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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