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Bison, Elephants, and Sperm Whales: Keystone Species in the Industrial Revolution

John R. McNeill *

Abstract: *»Bison, Elefanten und Pottwale: Schlüsseltiere der industriellen Revolution«.* Three giant-sized mammals, bison, African elephants, and sperm whales, faced sustained hunting in the 19th century. Demand for hides, ivory, and whale oil, all of which were useful in industrial production, animated the hunts. Most of the industrial production in question took place in the northeastern United States, while the hunts took place thousands of kilometers away, linking regions in what I call "ecological teleconnections." The hunts dramatically reduced the populations of all three species, most drastically the bison. For ten thousand years, bison had helped to regulate their biome, the North American prairie grasslands, playing a role of a keystone species. East African elephants on their savanna grasslands, and sperm whales in oceans, had functioned for even longer as keystone species. The sharp and sudden reductions in populations of these animals after 1800 produced a variety of indirect ecological effects, reshuffling the ecosystems in question, making for difficult times for human communities that had come to depend on them.

Keywords: Bison, elephants, sperm whales, hides, ivory, whale oil, industrialization, ecological teleconnections.

1. Introduction

Three monarchs of the biosphere in 1800 were the bison of North Americans grasslands, the elephants of East Africa's savannas, and the sperm whale of the tropical and temperate oceans. They had enjoyed lengthy reigns, helping to govern their domains as "keystone species" for millennia, but in the decades after 1800 they lost their thrones as a result of a revolution.[1] The bison, elephant, and sperm whale shared the misfortune that specific parts of their

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[1] A keystone species is one that plays an outsized role in influencing its habitat such as beavers, bees, or mangrove trees. The term was coined in the 1960s to refer to certain predators but is now used more generally. Thanks for critiques or suggestions on this paper to audiences at Princeton and Georgetown universities, and especially Francisco Céntola, Toshi Higuchi, Fabian Krautwald, Timothy Newfield, Andrew Ross, and Rachel Singer.

bodies served admirably in new, technically sophisticated processes developed during the 19th century's Industrial Revolution, particularly in its North American manifestations.

Bison hide, elephant tusk, and sperm whale oil helped to industrialize the US and to a lesser extent other lands. Properly tanned, bison hide made a better leather than cowhide in certain applications, such as boot soles and industrial belting. East African elephant tusk, sawn carefully, made attractive combs, cutlery handles, billiard balls, and above all, piano key veneer. Sperm whale oil, which is technically speaking not an oil but a wax, when suitably processed, made an excellent machine lubricant. It did not corrode metals, it retained its viscosity in both high and low temperatures, and so found applications in locomotives, power looms, watches, guns, and – in the 20th century – automobiles and aerospace.

In each of these three cases, industrialization ratcheted up demand for an animal body part. The invigorated markets in the heartlands of industry inspired intensified hunts for bison hide, elephant tusk, and sperm whale oil thousands of kilometers away. The result of these "ecological teleconnections," as I call them, was a series of "Late Holocene Depletions" of large animals, loosely analogous to the Late Pleistocene Extinctions some ten or twelve thousand years before.

On small scales, bison, elephant, and sperm whale hunting had existed before industrialization. The people who killed these animals before 1800 had their own reasons for doing so, unrelated to distant markets or factory production. New linkages in the 19th-century globalizing economy, however, brought a new logic, incentive, and urgency to these hunts.

Cheap energy, mainly in the form of coal, made these ecological teleconnections more powerful: watermills and steam engines cheapened factory production and railroad and steamship links cheapened transport. Meanwhile, the cheap energy of gunpowder made hunting for bison and elephants more efficient and less dangerous for hunters. While a few ecological teleconnections had existed before industrialization, as in sugar or furs for example, cheap energy after 1800 made such linkages more numerous and extended this sort of linkage to dozens of items such as fibers, minerals, dyestuffs, and so forth all over the world. The new scale of industrial demand intensified such teleconnections to the point where it radically reshuffled ecosystems with enduring consequences for both environments and the human societies that depended on them.

2. Bison

Bison[2] immigrated to North America from Siberia roughly 150,000 years ago, and for most of the remainder of the Pleistocene shared the grasslands of the Great Plains with a magnificent menagerie of megafauna: camels, mammoths, gigantic bears and wolves, and armadillos the size of small cars. However, shortly after the arrival of the first humans on the Great Plains, roughly 13,000 years ago, most of those megafauna species – a total of 38 genera – were swept into the dustbin of prehistory in a chapter of what are known as the Late Pleistocene Extinctions (Meltzer 2020). Among the victims was the horse, thereafter absent in the Americas until Columbus. By approximately 9000 BCE, bison stood as the largest animal in North America.

2.1 The Bison Steppe

The Late Pleistocene Extinctions opened a sprawling ecological niche into which the bison stampeded. Paleo-Indians helped to expand that niche – the prairie biome – further by their use of fire. Whereas northern Eurasia in the late Pleistocene became a "mammoth steppe," created mainly by climate conditions, maintained for 100,000 years by mammoths, and eventually destroyed partly by human hunters, in North America, climate (here meaning de-glaciation) and human hunting created a "bison steppe" by about 9000 BCE. It too would be destroyed, more than ten millennia later, by human hunters.

This deep history helps to explain why, until recently, so many bison thundered across North America. Their range extended across what is now more than 40 US states, 4 Canadian provinces, and the northernmost states of Mexico. Drought, disease, and perhaps other variables no doubt led bison numbers to wax and wane over the millennia, probably fluctuating around 20-40 million animals. Hunters took a very small toll, using fire to stampede herds over cliffs now and again. But bison-hunting on foot was a dangerous enterprise. Most of the time, paleo-Indians found better ways to ensure their subsistence.

In these ten millennia, plants and animals adjusted to the reign of bison. Pronghorn and deer came to use trails that bison plowed through deep snow, making deep winter on the grasslands less hazardous for them. Dozens of creatures learned to rely on bison wallows – depressions in flatlands that collected water – to get them through times of drought. Prairie dogs expanded their colonies in the short grass left behind by herds of munching bison, and hawks, eagles, coyotes, foxes, and snakes ate well in lands colonized by prairie dogs. Grouse and prairie owls also nested in the short grass. Other birds

[2] Popularly called "buffalo" in Canada and the US. The Linnaean name is *bison bison*.

lived off insects that accumulated on bison fur. The long-billed curlew protected their young by designing nests to look like bison "chips" (dried manure). Those bison chips were full of plant nutrients, which bison helpfully carried from locales brimming with nutrients, such as river banks, to those without, improving the prospects for vegetation far and wide. For many species trying to survive on the bison steppe, with its recurrent drought and fierce winter, these ten millennia with bison securely enthroned as a keystone species were the best of times (Knapp et al. 1999).

2.2 The Bison Hunt

The reign of the bison ended with many a bang. It is a story well told by several historians (Hornaday 2002 [1889]; Isenberg 2020; Flores 2016; Cunfer and Waiser 2016). After an absence of roughly eleven millennia, horses returned to North America with Hernán Cortés in 1519. By roughly 1730, they were running wild once more in their land of origin from northern New Spain to the Great Plains of what is now the US and Canada. Comanche and Kiowa in the west, and Lakota and Cheyenne in the east, edged out onto the plains, quickly developing equestrian cultures that included efficient bison hunting with bow and arrow. By about 1790, the bison population was probably in slow decline due to the skill of hunters on horseback, and to competition for succulent grasses from roughly 2 million wild horses, which, unlike antelope, eat much the same grasses as bison. The hunters gradually added guns to their arsenals and became yet more efficient. But as of 1840, some 15-20 million bison remained.

In the next 40 years, the bison came within a whisker of extinction. The decline came rapidly from 1840 to 1865, and then at warp speed from 1865 to 1881. Some 12-15 million remained in 1865 but by 1881 only about 1,000 animals were left, huddled in micro-herds from Chihuahua to Saskatchewan.

A small proportion of the post-1840 bison hunt was conducted by Native Americans seeking subsistence or the fluffy overcoat ("bison robe") available in wintertime when bison were at their shaggiest. They especially wanted fat, which inclined them to hunt females, ideally pregnant ones, which reduced the fertility and resilience of bison populations. By mid-century, white Americans were flowing across the prairies, aiming for California and Oregon, following trails that traced river courses. As access to alternative sources of food, especially in the river valleys of the Great Plains, became increasingly difficult, Plains Indians tightened their focus on bison-hunting. But even so, with each passing year, a larger share of the kill was conducted by market hunters aiming to turn dead bison into money.

2.3 The Bison Hide Market and Bison Slaughter

Several markets lay behind the bison hunt. North of the Missouri River, where perhaps 7 million bison roamed between the Rockies and the Red River, most of the hunters were Métis (descendants of both First Nations and French or French Canadians). They killed bison because its meat served as the key ingredient of pemmican, an energy-dense food essential to the cold-weather long-distance travel of the fur trade. The Hudson's Bay Company (HBC) needed endless supplies of pemmican for its traders as they paddled and walked across North America. The HBC also developed a side business in bison hides, selling them in Montreal and New York mainly after 1850. Métis hunters, too efficient for their own good, found bison increasingly scarce after 1860 (Colpitts 2015; Ray 1984; Ray 1998, 222-6; Dobak 1996; Binnema 2001; Foster 1992; Cowie 1913).

Further south, the hide market rather than pemmican inspired bison slaughter. Bison hunters in the 1840s and 1850s found modest markets for bison meat, robe, and hide. On the southern plains, bison populations were apparently in notable decline: Kiowa calendars, which were annual chronicles painted on bison robes, indicate so by the 1840s (Flores 2016, 129). Still, 12-15 million bison remained in North America at the time of the Civil War, the end of which unleashed thousands of marksmen in search of a living.

Between 1865 and 1885, some 5,000 bison hunters rode out onto the plains to cash in on the quickening hide market. From the 1850s, gradual technical improvements in the chemistry of leather tanning sharpened demand for raw bison hide in Europe. Liverpool importers began acquiring it in 1871; Le Havre in 1873; Hamburg in 1877. Tanning improvements took place in the US too, where the industry was concentrated in Pennsylvania and upstate New York where tree bark was cheap and big markets for leather existed nearby. Once they equaled their European counterparts in skill, American tanners took the vast majority of the bison hide business and hide exports to Europe diminished. Tanned bison leather was used for harnesses and saddles on a small scale. It made good, durable sole leather for shoes and boots, and according to some sources considerable quantities of tanned bison leather went to European armies in the 1870s, and perhaps as early as the Crimean War of 1853–1856 (Taylor 2011; Manning 1997, 84).

The other major destination for tanned bison hide was industrial belting in eastern North America and Europe. Textile mills in particular needed belting – an American innovation to factories' design – to impart power from waterwheels or steam engines to carding machines, power looms, and spindles. Factories with power saws, lathes, or almost any other big power machine needed heavy belting. Bison leather, tough but more elastic than cattle leather, formed the ideal ingredient, often called "machine leather" (Manning 1997, 84; Isenberg 2020, 130-1; Hansen 2016).

Habitat loss played only a tiny role in the bison's fate. The Great Plains in 1860 held about 160,000 settlers and less than 1% of the land was farmed. In 1880, about 20-40% of the total area of the plains states (not counting "Indian territory") was officially farmed, and around half of that was "unimproved" land, meaning left as woodland or grassland (United States 1880, xi-xii). The Canadian prairies had even thinner settlement as of 1880. Nor, contrary to popular belief, did the US Army do much to extinguish the bison. The famous quotation attributed to General Philip Sheridan, urging destruction of "the Indian's commissary," was a fabrication from 1907. Sheridan, in fact, in 1879 advised that the US Government should intervene to stop the slaughter (Flores 2016, 122-4, 131). The bison bone trade (for fertilizer) similarly had little impact, although it was briefly a sizeable business. The reason is that bone collectors followed a year or two after the hunters to collect bones cleaned by coyotes, buzzards, and bacteria; hunters did not collect bones, and even if they tried to return to the site of their kills, they could not count on getting to bison skeletons before someone else. They hunted for what they could get when they killed animals, which was mainly hides.

The hide trade inspired the slaughter, but other forces might have compounded the bison population collapse. A serious drought, 1858–1864, probably contributed to bison losses. Anthrax and bovine tuberculosis, presumably acquired from cattle herds, might have as well: they were present in the remnant herd in the late 1880s, but just when these infections made the jump to bison is unknown (Flores 2016, 127). Other infections might have ravaged herds too, although there is no evidence at all for this proposition. The relative roles of drought and disease are hard to assess, but most historians of the question, I think rightly, assign them marginal parts in the drama.

The dominant factor behind the end of the bison reign was an unregulated market for industrial ingredients in both North America and Europe. After dominating the prairies for 100 centuries, weathering all manner of climate change and epizootics, within the span of a few decades the bison fell victim to surging demand for industrial belting and boots, encouraged by new or improved technologies such as railroads, rifles, and leather tanning. Routine industrial production led to a biotic revolution on the prairies.

2.4 Ecosystem Impacts of Bison Slaughter

What happens when 99.99% of bison are suddenly subtracted from the prairie biome? In the short run, the slaughter of the bison brought a brief bonanza for buzzards, coyotes, and other scavenger species suddenly faced with a smorgasbord of several million quietly decomposing bison, conveniently stripped of their hides. No doubt hordes of insects and bacteria thrived as well for a few decades amid the archipelago of carcasses. Other species missed the bison, no longer scooping out wallows to collect water, no longer

snowplowing paths in deep winter, no longer serving up insect meals to birds. Pronghorn (commonly if incorrectly called antelope) in particular missed the bison, because they graze on forbs (not grass) that occur in patches here and there, so they need to move around, winter and summer, and in snowy winters had relied in snowplowing bison to make paths. Their numbers plummeted along with those of the bison, although since about 1950 they have made a modest comeback. Prairie dogs, which in 1800 probably numbered in the billions, also missed the bison. They need short grass with long vistas; tall grass hides predators such as snakes, coyotes, and ferrets. Bison had formerly chewed through tall grass, leaving a shaven landscape with good visibility for prairie dogs.

The plant world also felt the near-extinction of the bison. Bison no longer dispersed seeds, which reduced the plant biodiversity of the prairie. They no longer trampled bushy vegetation, so the grassland shrank and woody species spread. Without bison, the tallgrass became a tangled jungle harder to traverse for smaller species, including humans. Without bison, the fuel load of the prairie increased, making wildfires more intense. Without bison, no creature could efficiently carry nutrients from lands of plenty to lands starved of nitrogen and phosphorus. The prairie was by the 1880s already a different ecosystem, thanks to the market hunting undertaken by Native Americans, Métis, and above all, by roughly 5,000 Euro-Americans. It was rapidly becoming monocultures of wheat, corn, and cattle.

The remade prairie could not nourish the equestrian cultures invented by the Plains Indians between 1750 and 1850. The bison had served as a cultural keystone species for them, with both economic and spiritual importance. The purpose of the slaughter of the bison had been to make money, not to destroy Native American autonomy, power, and culture on the Great Plains – from the point of view of most of the market hunters that was a side benefit. But the slaughter did so anyway.

The Plains Indians' equestrian culture lasted for maybe ten human generations, between the arrival of horses and the demise of the bison. The more sedentary culture that followed, based on wheat, corn, and cattle, has now endured for roughly five generations. Since the 1940s, it has depended in large measure on pumped-up groundwater from the Ogallala Aquifer (and lesser underground water supplies). That water, accumulated drip by drip for millions of years, is now pumped up at a rate that shrinks the Aquifer by 1% every 18 months. That rate will climb if, as climate models predict, rains on the plains diminish in the decades ahead. It remains to be seen if the current plains culture can outlast its predecessor.

3. Elephants

In a remarkable quirk of recent evolutionary history, elephants in Mozambique's Gorongosa National Park have rapidly spread a genetic trait that results in mature female elephants without tusks. Hunting pressure in recent times, especially during Mozambique's civil war of 1975–1992, has selected ruthlessly against tusks (Campbell-Staton et al. 2021). Tuskless elephants now have much better chances of survival and reproduction than have tuskers. This turns several million years of elephant history, during which tusks were helpful to elephants, on its head. The origin of this extraordinary volte-face in natural history in East Africa is the invention of a mechanical saw and the maturation of the piano keyboard industry in the lower Connecticut River valley. Yankee ingenuity opened an era of intensified elephant slaughter in East Africa in the mid-19th century.

3.1 Elephants and Savannas

The earliest proto-elephant fossils are found in Africa and date back 40 million years. Representatives of the genus *loxodonta* have roamed the continent for the last 4 million years or so. Several species went extinct, in Africa, Europe, and Asia, within the past 12,000 years, leaving either two or three (there is debate) elephant species in Africa. (Asian elephants are from a different genus). *Loxodonta Africana*, the species that graces the East African savannas, appeared first in the late Pliocene as a forest species, but colonized the savannas of East Africa in the Pleistocene, beginning around 2.6 million years ago.[3]

The lion may rank as the king of the beasts, but the elephant once reigned over savanna ecosystems. Like the bison, it is a keystone species. Elephants govern the balance between grass and bush forest, because they knock over small and mid-sized trees to get at their tasty roots. Bull elephants can knock over six trees a day. They also use their tusks to strip off delicious bark, killing upright trees. In addition to preventing forest from spreading to every sufficiently moist landscape, elephants maintain trails through the bush. These serve as highways for other creatures, and as firebreaks that check the impact of wildfire. Elephants dig out waterholes that they and other animals use to stay hydrated during dry seasons. Elephants, more than smaller animals, disperse seeds, helping to regulate plant biodiversity. And, just by eating, defecating, and ultimately decomposing, elephants re-allocate soil nutrients from nutrient hotspots with more nitrogen and phosphorus than their plants can

[3] The famous war elephants of the ancient Mediterranean were likely not *Loxodonta africana* but a much smaller, and more easily trained, species native to North Africa, variously called North African forest elephant, Atlas elephant, Carthaginian elephant, and *Loxodonta africana pharaohensis*. It is long extinct.

use, to places where limiting nutrients are scarce. This applies not only to nitrogen and phosphorus: each grown elephant contains 200-300 lbs (90-136 kg) of calcium (much of it in tusks). Over millions of years, savanna plants and animals adapted to the presence of millions of elephants (Owen-Smith 1988).

In contrast to the situation in North America's bison history, no surge of Late Pleistocene extinctions changed the population balances among African animals, or suddenly opened niche space for lucky survivors. Elephant numbers rose and fell throughout the Pleistocene, and most of the Holocene, mainly with the rhythm of rains and drought. They drink prodigiously and cannot stray far from surface waters. When those dry up, elephants die in droves. Major droughts afflicted East Africa in the late 18th century, in the early 19th, and again in the 1870s and 1880s, and probably reduced elephant populations. But abundant rains ca. 1850–1870 provided lush forage and likely boosted elephant numbers.

The niche space occupied by livestock herds and herders also affected elephant population size. The prevalence of tsetse fly and trypanosomiasis in much of the mid-section of the African continent checked the geographical spread of livestock herding, leaving plenty of habitat for wild creatures including elephants. Tsetse fly species serve as vectors of African trypanosomiasis, an infection called sleeping sickness in humans and nagana in animals. Nagana made it difficult to raise livestock and for people to live as herders – a prominent way of life for more than 3,000 years in those parts of East Africa free of tsetse. In East Africa, wild animals have had about 35 million years to adjust genetically to trypanosomiasis and tsetse flies; domesticated animals have yet to do so (Steverding 2008). Sleeping sickness, a longtime scourge in equatorial Africa, is a debilitating infection that if untreated is fatal in humans. With livestock and pastoralism kept in check, elephants could roam widely. Lions, which can kill baby elephants that stray from their mothers, were their only non-human predators. With rare exceptions, humans prudently kept their distance from elephants, although Africans did occasionally hunt them for meat by digging big pits or using poison arrows. The best guesses suggest that in 1800, about 26 million African elephants strolled around their continent.

3.2 Elephant Hunting

A substantial commercial business in elephant hunting developed in the 1750s in Mozambique, financed by entrepreneurs from Gujarat who had plenty of cloth to trade and ready access to robust Indian markets for ivory (brides in Gujarat and Rajasthan ideally wore, and still wear, ivory bangles in profusion). This hunt took elephants from as far north as the shores of Lake Malawi to as far south as the hinterland of today's Maputo, and before its

demise about 1830, accounted for maybe 30,000 elephants, or a few hundred per year. This volume probably had a negligible overall impact on the targeted Mozambican herds, whose range extended into what is now southwestern Tanzania, and whose populations numbered (in this area) at least several hundred thousand (Machado 2014, 168-207).

Ivory hunting in East Africa, long a small-scale business, boomed after 1840. Local traders and leaders wanted cloth and guns as a route to wealth, power, and status. Ivory and slave exports were their means to these ends. By the 1830s, the Mozambique trade was fading away and Zanzibar emerged as the dominant ivory port of East Africa. European firms sold guns – perhaps 100,000 per year (Iliffe 2007, 187) – to Omani and Swahili entrepreneurs, who organized large-scale elephant hunts employing both wage and slave labor. These consisted of up to 4,000 men in militarized caravans. After marksmen killed elephants, porters – often 500 or 1,000 per caravan – carried the dead beasts' tusks to the coast. Animals could not do this heavy work because of the prevalence in these landscapes of tsetse fly and nagana. Nor did conveniently navigable rivers flow across East Africa north of the Zambezi, ruling out boat transport. These journeys could be nearly a thousand miles long and proved fatal to many porters. From little ports on the coast, boats then carried the ivory to warehouses (*godowns*) in Zanzibar, owned by Omani Arabs or Indians, often Gujaratis. They then sold the white gold to the highest bidders, by 1850 often buyers for Connecticut keyboard manufacturers. By some estimates, the Americans bought more than half the ivory on sale in Zanzibar between 1840 and 1920. By 1890, London, Liverpool, and Antwerp imported substantial quantities (hundreds of tons) annually, although almost all from Congo rather than Zanzibar. Some 70% of London's ivory imports were reexported; much of what stayed in England went to Sheffield, center of the cutlery industry (Great Britain 1895, 2). Zanzibar's ivory exports after 1850 required the deaths of tens of thousands of East African elephants annually. Many of them were mothers, whose newborns and toddlers would invariably die soon after their mothers.

By 1900, only about 10 million elephants remained in all of Africa, and in 2020 roughly half a million. Demand for ivory in centers of industry and the availability of guns account for a large share of the rapid decline of East Africa's elephant population. Habitat loss, in the form of the expansion of farming, would account for most of the remainder (Alpers 1975; Sheriff 1987).

3.3 Elephant Tusk and Ivory Manufacture

Until recently, almost all African elephants, male or female, had tusks. Big ones might weigh 200 lbs (80 kg) each. Average ones before 1880 came to 70 lbs (30 kg) per tusk, and by 1920 only about 50 lbs (20 kg), evidence of the

impact of hunters' preference for big tusks. A ton of ivory meant 15-20 dead elephants.

Tusks from female elephants made the best billiard balls. Big tusks from bull elephants, called *bori* in Swahili, made the best cutlery handles and piano key veneer (Moore 1931, 220). Between 1840 and 1930, the largest use for elephant ivory, outside of bangles made mainly of tusk from India's elephants, was piano keyboard manufacture. *The Book of Complete Information about Pianos* (1918, 10) summarized the virtues of ivory:

> Ivory is used for the white key-tops because it has a richer appearance than any other material and is more pleasant to the touch, there being very slight friction between the finger and the ivory key; besides, it is known to retain a remarkable evenness of temperature in all seasons. It does not become so cold in the winter as to be uncomfortable, yet it is always cool, even in the warmest weather. It seems to be affected very little by the changes of heat and cold. The best ivory is that cut from the tusks of freshly killed elephants. This is expensive. Besides, only certain portions of the tusks can be utilized for piano keys. There are parts of the tusks which are not of the proper color, and which, for other reasons, are not suitable.

A big elephant tusk, skillfully sawn, could cover the white keys of 45 pianos. An average one, well cut, might do for 35.

For millennia, ivory workers had used drills and chisels to craft fine objects. When they had a choice, they often preferred African ivory, which was softer and easier to work than the Asian variety. Then, Phineas Pratt, a church deacon with a full measure of Yankee ingenuity, devised a new saw in 1799. It could slice into ivory with precision and power and allowed an operator to make 400 ivory combs a day, nearly 100 times what could be achieved by hand. His ivory-sawing business created a new industry at the juncture of the Fall and Connecticut Rivers in what would become Ivoryton. Refinements to Pratt's saw permitted slicing tusks into wafer-thin veneer, 30 to an inch, opening the way to cheap mass production of ivory-paneled piano keys.

Between 1860 and 1930, two factories in the Connecticut River valley built most of the world's – not just America's – piano keyboards and with their orders determined the price of tusks in Zanzibar.[4] At their peak, around 1909, between them Pratt, Read & Co and Comstock, Cheney & Co. employed 1,400 workers who made upwards of 390,000 keyboards each year. (Today about 50,000 new pianos are sold annually in the US.) These two firms bought more than 90% of the ivory imported into the US, all of it from East Africa. When business was good, the Ivoryton factories bought 10,000 tusks a year, spelling the end for 5,000 elephants.

[4] Moore 1931, 207, giving no date (but likely around 1910) says a big tusk was worth $400 in Zanzibar.

3.4 Piano Popularity

Business was good for several decades. In the late 19th century, every bourgeois parlor, gospel church choir, and bordello in North America needed a piano. In 1918 former president Grover Cleveland explained his understanding of the place of the piano and its role for those seeking a ticket to the altar:

> In many an humble home throughout our land the piano has gathered about it the most sacred and tender associations. For it the daughters of the household longed by and day and prayed in dreams at night. For it fond parents saved and economized at every point and planned in loving secrecy. For it a certain Christmas day, on which the arrival of the piano gave a glad surprise, was marked as a red letter day in the annals of the household. With its music and simple song each daughter in her turn touched with love the heart of her future husband.[5]

One had to make one's own music in those days, whether one's taste ran to Johannes Brahms or Scott Joplin. But by the late 1920s, the popularity of pianos began to wane. Recorded music and radios gradually replaced homemade music (Roell 1989). The keyboard business shrank by almost 90% between 1922 and 1932, the deepest trough of the Great Depression. The two firms in Ivoryton merged in 1936, turned their expertise with wood and glue to making gliders during WWII, and limped into the 1950s, when the rise of cheap plastic piano keys finally killed off their business. The quantity of pianos built before the advent of plastic keys is summarized here:

Table 1 Piano Manufacture, 1850-1930 (in thousands)

Year	USA	Rest of the World	Total
1850	10	33	43
1870	24	61	85
1890	72	140	212
1910	370	230	600
1930	120	90	210

Source: Ehrlich 1990, 222.

The data in Table 1 show the peak of production, which came just before and after the First World War, the rapid ascent of the American piano industry, and the collapse begun in the late 1920s and confirmed by the Great Depression.

3.5 The Ivory and Cloth Trade

The East African ivory trade was funneled from the interior to several small ports from Kilwa to Mogadishu along the Swahili coast, and from there to Zanzibar. The island was then a sultanate run by a family, Bargash by name, of Omani origin. In the mid- and especially the late 19th century, Zanzibar

[5] Unnumbered dedicatory page in *The Book of Complete Information about Pianos* (1918).

was a cosmopolitan town with thousands of foreign residents, mostly from India. In 1885, eight of those foreigners were Americans, agents for New England merchant houses (Holmwood 1885, 421).

Their main business was ivory. Referring to the 12 months between mid-1883 and mid-1884, the US consul in Zanzibar wrote,

> [ivory] is brought down here in caravans from Central Africa to the coast and is shipped over here [Zanzibar] in dhows. Owing to the constant killing of the Elephants the supply is fast diminishing and consequently the price rises gradually from year to year. This year exported to the United States 174,000lbs and to England, India, and other places 326,000lbs in all some 500,000lbs valued at $1,500,000. (Cheney 1884)[6]

The German trade in ivory in 1886 amounted to about one-quarter of the American trade according to Edward Ropes, a shipping agent and sometime US consul in Zanzibar (Ropes 1886). That estimate would roughly accord with the volume of German piano production, centered in Leipzig, which ran about 40% the US total between 1850 and 1930 (Ehrlich 1990, 222).[7]

An important issue, on which information is scarce, is the volume of African ivory exported to India. As late as the 1860s, Zanzibar's trade to India consisted mostly of enslaved human beings. But in 1873, Britain negotiated a prohibition on slave trading in Zanzibari waters with Sultan Bargash, and Indian traders sought other goods to support their exports of textiles to East Africa. Dhows and steamers shuttled between Zanzibar and Bombay (often via Aden). Sultan Bargash owned five or six steamers plying this trade (Holmwood 1885, 422, 428). A longtime British resident in Zanzibar estimated in 1885 that in recent years India accounted for about a quarter or a third of the island's exports. But he did not mention ivory among them (Holmwood 1885, 422). China's imports of African ivory in the 19th and early 20th century were negligible.[8]

Many East Africans sold ivory because they wanted cloth, including American cottons. East African markets also valued beads, brass wire – both used in bodily ornamentation – and guns. From the 1830s to 1860, a variety of

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[6] The consul notes that "In giving the preceding figure it is impossible to be absolutely correct as no records of any kind are kept by the authorities and we can only take the best estimates […]."

[7] Europe's largest piano manufacturer, ca. 1853–1900, was Blüthner in Leipzig, but its maximum output was 5,000 in 1901, and in most years below 3,000 [inferred from the list of serial numbers on the company website: http://www.bluthner.co.uk/our-pianos/bluthner-piano-serial-numbers/ (Accessed 9 September 2022). That figure was also the maximum attained by Bechstein, another big European manufacturer based in Berlin and London. Bösendorfer of Vienna, the third great European manufacturer, built only a few hundred annually [Anonymous 1992 and https://www.boesendorfer.com/en/about/history-1 (Accessed 9 September 2022).. Steinway, in New York from 1853 and Hamburg as well from 1880, attained production of 6,000 per year and a total of 100,000 by 1901, 200,000 by 1920, and 300,000 by 1940. Ratcliffe 2002, 167; Kehl and Kirland 2011, 229.

[8] Jonathan Schlesinger, in personal email communication concerning Chinese ivory imports, 2022.

durable calico cotton cloth made in Massachusetts mills, and called *merekani* [American] in Swahili, came to dominate East African cloth markets, edging out Indian varieties. These exotic American imports conferred status and dignity upon their owners and wearers, paralleling the role of ivory objects, pianos included, in other parts of the world. In this way, American industry was doubly involved in East African elephant ecology, as a destination for ivory and a source of items traded for it. Cloth, especially durable varieties, also functioned as currency alongside Maria Theresa dollars in parts of East Africa, and allowed successful men to acquire cattle, wives, and retainers. Within East Africa, trading ivory for cloth, beads, wire, and guns was one of the more promising routes to socio-economic success for the ambitious – while ivory supplies lasted (Presthold 2008).

American cloth lost its market dominance during the US Civil War when shipments dwindled, and never fully recovered it. After the early 1860s, British and then Indian unbleached cloth took over the Zanzibar and East African markets. By the 1880s, about half of the output of Bombay's cotton mills went to Zanzibar, where it would be dyed, printed, and tailored to suit the latest African fashions (Presthold 2008).

3.6 Elephant Losses and Ecosystem Effects

The elephant hunt moved ever inland as tuskers proved ever hard to find (Coutu et al. 2016; Sheriff 1987). Tanganyika's herds had almost vanished by 1872 (Harms 2018, 301). Price series of ivory in Zanzibar show a sharp and sustained increase from the mid-1870s (Håkansson 2004, 571). By 1900, when the hunt was reaching its climax, expeditions stretched hundreds of miles from the coast, beyond Lake Victoria into the savannas and forests of Uganda and Congo. Most of the pachyderms on the savannas of Kenya, Tanganyika, and northern Mozambique had already perished (Håkansson 2004, 567, 569). The elephant population of all of Africa had fallen from about 26 million in 1800 to 10 million in 1900, a 63% decline, and most of that took place in East and southern Africa. A reasonable guess, then, is that between 1840, when ivory exports via Zanzibar began their rapid growth, and 1910 when the piano industry reached its apex, East Africa's elephant population fell faster, perhaps by roughly 75%.

When hunters obliterated the majority of East African elephants between 1840 and 1920 in order to supply the piano keyboard manufacturers, they inadvertently began a radical reorganization of East African ecosystems. With fewer elephants, there was soon more bush, and with more bush, more tsetse fly and sleeping sickness. It exploded into epidemics between 1896 and 1930 in many parts of Africa, abetted by the shortage of elephants, although many factors contributed (Hide 1999; Steverding 2008). The decades between 1890

and 1930 were dreadful ones for African disease history, and sleeping sickness played a significant part in that.

The sharp decline in elephant populations altered ecosystems in countless ways. The expansion of tsetse habitat brought not only sleeping sickness but nagana as well. Livestock herds suffered. Meanwhile, the ecosystem services elephants had performed – digging out watering holes, trampling trails, dispersing nutrients – became scarcer. Species well adapted to elephant savanna had to try to adjust to rapid changes in their environment. Species adapted to bush and forest, on the other hand, flourished.

In 1930, the repentant ivory buyer Ernst Moore wrote "it is not complimentary to our vaunted civilization and technical knowledge that our chemists and inventors cannot – though they have often tried – give us some material that in beauty and touch will prove a satisfactory alternate for the jewels of the noble elephant" (Moore 1931, 225). Moore's implicit wish was soon granted: By 1954, plastic coatings for piano keys had become so common that ivory imports to Connecticut's factories ceased altogether. Keyboard production shifted to the railroad junction town of Central, South Carolina,[9] where labor was cheaper, and the waste products associated with plastic use could be dumped with greater impunity, than in Connecticut. A peculiar interval in industrial history, that bound a little town in New England to the broad savannas of East Africa, came to an end.

Ivory, however, remained popular and expensive, so elephants enjoyed no respite. The networks of hunters and merchants remained, even if they now needed new markets. These were easy enough to find throughout the 20th century, despite various efforts to prohibit slaughter of elephants and sale of ivory. In the 21st century, by far the strongest market is the burgeoning wealthy class in China. Some 400,000 elephants remain in all of Africa, about one-quarter of them in Kenya, Tanzania, and Uganda (Martin 2019).

4. Sperm Whales

A shallow dive into the deep history of sperm whales shows that the ancestors of today's whales waded into the oceans about 50 million years ago. Forerunners of sperm whales swam into existence maybe 25 million years ago. Like the African elephant, (and *H. sapiens*) sperm whales (*Physeter microcephalus*) are the last survivors of a formerly more diverse genus. They are currently the planet's largest predator, the loudest animal anywhere, and possessors of the largest brains in the history of life on Earth. Like elephants, they have big bodies, big brains, long lives, thick skins, a penchant for travel, minimal

[9] Central is on the periphery of South Carolina but so-named because halfway between Atlanta and Charlotte on the railroad. Its population was under 1,500 in 1950 and in more recent censuses was 15-17% African-American.

worries about predators (except modern humans), and matrilineal social structure that leaves mature males out on their own. Mature males are about three times the size of females, whereas among African elephants the ratio is more like two to one. After age ten or so, they lead increasingly solitary lives, usually in higher latitudes (Whitehead and Rendell 2015, 157).

Topmost among sperm whales' preferred foods are squid. Ideally, that includes giant squid, which weigh about 300kg and swim in the deep and dark recesses of the oceans, and the even larger colossal squid, which with tentacles can be 12 meters from stem to stern. In some seas, sperm whales might get three-quarters of their food by hunting big squid (Clarke 1980; Ellis 2011; Whitehead 2003). But as a rule, they eat several varieties of squid, and other sea creatures too when big squid are hard to find. They need to eat food equivalent to 3% of their body mass per day, which for a mature male comes to about 800kg (Ellis 2011, 227; Whitehead 2003, 45-53).

4.1 The Whale Pump

Sperm whales are less of a keystone species than bison or elephants, but they help to regulate their environments through what specialists call the whale pump. Sperm whales spend at least half their lives deep below the waves, in the dark, hunting squid. Their dives last 40-60 minutes, punctuated by short breathing spells at the surface. Females and juveniles, in addition, meet, usually once per day, for a longer social gathering of several hours. Indeed, they spend most of their leisure (non-hunting) time basking and socializing on the surface of the ocean, and so that is where they normally release what is politely called a "fecal plume." It is rich in nutrients including nitrogen, phosphorus, and iron, which are typically the limiting nutrients for plant growth at sea.

In effect, sperm whales dredge up nutrients that without their deep-diving habits would be lost to the seafloor until such time – likely millions of years – as tectonic processes might get around to returning them to the biosphere. Their fecal plumes fertilize the upper parts of the oceanic water column, analogous to the horizontal and terrestrial nutrient transfer performed by bison and elephants. By injecting nutrients into the photic zone, the upper 200 meters of the ocean where sunlight can reach organisms, and photosynthesis can occur, the whale pump stimulates phytoplankton growth and the marine food webs based on plankton. The whale pump even has an effect on land because seabirds and anadromous fish carry nutrients – in their bodies – acquired from the sea to land and rivers. All whales, and some other marine mammals too, participate in keeping nutrients in the photic zone and off the seafloor, but big whales and deep divers do it far more efficiently than smaller creatures, and sperm whales, as carnivorous predators, carry the densest packages of nutrients up from the depths (Doughty et al. 2016).

4.2 The Sperm Whale Hunt and Population Losses

Nobody knows how many fish or whales are in the sea, let alone how many there were years ago. Expert opinion today converges on figures between 1.1 million and 2 million sperm whales in all the oceans as of 1700. The sperm whale hunting undertaken by coastal communities around the world, before 1800, was too intermittent and inefficient to have any but the slightest impact on populations. Whalers operated near the coasts, while the vast majority of sperm whales kept to deeper waters. Killer whales, on rare occasion, have been known to attack sperm whales, but usually without success. No animals – other than humans – prey on sperm whales, so their numbers throughout their history were controlled by food supply and whatever diseases might kill them or inhibit their fertility. We have no way to know how these variables behaved. My best guess is that sperm whales enjoyed a placid population history, with few dramatic ups or downs. The oceans consistently hosted somewhere around 25-50 million tons of sperm whale biomass.[10]

After 1800, sperm whales encountered stormier seas. The first recorded sperm whale catch came in 1712 off of Nantucket. In the 1730s, London began a program to check nocturnal crime by lighting its streets (Dolin 2007, 105). By 1780, London's streetlamps burned the oil from about 500 sperm whales annually (Zallen 2019, 24). Candlemakers and lighthouses also came to use sperm whale oil (Dolin 2007, 113, 120, 182). By 1800, sperm whaling was an organized business, dominated by New Englanders, and conducted from open boats with souped-up Paleolithic technology (harpoons). Sperm whale oil was in use as a machine lubricant and an illuminant – it burns cleaner and brighter than other whale oils. It greased the path for industrialization by allowing factory machinery to function smoothly, allowing industrial goods such as clocks, watches, and guns to work enduringly. It served as the preferred lubricant for millions of spindles in New England's cotton mills (Davis, Gallman, and Gleiter 1997, 344-6). It also kept lamps burning. Factory production could continue day and night with sufficient illumination in the workspaces. And illumination of the streets of factory towns made it easier to recruit a labor force, often female, that would on most days need to walk to and from work before the sun rose or after it set – or both. Sperm oil was usually too costly for home use in lamps, and more often used to brighten larger spaces (Davis, Gallman, and Gleiter 1997, 29).

French, British, and a very few others followed New Englanders into the hunt for sperm whales, which expanded into Pacific waters beginning in 1789. New England whaling peaked between 1830 and 1850, by which time sperm whale sightings were becoming scarce. The US whaling fleet tonnage

[10] Average sperm whale mass is about 40-45 tons for males and 14-16 tons for females. Juveniles are smaller, but sperm whales mature quickly and live to 80-100 years, so juveniles would not lower the total biomass much.

topped out ca. 1846–1850. Revenues peaked in 1851–1855 (Davis, Gallman, and Gleiter 1997, 6-7) when sperm whale oil's price reached its apex of nearly two dollars per gallon (Dolin 2007, 354). By the 1860s, sperm whale hunting, and sperm oil prices, entered a long decline. Petroleum-based lubricants (and illuminants) had begun to displace sperm oil in many routine uses, although for machinery with fine tolerances, such as watches, sewing machines, or high-end guns, or for machinery operating in very high or low temperatures, sperm oil remained the best option well into the 20th century (Dieterichs 1916, 22-3). It was also used in candle-making, leather manufacture, as a component in industrial cleansers, and from the 1950s through 1973 in cars' automatic transmission fluid.

The quest for marketable sperm oil, like that for bison hide and elephant ivory, led to mass slaughter. The numbers in question, however, are even more elusive than for elephants or bison. A careful student of the matter estimates that the global sperm whale population fell by about 30% due to hunting prior to 1880 (Whitehead 2003, 130-1). However, the rate at which whalers sighted sperm whales, as recorded in their logbooks, fell by about 60% between 1830 and 1850, so either whale populations had fallen faster than this estimate supposes, or whales were learning to avoid ships and boats. Sperm whales are no doubt smart enough to learn, and probably to communicate, the hazard presented by whaling ships (Whitehead and Rendell 2015).

4.3 A Weakened Whale Pump

The sperm whale hunt of the 19th century weakened the whale pump. Sperm whales in 1800 had ferried roughly 300 million tons of big squid from the depths to the surface each year. By 1880, their haul diminished to a little over 200 million tons. Their contribution to the fertilization of the upper levels of the oceans fell by roughly 30%, in proportion with their population decline. This alone, admittedly, probably had only a modest effect on marine food webs, although in certain locations where sperm whales had formerly cavorted *en masse*, such as the equatorial Pacific, the effect must have been much greater. In general, the deep oceans contain both near-deserts and patches teeming with life, almost like cities, which the whale pump helps to sustain.

After 1880, sperm whales enjoyed a reprieve that lasted about 70 years. As they are slow breeders, this did not allow much population recovery. The much larger, and technologically more sophisticated, whale hunt of ca. 1946–1988 reduced sperm whale populations severely, to perhaps one-third of the levels of 1800.

Of course, sperm whales were only one of several targets of 19th-century whalers. Other species were harpooned as well. The total impact on the efficacy of the whale pump in the 19th century was probably significant for

marine life, although that is hard to measure. Overall, from 1800 to 2015, across all whale species, the power of the whale pump to fertilize the oceans declined by about 80-90% (Doughty et al. 2016).

On some scale, then, the assault on sperm whales motivated by the lubrication and illumination markets altered marine life. Big squid and other sperm whale prey enjoyed a lull. But the photic zones of the ocean missed some of the nutrients that formerly supplied phytoplankton, as did all the animals that ultimately depend on phytoplankton. In some places, where sperm whales had once been most numerous and hunters most effective, such as the equatorial Pacific, this impoverishment of marine life could conceivably have affected the food supply of islanders who relied on fish, seabird eggs, and other foods ultimately dependent on phytoplankton. But this is mere speculation.

On a grander scale, the sperm whale hunt (and *a fortiori* the whale hunt across all whale species) reduced the net primary productivity of the oceans, and presumably reduced their carbon uptake – leaving more carbon for longer in the atmosphere, helping ever so slightly to warm the planet during the late 19th century and end the Little Ice Age. Once again, American entrepreneurial talent inspired megafauna slaughter and reorganized ecosystems far away from the centers of industry through an ecological teleconnection sustained over several decades.

5. Conclusions

These three stories involve radical and sudden reductions in animal biomass, far faster than the Late Pleistocene Extinctions. Bison, African elephants, and sperm whales did not go extinct, although the bison came very close. Roughly 20 million tons of bison, 50 million tons of elephant, and 10 million tons of sperm whale were subtracted from their environments between 1800 and 1920 in the Late Holocene Depletions (LHDs).

In every case, the LHDs resulted from industrial demand for specific animal body parts unleashed in what in the 19th century had become an open-access commons for men with access to financing, market knowledge, and transport and killing technologies. That population included Euro-American bison hunters, Arab and Omani elephant-hunting-caravan captains, and New England whalers. The industrial demand resulted from technical changes in the production and potential uses of leather, ivory, and sperm oil, all connected to the rise of American mills and factories – and the market connection of those factories to distant sources of supply of animal parts. Cheap energy, powering steamships and railroads (as well as guns), made the markets of the 19th century more global, more pervasive, and more powerful than ever before, a fact registered in the idolatry of markets characteristic of

economic thought in the first industrial societies. Technological ingenuity played a large role in creating the tools needed to process hides, tusks, and sperm oil into marketable products, and to move them from grasslands or oceans to factories and mills.

At the same time, no ingenuity restrained the slaughter to preserve the geese that laid the golden eggs. No institutions, laws, or powers limited participation in the 19th-century bison, elephant, or sperm whale hunt. No one with the power to restrain these slaughters had the will to do so. No one with the will to do so had the necessary power. Plains Indians, by some accounts, had hunted with restraint, at least before they became connected to hide markets, but they could not prevent Euro-Americans from killing millions of bison. Everyone else involved, bison hunters, elephant hunters, and whalers, faced incentives to hunt as fast and fully as possible, lest others get the hides, tusks, and sperm oil first. They responded to these incentives with lethal vigor.

As a result of the LHDs, longstanding ecological regimes on the North American prairies, East African savannas, and in all the world's oceans changed. The ramifying effects in the case of North America were profound for soils, grasses, trees, animals wild and domestic, and people too. Resulting ecosystems were both different and simpler, impoverished in terms of diversity, complexity, and biomass. The succeeding human system was catastrophic for the Plains Indians, who lost their autonomy, authority, and way of life, a shock to which one might say they are still adjusting. The post-bison North American prairies are in a transitory phase, rich in livestock and cash crops while the irrigation water lasts. In another century, perhaps, when irrigation water is scarce, grass and bison will return.

The changes in East Africa in many respects resemble those of North America, in that the radical reduction in elephant populations lowered biomass and simplified ecosystems. But the changes were less thorough, in part because the elephant slaughter, as of 1920, was less complete than that of the bison. Today the situation with respect to elephant populations more fully resembles that of the bison in the late 19th century: in East Africa, elephant numbers are now probably about 1-2% what they were in 1800. There is little prospect for recovery, what with a robust, if illegal, ivory market mainly in Asia and continual growth in demand for more farmland and cattle pasture in East Africa. With luck, and vigilant suppression of poaching in parklands, African elephants will survive in tiny numbers, like the bison ca. 1885 to the present. Without luck, they will go extinct.

The reorganization of the oceans on account of the sperm whale hunt was much more modest than the terrestrial cases of bison and elephants. Sperm whales were fewer to begin with, and they roamed over roughly 60% of the Earth's surface, far more area than ever inhabited by bison or elephants. The whalers lowered the sperm whale population by at most a third in the 19th

century, and by two-thirds by the end of the 20th, a slower and smaller decline than befell bison and East African elephants. Moreover, the keystone species functions that sperm whales performed were also provided by other whales and marine mammals, whereas no other creatures could do what bison and elephants did to regulate their grassy environments. The sperm whale slaughter also had minimal impacts on human communities, except for those of the slaughterers themselves in New England. In the 21st century, sperm whale populations, like those of bison, seem to be increasing slowly, and there is a good chance that in a few centuries – they reproduce languorously – their numbers will return to levels that prevailed before the Industrial Revolution, even if they move polewards as surface waters warm.

In addition to the ecosystem effects resulting from the LHDs, there will be durable genetic consequences. As we have seen, one has already emerged among tuskless East African elephants. Bison, elephants, and whales all experienced, and elephants are still experiencing, an erosion of genetic diversity – a genetic "bottleneck" that is an almost inevitable consequence of population decline. Today's North American bison, roughly half a million beasts, are descended from roughly 100 forebears. Some of the herds show loss of genetic fitness due to inbreeding (Hedrick 2009). Moreover, narrowed gene pools minimize the availability of potentially useful traits that might help bison populations adapt to future challenges, not least of which will be hotter and dryer climate on the North American plains. Similar constraints may face East African elephants, although the only populations studied, in South Africa's Kruger Park, do not show such effects (Santos et al. 2019). Sperm whales, because their population reduction was smaller, and because males roam widely, confront little narrowing of their gene pool, although their mitochondrial DNA, passed only from mothers to daughters, shows remarkably little diversity – a result of smaller ranges among females (Pinela et al. 2009). It seems that just as the deep histories of bison, elephants, and whales have some bearing on their experience when confronted with well-armed, highly motivated human hunters during the Industrial Revolution, so, too, will the experience of sharp population decline, at least in the case of bison, have some bearing on the distant future of these animals through modifications of their genomes. Teleconnections may exist in time as well as in space.

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