From unusual suspect to serial killer: Cyanotoxins boosted by climate change may jeopardize megafauna

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The recent mass mortality event of more than 330 African elephants in Botswana has been attributed to biotoxins produced by cyanobacteria; however, scientific evidence for this is lacking. Here, by synthesizing multiple sources of data, we show that, during the past decades, the widespread hypertrophic waters in Southern Africa have entailed an extremely high risk and frequent exposure of cyanotoxins to the wildlife within this area, which functions as a hotspot of mammal species richness. The hot and dry climatic extremes have most likely acted as the primary trigger of the recent and perhaps also of prehistoric mass mortality events. As such climate extremes are projected to become more frequent in Southern Africa in the near future, there is a risk that similar tragedies may take place, rendering African megafauna species, especially those that are already endangered, in risk of extinction. Moreover, cyanotoxin poisoning amplified by climate change may have unexpected cascading effects on human societies. Seen within this perspective, the tragic mass death of the world's largest terrestrial mammal species serves as an alarming early warning signal of future environmental catastrophes in Southern Africa. We suggest that systematic, quantitative cyanotoxin risk assessments are made and precautionary actions to mitigate the risks are taken without hesitation to ensure the health and sustainability of the megafauna and human societies within the region.

KEYWORDS: cyanobacteria toxin; climate change; eutrophication; mammal conservation; environmental health

The sudden deaths of at least 330 African savanna elephants (*Loxodonta africana*) in Botswana during May and June 2020 sparked much attention and concern worldwide (as seen in mainstream media, such as *New York Times*, *Washington Post*, *Chicago Tribune*, and *BBC News*. Viral and bacterial agents were initially suggested to be the most plausible cause of the tragic events, while the possibility of malicious poisoning, poaching, starvation, and anthrax was ruled out.[1] Aerial images and lab tests indicate that biotoxins or diseases are the culprit (see Text S1 for analyses of possible causes). Particularly, ingestion of cyanobacterial neurotoxins through drinking water rich in cyanobacteria is the suggested cause (see Text S2 for more information on cyanobacteria, cyanotoxins, and eutrophication).

However, questions remain as to the causal role of cyanotoxin poisoning in the elephant mass mortality event. Ideally, adequate measurements of water quality, cyanobacteria species, and cyanotoxin concentrations, combined with histopathological analyses, could have identified whether cyanotoxin poisoning was indeed the trigger of the mysterious mass deaths. However, the global coronavirus pandemic (COVID-19) and the remoteness of the mass mortality location render such measurements difficult. Also, most waters had gone dry, and many carcasses had already strongly decayed when the event started to attract attention. Here, we collected data on cyanotoxins and examined relevant historical records on the African continent and conducted a retrospective toxicity analysis to unravel how these pachyderms might have been killed. Then, using long-term meteorological records, we also examined the possibility of climate change as a trigger of this tragic event. Finally, we forecast the future risk of exposure of megafauna to cyanotoxins by identifying spatial congruence of hotspots of megafauna diversity, high cyanotoxins, hot and dry climates, and other factors favoring cyanobacteria growth.

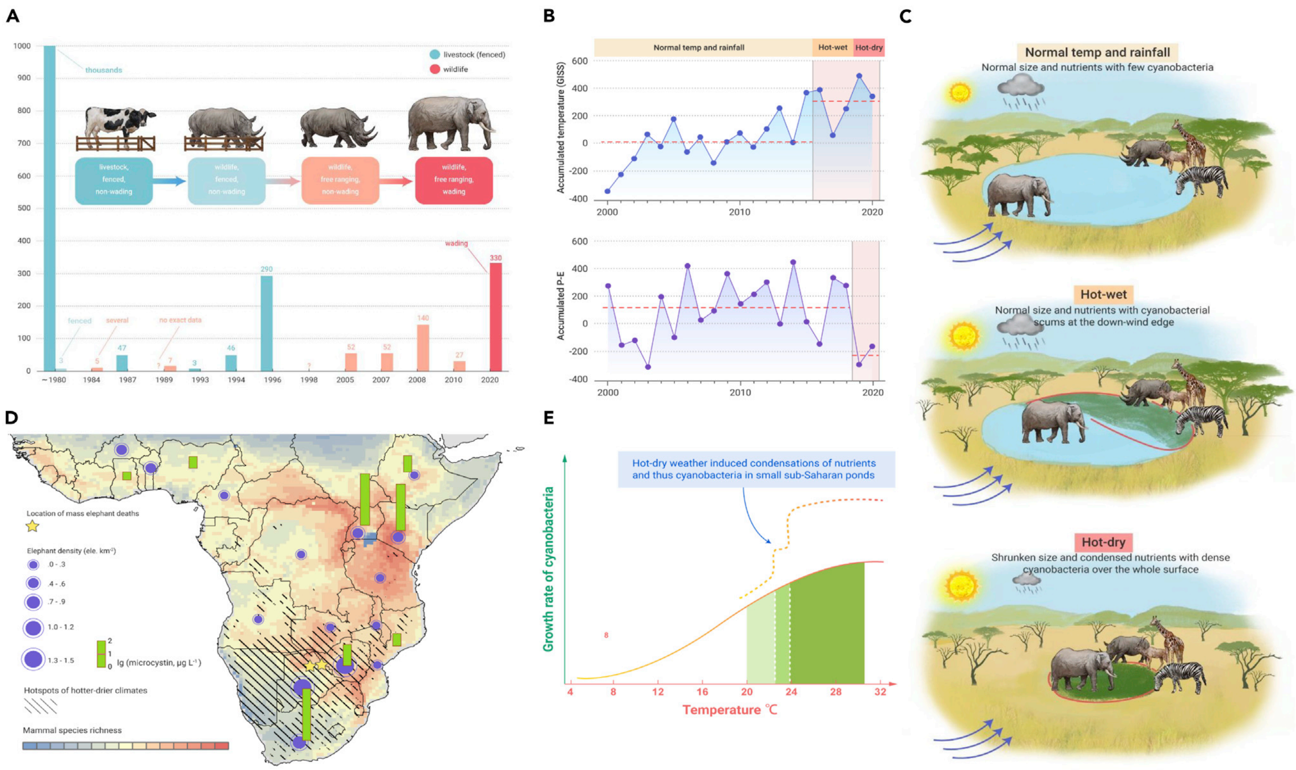

Figure 1. Lethal poisoning of cyanotoxin on megafauna in relation to changing environments Reported livestock and wildlife deaths in Africa with cyanotoxin poisoning as the suspected cause (A). Anomalies of effective accumulated temperature (°C days) and net precipitation (precipitation minus evaporation, mm) during 2000–2020 in the Seronga Village, Okavango Delta of Botswana, against the baseline climatology of 1986–2005 (B). Schematic representation of changes in vegetation, water area, and cyanobacteria concentrations and their poisoning risks to elephants under combined changing conditions of temperature and rainfall (C). Southern Africa identified as a hotspot of cyanotoxin risk at present and in the future (D). Response of cyanobacteria growth to climate warming (E).

High levels of cyanotoxins as a killer

One may doubt whether cyanobacteria in natural ecosystems are sufficiently toxic to kill hundreds of the world's largest terrestrial animals all at once. Indeed, cyanotoxin-induced mass mortalities have mostly been recorded for small-bodied animals such as fish, birds, and turtles.[2] Our literature review reveals that cyanotoxins have frequently been the suspected cause of the (mass) deaths of medium and large-sized terrestrial mammals in Africa, including livestock (cattle and sheep) as well as non-wading wild mammals (white rhinoceros, blue wildebeests, giraffes, zebras, and impalas) (Figure 1A) (see Table S1 for a compilation of historic events). Interestingly, due to vigilance against predators many of these species drink at the downwind edge of waters where dense cyanobacteria scum tends to accumulate, thus exposing them to high levels of cyanotoxins (Figure 1C). In contrast, elephants, being a wading species, tend to drink in the middle of the waters and are therefore expectedly less exposed to cyanotoxins if cyanobacterial scums are limited to the downwind edge. Hence, the behavior of the animals is expected to affect their susceptibility to toxic cyanobacteria.

Although *in situ* data on cyanotoxin concentrations in the elephant die-off locations are so far unavailable, our collected data on the water quality of relatively large waterbodies in Africa show that concentrations of cyanotoxin (using as a proxy microcystins, MCs for short, the most common and most toxic species) ranged between 0.36 and 124,460 $\mu g\ L^{-1}$. Most values were much higher (an 8,836 times average) than the provisional guideline value of 1.0 $\mu g\ L^{-1}$ recommended by the World Health Organization for mammals and humans (see Table S2 for details).[3] The situation is particularly serious in the southern part of Africa, where averaged MCs are over 13,400 times the guideline. Importantly, MCs in two waterbodies (103 and 124 mg L^{-1}) of southeastern Africa almost reached the acute lethal dose of 125 mg L^{-1} (see Table S2 for the derivation of acute lethal dose).[3] Similar results are found for the daily intake of toxins. In small ponds and puddles serving as important sources of drinking water for wild mammals, cyanotoxin concentrations are expected to be even higher due to accelerated water evaporation at high summer temperatures.[4] Such high concentrations of cyanobacteria/cyanotoxins in this region are not surprising, as hypertrophic (e.g., nitrogen-rich sewage and feces from wildlife resulting in ammonium levels as high as 273 mg L^{-1} in the Hartbeespoort Dam, which is 10 times the level of raw domestic sewage), hydrologically stagnant, and climatically hot conditions together create an ideal environment for cyanobacterial blooming in almost every aspect.

Our analysis indicates that cyanotoxins were indeed the most likely cause of this event, which would be the first confirmed case of cyanotoxin-induced elephant mass mortality. In a broader context, our retrospective analysis also demonstrates a likely increasing risk during the last decades, with mammal victims extending from fenced livestock to fenced wildlife, over free and non-wading wildlife, and finally to free and wading wildlife (Figure 1A). Despite a caveat of "survivorship bias," our findings nevertheless have profound implications, suggesting that cyanotoxins have rapidly become a life-threatening stressor for an increasingly wide range of African megafauna, including the largest species (i.e., the African savanna elephant). The consequences of cyanotoxin poisoning for the already endangered elephant could be catastrophic since the number of carcasses from the Botswana mass die-off was close to that of poaching (385 ± 54) (the primary cause of elephant deaths) in Botswana for a whole year.[5]

Hot and dry weather as a trigger

Cyanobacterial blooms, driven by eutrophication and global warming, have rapidly increased in frequency, intensity, and duration across the globe.[6,7] While hot weather is the primary trigger of dense cyanobacterial blooms, the high inputs of wildlife and livestock feces and sewage will lead to cyanobacterial growth spurts in Southern Africa. Our analysis of climate records reveals that hot and dry conditions occurred for multiple years in a row in the areas where most of the elephant carcasses in Botswana were found (Figure 1B).

This finding seems unlikely to be a coincidence because similar climatic conditions were also associated with mass mortalities of elephants in Zimbabwe and non-wading mammals in South Africa (Figure S1). Hot and dry weather could have boosted the production of cyanotoxins (Figure 1C). Also, the dry weather amplified the risk of poisoning—the shrinking water areas led to elevated cyanotoxin concentrations and an increasing demand for drinking water by the mammals. Our remote sensing analyses on the event area showed that, during March–July 2020, FAI (Floating Algae Index, an approximate indicator of cyanobacteria abundance) increased continuously along with shrinking water bodies (Figure S2). This demonstrates the increasing risk of cyanotoxin exposure associated with a drying trend of surface water cover.

Climate change as a risk amplifier

A critical question arising from the elephant mass die-off event in Botswana is how the ongoing climate change will influence the risks posed by cyanotoxins in the future. Our analysis identifies several "hotspots of cyanotoxin risks" in southeastern Africa where high megafauna diversity (including major elephant populations), high risks of exposure to cyanotoxins (MCs), and most historical cyanotoxin-related mortalities occur (Figure 1D). The first reported MC-attributed damage to human health under natural conditions also took place in this region (Zimbabwe).[8] Climate models project that, in the near future, this region will experience the highest warming rates across Africa, with a mean annual temperature increase of above 4°C and less precipitation than under the current conditions by 2070 predicted in a high-emission scenario SSP585 (Figure 1D; see also Figures S3 and S4). Of major concern is the circumstance that the poisoning risks will plausibly increase with the future warmer and drier climate. These hotter and drier climates will create more favorable conditions for cyanobacteria growth when both nutrient and cyanobacterial concentrations condense (Figure 1E).

With climate change, lake surface water temperatures are predicted to increase at a similar or even higher rate than the air temperatures.[9] Besides stimulating the release of toxins, warming will also promote dominance of a few highly toxic variants. At local scale, hot dry weather can drive more animals to gather more frequently around the remaining surface waters, which may accelerate eutrophication via feces and consequently further amplify the exposure risk (Figure 1C). In a worst-case scenario, the synergistic effects of warming and eutrophication promoting cyanobacteria growth and toxin release may create an existential risk for the vulnerable wildlife populations already subject to starvation and thirst induced by more frequent climate extremes.[10]

This study indicates an increased risk of mass die-off events with global warming, yet more research is needed to quantitatively predict the future (cyanotoxin-induced) mortality of African savanna elephants as well as other megafauna species that are prone to extinction with climate change. Interestingly, fossil records include evidence of prehistoric mass deaths of elephants and other megafauna in Pleistocene and Eocene lakes, which have been attributed to recurrent toxic cyanobacterial blooms, likely driven by climate change.[7] Further development of quantitative models on the link between cyanotoxins and animal death could provide robust explanations of these prehistoric mass mortality events as well as allow forecasts of future risks to wildlife populations.

In addition, cyanotoxin poisoning tragedies such as this tragic event may have unexpected cascading effects on humans and society. Thus, increasing exposure to cyanotoxins in polluted water will inevitably be harmful to the health and livelihoods of humans who rely on livestock and wildlife or use the polluted water for drinking or irrigation purposes. The substantial role of cyanotoxins in the Botswana die-off event emphasizes that more comprehensive and systematic (re-)assessments of the risks of cyanotoxins for both wildlife and humans are needed in the face of climate change to permit implementation of effective precautionary actions ameliorating the cyanotoxin threat to the vulnerable African socio-ecological systems.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

SUPPLEMENTAL INFORMATION

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