ARTICLE

Environmental drivers of biseasonal anthrax outbreak dynamics in two multihost savanna systems

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Abstract

Environmental factors are common forces driving infectious disease dynamics. We compared interannual and seasonal patterns of anthrax infections in two multihost systems in southern Africa: Etosha National Park, Namibia, and Kruger National Park, South Africa. Using several decades of mortality data from each system, we assessed possible transmission mechanisms behind anthrax dynamics, examining (1) within- and between-species temporal case correlations and (2) associations between anthrax mortalities and environmental factors, specifically rainfall and the Normalized Difference Vegetation Index (NDVI), with empirical dynamic modeling. Anthrax cases in Kruger had wide interannual variation in case numbers, and large outbreaks seemed to follow a roughly decadal cycle. In contrast, outbreaks in Etosha were smaller in magnitude and occurred annually. In Etosha, the host species commonly affected remained consistent over several decades, although plains zebra

(*Equus quagga*) became relatively more dominant. In Kruger, turnover of the main host species occurred after the 1990s, where the previously dominant host species, greater kudu (*Tragelaphus strepsiceros*), was replaced by impala (*Aepyceros melampus*). In both parks, anthrax infections showed two seasonal peaks, with each species having only one peak in a year. Zebra, springbok (*Antidorcas marsupialis*), wildebeest (*Connochaetes taurinus*), and impala cases peaked in wet seasons, while elephant (*Loxodonta africana*), kudu, and buffalo (*Syncerus caffer*) cases peaked in dry seasons. For common host species shared between the two parks, anthrax mortalities peaked in the same season in both systems. Among host species with cases peaking in the same season, anthrax mortalities were mostly synchronized, which implies similar transmission mechanisms or shared sources of exposure. Between seasons, outbreaks in one species may contribute to more cases in another species in the following season. Higher vegetation greenness was associated with more zebra and springbok anthrax mortalities in Etosha but fewer elephant cases in Kruger. These results suggest that host behavioral responses to changing environmental conditions may affect anthrax transmission risk, with differences in transmission mechanisms leading to multihost biseasonal outbreaks. This study reveals the dynamics and potential environmental drivers of anthrax in two savanna systems, providing a better understanding of factors driving biseasonal dynamics and outbreak variation among locations.

INTRODUCTION

Temporal dynamics in disease outbreaks occur across hosts, pathogens, and locations, where interannual and seasonal fluctuations in disease infections are commonly documented (Altizer et al., 2006; Kamo & Sasaki, 2005). Understanding transmission mechanisms underlying these dynamics is crucial to predicting or controlling future outbreaks (Lloyd-Smith et al., 2009). Temporal disease dynamics have been linked to host ecology or physiology, pathogen survival, and vector vital rates (Altizer et al., 2006; Dao et al., 2014; Fisman, 2012; Langwig et al., 2015; Liu et al., 2009). Among the causes of temporal disease dynamics, some of the main drivers are environmental forces, including rainfall, temperature, and vegetation. For example, high rainfall led to more cholera cases in Haiti (Eisenberg et al., 2013), and low rainfall was associated with outbreaks of chytridiomycosis in amphibians in Brazil (Moura-Campos et al., 2021). Seasons of high vegetation greenness in Alaskan and Canadian prairies were concordant with periods of more avian influenza cases (Lisovski et al., 2017), and low vegetation greenness was linked to an increased number of malaria cases in Bangladesh (Haque et al., 2010).

Environmental forces can interact with animal physiology or ecology and in turn affect infection patterns. These environmental fluctuations can drive disease dynamics through changes in host susceptibility or exposure to pathogens, and the ecology of animal hosts as well as their behaviors may be involved in these changes (Harvell et al., 2009; Shearer & Ezenwa, 2020). For instance, *Pseudogymnoascus destructans*, the fungal pathogen causing white-nose syndrome, thrives in cold temperatures when bats are hibernating (Langwig et al., 2015). Elk (*Cervus elaphus*) in the Greater Yellowstone Ecosystem in North America spend less time on supplemental feeding grounds after milder winters, limiting transmission risk at large social aggregations and leading to decreased brucellosis seroprevalence (Cross et al., 2007). These examples demonstrate how environmental fluctuations and interactions between environment and animal ecology can directly and indirectly alter transmission dynamics, complicating the detection of underlying mechanisms driving outbreak dynamics.

This study investigates the dynamics of anthrax cases in herbivorous wildlife, the environmental factors affecting anthrax infections, and between-species transmission/spillover in two national parks in southern Africa, Etosha National Park (ENP), Namibia, and Kruger National Park (KNP), South Africa. We evaluate potential transmission mechanisms based on environmental variation and between-species case correlations. Anthrax is a highly lethal, acute to peracute disease caused by the bacterium *Bacillus anthracis*. Anthrax only transmits via the environment, not directly between hosts (WHO, 2008), and hence presents a good model system to evaluate the effects of environment on disease dynamics. Transmission relies upon contact with environmental reservoirs, and spores released from anthrax carcasses can persist in the environment for years (Dragon & Rennie, 1995; Turner et al., 2016; WHO, 2008). Sites where high concentrations of spores can be found, such as anthrax carcass sites, serve as environmental reservoirs and transmission hotspots (Turner et al., 2014, 2016). All mammals can be infected with anthrax, although herbivorous mammals are the most common hosts and typically show higher susceptibility than carnivores (Hugh-Jones & de Vos, 2002; WHO, 2008). Herbivores are likely to die of anthrax within a few days to a week of a lethal exposure (Easterday et al., 2020; WHO, 2008). Although *B. anthracis* can infect a wide range of host species, a single outbreak typically involves one to a few species, while other susceptible species remain unaffected or marginally affected (Beyer & Turnbull, 2009; Driciru et al., 2020; Stears et al., 2021).

Anthrax outbreaks are reported from all continents except Antarctica, with considerable variation in interannual and seasonal outbreak dynamics across the pathogen's range (e.g., Blackburn & Goodin, 2013; Brownlie et al., 2020; Chen et al., 2016; Chikerema et al., 2012; de Vos, 1990; Hampson et al., 2011; Lindeque & Turnbull, 1994). Interannual anthrax outbreaks may follow multiyear cycles (de Vos & Bryden, 1996) or be linked to environmental fluctuations (Blackburn & Goodin, 2013; Hampson et al., 2011). Seasonally, anthrax infections in herbivores show biseasonality or bimodal seasonality—two annual peaks in infections—with dry and wet seasonal peaks (Lindeque & Turnbull, 1994; Turner et al., 2013). However, anthrax dynamics in different host species are not necessarily synchronized; each species tends to have only one seasonal peak, but those species-specific peaks may occur at different times of the year (Hampson et al., 2011; Lindeque & Turnbull, 1994; Turner et al., 2013). These patterns imply that not every species shares the same transmission source or infection pathway and that transmission mechanisms may be related to the ecology of each species.

Mechanisms driving the biseasonality of infectious diseases are potentially more complex than for single

infection peaks (Pascual & Dobson, 2005), involving two or more drivers. In wildlife diseases, demographic factors, such as age structure or the timing of parturition, have been commonly linked to a second seasonal peak. A second seasonal peak in raccoon (*Procyon lotor*) rabies was found to be concordant with a higher contact intensity period during dispersal of young (Ma et al., 2010; Torrence et al., 1992). A second peak of avian malaria infection in blue tits (*Cyanistes caeruleus*) or mycoplasmal conjunctivitis in house finches (*Carpodacus mexicanus*) may be attributed to postbreeding recruitment of immunologically naïve fledglings (Altizer et al., 2004; Cosgrove et al., 2008). Biseasonality within a guild of coexisting host species is rarely reported, possibly due to underreporting or a lack of research that integrates patterns among multiple host species. In a multihost system, the demographic structure of a single species is less likely to drive the disease seasonality. Instead, the abundance of total host species, weighted by their host competence, may play a larger role (Buhnerkempe et al., 2015; Keesing et al., 2006). One example of biseasonality in a multihost disease is avian influenza, predicted to have multiple peaks in North America because of the mixture of resident and migratory birds at stopover sites on the north- and south-bound migration routes (Brown et al., 2013). Multihost dynamics and their drivers can be more complex and less understood owing to variations in the ecology of host species as well as differences in species interactions (Buhnerkempe et al., 2015). The biseasonal pattern of anthrax dynamics would thus imply that there are multiple species-specific triggers in an anthrax system or that infection spreads from one host species into another.

Outbreak dynamics can be linked to transmission dynamics (Altizer et al., 2006), so to better understand anthrax dynamics, it is important to understand transmission routes and transmission modes. Various pathways have been proposed to explain anthrax transmission in wildlife, including contact with spores in the environment through grazing, browsing, bone handling, drinking, and inhalation. Hypothesized transmission mechanisms can be broadly categorized into four major groups, based on where hosts may contact spores and the routes of entry into the host bodies (Figure 1). First, hosts can contract pathogens directly at hotspot sites through foraging behavior (H1.1 in Figure 1) (Hugh-Jones & de Vos, 2002; Turner et al., 2013, 2014, 2016; Walker et al., 2020; WHO, 2008) or osteophagia (H1.2) (Turner et al., 2013). Second, animals can inhale spores through wind, dust, or close contact at hotspot sites (H2) (Barandongo et al., 2018; Turnbull et al., 1998). Third, spores can be relocated from hotspot sites through water (H3). For example, water flow concentrates spores at low-lying areas (Dragon & Rennie, 1995;
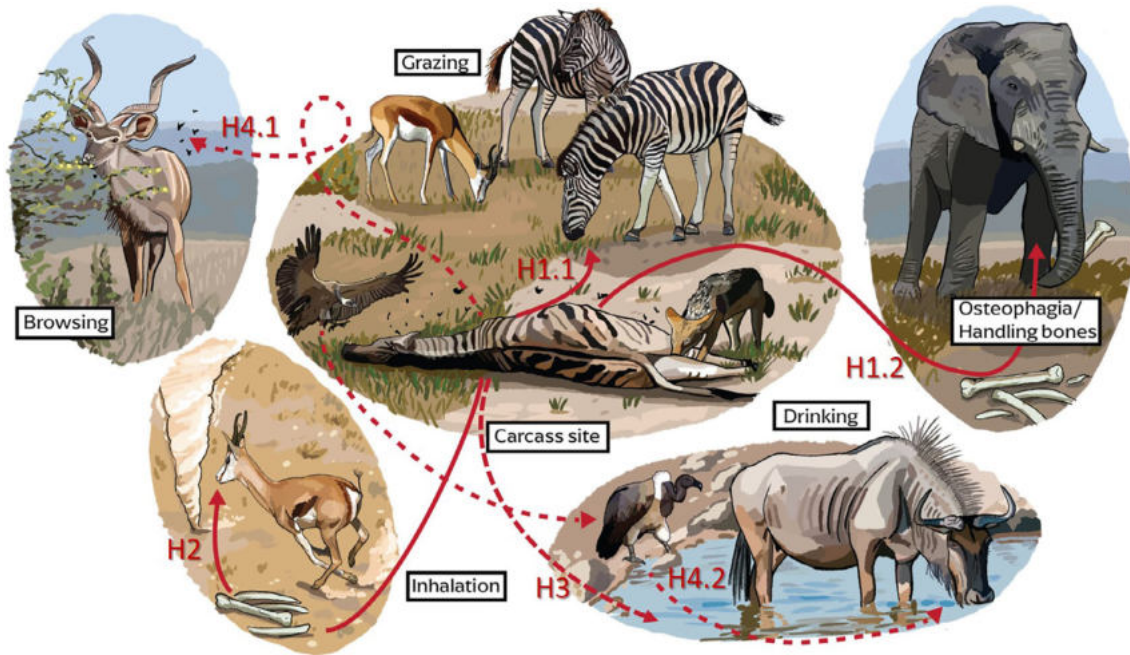
FIGURE 1 Common hypothesized mechanisms regarding anthrax transmission and dynamics in herbivorous wildlife. Solid arrows indicate exposures occurring at carcass sites; dashed arrows indicate exposures requiring biotic or abiotic vectors. Herbivores may contract pathogens directly at carcass sites through foraging behavior (H1.1) (Hugh-Jones & de Vos, 2002; WHO, 2008; Turner et al., 2013, 2014, 2016; Walker et al., 2020) or osteophagia/bone handling (H1.2) (Turner et al., 2013). Herbivores are also hypothesized to inhale spores through wind or dust bathing (H2) (Barandongo et al., 2018; Turnbull et al., 1998). Water may relocate *Bacillus anthracis* spores and increase their density in low-lying areas or dilute a hotspot area (H3) (Dragon & Rennie, 1995; de Vos & Bryden, 1996; Mongoh et al., 2007). Spores could be translocated to leaves via blowflies (H4.1) (Hugh-Jones & de Vos, 2002; Hugh-Jones & Blackburn, 2009) or to water via vultures (H4.2) (Hugh-Jones & de Vos, 2002; Hugh-Jones & Blackburn, 2009). In addition to the pathways shown in the figure, biting flies (tabanid flies) are hypothesized to translocate pathogens and cause cutaneous anthrax (Blackburn et al., 2010; Fasanella et al., 2010). Herbivore behavioral responses driving foraging behavior at infectious sites may be supported when there is association of anthrax mortalities with rainfall accumulated during 1–2 preceding months or vegetation index of the previous month. Water relocation may be supported when there is a correlation of cases with rainfall within 2 weeks prior. Associations of cases with environment for mechanisms involving spores translocated by organisms are largely unclear and potentially more complex.

Mongoh et al., 2007) or washes spores away (de Vos & Bryden, 1996). Fourth, living organisms, such as biting flies (Diptera: Tabanidae), scavenging blowflies (Diptera: Calliphoridae) (H4.1), or vertebrate scavengers, for example, vultures (Accipitriformes: Accipitridae) (H4.2), may translocate pathogens mechanically or biologically (Blackburn et al., 2010; de Vos & Bryden, 1996; Fasanella et al., 2010; Hugh-Jones & Blackburn, 2009; Hugh-Jones & de Vos, 2002). These mechanisms are not mutually exclusive, and more than one mechanism may coexist among host species or within a single species. The relative importance of each mechanism may also vary among species, systems, and spatial or temporal scales (Hugh-Jones & de Vos, 2002).

Investigating the time scales between an environmental signal and a subsequent disease outbreak can help identify underlying transmission mechanisms for acute diseases such as anthrax. Anthrax outbreaks have been linked to changes in rainfall or vegetation under both wetter- and drier-than-average conditions for a system (Blackburn & Goodin, 2013; Hampson et al., 2011; Huang et al., 2021; Hugh-Jones & Blackburn, 2009; Parkinson et al., 2003; Turner et al., 1999, 2013). These environmental signals are clearly linked, with vegetation growth stimulated by rainfall 1–2 months prior (Schmidt & Karnieli, 2000). A relationship between rainfall and anthrax mortalities occurring at short time intervals, with rainfall occurring 1–2 weeks prior to case detection, would be consistent with water transport of spores playing a role in anthrax transmission. This short time interval could encompass rainfall altering host exposure to the pathogen, infection, death (Easterday et al., 2020; WHO, 2008), and subsequent discovery of the carcass (Bellan et al., 2013). A positive relationship between rainfall and anthrax cases on this shorter time scale could be evidence of spore aggregation by water, while a negative relationship could indicate that water disperses spores, diluting spore concentrations at infectious sites and

reducing lethal contacts. Slightly longer time scales, around 2 months between rainfall and mortalities (or around 1 month from vegetation green-up to mortalities), would suggest that vegetation growth in response to rainfall alters transmission risk. In this time window, a positive or negative relationship between rainfall and mortalities suggests an increased or decreased exposure risk, respectively, as a result of changes in host foraging behavior or movement patterns, with the directionality (positivity or negativity) depending upon how hosts respond to the environmental cue and the interaction between behavior and disease risk.

Among the hypothesized transmission pathways for wildlife anthrax (Figure 1), we examined whether anthrax outbreaks could be linked to variation in rainfall and vegetation greenness index at different time lags, to investigate the transmission mechanisms involving spore transport via water movement and foraging behavioral responses to changes in vegetation (Figure 1, H1.1 vs. H3). For transmission mechanisms involving biotic vectors, that is, insects or vultures, relationships with the environment can be more complex (e.g., Reibe & Madea, 2010) and, hence, difficult to evaluate with only rainfall and remotely sensed vegetation data. We also did not consider inhalational anthrax since this transmission route is unlikely to occur through dust bathing or wind translocation in a natural system due to low concentrations of spores moved via this pathway (Barandongo et al., 2018; Turnbull et al., 1998).

It is challenging to infer causal relationships with traditional statistical analyses, for example, autoregressive regressions, assuming fixed effects between variables. Correlation can result from a confounding variable and does not reflect causation, and a lack of a direct correlation does not necessarily represent a lack of causality due to context-dependent relationships (Chang et al., 2017; Deyle, May, et al., 2016; Sugihara et al., 2012; Ye, Beamish, et al., 2015). Because of this challenge, we performed empirical dynamic modeling (EDM) to evaluate the potential causal associations between the environment and anthrax mortalities. EDM is an equation-free method that is not restricted by a set of equations or fixed relationships to analyze time-series data, and so it can flexibly infer patterns or context-dependent associations based on observations (Sugihara et al., 2012; Sugihara & May, 1990). With state-space reconstruction derived empirically, EDM could potentially provide insights into the mechanistic relationships of a system.

In addition to investigating relationships between environmental factors and anthrax cases, we evaluated correlational patterns in anthrax dynamics among species on different temporal scales. Case correlations among species can provide a better understanding of multihost dynamics, including which species are driving outbreaks, and the level of dependence or independence among outbreaks occurring in different species and in different seasons. Two species with a positive relationship in anthrax cases may indicate that similar or interrelated mechanisms are involved (Mutshinda et al., 2009) or that anthrax cases in one species drive cases in the other (Craft et al., 2008). Given the long persistence of *B. anthracis* spores in the environment, outbreaks occurring from one season to the next could be a continuation of an existing outbreak in the same or different species or a separate outbreak initiated through host–reservoir contact.

In this study, we analyzed patterns of anthrax mortalities in ENP and KNP. Leveraging two systems with different disease dynamics, yet many of the same host species, will help us to better understand the underlying environmental mechanisms that drive outbreaks (Turner et al., 2021). We first examined outbreak dynamics and biseasonal patterns in anthrax cases in both systems. We then explored whether there were associations among multihost dynamics by evaluating anthrax case correlations within and between species for each park, using autocorrelation functions and cross-correlation functions. Finally, we investigated the complexity of transmission mechanisms by evaluating the relationships between disease dynamics and fluctuations in environmental conditions, including rainfall and vegetation greenness, using EDM. By exploring the relationships between environmental variation and anthrax outbreaks across different time scales, we aimed to determine whether spore transport by water or host responses to vegetation dynamics were more likely transmission mechanisms driving the anthrax dynamics and whether these were consistent or variable between study areas and host species.

MATERIALS AND METHODS

Study areas and periods

This study was conducted in central ENP and northern KNP (Figure 2), where the highest incidence of anthrax mortalities is detected within the two parks (Ebedes, 1976; Ochai et al., 2022; Steenkamp et al., 2018). ENP and KNP are located at similar latitudinal ranges and have many species in common. Central ENP was defined as the Okaukuejo management section (Figure 2), where there is better mortality surveillance than in other sections of the park (Bellan et al., 2013). Central ENP is a semiarid savanna, with three seasons: wet season in January–April, dry season in May–August, and semidry season in September–December. Rainfall is strongly seasonal and occurs mainly between November and April, with the greatest
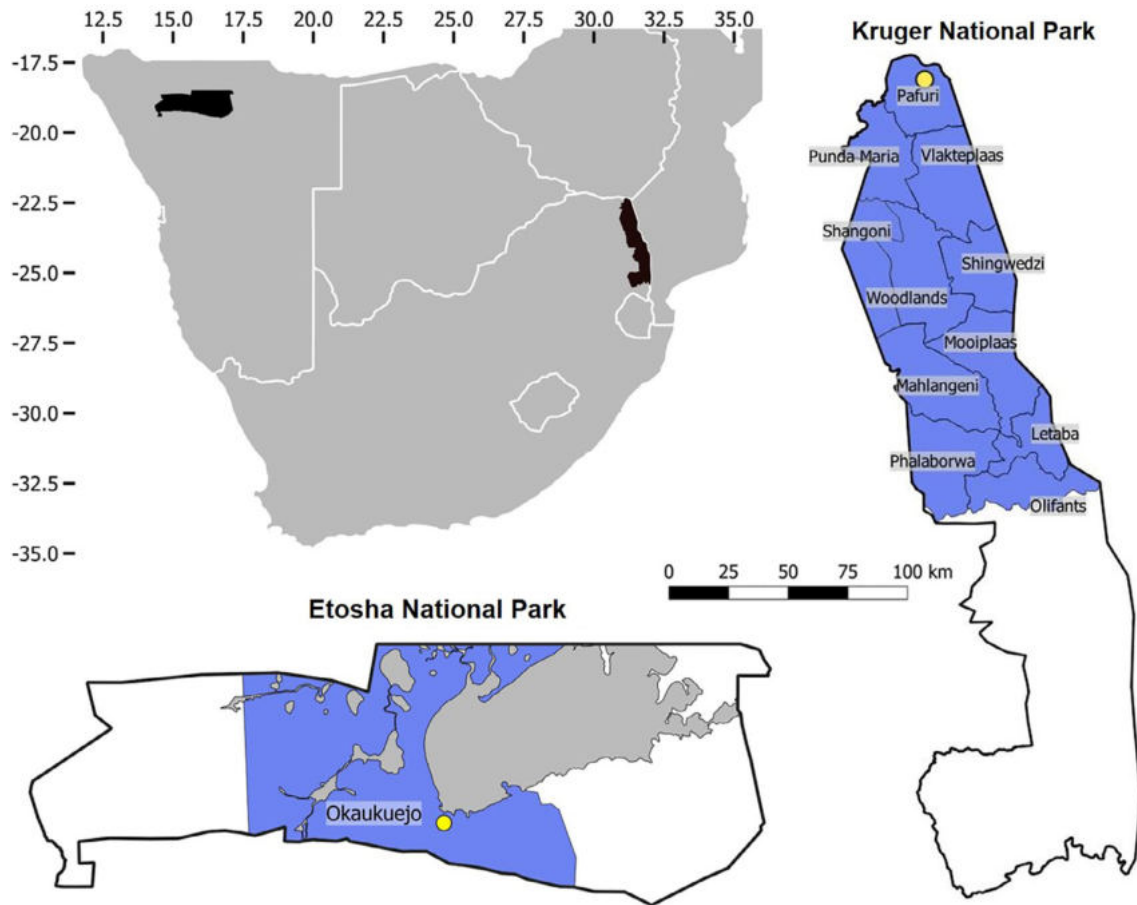
FIGURE 2 Map of study areas (blue), including central Etosha National Park (ENP), Namibia, and northern Kruger National Park (KNP), South Africa, in southern Africa. The management sections included in the study areas are labeled. The yellow circles are Okaukuejo station in ENP and Pafuri station in KNP, where the rainfall amounts were measured, and the gray areas in ENP are salt pans. The scale bar is related to the maps of the two parks. The numbers on the left and up to the map of southern Africa indicate degrees of latitude and longitude.

monthly rainfall occurring in January and February (Engert, 1997). Average annual rainfall is 358 mm (Okaukuejo station) (Huang et al., 2021). Animals rely on seasonal water from rainfall, or perennial water at boreholes, artesian or contact springs along salt pans (Auer, 1997). Much of central ENP is covered by mopane (*Colophospermum mopane*) shrubveld or treeveld and open grasslands and dwarf shrub savanna along a large salt pan that covers a fifth of the park. Anthrax mortalities occur every year, and plains zebra (*Equus quagga*), springbok (*Antidorcas marsupialis*), blue wildebeest (*Connochaetes taurinus*), and African elephant (*Loxodonta africana*) are common host species (Turner et al., 2013). Zebra, springbok, and wildebeest in ENP are likely to contract the disease through foraging at sites where animals previously died of anthrax (Turner et al., 2014, 2016), but where and how elephants get infected is largely unknown.

In this study, we defined northern KNP as all sections north of the Olifants River (Figure 2). Vegetation in

northern KNP is characterized by woody and shrubland savannas with mopane as the dominant tree species (Gertenbach, 1983), with higher canopy cover than in ENP. KNP also has higher water availability than ENP, from seasonal water and perennial boreholes, dams, springs, pools, and rivers flowing west–east (Gaylard et al., 2003). The seasons based on rainfall are 1 month earlier than ENP: wet season in December–March, early-dry season in April–July, and late-dry season in August–November (Owen-Smith, 2013). The average annual rainfall is 430 mm in northern KNP (Pafuri section) (Venter & Gertenbach, 1986), and, unlike ENP, there is still occasional rainfall during the dry period (Gertenbach, 1983; Zambatis & Biggs, 1995). In KNP, impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), and African buffalo (*Syncerus caffer*) are common anthrax host species, and the highest incidence of mortality occurs in the northernmost Pafuri section (Steenkamp et al., 2018), where habitats are composed of woodlands with dominant mopane and

other tree species and floodplains along the Luvuvhu and Limpopo rivers. Mechanisms of anthrax transmission in KNP may involve scavenging blowflies translocating spores to leaves of woody plant species or vultures translocating spores to water where they bathe (Basson et al., 2018; Braack & de Vos, 1990; de Vos, 1990; de Vos & Bryden, 1996). Anthrax dynamics in KNP are also suspected to be driven by host population density (de Vos & Bryden, 1996). KNP outbreaks followed a roughly decadal cycle with peaks in the dry seasons (de Vos & Bryden, 1996), although changes in the frequency and timing have occurred in recent years. Historical outbreaks, occurring before the mid-1990s, were large, impacting hundreds to thousands of animals in a single outbreak, where the kudu population was the most severely affected (de Vos & Bryden, 1996).

Anthrax mortality data

Animal mortality surveillance in both parks is opportunistic. In this study, anthrax mortality included anthrax confirmed cases from blood smear examination, bacterial culture, or molecular diagnosis from blood swabs, as well as anthrax suspected cases diagnosed by symptoms (i.e., blood exudation) (WHO, 2008) in cases where no samples were collected. We obtained anthrax mortality data from 1976 to 2014 in ENP and 1990 to 2015 in KNP through the Etosha Ecological Institute and Office of the State Veterinarian in KNP, respectively. We removed mortalities for which carcass discovery involved tracking the locations of scavengers with Global Positioning System (GPS) tags if the information was available to better standardize surveillance efforts over time. We analyzed case numbers and did not standardize these against population density, because population estimates were not available for all species and years. Given that anthrax in ENP occurs annually, we evaluated relationships between cases and environmental triggers using the entire period of the available mortality data. However, because of the large gaps between anthrax outbreaks in KNP, we took a two-pronged approach to evaluating relationships between the environment and outbreaks for this system. First, we limited our analyses to 2010–2015, a period during which anthrax mortalities were more frequent (Appendix S1: Figure S1). We then investigated the full time series to evaluate environmental factors behind the occurrence of anthrax outbreaks. The gaps in anthrax observations between large outbreaks could be a feature of the KNP system or surveillance not detecting low case numbers of anthrax. Because zebra and impala anthrax cases in KNP were aggregated within the Pafuri region (98.8% and 100% of cases in 2010–2015 of each species,

respectively, were in this area), the spatial extent of these two species was restricted to Pafuri for anthrax cases and vegetation index calculations. Cases in other species were more dispersed throughout the northern sections of the park, and case numbers and vegetation index calculations covered the entire study area.

We calculated the species compositions of anthrax mortalities over time in both parks. All cases in ENP, spanning the period 1976–2014, were included for the comparison. For KNP, we compared the mortality data in the periods 1990–1991, 1993–1994, 1999, and 2010–2015 (the four periods having larger outbreaks) (Appendix S1: Figure S1), with historical outbreaks in 1960 and 1970, using data extracted from Pienaar (1961) and de Vos (1990).

Environmental variability

We investigated relationships between environmental variability and anthrax case numbers at different scales. Because anthrax mortality peaked in different times of a year, we used system-specific rainfall years rather than calendar years when making comparisons at the interannual scale to better understand associations between anthrax mortalities and environmental variables (rainfall and vegetation index). Rainfall years in ENP are from July to June (e.g., July 2006–June 2007 is the 2007 rainfall year). In KNP, outbreaks occurred in the wet season more frequently in 1993–2015, so we also applied rainfall years from July to June. However, because outbreaks in 1990–1991 and historical outbreaks began anywhere from May to October (de Vos & Bryden, 1996), we defined rainfall years from October to September to better capture the variation in rainfall prior to the onset of the outbreaks.

Environmental variability was assessed using variables derived from daily rainfall measurements and remotely sensed vegetation greenness from the Normalized Difference Vegetation Index (NDVI). This index is used widely as a proxy for the spatiotemporal dynamics of photosynthetically absorbed radiation and makes it possible to estimate the greenness or the amount of chlorophyll in vegetation cover (du Plessis, 1999; Tucker et al., 1985). Both rainfall and NDVI allow for tracking changes in the quality and availability of vegetation and are often strongly correlated in dry environments (Nicholson et al., 1990). Rainfall also serves as a proxy for water availability and flow in systems. Although rainfall is the most commonly available estimate of environmental variation, it is generally not recorded at closely spaced localities, and therefore provides a poor spatial measure of rainfall variability, an important factor in semiarid ecosystems. NDVI provides better spatial coverage and resolution, which could make it a better variable than rainfall for investigating environmental fluctuations.

Rainfall, vegetation greenness, and anthrax case data were binned into two intervals per month: Days 1–15 and Day 16 to month's end. These intervals match the scale of NDVI data extracted from the Global Inventory Modeling and Mapping Studies (GIMMS) NDVI$_{3g}$ data set with a resolution of 1/12-degree latitude/longitude (Pinzon & Tucker, 2014; Tucker et al., 2005). For each bimonthly period we calculated the average daily rainfall and the average NDVI of composite estimates for the study areas, excluding the salt pans from central ENP (Figure 2). Although vegetation does emerge on parts of the saline pans, particularly in high-rainfall years (le Roux et al., 1988), the pans generally show very low NDVI values, with little seasonal variation; therefore, including them in the study area would have dampened the overall reflectance recorded and reduced the seasonal signal seen in surrounding habitats. We used rainfall measurements from management stations to characterize rainfall in the study areas. Daily rainfall was recorded at Okaukuejo station in central ENP and Pafuri station in northern KNP. The study period for ENP was restricted to rainfall years 1983–2014 for investigating associations between anthrax mortalities and environmental variables because vegetation index data were only available starting in 1981 and daily rainfall data were lacking for 1982.

Temporal correlations of anthrax cases within and between species

We assessed relationships of anthrax cases within and between species at different time lags to better understand the patterns in multihost disease dynamics in the two parks. We explored correlations at bimonthly intervals, with time lags ranging from 0 to 24 intervals (i.e., out to 1 year). We first calculated average daily cases by species to adjust for different numbers of days among intervals. We then applied autocorrelation functions (ACFs) and cross-correlation functions (CCFs) to evaluate the relationships of anthrax mortalities within and between species, respectively ($N = 936$ intervals for ENP and $N = 144$ intervals for KNP). We also investigated whether total case numbers drove outbreaks in certain species by examining correlations between total cases and cases that followed in those species. Therefore, we applied CCFs to investigate correlations between preceding total cases and cases in common host species. All analyses in this study were performed in R version 4.0.2 (R Core Team, 2020). We used the stats package (R Core Team, 2020) for both ACF and CCF.

Associations of anthrax cases with environmental variables

We evaluated associations of anthrax cases with environmental variables to determine possible transmission mechanisms. This method has its limitations and is unable to detect every proposed transmission pathway (Figure 1); thus, the evaluated mechanisms included only spore transport via water and host behaviors in response to vegetation dynamics. We performed EDM to assess relationships between anthrax mortalities of common host species and both rainfall and NDVI. With state-space reconstruction, EDM can reveal and reconstruct dynamics in an attractor from a time-series variable, using single (univariate) or multiple (multivariate) variables (Deyle & Sugihara, 2011; Sugihara, 1994; Sugihara et al., 2012; Sugihara & May, 1990; Takens, 1981). The concept behind EDM is that the dynamics of an attractor are composed of a set of states and deterministic rules, and they collectively project the dynamics (Ye, Beamish, et al., 2015). To use EDM, an attractor cannot be entirely stochastic, though it is allowed to have some stochasticity (Munch et al., 2020). EDM approaches to reconstructing a variable include simplex projection and S-map, which are based on nearest-neighbor regression and nonlinear state dependence with a weighting function, respectively (Cenci et al., 2019; Sugihara, 1994; Sugihara & May, 1990).

In addition to forecasting, EDM can also be used to assess potential causal relationships between time-series variables. Not assuming a fixed effect, EDM is particularly suitable for systems with nonequilibrium dynamics and nonlinear state-dependent relationships between variables (Chang et al., 2017; Sugihara et al., 2012). One EDM approach, convergent cross-mapping (CCM), can be used when aiming to identify relationships between two variables (Sugihara et al., 2012). This approach constructs two "shadow attractors" based on each variable. The concept of a conjectural causal relationship in CCM is that if A causes B, the shadow attractor constructed by B can have dynamic features of A and potentially predict the dynamics of A (Sugihara et al., 2012). Though the use of EDM is still relatively uncommon, it has been used for studying diseases or vectors and climatic/weather drivers (Deyle, Maher, et al., 2016; Grziwotz et al., 2018; Nova et al., 2021).

We only selected anthrax cases in common host species based on the results of species composition calculations. In the preparation of the data sets for analyses, we calculated average daily anthrax mortalities by species to adjust for different numbers of days by interval, based on the data from the bimonthly intervals ($N = 768$ intervals for central ENP; $N = 144$ intervals for northern KNP). We also attempted to extend the period to 1990–2015 for

KNP to evaluate whether the environmental variables could explain the large interannual variation in outbreaks ($N = 624$ intervals). For the KNP data set with a longer time period, only NDVI was assessed due to discontinuity of available rainfall data in the 2000s, so we were unable to test spore translocation by water for this data set. We standardized variables of anthrax cases, rainfall, and NDVI, with center at zero and standard deviations equal to one. For the EDM approaches, we followed and modified the procedures from Chang et al. (2017) and Nova et al. (2021). We first decided on an optimal embedding dimension between 1 and 10, for anthrax mortality by species and park using simplex projections, based on the highest Pearson's correlation coefficient with out-of-sample predictions using one time lag (Chang et al., 2017; Ye, Deyle, et al., 2015). We then applied CCM to assess relationships of anthrax cases with rainfall and NDVI at different time lags. For the environmental variables with best-performing time lags, we forecasted corresponding anthrax mortalities using nonlinear state dependence relationships with S-map, based on the same embedding dimensions predicted earlier, and weighting functions with the highest Pearson's correlation coefficients from out-of-sample predictions. If the Pearson's correlation coefficient between observed and predicted anthrax mortalities was higher than 0.1, then we applied partial derivatives of anthrax mortalities with respect to environmental predictors in the forecasting models to investigate the interactions of the environmental variables and anthrax mortality, or the effects of the environmental predictors on the magnitude of anthrax mortality (Deyle, May, et al., 2016). Finally, based on the general directionality (positivity or negativity) of the environmental effects on anthrax mortalities and the best-performing time lags, we assessed which transmission mechanisms were most plausible for the species and park (H1.1 vs. H3 in Figure 1).

Convergent cross-mapping

Using anthrax mortalities to reconstruct NDVI and rainfall dynamics with time-lags from one to six intervals (2 weeks to 3 months), we repeatedly conducted CCM to evaluate relationships and the most important time lags for the environmental variable (Wang et al., 2018; Ye, Deyle, et al., 2015). We used the Pearson's correlation coefficient ρ (cross-mapping skill) between predicted and observed environmental values as the index to evaluate the relationships (Nova et al., 2021; Sugihara et al., 2012; Ye, Deyle, et al., 2015). To calculate ρ, 500 samples were randomly selected for each library size (i.e., number of total intervals calculated) in CCM. We compared ρ at the

maximum library size among different time lags to identify the best-performing time lags. The time lag with the highest ρ for either rainfall or NDVI was further examined with two criteria to confirm the relationships. First, ρ at maximum library size of CCM using observed data were significantly different from ρ of CCM using seasonal null models (Deyle et al., 2016) with a Kolmogorov–Smirnov test. Seasonal null models were created for rainfall and NDVI with the mean seasonal trends, smoothing splines, and additive Gaussian noise with 0.5 SDs. Second, a Mann–Kendall trend test showed $\tau > 0$ and significance of ρ of observed data, indicating convergent ρ, as ρ increased monotonically then reached a plateau along with the increase in library size (Grziwotz et al., 2018). No environmental variable showed significant differences between observations and seasonal null models in CCM for KNP from 1990 to 2015, and thus this larger data set was not evaluated with the following procedures.

Multivariate S-map forecasting

For any environmental variables with best-performing and significant time lags identified from CCM, we used these variables to forecast anthrax mortalities with nonlinear relationships using multivariate S-map to examine their predictive capability. When only one significant variable was identified as an important predictor from CCM, we included only that environmental variable in the model. When rainfall and NDVI were both identified as important predictors, we included one and both variables in a model. If an embedding dimension was more than the number of environmental variables, we added time-lagged anthrax mortality of the target species from $t-1$ to earlier intervals in a model, until the number of predictors equaled the embedding dimension. For example, if the embedding dimension was four, a model including two environmental variables used $NDVI_{t-lagN}$, $rainfall_{t-lagR}$, anthrax mortality$_{t-1}$, and anthrax mortality$_{t-2}$ to forecast anthrax mortality$_t$. For ENP, we used rainfall years 1983–2005 to build a model to predict anthrax mortality data based on environmental variables and forecasted anthrax mortality from 2006 to 2014. For KNP, we built a model based on data from calendar years 2010–2013 and forecasted for 2014 to 2015. Pearson's correlation coefficient ρ (forecasting skill) between predicted and observed values was used to evaluate the predictive power of our models.

We wanted to know not only which environmental drivers (and time lags) might have caused disease outbreaks but also how they affected the disease dynamics. Following the forecast with S-map, we estimated the

interaction strengths between environmental variables and anthrax mortality. Chang et al. (2021) recently proposed a method (multiview distance regularized S-map) for more accurate estimation of interaction when there was high embedding dimensionality. However, since our systems had relatively low dimensionality, we applied partial derivatives of anthrax cases with respect to environmental variables during the prediction periods (2006–2014 for ENP and 2014–2015 for KNP) using the coefficients of S-map to measure the interaction strengths between the environment and anthrax mortality (Deyle, May, et al., 2016). From the partial derivatives we determined the directionality of estimated environmental effects on anthrax mortalities. We then explored whether the effects varied with the seasons. EDMs and seasonal null models were run using the rEDM package (Park et al., 2020). Kolmogorov–Smirnov and Mann–Kendall trend tests were done using the packages stats (R Core Team, 2020) and Kendall (McLeod, 2011), respectively.

RESULTS

Seasonality and dynamics in anthrax cases

KNP experienced large interannual variation in anthrax outbreak occurrence and intensity, with larger outbreaks occurring less frequently, whereas ENP experienced relatively smaller outbreaks, which occurred annually (Appendix S1: Figure S1). KNP saw large outbreaks in 1990–1991, 1993–1994, 1999, and 2010–2015, with on average more than 100 individuals affected per year during these outbreaks, but between these periods, anthrax cases were infrequently detected (Appendix S1: Figure S1b).

Large interannual variation in anthrax mortalities was observed for elephant in ENP, as well as host species in KNP such as zebra, impala, kudu, and buffalo (Appendix S1: Figures S2 and S3). In ENP, there was a big anthrax outbreak in elephant in 1982, with more than 60 mortalities detected, and another smaller outbreak in 1990 (Appendix S1: Figure S2). However, since then, only sporadic elephant anthrax cases have been observed, and relative to other species, elephant cases have declined over time (Figure 3a, Appendix S1: Figure S4). In contrast, although zebra has always been the most common host in ENP, its proportional contribution to outbreaks has increased over time (Figure 3a, Appendix S1: Figure S4). In KNP, outbreaks in 1960, 1970, and 1990–1991 affected mostly kudu and sometimes buffalo, with small proportions of waterbuck (*Kobus ellipsiprymnus*), impala, roan antelope (*Hippotragus equinus*), or nyala (*Tragelaphus angasii*) (Figure 3b). However, there seemed to be a switch in the dominant host species in the 1990s to 2000s, with

impala replacing kudu as the most common host species in KNP. Although kudu was the most impacted species in the 1999 outbreak, the majority of cases in 1993–1994 and 2010–2015 were impala (Figure 3b). Zebra and elephant were also proportionally more affected in the more recent outbreaks (Figure 3b). Descriptive statistics of anthrax cases in host species commonly affected during the study periods are summarized in Table 1.

Anthrax cases across the herbivore guild in both parks can occur almost throughout the year, but each species had an apparent seasonal peak (Figure 4). For the common host species shared between parks, zebra anthrax mortalities peaked in wet seasons and elephant mortalities in dry seasons (semidry in ENP and late-dry in KNP) in both study areas (Figure 4). Anthrax mortalities of kudu and buffalo in KNP peaked in the dry season, while springbok and wildebeest in ENP and impala in KNP had wet-season peaks (Figure 4). The wet-season anthrax peaks were concordant with the NDVI peaks, occurring 1 to 2 months after peaks of rainfall (Figure 4).

Temporal correlations of anthrax cases within and between species

In both parks, temporal correlation analyses examining relationships between total anthrax cases or cases in the dominant host species and cases in other species showed similar patterns (Figure 5), likely due to the dominant contribution of the main host to total cases in each system. Positive correlations around the zero time lag (≤ 4 intervals or 2 months) indicated synchronization of cases between species. For both parks, synchronization in cases can be observed between species sharing the same seasonal peaks (Figure 5). An exception was seen for elephant in northern KNP, which had weaker correlations with other species around the zero time lag (Figure 5i), suggesting low to no synchronization even for species with cases occurring in the same season (i.e., kudu and buffalo). Synchronization between two species may suggest either a more immediate direct relationship (mortalities in one species affect the other) or an indirect relationship (cases in both species are driven by the same covariate, such as an increased or decreased amount of rainfall).

Patterns in case correlations within or between species in ENP tended to be less complex than in KNP. In ENP, there was more synchronization among cases, with an additional peak in correlations occurring around a year later within or between species (Figure 5a–c). One exception to this is the correlation between zebra cases and wildebeest cases following 6–7 months later (Figure 5a). In KNP, preceding impala and kudu cases
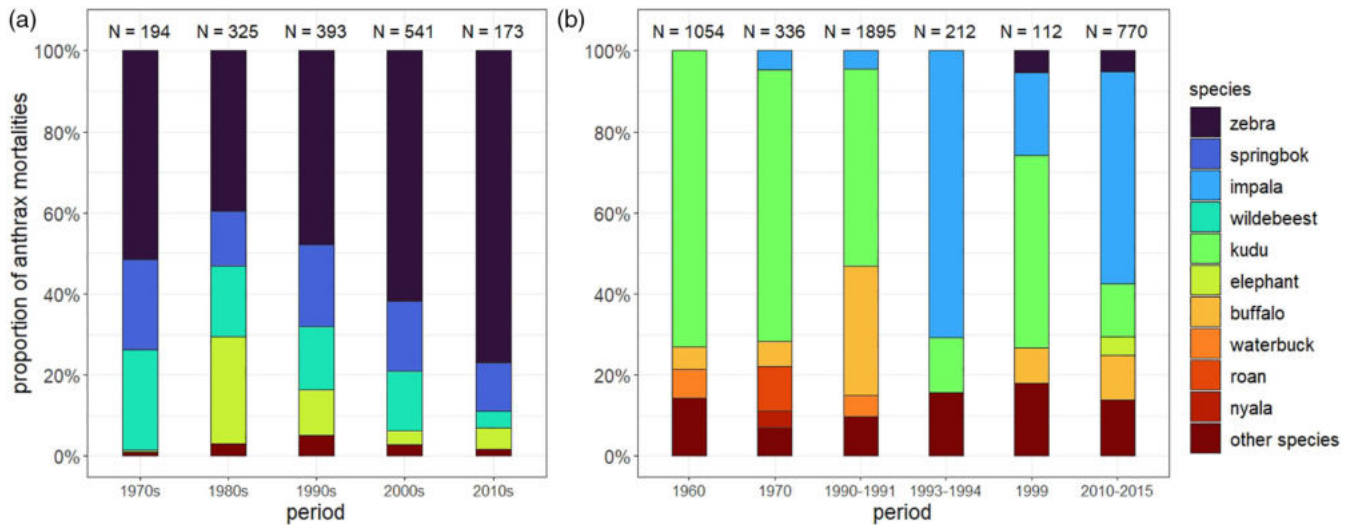
FIGURE 3 Species compositions of anthrax mortalities over time in (a) central Etosha National Park (ENP), Namibia, 1976–2014 (rainfall years; July–June) and (b) sporadic outbreaks in northern Kruger National Park (KNP), South Africa, 1960, 1970, 1990–1991, 1993–1994, 1999, and 2010–2015 (calendar years as onsets of outbreaks). Periods in ENP were divided into decades. For KNP, mortality data (1990–1991, 1993–1994, 1999, and 2010–2015) were compared to historical outbreaks in 1960 and 1970 (data from Pienaar [1961] and de Vos [1990]). Total number of individuals affected is shown on top of each bar. For ENP, four species were always the most common host species across decades, and they were thus shown with other species grouped together. For KNP, common host species varied over time, and species grouped together included herbivore species whose proportions were lower than 4% in each period or outbreak.

correlated with impala and zebra cases after almost a year (Figure 5g,h). The relationships between elephants and other species are difficult to decipher from these correlations. Elephant cases both preceded anthrax mortalities of impala and zebra by around 2 months and followed around 2 and 4 months after cases in zebra, impala, and elephant (Figure 5f,g,i).

Associations of anthrax cases with environmental variables

Years with higher rainfall in ENP generally showed a trend of more zebra anthrax cases, whereas lower-rainfall years had fewer cases (Figure 6a). No patterns were evident between annual cases and rainfall for springbok or wildebeest (Figure 6b,c). The large outbreak for elephant in ENP occurred in the year with the latest onset of rainfall, only starting in early January (Figure 6d). In KNP, years with large outbreaks did not show obvious differences or consistent patterns in rainfall measures from nonoutbreak years (Figure 6e,f).

Convergent cross-mapping

CCM, which can recognize potential causality, identified the time intervals with the highest correlations between rainfall and NDVI variables and anthrax cases (Figure 7).

Among the time lags with the highest correlation coefficients (i.e., the highest mapping skill), the significant differences detected from seasonal null models with Kolmogorov–Smirnov tests included $NDVI_{t-1}$ and $rainfall_{t-4}$ for zebra in central ENP, $NDVI_{t-2}$ and $rainfall_{t-3}$ for springbok in ENP, $NDVI_{t-2}$ for elephant in ENP, $NDVI_{t-2}$ and $rainfall_{t-4}$ for elephant in northern KNP, and $rainfall_{t-1}$ for buffalo in KNP (Table 2, Figure 7, Appendix S1: Figure S5). For these species–environment relationships, Mann–Kendall tests all showed convergence of ρ (Appendix S1: Figure S5). We extended the period to 1990–2015 for impala, kudu, and buffalo in KNP, the three most common host species contributing to outbreaks throughout this period. However, no significant difference of environmental effects from seasonal null models was detected, indicating that interannual variation or large outbreaks in KNP were less likely to be driven by the vegetation dynamics.

Multivariate S-map forecasting

We explored how well the environment could predict numbers of anthrax mortalities, assuming nonlinear relationships using multivariate S-map, for the anthrax mortality–environment relationships detected. We partitioned the data sets using the environmental variables from 1983 to 2005 for ENP or 2010 to 2013 for KNP to build models to predict for 2006–2014 for ENP or 2014–2015 for KNP. The environmental variables had better

TABLE 1 Descriptive statistics of anthrax cases at annual and bimonthly intervals

| Species[a]	No. intervals	Median	Mean	Minimum	Maximum	Percentage zeros
Annual cases in central Etosha National Park, 1976–2014						
Zebra	39	20	22.7	4	63	0
Springbok	39	6	7.2	0	25	2.6
Wildebeest	39	6	6.5	0	14	2.6
Elephant	39	2	4.1	0	61	12.8
Bimonthly cases in central Etosha National Park, 1976–2014						
Zebra	936	0	0.9	0	31	68.8
Springbok	936	0	0.3	0	11	81.1
Wildebeest	936	0	0.3	0	7	82.6
Elephant	936	0	0.2	0	31	90.5
Annual cases in northern Kruger National Park, 1990–2015						
Zebra	26	0	2.0	0	32	73.1
Impala	26	1.5	23.0	0	266	38.5
Kudu	26	0.5	42.7	0	609	50.0
Elephant	26	0	2.1	0	13	57.7
Buffalo	26	0	27.2	0	321	53.8
Bimonthly cases in northern Kruger National Park, 1990–2015						
Zebra	624	0	0.1	0	13	96.8
Impala	624	0	1.0	0	89	82.7
Kudu	624	0	1.8	0	128	87.5
Elephant	624	0	0.1	0	2	92.6
Buffalo	624	0	1.1	0	101	89.6
Bimonthly cases in northern Kruger National Park, 2010–2015						
Zebra	144	0	0.3	0	13	92.4
Impala	144	0	2.8	0	89	65.3
Kudu	144	0	0.7	0	15	77.1
Elephant	144	0	0.2	0	2	79.2
Buffalo	144	0	0.6	0	10	76.4

Note: Data were from central Etosha National Park (ENP), Namibia 1976–2014 (rainfall years; July–June) and northern Kruger National Park (KNP), South Africa, 1990–2015 (calendar years). Bimonthly data from KNP 2010–2015 are also included in this table because they were frequently used for analyses.

[a]Common and scientific names of host species: plains zebra (*Equus quagga*), springbok (*Antidorcas marsupialis*), blue wildebeest (*Connochaetes taurinus*), African elephant (*Loxodonta africana*), impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), and African buffalo (*Syncerus caffer*).

predictive capability for zebra anthrax mortalities in ENP than for other species (Table 2). For zebra in ENP, the NDVI model had better predictive power than rainfall, and the model with both NDVI and rainfall offered even better prediction (Table 2, Appendix S1: Figures S6 and S7). For springbok in ENP and elephant in KNP, the rainfall models performed slightly better than NDVI, and there was slight improvement in predictive power when both variables were used for forecasting (Table 2, Appendix S1: Figures S6 and S7). The NDVI and rainfall models had almost no forecasting capability for elephant in ENP and buffalo in KNP, respectively ($\rho < 0.1$; Table 2, Appendix S1: Figures S6 and S7), possibly due to the fact that relatively few cases were observed for these species during the prediction periods.

Partial derivatives from the forecast models estimated the effects of environmental variables on the numbers of anthrax mortalities. Elephant in ENP and buffalo in KNP were excluded from these procedures since there was no predictive power in their forecast models. The partial
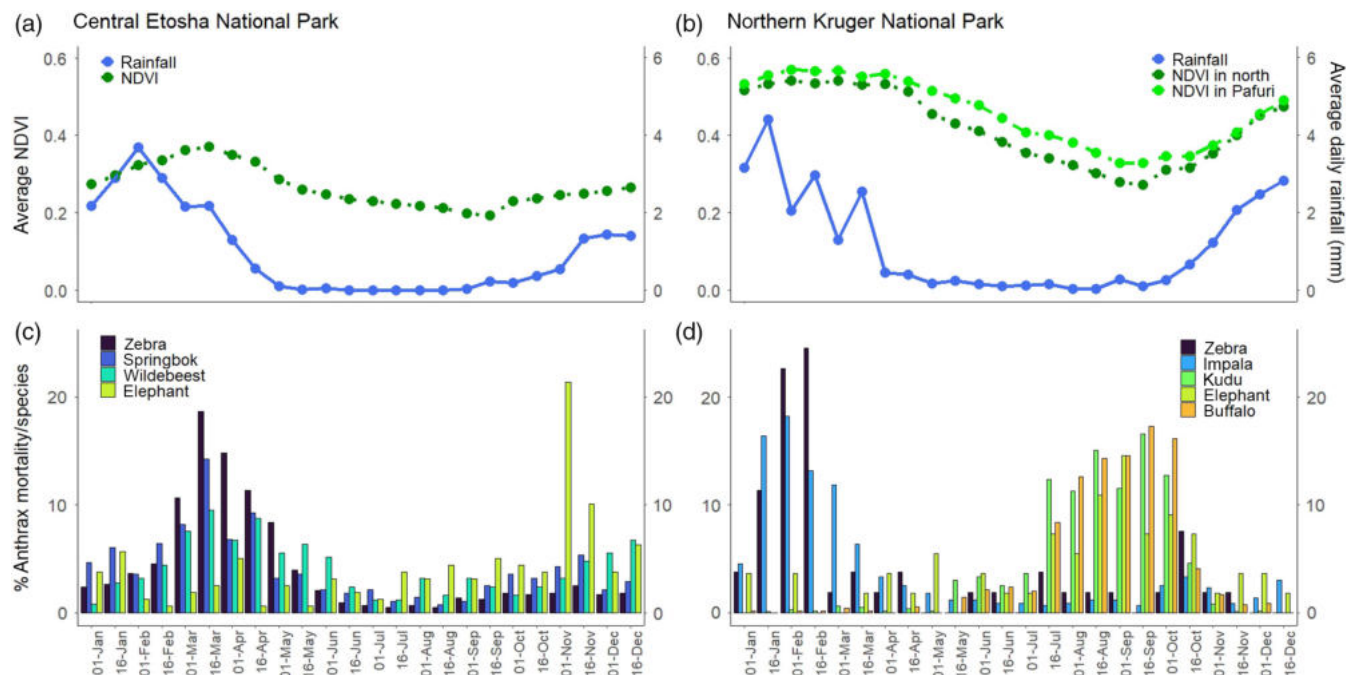
FIGURE 4 Seasonality in Normalized Difference Vegetation Index (NDVI) (a remote-sensing index of vegetation greenness) and rainfall (a, b) and anthrax mortality (c, d) from central Etosha National Park (ENP), Namibia (a, c; 1983–2014 for upper panel and 1976–2014 for lower panel; rainfall years; July–June), and northern Kruger National Park (KNP), South Africa (b, d; 1990–2015; calendar years). The data shown are averages for each bimonthly interval of a year. The anthrax mortality was calculated by total cases at an interval divided by overall cases per species to better show the seasonality.

derivatives were calculated from a multivariate S-map with only one environmental variable for zebra and springbok in ENP, and elephant in KNP. Environmental effects on anthrax mortalities were categorized based on the seasons of the anthrax mortality intervals. General directionality of the effects did not vary over seasons (Figure 8). The majority of both NDVI and rainfall effects on zebra and springbok anthrax mortalities in ENP was positive (Figure 8a–d). On the other hand, elephant cases in KNP were generally negatively affected by prior values for NDVI and rainfall (Figure 8e,f). Comparing these to models that include only a single environmental variable, the effects of NDVI estimated from models with two environmental variables were much closer to zero (Appendix S1: Figure S8), probably because of the interaction between the two environmental variables, with NDVI and rainfall acting as proximate and distal causes, respectively.

For these species–location pairings (zebra and springbok in ENP; elephant in KNP), the time intervals between environmental signal and anthrax cases (time lags within 1 month of NDVI or around 2 months of rainfall) suggest that the underlying transmission mechanisms for these species involve host behavioral responses to vegetation dynamics. However, the directionality of the effects indicated that these three species respond differently to vegetation change. Based on the predicted environmental effects on cases, zebra and springbok generally had more anthrax mortalities following higher NDVI or rainfall, while elephant generally had more cases following lower NDVI or rainfall. In addition, although rainfall had no predictive power for buffalo anthrax cases in KNP, we did detect potential causality from rainfall at a two-week time lag with CCM (Table 2, Figure 7, Appendix S1: Figure S5), and thus we cannot rule out the hypothesis that water translocation of spores contributes to buffalo anthrax cases in KNP.

DISCUSSION

In this study, we evaluated patterns and drivers of disease dynamics and biseasonality in anthrax infections in two multihost systems. In central ENP, common host species were the same over nearly 40 years, with a relatively small outbreak occurring every year. In northern KNP, historical outbreaks affected mostly kudu and followed a roughly decadal cycle, but turnover in host composition occurred in the 1990s and 2000s, with impala replacing kudu. Seasonally, the two parks showed similar bimodal seasonality. While anthrax cases in zebra, springbok, wildebeest, and impala peaked in wet seasons, anthrax cases in elephant, kudu and buffalo peaked in dry seasons. Except for elephant, species peaking in the same season showed synchronization of cases, indicating interrelated mechanisms behind the dynamics. Of the transmission
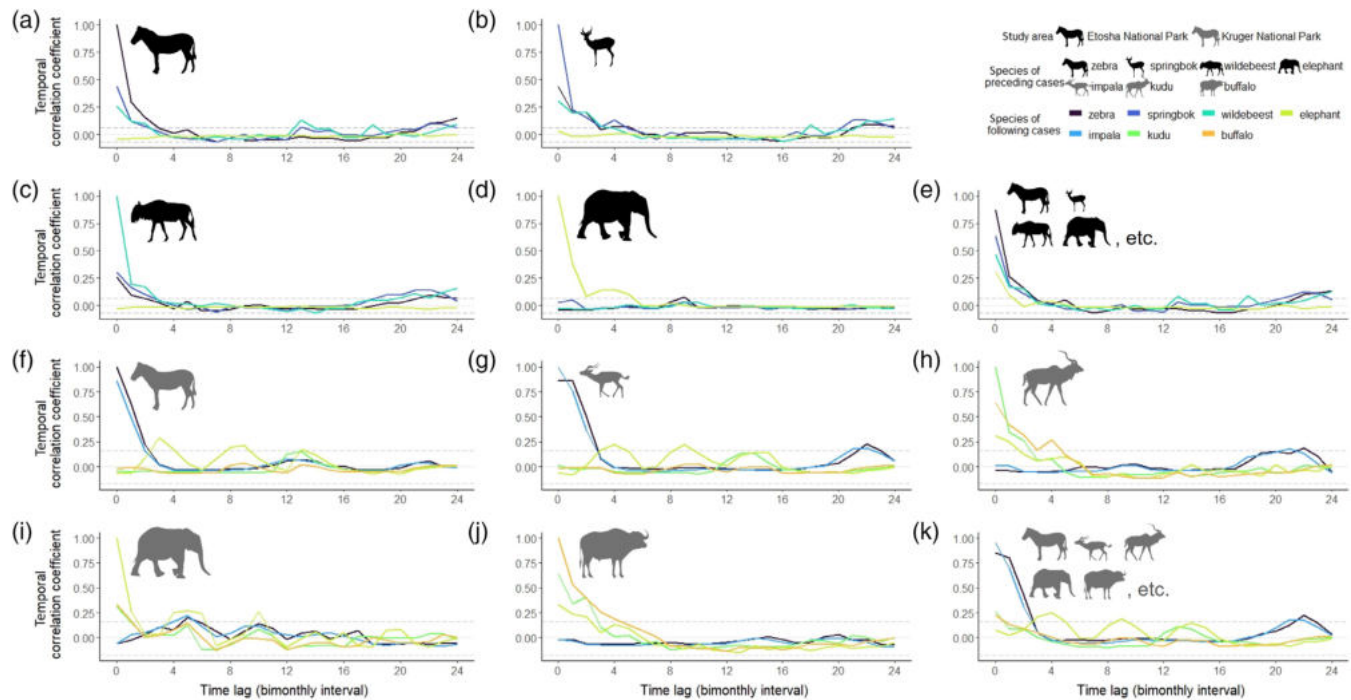
FIGURE 5 Temporal correlations between preceding cases of certain species and following cases of the same or different species with time lags in central Etosha National Park (ENP), Namibia, 1976–2014 (rainfall years; July–June), and northern Kruger National Park (KNP), South Africa, 2010–2015 (calendar years). Preceding cases were of (a) zebra, (b) springbok, (c) wildebeest, (d) elephant, and (e) all species in ENP; (f) zebra, (g) impala (h) kudu, (i) elephant, (j) buffalo, and (k) all species in KNP. Autocorrelation functions and cross-correlation functions were used to calculate within- and between-species correlations, respectively, with time lags ranging from 0 to 24 bimonthly intervals (i.e., out to 1 year). Different colors of lines represent different species of following cases. Dashed lines indicate upper and lower boundaries of 95% confidence intervals. Due to multiple time lags and multiple species, the 95% confidence intervals are less conservative in this case.

mechanisms considered, we found the strongest evidence linking outbreaks to changes in rainfall-driven vegetation dynamics, with zebra and springbok cases linked to higher rainfall and increased greenness and elephant cases linked to lower rainfall and reduced greenness. Put another way, wetter conditions were linked with more anthrax cases for zebra and springbok, whereas drier conditions were linked with more elephant cases. These relationships between anthrax dynamics and environmental fluctuations indicate that host behavioral responses to vegetation changes are likely important mechanisms behind anthrax dynamics for zebra, springbok, and elephant and that different seasonal peaks can result from divergent host responses to vegetation green-up. This study suggests that divergent transmission mechanisms and possible interactions between species may lead to the dynamics and biseasonal patterns in anthrax infections.

Seasonality and dynamics in anthrax cases

Though anthrax outbreaks in northern KNP followed a roughly decadal cycle, with large outbreaks occurring every 10 to 20 years, outbreaks in central ENP occurred annually with fewer cases. However, with fewer than 40 years of data, we cannot be certain that large outbreaks in ENP did not follow a multiyear cycle. Nonetheless, although these two parks seemed to have different interannual patterns, they both showed bimodal seasonality in anthrax infections. Species differed in their seasonality, with some peaking in wet seasons (zebra, springbok, wildebeest, and impala) and others peaking in dry seasons (elephant, kudu, and buffalo).

In long-term trends, the species composition for anthrax cases changed over decades in both parks. In ENP, the proportion of elephant cases declined, while the proportion of zebra cases increased over recent decades. This shift may be due to long-term rainfall patterns and the association of each species with environmental conditions. ENP experienced a period of drought in the 1980s–1990s when elephant case numbers were relatively higher, followed by a wet period from 2000–2012 with both higher zebra anthrax mortality and lower elephant anthrax mortality. In addition to rainfall patterns, we cannot exclude the possibility that the trends in species composition were driven by population abundance of the host species. Furthermore, a more dramatic change in host species was observed in KNP, which in the
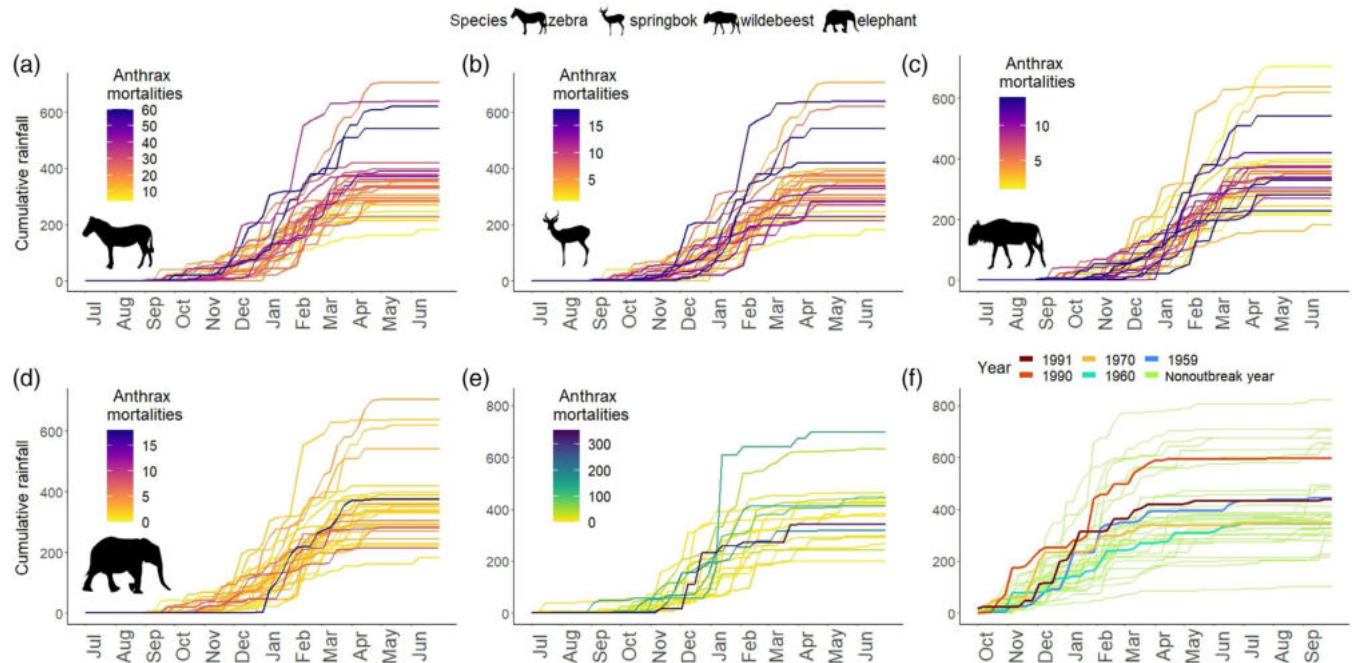
FIGURE 6 Anthrax mortalities in relation to cumulative rainfall in different rainfall years for (a) zebra, (b) springbok, (c) wildebeest, and (d) elephant in central Etosha National Park (ENP), Namibia 1983–2014, and (e) total cases in northern Kruger National Park (KNP), South Africa 1993–2015, and (f) outbreak years versus nonoutbreak years in KNP 1955–1991. Rainfall years of July to June were used for ENP and KNP 1993–2015; and rainfall years of October to September were used for KNP 1955–1991. Outbreak years 1990 and 1991 were compared with historical outbreaks because they primarily comprised kudu and buffalo in dry seasons. Rainfall years 1969, 1972, 2000, 2003, 2004, and 2005 in KNP were excluded due to unavailable rainfall data.

1990s–2000s shifted from dry-season kudu outbreaks to wet-season impala outbreaks, following large outbreaks in kudu in 1990–1991 and 1999. This switch in the dominant anthrax host species may have occurred due to decreased kudu population density, especially after the large outbreaks, and a consistently abundant impala population (Kruger et al., 2008; Owen-Smith & Mills, 2006). Other possible factors altering the KNP anthrax system could include extreme weather events, such as a severe drought in 1991–1992 or widespread flooding in 2000 (Parsons et al., 2005), after which few anthrax cases were recorded over the next decade (Appendix S1: Figure S1). Whether anthrax in KNP will return to a kudu-dominated dry-season system or remain an impala-dominated wet-season system remains to be seen.

Temporal correlations of anthrax cases within and between species

In both parks, anthrax dynamics were synchronized (within 2-month time lags) within seasonal peaks. The synchrony of cases within a season may be attributed to similar transmission mechanisms or common infectious sources, and the biseasonal patterns suggest that there are several mechanisms of anthrax transmission or dynamics, such as divergent responses to vegetation availability in different seasons. The exception to this case synchrony was elephant cases in northern KNP, which were less synchronized with other dry-season anthrax species and, thus, suggest potentially different transmission routes from other dry-season species. In KNP, case synchrony among species can also be observed at different temporal or spatial scales. For example, kudu and buffalo cases co-occurred in historical outbreaks. Zebra cases became more common after impala became the dominant host, and cases in these two species showed a similar geographical distribution, concentrated in the Pafuri region.

In central ENP, we did not observe positive correlations in anthrax dynamics for host species with cases peaking in different seasons. For the wet-season anthrax hosts, when there were more zebra cases, wildebeest experienced higher risk 6–7 months after the zebra cases. Wildebeest have a higher tendency to remain in open habitats even in dry seasons (Arsenault & Owen-Smith, 2008), and the habitat type they prefer corresponds to high-risk habitats in ENP (Huang et al., 2021). Big wet-season outbreaks in zebra potentially heighten the pathogen concentrations in those habitats and the probability of spillover to wildebeest in the following season.
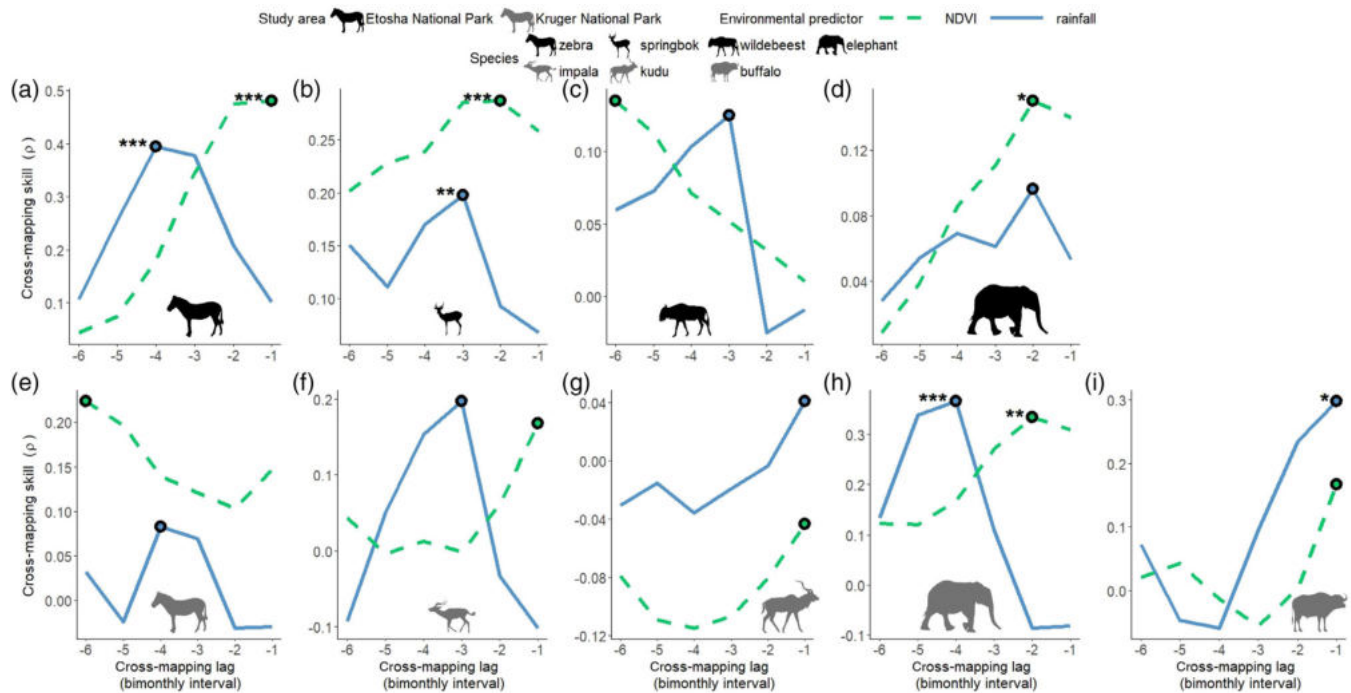
FIGURE 7 The strengths of the relationships between environmental variables with different time lags and anthrax mortalities. Plots show Pearson's correlation coefficients ρ (cross-mapping skill) between observed environmental variable values and predicted values by anthrax mortalities at maximal library size for different time lags from one to six bimonthly intervals (around 2 weeks to 3 months) of Normalized Difference Vegetation Index (NDVI) (a remote-sensing index of vegetation greenness; green dashed lines) and rainfall (blue solid lines) variables, using convergent cross-mapping. These analyses were performed to evaluate environmental causes of anthrax mortalities of (a) zebra, (b) springbok, (c) wildebeest, and (d) elephant in central Etosha National Park (ENP), Namibia, 1983–2014 (rainfall years; July–June); and (e) zebra, (f) impala, (g) kudu, (h) elephant, and (i) buffalo in northern Kruger National Park (KNP), South Africa, 2010–2015 (calendar years). Time lags with highest cross-mapping skill were highlighted with black circles, and they were further compared with seasonal null models. One, two, and three asterisks represent p values less than 0.05, 0.01, and 0.001, respectively, compared to seasonal null models with Kolmogorov–Smirnov tests.

TABLE 2 Results of empirical dynamic modeling for relationships between anthrax mortalities and environmental variables with best-performing time lags, which were significantly different from seasonal null models with convergent cross mapping, using Kolmogorov–Smirnov tests

Park	Species[a]	Environmental variable	Best-performing time lag	Two-tailed p value compared to seasonal null models	Predictive power using one environmental variable (ρ)	Predictive power using two environmental variables (ρ)
Etosha	Zebra	NDVI	$t-1$	<0.001	0.345	0.481
		Rainfall	$t-4$	<0.001	0.268	
Etosha	Springbok	NDVI	$t-2$	<0.001	0.200	0.240
		Rainfall	$t-3$	<0.05	0.217	
Etosha	Elephant	NDVI	$t-2$	<0.01	0.053	N/A
Kruger	Elephant	NDVI	$t-2$	<0.01	0.278	0.301
		Rainfall	$t-4$	<0.001	0.292	
Kruger	Buffalo	Rainfall	$t-1$	<0.05	0.035	N/A

Note: The predictive power was evaluated based on Pearson's correlation coefficients ρ between predicted and observed values, using S-map to forecast. The predictive models were built upon data from central Etosha National Park (ENP), Namibia, 1983–2005 (rainfall years; July–June), or northern Kruger National Park (KNP), South Africa, 2010–2013 (calendar years), to forecast 2006–2014 for ENP or 2014–2015 for KNP.

[a]Common and scientific names of host species: plains zebra (*Equus quagga*), springbok (*Antidorcas marsupialis*), African elephant (*Loxodonta africana*), and African buffalo (*Syncerus caffer*).

Abbreviation: NDVI, Normalized Difference Vegetation Index.
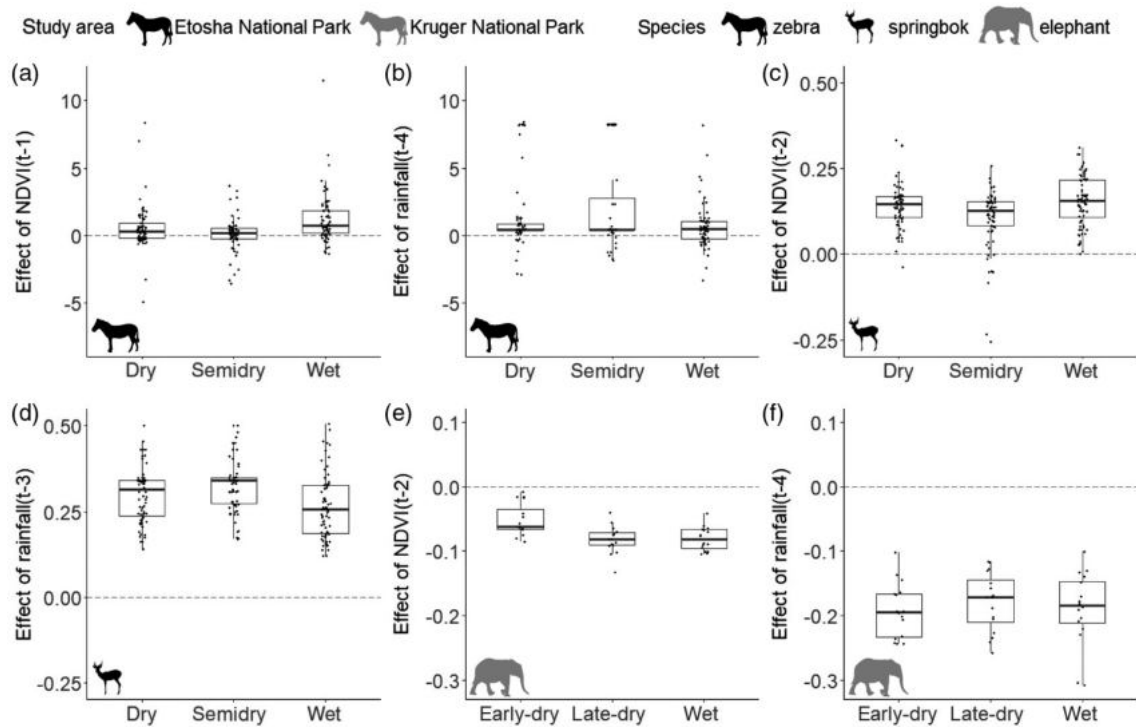
FIGURE 8 Predicted effects of Normalized Difference Vegetation Index (NDVI) (a remote-sensing index of vegetation greenness) or rainfall in different seasons on (a, b) zebra anthrax mortalities in central Etosha National Park (ENP), Namibia, (c, d) springbok in ENP, and (e, f) elephant in northern Kruger National Park (KNP), South Africa, shown with conventional boxplots. These environmental effects were estimated by partial derivatives from the multivariate S-map forecast models with one environmental variable (NDVI or rainfall) for the prediction period (2006–2014 for ENP and 2014–2015 for KNP) with anthrax cases, rainfall, and NDVI standardized with center at zero and standard deviations equal to one. These effects were grouped into different seasons based on case intervals.

When comparing correlations in cases contrasting species with cases peaking in different seasons in northern KNP, we observed positive correlations with longer time lags (2–11 months later). These lagged correlations imply that anthrax mortalities of one species may contribute to or amplify the force of infection in other species. These relationships suggest that anthrax transmission dynamics in KNP are complex—more complex than observed in ENP—and that cases in different synchronized seasonal groups are still interrelated.

Associations of anthrax cases with environmental variables

We were able to detect associations between environmental variables and anthrax mortalities for zebra and springbok cases in central ENP, buffalo in northern KNP, and elephant in both parks. These relationships indicate potential transmission mechanisms for anthrax tied to rainfall-driven vegetation dynamics and spore translocation by water. Transmission mechanisms based on environmental variables for other host species remain unclear. Shorter time

periods for analyses and large variations in outbreak frequency, especially in northern KNP, may limit our ability to identify potential environmental links. For those species for which anthrax cases showed potential causality with the environment, the best-performing time lags in EDM were mostly within 1 month prior to anthrax mortalities for NDVI or around 2 months prior to anthrax mortalities for rainfall (Figure 7), consistent with the hypothesis that transmission is related to behavioral responses to vegetation fluctuations. The only exceptions to this hypothesis were buffalo cases in KNP, for which the best-performing time lag was 2 weeks for rainfall, implying that the transmission mechanism for buffalo may involve water flow translocating spores, despite the limited predictive power. Among years, anthrax outbreaks in KNP were not associated with rainfall or NDVI, and environmental variables failed to explain the occurrence of these sporadic, large anthrax outbreaks. Across the scales of the different analyses, our KNP findings suggest that the environment modulates the intensity of an outbreak when it occurs but cannot be used to predict when infrequent outbreaks will occur. Thus, the environment is unlikely to be the primary trigger of large outbreaks in KNP; instead, the main driver

may be other factors, such as host population density (de Vos & Bryden, 1996) or an interaction between host density and environment.

In ENP, anthrax cases seem to be driven by zebra and, potentially, springbok and their interactions with the environment and may spill over into wildebeest through their shared space use. Zebra in ENP are attracted to habitats with higher anthrax risk in response to vegetation growth in wet seasons (Huang et al., 2021), exhibit higher-risk foraging strategies (Havarua et al., 2014; Turner et al., 2013), and selectively forage at anthrax carcass sites (Turner et al., 2014). These behavioral responses at both the landscape and the local patch scales result in mostly positive effects of rainfall and NDVI on the number of zebra anthrax cases. These zebra cases are triggered by the environment, synchronized with springbok and wildebeest cases, and correlated with wildebeest cases into the following dry season.

We were not able to determine specific behavioral changes that alter the exposure to *B. anthracis* for springbok in ENP or elephant in KNP. However, the effects of NDVI and rainfall on springbok and elephant cases determined here do suggest potential mechanisms that warrant further study. The directionality of the environmental effects on anthrax mortalities indicates that springbok have higher disease exposure during periods of wetter conditions and that elephant have higher exposure during drier conditions. Springbok selectively forage at zebra anthrax carcass sites in reaction to vegetation growth, a pattern not observed for elephants (Turner et al., 2014). Springbok shift their diet or potentially use different habitats across seasons (Bigalke, 1972; Lyons et al., 2013; Nagy & Knight, 1994; Panagis & Stander, 1989), and elephant populations are known to switch resource selection seasonally (Codron et al., 2006; Kaszta et al., 2021; Robson & van Aarde, 2018; Tsalyuk et al., 2019). Thus, changes in habitat or patch use, as well as foraging strategies, of these mixed-feeding herbivores could contribute to the differential exposure to *B. anthracis*.

Transmission mechanisms for elephants appear to be different from those of the other host species. Why elephants are not more correlated with other dry-season species remains an interesting question. The correlations at longer time lags in KNP suggest that outbreaks may move from one host species to another over several months. Moreover, in KNP, the environment cannot predict when an outbreak will occur. Outbreaks in KNP seem to emerge from complex interactions between host populations, the environment, host interactions with that environment, and subsequent interactions among species.

Unevaluated mechanisms behind dynamics

Using relationships between environmental variables and anthrax mortalities to evaluate transmission mechanisms has its limitations. Anthrax cases in wildebeest, impala, and kudu did not show significant associations with the environment. In addition to small sample sizes, this could be because not every transmission mechanism can be evaluated using associations with rainfall and NDVI. For example, transmission may be driven by host population density or involve translocation by vultures or insects (Figure 1), or other mechanisms and pathways that scientists have not yet considered. Furthermore, environmental variation may have uneven impacts on transmission risk across a heterogeneous landscape. For instance, if water dilutes spores at some infectious sites but hosts are attracted by abundant plant biomass at other infectious sites after rainfall, the relationships with the environment may be masked and not revealed by correlations averaged across a large spatial extent.

The timing of parturition has been noted as a common factor for biseasonality in wildlife diseases, where a pulse of immunologically naïve individuals is added to the population (Altizer et al., 2004; Cosgrove et al., 2008). For the species in our study, though there is no obvious breeding season for elephant, the birth peaks of the other ungulate host species are mostly during wet seasons (Fairall, 1968; Gasaway et al., 1996). This recruitment of potential host individuals may contribute to wet seasonal peaks in anthrax infections. However, most anthrax mortalities are adults (Clegg et al., 2007; Lindeque & Turnbull, 1994; Salb et al., 2014), and adults are potentially more likely to die of anthrax than younger individuals (Lindeque & Turnbull, 1994). Thus, even though we cannot rule out the effect of individual recruitment from birth peaks on anthrax seasonality, it may be only minimal.

Another common hypothesis for explaining the mechanisms of anthrax dynamics is that stress heightens host susceptibility, leading to anthrax outbreaks (Dragon & Rennie, 1995; Hugh-Jones & de Vos, 2002). Two common forms of stress are nutritional deprivation and reproduction (Plowright et al., 2008). For the host species in this study, while there are mismatches between periods of low nutrient availability and anthrax outbreaks, especially for wet-season anthrax species, for example, zebra and springbok in ENP (Cizauskas et al., 2015), these two periods are potentially concordant for dry-season anthrax species, for example, elephant in KNP (Viljoen et al., 2008). These differences suggest that stress-related responses due to nutritional deprivation may vary with species, and there could be a causal link

for species in the dry-season group. The largest elephant outbreak in ENP corresponded to the year with the latest start of rainfall during the study period. However, confirmation of these relationships will require an analysis of different scales using longer-term data sets of outbreaks across years. Additionally, if stress from pregnancy and lactation is a major driver of cases, female-biased anthrax mortalities should be observed. Though sex biases are reported, they are variable across species or areas (Bagamian et al., 2013). For example, impala anthrax cases during a large outbreak in Malilangwe Wildlife Reserve, Zimbabwe, were skewed to males, whereas kudu in the same area were skewed to females (Clegg et al., 2007). Springbok, wildebeest, and elephant anthrax cases in ENP are skewed toward males, whereas zebra cases show no sex bias (Lindeque & Turnbull, 1994). However, the sex ratio of zebra in the Samburu district, Kenya, are skewed toward females (Muoria et al., 2007). This mixed sex skewness indicates that sex-specific stressors may not be the main contributing factors to anthrax mortalities or that the effects of sex on anthrax mortality may vary by species and area.

Even though host susceptibility may contribute to anthrax outbreaks for some species, exposure to high concentrations of pathogens may be equally important. Zebra in ENP move between habitats in reaction to rainfall fluctuations (Huang et al., 2021). They primarily use low-risk habitats when individuals are more susceptible to anthrax infection during drier seasons or a drought (Huang et al., 2021). As a result, anthrax outbreaks in this population generally occur when there is better forage availability. Therefore, while stressors can alter individual susceptibility to anthrax, confirming that habitats used by the host populations have high risks and identifying transmission hotspots are essential.

Variable surveillance effort in long-term wildlife mortality data makes it challenging to link environmental variation to disease outbreaks, and variation in case detection may obscure patterns between environmental factors and disease outbreaks. Though standardized mortality surveys across a large area are certainly desirable, they may not be practical or feasible. Despite these limitations, EDM is useful for detecting nonlinear or context-dependent relationships, since it provides more flexibility in identifying linkages between variables than traditional correlational analyses (e.g., generalized linear model analyses shown in Appendix S1). In addition, long-term mortality data can be useful for evaluating the effects of factors such as human activities and roads (Ashley & Robinson, 1996; Gilhooly et al., 2019) or diseases (Hall & Saito, 2008; Kuisma et al., 2019) on animal populations, especially when multiple species are considered. Despite the potential challenges of working with long-term

mortality data sets, we encourage wildlife scientists and managers to collect them and to explore the data sets at different spatial and temporal scales with statistical and modeling methods to retrieve underlying information.

Summaries and future research

This study showed bimodal seasonality in anthrax mortality among African herbivore species and the characteristics and complexities of anthrax outbreak dynamics from two separate systems. Our results suggest potential causal relationships between rainfall and vegetation greenness and anthrax transmission mechanisms for different species. The mortality of species in different seasonal peaks (i.e., zebra and springbok vs. elephant) has opposite relationships with rainfall and NDVI, suggesting that a difference in animal ecology may lead to variable seasonality in infectious diseases. The underlying mechanisms that lead to anthrax infection for many of these herbivore species remain largely unknown. We recommend future studies to explore spatiotemporal patterns in anthrax infections, as well as the population biology of the host populations across seasons and years, to confirm the potential change in behavioral responses to vegetation fluctuations through monitoring movement, behavior, and serostatus and to directly evaluate vector-involved transmission pathways. Despite the complexity of pathways that can lead to transmission in this multihost, environmentally transmitted disease, this study revealed that biseasonal anthrax infections could emerge from two systems with very different disease outbreak dynamics. Finally, the different patterns in interannual outbreak dynamics in these systems is a reminder that we should be cautious in generalizing patterns or processes of a disease from the characteristics observed in a single system.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data (Huang et al., 2022a) are available in Dryad at https://doi.org/10.5061/dryad.zkh1893br. Code (Huang et al., 2022b) is available in Zenodo at https://doi.org/10.5281/zenodo.5812311.

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REFERENCES
Altizer, S., A. Dobson, P. Hosseini, P. Hudson, M. Pascual, and P. Rohani. 2006. "Seasonality and the Dynamics of Infectious Diseases." *Ecology Letters* 9(4): 467–84. https://doi.org/10.1111/j.1461-0248.2005.00879.x.

Altizer, S., W. M. Hochachka, and A. A. Dhondt. 2004. "Seasonal Dynamics of Mycoplasmal Conjunctivitis in Eastern North American House Finches." *Journal of Animal Ecology* 73: 309–22. https://www.jstor.org/stable/3505566.

Arsenault, R., and N. Owen-Smith. 2008. "Resource Partitioning by Grass Height among Grazing Ungulates Does Not Follow Body Size Relation." *Oikos* 117(11): 1711–7. https://doi.org/10.1111/j.1600-0706.2008.16575.x.

Ashley, E. P., and J. T. Robinson. 1996. "Road Mortality of Amphibians, Reptiles and Other Wildlife on the Long Point Causeway, Lake Erie, Ontario." *Canadian Field Naturalist* 110(3): 403–12.

Auer, C. 1997. "Chemical Quality of Water at Waterholes in the Etosha National Park." *Madoqua* 20(1): 121–8. https://hdl.handle.net/10520/AJA10115498_463.

Bagamian, K. H., K. A. Alexander, T. L. Hadfield, and J. K. Blackburn. 2013. "Ante- and Postmortem Diagnostic Techniques for Anthrax: Rethinking Pathogen Exposure and the Geographic Extent of the Disease in Wildlife." *Journal of Wildlife Diseases* 49(4): 786–801. https://doi.org/10.7589/2013-05-126.

Barandongo, Z. R., J. K. E. Mfune, and W. C. Turner. 2018. "Dust-Bathing Behaviors of African Herbivores and the Potential Risk of Inhalational Anthrax." *Journal of Wildlife Diseases* 54(1): 34–44. https://doi.org/10.7589/2017-04-069.

Basson, L., A. Hassim, A. Dekker, A. Gilbert, W. Beyer, J. Rossouw, and H. van Heerden. 2018. "Blowflies as Vectors of *Bacillus anthracis* in the Kruger National Park." *Koedoe* 60(1): 1–6. https://doi.org/10.4102/koedoe.v60i1.1468.

Bellan, S. E., O. Gimenez, R. Choquet, and W. M. Getz. 2013. "A Hierarchical Distance Sampling Approach to Estimating Mortality Rates from Opportunistic Carcass Surveillance Data." *Methods in Ecology and Evolution* 4(4): 361–9. https://doi.org/10.1111/2041-210x.12021.

Beyer, W., and P. C. B. Turnbull. 2009. "Anthrax in Animals." *Molecular Aspects of Medicine* 30(6): 481–9. https://doi.org/10.1016/j.mam.2009.08.004.

Bigalke, R. C. 1972. "Observations on the Behaviour and Feeding Habits of the Springbok, *Antidorcas marsupialis*." *African Zoology* 7(1): 333–59.

Blackburn, J. K., A. Curtis, T. L. Hadfield, B. O'Shea, M. A. Mitchell, and M. E. Hugh-Jones. 2010. "Confirmation of *Bacillus Anthracis* from Flesh-Eating Flies Collected during a West Texas Anthrax Season." *Journal of Wildlife Diseases* 46(3): 918–22. https://doi.org/10.7589/0090-3558-46.3.918.

Blackburn, J. K., and D. G. Goodin. 2013. "Differentiation of Springtime Vegetation Indices Associated with Summer Anthrax Epizootics in West Texas, USA, Deer." *Journal of Wildlife Diseases* 49(3): 699–703. https://doi.org/10.7589/2012-10-253.

Braack, L. E., and V. de Vos. 1990. "Feeding Habits and Flight Range of Blow-Flies (*Chrysomyia* Spp.) in Relation to Anthrax Transmission in the Kruger National Park, South Africa." *The Onderstepoort Journal of Veterinary Research* 57(2): 141–2.

Brown, V. L., J. M. Drake, D. E. Stallknecht, J. D. Brown, K. Pedersen, and P. Rohani. 2013. "Dissecting a Wildlife Disease Hotspot: The Impact of Multiple Host Species, Environmental Transmission and Seasonality in Migration, Breeding and Mortality." *Journal of the Royal Society Interface* 10(79): 20120804. https://doi.org/10.1098/rsif.2012.0804.

Brownlie, T., T. Bishop, M. Parry, S. E. Salmon, and J. C. Hunnam. 2020. "Predicting the Periodic Risk of Anthrax in Livestock in Victoria, Australia, Using Meteorological Data." *International*

Journal of Biometeorology 64(4): 601–10. https://doi.org/10.1007/s00484-019-01849-0.

Buhnerkempe, M. G., M. G. Roberts, A. P. Dobson, H. Heesterbeek, P. J. Hudson, and J. O. Lloyd-Smith. 2015. "Eight Challenges in Modelling Disease Ecology in Multi-Host, Multi-Agent Systems." *Epidemics* 10: 26–30. https://doi.org/10.1016/j.epidem.2014.10.001.

Cenci, S., G. Sugihara, and S. Saavedra. 2019. "Regularized S-Map for Inference and Forecasting with Noisy Ecological Time Series." *Methods in Ecology and Evolution* 10(5): 650–60. https://doi.org/10.1111/2041-210X.13150.

Chang, C.-W., T. Miki, M. Ushio, P.-J. Ke, L. Hsiao-Pei, F.-K. Shiah, and C.-h. Hsieh. 2021. "Reconstructing Large Interaction Networks from Empirical Time Series Data." *Ecology Letters* 24(12): 2763–74. https://doi.org/10.1111/ele.13897.

Chang, C.-W., M. Ushio, and C.-h. Hsieh. 2017. "Empirical Dynamic Modeling for Beginners." *Ecological Research* 32(6): 785–96. https://doi.org/10.1007/s11284-017-1469-9.

Chen, W.-J., S.-J. Lai, Y. Yang, K. Liu, X.-L. Li, H.-W. Yao, Y. Li, H. Zhou, L.-P. Wang, and D. Mu. 2016. "Mapping the Distribution of Anthrax in Mainland China, 2005–2013." *PLoS Neglected Tropical Diseases* 10(4): e0004637. https://doi.org/10.1371/journal.pntd.0004637.

Chikerema, S. M., D. M. Pfukenyi, G. Matope, and E. Bhebhe. 2012. "Temporal and Spatial Distribution of Cattle Anthrax Outbreaks in Zimbabwe between 1967 and 2006." *Tropical Animal Health and Production* 44(1): 63–70. https://doi.org/10.1007/s11250-011-9888-z.

Cizauskas, C. A., W. C. Turner, N. Pitts, and W. M. Getz. 2015. "Seasonal Patterns of Hormones, Macroparasites, and Microparasites in Wild African Ungulates: The Interplay among Stress, Reproduction, and Disease." *PLoS One* 10(4): e0120800. https://doi.org/10.1371/journal.pone.0120800.

Clegg, S. B., P. C. B. Turnbull, C. M. Foggin, and P. M. Lindeque. 2007. "Massive Outbreak of Anthrax in Wildlife in the Malilangwe Wildlife Reserve, Zimbabwe." *Veterinary Record* 160(4): 113–8. https://doi.org/10.1136/vr.160.4.113.

Codron, J., J. A. Lee-Thorp, M. Sponheimer, D. Codron, R. C. Grant, and D. J. de Ruiter. 2006. "Elephant (*Loxodonta africana*) Diets in Kruger National Park, South Africa: Spatial and Landscape Differences." *Journal of Mammalogy* 87(1): 27–34. https://doi.org/10.1644/05-MAMM-A-017R1.1.

Cosgrove, C. L., M. J. Wood, K. P. Day, and B. C. Sheldon. 2008. "Seasonal Variation in *Plasmodium* Prevalence in a Population of Blue Tits *Cyanistes caeruleus*." *Journal of Animal Ecology* 77(3): 540–8. https://doi.org/10.1111/j.1365-2656.2008.01370.x.

Craft, M. E., P. L. Hawthorne, C. Packer, and A. P. Dobson. 2008. "Dynamics of a Multihost Pathogen in a Carnivore Community." *Journal of Animal Ecology* 77(6): 1257–64. https://doi.org/10.1111/j.1365-2656.2008.01410.x.

Cross, P. C., W. H. Edwards, B. M. Scurlock, E. J. Maichak, and J. D. Rogerson. 2007. "Effects of Management and Climate on Elk Brucellosis in the Greater Yellowstone Ecosystem." *Ecological Applications* 17(4): 957–64. https://doi.org/10.1890/06-1603.

Dao, A., A. S. Yaro, M. Diallo, S. Timbine, D. L. Huestis, Y. Kassogue, A. I. Traore, Z. L. Sanogo, D. Samake, and T. Lehmann. 2014. "Signatures of Aestivation and Migration in Sahelian Malaria Mosquito Populations." *Nature* 516(7531): 387–90. https://doi.org/10.1038/nature13987.

de Vos, V. 1990. "The Ecology of Anthrax in the Kruger National Park, South Africa." Proceedings of the International Workshop on Anthrax: Winchester, England, April 11–13, 1989 68: 19–23.

de Vos, V., and H. B. Bryden. 1996. "Anthrax in the Kruger National Park: Temporal and Spatial Patterns of Disease Occurrence." *Salisbury Medical Bulletin* 87: 26–31.

Deyle, E. R., M. C. Maher, R. D. Hernandez, S. Basu, and G. Sugihara. 2016. "Global Environmental Drivers of Influenza." *Proceedings of the National Academy of Sciences of the United States of America* 113(46): 13081–6. https://doi.org/10.1073/pnas.1607747113.

Deyle, E. R., R. M. May, S. B. Munch, and G. Sugihara. 2016. "Tracking and Forecasting Ecosystem Interactions in Real Time." *Proceedings of the Roayl Soceity B: Biological Sciences* 283(1822): 20152258. https://doi.org/10.1098/rspb.2015.2258.

Deyle, E. R., and G. Sugihara. 2011. "Generalized Theorems for Nonlinear State Space Reconstruction." *PLoS One* 6(3): e18295. https://doi.org/10.1371/journal.pone.0018295.

Dragon, D. C., and R. P. Rennie. 1995. "The Ecology of Anthrax Spores: Tough but Not Invincible." *The Canadian Veterinary Journal* 36(5): 295–301.

Driciru, M., I. B. Rwego, S. A. Ndimuligo, D. A. Travis, E. R. Mwakapeje, M. Craft, B. Asiimwe, J. Alvarez, S. Ayebare, and K. Pelican. 2020. "Environmental Determinants Influencing Anthrax Distribution in Queen Elizabeth Protected Area, Western Uganda." *PLoS One* 15(8): e0237223. https://doi.org/10.1371/journal.pone.0237223.

du Plessis, W. P. 1999. "Linear Regression Relationships between NDVI, Vegetation and Rainfall in Etosha National Park, Namibia." *Journal of Arid Environments* 42(4): 235–60. https://doi.org/10.1006/jare.1999.0505.

Easterday, W. R., J. M. Ponciano, J. P. Gomez, M. N. Van Ert, T. Hadfield, K. Bagamian, J. K. Blackburn, N. C. Stenseth, and W. C. Turner. 2020. "Coalescence Modeling of Intrainfection *Bacillus anthracis* Populations Allows Estimation of Infection Parameters in Wild Populations." *Proceedings of the National Academy of Sciences of the United States of America* 117(8): 4273–80. https://doi.org/10.1073/pnas.1920790117.

Ebedes, H. 1976. "Anthrax Epizootics in Etosha National Park." *Madoqua* 10(2): 99–118.

Eisenberg, M. C., G. Kujbida, A. R. Tuite, D. N. Fisman, and J. H. Tien. 2013. "Examining Rainfall and Cholera Dynamics in Haiti Using Statistical and Dynamic Modeling Approaches." *Epidemics* 5(4): 197–207. https://doi.org/10.1016/j.epidem.2013.09.004.

Engert, S. 1997. "Spatial Variability and Temporal Periodicity of Rainfall in the Etosha National Park and Surrounding Areas in Northern Namibia." *Madoqua* 20(1): 115–20.

Fairall, N. 1968. "The Reproductive Seasons of some Mammals in the Kruger National Park." *African Zoology* 3(2): 189–210.

Fasanella, A., D. Galante, G. Garofolo, and M. Hugh-Jones. 2010. "Anthrax Undervalued Zoonosis." *Veterinary Microbiology* 140(3–4): 318–31. https://doi.org/10.1016/j.vetmic.2009.08.016.

Fisman, D. 2012. "Seasonality of Viral Infections: Mechanisms and Unknowns." *Clinical Microbiology and Infection* 18(10): 946–54. https://doi.org/10.1111/j.1469-0691.2012.03968.x.

Gasaway, W. C., K. T. Gasaway, and H. H. Berry. 1996. "Persistent Low Densities of Plains Ungulates in Etosha National Park,

Namibia: Testing the Food-Regulating Hypothesis." *Canadian Journal of Zoology* 74(8): 1556–72. https://doi.org/10.1139/z96-170.

Gaylard, A., N. Owen-Smith, and J. Redfern. 2003. "Surface Water Availability: Implications for Heterogeneity and Ecosystem Processes." In *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*, edited by J. T. du Toit, K. H. Rogers, H. C. Biggs, A. R. E. Sinclair, and B. Walker. Washington, DC: Island Press.

Gertenbach, W. P. D. 1983. "Landscapes of the Kruger National Park." *Koedoe* 26(1): 9–121. https://doi.org/10.4102/koedoe.v26i1.591.

Gilhooly, P. S., S. E. Nielsen, J. Whittington, and C. C. St. Clair. 2019. "Wildlife Mortality on Roads and Railways Following Highway Mitigation." *Ecosphere* 10(2): e02597. https://doi.org/10.1002/ecs2.2597.

Grziwotz, F., J. F. Strauß, C.-h. Hsieh, and A. Telschow. 2018. "Empirical Dynamic Modelling Identifies Different Responses of *Aedes polynesiensis* Subpopulations to Natural Environmental Variables." *Scientific Reports* 8(1): 16768. https://doi.org/10.1038/s41598-018-34972-w.

Hall, A. J., and E. K. Saito. 2008. "Avian Wildlife Mortality Events Due to Salmonellosis in the United States, 1985–2004." *Journal of Wildlife Diseases* 44(3): 585–93. https://doi.org/10.7589/0090-3558-44.3.585.

Hampson, K., T. Lembo, P. Bessell, H. Auty, C. Packer, J. Halliday, C. A. Beesley, et al. 2011. "Predictability of Anthrax Infection in the Serengeti, Tanzania." *Jouranl of Applied Ecology* 48(6): 1333–44. https://doi.org/10.1111/j.1365-2664.2011.02030.x.

Haque, U., M. Hashizume, G. E. Glass, A. M. Dewan, H. J. Overgaard, and T. Yamamoto. 2010. "The Role of Climate Variability in the Spread of Malaria in Bangladeshi Highlands." *PLoS One* 5(12): e14341. https://doi.org/10.1371/journal.pone.0014341.

Harvell, D., S. Altizer, I. M. Cattadori, L. Harrington, and E. Weil. 2009. "Climate Change and Wildlife Diseases: When Does the Host Matter the Most?" *Ecology* 90(4): 912–20. https://www.jstor.org/stable/25592578.

Havarua, Z., W. C. Turner, and J. K. E. Mfune. 2014. "Seasonal Variation in Foraging Behaviour of Plains Zebra (*Equus quagga*) May Alter Contact with the Anthrax Bacterium (*Bacillus anthracis*)." *Canadian Journal of Zoology* 92(4): 331–7. https://doi.org/10.1139/cjz-2013-0186.

Huang, Y.-H., H. Joel, M. Küsters, Z. R. Barandongo, C. C. Cloete, A. Hartmann, P. L. Kamath, et al. 2021. "Disease or Drought: Environmental Fluctuations Release Zebra from a Potential Pathogen-Triggered Ecological Trap." *Proceedings of the Roayl Soceity B: Biological Sciences* 288(1952): 20210582. https://doi.org/10.1098/rspb.2021.0582.

Huang, Y.-H., K. Kausrud, A. Hassim, S. O. Ochai, O. L. van Schalkwyk, E. H. Dekker, A. Buyantuev, et al. 2022a. "Environmental Drivers of Biseasonal Anthrax Outbreak Dynamics in Two Multi-Host Savanna Systems." Dryad, dataset. https://doi.org/10.5061/dryad.zkh1893br.

Huang, Y.-H., K. Kausrud, A. Hassim, S. O. Ochai, O. L. van Schalkwyk, E. H. Dekker, A. Buyantuev, et al. 2022b. "Environmental Drivers of Biseasonal Anthrax Outbreak Dynamics in Two Multi-Host Savanna Systems." Zenodo, software. https://doi.org/10.5281/zenodo.5812311.

Hugh-Jones, M. E., and V. de Vos. 2002. "Anthrax and Wildlife." *Revue Scientifique et Technique-Office International des Epizooties* 21(2): 359–83. https://doi.org/10.20506/rst.21.2.1336.

Hugh-Jones, M., and J. Blackburn. 2009. "The Ecology of *Bacillus anthracis*." *Molecular Aspects of Medicine* 30(6): 356–67. https://doi.org/10.1016/j.mam.2009.08.003.

Kamo, M., and A. Sasaki. 2005. "Evolution toward Multi-Year Periodicity in Epidemics." *Ecology Letters* 8(4): 378–85. https://doi.org/10.1111/j.1461-0248.2005.00734.x.

Kaszta, Ż., S. A. Cushman, and R. Slotow. 2021. "Temporal Non-stationarity of Path-Selection Movement Models and Connectivity: An Example of African Elephants in Kruger National Park." *Frontiers in Ecology and Evolution* 9: 207. https://doi.org/10.3389/fevo.2021.553263.

Keesing, F., R. D. Holt, and R. S. Ostfeld. 2006. "Effects of Species Diversity on Disease Risk." *Ecology Letters* 9(4): 485–98. https://doi.org/10.1111/j.1461-0248.2006.00885.x.

Kruger, J. M., B. K. Reilly, and I. J. Whyte. 2008. "Application of Distance Sampling to Estimate Population Densities of Large Herbivores in Kruger National Park." *Wildlife Research* 35(4): 371–6. https://doi.org/10.1071/wr07084.

Kuisma, E., S. H. Olson, K. N. Cameron, P. E. Reed, W. B. Karesh, A. I. Ondzie, M.-J. Akongo, S. D. Kaba, R. J. Fischer, and S. N. Seifert. 2019. "Long-Term Wildlife Mortality Surveillance in Northern Congo: A Model for the Detection of Ebola Virus Disease Epizootics." *Philosophical Transactions of the Royal Society B: Biological Sciences* 374(1782): 20180339. https://doi.org/10.1098/rstb.2018.0339.

Langwig, K. E., W. F. Frick, R. Reynolds, K. L. Parise, K. P. Drees, J. R. Hoyt, T. L. Cheng, T. H. Kunz, J. T. Foster, and A. Marm Kilpatrick. 2015. "Host and Pathogen Ecology Drive the Seasonal Dynamics of a Fungal Disease, White-Nose Syndrome." *Proceedings of the Royal Society B: Biological Sciences* 282(1799): 20142335. https://doi.org/10.1098/rspb.2014.2335.

le Roux, C. J. G., J. O. Grunow, G. J. Bredenkamp, J. W. Morris, and J. C. Scheepers. 1988. "A Classification of the Vegetation of the Etosha National Park." *South African Journal of Botany* 54(1): 1–10. https://doi.org/10.1016/s0254-6299(16)31355-2.

Lindeque, P. M., and P. C. B. Turnbull. 1994. "Ecology and Epidemiology of Anthrax in the Etosha National Park, Namibia." *Onderstepoort Journal of Veterinary Research* 61(1): 71–83. http://hdl.handle.net/2263/33072.

Lisovski, S., B. J. Hoye, and M. Klaassen. 2017. "Geographic Variation in Seasonality and its Influence on the Dynamics of an Infectious Disease." *Oikos* 126(7): 931–6. https://doi.org/10.1111/oik.03796.

Liu, A., V. Lee, D. Galusha, M. D. Slade, M. Diuk-Wasser, T. Andreadis, M. Scotch, and P. M. Rabinowitz. 2009. "Risk Factors for Human Infection with West Nile Virus in Connecticut: A Multi-Year Analysis." *International Journal of Health Geographics* 8(1): 67. https://doi.org/10.1186/1476-072X-8-67.

Lloyd-Smith, J. O., D. George, K. M. Pepin, V. E. Pitzer, J. R. C. Pulliam, A. P. Dobson, P. J. Hudson, and B. T. Grenfell. 2009. "Epidemic Dynamics at the Human-Animal Interface." *Science* 326(5958): 1362–7. https://doi.org/10.1126/science.1177345.

Lyons, A. J., W. C. Turner, and W. M. Getz. 2013. "Home Range Plus: A Space-Time Characterization of Movement over Real Landscapes." *Movement Ecology* 1(1): 2. https://doi.org/10.1186/2051-3933-1-2.

Ma, X., J. D. Blanton, S. L. Rathbun, S. Recuenco, and C. E. Rupprecht. 2010. "Time Series Analysis of the Impact of Oral Vaccination on Raccoon Rabies in West Virginia, 1990–2007." *Vector-Borne and Zoonotic Diseases* 10(8): 801–9. https://doi.org/10.1089/vbz.2009.0089.

McLeod, A. I. 2011. "Kendall: Kendall Rank Correlation and Mann-Kendall Trend Test." https://CRAN.R-project.org/package=Kendall.

Mongoh, M. N., N. W. Dyer, C. L. Stoltenow, and M. L. Khaitsa. 2007. "Characterization of an Outbreak of Anthrax in Animals in North Dakota." *The Bovine Practitioner* 41: 101–9. https://doi.org/10.21423/bovine-vol41no2p101-109.

Moura-Campos, D., S. E. Greenspan, G. V. DiRenzo, W. J. Neely, L. F. Toledo, and C. Guilherme Becker. 2021. "Fungal Disease Cluster in Tropical Terrestrial Frogs Predicted by Low Rainfall." *Biological Conservation* 261: 109246. https://doi.org/10.1016/j.biocon.2021.109246.

Munch, S. B., A. Brias, G. Sugihara, and T. L. Rogers. 2020. "Frequently Asked Questions about Nonlinear Dynamics and Empirical Dynamic Modelling." *ICES Journal of Marine Science* 77(4): 1463–79. https://doi.org/10.1093/icesjms/fsz209.

Muoria, P. K., P. Muruthi, W. K. Kariuki, B. A. Hassan, D. Mijele, and N. O. Oguge. 2007. "Anthrax Outbreak among Grevy's Zebra (*Equus grevyi*) in Samburu, Kenya." *African Journal of Ecology* 45(4): 483–9. https://doi.org/10.1111/j.1365-2028.2007.00758.x.

Mutshinda, C. M., R. B. O'Hara, and I. P. Woiwod. 2009. "What Drives Community Dynamics?" *Proceedings of the Royal Society B: Biological Sciences* 276(1669): 2923–9. https://doi.org/10.1098/rspb.2009.0523.

Nagy, K. A., and M. H. Knight. 1994. "Energy, Water, and Food Use by Springbok Antelope (*Antidorcas marsupialis*) in the Kalahari Desert." *Journal of Mammalogy* 75(4): 860–72. https://doi.org/10.2307/1382468.

Nicholson, S. E., M. L. Davenport, and A. R. Malo. 1990. "A Comparison of the Vegetation Response to Rainfall in the Sahel and East Africa, Using Normalized Difference Vegetation Index from NOAA AVHRR." *Climatic Change* 17: 209–41. https://doi.org/10.1007/BF00138369.

Nova, N., E. R. Deyle, M. S. Shocket, A. J. MacDonald, M. L. Childs, M. Rypdal, G. Sugihara, and E. A. Mordecai. 2021. "Susceptible Host Availability Modulates Climate Effects on Dengue Dynamics." *Ecology Letters* 24(3): 415–25. https://doi.org/10.1111/ele.13652.

Ochai, S. O., J. E. Crafford, A. Hassim, C. Byaruhanga, Y.-H. Huang, A. Hartmann, E. H. Dekker, et al. 2022. "Immunological Evidence of Variation in Exposure and Immune Response to *Bacillus anthracis* in Herbivores of Kruger and Etosha National Parks." *Frontiers in Immunology* 13: 814031. https://doi.org/10.3389/fimmu.2022.814031.

Owen-Smith, N. 2013. "Daily Movement Responses by African Savanna Ungulates as an Indicator of Seasonal and Annual Food Stress." *Wildlife Research* 40(3): 232–40. https://doi.org/10.1071/WR13024.

Owen-Smith, N., and M. G. L. Mills. 2006. "Manifold Interactive Influences on the Population Dynamics of a Multispecies Ungulate Assemblage." *Ecological Monographs* 76(1): 73–92. https://doi.org/10.1890/04-1101.

Panagis, K., and P. E. Stander. 1989. "Marking and Subsequent Movement Patterns of Springbok Lambs in the Etosha National Park, South West Africa/Namibia." *Madoqua* 1989(1): 71–3.

Park, J., C. Smith, G. Sugihara, and E. Deyle. 2020. "rEDM: Empirical Dynamic Modeling ('EDM')." https://CRAN.R-project.org/package=rEDM.

Parkinson, R., A. Rajic, and C. Jenson. 2003. "Investigation of an Anthrax Outbreak in Alberta in 1999 Using a Geographic Information System." *The Canadian Veterinary Journal* 44(4): 315–8.

Parsons, M., C. A. McLoughlin, K. A. Kotschy, K. H. Rogers, and M. W. Rountree. 2005. "The Effects of Extreme Floods on the Biophysical Heterogeneity of River Landscapes." *Frontiers in Ecology and the Environment* 3(9): 487–94. https://doi.org/10.1890/1540-9295(2005)003[0487:TEOEFO]2.0.CO;2.

Pascual, M., and A. Dobson. 2005. "Seasonal Patterns of Infectious Diseases." *PLoS Medicine* 2(1): e5. https://doi.org/10.1371/journal.pmed.0020005.

Pienaar, U. D. V. 1961. "A Second Outbreak of Anthrax amongst Game Animals in the Kruger National Park. 5th June to 11th October, 1960." *Koedoe* 4(1): 4–17. https://doi.org/10.4102/koedoe.v4i1.824.

Pinzon, J. E., and C. J. Tucker. 2014. "A Non-Stationary 1981–2012 AVHRR NDVI3g Time Series." *Remote Sensing* 6(8): 6929–60. https://doi.org/10.3390/rs6086929.

Plowright, R. K., H. E. Field, C. Smith, A. Divljan, C. Palmer, G. Tabor, P. Daszak, and J. E. Foley. 2008. "Reproduction and Nutritional Stress Are Risk Factors for Hendra Virus Infection in Little Red Flying Foxes (*Pteropus scapulatus*)." *Proceedings of the Roayl Soceity B: Biological Sciences* 275(1636): 861–9. https://doi.org/10.1098/rspb.2007.1260.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.

Reibe, S., and B. Madea. 2010. "How Promptly Do Blowflies Colonise Fresh Carcasses? A Study Comparing Indoor with Outdoor Locations." *Forensic Science International* 195(1–3): 52–7. https://doi.org/10.1016/j.forsciint.2009.11.009.

Robson, A. S., and R. J. van Aarde. 2018. "Changes in Elephant Conservation Management Promote Density-Dependent Habitat Selection in the Kruger National Park." *Animal Conservation* 21(4): 302–12. https://doi.org/10.1111/acv.12393.

Salb, A., C. Stephen, C. Ribble, and B. Elkin. 2014. "Descriptive Epidemiology of Detected Anthrax Outbreaks in Wild Wood Bison (*Bison bison athabascae*) in Northern Canada, 1962–2008." *Journal of Wildlife Diseases* 50(3): 459–68. https://doi.org/10.7589/2013-04-095.

Schmidt, H., and A. Karnieli. 2000. "Remote Sensing of the Seasonal Variability of Vegetation in a Semi-Arid Environment." *Journal of Arid Environments* 45(1): 43–59. https://doi.org/10.1006/jare.1999.0607.

Shearer, C. L., and V. O. Ezenwa. 2020. "Rainfall as a Driver of Seasonality in Parasitism." *International Journal for Parasitology: Parasites and Wildlife* 12: 8–12. https://doi.org/10.1016/j.ijppaw.2020.04.004.

Stears, K., M. H. Schmitt, W. C. Turner, D. J. McCauley, E. A. Muse, H. Kiwango, D. Mathayo, and B. M. Mutayoba. 2021. "Hippopotamus Movements Structure the Spatiotemporal Dynamics of an Active Anthrax Outbreak." *Ecosphere* 12(6): e03540. https://doi.org/10.1002/ecs2.3540.

Steenkamp, P. J., H. van Heerden, and O. L. van Schalkwyk. 2018. "Ecological Suitability Modeling for Anthrax in the Kruger National Park, South Africa." *PLoS One* 13(1): e0191704. https://doi.org/10.1371/journal.pone.0191704.

Sugihara, G. 1994. "Nonlinear Forecasting for the Classification of Natural Time Series." *Philosophical Transactions of the Royal Society of London. Series A: Physical and Engineering Sciences* 348(1688): 477–95. https://doi.org/10.1098/rsta.1994.0106.

Sugihara, G., and R. M. May. 1990. "Nonlinear Forecasting as a Way of Distinguishing Chaos from Measurement Error in Time Series." *Nature* 344(6268): 734–41. https://doi.org/10.1038/344734a0.

Sugihara, G., R. May, H. Ye, C.-h. Hsieh, E. Deyle, M. Fogarty, and S. Munch. 2012. "Detecting Causality in Complex Ecosystems." *Science* 338(6106): 496–500. https://doi.org/10.1126/science.1227079.

Takens, F. 1981. "Detecting Strange Attractors in Turbulence." In *Dynamical Systems and Turbulence, Warwick 1980*, edited by D. Rand and L.-S. Young, 366–81. Berlin, Heidelberg: Springer.

Torrence, M. E., S. R. Jenkins, and L. T. Glickman. 1992. "Epidemiology of Raccoon Rabies in Virginia, 1984 to 1989." *Journal of Wildlife Diseases* 28(3): 369–76. https://doi.org/10.7589/0090-3558-28.3.369.

Tsalyuk, M., W. Kilian, B. Reineking, and W. M. Getz. 2019. "Temporal Variation in Resource Selection of African Elephants Follows Long-Term Variability in Resource Availability." *Ecological Monographs* 89(2): e01348. https://doi.org/10.1002/ecm.1348.

Tucker, C. J., C. Li Vanpraet, M. J. Sharman, and G. van Ittersum. 1985. "Satellite Remote Sensing of Total Herbaceous Biomass Production in the Senegalese Sahel: 1980–1984." *Remote Sensing of Environment* 17(3): 233–49. https://doi.org/10.1016/0034-4257(85)90097-5.

Tucker, C. J., J. E. Pinzon, M. E. Brown, D. A. Slayback, E. W. Pak, R. Mahoney, E. F. Vermote, and N. El Saleous. 2005. "An Extended AVHRR 8-Km NDVI Dataset Compatible with MODIS and SPOT Vegetation NDVI Data." *International Journal of Remote Sensing* 26(20): 4485–98. https://doi.org/10.1080/01431160500168686.

Turnbull, P. C. B., P. M. Lindeque, J. Le Roux, A. M. Bennett, and S. R. Parks. 1998. "Airborne Movement of Anthrax Spores from Carcass Sites in the Etosha National Park, Namibia." *Journal of Applied Microbiology* 84(4): 667–76. https://doi.org/10.1046/j.1365-2672.1998.00394.x.

Turner, A. J., J. W. Galvin, R. J. Rubira, and G. T. Miller. 1999. "Anthrax Explodes in an Australian Summer." *Journal of Applied Microbiology* 87(2): 196–9. https://doi.org/10.1046/j.1365-2672.1999.00869.x.

Turner, W. C., P. Imologhome, Z. Havarua, G. P. Kaaya, J. K. E. Mfune, I. D. T. Mpofu, and W. M. Getz. 2013. "Soil Ingestion, Nutrition and the Seasonality of Anthrax in Herbivores of Etosha National Park." *Ecosphere* 4(1): 1–19. https://doi.org/10.1890/es12-00245.1.

Turner, W. C., P. L. Kamath, H. van Heerden, Y.-H. Huang, Z. R. Barandongo, S. A. Bruce, and K. Kausrud. 2021. "The Roles of Environmental Variation and Parasite Survival in Virulence-Transmission Relationships." *Royal Society Open Science* 8(6): 210088. https://doi.org/10.1098/rsos.210088.

Turner, W. C., K. L. Kausrud, Y. S. Krishnappa, J. P. G. M. Cromsigt, H. H. Ganz, I. Mapaure, C. C. Cloete, et al. 2014. "Fatal Attraction: Vegetation Responses to Nutrient Inputs Attract Herbivores to Infectious Anthrax Carcass Sites." *Proceedings of the Royal Society B: Biological Sciences* 281(1795): 20141785. https://doi.org/10.1098/rspb.2014.1785.

Turner, W. C., K. L. Kausrud, W. Wolfgang Beyer, R. Easterday, Z. R. Barandongo, E. Blaschke, C. C. Cloete, et al. 2016. "Lethal Exposure: An Integrated Approach to Pathogen Transmission Via Environmental Reservoirs." *Scientific Reports* 6: 27311. https://doi.org/10.1038/srep27311.

Venter, F. J., and W. P. D. Gertenbach. 1986. "A Cursory Review of the Climate and Vegetation of the Kruger National Park." *Koedoe* 29(1): 139–48. https://doi.org/10.4102/koedoe.v29i1.526.

Viljoen, J. J., A. Ganswindt, R. Palme, H. C. Reynecke, J. T. Du Toit, and W. R. Langbauer, Jr. 2008. "Measurement of Concentrations of Faecal Glucocorticoid Metabolites in Free-Ranging African Elephants within the Kruger National Park." *Koedoe* 50(1): 18–21. https://doi.org/10.4102/koedoe.v50i1.129.

Walker, M. A., M. Uribasterra, V. Asher, J. M. Ponciano, W. M. Getz, S. J. Ryan, and J. K. Blackburn. 2020. "Ungulate Use of Locally Infectious Zones in a re-Emerging Anthrax Risk Area." *Royal Society Open Science* 7(10): 200246. https://doi.org/10.1098/rsos.200246.

Wang, Y., J. Yang, Y. Chen, P. de Maeyer, Z. Li, and W. Duan. 2018. "Detecting the Causal Effect of Soil Moisture on Precipitation Using Convergent Cross Mapping." *Scientific Reports* 8(1): 1–8. https://doi.org/10.1038/s41598-018-30669-2.

WHO. 2008. *Anthrax in Humans and Animals*. Geneva: World Health Organization, World Organisation for Animal Health, Food and Agriculture Organization of the United Nations.

Ye, H., R. J. Beamish, S. M. Glaser, S. C. H. Grant, C.-h. Hsieh, L. J. Richards, J. T. Schnute, and G. Sugihara. 2015. "Equation-Free Mechanistic Ecosystem Forecasting Using Empirical Dynamic Modeling." *Proceedings of the National Academy of Sciences of the United States of America* 112(13): E1569–76. https://doi.org/10.1073/pnas.1417063112.

Ye, H., E. R. Deyle, L. J. Gilarranz, and G. Sugihara. 2015. "Distinguishing Time-Delayed Causal Interactions Using Convergent Cross Mapping." *Scientific Reports* 5(1): 1–9. https://doi.org/10.1038/srep14750.

Zambatis, N., and H. C. Biggs. 1995. "Rainfall and Temperatures during the 1991/92 Drought in the Kruger National Park." *Koedoe* 38(1): 1–16. https://doi.org/10.4102/koedoe.v38i1.301.

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