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Assessing the distribution pattern of African elephant (*Loxodonta africana*) carcasses in Etosha National Park and its implications for management

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ABSTRACT Mortality is an important component of understanding elephant population dynamics and disease ecology. We use carcass location data from Etosha National Park, Namibia, collected under the CITES Monitoring the Illegal Killing of Elephants programme, to assess the spatial distribution of elephant deaths, as identified through automated surface feature selection, and explore implications for park management. We modelled carcass location data using a regression spline framework, with targeted flexibility, a spatial term and additional environmental covariates (annual rainfall, distance to water and roads). The novel modelling approach chosen acknowledges the localised and patchy distribution of carcasses and recognises physical barriers (Etosha pan) to substantially reduce the risk of false conclusions about the location of elephant deaths in the park. Our results showed high carcass intensity close to waterholes (< 2.5 km) and roads (< 5 km) and in areas of the park with average rainfall (~450 mm annually). Some high-risk areas were identified, particularly in the north-east of the park, and the mortality risk did not always coincide with elephant distribution. These findings are useful for understanding population dynamics and drivers for the park's elephant population and park management, particularly for disease surveillance.

KEYWORDS African elephant; CITES MIKE program; disease; mortality distribution; Namibia; presence-only data; spatially adaptive

INTRODUCTION

The African elephant (*Loxodonta africana*) occurs across 37 African countries. Southern Africa holds the largest number of elephants on the continent (Thouless et al. 2016). It is the largest living terrestrial mammal species and is of great conservation concern (Guldemond et al. 2017, Skinner & Chimimba 2005). On a continental scale, elephant populations are declining rapidly. As a result, the International Union for the Conservation of Nature (IUCN) recently reclassified the species' conservation status as Endangered (Gobush et al. 2022). Reasons for this decline include habitat fragmentation and loss, unsustainable hunting, conflict with humans, and increasingly scarce resources due to a changing climate (Ripple et al. 2015, Chase et al. 2016).

Mortality is a key factor in understanding elephant population dynamics and monitoring disease. The recent Kavango-Zambezi (KAZA) elephant survey noted a large proportion of elephant carcasses compared to previous surveys (Bussière & Potgieter 2023). Poaching has often been the major focus of elephant mortality studies (Douglas-Hamilton 1987, Wittemyer et al. 2014, Beale et al. 2018, Kuiper et al. 2020), with other causes such as human-elephant conflicts, accidents and natural processes (e.g. disease) less studied. With few non-human predators, natural elephant mortality is often a consequence of food scarcity and water stress during droughts (Mukeka et al. 2022) or of diseases such as anthrax (Huang et al. 2023). However, accurately determining the true distribution of natural mortality may be challenging due to varying patrol effort and distribution of elephants being driven by resource availability and preferences (Kuiper et al. 2020).

In contrast to the rest of Africa, there has been little to no poaching of elephants reported in Etosha National Park (ENP), and the population in the country is apparently increasing (Craig et al. 2021). Elephant mortalities are mostly attributed to resource deficiencies, drought, and disease (Huang et al. 2023). Anthrax (*Bacillus anthracis*) is endemic to the park and a major cause of herbivore mortality, in particular elephant mortality (Lindeque & Turnbull 1994; Turner et al. 2013). The Convention on International Trade in Endangered Species (CITES) Monitoring of Illegal Killing of Elephants (MIKE) programme has been active in ENP for over a decade, and substantial resources are used to collect relevant abundance and mortality data through dedicated aerial surveys under strict survey protocols. Additionally, as part of routine park activities, opportunistic data and carcass detections from biennial helicopter block count surveys are also recorded. Together these form the elephant mortality database for ENP. To date, these data have only been reported to the MIKE project and not analysed on a spatial scale. Analysis of carcass distribution and density could be advantageous for management of elephants, their resources and disease in ENP.

Statistical modelling of these data is useful since the park is very large (~23 000 km^2) and regardless of the survey regime, the observed counts will undoubtedly comprise a subset of total mortalities. Reliable modelling results which accurately estimate the magnitude and location of elephant mortality in ENP are also not guaranteed and require careful consideration of two important factors, namely the largely unused salt pan and the heterogeneous distribution of elephants due to habitat selection and the presence of surface water. Failing to account for the possibly unusual spatial patterns in these data and/or assuming points across the pan are as closely linked as equidistant points without a physical barrier, can unwittingly lead to false conclusions about the magnitude and location of elephant deaths in the park.

This study uses the Complex Region Spatial Smoother (CReSS) to analyse elephant mortality patterns in ENP while considering linear and non-linear covariates. CReSS is a regression spline based statistical modelling method equipped to address both aspects of these data (Scott-Hayward et al. 2014). Spline based regression is a well-established method for estimating relationships when the relationship between the response (mortality) and a set of covariates is unknown and likely non-linear. Splines can return reasonable results with few parameters but can also approximate a wide range of smooth functions. In a regression spline approach the curve flexibility is determined by judicious placement and number of 'knots'. In the CReSS method, straight-line (Euclidean) or 'around the salt pan' (Geodesic) distances can be used to underpin the fitted surface and the method is 'spatially adaptive', which means the flexibility can be targeted to accommodate any particularly patchy trends and/or local surface features (Scott-Hayward et al. 2014, 2015).

While useful, the CReSS method undertakes the crucially important model selection process using a model-averaging approach which can be computationally intensive. Use cases have also shown that this can mask unusual spatial patterns. Walker et al. (2010) presented an algorithm for adaptively placing knots called SALSA (Spatially

Adaptive Local Smoothing Algorithm). This 'adaptive knot selection' approach, results in a number and location of the knots which combines a local-search strategy with a restricted forward/backward regression approach for efficient selection. In this paper, we propose using CReSS with a novel automated model selection approach, SALSA2D, (based on Walker et al. (2010)), to identify atypical spatial distributions and reveal patterns, which have implications for park management in this case.

The aim of this study is to investigate the spatial distribution of carcass locations in ENP and whether the distribution and density of elephant carcasses is related to annual rainfall, their distance from waterpoints and distance from roads. We use the CReSS radial basis function (Scott-Hayward et al. 2015), introduce the novel SALSA2D algorithm, for model selection, and apply these methods to presence-only data – the spatial locations of carcasses (presences) – to develop a spatial model to predict the risk of elephant mortality across the park. In a large national park, early detection of carcasses allows for enhanced monitoring and management interventions. We hypothesise that elephant deaths are influenced by environmental factors and not merely by the distribution and density of live elephants in ENP.

METHODS

Study Area

ENP covers over 22 000 km² of Namibia's northern arid savanna. Rainfall varies from approximately 500 mm per annum in the east, decreasing westwards to about 250 mm. The Etosha Salt Pan covers 4 812 km² and is largely void of vegetation and mostly dry, except for small periods of the rainy season from January to April. The park sustains important populations of most of Africa's large mammals, including a high density of southern black rhino (*Diceros bicornis bicornis*) and an elephant population of approximately 2 900 (Craig et al. 2021). The population is growing slowly at approximately 1.75% per year, compared to 4.75% in the Zambezi region and 4.85% in the Khaudum-Nyae-Nyae complex (Craig et al. 2021). Most surface water is pumped from underground into artificial waterholes where large herds of wildlife congregate to drink. A small number of natural springs occur mostly in the east. An extensive road network covers the central and east of the park with limited management roads and firebreaks across the remaining area.

Data Description

The MIKE data (MIKE 2018) consists of 320 carcass locations observed between February 2000 and March 2017 in ENP. The survey protocol for MIKE was published by Craig (2012) and these dedicated aerial surveys are supplemented by approximately biennial helicopter block count surveys, during which carcasses may be recorded. As most of the carcass data are from dedicated surveys, this minimises the possibility of patrol bias driving the distribution of carcasses. The observed fatalities were recorded as being due to anthrax, natural (age-related) causes, poaching and unknown. While a substantial proportion of the carcasses were recorded as being for 'unknown' reasons (54%) the largest known cause of death is from anthrax (27.8%; 12.5% confirmed cases and 15% suspected). Less than 1% of the carcasses were confirmed as poached. All reported carcasses were used in the analysis regardless of type. Disregarding 2017 as it was only a partial year, 2006 and 2014 had the fewest recorded carcasses (7–8), whilst 2002, 2003, 2005 and 2011 had the highest recorded (27–28) (Figure 1). As there were a relatively small number of observations per year, no guarantee the deaths occurred in the year of detection and no obvious changes in the spatial pattern of observations, the data were pooled across all years. There was also no evidence that

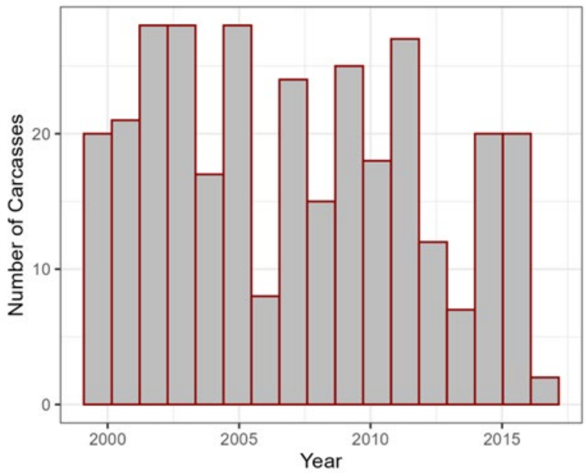

Figure 1 Number of elephant carcasses detected in Etosha National Park, by approximate year of death. The years are estimated based on the condition of the carcasses when found.

there were any differences in spatial patterns when dividing the time series into three equal time periods (2000–2005, 2006–2011, 2012–2017) (space-time Monte Carlo test; $p > 0.95$; Diggle et al. 1995).

Coordinates were converted from WGS84 (World Geodetic System) to Universal Transverse Mercator (UTM) zone 33S and the study region was extended beyond the ENP boundary by 20 km to include carcasses just outside the park. Additionally, the large salt pan was reduced in size by 2 km to include carcasses found near the edge of the pan. The data show that carcasses seem to occur near roads (or, at least, are more commonly observed there) and waterholes (Figure 2). While it is possible that these patterns are due to opportunistic reporting of carcasses as a result of park vehicles moving along the roads, the data were from both opportunistic and dedicated surveys, which are carried out without reference to roads Furthermore, the movement patterns of collared elephant in ENP do utilise roads/tracks and fire breaks extensively and are known to frequent waterholes (Chamaillé-Jammes et al. 2007, Tsalyuk et al. 2019). Anthrax-related deaths appear to be particularly well correlated with waterholes (Figure 2).

Data Analysis

Density of elephant carcasses, based on the presence and (pseudo-) absence of carcass locations, was modelled using four candidate covariate terms: distance from the nearest road, distance from the nearest water point, mean annual rainfall and a spatial term based on spatial coordinates. Distance from nearest road and nearest waterhole metrics were considered as candidates in the model to reflect differential mortality rates near roads and waterholes, where that exists. Mean annual rainfall was based on rainfall data collected from 168 rain gauges distributed across ENP which are visited annually, when possible. When annual data were unavailable, this metric was averaged across years for each gauge before detailed interpolation ($df = 150$) to indicate areas with persistently high or low rainfall. Details on the rainfall interpolation can be found in Section 1 of Appendix 1.

Proximity to waterholes was included since elephants frequent waterholes, particularly in the dry season (Tsalyuk et al. 2019) and inhabit areas close to water (Harris et al. 2008). In addition to distribution-based mortality it is thought that anthrax-related deaths may be related to the presence of waterholes (Zidon et al. 2017). The reasons for trialing proximity to roads in the model were due to elephant use of roads for travel (Tsalyuk et al. 2019), and therefore possible increased detection near roads (e.g. easier to observe).

The spatial term was considered to represent spatial patterns in mortality which are not adequately explained by proximity to the other covariates. This term is crucial here - correctly identifying systematic spatial patterns in mortality might provide insights about park features not

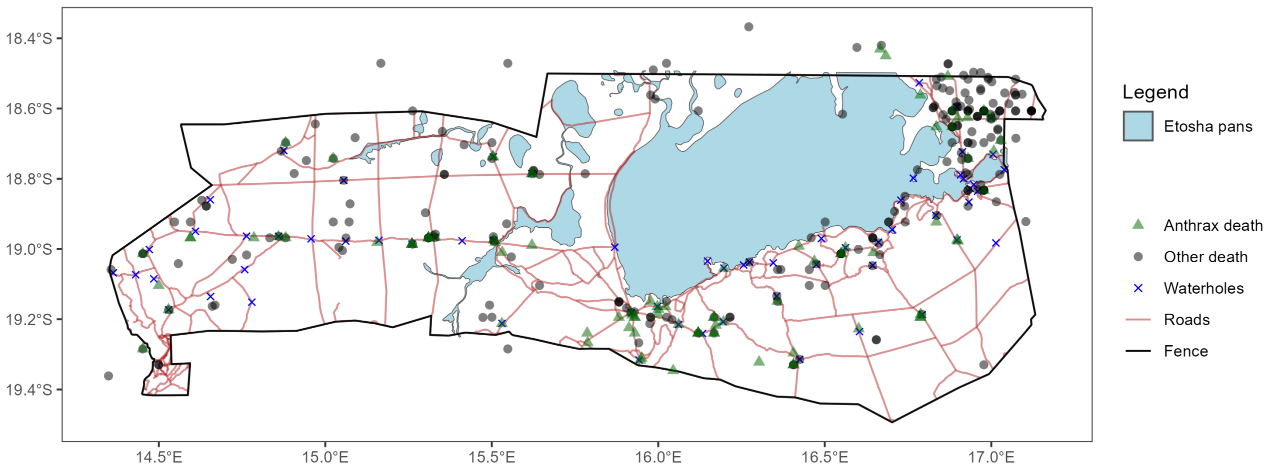

Figure 2 The study area with carcass locations. Green triangles show confirmed or suspected anthrax cases and grey circles all other types of death (natural causes, poaching and unknown). To visualise overlapping points, the colours are semi-transparent, therefore a darker shape indicates overlapping carcass locations.

currently thought related to mortality and overlooking these prevents the mitigation of future elephant mortalities, particularly those related to poaching.

In this dataset, while the carcass locations were available, the survey tracks were not, and so carcass-free locations were estimated for subsequent modelling. The number of carcass locations per unit area ('intensity') was modelled against selected covariates in the study region. 'Intensity' is a relative measure and gives the expected abundance of carcass sightings for a given area. Here, we also use the link between logistic regression and an inhomogeneous Poisson point process model (PPM; Warton & Shepherd (2010)) and the downweighted Poisson regression method (Renner & Warton 2013) to fit a Poisson PPM using a pure regression generalised additive model (GAM) framework. This results in a basic PPM with flexible smooth terms (sometimes referred to as resource selection functions). Pseudo-absences play the role of quadrature points in point process modelling and were selected as a regular grid and the number was based on convergence of the likelihood (Renner & Warton 2013).

Method description

The CReSS approach fits pure spatial regression models to a set of coordinates $\mathbf{z}_i$ of the form:

$$g(\mathbf{y}_i) = \eta_i = \beta_0 + s(\mathbf{z}_i) = \mathbf{X}_i\boldsymbol{\beta} \qquad (1)$$

where g is the link function and η the linear predictor. $\mathbf{s}$ is a two-dimensional surface approximated by a linear combination of K exponential basis functions, $bE(h,r)_k$. Each of the k basis functions can be considered as a covariate in the linear predictor and so in matrix form, $\mathbf{X}$ is the design matrix with $K+1$ columns (K bases and the intercept) and $\boldsymbol{\beta}$ the vector of coefficients.

In each basis function, the range parameter, r, dictates the extent of the decay of the exponential function with distance between points, and thus the extent of its local nature. h indicates a geodesic or Euclidean distance (for some observation i and the k-th knot location). Optional distance metrics are a very useful feature of the CReSS approach as the large salt pan effectively acts as a hole in the domain. This means that distances between points must be incorporated as the elephant travels (geodesic), not as the crow flies.

Parameter r takes values such that if r is small the model will have a set of relatively local basis functions and if r is large the model will have a set of relatively global basis functions. The exact values of r are dependent upon the range and units of the spatial covariates.

Every data point can be chosen as a knot location, so deciding which basis functions to include in the surface is a standard covariate selection problem. The CReSS with model averaging procedure (Scott-Hayward et al. 2015) fits multiple models with each model evaluated at one of a variety of parameter values for the number of space-filled knots, K, and the effective range parameter r_k. This paper presents CReSS with SALSA2D, which uses the same model framework as for model averaging (Equation 1) but where the best knot locations are chosen using automatically using an iterative procedure. The SALSA algorithm is not a complex modelling algorithm, rather it is a covariate selection method with three intuitive steps and is presented here as it provides an effective tool for non-technical modellers to automatically select which knots to include in the spatial surface.

The algorithm works in (at least) two dimensions and begins with space-filled knots to facilitate spatial coverage and then adaptively moves, adds and drops knots into, or from, locations in line with poor model fit (evidenced by large residuals) and an objective fit criterion. At each stage, the global/local extent of each basis function, via the r value employed, can also be revised as part of the search for a more appropriate surface. So, unlike the model averaging approach, SALSA2D returns one model with specifically selected K and r_k enabling standard regression methods for assessment of fit and uncertainty estimation. Further details on the algorithm and a full comparison of the model averaging vs SALSA2D approach can be found in Section 3 of the supplementary material, Appendix 1.

The SALSA2D algorithm is implemented inside the MRSea R package (Scott-Hayward et al. 2024, R Core Team 2024) for easy use by practitioners (http://lindesaysh.github.io/MRSea/).

Model specification

We modelled the intensity of elephant carcass locations as a function of distance to water, roads, mean annual rainfall and as a spatially adaptive smooth function of spatial coordinates. The locations of the carcasses were modelled jointly with the pseudo-absences by maximising the following weighted Poisson log-pseudolikelihood (Berman & Turner 1992):

$$l(\boldsymbol{\beta};\mathbf{X}) = \sum_{i=1}^{N} w_i \left(y_i \log(\lambda(\mathbf{X}_i)) - \lambda(\mathbf{X}_i) \right) \qquad (2)$$

where $\lambda(\mathbf{X}_i))$ is the intensity at location i, $\mathbf{X}_i$ represents the design matrix at location i, N is the total number of points (presence and pseudo-absence), $\mathbf{w} = \{w_1, \cdots, w_N\}$ are quadrature weights. $y_i = \frac{1}{w_i}$ if i is a presence location and $y_i = 0$ for a pseudo-absence.

The log-pseudolikelihood in Equation 2 is a re-expression of the Poisson PPM log-likelihood (Cressie 1993), which means that models can be fitted using standard software. Here we model the expected number of carcasses per km² and so the weights for the pseudo-absence points are specified as the area of the study region, 37 872 km² (ENP plus the 20 km buffer) divided by the number of pseudo-absences. The weights for presence points are set to some small value (10^{-6}).

Likelihood convergence was used to determine the number of pseudo-absences which was estimated to be 9 644 (a grid spacing of 2 km). For more details see Section 2 of Appendix 1.

The GAM model specification was:

$$\begin{aligned} \log(\lambda(\mathbf{X}_i)) &= \eta_i \\ &= \beta_0 + s_1(\text{distWater}_i) + s_2(\text{rainfall}_i) + s_3(\text{distRoads}_i) + s_4(\mathbf{z}_i) \\ &= \mathbf{X}_i\boldsymbol{\beta} \end{aligned}$$

In this case, $\lambda(\mathbf{X}_i)$ is the intensity at location i and X_i represents the coordinates and environmental covariates (design matrix). s_1 - s_3 represent one-dimensional basis functions, while $s_4(\mathbf{z})$ represents a two-dimensional exponential basis function for the spatial coordinates. $\boldsymbol{\beta}$ is a vector of model parameters associated with all columns of the design matrix, $\mathbf{X}$. The columns of $\mathbf{X}$ comprise the intercept, spline bases for water, rainfall and roads and the exponential radial bases for the spatial term.

Specifically, quadratic B-splines with SALSA based knot selection (Walker et al. 2010) were used to implement the one-dimensional smooth terms for water, rainfall and roads. The two-dimensional smooth was an exponential basis with Euclidean distances. Knot number, their locations and r_k values were chosen using the SALSA2D algorithm. We used the outputs from a small methods comparison exercise to determine the starting parameters for SALSA2D. The details of this study can be found in Section 3 of Appendix 1. The Bayesian Information Criterion (BIC; Schwarz 1978) was used to govern model selection in all cases. BIC is an information criterion approach to model selection that trades off model fit (the loglikelihood of the model; LL) with the number of estimated parameters (k):

$$\text{BIC} = \text{-2LL} + \text{klog(n)}$$

Where n *is* the number of data points and in this study is equal to the number of carcass locations, 320. Models with a smaller BIC score are selected for.

Lastly, to determine areas of poor fit, the exchange step requires the calculation of residuals. This was achieved by creating a neighbourhood around each knot location, k, and comparing the observed number of points with the sum of the estimated intensities in the same area. For more details, see Section 3.3 of Appendix 1.

RESULTS

Carcass intensity, the expected abundance of carcass sightings for a given area, is clearly highest near waterholes, roads and locations where annual rainfall is approximately 450 mm (Figure 3). Of these three covariates, the distance to waterhole term has the strongest influence on carcass intensity. Specifically, intensity decreases steeply with the distance from water until approximately 5 km when the relationship subsides. Distance to roads has a smaller effect on carcass intensity and with a less steep decline in intensity to that of distance to water. The relationship flattens off toward zero intensity at approximately 10 km.

The addition of distance from waterholes, distance from roads and mean annual rainfall to the spatial term, improved model results when compared with model results based on a SALSA2D-based spatial term alone (Models 2 vs 3 in Table 1; the BIC scores substantially improved from 11 038 to 2 021).

The spatial term also contributed positively to the model, despite the extra parameters required (Table 1); the BIC score decreased from 2 144 for the univariate model (Model 1) to 2 021 when the spatial term was included (Model 2). The practical consequences of its inclusion were clearly evidenced by tempering the 'global' effect of roads and water which was implicit in the model that included the additional variables (Figure 4a). In some cases, the road and water effects diminished altogether where carcasses were not seen in the data. Crucially, this spatial term also better accommodates carcass locations which are not explained by only their proximity to water, distance to roads or average annual rainfall. Figure 5 shows that in Model 1, the waterhole relationship dominates with a peak of intensity at each one. When the spatial term is added, the waterhole peak is suppressed at a number of waterholes and even increased at others. The peak in intensity is shifted to the north which is in keeping with the high number of carcasses observed there. Overall, our modelling shows that most, but not all, waterholes and some roads have high carcass intensity. Figure 4b shows the top 5% highest carcass intensity areas which form the highest risk areas in the park. These are mainly in the northeast of the park and in the area around Okaukuejo (central south of the pan).

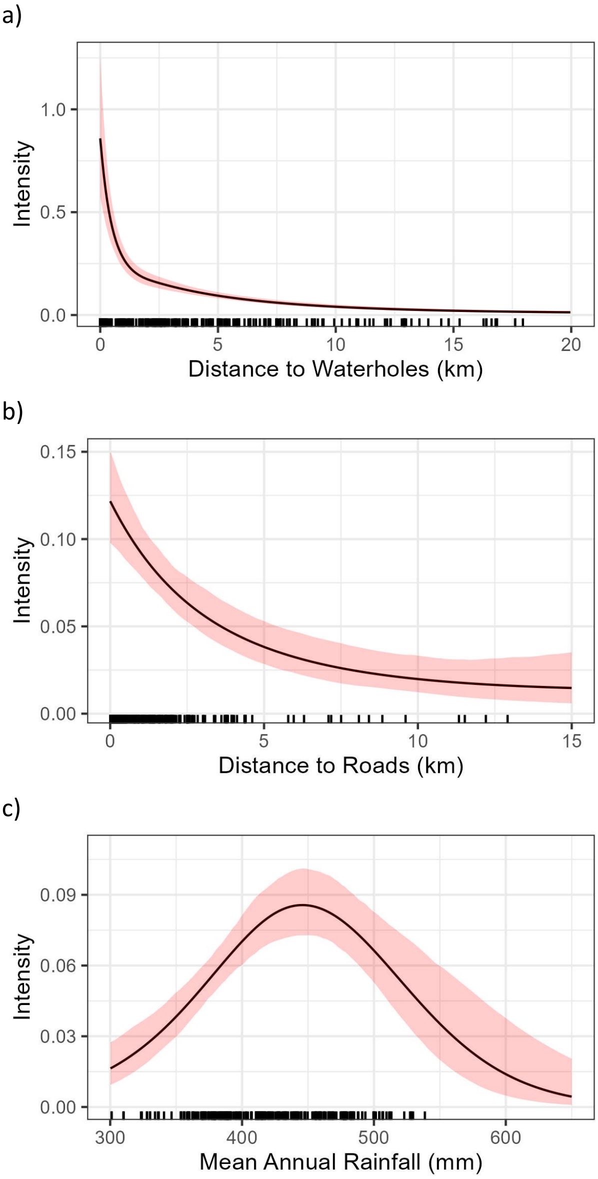

Figure 3 The estimated relationships, from the best model, of each variable to carcass intensity: (a) waterholes, (b) roads and (c) annual rainfall. The red shaded area/line is a 95% confidence interval about the estimated relationship. Tick marks at the bottom of each plot show the distribution of the observed carcass locations across each covariate.

DISCUSSION

We have demonstrated a strong relationship between mortality of elephants and distance to waterholes. Elephants are highly dependent on surface water for drinking, thermoregulation and parasite control (Bothma & du Toit 2010). It is therefore not surprising that carcasses are mostly found near waterholes as a direct factor of distribution density. This relationship extends to

Table 1 Model selection results for the one dimensional smoother-based relationships only (Model 1) and the model with both one and two-dimensional smoothers (Model 2). Model 3 is the model with only a two dimensional smooth. *df* is degrees of freedom of each model term and LL is the Log-Likelihood score. The BIC score in bold is the best selected model.

Model	Term	*df*	χ^2 *p*-value	LL	BIC
1	s(rainfall)	3	< 0.0001	-1048.7	2143.5
	s(distRoads)	3	< 0.0001		
	s(distWater)	3	< 0.0001		
2	s(rainfall)	3	< 0.0001	-886.3	**2020.6**
	s(distRoads)	3	< 0.0001		
	s(distWater)	3	< 0.0001		
	s(xcoord, ycoord)	35	< 0.0001		
3	s(xcoord, ycoord)	52	< 0.0001	-5496.4	11038

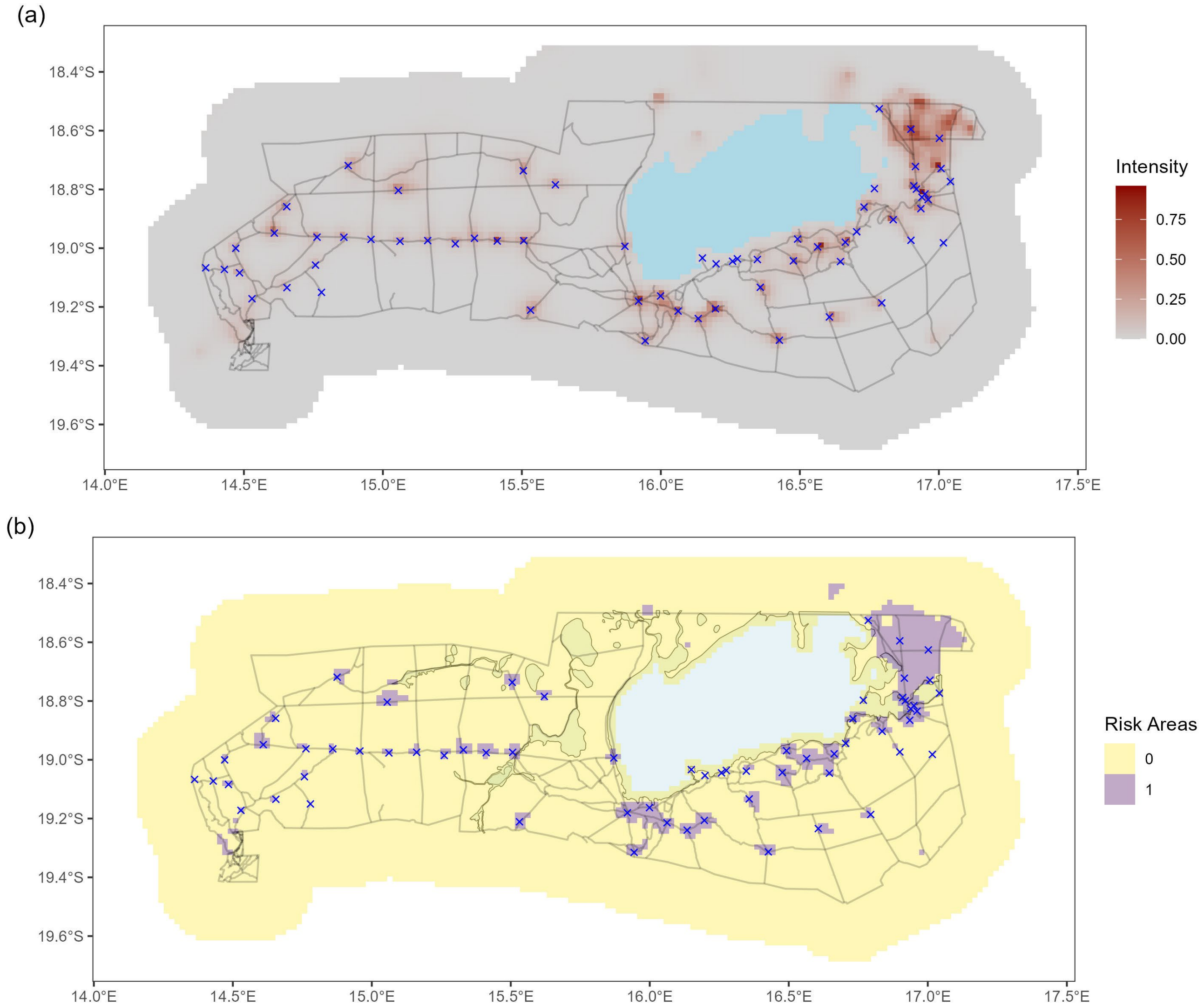

Figure 4 (a) Estimated carcass intensity (the expected number of carcass sightings in a 4 km² area), throughout the study region using the best model, Model 2. (b) The top 5% intensity areas are highlighted to show the areas with the highest risk of mortality in the park. The blue is the Etosha salt pan, the blue crosses are waterholes, and the black lines are roads.

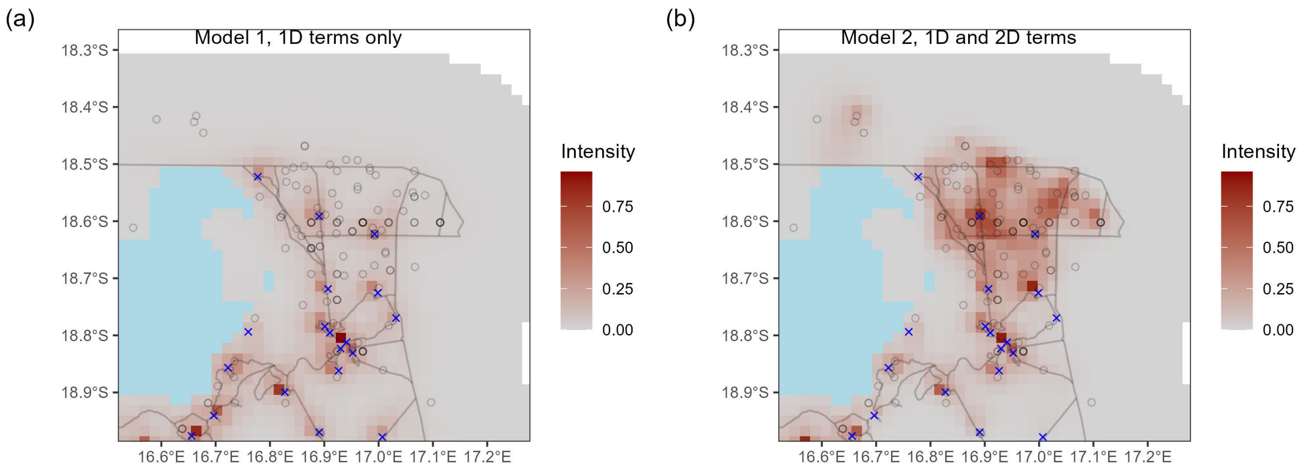

Figure 5 The estimated carcass intensity (the expected number of carcass sightings in a 4 km² area), for the north-east part of the study region for (a) Model 1 (1D variables only) and (b) Model 2 (1D variables and spatial term).

roads, albeit not as strongly as for waterholes. Many waterholes are provided along tourist roads to increase wildlife viewing potential; hence the distribution of waterholes and roads are similar, resulting in a similar probability of carcasses from each variable. Outside of protected areas, elephants often avoid roads to reduce the risk of persecution (Cushman et al. 2010), however, ENP's elephants face few anthropogenic threats and are habituated to tourist vehicles. The elephants likely use the roads to traverse the landscape when the pan and clay areas adjacent are muddy or waterlogged or bush is particularly dense.

Generally, and especially in large parks, wildlife data collection effort is often heavily biased by the spatial extent of roads (Bothma & Du Toit 2010) and can lead to patrol bias, giving a false sense of the true distribution and density of carcasses. The majority of the carcass data analysed here were from dedicated surveys, designed to reduce the potential effects of bias from using roads/tracks. Patrol bias is therefore considered to be minimised in this case.

Simply including proximity to waterholes and roads in the model assumes that any relationships pertain to all waterholes/roads regardless of their location. However, not all roads/waterholes have been associated with carcasses. The addition of the spatial term, with novel spatially adaptive knot selection using SALSA2D was able to suppress/enhance the global relationships with the environmental covariates in particular areas. This resulted in the identification of some critical areas of the park, which is important for effective park management – for example, in terms of disease outbreak, which after 'unknown' was the largest category in the data. It is impossible to patrol the large park area at random and there are areas of the park identified here (particularly those accessed by a subset of roads/waterholes) that are shown to necessitate more monitoring efforts than others.

Elephants are highly mobile and so early detection of carcasses, in particular anthrax-related deaths, is important to identify and monitor disease outbreaks across the park (Lindeque & Turnbull 1994). The area of high intensity of carcasses to the south of the main pan matches well with the area of high anthrax risk identified by Dougherty et al. (2022). This is also the area where the majority of anthrax or suspected anthrax cases were found in our database. Specifically, we show here that within this anthrax risk area the highest intensity of carcasses is near the waterholes. This is in line with the findings of Ebedes (1976) and Lindeque & Turnbull (1994) where animal activity in the overgrazed bare soil areas around Etosha's artificial waterholes stir up dust-borne anthrax spores which are inhaled by wildlife. In addition, the finding of carcasses closely associated with waterholes is not surprising given several studies report a preference for animals to be close to water (e.g. Harris et al. 2008, Wilson et al. 2021).

In the critical high carcass intensity area identified in the north-east of the park, the cause of death is less clear as the majority of carcasses were of unknown cause. This could be because many of these carcasses were detected during aerial surveys and samples collected were of inadequate quality to establish disease as the cause of death. However, it is interesting to note that the water sources in ENP are a mix of boreholes and springs, with most springs occurring in the north-east. It is possible that in this region, there is higher water stress during drought which may play a role in mortality.

Whilst the density of elephants across the park is shown to be fairly constant (Craig et al. 2021), we have found that the density of carcasses is not. Mortality is one of the key components in population dynamics models and the effects of spatial and temporal heterogeneity must be accounted for to have accurate predictive models for use in conservation and park management (Sibly et al. 2009). This provides valuable input into better understanding dynamics in ENP's elephant population. For example, it is well known that surface water availability drives the distribution and abundance of elephants, and that artificial manipulation of water availability is one of the tools available for the management of elephant populations (Chamaillé-Jammes et al. 2007). ENP, however, has adopted a mostly passive management strategy, which may preclude water source manipulation as a management tool. In light of the probable impacts of climate change on surface water availability, understanding the linkage will be important for park management. It would also be of value to look at the carcass distribution of other large mammals to determine whether population-driven mortalities, anthropogenic factors, environmental factors, or a combination of these play a role. In this arid savanna system, rainfall is low and erratic, and a key driver of wildlife movements (Hering et al. 2022). The impact of this on anthrax epidemiology is also not well understood and rainfall as a factor could assist predictive elephant population dynamics aiding management of the species in ENP.

If the deaths are natural and, for instance, disease-related (e.g. anthrax) then this provides valuable information about the prevalence and locale of disease in the park. Endemic anthrax occurs in ENP annually (Turner et al. 2013) and plays an important role in elephant population regulation or limitation. The monitoring of the prevalence of anthrax in elephants is important, because it advances our knowledge of a top-down factor limiting a mega-herbivore.

Even though the poaching of elephants in ENP is low (20 deaths reported to MIKE in 2018 and none poached), the general trend of animal poaching in Namibia in more recent years is increasing (GRN 2023). As the number of human-related elephant deaths increases it is very useful knowledge to have a baseline distribution of natural deaths. It is also very important in light of the mass death events seen in Botswana in 2020 and 2021 (Karombo 2021). Understanding the prevalence of natural mortality may provide insights should such events ever occur in ENP.

Critchlow et al. (2017) developed a method for improving the efficiency of ranger patrols using ranger-collected monitoring data. Ranger patrols are not just important for law enforcement but also the conservation of key species as well as ecological monitoring. With limited resources available for patrols, the key is to ensure that the patrol effort is efficient with respect to the activity one wishes to combat. The starting point for the method presented by Critchlow et al. (2017) is a least one geographical map of illegal activity occurrence. However, the activity does not need to be an illegal one and in this case the activity of interest could be risk of disease outbreak. Along with a map of existing ranger effort, the carcass intensity maps presented here could be used to assess and target the existing ranger effort in the park without the need for increased resources. Natural mortalities may be indicative of underlying ecological or anthropogenic problems, which adaptive park management could address.

In future studies, if a more precise date of death is available, it is possible that the use of more dynamic predictor variables, such as NDVI or fire risk, could improve the model-based outputs. In addition, recording and acknowledging the effort associated with collecting the data (i.e. reporting tracks flown) would enable known zeros (absence of carcass) to be included in the modelling framework and likely further improve estimation. Should poaching increase in ENP, then the novel methods presented here can provide necessary information about the prevalence, locale and patterns of these deaths. Moreover, should poaching occur in areas of low natural mortality risk, then increased or targeted mitigation measures can be efficiently actioned. From a practical perspective, understanding both the magnitude and spatial patterns of elephant deaths in ENP may assist in adapting patrol efforts in and around the park to track the anthrax disease and/or combat any poaching activities.

SUPPLEMENTARY MATERIAL

See Appendix 1 Section 1 for information on the rainfall model, Section 2 for pseudo-absence selection and Section 3 for more detailed SALSA2D information and the model averaging vs SALSA2D comparison.

The code and data for the analyses in this paper can be found at the github site of the corresponding author: https://github.com/lindesaysh/Elephant_carcass_paper.

AUTHOR CONTRIBUTIONS

LSH, MLM and CGW contributed to method development, analysis and manuscript writing. MH contributed to interpretation of results and manuscript writing. CC, GS, JWK and PdP contributed to data collection, local information, reviewed and edited the manuscript.

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