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Prolonged drought results in starvation of African elephant (*Loxodonta africana*)

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ABSTRACT

Elephant inhabiting arid and semi-arid savannas often experience periods of drought, which, if prolonged, may cause mortality. During dry periods, elephant aggregate around water sources and deplete local forage availability. However, the relationships between adult elephant mortality and both high local elephant density and forage availability close to water during dry periods remain unexplored. We hypothesized that elephant mortality is higher: a) when dry periods are longer, b) closer to water points, and c) in areas with higher local elephant density. Using nine years of elephant carcass data from Tsavo Conservation Area in Kenya, we analysed the probability of adult elephant mortality using maximum entropy modelling (MaxEnt). We found that elephant carcasses were aggregated and elephant mortality was negatively correlated with four months cumulative precipitation prior to death (which contributed 41% to the model), Normalised Difference Vegetation Index (NDVI) (19%) and distance to water (6%), while local elephant density (19%) showed a positive correlation. Three seasons (long dry, short dry and short wet seasons) showed high probability of elephant mortality, whereas low probability was found during long wet seasons. Our results strongly suggest that elephants starve to death in prolonged drought. Artificial water holes may lead to lower mortality, but also to larger populations with subsequent high browsing pressure on the vegetation. Our results suggest that elephant populations in arid and semi-arid savannas appear to be regulated by drought-induced mortalities, which may be the best way of controlling elephant numbers without having to cull.

1. Introduction

Human-induced climate change is threatening wildlife communities globally (Thuiller et al., 2006). For example, incidents of drought occur more frequently globally and, particularly, in Africa over the last 25 years (Collier et al., 2008). Recent studies predict that failure of long rains in East Africa may become a frequent occurrence in the future (Yang et al., 2014). Although drought is an integral part of arid and semi-arid systems, prolonged periods without rainfall may result in mass die-offs of wildlife (Knight, 1995). To prevent mass wildlife die-offs due to the predicted increase in drought periods, there is a need to better understand the causes of drought-induced mortality. In this paper, we aim to unravel the drought-related causes of mortality of the African elephant (*Loxodonta africana*). Although some studies have investigated elephant mortalities as a result of drought (Caughley et al., 1985; Moss, 2001; Foley et al., 2008), and the effect of environmental factors such as spatial and temporal variability in drinking water, food distribution (extrinsic drivers) and local population density (intrinsic driver) (Young and Van Aarde, 2010), few studies have focussed on long-term drought events, particularly on adult elephant mortality. This is because elephant mortality data were mainly from unpredictable, opportunistic single-drought events, whereas long-term, consistent records of elephant mortality are rare (Dudley et al., 2001, Foley et al., 2008, but see Aleper and Moe, 2006).

Continent-wide declines in African elephant populations are attributed largely to elephant poaching for ivory (Prins et al., 1994; Kahindi et al., 2010; Bouche et al., 2011; Burn et al., 2011; Maingi et al., 2012; Wittemyer et al., 2014) and loss of habitat associated with increased human population (Douglas-Hamilton, 1987; de Boer et al., 2013), but rarely to abiotic factors such as rainfall variability. Given the predicted increase in drought periods, the mortality of wildlife will likely rise, especially for species that are relatively more water dependent than others and those that require large amounts of daily food (Okello et al., 2015). For instance, in Kenya's Amboseli National Park, the droughts of 2007 and 2009 drastically reduced the population of large mammals, and species such as wildebeest (*Connochaetes taurinus*) declined by over

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50% (Okello et al., 2015). Elephant mortality as result of drought over the past few decades remains unprecedented (Corfield, 1973; Dudley et al., 2001; Walker et al., 1987; Foley et al., 2008). For example, drought is suspected to have contributed substantially to the elephant population drop in Tsavo from 35,000 elephants in 1974 (Cobb, 1976; Blanc et al., 2007) to below 12,000 elephants in 2011 (Ngene et al., 2011).

Given their large body size and long generation time, survival of an adult elephant may be buffered against temporal variation in limiting resources (Gaillard et al., 1998; Gaillard et al., 2000; Prins and Van Langevelde, 2008; Moss and Lee, 2011). In the dry season, for instance, elephants shift their diet from a predominance of grass towards increasing amounts of woody browse (Lindsay, 1994; Moss et al., 2011; Kohi et al., 2011). This diet shift enables elephants to cope with prolonged drought. However, elephant feeding requirements and the patchy distribution of resources in savannas may cause heterogenous elephant aggregation across the landscape (Wittemyer et al., 2007; Chamaillé-Jammes et al., 2008). Consequently, at high densities, elephant may deplete local forage resources, often in the proximity of waterholes and rivers, particularly during the dry season (De Beer et al., 2006; Chamaillé-Jammes et al., 2008). Several previous studies identified distance to water as the primary environmental factor influencing the density of elephant during the dry season (Verlinden and Gavorv, 1998; Maingi et al., 2012), but the relationships between adult elephant mortality and both high local elephant density and forage availability close to water during dry periods remain unexplored.

This study therefore investigates whether elephant natural mortality varies seasonally, whether elephant carcasses are clustered around water points, and what are the relationships between observed patterns of elephant mortality and precipitation, distance to water, forage and local elephant density? Water is scarce in arid and semi-arid savannas and most seasonal rivers and water holes dry up during prolonged drought. Consequently, elephant, especially the breeding herds, are constrained to close proximity of the remaining permanent water sources (O'Connor et al., 2007; Young and Van Aarde, 2010). We therefore hypothesize that elephant mortality will be higher: a) when dry periods are longer, b) closer to water points, and c) in areas with higher local elephant density.

2. Materials and methods

2.1. Study area

We conducted this study in the Tsavo Protected Area (~48,300 km^2), located at 2–4° S and 37.5–39.5° E in the southern part of Kenya (Omondi et al., 2008). It is an arid ecosystem with bi-modal rainfall from mid-March to May and from November to December (Omondi et al., 2008; Tyrrell and Coe, 1974). The long dry season typically ranges from June through October, whereas the short dry season occurs from January to March (Leuthold and Leuthold, 1978; Tyrrell and Coe, 1974). The mean annual rainfall in Tsavo ranges from 250 to 500 mm (Ngene et al., 2014). Tsavo Protected Area is dominated by a flat and undulating terrain with a difference in altitude of 100–500 m that is interrupted by granitic hills and inselbergs with the highest peak of Taita hills standing at ~2220 m above sea level (Mukeka, 2010). The perennial Galana River flows at the foot of the Yatta plateau situated in the northern part of the Protected Area. The vegetation consists of remnants of *Commiphora-Acacia* woodlands that dominated the landscape in the past and is thought to have been thinned by elephant (Bax and Sheldrick, 1963; Leuthold and Sale, 1973; Cobb, 1976). Tsavo hosts a third of Kenya's estimated 38,000 elephants (Omondi et al., 2008; Ngene et al., 2011).

2.2. Data

We extracted adult elephant mortality data from the Tsavo Protected Area database. These data were generated from daily foot-and-vehicle patrols that were carried out by security personnel in Tsavo Protected Area for nine consecutive years (2004–2012). The study area was historically divided into five sections for ease of patrol (Fig. 1). A team comprising of between 5 and 25 rangers patrolled each of these sections daily using a combined vehicle-and-foot patrol. Furthermore, the park authorities received information on elephant mortalities from local people and tourists; these reports were also accepted if the carcass was confirmed by one of the patrol teams. We used elephant carcasses that were approximately less than four months old in our analysis. Most carcasses were fresh and were estimated to be less than a month old. A few were estimated to be >4 months old and these carcasses at least had remnants of skins and the bones not fully disintegrated, which enabled us to estimate the approximate death date. The elephant carcasses we used in this paper are from elephants of ages ranging from 3 years to 60 years (estimated ages) and over 80% of the carcasses were from adult elephant.

The following information was recorded for each carcass: date, area name, sex (for fresh carcasses), likely cause of death, estimated age, and GPS coordinates. An elephant was assumed to have died of a natural cause if the carcass had no snare, spear, gun or poison arrow wound and if it was declared by the resident veterinary officer that it had not died of any disease. Although climatic conditions such as temperature change or lack of sufficient food in dry periods play a role in wildlife susceptibility to diseases (Harvell et al., 2002), we excluded all elephant deaths due to diseases, which were <1% of the total recorded mortalities, and used only records of mortality other than poaching and diseases in our analysis. In total, we used 221 elephant carcasses in this study (Fig. 1C).

Analysis of wildlife mortality data may violate a number of assumptions that underlie standard statistical tests. This is because there are many sources of biases from, for instance, variable patrol efforts (Burn et al., 2011; Huso, 2011) and imperfect carcass detection. The sources of bias were reduced by dividing the study area into sections and conducting systematic carcass searches with equal search efforts (number of rangers and duration of patrol) (no differences between the sections: ANOVA, $F_{4,69} = 2.24$, $P > 0.05$). Furthermore, the big size of the elephant carcass, its immobility, the open savanna landscape that dominates the Tsavo ecosystem, the strong smell from the rotting cadaver, vultures overflying and feeding on fresh carcasses, and the intensive and systematic patrols collectively minimized the bias as a result of imperfect detectability. We therefore assumed minimal detectability bias (MacKenzie and Royle, 2005), and used maximum entropy modelling with MaxEnt, which is a rigorously proven inference procedure based on presence-only data that yields least-biased predictions of occurrences (Harte and Newman, 2014).

We mapped all the water sources in the study area and categorized them as permanent (perennial rivers – Fig. 1D – and boreholes) or seasonal (rain-fed ephemeral water pools and seasonal rivers). Permanent water sources have a water supply throughout the year, whereas seasonal water sources hold water for a maximum of four months in the rainy season (Ayeni, 1975). Boreholes are located near tourist facilities and supply water throughout the year. Using ArcGIS Spatial Analyst Tool (Esri, 2011), we made a map with the distance from grid cells (resolution of 250 m), including the elephant mortality locations, to the permanent rivers, boreholes and seasonal water sources separately. To reduce edge effects (Griffith, 1985), we generated a 10 km buffer around the study area and used it to clip the spatial extent of all other subsequent maps used in this study.

We obtained monthly rainfall data from rain gauges distributed in different sites in the study area to capture the variation in rainfall amounts across the study area. We classified seasons in the study area into long wet, short wet, long dry and short dry seasons following Wittemyer et al. (2005) and Moss et al. (2011). We created point maps from rain gauge records for all the months where elephant mortality had occurred. Using kriging (Esri, 2011), we developed a rainfall grid (resolution of 250 m) for each of these months (see Fig. 1E as an example). We extracted rainfall values from these rainfall grids for all 221

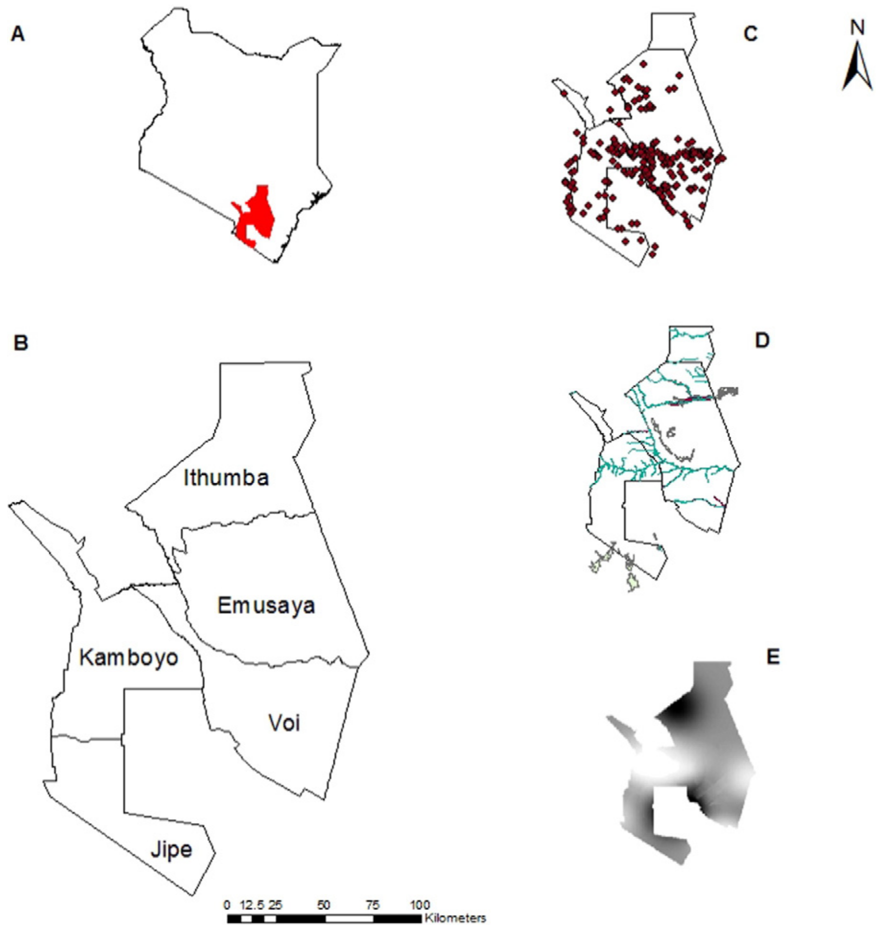

Fig. 1. Maps of A) Kenya showing the location of Tsavo Conservation Area (TCA), B) the five management sectors of T CA where security patrols were carried out, C) elephant carcass locations, D) major rivers and, E) kriged rainfall amount of January 2009; dark shades representing high rainfall amount (see text for explanation).

elephant carcasses at the time of their estimated death. To account for effects of past rainfall amounts on elephant mortality, we also kriged the rainfall values from rain gauge records for one, two, three, four and five months prior to each elephant's death. We calculated the cumulative rainfall from one month up to five months prior to each death and linked the values to the particular elephant carcass.

Several studies analysing the relationships between elephant and vegetation have successfully applied the satellite-derived Normalised Difference Vegetation Index (NDVI) as a proxy for available forage (Loarie et al., 2009; Maingi et al., 2012). We used the NDVI images from the MODIS product (MOD13Q1), which is a 16-day composite of highest-quality pixels from daily images available at a spatial resolution of 250 m. The MODIS NDVI images were downloaded from the USGS Land Processes Distributed Active Archive Center (LP DAAC). For all 221 elephant mortality records, we extracted NDVI values at the time of each elephant's death.

The variable for local elephant density was derived from 2005, 2008 and 2011 total aerial elephant censuses conducted in Tsavo Ecosystem in the dry season (Omondi et al., 2008; Ngene et al., 2011). We generated kernel-density surfaces using ArcGIS Spatial Analyst Tool (ESRI, 2011) for local population densities of elephants in Tsavo on the basis of these three elephant censuses, and averaged the kernel density grid values. We then extracted a single estimated elephant density value for each of the 221 elephant mortality locations.

2.3. Data analysis

We used point pattern analysis to evaluate whether the spatial pattern of elephant carcasses in Tsavo ecosystem was random, clustered or dispersed (Wong and Lee, 2005) and to evaluate the distances at which the clustering is most pronounced using Moran's I in ArcGIS's incremental spatial autocorrelation tool (ESRI, 2011). Besides, we modelled the occurrence of an elephant carcass as a function of distance to water, NDVI, local elephant density, season and amount of precipitation in preceding months using MaxEnt v. 3.3.3e. MaxEnt has been used widely in analysis of presence-only data (Phillips et al., 2006; Phillips and Dudík, 2008; Elith et al., 2011). MaxEnt relates environmental variables at presence locations with random locations in the whole study area and generates a spatial probability distribution of occurrence (Phillips et al., 2006; Coppes and Braunisch, 2013; Ngene et al., 2014), in our case the probability of carcass occurrence which we call probability of elephant mortality in the paper. We used the area under the curve (AUC) of the receiver operating characteristic (ROC) plot (Phillips and Dudík, 2008) to assess the accuracy of the model. We used the default convergence threshold of 10^{-6}, maximum number of iterations of 5000 and the default logistic model to ensure that predictions gave estimates between 0 and 1 of the probability of elephant mortality in the study area. We generated 10,000 random points using Geospatial Modelling Environment (GME) (Beyer, 2010) from the entire study area that we used as background data in the MaxEnt modelling. For these 10,000 random points, we extracted data on local elephant density and distance to water. As we had time series of rainfall and NDVI, we randomly selected 20 elephant carcasses that represented different dates from 2004 to 2012. For each of these dates, we randomly drew 500 points from the rainfall and NDVI maps so that we could link rainfall and NDVI data to each of the random locations.

We ran our model using a 10-replicate cross-validation setting. We randomly selected 70% of the elephant mortality locations as training data and used the remaining 30% for testing the resulting model. We tested for the correlations between all variables and found that all rainfall variables were highly correlated ($r > 0.5$). In the final model, we selected the rainfall variable that had the highest contribution in explaining the occurrence of elephant carcasses. There was also a correlation between NDVI and rainfall ($r > 0.5$) but we accounted for this in our analysis by showing results of each variables separately holding all other variables constant.

3. Results

Results from the Moran's I analysis (Moran's I = 0.316, Z score 6.74, $P < 0.05$) showed that elephant mortality mainly occurred within a distance of 1 to 8 km from each other in the Tsavo Protected Area, with maximum clustering occurring at a distance of ~8 km (Fig. 2). Our MaxEnt model had an AUC of 0.956 (Fig. 3). The four months cumulative precipitation prior to an elephant's death (41% contribution), NDVI (19% contribution) and the distance to nearest permanent rivers (6% contribution) negatively correlated with the mortality of elephants, whereas local elephant density (19% contribution) showed a small positive correlation with elephant mortality (Fig. 4). Furthermore, with exception of the long wet season, all other seasons showed a high (>0.5) probability of elephant mortality (Fig. 5). Based on this analysis, the probability of finding an elephant carcass is not uniform in Tsavo Conservation Area (Fig. 6), and the highest mortality occurs around permanent water and at low NDVI values.

We tested for the change in NDVI values with an increase in distance from the Galana River (at 5 km interval from 1 km to 50 km) for the driest recorded month of September 2009. NDVI was the lowest in this month and much lower than at the end of wet season. NDVI values were not significantly different with an increase in distance from the Galana river (ANOVA, $F_{6,133} = 0.362$, $P = 0.90$), suggesting that food availability was equally low close to the river compared to further away from the river.

4. Discussion

Elephants are bulk feeders and require large amount of food to survive (Barnes, 1983; Jachmann and Bell, 1985; Jachmann, 1989; Osborn, 2004). They are also water dependent and must drink water frequently; mostly every two days (De Knegt et al., 2011; Skarpe et al., 2014). In arid and semi-arid savannas where both water and forage are deficient in the dry season, elephant are faced with two major challenges: starvation or dehydration. The results of this study show that elephant mortality was high during long drought periods, i.e., at least four consecutive months with low or no rainfall (<150 mm). Moreover, elephant carcasses were aggregated and elephant mortality was high in areas with high local elephant density, low NDVI and in close proximity to permanent rivers. With the predicted increasing frequency of droughts in (East) Africa (Collier et al., 2008; Yang et al., 2014), these findings are vital for effective conservation of the African elephant.

Although drought-related elephant mortality is frequently observed (Dudley et al., 2001; Foley et al., 2008; Moss et al., 2011), and short-term studies on the role of extrinsic (environmental) and intrinsic (density-dependent) factors exists (Young and Van Aarde, 2010), long-term studies focussing on adult elephants are rare. This has been a major issue in understanding the repercussions of the infamous Tsavo Elephant disaster of the 1970s which often has been interpreted solely as the outcome of 'overpopulation' and has been used a proof of density dependency in elephant (Myers, 1973; Corfield, 1973). Our results support the role of high densities especially around permanent water during dry seasons. It has been observed that elephant aggregate in the proximity of rivers, particularly during the dry season (O'Connor et al., 2007; Young and Van Aarde, 2010). This 'crowding' effect can lead to depletion of local food resources (De Beer et al., 2006; Chamaillé-Jammes et al., 2008) and probably a high elephant mortality around water points. These observations corroborate with our finding that carcasses are aggregated and that mortality probability of elephants is higher closer to water. In our study, permanent rivers, specifically the Galana and Tiva rivers, seem to be the determinants for the heterogeneous distribution of elephant in the Tsavo landscape with high densities consistently recorded in close proximity to these rivers during the dry season. Our results further suggest that elephant mortalities are not likely to be explained by dehydration as elephant aggregate around permanent water, but that elephant mortalities are likely due to starvation. Our data shows that NDVI is low during dry periods close to rivers and further away. Although NDVI does not give any information about plant species composition and availability of palatable plants, it has previously been used as measure of vegetation productivity and therefore a proxy measure of available forage (e.g., Rasmussen et al., 2006; Young

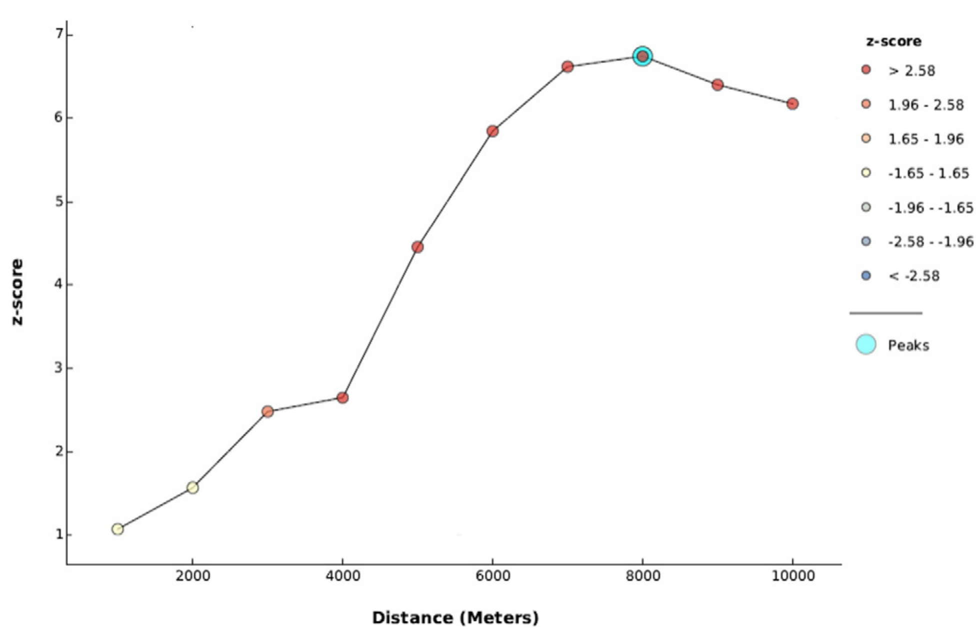

Fig. 2. Incremental spatial autocorrelation of elephant-carcass locations for the 2004–2012 period showing clustered elephant mortality pattern in the Tsavo Protected Area. The graph's peak at ~8 km indicates the distance of highest clustering of elephant carcasses.

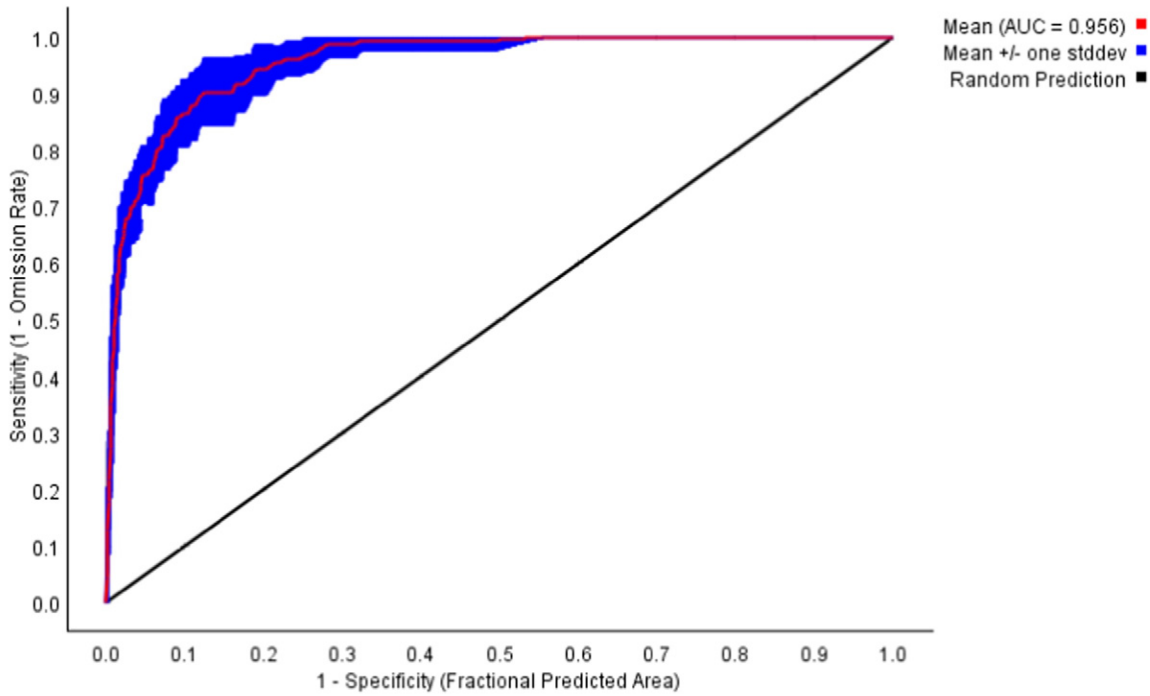

Fig. 3. The Area Under the Curve (AUC) of the best fitting model using MaxEnt to predict probability of natural elephant mortality in Tsavo Protected Area.

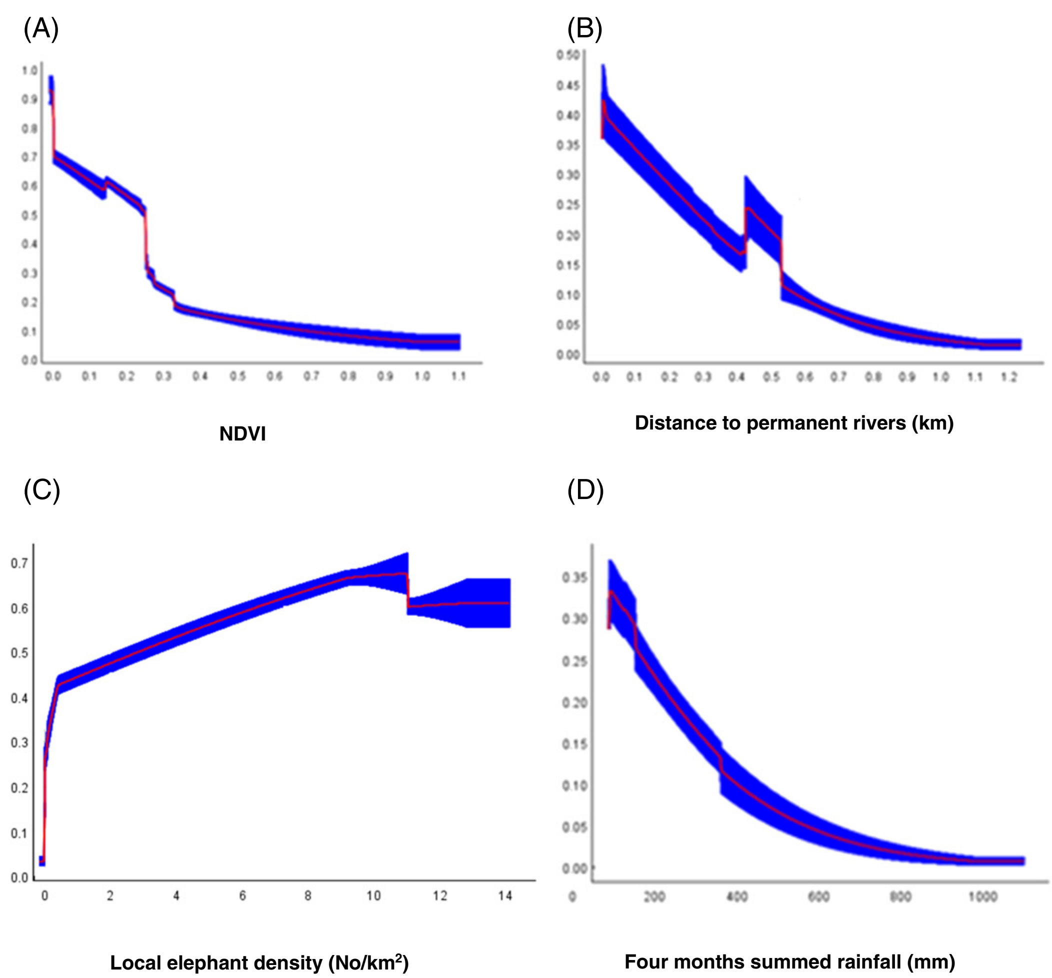

Fig. 4. The probability of elephant mortality in Tsavo as function of several environmental variables: (a) NDVI, (b) distance to permanent water, (c) local elephant density, and (d) cumulative precipitation for the past four months. For each panel, all environmental variables other than the one for which the effect is shown were kept at their average sample value in the MaxEnt model. The curves show the mean response of the 10 replicate MaxEnt runs and the mean ± one standard deviation (shades).

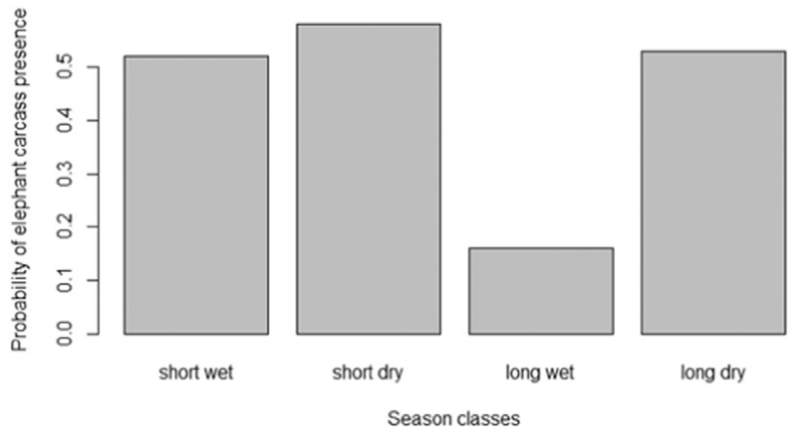

Fig. 5. Probability of elephant mortality for each of the four seasons in Tsavo Protected Area for the period 2004–2012.

et al., 2009; Young and Van Aarde, 2010). Our findings therefore support the hypothesis that forage limitation in prolonged drought may result in elephant starvation (Gough and Kerley, 2006; Young and Van Aarde, 2010), which appears to be intensified by local density. Effects of diseases and poaching are ruled out due to the selection of the carcasses.

We found a large effect of the cumulative precipitation of four months before an elephant's death. Similarly, Dudley et al. (2001) reported that it is the effective duration of the rainy season and not the total annual precipitation that determines elephant mortality during dry periods. A typical long dry season in Tsavo Conservation Area lasts for 5 months (June–October) (Omondi et al., 2008; Ngene et al., 2014). Rasmussen et al. (2006) showed that NDVI, which is a proxy measure of available browse, peaks at around 80 days after the onset of the rains. This implies that by the end of the long rainy season in May, there is probably sufficient forage and water for elephants, which may remain available up to about 3 months into the dry period (Rasmussen et al., 2006). Therefore, elephants have to cope with the remaining two dry months of declining food availability assuming that the short rains (November-December) come on time. Elephant is a coarse feeder and can survive for long on poor quality forage and during the long dry season when the fibre content of the grass is high, they switch to browse and herbs (Beekman and Prins, 1989; Moss et al., 2011). Sometimes the amount of rainfall in the long wet season may be too low to yield enough plant growth and fill the water points or the short rains may come late. Our results imply that, if the period of dry months extends beyond three months, it may lead to starvation of elephants, especially when local elephant density is high. For the nine years that this study covered, each year had an annual rainfall of over 250 mm, which is the average minimum rainfall reported for the Tsavo Conservation Area (Ngene et al., 2014). However the highest cumulative elephant deaths occurred in October of the year 2009. This year had the lowest rainfall during the long wet season, yielding 69 mm of annual rainfall. Because aboveground net primary production in arid and semi-arid environments is closely related to the amount of precipitation (Rosenzweig, 1968; Rasmussen et al., 2006; Moss et al., 2011), the amount of rainfall during the long wet season in 2009 may not have been enough to produce sufficient woody browse to take the elephants through the long dry season. This finding suggests that the long wet season determines the number of months that the forage will remain available in the long dry season before elephants succumb to starvation. Although we expected that the five months cumulative precipitation would show an even stronger correlation with elephant mortality, its effect was likely smaller than when considering four months cumulative precipitation: forage insufficiency did not last more than four months in the entire period that was covered by this study.

Fig. 6. Predicted probability of elephant mortality in Tsavo Protected Area, based on the MaxEnt model. Dark shades represent high probability (close to permanent water, Fig. 1D) and light shades representing low probability.

Although this study was conducted in Tsavo Conservation Area, the findings from this study can be generalized to other arid and semi-arid savannas where elephants occur. Because water is a key determinant of elephant distribution in these areas (Verlinden and Gavorv, 1998), it has long been used as management tool to manipulate impact of elephants on the vegetation, for example in Kruger National Park in South African (Smit and Grant, 2009; Smit and Ferreira, 2010; Hilbers et al., 2015). Although artificial water holes may lead to lower mortality, it is argued that the increase of water points is indirectly causing vegetation degradation by attracting and building up elephant densities around them (Smit and Ferreira, 2010). The closure of artificial waterholes in Kruger National Park to induce spatial redistribution of elephants in the landscape have resulted in increased elephant densities around large perennial rivers and large seasonal rivers as compared to smaller streams and areas far removed from rivers (Smit and Ferreira, 2010). Because there are few artificial water holes in the Tsavo Conservation Area, the trends in elephant distribution show opposite patterns to Kruger National Park, with very high elephant densities and mortalities around the perennial rivers.

Even though prolonged droughts usually result in high elephant mortality, the resilience of these dry ecosystems may perhaps improve as a result of these deaths that release the vegetation from high browsing pressure and give it a window to regenerate. Our results suggest that elephant populations in arid and semi-arid savannas appear to be regulated by drought-induced mortalities, which may be the best way of controlling elephant numbers without having to cull. This implies that arid and semi-arid savannas may in fact be sustained by growth and crashes of herbivore populations, which is predicted by the non-equilibrium hypothesis for rangelands (e.g., Vetter, 2005): non-equilibrium rangelands are thought to be mainly determined by stochastic abiotic factors, especially variable rainfall, which result in highly variable and unpredictable primary production, and population sizes of large herbivores rarely reach equilibrium with their fluctuating resource base. Maintaining these system as natural as possible may therefore keep elephant populations in savannas sustained for posterity.

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