison is often used in retaliation killing against damage-causing animals such as lions and hyenas, but non-target wildlife is also heavily affected. With an ongoing intensification and spread of wildlife poisoning over the past three decades, there is substantial evidence of corresponding population declines in lions, hyenas, vultures, other scavenging raptors such as tawny eagles, and other scavenging mammals. Poisoning is therefore one of the greatest threats to carnivore and scavenger populations across Africa (Murn and Botha, 2018; Blackburn et al., 2016; Ogada, 2014; Frank et al., 2011; Kendall & Virani, 2012; Margalida, 2012; Kissui, 2008).

Vultures are the only extant vertebrate obligate scavengers. They have evolved highly specialised morphology and behaviour to allow them to exploit unpredictable and highly dispersed food more efficiently than other facultative scavengers (Dermody et al., 2011; Ruxton and Houston, 2004; Houston, 1979), putting them at greater risk for finding poisoned carcasses. Poisoning is the most significant threat to vulture populations, because individual poisoned carcasses can kill large numbers of individuals, particularly for species that aggregate at carcasses (Murn and Botha, 2018; Ogada, 2014; Kendall & Virani, 2012; Margalida, 2012). In Africa, white-backed vultures (*Gyps africanus*), a highly social species, are the most recorded species found at large contaminated carcasses (Ogada et al., 2016). Free from human influence, African vultures have high adult survival, but due to catastrophic poisoning events vulture annual mortality can be >25 % (Ogada et al., 2016; Kendall & Virani, 2012). A single event can kill up to 600 birds and 100 individuals killed at a poisoning incident is common (African Wildlife Poisoning Database, 2020). Population declines >95 % over 10 years have been observed in vultures across the Indian subcontinent due to poisoning by the veterinary drug diclofenac (Green et al., 2004; Oaks et al., 2004; Pain et al., 2003; Prakash et al., 2003). In eastern and southern Africa vultures are killed incidentally at poisoned baits targeted primarily at carnivores to protect livestock (Ogada et al., 2012; Virani et al., 2011). In addition, there is evidence that some ivory poachers now intentionally poison vultures to prevent law enforcement being alerted to carcasses through vultures' conspicuous circling and landing, referred to as 'sentinel poisoning' (Ogada et al., 2016; Roxburgh & McDougall, 2012), and that some vulture poisonings may be linked to trade in vulture body parts for uses such as traditional medicine (McKean et al., 2013; Ogada, 2014; Saidu and Buij, 2013). Although identified as the greatest threat to sustainable vulture populations, information pinpointing where poisoning risk is greatest is largely lacking but vital to target anti-poisoning interventions.

A key challenge to our understanding of poisoning risk is the scarcity of data on poisoning events: most poisoning events are never found, reported, or confirmed (Ogada et al., 2016; Ogada, 2014; Vyas, 1999). Poisoned carcasses are often found weeks after they were initially set. Poisoned vultures can be in an advanced state of decay or no longer present, making it difficult to estimate the full extent of the poisoning across the landscape needed to fully understand the effects of poisoning on species' population and demographics (Ogada et al., 2016; Roxburgh & McDougall, 2012). Through demographic modelling, Green et al.

(2004) demonstrated that large-scale declines (22–50 % annually) in Asian vultures could be caused by as little as 0.13 % of carcasses available to vultures being poisoned. This percentage was sensitive to assumptions about bird feeding frequency and the assumed adult survival rate in a healthy population, but even with the highest adult survival (0.99) and longest feeding interval (1 feed per 4 days) the percentage of carcasses required to cause catastrophic declines did not reach 1 %. Similarly, Murn and Botha (2018) estimated vulture population extinction in Southern Africa would occur in just 50 years with only one poisoned elephant carcass every 2 years. Such extreme sensitivity to rare poisoning events are a consequence of vulture's unique social foraging strategy that enables large numbers of birds to congregate at a carcass shortly after the first bird discovers it (Ogada, 2014; Groom et al., 2013; Newton, 2010; Mundy, 1992) and presents a considerable challenge for establishing effective interventions across the entirety of vulture foraging ranges.

While these models demonstrate that infrequent poisoning is sufficient to have catastrophic effects on vulture populations, they do not consider spatial implications of a poisoning event, implicitly assuming that poisoned carcasses are equally likely to be encountered by vultures across the landscape (Murn and Botha, 2018; Green et al., 2004). Given that vultures show clear foraging preferences, understanding the differences in the probability vultures encounter a given carcass could be important for targeting poisoning interventions. The detection probability of a carcass is spatially variable and will depend on carcass availability and density as well as habitat factors and vulture behaviour (Kendall et al., 2014; Kendall 2013; Kendall et al. 2012). It seems plausible that if poisoning events are rare in heavily used areas, vulture populations could be sustained despite poisoning levels above those identified as catastrophic by Green et al. (2004). As wide-ranging species with extremely efficient soaring flight, vultures have large foraging radius but can also be selective within their range (Zvidzai et al., 2020; Houston, 1974; Pennycuick, 1971). Large portions of *Gyps* vulture's range are found to be outside of protected areas across the African continent (Kane et al. 2022). Peters et al. (in review) showed that vultures forage frequently outside protected areas. Understanding variation in carcass use across the landscape (i.e. potential exposure) particularly in relation to buffer zones, can thus provide insight into variation in poisoning risk.

Here, we seek to provide a spatially explicit estimate of poisoning risk for white-backed vultures in southern Tanzania. Modern risk assessment methodology is based on separately estimating the exposure and the threat, with the overlap forming the risk (Piet et al., 2017; Harman, 2014; Samhouri and Levin, 2012). We combine data on time spent in a given area and spatially explicit estimates of carcass detection probability (predicted from vulture telemetry data and assumed carcass availability) to estimate the exposure of vulture populations. We use human footprint as a proxy of poisoning threat and identify the areas of overlap between exposure and threat to identify where poisoning risk is greatest. We then use recorded poisoning events to test our predictions for areas of high poisoning risk. We predict that locations with the greatest risk will be those where natural carcass densities are intermediate - sufficiently high to maintain a reasonable density of foraging vultures, but sufficiently low to ensure a large proportion of vultures in the area will congregate on any given carcass. This is likely to occur at the edge of national parks or in and around lesser protected areas like game reserves, which are areas where human-wildlife conflict is often highest (Santangeli et al., 2019; Kolowski and Holekamp, 2006). We use our risk maps to determine the ideal size of buffer zones to maximise conservation outcomes while minimising the area that needs to be protected. We further predict that priority areas identified using our risk assessment framework will cover a smaller geographic area than simple spatial buffers often used to prioritize interventions for human-wildlife conflicts, demonstrating the value of this type of risk assessment for reducing resources needed to conserve endangered scavengers and carnivores (Santangeli et al., 2019; Blackburn et al., 2016; Balme et al.,

2010; Alexandre et al., 2010; Kolowski and Holekamp, 2006; Martino, 2001). Finally, our assessment will allow us to identify priority areas for anti-poisoning interventions in southern Tanzania.

2. Methods

2.1. Estimating exposure

To estimate exposure to poisoning, we need to know both where vultures forage and the probability that they visit a given carcass within those foraging areas, because time spent in areas of high poisoning risk is only a threat if vultures are foraging or feeding (Santangeli et al., 2017; Ogada et al., 2016; Virani et al., 2011). Therefore, we defined exposure to potential poisoning as areas where vultures are likely to find a carcass within the space they use. We first collected data on vulture movements with GPS tags to identify regional use, likely carcass locations and then estimate carcass detection probabilities. Once obtained, we used this to calculate exposure by multiplying the proportion of days spent per region of all tagged vultures by the daily probability that an individual carcass is detected by a given vulture (see calculation described below), to overlay where vultures are versus where they are most likely to find carcasses.

2.1.1. Telemetry data

We captured and fitted 47 African white-backed vultures (*Gyps africanus*), two hooded vultures (*Necrosyrtes monachus*) and two white-headed vultures (*Trigonoceps occipitalis*) with 70 g Microwave Telemetry solar-powered ARGOS-GPS tags between 2015 and 2021. We trapped and tagged birds in Ruaha and Katavi National Parks and Rukwa, Lukwati-Piti and Selous Game Reserves, Tanzania. Trapping procedure and harnessing methods used here have been described elsewhere (Kendall et al., 2014). GPS tags recorded 14 locations at hourly intervals during the day plus a single overnight point. We downloaded movement data from Movebank (Study ID 103394406) and data manipulation, cleaning, and analysis were run in R (v 4.0.2, R Core Team, 2020).

2.1.2. Carcass detection probability

To determine how likely a vulture would be to find a poisoned carcass, we calculated probabilities that a carcass in an area visited by a given individual would be detected by that individual vulture: essentially the probability that an individual bird encountered a specific (potentially poisoned) carcass on any one day. This required a two-stage process: identification of individual carcasses from clusters within the telemetry data, and a capture-recapture abundance model to determine detection probability by geographic region.

2.1.2.1. Identification of carcasses from GPS.
To first identify possible carcass locations from vulture telemetry data, we distinguished clusters in ArcGIS using purpose written python code. This code first filters GPS points by specified date range to identify where fixes were recorded for one or more vultures within 250 m and within 90 days of each other, between 08:00 and 16:00, when birds are most likely to be feeding, and where distance between hourly points is <1 km (travelling speed). This buffer is created around each individual point for each unique bird and then all overlapping buffers are joined to group together overlapping clusters of individual points. In the case where a single bird is responsible for a cluster the buffer was created around each individual GPS point for that single bird. The mean centre for the cluster was recorded as a potential carcass with additional information such as time of first and last visit by bird, number of visits, and total number of birds visited. We did this across all bird locations between September 2015 to August 2021. These clusters were then cleaned by deleting known nests, locations of known mortalities, omitting one vulture that left Tanzania, removing clusters that birds used for longer than 90 days as even the

largest carcass would not persist in the landscape for more than this, and deleting clusters with only one bird present for less than three hours as these are more likely to be resting or non-carcass roosts. This left a total of 23,825 clusters.

Between 2018 and 2021, 607 clusters were checked in the field by WCS plane or on foot to verify carcass presence and identity. These ground-truthed points represented clusters of 1–6 birds present over a total time of 3–139 h. The clusters were checked over a period of 1–87 days after the date of last use by vultures. Carcasses were classified to species level if possible, or otherwise classified simply as unknown carcass (evidence of bones, animal material, etc.) or non-carcass (bathing site, roost, including nothing found). 287 of checked clusters were confirmed carcasses to a species level, 63 were unknown carcasses, and at 257 no sign of a carcass was found (though it may have been present previously). To improve our carcass dataset we used the information collected on ground-truthed clusters to predict whether the unchecked clusters were carcasses or not, using a discriminant analysis. Linear discriminant analysis (LDA) (Balakrishnama and Ganapathiraju, 1998; Tharwat et al., 2017) is used to classify objects with associated probability, based on linear combinations of one or multiple predictor variables.

Using a random sample of 20 % of the data, we trained a LDA model with the ground-truthed data, including number of vultures present in the cluster, total hours of vulture presence, distance to rivers, distance to ranger stations, and tree cover.

For distance to rivers, we downloaded the African Rivers dataset available on the World Agroforestry Centre's landscape portal (available at http://landscapeportal.org/layers/geonode:africa_rivers_1#more). Distances to ranger stations in Ruaha National Park have previously shown to be correlated with clusters of carcasses, specifically large carcasses (Beale et al., 2018). We included this to assess if distance to ranger station was predictive of caracass versus non-carcass clusters in our study as well. Ranger post data was provided by Tanzania National Parks Authority (TANAPA). Both datasets were rasterized to 100 m resolution, cropped to Tanzania, and distances between checked clusters and rivers or ranger posts were calculated in RStudio. We extracted tree cover data from the Hansen UMD global forest cover dataset for 2015 (Hansen et al., 2013; available at http://earthenginepartners.appspot.com/science-2013-global-forest), accessed via Google Earth Engine (Gorelick et al., 2017) at a resolution of 100 m.

Although we only needed to identify carcass and non-carcass among candidate cluster locations, accuracy may be improved by classifying the diversity of true carcasses separately before recombination to carcass/non-carcass. Consequently, we built a series of LDA models that assessed classification into 2 to 6 separate classes for carcass type and compared model accuracy. The LDA with 5 classes provided good model accuracy and distinguished classes and so was chosen for further use (Appendix S1).

The chosen class distinctions were:

1. Very Large carcasses weighing over 2000 kg
2. Large carcasses between 900 kg–1900 kg
3. Medium sized carcasses, including most ungulates (100 kg–900 kg)
4. Small carcasses including small antelopes (below 100 kg)
5. Non-carcass

Ground truthed carcasses that were of unknown type were removed for analysis as they lowered the confidence of our class identification model since size was unknown.

To validate our LDA model, we tested classification accuracy against the test set seeking to distinguish between carcasses and non-carcasses. We measured model performance using the Area Under the Receiver Operating Curve (AUC).

We used our validated LDA to predict carcass class type for each of the clusters that had not been verified by ground-truthing. To generate a conservative dataset of estimate of carcass locations, we removed cluster

locations with probabilities ≥40 % of being a non-carcass. We then combined this dataset with the 544 ground-truthed verified carcasses to produce a data set of all known and predicted carcasses. After this process, we retained 1876 cluster locations as likely carcasses.

This conservative method of identifying carcasses is likely to be an underestimate of the true number of carcasses in the landscape, both because we might exclude clusters that are genuine carcasses if they did not fit our criteria (e.g. being removed in under three hours), and because not all carcasses will be visited by vultures (Robertson & Boshoff, 1986). However, it is likely to provide accurate information about the spatial distribution of medium to larger carcasses which are often those poisoned, which was the aim here given our focus on assessing exposure. To assess the degree to which our methods underestimated carcasses, we compared the frequency with which individual tagged birds visited assumed carcasses against their minimal energetic needs (Brink et al., 2020; Spiegel et al., 2013; Prinzinger et al., 2002; Ruxton & Houston, 2002). We summarised individual tagged birds feeding frequency at assumed carcasses and computed basic summary statistics on average and standard deviation for number of days fed and time between feedings for each individual.

2.1.2.2. Capture-recapture analysis. Having assessed carcass location, we estimated carcass detection probability by administrative region. To do this, we computed the actual number of tagged vultures using a given carcass selected from the total number in the area, based on telemetry locations for tagged birds. We computed detection probabilities separately for each region of Tanzania (available at https://datacatalog.wo rldbank.org/dataset/tanzania-region-district-boundary-2012) and their associated protected areas (from The World Database on Protected Areas, WDPA: available at https://www.protectedplanet.net/) and limited the analysis to only the major protected areas tagged vultures in this study used which were: Serengeti National Park (NP), Ngorongoro Conservation Area, Tarangire National Park, Selous Game Reserve (GR) (parts of which have now been upgraded to form Nyerere National Park: Tanzania National Parks 2019), Ruaha National Park, Rungwa Game Reserve, Katavi National Park, Moyowosi Game Reserve, Lwafi Game Reserve, Nkamba Forest Reserve, Piti Open Area East and West, and Lukwati Game Reserve. Although we could have defined regions based on homogenous grids across the study area, we chose to model units as important management areas as these results are more applicable to conservation planning than an arbitrary grid. Regions vary in size, and this may drive differences in detection probabilities for each region.

We used a Bayesian capture-recapture model to estimate the number of carcasses and carcass detection probability by an individual vulture in a given region. Traditional capture-recapture analysis uses the frequency distribution of repeated captures of wild animals to estimate quantities of interest (e.g. population size, survival rate). For our capture-recapture analysis we used the birds as "traps", carcass encounters as a "capture" event, and multiple birds visiting as a "recapture". The number of carcasses "captured" is used to estimate the total carcasses available per region. In the same way as individual animals are imperfectly detected in trapping events in conventional capture-recapture analyses, existing animal carcasses are imperfectly detected by vultures in the local area. Therefore, the true number of carcasses in an area is likely to be greater than the number detected by vultures. In this study we use a capture-recapture framework to analyse the 'captures' of carcasses by vultures: to estimate the 'detection probability' of carcasses by an individual vulture, and the true 'population size' of carcasses (Kery and Schaub, 2011).

Capture histories were constructed using the telemetry location data, date, and carcass information. In a conventional capture history, the elements record whether an individual (rows) was captured on a particular trapping event (columns). Here, we identify trapping events by individual vulture rather than by time: i.e. the elements of the capture history record whether a carcass (rows) was visited by a particular

vulture (columns), at any point over the time the carcass was known to be in existence.

In capture-recapture modelling it is important to take into account when trapping events occurred; i.e. when individuals could have been observed by a given trap. In our framework this means taking into account whether a given carcass could have been observed by a given vulture. Not all carcasses could have been visited by all GPS-tagged vultures, because not all GPS tags were active for the entire study period and because each day a vulture only visited one or a few regions. Omitting this information would cause an under-estimation of the detection probability. Therefore, we computed an 'availability history' documenting the individual birds present in the region during the period when each carcass was present; if a vulture was present in the same region as the carcass during the period for which the carcass was known, the carcass could have been detected by that vulture. For the time period a given carcass was known to be in existence, a data frame of each carcass (rows) and total number of birds present in each region/protected area (columns) was created. The elements of this availability history record whether a given vulture was known to be present (from the telemetry data) in the same region as the carcass, on at least one of the days for which a given carcass was known to be in existence. Any repeat visits to the same carcass by the same bird were removed, and only the first date of attendance was considered.

A closed-population capture-recapture model (Kery and Schaub, 2011) was fitted to the capture and availability histories. This was carried out by data augmentation: adding a number of unobserved 'potential' carcasses, with all-zero capture histories, to the full capture history (Royle et al., 2007), which effectively converts a closed-population capture-recapture model into an occupancy model; one then estimates occupancy rather than abundance. The analysis proceeds by estimating, for each individual carcass in this augmented capture history, the probability whether it is real or not; the expectation of N is equivalent to the sum of these probabilities across all real and potential carcasses.

A key decision in data augmentation is how many all-zero rows to add to the capture history. Enough rows must be added such that all reasonable parameter space for N can be explored. However, adding more rows adds computation time. Here, 1000 rows were added to each region's capture history respectively. This allowed reasonable computation time, while also ensuring that the upper end of the posterior probability distribution of N was not truncated for any region.

For the full augmented capture history, the observed presence y of a carcass was assumed to be a Bernoulli-distributed random variable. The parameter of this distribution was the product of the true existence z of the carcass, the detection probability p, and the availability a of the carcass to be detected by vultures present in the region during its existence. For region h, carcass i and vulture j,

$$y_{h,i,j} \sim Bernoulli\left(z_{h,i}p_{h}a_{h,i,j}\right)$$

The true existence z of a carcass was assumed to be a Bernoulli distributed random variable with parameter Ω. Ω is a nuisance parameter, termed 'inclusion probability' (Kery and Schaub, 2011), and has no ecological meaning. Ω (for each region) was given a uniform prior with minimum 0 and maximum 1. For each region, the estimated number of carcasses N is the sum of the set of z in that region. For region h and carcass i,

$$z_{h,i} \sim Bernoulli(\Omega_{h})$$

Detection probability p was assumed to vary by region, and p (for each region) was given a uniform prior with minimum 0 and maximum 1.

Inference was carried out using MCMC. For each parameter, three separate chains were run for 100,000 iterations. The first 50,000 iterations were discarded as 'burn-in'. Autocorrelation in the chains was reduced by thinning the iterations: retaining only every twentieth

iteration. Convergence was assessed by eye and using the Gelman-Rubin statistic 'R-hat'. If R-hat was below 1.1 then it was assumed that the chains had converged on their posterior probability distribution. When assessing convergence by eye, it was particularly important to check that the upper limits for the population size estimates were not truncated by insufficient extra rows added during data augmentation. Models were fitted in WinBUGS accessed from R, using the package R2WinBUGS (Sturtz et al., 2005). Convergence was generally good, except for regions which had very few vultures and/or carcasses. These regions were removed from the model, and the full model was run again without the data-poor regions.

From this, we determined exposure by multiplying the proportion of days a region had any vulture present over the tagging period with the individual carcass detection probabilities from the capture-recapture analysis. We also calculated the total carcasses likely (Table 1) using the mean number of carcasses estimated from the analysis, divided by the proportion of time tagged birds spent in each region, as a measure of variation in carcass density by region.

2.2. Estimating threat

Simply understanding where vultures feed does not accurately portray real poisoning risk, because there is only a risk of poisoning where feeding and poisoning overlap (Santangeli et al., 2017; Ogada et al., 2016; Virani et al., 2011). Because poisoning is driven by human activities such as lethal predator population control, poaching, and wildlife trade in East Africa (Ogada, 2014; Ogada et al., 2012; Virani et al., 2011) we used the human footprint index ((Venter et al., 2016), available from https://sedac.ciesin.columbia.edu/data/set/wildareas-v3-2009-human-footprint/data-download) as a metric for where poisoning was possible. We chose human footprint data over human population density as it is a more accurate measure of the areas used by people even if they do not reside there, such as inside National Parks (Venter et al., 2016).

2.3. Estimating risk

Risk of poisoning in a given area was determined by areas with high exposure and high threat of poisoning. After defining and identifying exposure and threat of poisoning, we combined both these values to determine risk. We then tested different thresholds of the maximum risk value to determine high-risk hotspots, i.e. areas most likely for a vulture to find a poisoned carcass, and chose a threshold of >10 % of the maximum risk value as this sufficiently refined our risk areas while still including areas of interest (Appendix S3). To test whether our method generated more precise estimates of risk than traditional buffers around protected areas we created a series of buffer areas extending 10–50 km from the core protected areas in 10 km steps. Core protected areas were defined as the main protected areas of interest that vultures used frequently: Katavi NP, Tarangire NP, Ruaha NP, Rungwa GR, Selous GR, Serengeti NP, Lukwati GR, and Ngorongoro CA (seen outlined in green in Fig. 1). We calculated the percent of high-risk areas that fell inside buffer areas, and what percentage of the buffer area was considered high-risk (Appendix S2). We also identified the locations of known poisoning events within our study area using mortalities from tagged birds and African Wildlife Poisoning Database (African Wildlife Poisoning Database, 2020). We determined the length of the ideal buffer based on where the distance maximised protection for vultures by covering a majority of known poisoning events and high-risk areas at the smallest total distance. Finally, to evaluate our risk calculation, we compared the estimated risk score at known poisoning locations to the risk at a random distribution of points across the same area with a Wilcoxon signed-rank test.

3. Results

3.1. Exposure

3.1.1. Telemetry data

Tagged birds spent 62 % of their time in Protected Areas (Fig. 1A). Raw telemetry location data showed that tagged vultures spent most of their time (38.5 %) in Ruaha National Park (NP), followed by Morogoro (11.5 %) and Iringa (8.6) regions. Western birds spend a high proportion of their time in Ruaha and Katavi NP and Rungwa GR but also in the border zones of the protected areas of Mbeya, Iringa, and Katavi regions (Table 1, Fig. 1A). Eastern birds spent most of their time in Selous GR and in the bordering regions of Pwani and Morogoro (Table 1, Fig. 1A).

3.1.2. Carcass detection probability

When ground truthing on foot all recent and accessible clusters, most

Table 1
Results of capture-recapture for all carcasses from 2015 to 2021: regions are shown with carcasses observed (number of carcasses in dataset including ground-truthed and predicted), mean carcasses estimated (population estimate from capture-recapture analysis), individual carcass detection probability (p from the capture-recapture analysis), proportion of days with birds (number of days with at least 1 bird over the whole tagging period), total carcasses likely (mean carcasses estimated/proportion of days with birds), percent of carcasses found (carcasses seen divided by total estimated), and exposure (proportion of days with birds multiplied by the detection probability).

| Region	Carcasses observed	Carcasses estimated (mean)	Probability of detection	Proportion of days with birds	Total carcasses likely	% found	Exposure
Iringa	72.00	72.25	0.55	0.84	85.67	84.04	0.46
Ruaha National Park	289.00	293.50	0.35	0.90	327.61	88.21	0.31
Rungwa G.R.	25.00	25.50	0.48	0.50	51.13	48.90	0.24
Katavi National Park	68.00	74.32	0.35	0.58	127.48	53.34	0.21
Mbeya	59.00	59.26	0.45	0.44	135.90	43.42	0.19
Lukwati G.R.	18.00	19.13	0.69	0.26	74.55	24.14	0.18
Selous G.R.	91.00	93.25	0.35	0.47	199.59	45.59	0.16
Pwani	146.00	149.42	0.33	0.41	360.71	40.48	0.14
Morogoro	213.00	230.87	0.24	0.48	477.97	44.56	0.12
Katavi	34.00	46.28	0.23	0.50	92.34	36.82	0.12
Tarangire National Park	178.00	204.13	0.51	0.20	1025.92	17.35	0.10
Manyara	227.00	262.94	0.36	0.26	1013.61	22.40	0.09
Arusha	55.00	57.99	0.63	0.12	491.07	11.20	0.07
Tanga	19.00	19.20	0.78	0.09	225.63	8.42	0.07
Simiyu	10.00	21.93	0.76	0.03	760.96	1.31	0.02
Ngorongoro Conservation Area	15.00	20.31	0.86	0.02	840.02	1.79	0.02
Serengeti National Park	173.00	525.57	0.15	0.10	5115.38	3.38	0.01
Mara	41.00	127.29	0.28	0.03	4345.99	0.94	0.01

A)

B)

C)
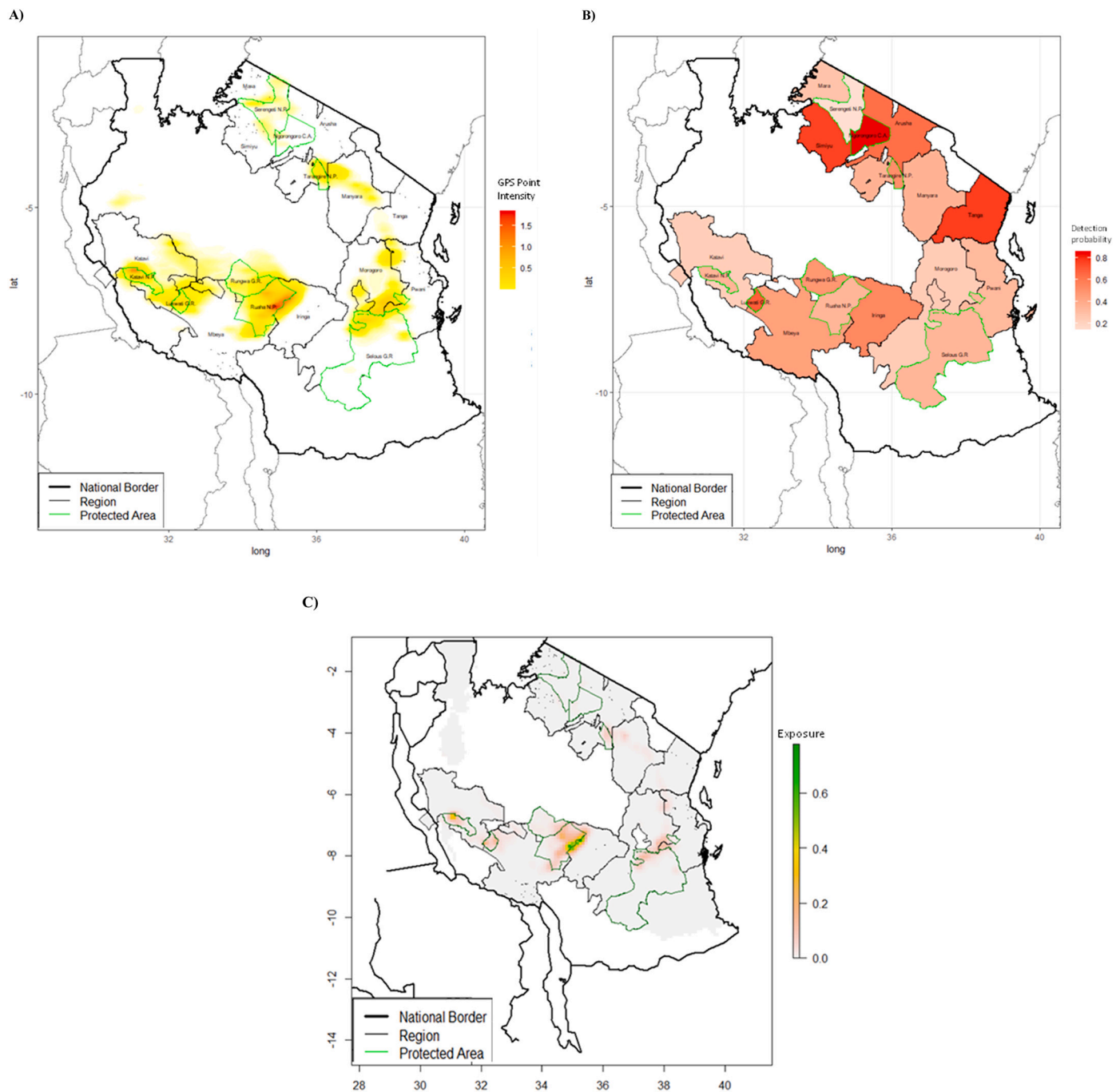
Fig. 1. A) GPS point intensity B) Map of individual carcass detection probability (*p*) as determined by the capture-recapture analysis, only regions with sufficient data have been included. C) Overlapping hotspots of vulture GPS points and individual detection probability to determine exposure - how likely vultures are to use an area and find a high proportion of existing carcasses.

were found to be carcasses. Of 60 points checked on foot, 39 were identified as carcasses (65 %) and 21 were non-carcasses including nothing found (35 %). Aerial checks present more difficulty in identifying small or completely scavenged carcasses, and may thus be less accurate, as visibility and search ability is less and time interval between checking and date of last use by vultures was often longer. However, aerial checks were most feasible to reach the majority of points due to the size of the area being checked, lack of ground infrastructure and complicated logistics associated with any ground effort. Of 452 points checked, 311 were carcasses (including unknown carcass type) (57 %), 13 were non-carcasses (2.3 %) and nothing was found at the remaining 223 clusters (40.7 %). For 48.1 % of locations, our chosen LDA correctly

classified clusters into their carcass class (Appendix S1). Based on our carcass dataset, we determined that vultures were present at likely carcass locations on an average of 18.8 % of days over the tagging period, or approximately one feeding event every 6 days (assuming even distribution) (Appendix S5). As a minimum estimate of feeding requirements, vultures can feed on up to 2 kg of meat in one feeding event (Ruxton & Houston, 2002) and energetically need at least 0.4 kg food per day (Brink et al., 2020), although they can go 10–14 days without feeding (Spiegel et al., 2013; Prinzinger et al., 2002; Bahat, 1995). Based on these minimal vulture energetics, we would expect vultures to feed every 3–5 days. Our feeding encounters are thus slightly lower than we would expect based on energetic needs and suggest that our results may

underestimate feeding. In particular, smaller carcasses, used for short time periods, may be missed by our methods.

3.1.2.1. Capture-recapture analysis. Detection probability (*p*) of a carcass was highest in Simiyu, Tanga, and Ngorongoro Conservation Area and lowest in Morogoro, Katavi region, and Serengeti NP (Table 1,

Fig. 1B). Using the mean number of carcasses estimated from our analysis over the proportion of time tagged birds spent in each region we calculated the total number of carcasses that likely existed. Regions with the most total carcasses were Serengeti NP, Mara, and Tarangire NP (Table 1). Regions with the lowest total carcasses were Iringa, Lukwati GR, and Rungwa GR (Table 1). Birds were best at finding a high proportion of carcasses in Ruaha NP, Iringa region, and Katavi NP due to
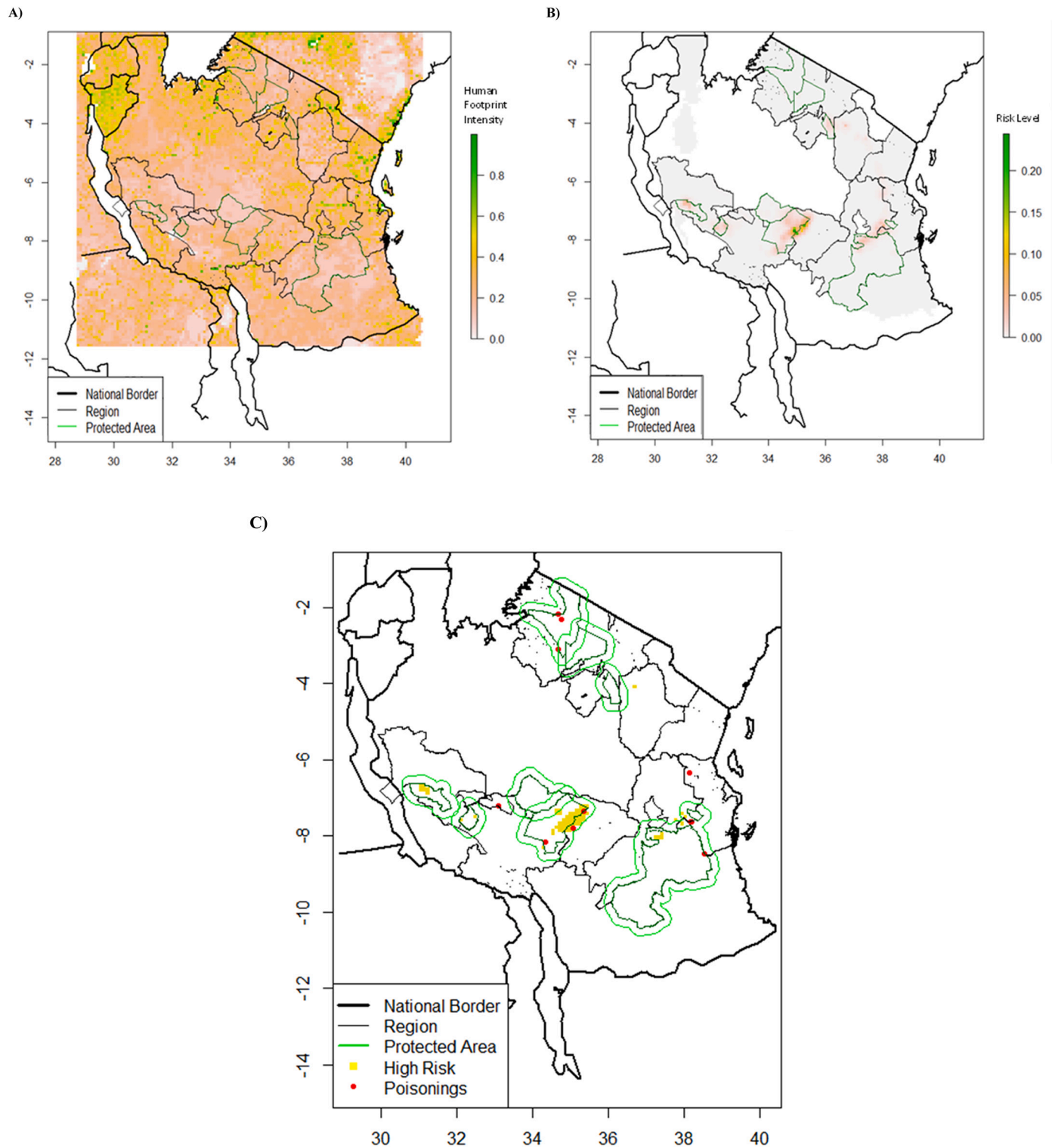

Fig. 2. A) Human footprint which we used as proxy for poisoning (threat). B) Risk map calculated from overlapping threat and exposure. C) Our determined high-risk areas (using threshold of >10 % of the maximum risk value) with 20 km buffer zones around protected areas, and known poisoning occurrences in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

constant vulture presence in the area despite these regions having a lower individual detection probability, and worst at finding carcasses in Ngorongoro Conservation Area, Simiyu, and Mara (Table 1). Regions that had very few vultures and/or carcasses that were removed from the model were Piti OA(E), Piti OA (W), Lwafi GR, Nkamba FR, Moyowosi GR, Lindi. Regions with the highest exposure rates were Iringa, Ruaha NP, and Rungwa GR and lowest were Ngorongoro Conservation Area, Serengeti NP, and Mara (Table 1, Fig. 1C).

3.2. Threat

Using human footprint as a proxy for poisoning threat, we compared mean values of footprint inside protected areas, in buffer zones, and outside both. The mean value of human footprint inside protected areas was 0.16, inside buffer zones that were 10–50 km from protected area borders was 0.20, and outside both areas for the rest of Tanzania was 0.23 (Fig. 2A). Therefore, human impact was lower in protected areas than outside, but surprisingly only slightly lower in buffer areas than surrounding areas.

3.3. Risk

Our identified high-risk areas covered only 6500km² , a much smaller area in comparison to traditional buffer zones around core protected areas of interest: 50 km buffer of approximately 200,332km² total (3 %) and 10 km buffer of approximately 38,917km² total (16 %) (Appendix S2). 2265km² (34.8 %) of this high-risk area was outside protected areas while 4235km² (65.2 %) was inside. Out of 10–50 km, we identified 20 km buffer as most appropriate to capture the majority of poisoning events and high-risk areas. 30.3 % of our high-risk areas fell into a 20 km buffer zone, while almost all the remaining (65.1 %) fell into protected areas (Ruaha National Park specifically) (Fig. 2, Appendix S3). However, only 1969km² (2.5 %) of the 20 km buffer zone (77557km² total) was identified as high-risk by our computation. 7 of the 13 known poisoning events that have occurred in Tanzania happened within a 50 km buffer area of our protected areas of interest, while 3 of them occurred within a National Park and 3 were neither in a buffer area nor a national park of interest. 6 poisoning events were found in a 20 km buffer (totalling 77557km²) while a risk threshold >3 % of the maximum risk value identified 6 poisonings within an area of only 25418km² (Appendix S3). Only one known poisoning event happened within our identified high-risk area (>10 % of the maximum risk value) (Appendix S3). However, when comparing to a random distribution of points across the risk area with a Wilcoxon signed-rank test, we found that our risk areas were better associated with poisoning events (p-value = 5.88e-7) than a 20 km buffer zone (p-value = 3.34e-4). The median risk value for the 13 known poisoning events that happened within our study area was 0.0058 with an interquartile range of 0.0085, compared to random points across the study site which had a median risk value of 1.85e-5 and an interquartile range of 0.0003.

4. Discussion

We found that a 20 km buffer size could maximise protection for scavengers while covering most of the high-risk areas and known poisoning events. Our identified high-risk border areas outside of protected areas (2265km²) are much smaller than (only 3 % of) the 20 km (77,557 km²) buffer area and thus provide a more fine-scale assessment of the spatial extent of poisoning. We found that within Tanzania, locations with the greatest risk of poisoning were at the periphery of protected areas but not all border areas were found to be high-risk. Finally, we used our analysis to identify priority areas for anti-poisoning interventions in southern Tanzania. These main areas of interest were: the northern area of Katavi National Park, the north-eastern buffer area of Ruaha National Park, and the northern buffer area of Nyerere National Park (formerly part of Selous Game Reserve).

As expected from previous studies (Ruxton and Houston, 2004; DeVault et al., 2003; Houston, 1979), we found that vultures are highly efficient at finding carcasses. Even if individual detection probability may be low, the likelihood of vultures detecting almost all large carcasses can be very high in areas frequented by even a small number of birds. As vultures are social foragers and can aggregate in large numbers on one carcass, this supports the notion that only a small number of vultures are needed to discover the majority of carcasses even in a large area. This is apparent in regions such as Ruaha National Park where despite the low probability of a given individual vulture detecting a specific carcass, we found a high exposure rate and a high proportion of all carcasses are found, as this is a heavily used area (Table 1). Indeed, even in the Katavi region where individual carcass detection probability was low, we estimate that 11 vultures using this area everyday would detect >95 % of medium and large carcasses. Thus, we expect a high proportion of birds present in the region to visit any individual carcass, which creates a high-risk on the occasion that it is poisoned.

Administrative regions that include protected areas had birds present for a higher proportion of days compared to regions further away (Table 1). Vultures spend much of their time in protected areas such as National Parks for important behaviours such as nesting and roosting, but frequently travel outside into buffer zones or unprotected areas for foraging, feeding, or travelling and therefore may be at risk of encountering poison (Carneiro et al., 2020; Henriques et al., 2018; Broekhuis et al., 2017; Santangeli et al., 2017; Pomeroy et al., 2015; Phipps et al., 2013; Virani et al., 2011; Bamford et al., 2009; Monadjem and Garcelon, 2005). Rather than avoiding low quality areas, these wide-ranging scavengers appear to utilise buffer zones, which may act as population sinks. Areas bordering protected areas usually have lower densities of wildlife and potential food sources than the protected areas (Veldhuis et al., 2019; Ogutu et al., 2011). We found that these regions had an intermediate number of total predicted carcasses and a high individual detection probability, and the highest exposure rates excluding protected areas (Table 1). This overlapped with the threat of poisoning (human footprint) along the protected area border zones as well, creating a high-risk area for vultures (Fig. 1C, Fig. 2). Because we estimated that these areas have intermediate carcass availability (Table 1) they are likely to have sufficient food to maintain regular use by foraging vultures, but sufficiently low food availability that a larger proportion of vultures will congregate on any one carcass in the area: a scenario that may pose the greatest overall risk to vultures.

From our capture-recapture analysis, we can have confidence that we identified most large carcasses in the study area. However, because we would expect around two feeding bouts per week but only identified one, we may be missing shorter feeding events or smaller carcasses. Vultures can finish a carcass in under 30 min (Houston, 2009) and in experiments done in southern Tanzania, vultures finished a large goat carcass in under 10 min (Peters unpubl. data). Because our satellite tags are limited to hourly data points, the cluster analysis will be unable to identify carcasses at which vultures spend a small period. Based on our feeding data frame results, we can assume that cluster analysis is most likely identifying nearly all medium and large sized carcasses that birds spend >3 h at or that multiple birds visit. Spiegel et al. (2013) found in Israel that European griffon vultures (*Gyps fulvus*) fed every 3 days but could go up to 10 days without feeding, Arkumarev et al. (2021) found that in Bulgaria griffons feed once every 1.5–6 days, and in France Fluhr et al. (2021) found that this was approximately every 1.6–3.5 days. If we assume that vultures feed every 3–5 days this supports the suggestion that we are missing the shorter feeding events/smaller carcasses. Although we may be missing the smaller carcass feeding events, according to the African Wildlife Poisoning Database (2020) of the known baits used for poison events in Tanzania the most common is cattle and medium sized ungulate carcasses. Similarly, Santangeli et al. (2019) found that medium to large sized carcasses of herbivores (>53 kg) were poisoned most often to kill vultures. In addition, we would not expect that exclusion of these smaller feeding bouts would dramatically change

our understanding of the exposure which also incorporates time spent in different areas. Therefore, even if our analysis is missing smaller carcass feeding events, our results related to poisoning risk are unlikely to be affected.

Protected area buffers are typically spaces where humans and wildlife are most likely to come into contact and result in conflict (Watson et al., 2013; Mateo-Tomás et al., 2012; Dickman, 2008). Poisoning in East Africa is strongly linked to human-wildlife conflict which tends to occur in the boundaries of protected areas, where humans with livestock and carnivores meet (Santangeli et al., 2019; Broekhuis et al., 2017; Kolowski and Holekamp, 2006). As protected areas can be large, patrolling all border areas may not be feasible. Properly identifying the appropriate size of bordering areas, along with high-risk conflict areas within the landscape is therefore a conservation priority. We successfully used new methods to analyse telemetry animal movement data and identify priority areas where conservation interventions to protect vultures from poisoning are most important.

This analysis identified 20 km as the ideal buffer range for vulture conservation around protected areas and pinpointed the 3 % within the 20 km buffer zone that is of greatest risk for vultures, providing a smaller region that could be more effectively targeted for protection. Focusing poison reduction efforts and use of rapid poison response teams in these areas will be critical for vulture conservation (Murn and Botha, 2018). This approach may also be useful in prioritising locations for formations of Vulture Safe Zones (VSZ): a poison-free area that completely covers vulture foraging ranges (Bhusal, 2018). In addition, our results highlight the need to mitigate threats both within and adjacent to protected areas and community-focused solutions for threat reduction for endangered species such as vultures (Henriques et al., 2018; Broekhuis et al., 2017; Santangeli et al., 2017; Pomeroy et al., 2015; Phipps et al., 2013; Virani et al., 2011; Monadjem and Garcelon, 2005). Collaboration with local communities in management decisions has shown to increase compliance with protected area regulations, and areas that focus on co-management and integration of local people as stakeholders, along the boundaries of protected areas, have shown to be more effective at achieving conservation goals than strict and exclusionary approaches (Oldekop et al., 2016; Andrade and Rhodes, 2012).

Our results highlight priority areas for addressing poisoning for more effective vulture conservation with careful consideration of carcass use by vultures. As wide-ranging species, conservation of vultures is dependent on the ability to identify and mitigate high-risk hotspots. While protected area buffer zones often include areas of greater poisoning risk, not all buffer zones are used equally by vultures. Our methods help to identify areas that have both high threat and high exposure to better understand risk. This study is important as it demonstrates the ability to use telemetry animal movement data and accurately overlay space-use and threat existence to identify high-risk areas to an endangered species.

CRediT authorship contribution statement

Natasha Peters, Corinne J Kendall, Colin Beale Conceptualization; Cliare Bracebridge, Msafiri Mgumba, Natasha Peters Data curation; Jacob G Davies, Natasha Peters, Colin Beale Formal analysis; Corinne Kendall, Natasha Peters Funding acquisition; Natasha Peters, Corinne J Kendall, Colin Beale Methodology; Colin Beale and Corinne Kendall Supervision; Natasha Peters, Corinne J. Kendall, Colin M. Beale Roles/Writing - original draft; Natasha Peters, Corinne J. Kendall, Jacob G. Davies, Claire Bracebridge, Aaron Nicholas, Msafiri P. Mgumba, Colin M. Beale Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109828.

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