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Pleistocene extinctions: the pivotal role of megaherbivores

Norman Owen-Smith

Abstract.—Two alternative hypotheses have been advanced to explain the demise of about half of the mammalian genera exceeding 5 kg in body mass in the later Pleistocene. One hypothesis invokes climatic change and resulting habitat transformations. This fails to predict the increased likelihood of extinctions with increasing body size, greater severity in both North and South America than in Eurasia or Australia, lack of simultaneous extinctions in Africa and tropical Asia, and the absence of extinctions at the end of previous glacial periods. The other hypothesis invokes human predation as the primary cause. This fails to explain the simultaneous extinctions of a number of mammalian and avian species not obviously vulnerable to human overkill. I propose a "keystone herbivore" hypothesis, based on the ecology of extant African species of megaherbivore, (i.e., animals exceeding 1,000 kg in body mass). Due to their invulnerability to non-human predation on adults, these species attain saturation densities at which they may radically transform vegetation structure and composition. African elephant can change closed woodland or thicket into open grassy savanna, and create open gaps colonized by rapidly-regenerating trees in forests. Grazing white rhinoceros and hippopotamus transform tall grasslands into lawns of more nutritious short grasses. The elimination of megaherbivores elsewhere in the world by human hunters at the end of the Pleistocene would have promoted reverse changes in vegetation. The conversion of the open parklike woodlands and mosaic grasslands typical of much of North America during the Pleistocene to the more uniform forests and prairie grasslands we find today could be a consequence. Such habitat changes would have been detrimental to the distribution and abundance of smaller herbivores dependent upon the nutrient-rich and spatially diverse vegetation created by megaherbivore impact. At the same time these species would have become more vulnerable to human predation. The elimination of megaherbivore influence is the major factor differentiating habitat changes at the end of the terminal Pleistocene glaciation from those occurring at previous glacial-interglacial transitions.

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Introduction

There has recently been renewed interest in the episodic extinctions that characterize the fossil record, and in the processes responsible for them. The most recent episode occurred at the end of the Pleistocene, when about half of the genera of large mammals became extinct. The causal processes responsible for the disappearance of much of the world's terrestrial macrofauna at this time remain controversial.

One hypothesis claims that the climatic change occurring at the end of the last ice age was sufficient to precipitate the extinctions through its effects on habitat conditions, although human predation may have accelerated the process. An alternative hypothesis proposes that human predation was a necessary factor in the extinctions, the climatic shift merely making populations more vulnerable to overkill. A third viewpoint holds

that it was the temporal coincidence of human hunting at a time when populations were vulnerable because of habitat deterioration that brought about the extinctions, which neither factor alone would have caused (see various papers in Martin and Klein 1984). The problem is thus to resolve which of the two factors, climatic change and predation, was primary and which secondary as causes of the extinctions, or whether both were necessary.

All three hypotheses have major shortcomings. Protagonists of climatic change as the primary causal factor have yet to explain satisfactorily why no increase in extinction rate occurred at previous glacial-interglacial transitions. The human predation hypothesis fails to account for the extinctions of mammalian and avian species that were not obvious prey species of human hunters. The coincidence-of-factors hypothesis does not ex-
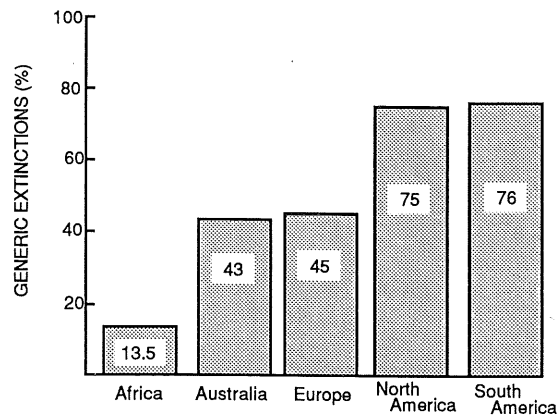
FIGURE 1. Geographic distribution of late Pleistocene extinctions of mammalian large herbivore genera (including all extinctions during the last 130,000 years of the Pleistocene of genera with body masses (>5 kg). Data from E. Anderson (1984), Klein (1984a, b), Martin (1984a).
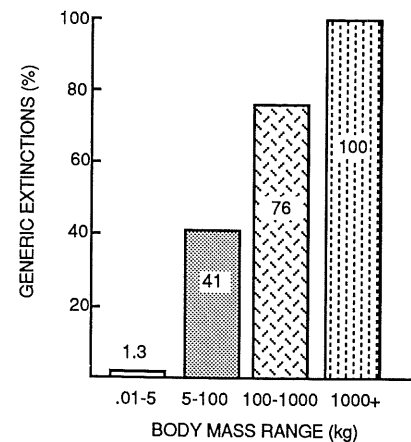

FIGURE 2. The influence of body size on generic extinctions of large mammalian herbivores in North America, South America, Europe and Australia. Sources as in Fig. 1.

plain the asynchronous disappearance of species in different regions of the world, relative to human arrival. For example, in Australia the main wave of extinction occurred some 7,000 years earlier than it did in Europe and the Americas, and about 10,000 years after the arrival of humans (Horton 1984).

In this paper I reconsider the causal processes involved in the late Pleistocene extinctions from the perspective of a neontologist familiar with the ecology of African large herbivores. The kinds of evidence that I draw together come from two sources: the pattern of the extinctions, including their geographic distribution and relation with body size as well as their timing; and the ecology of extant mammalian herbivores. I restrict my attention to species exceeding a size limit of 5 kg, i.e., about the size of the smallest antelope. Such animals are directly sensitive both to vegetation change and to human hunting pressures. Large mammalian carnivores in turn depend upon the availability of herbivores as prey. In particular I emphasize the very large mammals that I have termed "megaherbivores" (Owen-Smith, In Press). This term encompasses those species that typically attain an adult body mass in excess of a megagram, i.e., 10^6 grams, 1,000 kg or one metric tonne. It includes elephants, rhinoceroses, hippopotamus, and perhaps giraffe, among extant species, and a variety of proboscideans, perissodactyls, edentates and other forms among extinct species.

Pattern of Extinctions

Geographic distribution.—Extinctions of large mammalian herbivores were most severe in North and South America, where about three-quarters of previously extant genera disappeared during the late Pleistocene. In Europe and Australia, over 40% of genera were lost. In Africa only 14% of genera went extinct at this time (Fig. 1). Data are unavailable in an accessible form for tropical Asia.

Body size relation.—In those continents that incurred severe extinctions, the likelihood of generic extinction increased with increasing body size. All species exceeding 1,000 kg in adult body mass—i.e., all megaherbivores—disappeared from the Americas, Europe and Australia, together with three-quarters of herbivore genera with weights typically in the range 100–1,000 kg. Among mammalian herbivores weighing under 5 kg, less than 2% of genera became extinct (Fig. 2).

During the preceding Pliocene and Pleistocene, megaherbivores had remained both numerically abundant and species-rich. Over this four million year period, the number of genera extant worldwide declined only slightly, from 27 to 22, due mostly to a reduction in the number of proboscidean genera. At the end of the Pleistocene, megaherbivores were reduced precipitously to seven genera represented by eight species, all confined to Africa or tropical Asia (Fig. 3).

Temporal distribution.—In North America,

the more reliable terminal dates for extinct species fall mostly into a time range between 11,000 and 10,000 years BP (Haynes 1984; Mead and Meltzer 1984). The most precise dates for a local region, from Rancho La Brea, California, span a narrow range between 11,200 and 10,800 years BP (Martin 1984b). Extinctions included four genera of megaherbivore: *Mammuthus* (Elephantidae), *Mammut* (Mammutidae), *Cuvieronius* (Gomphotheriidae) and *Eremotherium* (Megatheriidae). *Mammuthus* was represented by two species, *M. primigenius* and *M. columbii* (Agenbroad 1984). Also disappearing during this period were genera of smaller edentate, and several species each of cervid, bovid, antilocaprid, camelid and equid (Martin 1984a).

Terminal dates for South American forms appear to span a similar time range to those in North America (Gruhn and Bryan 1984; Markgraf 1985). Six genera of megaherbivore vanished, including *Cuvieronius, Haplomastodon* and *Stegomastodon* (all Gomphotheriidae), the giant ground sloths *Eremotherium* and *Megatherium* (Megatheriidae), and the hippopotamus-like notoungulate *Toxodon* (Toxodontidae). Other forms of large herbivore becoming extinct included litopterns, camelids, cervids and equids (E. Anderson 1984; Martin 1984a).

In Europe the woolly mammoth *Mammuthus primigenius* persisted in Russia until around 11,000 years BP, although disappearing from western Europe somewhat earlier. This species, together with the woolly rhinoceros *Coelodonta antiquitatis*, became extinct in Siberia at about 11,000 years BP (Vereshchagin and Baryshnikov 1984). The giant grazing rhinoceros *Elasmotherium* disappeared from the steppes of Manchuria some time in the late Pleistocene, although precise dates are unavailable (Fortelius 1982). Medium-sized ungulates becoming extinct in Europe at the end of the last Pleistocene glacial included *Megaloceros* (Cervidae), *Equus* (Equidae), *Ovibos* and *Saiga* (Bovidae). However *Ovibos* survived in North America, and *Equus* and *Saiga* on the steppes of central Asia. An earlier wave of extinctions was associated with the end of the Eemian interglacial some 100,000 years BP, involving species of *Elephas* (Elephantidae), *Dicerorhinus* (Rhinocerotidae) and *Hippopotamus* (E. Anderson 1984; Martin 1984a). Dwarf elephants (*Elephas falconeri*) and similarly dwarfed
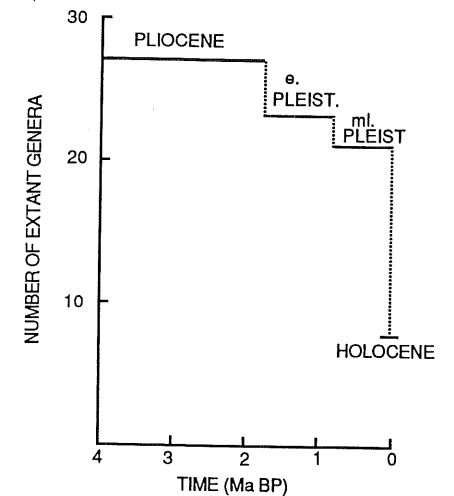
FIGURE 3. Number of genera represented by megaherbivores extant during the Pliocene and different periods of the Quaternary. Data from E. Anderson (1984), Kurtén (1968), Kurtén and Anderson (1980), Maglio (1978), Martin (1984a).

hippos survived in Sicily and on other Mediterranean islands until as recently as 8,000 years BP (Davies 1985).

In Australia, a sequence of extinctions occurred between 26,000 and 15,000 years BP. This included the rhinoceros-sized *Diprotodon*, giant wombats, and several species of giant kangaroo. Extinctions were associated with hyperarid conditions coincident with the coldest phase of the last glaciation (Hope 1984; Horton 1984).

In southern Africa, three genera of large herbivore became extinct at the end of the Pleistocene between 12,000 and 9,500 years BP: the giant buffalo *Pelorovis*, the giant hartebeest *Megalotragus* (both Bovidae), and a giant warthog (*Metridiochoerus*). Other ungulate species becoming extinct at this time include the giant Cape horse *Equus capensis,* and two species of springbok (*Antidorcas australis* and *A. bondi*). *Pelorovis* became extinct in East Africa at about the same time, but persisted in the Sahara region until about 4,000 years BP, its final extinction coinciding with advancing desert conditions. In Africa there was an earlier pulse of extinctions between the Early and Middle Stone Age, some time between 200,000 and 130,000 years BP. This encompassed *Elephas recki, Hippopotamus gorgops, Sivatherium* spp., the hartebeest genus *Parmularius,* and several large suids (Klein 1984a,b; Martin 1984a).

Further waves of extinction occurred in Madagascar and New Zealand around 1,000 years BP. In Madagascar these included a dwarf hippopotamus as well as giant lemurs and the elephant bird *Aepyornis* (Dewar 1984). In New Zealand, where mammals apart from bats were absent, extinctions involved in particular the giant herbivorous birds known as moas (Dinorthidae) (A. Anderson 1984; E. Anderson 1984; Martin 1984a).

Geographic Expansion of Human Populations

The genus *Homo* originated in Africa some time around the beginning of the Pleistocene, spread to tropical Asia during the mid Pleistocene, and steadily expanded its range northwards in Eurasia during the course of the late Pleistocene. Humans had reached 50°N latitude by about 40,000 years BP, and attained the northern-most extremes of Russia and Siberia about 15,000 years BP (Muller-Beck 1982). Unequivocal stone artefacts occur in Alaska dated at 13,000 years BP, suggesting that humans crossed the Bering land-bridge into North America around this time (West 1984). However, there is mounting evidence that people of unknown origin were present in South America as early as 32,000 years BP (Guidon and Delibrias 1986). Stone spear-points of the Clovis culture became abundant throughout the United States around 11,500 years BP, but were abruptly replaced by somewhat different artefacts of the Folsom and other cultures around 11,000 years BP.

Entry of the ancestral Aborigines into Australia occurred some time between 40,000 and 30,000 years BP, and humans had spread as far south as Tasmania by 25,000 years BP (Horton 1984). Human colonization of both Madagascar and New Zealand occurred around 1,000 years BP (Dewar 1984; Trotter and McCulloch 1984).

Ecology of Extant Megaherbivores

Distribution and abundance.—The African elephant (*Loxodonta africana*) was distributed over the whole of the African continent, from the Cape to the Mediterranean, in early historic times. Despite recent reductions in distribution, the species still occupies habitats ranging from subdesert in Namibia through various forms of savanna to rainforest in central and west Africa. The African black rhinoceros (*Diceros bicornis*) was also widely distributed from Mediterranean shrublands in the Cape and semidesert in Namibia, Somalia and adjoining countries, to moist savanna in parts of east, west and southern Africa, but was absent from moist forest. The African white rhinoceros (*Ceratotherium simum*) was historically restricted to subpopulations separated by a distribution gap of over 2,000 km through East Africa. However, the species is abundant in fossil deposits at Olduvai Gorge in Tanzania (Hooijer 1978), and its Pleistocene range extended from the Cape to Algeria. Isolated teeth suggest its persistence in East Africa into the Holocene (Hooijer and Patterson 1972). Asian elephant (*Elephas maximus*) and the two Asian species of rhinoceros (*Rhinoceros unicornis* and *R. sondaicus*) show restricted distributions but, except for *R. unicornis,* these species occurred far more widely through southeastern Asia in recent historic times (Owen-Smith, In Press). (The third Asian rhinoceros, *Dicerorhinus sumatrensis,* does not fall into the megaherbivore category).

These megaherbivores are supreme generalists not only in their habitat tolerance, but also in their dietary acceptance of a wide range of plant species and parts. In particular they can support themselves on nutrient-poor tissues such as bark, stems, and tall mature grasses, due to their low specific metabolic rates, a direct consequence of large body size. However, while both species of elephant, together with the Indian one-horned rhino, are mixed-feeders eating both grasses and woody plants, white rhinos and hippos are grazers restricting their diet to graminoids. The African black rhino and Javan one-horned rhino, together with giraffe, are browsers eating very little grass.

The extinct woolly mammoth likewise had a huge geographic range, extending across three continents from western Europe through Siberia to the United States. The woolly rhinoceros had a wide distribution from northern China through Siberia and northern Europe, but did not enter North America.

Demography.—Maximum rates of population increase decline with increasing body size (Blueweiss et al. 1978). For African elephants maximum sustained rates of population growth of 6–7 percent per annum have been recorded and for white rhino just over 9 percent (Owen-Smith, In Press). Comparable data are unavailable for other species.

A special feature of the population dynamics of African elephants, white rhinos, and hippos is their flexibility in reproduction in relation to prevailing conditions. Conceptions may be synchronized more with favorable years than with favorable seasons, resulting in variable birth intervals. Growth to sexual maturity is also retarded when levels of food resources are low relative to population demands. Adult survival is buffered against nutritional deficiencies by large size and low specific metabolism, coupled with tolerant feeding habits. Dispersal movements alleviate situations of progressive resource depletion (Owen-Smith, In Press).

Episodes of high mortality may occur during severe droughts, but less frequently than for smaller herbivores. In Tsavo (East) National Park in Kenya, one third of the elephant population, consisting mainly of adult females and young, died from starvation during a severe drought over 1970–71 (Corfield 1973; Parker 1983). However no population crash occurred in the adjoining Tsavo (West) National Park, where annual rainfall during the drought was somewhat higher. Population levels of elephant in Kruger Park and white rhino at Umfolozi were almost unaffected by the severe drought experienced in southern Africa over 1981–83 (Walker et al., In Press). In the Namib Desert region of South West Africa, elephant and black rhino showed more resilience to drought than medium-sized ungulates (Owen-Smith 1986). The mass mortality at Tsavo (East) seems to have been the result of a situation where elephants were compressed into a marginal region with a mean annual rainfall of under 400 mm by surrounding human disturbance (Corfield 1973; Parker 1983).

Anti-predator responses.—Adult elephants and rhinos are almost invulnerable to carnivores such as lions or tigers, and solitary adults show little response to the nearby presence of such predators. However this invulnerability does not extend to calves and younger subadults. Female elephants form a protective ring of adults around calves, while groups of white rhinos stand in a defensive rump-against-rump formation. Both elephants and rhinos attack and kill threatening carnivores in defense of their young.

Elephants and rhinoceroses also respond aggressively when threatened by nearby humans. However, the white rhino is an exception. In the presence of humans white rhinos waver between standing their ground defensively and fleeing. The fleeing response is restricted to humans, and is not shown in the presence of other potential predators (Owen-Smith, In Press).

Habitat impact.—Being relatively little affected by predators or weather, megaherbivore populations tend to reach saturation levels at which further increase becomes restricted by nutritional deficiencies. At such densities food resources are severely impacted, while other vegetation components may be damaged by trampling or breakage.

In higher rainfall regions with soils allowing good water infiltration, the effect of elephant damage has been to convert stands of mature woodland into shrub coppice. The shrubby woodland provides a higher biomass of accessible forage than mature woodland does, and genera of woody plants such as *Brachystegia* are able to persist in the shrub coppice form for extended periods of time (Bell 1984; Jachmann and Bell 1984, 1985). In Chizarira Game Reserve in Zimbabwe, elephants at a local density of about 1 per km² converted a *Brachystegia* woodland with a tree density of 1,180 per km² into an open tree-coppice grassland within ten years (Thompson 1975; Cumming 1981).

Colophospermum mopane, which dominates woodlands on shallow clayey soils in parts of south-central Africa where some of the highest elephant densities occur, similarly develops a shrub coppice form in response to elephant damage, and may even set seed in this growth stage. However, certain sensitive tree and shrub species may be eliminated. In the Luangwa Valley in Zambia, the elephant population showed signs of malnutrition at a regional density of about 3 per km², associated with structural modification of extensive areas of *Colophospermum mopane,* and near-annihilation of baobab (*Adansonia digitata*) and *Acacia* spp. (Naylor et al. 1973; personal observations 1983). In the Sengwa Research Area in Zimbabwe, elephants at a density of about 1 per km² reduced the biomass of mopane by only 6%, but halved the biomass of *Brachystegia* and riparian woodland (Guy 1981). In Ruaha National Park in Tanzania, elephants at a local density of 3 per km² removed 95 percent of *Commiphora* shrubs over a ten year period, and severely depleted stands of *Acacia*

albida and baobab (Barnes 1985). In Kruger National Park in South Africa, elephant damage to trees and opening up of *Acacia* and *Combretum* woodlands has been a steadily worsening problem, even though the elephant population is tightly managed to keep it below a regional density of 0.4 per km² (van Wyk and Fairall 1966; Coetzee et al. 1979).

On nutrient-rich, clayey soils with restricted water infiltration, the result of elephant damage may be the elimination of *Acacia* woodlands, aided by fire. In Murchison Falls National Park in Uganda, elephant breakage and debarking of trees, coupled with fire, converted regions of *Acacia* or *Terminalia/Combretum* savanna into open grassland, with reduced carrying capacity for elephants (Laws et al. 1975). In Masai Mara National Park in Kenya, a well-wooded *Acacia* savanna was transformed into open grassland by the combined impact of fire and elephant browsing (Dublin 1984). Similar changes have been recorded in parts of the adjoining Serengeti National Park in Tanzania, caused by a local density of elephant bulls of only 0.2 per km² (Pellew 1983). The Rwindi-Rutshuru plain of Virunga National Park in Zaire provides another example, strikingly depicted by the paired photographs presented by Bourlière (1965).

In forest habitats, both African and Asian elephants promote the replacement of slow-growing, shade-tolerant trees by more rapidly growing, gap-colonizing trees, shrubs and herbaceous plants (Mueller-Dombois 1972; Laws et al. 1975). Fast-growing plants tend to be less well defended by secondary metabolites such as tannins than slow-growing species (Coley et al. 1985).

Browsing black rhinoceros may exert a severe impact on regenerating woody scrub; but at the maximum densities they attain (about 1 per km²) this does not appear sufficient to alter woodland density (Mukinya 1977; B. P. O'Regan, pers. comm. 1985).

In the Umfolozi Game Reserve in Zululand, expansion of the white rhinoceros population has been associated with extensive conversion of stands of medium-tall *Themeda* grassland to short grass lawns, with consequent exposure of soils to increased erosion (Owen-Smith, In Press). In Queen Elizabeth National Park in Uganda, grazing pressure by hippopotamus at local densities of 15–

20 per km² converted tall grassland into short grassland with greatly accelerated soil erosion (Thornton 1971; Lock 1972). Because short grass areas fail to sustain fires, the habitat becomes vulnerable to invasion by woody scrub, which can result in the transformation of an open grassy savanna into a densely wooded thicket (Walker et al. 1981; Pellew 1983).

Apart from megaherbivores, no other wild ungulate species has brought about major changes in African savanna vegetation, except in circumstances where populations have been restricted by fencing to small areas, affected by provision of artificial water supplies, or influenced by the elimination of predators (Cumming 1982).

Effects on other large herbivores.—Habitat changes may have positive or negative effects on smaller animal species. The conversion of the bush thickets of Tsavo (East) into an open grassy steppe was associated with declines in populations of browsing ungulates, including black rhinoceros and lesser kudu, and corresponding increases by grazing ungulates, such as Grevy's zebra and oryx (Parker 1983). However, in Addo National Park in the Cape, opening up of dense thickets by elephants at a density of 4 per km² resulted in increases by browsers, including kudu and eland, probably because more browse became accessible (Hall-Martin, pers. comm. 1985). Along the Chobe River in Botswana, elephants attain a dry season density of over 7 per km², but the only animal species to suffer has been bushbuck (*Tragelaphus scriptus*) due to the opening up of thickets (D. Work, pers. comm. 1986).

In the Umfolozi Game Reserve, expansion of the white rhino population was accompanied by increased numbers of other grazers, including wildebeest, zebra and impala, but tall-grass-dependent species such as waterbuck and reedbuck declined (Brookes and Macdonald 1983). Following recovery of the hippopotamus population on the Mweya Peninsula in Queen Elizabeth National Park, Uganda, densities of elephant, buffalo and waterbuck declined, while warthog remain unchanged. The species declining were those dependent on taller grass (Eltringham 1980).

Discussion

Climatic changes hypothesis.—Episodes of extinction seem to be associated frequently with periods of climatic change. For example, the wave

of mammalian extinctions that took place in North America at the end of the Miocene (Clarendonian), and at the end of the Pliocene (late Hemphillian), occurred around times of major climatic shifts. However, these differed from the extinction episode at the end of the Pleistocene in that all size classes of mammal were affected equally. Furthermore, these earlier extinction events did not bring about much decline in generic diversity, since terminated genera were replaced by new genera through immigration (Martin 1984a; Webb 1984). In Africa, episodes of extinction and speciation among bovids during the Pleistocene tended to be associated with periods of change between wet and dry conditions, synchronous with the glacial/interglacial alternation (Vrba 1985). In contrast, the late Pleistocene extinctions occurred without replacement.

Major habitat changes at the end of the Pleistocene involved more than simply the latitudinal migration of biomes. The associations of animals and plants during the late Pleistocene were somewhat different from those found in modern times (Graham and Lundelius 1984). Species which today have disparate distributions restricted to either subtropical or cool-temperate regions coexisted then in the same faunas. For example, in the Appalachian region of North America, grazers like mammoth, equids and bison coexisted alongside browsers such as mastodont, ground sloth, tapir and cervids, together with mixed feeders like caribou and muskox (Guilday 1984). Pollen evidence indicates the co-occurrence of conifers, broadleaf hardwoods and graminoids, suggesting an open parkland in a broad belt across the United States from the Appalachians to the Rockies (Wright 1984). Remnants of this vegetation formation still persist in small areas in Siberia (Yurtsev 1982). The prairie grasslands of today are a novel formation with no paleontological counterpart (Stebbins 1981).

Changes in animal and plant distributions have led observers to infer that modern climates are more intensely seasonal than those of the Pleistocene. It has been suggested that the climatic shift at the end of the Pleistocene was more extreme in either magnitude or rate than the shifts that had occurred at previous glacial-interglacial transitions (Guthrie 1984; Graham 1986). However, there is no independent evidence in support of this contention. The temperature

change as reflected by ¹⁸O ratios preserved in the Antarctic ice cap, and by foraminifera from the Pacific sea floor, appears no more extreme or rapid at the end of the Pleistocene than at the termination of the previous (Illinois/Saal) glaciation 140,000 years BP (Shackleton et al. 1983; Lorius et al. 1985). On the contrary, the Sangamon/Eem interglacial appears to have been somewhat warmer at the start than the Holocene, so that the climatic change leading into it was perhaps more extreme than that at the Holocene transition. Yet no increase in extinctions took place at the end of the Illinoisian glaciation.

Guthrie (1984) proposed that a common factor in the extinctions was the transformation of a previously mosaic interspersion of vegetation communities into a more uniform zonal distribution. The reduced habitat diversity made it difficult for sedentary herbivores to secure their food requirements at different seasons within a restricted home range. Notably, among surviving species bison and caribou migrate over extensive areas, while mountain sheep and mountain goat find a compressed zonal gradient in mountainous areas.

It has also been suggested that increased climatic seasonality could have created problems of reproductive synchrony among larger mammals with gestation periods exceeding about one year (Guthrie 1984; Kiltie 1984). However, this does not explain the disappearance of such animals from the milder climates of the southern United States and Central and South America, as well as from the far north. Prolonged gestation periods also restrict maximum rates of population growth, with consequences to be examined below.

Climatic causation does not explain the geographic variability in the severity of extinctions. The recent expansion of forest in South America would be less favorable to large mammalian herbivores than the savannas persisting in Africa. However elephants persist in moist forested regions in Africa, India and other parts of southeast Asia, while gomphotheres vanished from South and Central America. Horse, ass, camel, yak and saiga remained on the steppes of central Asia, while their counterparts disappeared from the prairies of North America. Finally, no satisfactory explanation has been put forward to suggest why megaherbivores, with their wide habitat and trophic tolerance, should have been

so much more vulnerable to the habitat changes of the late Pleistocene than smaller species of herbivore.

Human predation hypothesis.—Megaherbivores are indisputably more vulnerable to sustained human predation than smaller species. Their maximum rate of population recruitment is under 10 percent per annum, and any harvest level exceeding this must inevitably drive populations downwards. They are large, conspicuous animals, unable to seclude themselves when populations become rare. The kinds of anti-predator defenses used to protect immature animals against carnivores would be ineffective against an organized group of humans, capable of hurling projectile weapons. Species that had evolved in the New World in the absence of humans were confronted relatively suddenly by organized hunters that had perfected their techniques on the megafauna of Eurasia.

The geographic pattern of the late Pleistocene extinctions is also concordant with the pattern of human occupation. The megaherbivores of Africa and southern Asia coevolved alongside early humans and so had ample time to develop effective defenses (although the example of the white rhino suggests that species might become evolutionarily trapped into inappropriate responses). The Middle and Late Stone Age people inhabiting Africa between 130,000 BP and the early Holocene hunted small to medium-sized ungulates, but avoided elephants and rhinos (Klein 1977, 1984a). In Europe there was gradually increasing contact as humans expanded northward during the Pleistocene. Cave paintings in France depict the hunting of mammoths around 20,000 years BP, while earlier associations of mammoth bones with stone spear-heads suggest that human hunting of this species was well established in southern Europe as early as 80,000 years BP (Muller-Beck 1982). Mammoth and woolly rhino, along with horse, bison and reindeer, are among the characteristic species found at human occupation sites in northern Europe and Siberia, and in some places dwellings were constructed from the abundant mammoth bones (Vereshchagin and Baryshnikov 1984). In North America, Clovis points are commonly associated with mammoth remains, and there is also clear evidence for the hunting of mastodonts (Haynes 1982; Agenbroad 1984; Fisher 1984). Associ-

ations of gomphothere and ground sloth remains with human artefacts occur in Venezuela and Patagonia (Gruhn and Bryan 1984; Markgraf 1985). In Australia, in contrast, human artefacts are rarely found in association with abundant vertebrate fossils, although bones of large vertebrates do occur at archeological sites (Horton 1984).

The earlier disappearance of *Elephas recki, Sivatherium* and certain other large herbivores in Africa during the Middle Stone Age cannot be ascribed directly to human hunting. Nevertheless, humans were becoming increasingly proficient at hunting medium-sized ungulates at this time, and there may well have been indirect effects. For example, human control of fire was evidently widespread in Africa by 130,000 years BP (Volman 1984). *E. recki* as a grazer would have been especially vulnerable to reductions in the standing biomass of the grass that it probably depended on to sustain it through the dry season. On the other hand, the demise of *Elephas* and *Dicerorhinus* in Europe at the end of the Eemian interglacial is more readily related to the increased capabilities of human hunters of the region in tackling such large prey. Populations of these species retreating southward at the end of the interglacial could have come into contact relatively suddenly with humans spreading northward.

Variations in the timing of extinctions between different regions relative to human arrival could be explained in terms of the time required for human populations to reach the critical densities at which their hunting pressure exceeded the replacement potential of prey species. A possible scenario might encompass (1) a prey density averaging under 2 per km², (2) a human density of around one person per 20 km², and (3) a kill rate of one person per band of 25 people per week. The human density suggested above is that estimated to have prevailed in Europe during the paleolithic (Muller-Beck 1982). The precise timing of the extinctions could be influenced by either a depression in megaherbivore populations, or a restriction on their distribution, due to the deteriorating habitat conditions of the late Pleistocene.

While the elimination of megaherbivore populations by human overkill is thus readily explained, the simultaneous extinction of more

abundant smaller species with higher rates of population recruitment at the same time through the same agency is more difficult to support. I thus turn to a third hypothesis, which incorporates elements of both the climatic and human predation explanations.

The keystone herbivore hypothesis.—The dramatic effects that megaherbivores can have on habitats is widely evident in Africa today. This is the case even though elephant populations have attained saturation levels in very few areas, due to their depression during the ivory hunting era of the eighteenth and nineteenth centuries. Moreover, only rarely does the impact of elephants on woodlands occur in conjunction with the effects of an equally destructive grazer on grassland; and, with the widespread elimination of white rhino, these regions are restricted to narrow zones adjoining rivers or lakes where hippos concentrate their grazing. Notably one of these areas, Queen Elizabeth National Park in Uganda, supported the highest animal biomass yet recorded for a natural ecosystem (until poachers intervened; Field and Laws 1970).

By felling or damaging trees, elephants can transform wooded savanna to open grassy savanna or shrubby regrowth, and create openings in forests. Fire may have a secondary effect in opening up such woodlands. Grazers like white rhinos and hippos convert medium-tall grasslands to short grass lawns, suppressing fires and thereby making grasslands vulnerable to invasion by woody plants. The combined effects of both grazing and browsing megaherbivores is to create open short-grass savannas dominated by rapidly regenerating woody plants and herbs. The kinds of habitat change that these species induce are not necessarily detrimental to other large herbivores. On the contrary, the coppice or gap-colonizing woody plants promoted by elephant damage offer more accessible foliage and new stems and lowered chemical defenses compared with the mature trees they replace. Short decumbent grasses offer higher growth rates and a more favorable ratio of protein to fiber than taller grasses. A high biomass of very large herbivores could furthermore accelerate the recycling of nutrients for further plant growth (Botkin et al. 1981). Thus the disturbing effects of megaherbivores on vegetation can promote higher rates of production of more nutritious forage than occurs in their

absence, and these habitat changes may benefit other mammalian herbivores with similar but more selective feeding habits.

In North America during the Pleistocene, the megaherbivore fauna included grazing mammoths plus browsing mastodonts, gomphotheres and ground sloths. In South America, grazers, including *Stegomastodon* and *Mylodon* ground sloths, complemented browsing *Haplomastodon, Cuvieronius* and *Megatherium*. In northern Eurasia, grazing mammoth and woolly rhino coexisted, while during the earlier part of the Pleistocene there were also browsing elephants and browsing rhinos. The combined impact of these species at nutritionally limited densities could have been vastly greater than anything yet documented in Africa.

Following the demise of megaherbivores, by whatever agency, what changes in vegetation would have resulted? Reversing the changes that have been observed in Africa following megaherbivore increases, these would have involved the elimination of open glades in forests, while in grasslands a mosaic of tall and short grass zones would have grown out to a more uniform tall grassland. The latter would furthermore have sustained more frequent and fierce fires than the former grassland mosaic, further depressing any remnant tree or shrub stands. These seem to be just the kinds of changes in vegetation documented by the fossil pollen record.

Thus the unique features of the vegetation changes that occurred between the late Pleistocene and the Holocene appear to be closely in accord with those to be expected following the elimination of a pre-existing regime of severe and widespread disturbance maintained by megaherbivores. The changes in animal distributions that occurred over this period could in some cases be a consequence of the vegetation change, rather than of reduced climatic equability.

The keystone herbivore hypothesis does not entail necessary acceptance of either habitat change or human predation as the primary cause of the extinctions of lesser herbivores. Megaherbivore-impacted vegetation must have been a consistent feature of habitats throughout the evolutionary history of these species, so that many of them were probably adapted to exploit the quick-growing, chemically-undefended shrubs and grasses that were prevalent. Elimination of mega-

herbivores would result in the contraction of such vegetation to sites where other disturbing factors promoted these kinds of plants. The restriction of associated herbivores to relatively isolated pockets would have made these herbivore species more susceptible to chance events, and may have blocked the migratory routes they needed to follow shifting vegetation zones. At the same time, these restricted populations would have been vulnerable to human hunters, especially if their antipredator responses were poorly adapted to this novel predator. Humans may well have turned increasingly to these species following the demise of the larger animals that had been their preferred prey. Rather than being ripe for speciation, these small isolated populations may have been pushed over the brink towards extinction by the additional pressure of sustained human predation.

Those who have witnessed the abundant African megafauna still persisting in protected National Parks today may find it hard to imagine that many of these species could disappear if elephants, rhinos and hippos were eliminated. In much of savanna Africa, edaphic and climatic variability, coupled with fire and human exploitation of woodlands for fuelwood, help maintain the diverse mosaic of grasses and trees. Nevertheless, in the Hluhluwe Game Reserve in Natal, where the rainfall is relatively high (c. 950 mm), elephants have recently been reintroduced with the aim of halting a steadily worsening trend toward closed woodland and forest. Following 100 years or so without elephants, three species of antelope have become locally extinct, while open country grazers such as wildebeest and waterbuck have been reduced to low numbers. Among browsers, black rhino and kudu have shown steadily declining numbers, although thicket-inhabiting species have maintained their numbers or increased (Brooks and Macdonald 1983).

The scenario that I have outlined supports the coincidence-of-events hypothesis for the disappearance of medium-sized herbivores, but with this twist. The habitat change was necessarily coincident with human predation pressure, because human hunting induced the habitat transformation by exterminating the megaherbivore component. Australia, with only one megaherbivore species, provides an exception. Here extinctions were delayed for some time after human

arrival, until populations became restricted in their distribution due to a hyperarid period.

Evidence in support of the keystone herbivore hypothesis may be sought from two sources:

1. The kinds of vegetation change that occurred during the late Pleistocene, and whether these are best explained by climatic change or as a consequence of the elimination of megaherbivore disturbance.

2. The precise relation between the timing of the extinctions of megaherbivores and the disappearance of smaller mammalian species. If the latter generally preceded the former, the keystone herbivore hypothesis would be refuted.

Whatever the outcome of this evidence, there is one indisputable point that needs to be made in conclusion. The relatively sudden disappearance of a variety of megaherbivore species, through whatever agency, must have had major effects on pre-existing vegetation patterns. The elimination of their impact, which had been a persistent feature during past evolutionary time, needs to be taken into account, in addition to climatic shifts, in explaining the vegetation transformations that occurred at the end of the Pleistocene.

Acknowledgments

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CONTENTS