Megaherbivores

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Abstract

Megaherbivores were abundant and diverse worldwide until the end of the Pleistocene. They represent a distinct adaptive syndrome in: (1) life history allometry; (2) invulnerability to predation as adults; (3) population regulation; (4) dietary tolerance; (5) dominance of large herbivore biomass; and (6) impacts on vegetation and ecosystem structure and dynamics. Their demise probably contributed to cascading extinctions among other species. Surviving populations of elephants and rhinos remain vulnerable to human overkill.

Glossary

Allometry How a biological feature is related to body sizes?; for example, basal metabolic rate varies with body mass raised to the power three-quarters rather than in direct proportion with body mass, so that an animal twice as large requires less than twice the amount of food to supply its metabolic needs.
Graminoids Grasses plus grass-like plants such as reeds and sedges.
Holocene The epoch in time extending from 11,700 years ago, approximately when the last ice age ended, to the present.
Home range The area typically traversed by an animal in meeting its life requirements over some period.
Keystone A species or some other entity (such as a habitat) that has a disproportionate influence on maintaining or influencing a structure, for example, the species composition and functioning of an ecosystem.
Pleistocene The epoch or period in time from approximately 2.5 million to 11,700 years ago, which included a series of glacial advancements or ice ages separated by interglacial periods.

Key Points

- There are fundamental transitions in physiology, diet, susceptibility to predation and life history schedules of large herbivores once their body mass exceeds $\sim$1000 kg.
- Large terrestrial herbivores attaining an adult body mass exceeding 1000 kg are no longer subject to carnivore predation on the adult segment.
- These megaherbivores are digestively tolerant of structural vegetation components high in fiber.
- Consequently, they typically dominate the total biomass of large herbivores within local ecosystems.
- They generally exhibit gestation times exceeding one year and thus only weakly entrained by seasonal cycles.
- Other life history features, including time to attain reproductive maturity, interbirth intervals and potential lifespans, are allometrically extended over longer time frames than shown by less-large mammals.
- Due to their correspondingly slowed population growth rates, these very large mammals are especially vulnerable to overkill when hunted by humans for products like ivory.

Introduction

The label "megafauna" has been applied widely to animals weighing over 44 kg (100 lbs), following Martin (1966, 1967). However, this demarcation was somewhat arbitrary, and different size thresholds are needed to differentiate the largest species among different kinds of organisms (Moleon *et al.*, 2020). The label "megaherbivore" applies more strictly to plant-eating mammals attaining over 1000 kg (a metric ton or 10^6 g), in adult body mass. Several biological distinctions become effective among large herbivores exceeding this size threshold (Owen-Smith, 1988). Gestation periods lengthen beyond one year, so that reproduction is no longer synchronized with the annual seasonal cycle. Once they reach adulthood, animals become too large to be killed by even the largest carnivores. Large size enables animals to extract sufficient nutrition from structural plant parts that are inadequate in metabolizable energy and protein content to support smaller herbivores. As a consequence of these features, animals weighing over a mega-gram typically dominate the biomass of large herbivore assemblages (Owen-Smith, 1988). Moreover, megaherbivores have the capacity to transform ecosystems by toppling trees and mowing down tall grasses, altering habitat conditions for other animals. These features in combination define the "megaherbivore syndrome" (Owen-Smith, 1988). They also raise conservation dilemmas.

Megaherbivores were once far more abundant and diverse than they are today, and were present on all continents. Especially prominent were elephants and elephant-like forms placed in the order Proboscidea (**Table 1**). Numerous members of the Perissodactyla (odd-toed ungulates), including rhinoceroses and their allies, also attained megaherbivore size, along with some of the largest artiodactyls (even-toed ungulates) and edentates (ground sloths and glyptodons). Anthracotheres, possibly ancestral to hippos, also included species within the megaherbivore size range. Several of the extinct species exceeded the modern African savanna elephant in size. *Paraceratherium*, related to rhinos and extant during the Oligocene, attained a shoulder height of approximately 5.5 m and body mass of perhaps as much as 20 tons, making it the largest land mammal ever.

Numerous megaherbivores survived into the Late Pleistocene, which spans the period from 130,000 years ago until as recently as 11,000 years ago, after the last glacial advance ended (**Table 2**). Among them were several species of elephants and mammoths along with allied gomphotheres, spread worldwide. Three species of rhinoceros occurred in Europe. Giant ground sloths and glyptodons were present within South America and southern North America, along with *Toxodon*, a hippo-like notoungulate confined to South America. Within Australia, only a giant wombat-like marsupial, *Diprotodon*, attained rhinoceros size.

Today, terrestrial megaherbivores are confined to Africa and tropical Asia (**Table 3**). They include the African elephants, recently proposed to represent two distinct species (*Loxodonta africana and L. cyclotis*; Rohland *et al.*, 2010); the Asian elephant *Elephas maximus*; four rhinoceros species within this size range; the hippopotamus *Hippopotamus amphibius*; and, marginally, the giraffe *Giraffa camelopardalis*. Megaherbivores are missing from the modern faunas of North and South America, Europe, northern Asia, and Australasia.

My doctoral research on the behavioral ecology of the white rhinoceros raised my awareness of the common ecological features shared among elephants, hippos, and rhinos, and also of some of the concerns involved in the conservation of these species. But, why did these previously so successful forms of animals disappear from ecosystems outside Africa and tropical Asia late in the Pleistocene? How can surviving representatives be accommodated, or even restored, within the fragments of ecosystems increasingly compressed by human population expansion? (Owen-Smith, 1981; Donlan *et al.*, 2006; Owen-Smith *et al.*, 2006).

Life History and Population Dynamics

Life history stages inevitably lengthen as body size increases. This is because the temporal scaling of vital rates with body size follows allometric principles, derived from relationships between surface areas and volumes (Calder, 1984; Duncan *et al.*, 2007). Specifically, time durations become lengthened as a function of body mass raised to the power one-quarter. Gestation periods get prolonged, reproductive maturity is reached later and animals live for longer.

Gestation lasts as long as 22 months for both elephant species, 16 months for white rhinos and 15 months for giraffes and black rhinos. Hippos are exceptional with gestation lasting only 8 months. Once gestation time exceeds 12 months, animals can no longer reproduce annually, so that births are no longer synchronized with the seasonal cycle. The briefest birth intervals shown by elephants and rhinos fall close to the allometric trend extrapolated from smaller species, but mean birth intervals observed are somewhat longer (**Fig. 1**(a)).

The age at which reproduction commences is also delayed. While medium-sized ungulates generally first conceive after reaching two years of age, white rhinos usually don't conceive until they have attained around six years of age, while among elephants conception is typically delayed until animals are ten years of age or older (**Fig. 1**(b)). Even the youngest reproductive ages recorded for elephants and rhinos tend to be greater than projected from allometric extrapolations. The earliest age at first reproduction (8 years) and shortest birth interval (3 years) were recorded in the growing elephant population established in the Hluhluwe-iMfolozi Park in South Africa (Druce *et al.*, 2017).

Ungulates below megaherbivore size mostly reproduce annually, with offspring born during the wet season when conditions are most favorable nutritionally for the elevated demands of late gestation and lactation (Owen-Smith and Ogutu, 2013). For megaherbivores, the critical nutritional periods become extended and births get spread more widely through the year. Seasonal peaks in parturition may still be evident, apparently governed by the proximate effects of food quality on estrous cycling and hence conceptions (Owen-Smith, 1988). African elephants, with a 22-month delay between conception and birth, show a concentration of births early in the wet season, following a conception peak 2 months into the wet season (Wittemyer *et al.*, 2007). Asian

Table 1 Megaherbivore genera extant during the earlier part of the Tertiary period

Order	*Family*	*Genus*	*Place*	*Period extant*
Proboscidea	Barytheriidae	*Barytherium*	Egypt	Eocene–Oligocene
Proboscidea	Palaeomastodontidae	*Palaeomastodon*	Africa	Eocene–Oligocene
Proboscidea	Palaeomastodontidae	*Phiomia*	Africa	Eocene-Oligocene
Proboscidea	Deinotheriidae	*Deinotherium*	Africa, Eurasia	Miocene–Pleistocene
Proboscidea	Deinotheriidae	*Prodeinotherium*	Africa	Miocene
Proboscidea	Mammutidae	*Hemimastodon*	Africa	Miocene
Proboscidea	Mammutidae	*Eozygodon*	Africa	Miocene
Proboscidea	Mammutidae	*Zygolophodon*	Africa, Eurasia, North America	Miocene
Proboscidea	Gomphotheriidae	*Gomphotherium*	Africa, Eurasia, North America	Miocene
Proboscidea	Gomphotheriidae	*Platybelodon*	Africa, Eurasia, North America	Miocene
Proboscidea	Gomphotheriidae	*Gnathabelodon*	North America	Miocene
Proboscidea	Gomphotheriidae	*Amebelodon*	Africa, Asia, North America	Miocene
Proboscidea	Gomphotheriidae	*Anancus*	Africa, Eurasia	Miocene–Pleistocene
Proboscidea	Gomphotheriidae	*Zyglolophodon*	Africa, Eurasia, North America	Miocene
Proboscidea	Gomphotheriidae	*Sinomastodon*	Asia	Miocene-Pleistocene
Proboscidea	Gomphotheriidae	*Rhynchotherium*	North America	Miocene
Proboscidea	Gomphotheriidae	*Notiomastodon*	South America	Pleistocene
Proboscidea	Gomphotheriidae	*Tetralophodon*	Africa, Eurasia	Miocene–Pliocene
Proboscidea	Stegodontidae	*Stegolophodon*	Asia	Miocene
Proboscidea	Stegodontidae	*Stegotetrabelodon*	Africa	Miocene
Proboscidea	Stegodontidae	*Stegodibelodon*	Africa	Miocene
Proboscidea	Elephantidae	*Primelephas*	Africa	Miocene–Pliocene
Perissodactyla	Hyracodontidae	*Urtinotherium*	Asia	Oligocene
Perissodactyla	Hyracodontidae	*Paraceratherium*	Eurasia	Eocene–Oligocene
Perissodactyla	Brontotheriidae	*Brontotherium*	North America	Eocene
Perissodactyla	Brontotheriidae	*Megacerops*	North America	Eocene
Perissodactyla	Brontotheriidae	*Dianotitan*	China	Eocene
Perissodactyla	Brontotheriidae	*Notiotitanops*	North America	Eocene
Perissodactyla	Brontotheriidae	*Embolotherium*	Mongolia	Eocene
Perissodactyla	Brontotheriidae	*Aktautitan*	Kazakstan	Eocene
Perissodactyla	Brontotheriidae	*Gnathotitan*	Mongolia	Eocene
Perissodactyla	Brontotheriidae	*Rhinotitan*	Mongolia	Eocene
Perissodactyla	Brontotheriidae	*Diplacodon*	North America	Eocene
Perissodactyla	Brontotheriidae	*Pachytitan*	Mongolia	Eocene
Perissodactyla	Brontotheriidae	*Hyotitan*	Mongolia	Eocene
Perissodactyla	Brontotheriidae	*Brachydiastematherium*	North America, Europe	Eocene
Perissodactyla	Brontotheriidae	*Epimanteoceras*	Mongolia	Eocene
Perissodactyla	Rhinocerotidae	*Teleoceras*	North America	Miocene–Pliocene
Perissodactyla	Rhinocerotidae	*Elasmotherium*	Asia	Pliocene–Pleistocene
Perissodactyla	Rhinocerotidae	*Diceratherium*	North America	Oligocene
Perissodactyla	Rhinocerotidae	*Aceratherium*	Africa, Asia	Oligocene–Pliocene
Perissodactyla	Rhinocerotidae	*Brachydiceratherium*	Europe	Oligocene–Miocene
Perissodactyla	Rhinocerotidae	*Diaceratherium*	Europe	Miocene
Perissodactyla	Rhinocerotidae	*Brachypotherium*	North America, Europe, Africa	Miocene–Pliocene
Perissodactyla	Rhinocerotidae	*Aphelops*	North America	Miocene-Pliocene
Perissodactyla	Rhinocerotidae	*Peraceras*	North America	Miocene
Perissodactyla	Rhinocerotidae	*Chilotherium*	Eurasia	Miocene–Pliocene
Perissodactyla	Rhinocerotidae	*Floridaceras*	North America	Miocene
Artiodactyla	Anthracotherriidae	*Libycosaurus*	Africa	Miocene
Artiodactyla	Anthracotherriidae	*Merycopotamus*	Asia	Miocene–Pliocene
Artiodactyla	Giraffidae	*Libytherium*	Africa	Pliocene

elephants kept in captivity in India and Myanmar have a birth peak spread into the early dry season, following a peak in conceptions during the monsoon rains (Sukumar, 1989). Indian rhinos in Nepal show a similar seasonal concentration of births in the early dry season, despite a shorter gestation than elephants Dinerstein, 2003). White rhinos, black rhinos, and giraffes, with gestation lasting 15–16 months, exhibit birth peaks during the early part of the dry season, following conceptions concentrated during the rains. In contrast, hippos show a conception peak early in the dry season, resulting in births during the rains.

Lifespans are also prolonged. Elephants of both species live up to 65–70 years (Moss, 2001; Sukumar, 2003), while the potential longevity of rhinos and hippos is 45–50 years (Owen-Smith, 1988). The highest recorded age for a giraffe is 28 years. Aside from primates and cetaceans (whales and dolphins), other mammals do not live much longer than 20 years.

Table 2 Megaherbivores becoming extinct during the late Pleistocene

Order	*Family*	*Species*	*Location*	*Last recorded (years BP)*
Proboscidea	Elephantidae	*Elephas iolensis*	Africa	34,000
Proboscidea	Elephantidae	*Palaeoloxodon antiquus*	Europe, Asia	40,000
Proboscidea	Elephantidae	*Mammuthus primigenius*	Eurasia, North America	10,000
Proboscidea	Elephantidae	*Mammuthus columbi*	North America	10,500
Proboscidea	Stegodontidae	*Stegodon* spp	Asia	11,000
Proboscidea	Mammutidae	*Mammut americanum*	North America	10,500
Proboscidea	Gomphotheriidae	*Stegomastodon platensis*	South America	11,000
Proboscidea	Gomphotheriidae	*Stegomastodon waringi*	South America	11,000
Proboscidea	Gomphotheriidae	*Cuvieronius hyodon*	South America	11,900
Perissodactyla	Rhinocerotidae	*Dicerorhinus hemitoechus*	Southern Europe	24,000
Perissodactyla	Rhinocerotidae	*Dicerorhinus kirchbergensis*	Southern Europe	24,000
Perissodactyla	Rhinocerotidae	*Coelodonta antiquitatis*	Eurasia	10,700
Artiodactyla	Hippopotamidae	*Hippopotamus gorgops*	Africa	130,000
Artiodactyla	Giraffidae	*Sivatherium maurusium*	Africa	8000
Notoungulata	Toxodontidae	*Toxodon platensis*	South America	13,000
Edentata	Megatheriidae	*Megatherium americanum*	South America	8500
Edentata	Megatheriidae	*Eremotherium mirabile*	South & North America	13,200
Edentata	Megatheriidae	*Glossotherium harlani*	South and North America	12,500
Edentata	Megatheriidae	*Mylodon robustus*	South America	12,000
Marsupiala	Diprotdontidae	*Diprotodon optatum*	Australia	45,000

Table 3 Megaherbivores still extant

Common name	*Scientific name*	*Adult body mass (kg)*		*Historic distribution*	*Status*
		Female	Male		
African savanna elephant	*Loxodonta africana*	2800–4000	5000–8000	Africa-wide	Still widespread and locally abundant
African forest elephant	*Loxodonta cyclotis*	2500	4500	Forested regions of Africa	Declining under hunting
Asian elephant	*Elephas maximus*	2500–4000	4000–5400	India, Burma, Thailand, Malaysia, Vietnam, Sri Lanka	Locally common but insecure
Hippopotamus	*Hippopotamus amphibius*	1350–2350	1500–2600	Africa-wide	Abundant
White rhinoceros	*Ceratotherium simum*	1600–1800	2200–2400	Southern and northeastern Africa	Secure in south, extinct in north
Great Indian rhinoceros	*Rhinoceros unicornis*	1600	2100	India, Nepal	Restricted to reserves
Black rhinoceros	*Diceros bicornis*	1000–1300	1000–1300	Most of Africa	Uncommon and endangered
Javan rhinoceros	*Rhinoceros sondaicus*	1300	1300	Java	Rare and endangered
Giraffe	*Giraffa camelopardalis*	825–1125	1200–1400	Southern and east-central Africa	Common and secure

Slow reproduction restricts the proportional rate at which megaherbivore populations can grow. The maximum growth rate for an African elephant population is approximately 6.5% per year, assuming minimal mortality, whereas for a white rhino population the maximum sustainable rate is 9% per year (Owen-Smith, 1988). Temporary population increases exceeding these levels may be produced by pulses in reproduction or distortions in the population structure (Slotow *et al.*, 2005; Foley and Faust, 2010; Wittemyer *et al.*, 2013). Realized population growth rates in the long term are likely to be somewhat slower than the maximum potential rates due to environmental variation and resultant mortality, especially among calves (Moss, 2001).

The growth rates of megaherbivore populations do not respond to density feedbacks until quite high densities have been attained (Fowler, 1987; Gough and Kerley, 2006; **Fig. 2**), a pattern shared with whales (Chapman, 1981). Nevertheless, African elephants crowded within protected areas by human settlements and hunting outside have shown a delay in the age at first reproduction and lengthened birth intervals (Laws and Parker, 1968). Chronic malnutrition may also slow potential population growth rates (Turkalo *et al.*, 2017). Among forest elephants, median inter-birth intervals are a year longer than the 4 years typical of growing savanna elephant populations, lengthened a further year among females older than 40 years (Turkalo *et al.*, 2018). Age at first reproduction occurs at a median age of 23 years, double the 10 years typical of savanna elephants (Wittemyer *et al.*, 2013). But the slower reproduction of forest elephants is compensated by very high offspring survival, perhaps due to the constant conditions coupled with the scarcity of large predators in forests. Asian elephants confined largely to forests by human settlements and cultivation show similarly slow population growth rates, likewise ascribed to malnutrition (Sukumar, 1989, 2003).

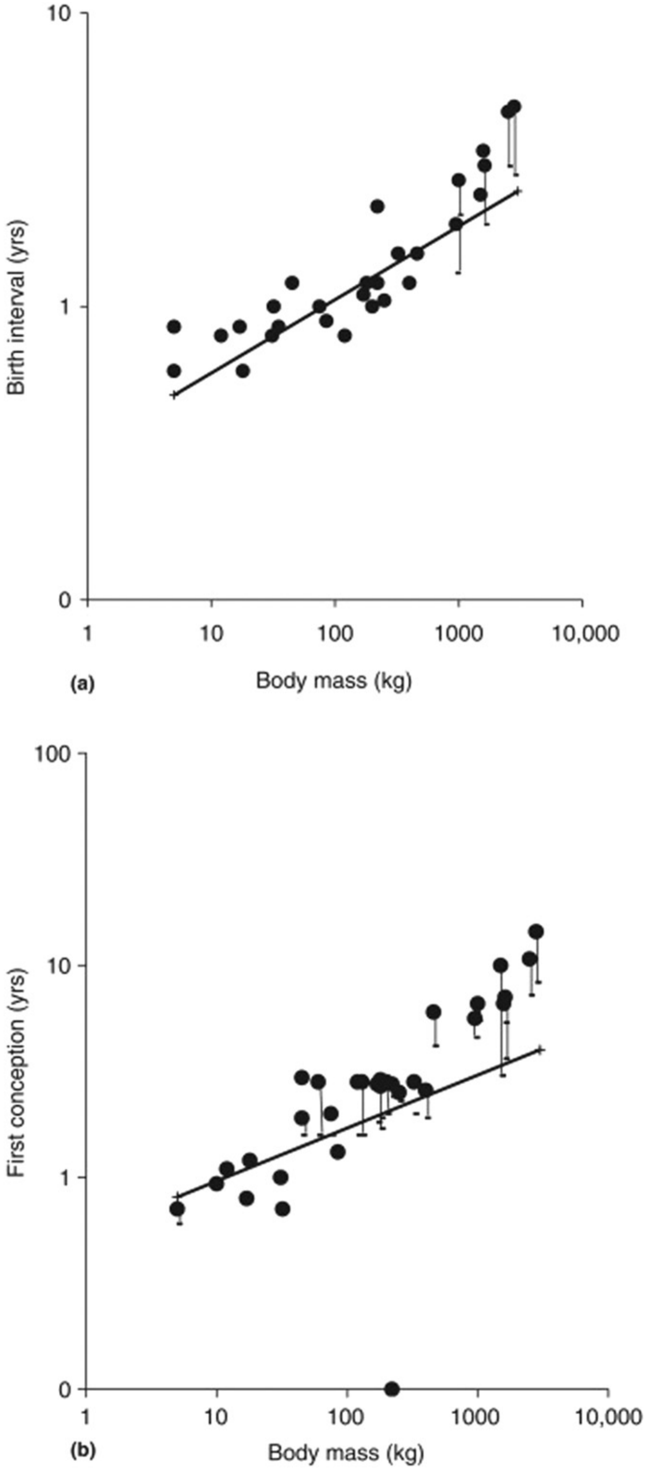

Fig. 1 Allometric trends among large mammalian herbivores in (a) interval between births and (b) age at first conception. Circles represent the population averages; lines below indicate minimum records. Trend lines shown have a slope proportional to body mass raised to the power three-quarters.

Food deficiencies were apparently responsible for the shrinking population of black rhinos in the Hluhluwe-iMfolozi Park in South Africa, in striking contrast with the growing population of white rhinos there (Hitchins and Anderson, 1983; Owen-Smith, 1988). Indian rhinos in Nepal show substantially longer calving intervals than is typical of growing white rhino and black rhino populations, although their age at first reproduction differs little (Dinerstein, 2003).

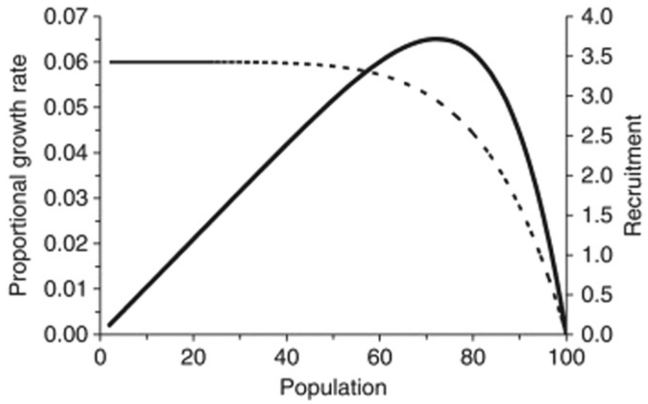

Fig. 2 Relationship between the population growth rate and the population size expected for megaherbivores, showing delayed onset of the density-dependent reduction in the relative growth rate (dotted line), and the corresponding right-skewed recruitment curve (i.e., the numerical growth increment; solid line).

Megaherbivore populations show less response to annual variation in rainfall conditions than smaller ungulates. Nevertheless, drought conditions can result in the deferment of conceptions, leading to fewer calves being born a year or two later, along with increased calf mortality (Conybeare and Haynes, 1984; Dudley *et al.*, 2001; Foley *et al.*, 2008). Predation losses among calves may increase when animals become forced to travel substantial distances between food and water (Loveridge *et al.*, 2006; Young and van Aarde, 2010). During very severe droughts, even adult elephants can incur increased mortality due to malnutrition. A die-off of elephants occurred in Tsavo East National Park in Kenya when severe drought conditions persisted through two successive years in this semiarid region (Corfield, 1973). Total mortality amounted to approximately 20% of the population and was concentrated near rivers in the driest region of the park. This mortality was accentuated by the compression of elephants into the park by hunting activities outside (Myers, 1973; Parker, 1983). Similar episodes of mortality accounting for about 15% of the population have been recorded at Samburu and Amboseli in Kenya in regions that are likewise quite arid (Wittemyer *et al.*, 2013).

The white rhino population the Hluhluwe-iMfolozi Park continued to increase at its maximum potential rate during the late 1960s, despite the prevailing drought conditions, perhaps because less rain meant that the grass produced was more nutritious (Owen-Smith, 1988). Hippos are rather more susceptible to drought-related mortality than other megaherbivores because of their grazing restriction to the vicinity of rivers, where forage becomes most severely depleted. Shorter calving intervals and earlier reproduction than other megaherbivores enables hippos to recover sooner from population crashes.

Disease has had little or no impact on the population dynamics of elephants and rhinos, although white rhinos relocated into East Africa are vulnerable to infection by trypanosome blood parasites responsible for sleeping sickness. An exception exists in Namibia's Etosha National Park, where periodic mortality from anthrax has kept elephant numbers relatively constant (Lindeque and Turnbull, 1994). Hippos are subject to outbreaks of anthrax in the crowded pools where they seek daytime refuge (Wafula *et al.*, 2007).

Stabilization of the growth of African elephant populations may eventually come about as a result of density-related reproductive changes, coupled with episodic mortality during severe drought years (Owen-Smith *et al.*, 2006; Wittemyer *et al.*, 2007, 2013; Trimble *et al.*, 2009). The robust growth rates shown by elephant populations protected from poaching could be partly an outcome of the exceptionally favorable, low-density conditions that these animals have experienced since birth. Cohort effects, whereby animals born under adverse conditions show lower survival and reproductive success throughout their lives (Lindstrom and Kokko, 2002), could eventually come into play once animals start experiencing chronic malnutrition, perhaps due to the depletion of the tree cover. Whether nutritional regulation can operate effectively within the confines of protected areas remains a leading conservation issue.

Home Ranges and Dispersal

When not restricted by human settlements or fences, elephants roam widely. In somewhat arid regions, their seasonal home ranges can cover 2000 km^2 in the wet season, contracting to 500–1000 km^2 during the dry season when access to surface water is restricted, but are somewhat smaller in wetter savannas (Young *et al.*, 2009; Grogan *et al.*, 2020). In arid regions of Namibia, total annual ranges traversed may encompass as much as 6000 km^2 for females and 12,000 km^2 for males, although only a fraction of this area is actually utilized (Leggett, 2006). During the wet season, elephant herds concentrate opportunistically in places where rainfall has produced local greening of the vegetation (Loarie *et al.*, 2009). Home ranges recorded for Asian elephant herds cover 100–800 km^2 (Sukumar, 2003).

White rhinos are much more sedentary than elephants. In the Hluhluwe-iMfolozi Park, females moved over overlapping home ranges encompassing 10–20 km^2, whereas males occupied smaller discrete territories (Owen-Smith, 1975). However, home ranges covering up to 90 km^2 have been recorded for white rhinos elsewhere where population densities are lower (van Gysegem, 1984; Pienaar *et al.*, 1993). Black rhino home ranges are typically under 50 km^2 in extent, but may expand to as much as 500 km^2 in desert regions (Owen-Smith, 1988). Home ranges occupied by Indian rhinos are similar in size to those of the African species. Giraffe home ranges typically cover approximately 100–200 km^2, but may expand to as large as 1950 km^2 in desert regions (Fennessy, 2009; Knusel *et al.*, 2019).

Dispersal movements contribute to the longer term redistribution of elephant populations, responding to changing food and water resources (Laws, 1969; van Aarde and Jackson, 2007; Chamaille-Jammes *et al.*, 2008). The regional population of almost 150,000 elephants spread through northern Botswana, western Zimbabwe, eastern Namibia, and adjoining regions of Angola and Zambia, has been growing in numbers, but not in density, indicating dispersal outward (Junker *et al.*, 2008). The growth of the elephant population within Kruger Park has also slowed as animals shifted into areas to the east and west, opened to them following the establishment of the Greater Limpopo Transfrontier Park. White rhinos dispersing from the high-density population core into outlying areas consisted mostly of subadult animals of both sexes, along with some mature males (Owen-Smith, 1988). Hippos have been recorded transferring between water bodies in response to changing conditions. Dispersal movements can play the major role in preventing megaherbivores from reaching excessively high densities, recognizing that reproductive changes are slow to take effect.

Susceptibility to Predation

Elephants, rhinos, and hippos hardly feature among predator kills recorded in the Kruger National Park (Owen-Smith and Mills, 2008). Although giraffes are frequently killed by lions (*Panthera leo*) in Kruger Park, this rarely happens in Serengeti National Park (Hopcraft, 2010). Their body size is transitional, with adult males weighing up to 1200 kg, but females only up to 825 kg.

However, young animals that have not yet attained adult size remain susceptible to predation. In Botswana's Chobe National Park, a large pride of lions specialized in killing partly grown elephants, no longer protected by their mothers, near waterholes at night during the late dry season (Joubert, 1986; Power and Compion, 2009). Young hippos can constitute a substantial proportion of lion kills in Zambia and Congo (Bourliere and Verschuren, 1960). Attacks by lions on near-adult rhinos of both African species have been recorded (Goddard, 1976; Pienaar, 1970; Joubert and Eloff, 1971; Brain *et al.*, 1999), but remain rare. Black rhino calves seem vulnerable to being killed by spotted hyenas (*Crocuta crocuta*; Hitchins and Anderson, 1983). A substantial proportion of Indian rhino calves are killed by tigers (*Panthera tigris*; Dinerstein, 2003), and tigers are also a threat to young Indian elephants (Sukumar, 2003).

The cohesive family groups formed by elephants help protect offspring from predator attacks. Bur adult rhinos of all species remain mostly solitary, apart from associations of mothers with their most recent offspring. Nevertheless, subadult white rhinos do form groups, numbering from 2 to 3 animals up to 12 or more, sometimes along with an adult female lacking a calf. When threatened, these animals stand with rumps together and horns pointing outward, positioned to resist predator attacks. Hippos move independently while feeding on land at night (Owen-Smith, 1988).

Nevertheless, megaherbivores die eventually of old age and their carcasses provide food for carnivores. Although the larger saber-toothed felids, now extinct, are regarded as having been predators on thick-skinned herbivores (Turner and Anton, 2004), I suspect that their lengthened and flattened upper canines were adapted to facilitate access to muscular tissues beneath the thick hides of animals that had died. Elephants and hippos have repeatedly become dwarfed in size on islands lacking large predators (Simmons, 1988; Stuart, 1991), which indicates how predation risk has been a factor promoting very large size.

The arrival of humans organized in groups with projectile weapons breached the basic defense that megaherbivores had evolved against predation: standing their ground to fend off attacks. Humans could launch spears until animals became weakened by the wounds inflicted, and eventually killed. Modern elephants and rhinos largely ignore nearby carnivores, but flee from approaching humans. As a consequence of their resistance to predation, elephants and rhinos can move about securely during both daylight and darkness, and exploit resources within both open and wooded environments.

Nutritional Physiology and Dietary Tolerance

Because metabolic rate increases allometrically as a function of body mass raised to the power three-quarters, specific metabolic requirements for energy and nutrients per unit of body mass diminish with increasing body size. This means that larger animals need less food in proportion to their size, despite the huge amounts of food each individual consumes. Furthermore, larger animals can gain adequate nutrition from food that is lower in nutritional yield than required by smaller animals. Thus, megaherbivores can utilize fibrous bark and tall stemmy grasses, although they do favor higher quality plant parts when available. By utilizing a large fraction of the plant matter produced annually, they can attain greater biomass densities than smaller herbivores.

All megaherbivores, apart from giraffe, are non-ruminants, and most rely on fermentation taking place in the hindgut, specifically the colon and cecum, to provide energy (Langer, 1988). Larger size means that the forage consumed takes longer to pass through the gut, enabling it to be digested more completely. The extent of fiber digestion achieved by white rhinos resembles that of medium-sized antelope, but is less than exhibited by large ruminants like cattle and wild bovines (Foose cited by Owen-Smith, 1988;

Steuer *et al.*, 2010). Hippos ferment forage within an expanded foregut without the benefit of rumination, relying on prolonged retention to achieve adequate digestive efficiency. In contrast, elephants pass food rapidly through the digestive tract, including indigestible fiber (Clauss *et al.*, 2007a). Because cattle and wild bovines are capable of digesting almost all of the plant foliage that is potentially fermentable, there is no benefit for a ruminant to grow into the megaherbivore size range (Demment and Van Soest, 1985; Clauss *et al.*, 2003).

Elephants are mixed feeders consuming both tree and grass parts, but distinguished by their ability to fall back on fibrous twigs, bark and roots during the late dry season when green leaves are sparse (Barnes, 1982; Owen-Smith and Chafota, 2012). White rhinos, Indian rhinos, and hippos remain mainly grazers year-round. Black rhinos are browsers consuming woody twigs along with leaves, plus succulent euphorbias. The extinct mammoths were more specialized for grazing in their dentition than modern elephants, and the extinct woolly rhinoceros was also mainly a grazer. Among gomphotheres and giant ground sloths, some species favored grass and others browse (MacFadden, 2000; Prado *et al.*, 2005).

However, the lowered digestive efficiency of black rhinos leads to greater losses of minerals including sodium in feces than shown by smaller hindgut fermenters, like horses (Clauss *et al.*, 2007b). This helps explain why black rhinos are most common in dry savannas and shrublands, where evaporation concentrates salts in soils (Owen-Smith, 1988). A similar need for sodium could also account for the historic absence of white rhinos from the cooler Highveld grasslands in southern Africa. Also notable is that elephants prefer to drink from waterholes with higher sodium contents (Weir, 1972), and ingest sodium-rich soil in regions where water supplies are lacking in sodium (Holdo *et al.*, 2002). Forest elephants frequently visit the open glades called bais where mineral nutrients including sodium are concentrated.

Transforming Vegetation and Ecosystem Processes

Typically, megaherbivores constitute 40%–70% of the total herbivore biomass in African savanna ecosystems where their populations have not been decimated by past or current human hunting (**Fig. 3**). In the absence of such human interference, about half of the total amount of the vegetation consumed by all large herbivores passes through the digestive systems of a megaherbivore. Reintroduced white rhinos have become the third most abundant herbivore in biomass within Kruger National Park, after elephants and buffalos. The domination of the Serengeti ecosystem by migratory wildebeest is exceptional. Missing are the white rhinos that were formerly abundant there, as testified by their fossilized remains in Olduvai Gorge (Leakey, 1965). There is no indication that a high biomass of elephants and white rhinos suppresses the abundance of less-large herbivores (Skarpe *et al.*, 2004; Arsenault and Owen-Smith, 2012).

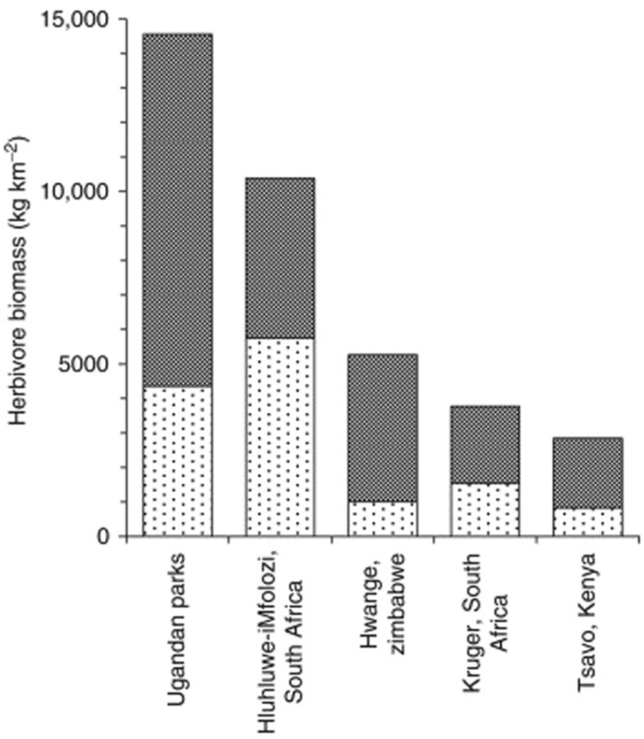

Fig. 3 The contribution of megaherbivores (dark shade) to total large herbivore biomass in relatively intact African ungulate assemblages. Uganda is represented by combined data for Queen Elizabeth and Murchison Falls national parks.

The high abundance and physical strength of megaherbivores mean that they operate as habitat engineers modifying structural aspects of vegetation. Elephants can radically reduce the tree cover, and also the composition of remaining woodlands, through the damage they impose (Laws, 1970; Teren *et al.*, 2018; Owen-Smith *et al.*, 2019). Quite large sections of regional landscapes have been transformed from wooded savanna into open grassland or shrub coppice, depending on soils and rainfall (Bell, 1981; McShane, 1989; Western, 2007). Intense fires burning the grass layer help suppress the woody plant regeneration (Dublin *et al.*, 1990; Holdo, 2007). Nevertheless, the effects of elephants are overriding, as demonstrated in Uganda (Smart *et al.*, 1985) and in Kruger Park in South Africa (Asner and Levick, 2012; Pelegrini *et al.*, 2015). The breakage of leader shoots by elephants generates stands of coppicing shrubs, interpreted as "browsing lawns" or "hedges" (Cromsigt and Kuijper, 2011; du Toit and Olff, 2014), enhancing food availability for elephants and smaller browsers (Makhabu *et al.*, 2006). Vulnerable tree species may become restricted to steep slopes or places far from water where they are less likely to be encountered by foraging elephants (Edkins *et al.*, 2007). Asian elephants have somewhat less impact on the woodlands and forests to which they are largely confined, but can depress the abundance of favored understory trees in deciduous woodlands (Sukumar, 2003). Black rhinos can topple succulent euphorbias (Luske *et al.*, 2009), while giraffes can restrict the distribution of sensitive tree species (Bond and Loffell, 2001; Wiseman *et al.*, 2004).

Grazing impacts by white rhinos have transformed areas formerly supporting tall grassland in the Hluhluwe-iMfolozi Park into a mosaic of short grass areas or "grazing lawns" interspersed with taller grass patches (Owen-Smith, 1988; Waldram *et al.*, 2007), and are doing the same in parts of Kruger Park (Cromsigt and te Beest, 2014). Hippos likewise promote extensive grazing lawns near the water bodies where they seek day-time refuge (Lock, 1972; Olivier and Laurie, 1974). Grazing by hippos near rivers, and by white rhinos more widely, helps suppress the spread of fires, facilitating regeneration of the trees damaged by elephants. Grazing lawns support more nutritious grasses, drawing concentrations of smaller grazers (Verweij *et al.*, 2006; Arsenault and Owen-Smith, 2012).

However, no place bears testimony to the ultimate state of the landscapes produced by the combined impacts of browsing and grazing megaherbivores, both at their maximum abundance levels, even in Africa. Highest local densities were attained by hippos in Queen Elizabeth National Park in Uganda, but confined to the immediate vicinity of the lakes that served as their daytime refuges (Lock, 1972). Densities attained by white rhinos in the Hluhluwe-iMfolozi Park have been capped by live removals undertaken to restrict population growth (Linklater and Shrader, 2017). The reintroduced elephant population there is still growing (Druce *et al.*, 2017). Elephants reach their highest local densities of around 5 animals per km^2 in parts of the Addo National Park in the Eastern Cape where the prevailing vegetation is largely evergreen thicket (Gough and Kerley, 2006).

During the Pleistocene epoch when megaherbivores of many species had been abundant, areas of North America covered today by fairly uniform forests showed a mix of conifers, broadleaf hardwoods, and graminoids, indicating a former parkland mosaic (Wright, 1984; Gill *et al.*, 2009). The prairie grasslands that predominate today in western America were evidently less uniform in the past. The grassy steppe tundra that once stretched from Alaska through Siberia into northern Europe has been replaced by the dense assemblage of shrubs, mosses, and bogs that characterizes the modern wet tundra (Zimov *et al.*, 1995). In the Appalachian region, grazing mammoths, equids, and bison coexisted alongside browsing mastodons, ground sloths, tapirs, and deer, plus mixed feeders like caribou and muskoxen (Guilday, 1984). The mosaic interspersion of vegetation types of the Pleistocene has become transformed into zonal vegetation bands, largely reflecting climatic controls (Guthrie, 1984).

In northwestern Europe, pollen and animals indicative of open vegetation suggest that grassy meadows had been quite common in the landscape, in contrast to the current predominance of closed forest in areas undisturbed by humans (Svenning, 2002; Vera *et al.*, 2006). Today, grazing and browsing by cattle and horses suppress tree regeneration locally, helping to maintain grassy gaps and promote cyclic succession (Olff *et al.*, 1999). The disappearance of the northern grassland steppe has been ascribed to the absence of megaherbivore impacts maintaining an open soil cover, and thereby restricting permafrost development (Zimov *et al.*, 1995). Through opening the forest cover, megaherbivores facilitated the penetration of fire, which further modified habitats (Svenning, 2002; Gill *et al.*, 2009).

The vegetation changes induced by megaherbivores facilitate the coexistence of smaller, more selective grazers and browsers, by bringing more of the vegetation within the height range favored by the latter (Rutina *et al.*, 2005). Moreover, regenerating plant parts are fundamentally more nutritious than the vegetation components removed (Makhabu *et al.*, 2006). The overall energy flow through the large herbivore assemblage can thereby be greatly enhanced by the presence of megaherbivores, at the expense of the amount recycled more slowly through termites and other soil organisms, or incinerated by fire. Hence, megaherbivores can make a pivotal contribution towards enhancing both habitat productivity and a diversity of other species (Owen-Smith, 1987,1989; Galetti *et al*, 2018). Nevertheless, because of their water dependency, areas remote from perennial sources may persist largely free from these impacts, contributing to the broader vegetation mosaic.

Late Pleistocene Extinctions

During the Late Pleistocene, all megaherbivore species weighing more than 1000 kg, and 80% of macroherbivores in the size range 100–1000 kg, were eliminated throughout all continents except Africa and tropical Asia (Owen-Smith, 2013; **Fig. 4**). Around half of the species weighing between 10 and 100 kg disappeared from North America and Australia, but few losses in this size range occurred in Eurasia and South America. Extinctions of carnivores and scavenging birds followed that of their herbivore prey (Martin, 1967). In Australia, giant emus vanished along with the marsupial mammals (Flannery and Roberts, 1999). Africa lost the last of the grazing *Elephas iolensis* in Tunisia approximately 34,000 years ago (Todd, 2005). Four genera of macroherbivores also became extinct in Africa between 100,000 and10,000 years ago: the antlered giraffe *Sivatherium*; the giant buffalo *Pelorovis*; the giant hartebeest *Megalotragus*; and the giant warthog *Metridiochoerus*.

In tropical Asia, the elephant-like *Stegodon* disappeared approximately 11,000 years ago. In Europe, the last recorded date for the straight-tusked elephant *Palaeoloxodon antiquus* was approximately 40,000 years ago, whereas two rhinoceros species vanished around 20,000 years ago (Stuart, 1991, 2005). The woolly mammoth and woolly rhino persisted in northern Europe and Siberia until as recently as 11,000–10,000 years ago, and, in dwarfed form, on Wrangel Island until 3700 years ago (Vartanyan *et al.*, 1993; Orlova *et al.*, 2004). In North America, the major pulse of megafaunal extinctions occurred within a narrow time window between approximately 12,500 and 11,500 years ago (adjusted radiocarbon dates, reported by Stuart, 1991). Dwarfed mammoths persisted in islands off California, and dwarfed ground sloths in the Caribbean, until somewhat later. In South America, the extinction wave apparently intensified slightly earlier, between 14,000 and 11,000 years ago (Barnovsky and Lindsey, 2010). The gomphotheres *Cuvieronius* and *Haplomastodon* were last recorded in Chile and Venezuela, respectively between 14,000 and 13,000 years ago, whereas the giant ground sloth *Megatherium* persisted in Argentina until perhaps as late as 8500 years ago. In Australia, the extinction wave began shortly after 50,000 years ago (Bowler *et al.*, 2003). All of these species had persisted through previous glacial–interglacial transitions, despite temperature regimes similar to those ending the Pleistocene. Species in the megaherbivore size range should be least vulnerable to climatic influences on habitat conditions, because of their wide food tolerance and broad distributions. The crucial factor distinguishing the last glacial advance and its retreat was not the severity of the climate, but rather the presence of humans dispersing from Africa and eventually colonizing the Americas.

A contingent of *Homo sapiens sapiens* moved out of Africa through tropical Asia to reach Australia by 50,000 years ago (Finlayson, 2005). By 40,000 years ago, modern humans had spread westward into Europe. By 15,000 years ago, people had entered North America from Siberia via the Beringian land bridge, and had reached the southern tip of South America quite soon thereafter (Goebel *et al.*, 2008). The large mammals they met had never encountered such a strange predator before. Megaherbivores would have responded to the threat by standing their ground to protect their offspring, like white rhinos do. Thus, they became stationary targets for hunters launching spears until losses of blood weakened the recipients. African forms, which evolved alongside early humans honing their hunting skills, respond aggressively to human presence at close quarters. The Neanderthal people, who had lived in Europe for half-a-million years, apparently depended on short stabbing spears to kill their prey, inadequate for dispatching the largest mammals (O'Driscoll and Thompson, 2018).

The terminal Pleistocene was a time of climatic turmoil as global cooling tended towards its greatest extreme and then receded, with rapid warming interludes (Cooper *et al.*, 2015). But there is no evidence that climatic conditions were more extreme than they had been during the preceding glacial maximum prior to 130,000 years ago – not only in the frigid north, but right through the Americas – arctic, temperate or tropical. The feature distinguishing the end of the Pleistocene was the presence of modern humans, who had become skilled as hunters. Of course, herbivores were most likely nutritionally stressed by the extreme climatic disruptions; but so also were people under conditions that would have been less amenable for harvesting plant products. Human overkill under these conditions provided the sustained pressure forcing megaherbivores populations with limited growth potential into progressive decline, until the last animal was gone. This happened because humans, as omnivores, could still exploit plant food resources while they sought out their desire for animal protein (Owen-Smith, 1999). Many less-large herbivores also went extinct. The greater vulnerability of dietary tolerant megaherbivores was not due to food deficiencies, but to sustained predation. "Allee effects," manifested through a reduction in the potential growth rate with diminishing density and hence vegetation impacts, may have contributed to the slide toward extinction (Owen-Smith, 1999).

Fungal spores typical of large mammal dung fade out rapidly after 14,000 years ago in eastern North America, followed thereafter by a rise in charcoal, indicating extensive fires, coupled with greater representation of hardwood tree pollen (Robinson *et al.*, 2005; Gill *et al.*, 2009). Last recorded dates of Columbian mammoths after 10,000 years ago come either from the prairie region along the Canadian border or the arid region near the Mexican border, where more open conditions remained (Agenbroad, 2003). A few woolly mammoths may have persisted also in Alaska after 10,000 years ago (Haile *et al.*, 2009). Extinctions of numerous large mammals were closely associated with human arrival in the pampas of Argentina and Uruguay, and in Patagonia. Humans and large mammals apparently coexisted for several thousand years elsewhere in South America, perhaps because humans were less dependent there on hunting (Barnovsky and Lindsey, 2010).

The vegetation changes that occurred at the end of the Pleistocene cannot be related solely to climate, because large herbivore impacts and fire also substantially modify vegetation structure and composition (Owen-Smith, 1987; Bond, 2005; Johnson, 2009). In Siberia, there are indications that areas of open steppe-tundra that had persisted through previous interglacials became entirely replaced by boggy tundra after the end of the last ice age (Sher, 1997, reported by Stuart, 2005). The megafaunal extinction by human hunting could have contributed to this radical vegetation transition from graminoid to shrub and moss dominance (Zimov *et al.*, 1995; van der Wal *et al.*, 2004). As noted earlier (*see* Vegetation Transformation and Ecosystem Processes), disturbance by megaherbivores promotes not only structural vegetation diversity but also greater vegetation productivity, at least in the form of regenerating tissues most supportive of smaller herbivores. Hence, deterioration in habitat conditions for macroherbivores may have followed the elimination of megaherbivores by human hunters, making these other species more vulnerable to hunting pressure, especially at a time when suitable habitats were potentially shifting in location in response to climate change.

But this "keystone herbivore" hypothesis (Owen-Smith, 1987) would not apply in Australia, where only a single, rather minor megaherbivore was lost and the use of fire by aboriginal people has been emphasized as playing a major role in the megafaunal extinctions (Bowman, 1998). Within Africa, the disappearance of the grazing *E. iolensis* earlier in the Pleistocene could likewise have been a consequence of widening use of fire by humans, depleting forage during the dry season bottleneck.

Hence, megaherbivores surely played a pivotal role in the late Pleistocene extinctions, both through being the animal type most susceptible to extinction by human hunters and by contributing to the demise of other species through the vegetation changes that ensued. Their broad dietary and habitat tolerance negates claims that climatic factors were primarily responsible for the extinction wave affecting mainly the largest mammals. Climatic extremes could have contributed to the timing of the large mammal extinctions in North and South America, but through increased human dependency on hunting rather than directly through vegetation changes (Koch and Barnovsky, 2006). Without the presence of skilled human hunters, the late Pleistocene extinctions of large mammals would not have occurred (Sandora *et al.*, 2014; Becarra-Valdivia and Higham, 2020).

Recent Human Impacts

Recent human hunting of megaherbivores has been aimed at securing valued products in the form of ivory and horns, and rarely meat. Trade in ivory was initiated by Greeks and Phoenicians around 800 BCE, initially exploiting African elephants then still extant in Syria and Asian elephants in India, although later the source shifted to North Africa (Spinage, 1994). The Roman Empire dominated the demand for ivory during the early few centuries CE, but after elephants disappeared from North Africa the supply became transferred to East Africa and India. By 900 CE, Arab traders were importing ivory from East Africa into India and China because Asian elephants had become scarce. During the seventeenth century, Portuguese traders became involved in the ivory traffic, initially in West Africa, extending later to East Africa and southward, closely linked to the slave trade. European hunters played a major role during the nineteenth century, making a living largely from ivory and supplying guns to local people to increase the supply. The amount of ivory leaving Africa was estimated to be approximately 800 tons per year by the late nineteenth century, leading to the elimination of elephants through much of eastern and southern Africa (Spinage, 1994). In South Africa, a few herds survived in forests of the Southern Cape and two or three herds in the region adjoining Mozambique that became the Kruger Park. Elephants disappeared from Botswana and most of Zimbabwe and Namibia. Elephants are still killed for their ivory today, despite the international ban on trade, so that their numbers north of the Zambezi River continue to shrink. South of the Zambezi, better-protected elephant populations have grown to abundance levels widely regarded as excessive. The ivory trade affected Asian elephants less for the simple reason that females of this species lack tusks. Although male Asian elephants do get killed for their ivory, this has less effect on populations than the slaughter of African elephants encompassing both sexes.

Hunting activities during the nineteenth century also encompassed rhinos, with their horns being traded for various uses (Selous, 1899). White rhinos were abundant throughout savanna regions south of the Zambezi River early in the nineteenth century, but by the end of this century had been extirpated everywhere save for perhaps 50 animals in the newly proclaimed Umfolozi Game Reserve (the original name), plus a few survivors in a remote region of Mozambique (Owen-Smith, 1988). The existence of the northern white rhino subspecies was discovered only in the early twentieth century to the west of the Nile River, but recently these animals have become effectively extinct. Black rhinos, secluded in bushy habitats, survived somewhat better, and their elimination through most of Africa took place during the twentieth century largely as a result of the expanding demand for rhino horns in the Far East.

An intriguing feature of the distribution of white rhinos is their historical absence from a broad region through central and eastern Africa, where numerous other grazers and browsers remain abundant. Rock art in Algeria and Tanzania suggests that white rhinos survived in eastern and northern Africa until merely a few thousand years ago (Lang, 1923; Leakey, 1983). Since habitat conditions seem quite suitable through much of the distribution gap (confirmed by successful reintroductions of the species), it seems likely that white rhinos were eliminated from this region through hunting by early Bantu-speaking people moving from central Africa, armed with iron-tipped spears. By the time these people had colonized southern Africa around 1000 CE, they had become agro-pastoralists and no longer dependent routinely on wildlife for protein.

Conservation Dilemmas

The conservation problems associated with megaherbivores are acutely manifested with respect to both elephants and rhinos (Owen-Smith, 1981; Owen-Smith *et al.*, 2006; Scholes and Mennell, 2008). Throughout eastern Africa, widening poaching for ivory and horns has greatly reduced elephant numbers, while black rhinos have become restricted to very few localities. Illegally traded ivory has been sourced largely from forest elephants in central African countries. In southern Africa, elephant numbers have grown under effective protection to a situation where progressively worsening consequences of their vegetation impacts are feared (Whyte, 2001; Mosugelo *et al.*, 2002), and their range expansion is exacerbating conflicts with people (O'Connell-Rodwell *et al.*, 2000; Sitati, 2007). White rhino numbers had recovered to levels allowing hunting to be permitted as a legitimate activity outside of protected areas, before the recent poaching wave, and even black rhinos were recovering well across southern Africa. But, fueled by the extremely high prices fetched for rhino horns used for various purposes in the Far East, rhino numbers are declining once more. Both species are now restricted mostly to South Africa and Namibia. Indian rhinos persist under fortress protection only in sanctuaries established in India and Nepal.

Despite these initiatives, a major conservation issue is the conflicts that arise between rural people and elephants with regard to crop damage, in India as well as in Africa (Sukumar, 2003; Dublin and Hoare, 2004). This tension is increasing where elephant populations are growing and expanding their range into settled areas. It is unclear how an eventual resolution will be achieved, except by fencing elephants out or people in, and by allowing the killing of elephants transgressing boundaries.

Final Perspectives

Very large mammals falling within the megaherbivore size range (> 1000 kg) were once a major feature of terrestrial faunas in all parts of the world. Megaherbivores still vastly dominate large herbivore biomass in parts of Africa. Their grazing, browsing, and damaging impacts can transform uniform forests or grasslands into a mosaic interspersion of woodland, meadow, and savanna parkland. The enhanced habitat heterogeneity and productivity generated by such disturbance of vegetation can be favorable for the coexistence of numerous other mammalian herbivores, although plant diversity may be reduced locally.

This life form was eliminated outside of Africa and tropical Asia by the wave of extinctions that took place during the Late Pleistocene, differentially concentrated on the largest mammals. The disparate timing of species losses in different regions of the world means that there is no consistent climatic relationship (Owen-Smith, 1987; Alroy, 1999; Barnovsky *et al.*, 2004; Carrasco *et al.*, 2009). The arrival of modern humans skilled as hunters was the key influence on their demise.

Ecological conditions and processes operating within regions lacking megaherbivores differ vastly from those that prevailed in past times, before human hunting intruded. The transforming influences of human settlements and cultivation on landscapes have largely replaced the impacts of megaherbivores. The ultimate resolution of the conflicts with humans in southern Africa where elephants are recovering their numbers and expanding their distribution remains unclear. Elsewhere in Africa, elephants and rhinos seem to be on a continuing downward slide towards extinction, unless more effective conservation measures can be deployed.

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