

ADVANCES IN VERTEBRATE PALEOBIOLOGY

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New York, New York

Kluwer Academic / Plenum Publishers
New York, Boston, Dordrecht, London, Moscow

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1999

CHAPTER 3

The Interaction of Humans, Megaherbivores, and Habitats in the Late Pleistocene Extinction Event

NORMAN OWEN-SMITH

1. Introduction

The extinction pulse during the late Pleistocene exhibited the following special features: (1) extinction likelihood was strongly dependent on body size, (2) the severity of the extinctions varied markedly between continents, and (3) extinctions were associated in time with the appearance of humans, and also with a period of climatic and hence habitat change (Owen-Smith, 1987). Causal explanations must be judged by their ability to predict these patterns.

My contribution to this volume will emphasize the ecological processes that potentially led to these species extinctions. Extinctions may result from climatic shift, habitat loss, competition, predation, or disease outbreaks. Competition has not been invoked as a factor in the late Pleistocene (except possibly between human hunters and other predators), and disease panzootics seem unlikely to have been involved (but for a contrary view, see MacPhee and Flemming, this volume). The central issue to be addressed concerns the relative importance of human predation, versus consequences of the climatic shift at the end of the last ice age for habitat conditions (see papers in Martin and Klein, 1984).

My focus is on large mammalian herbivores, as these are both directly responsive to habitat change, and potential prey for human hunters. The time period I cover extends from somewhat after the end of the Sangamonian/Eemian Interglacial into the early Holocene, i.e., from about 100,000 yrbp to perhaps 5000 yrbp.

2. Pattern of the Late Pleistocene Extinctions

Toward the end of the Pleistocene, over half of the species of large mammalian herbivores occupying North America, South America, and Australia became extinct. North-

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Extinctions in Near Time, edited by MacPhee. Kluwer Academic/Plenum Publishers, New York, 1999.

ern Eurasia (i.e., Europe plus Siberia) lost 37% of its meager fauna of large herbivores, while Africa incurred only a 10% loss (Fig. 1; data for tropical Asia unavailable). The lower size limit of 10 kg that I have used is arguably a more natural subdivision than Martin's (1966, 1967) criterion of 44 kg (see Fig. 17.1 in Owen-Smith, 1988, and Fig. 24 in Stuart, 1991). It encompasses most bovids and macropods, while excluding most rodents and lagomorphs.

Notable distinctions existed in body size distributions among continental Pleistocene herbivore faunas (Fig. 1). Both North and South America exhibited predominantly medium to large species weighing over 100 kg. Africa was and is especially species-rich in the size range of 10–100 kg, while retaining as many medium–large species as formerly in the Americas. Australia formerly had about as many medium–small species as Africa, but very few large species. Eurasia was generally depauperate in species, despite its vast area. Africa's past and present richness lies especially in the radiation of medium-sized bovids, with 16 modern genera represented by almost 50 species in the size range 10–100 kg. North and South America were formerly as species-diverse as Africa in the size range 100–1000 + kg, but lost most of these species at the end of the Pleistocene.

The extinctions took out all megaherbivores (species attaining over 1000 kg in adult body weight), plus over 80% of species weighing 100–1000 kg, throughout the Americas, Eurasia, and Australia. In Africa a pulse of extinctions between the Early and Middle Stone Age, somewhat prior to 100,000 yrbp, involved the disappearance of *Elephas recki*, *Hippopotamus gorgops*, *Sivatherium*, *Hipparion*, the hartebeest *Parmularius*, and several large suids (Klein, 1984a,b). Near the end of the Pleistocene, a giant horse (*Equus capensis*), long-horned buffalo (*Pelorovis antiquus*), giant hartebeest (*Megalotragus priscus*), giant warthog (*Phacochoerus* [*Metridiochoerus*] *compactus*), two medium-sized bovids (*Damaliscus niro* and *Antidorcas bondi*), and an ass (*Equus* c.f. *asinus*) became extinct in southern and eastern Africa (Klein, 1977, 1984a,b; Marean and Gifford-Gonzalez, 1991; Brink, 1994), although *Pelorovis* lingered into the Holocene in the Sahara region. Tropical Asia lost *Stegodon* (a proboscidean) and *Elasmotherium* (a rhinoceros) sometime during the late Pleistocene (Anderson, 1984).

In southern Europe the straight-tusked elephant (*Palaeoloxodon antiquus*) survived until about 40,000 yrbp and the steppe rhinos (*Dicerorhinus hemitoechus* and *D. kirchbergensis*) until about 20,000 yrbp (Stuart, 1991). The woolly rhino (*Coelodonta antiquitatis*) and woolly mammoth (*Mammuthus primigenius*) persisted in Europe until 12,000 yrbp. Mammoths remained in continental Siberia until nearly 10,000 yrbp, and on Wrangel Island until perhaps 4000 yrbp (Vartanyan *et al.*, 1993). *Hippopotamus amphibius* disappeared from Europe around 80,000 yrbp, whereas the giant deer *Megaloceros giganteus* persisted in Ireland until 10,500 yrbp (Stuart, 1991).

In North America, extinctions were concentrated within a narrow time window between 11,500 and 10,500 yrbp (Stuart, 1991). Terminal dates for South America suggest a similar or even slightly earlier timing for extinctions (Markgraf, 1985), but need to be confirmed. Notably only two grazing ungulate species survive today in South America, both very localized: the vicuña (*Vicugna vicugna*) and the pampas deer (*Ozotoceros bezoarticus*). In Australia the extinctions apparently occurred prior to 35,000 yrbp (Flannery and Roberts, this volume). No species weighing over 100 kg survived.

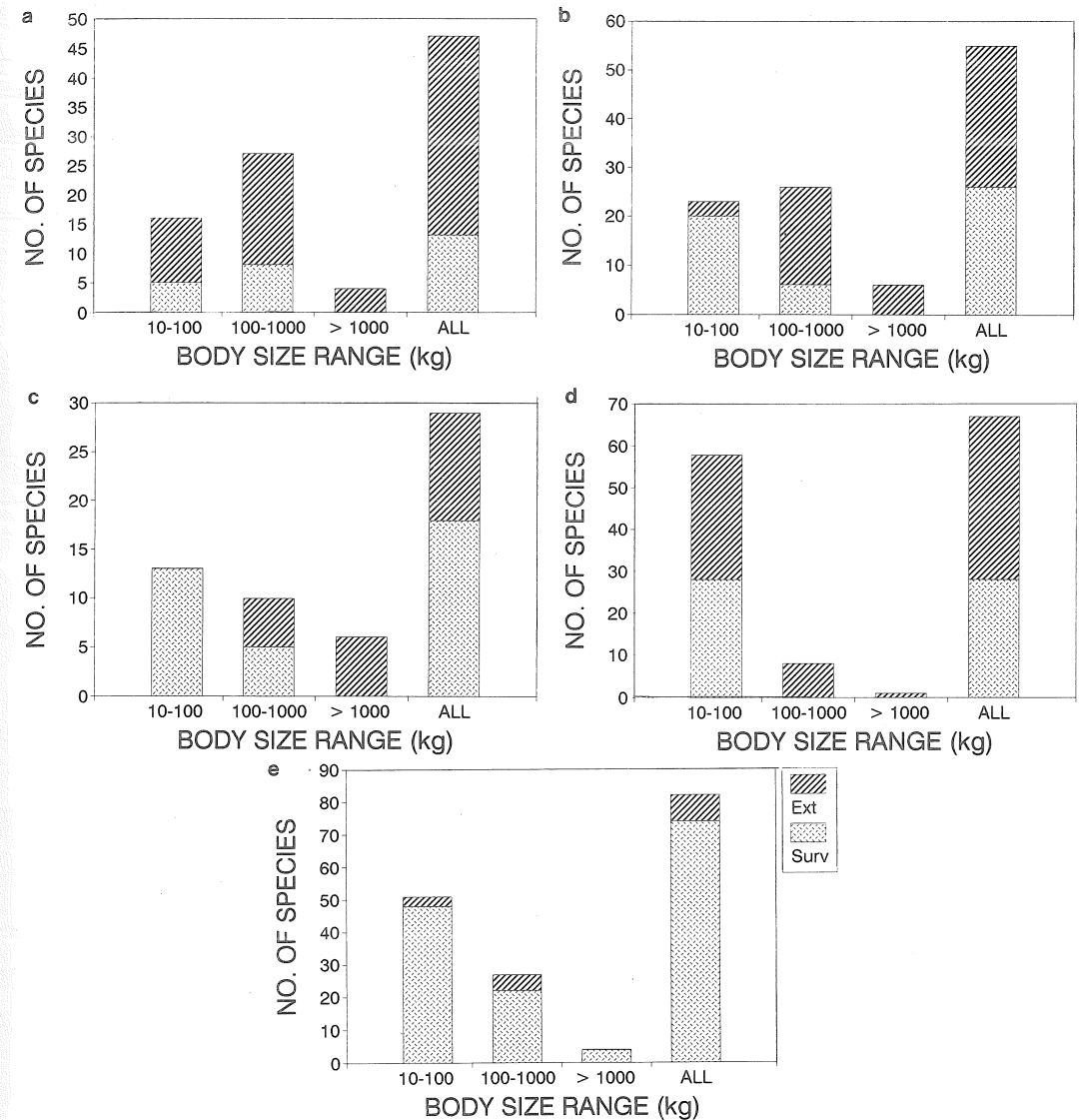


FIGURE 1. (a) North America; (b) South America; (c) Eurasia; (d) Australia; (e) Africa. Body mass distribution of late Pleistocene versus surviving species of large mammalian herbivores in different continents. Eurasia represents Europe plus Siberia. Africa excludes the Mediterranean region. Extinctions tallied from about 100,000 yrbp (i.e., following the Sangamonian/Eemian Interglacial) into the Holocene. For South America, one species per extinct genus was assumed where species-level tallies were unavailable (from Anderson, 1984; Klein, 1984a,b; Macdonald, 1984; Marean and Gifford-Gonzalez, 1991; Murray, 1991; Stuart, 1991).

3. Predation-Induced Extinctions

For predation to drive prey to extinction, three conditions must apply: (1) population losses must exceed recruitment, (2) this imbalance must be maintained even when prey become rare, and (3) no predator-free refuges must exist. Density-dependent recruitment models applied to fisheries highlight the distinction between sustainable and unsustainable harvests. Assuming a simple logistic model, maximum "sustained" yield (MSY) is obtained at a population level equal to half of the equilibrium carrying capacity in the absence of harvests, at a rate equivalent to half of the maximum rate of population growth. But large mammals generally show a right-skewed recruitment curve, so that maximum yield occurs somewhat closer to the equilibrium density than suggested by the logistic model (Fowler, 1981; Fig. 2).

If harvests reduce the resource population below the MSY level, the population collapses, unless the quota is reduced promptly and sufficiently. In natural environments, recruitment success can vary widely over time, so that a quota set initially below the theoretical MSY sooner or later exceeds the sustainable threshold. The history of human resource exploitation shows that, because of uncertainties and economic pressures, an effective response is usually delayed until too late (Ludwig *et al.*, 1993). Accordingly, fisheries have notoriously failed to conserve stocks of fishes and whales. Yet species have not been driven to extinction, because harvesting becomes economically inefficient once the resource gets scarce.

Even in natural predator-prey systems, circumstances may push the prey population into a "predator pit," i.e., a level maintained well below that set by food resources. This may arise from a strongly density-dependent increase in predation rate at low density, sufficient to exceed the resource-dependent recruitment rate (Fig. 3). When prey becomes scarce, predators either switch to other prey species, or decline numerically because of insufficient food. Toward higher prey abundance, individual predators become satiated, and predator populations may reach a density limit set by social factors (e.g., territorial exclusion). A North American example is the moose-wolf interaction, with moose held at a density of under 0.4 per km² by the combined impacts of wolves, bears, and human hunters, despite being capable of attaining a food-limited density of over 2 per km² (Messier, 1994). In Africa, the contrasting population levels of migratory versus sedentary wildebeest in the Serengeti region of Tanzania may have a similar explanation (Fryxell *et al.*, 1988).

Prey switching will not alleviate predation pressure on favored prey species when these and alternative prey occur together in the same habitat. Accordingly, whether keystone predators enhance or reduce prey diversity depends on the relative abundance of preferred versus alternate prey, and on the capacity of the latter to support the predator population (Begon *et al.*, 1996, Chapter 21). Notably, in the places where wolves depress moose populations, deer or other species provide alternative prey (Messier, 1994). An unpublished South African example of near-extinction of a prey species by a mammalian predator, from the Suikerbosrand Nature Reserve near Johannesburg, is instructive. Following the introduction of cheetah (*Acinonyx jubatus*), blesbok (*Damaliscus dorcas*) declined precipitously to low numbers, at which point the cheetahs started concentrating their hunting on springbok (*Antidorcas marsupialis*). Extinction of the blesbok was avoided by removal of the cheetahs.

A predator-maintained prey density below half of the saturation density of the prey is inherently unstable, unless habitats are sufficiently heterogeneous. Typically the prey species persists in localities where it can effectively evade predation. For example, wilde-

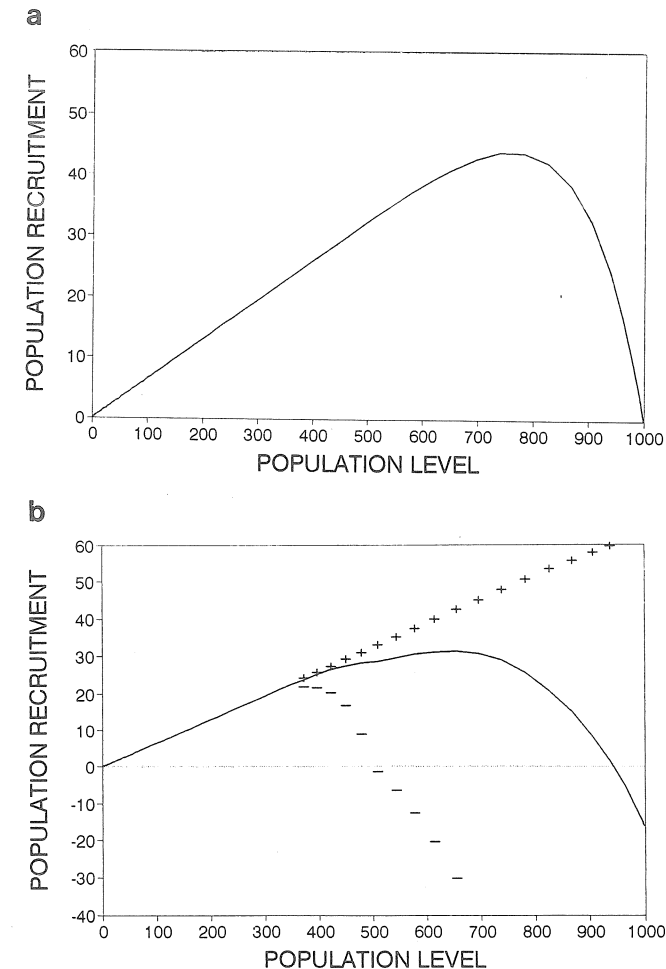


FIGURE 2. Shape of recruitment curve typical for large mammalian herbivores, which also represents potential harvests. (a) Population with a maximum rate of population growth of 6.5% in a constant environment with an equilibrium density ("carrying capacity") of 1000 units (units may represent numbers, density, biomass, or whatever). The maximum sustainable harvest is 44 units from a population level of about 750 units. (b) Population with the same intrinsic growth rate under conditions where the "carrying capacity" varies stochastically between extremes of 0.5 and 1.5 times the mean level of 1000. +, recruitment curve under best conditions (carrying capacity 1500); -, recruitment curve under worst conditions (carrying capacity 500); solid line is the mean recruitment averaged over the range in conditions. Environmental variability reduces the maximum sustainable harvest to on average 33 units. However, to avoid overexploitation in the worst years, the harvest quota would need to be reduced to no more than 22 units, in this specific example.

beest avoid wooded areas providing cover for lions, despite the food resources they offer (Talbot and Talbot, 1963). Deer alleviate predation by wolves by occupying boundary regions between adjacent wolf pack territories (Mech, 1977). Such habitat restrictions underlie the classical distinction between the fundamental and realized niche of a species (Hutchinson, 1957).

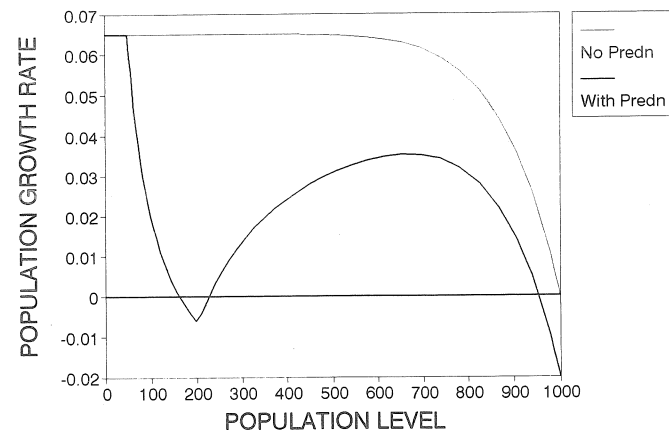


FIGURE 3. Change in population growth rate with increasing population level, indicating a “predator pit” brought about by density-dependent predation, for population parameters as in Fig. 2. Predation level increases more steeply than prey abundance at low prey density, but with predators tending to become satiated toward high prey densities. This generates two alternative equilibrium levels where the net population growth of the prey is zero: (1) a high level of about 950 units with a predation level of about 2% and (2) a low level of about 160 units maintained by the predation of about 10 units per year. The lower population equilibrium is referred to as the predator pit (not the bottoming out of the net recruitment curve, where population growth is negative!).

When populations are depressed to low densities, the “Allee effect,” i.e., reduced recruitment rate at low density, may come into operation. The population growth rate of white rhinos in the Hluhluwe–Umfolozzi Park in South Africa was evidently lower when the population was small than after high densities had been attained (Fig. 4). Furthermore, white rhinos introduced into other wildlife parks have exhibited longer intercalving intervals than those typical of the dense Umfolozzi population (Owen-Smith, 1988). This pattern could be related either to difficulties in finding mates at low densities, or to improvements in food resources brought about by the feeding impacts of the rhinos on vegetation. Notably, the depressed blue whale population has failed to recover, despite cessation of all harvesting. Through “Allee effects,” effective population extinguishment may occur well before the last few individuals have been killed.

Refuge habitats (“enemy-free space,” Jeffries and Lawton, 1984) may permit prey persistence despite efficient predators. This may also occur dynamically, with prey colonizing vacant habitat patches one step ahead of predators (Huffaker, 1958). Metapopulation extinction (regional extirpation, as opposed to local population extinguishment) occurs only if all suitable habitat is persistently occupied by predators, so that new colonists encounter waiting hunters. This requires that the predator population be maintained by alternate food resources resistant to depletion.

4. Habitat-Induced Extinctions

Here the focus is on habitat components such as food resources and vegetation physiology, while recognizing that predators also influence habitat suitability. Spatial varia-

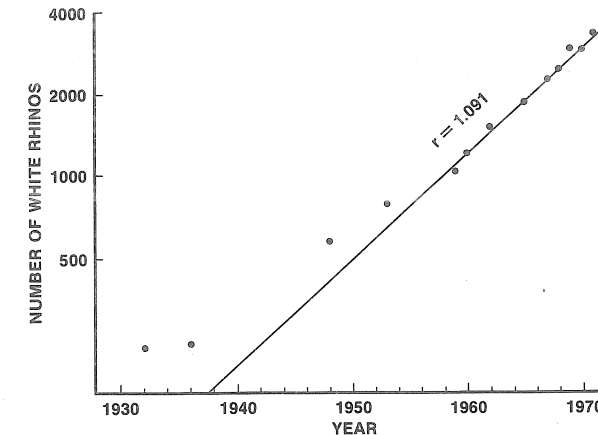


FIGURE 4. Population increase of white rhinos in the Hluhluwe–Umfolozzi Park in South Africa, showing indication of an “Allee effect,” i.e., reduced population growth rate at low density. The growth rate of the white rhino population increased from about 6.5% per year when the population size was about 200 toward 9.5% per year when the population size exceeded 1000 animals (from Owen-Smith, 1988).

tion in these features underlies the distinction between source and sink habitats, and intervening nonhabitat (Pulliam and Danielson, 1991). Source habitats are places sufficiently favorable to support thriving populations of particular species. Surplus individuals from these localities disperse into surrounding less suitable regions, where population growth would be negative in the absence of continuing immigration. Areas of nonhabitat may be traversed by migrants, but do not support breeding groups.

Environmental fluctuations in precipitation or temperature may cause localities to vary over time in their habitat suitability. A progressive climatic change could bring about species extinctions by (1) transforming formerly source habitat into sink habitat, leading to (2) remaining patches of source habitat becoming isolated, so that (3) local populations become vulnerable to stochastic small-population effects. Isolation retards recolonization following local population extirpation. Unless adequate areas of suitable habitat persist somewhere within the range, species extinction may ultimately result.

The change from glacial to interglacial conditions at the end of the Pleistocene entailed not only a rise in global mean temperatures, but also a widespread increase in precipitation in both high and low latitudes (Ritchie and Cwynar, 1982; Markgraf, 1985; Partridge *et al.*, 1990; deMenocal, 1995). In midlatitudes of North America, vegetation changed from the diverse mosaic of conifers, hardwoods, and grasses that was widespread during the Pleistocene, into the relatively uniform conifer or broadleaf forests and prairie grasslands found today (Guthrie, 1984; Wright, 1984). Such changes were associated in time with a reduction in the ranges occupied by the woolly mammoth and associated grazing ungulates, plus certain low-level browsers, which typified the “mammoth steppe” fauna of North America and Eurasia (Guthrie, 1982; Stuart, 1991). In the tropical and subtropical latitudes of eastern and southern Africa and South America, extensive dry grasslands or open woodlands gave way to expanding forest and moister woodlands around this time (Klein, 1984a; Mark-

graf, 1985). The general result was a contraction in physiognomically open habitat in favor of closed woodland or forest.

The regional vegetation pattern (biome type) is determined by climatic conditions (temperature and precipitation), whereas local vegetation physiognomy is influenced by topography and soils. The spatial heterogeneity notable within African savannas is largely a result of soil differences determined by underlying geology and downslope sediment movements (catenary patterns). These are in turn a consequence of the high elevation of much of southern and east-central Africa. Toward higher (above 800 mm) and lower (below 400 mm) annual rainfall, soil parent material becomes less influential, because of nutrient and clay leaching, or lack thereof. Superimposed on geophysical factors are the important modifying effects of fire and herbivory on vegetation (Scholes, 1991; Bond, 1997; Owen-Smith, 1997).

Over much of North America and Eurasia, soils are derived from wind-blown loess or former lake and sea beds. Accordingly, disturbance by fire or herbivory may have been relatively more influential in modifying vegetation patterns than in Africa. South America and Australia are mostly low-lying, except for mountain ranges, with soils intensely weathered and especially depauperate in phosphorus and other nutrients (Medina and Silva, 1991; Flannery and Roberts, this volume). Large herbivores concentrate in localities where nutrients accumulate, such as floodplains, as evidenced within regions of nutrient-poor (moist/dystrophic) savanna in Africa today (Huntley, 1982; Scholes and Walker, 1993; Owen-Smith, 1997). The tendency toward large body size in South America's Pleistocene fauna is matched by the pattern typical of the large herbivore guild in regions of nutrient-poor savanna in Africa today (Bell, 1982). The relatively small body size of Australia's mammalian herbivore fauna is perhaps a reflection of widespread aridity. Australian habitats were altered following a drastic increase in burning around 38,000 yrbp following the arrival of humans, with sclerophyllous woodlands almost totally replacing rain forest over extensive regions (Kershaw, 1986).

African elephants at high densities can transform wooded savanna to open savanna, shrubland, or grassland within a few decades (Bourlière, 1965; Laws *et al.*, 1975; Thompson, 1975; Cumming, 1981; Owen-Smith, 1988). Although fire promotes open grassland conditions, elephants contribute significantly by suppressing woody regeneration (Dublin *et al.*, 1990). Within forests, elephants create and maintain open grassy glades, where other ungulate species congregate (Turkalo and Fay, 1995). Heavy grazing pressure by white rhinos and hippos transforms medium-tall grassland into extensive areas where lawnlike grassland predominates (Lock, 1972; Owen-Smith, 1988). As a result, fires are suppressed, promoting invasion by woody plants. The general result of megaherbivore feeding, trampling, and breakage is the creation of a mosaic interspersion of habitat patches characterized by rapidly regenerating relatively nutritious grasses, shrubs, or tree saplings.

However, Africa does not bear witness to the extreme effects that megaherbivores may exert on vegetation and landscapes, except in limited areas, because of historically widespread hunting, and continuing management culling of such species. Nowhere recently in Africa has there been a coexistence of both browsing and grazing megaherbivores at high abundance, except briefly in western Uganda (Laws *et al.*, 1975), eastern Zaire (Bourlière, 1965), and the Luangwa Valley of Zambia (Naylor *et al.*, 1973). The severity of the vegetation transformation associated with the co-occurrence of grazing and browsing pro-

boscideans, ground sloths, rhinos, and other large species through much of the Americas and northern Eurasia would have been more extreme than anything yet documented in Africa. Indeed, Zimov *et al.* (1995) propose that the transformation of the grassy mammoth steppe into the nutrient-deficient shrub tundra found in high northern latitudes today was largely a result of the demise of the grazing megafauna.

5. Interactions

Through attaining a body size exceeding the threshold of 1000 kg, megaherbivores largely escape carnivore predation on adults, at the demographic cost of birth intervals spanning 2 to 4 years (Owen-Smith, 1988, 1989b). Accordingly, maximum population growth rates vary from just over 6% per year for African elephants to 9–10% per year for rhinos and hippos (Owen-Smith, 1988). Harvests exceeding 3–5% per year would be sufficient to drive these populations into decline if sustained. For kudu (*Tragelaphus strepsiceros*), a 180-kg browsing antelope, annual mortality rates ascribed to predation in South Africa's Kruger National Park amounted to 7% per year for prime-aged females, and 12% per year for the overall population, under conditions of high resource abundance, despite the species not being a favored prey of any predator (Owen-Smith, 1990, 1993).

However small the initial founder numbers of humans in the Americas, the population of these hunters will have increased steadily in response to the abundant food resources encountered. With an annual growth rate of 3%, populations would double ten times within 250 years, i.e., 100 founders would end up as 100,000 descendants. Once humans had become sufficiently skilled predators of megaherbivores, it was inevitable that their offtake would eventually rise beyond the sustainable limit for these species having low rates of population increase. Notably, humans are unique in being the only omnivore that is also an effective predator, enabling their populations to be maintained even when prey became scarce. The onslaught by skilled and effective predators, in the form of human hunters, in effect breached the realized niche of megaherbivores.

Within Africa, elephant and rhino species had more time to evolve deterrent responses toward human hunters, until firearms breached this defense. Notably, the relatively inoffensive white rhino persisted precariously, being restricted to the remote southern and northwestern limits of nutrient-rich savanna within historic times. This contrasts with the abundance of this species in Pleistocene fossil deposits at Olduvai Gorge and elsewhere in east-central Africa. Teeth of seemingly modern white rhinos collected from surface deposits in Kenya (Hooijer and Patterson, 1972) suggest that the species survived there into the early Holocene, perhaps being eliminated by early Iron Age hunters. By the time Iron Age people armed with spears colonized southern Africa, they had large herds of livestock, and were no longer dependent on hunting for subsistence.

The prior Stone Age people occupying southern Africa seldom hunted animals above buffalo size (Klein, 1977, 1984b), although a rock painting depicts an elephant being attacked by hamstringing (Woodhouse, 1976). The benefits of killing very large animals are limited in tropical latitudes, because much of the meat would become rotten before it could be consumed by small bands of people. In tropical South America and Australia, this may have been counterbalanced by the great ease of hunting the naive fauna.

Extant megaherbivores are not numerically rare, contrary to common assumptions. White rhinos exhibited a regional density of 3.5 per km², with local densities exceeding 5 per km², in Umfolozi Game Reserve (Owen-Smith, 1988). African elephants (*Loxodonta africana*) attain regional densities of over 1 per km², and sustain local densities up to 3 per km² (Owen-Smith, 1988). Such densities are above those generally attained by kudus (*Tragelaphus strepsiceros*), a medium-sized browsing antelope widespread through most of southern Africa.

Coexistence of humans and megafauna for millennia does not preclude human involvement in later extinctions. Effective hunting of very large mammals may require appropriate technology, as well as conditions under which prey populations become vulnerable to extinction. A change in stone tool technology defining the transition from the Early to Middle Stone Age was roughly concurrent with the demise of *Elephas recki* and *Hippopotamus gorgops* in Africa, which may have taken place around the time of climatic change associated with the previous glacial–interglacial transition. The disappearance of *Palaeoloxodon* in southern Europe around 40,000 yrbp followed the appearance in the region of modern humans, who displaced Neanderthal hunters, and was coincident with the beginning of the coldest phase of the last glacial. The ancestors of the Aborigines arriving in Australia perhaps 50,000 yrbp may have lacked prior skills in hunting large open-country mammals, in contrast to the Amerindian ancestors colonizing the Americas toward the end of the last glacial. Accordingly, they may have required more time to become devastating predators.

Ascribing the disappearance of numerous smaller, fleeter, and potentially more rapidly reproducing ungulates solely to human predation is somewhat more problematic. Provided a species remains widely distributed, some populations are likely to persist beyond the range of predators. Habitat changes may have contributed to their demise through range contraction, thereby influencing also the timing of extinctions.

This is where the habitat changes consequent on the elimination of megaherbivores through human predation were probably influential (Owen-Smith, 1987, 1988). In particular, the transformation of the mosaic diversity typical of the Pleistocene into the zonal diversity of modern times (Guthrie, 1984; Graham and Lundelius, 1984) is what would be expected following the removal of the patch-scale effects on vegetation. Climate cannot sustain such small-scale diversity, except in mountainous or hilly terrain.

Without the ecosystem engineering by megaherbivores, grassy glades would revert to closed-canopy forest, while tree and shrub patches within grasslands would become eliminated by hot fires. Loss of local habitat diversity would be detrimental for the survival of medium-sized herbivores with restricted home ranges. Notably, most of the herbivore species becoming extinct in the Americas and Eurasia were open country grazers or browsers, likely to have been sedentary. Even the equids were typically short-limbed (Guthrie, 1984; Anderson, 1984). Surviving species are mainly woodland browsers (e.g., various deer), migratory grazers or low browsers (e.g., bison and reindeer/caribou), or inhabitants of mountainous terrain (various sheep and goats). In Australia, in contrast, extinctions took out most of the browsers, corresponding with the fire-induced change from forest to open woodland and savanna. The low magnitude of the late Pleistocene extinctions in Africa, involving some 10% of the large herbivore fauna, indicates the upper limit to solely climatically related extinctions, although even here human agency cannot be excluded (Klein, 1977).

6. Conclusions

Ecological transformations rarely have single causes. They are subject to contingencies, coincidences of events, interactions between factors, and multiplier effects (Walker, 1993). An ecologically sophisticated explanation must take cognizance of this, in explaining patterns that are richly complex in detail. Habitat changes surely contributed to extinctions of large mammalian herbivores in the late Pleistocene. The climatic shift at the end of the glacial period must have had a strong influence on habitat conditions. But its effects were drastically modified by the elimination of the disturbing influence of megaherbivores on vegetation, especially in the Americas. An increase in fire incidence through human agency may have contributed importantly in Australia. Thus, human presence, in various ways, was the decisive factor transforming a minor extinction pulse into a major extinction cascade.

The processes involved in the late Pleistocene extinction event still operate today. The numbers and distribution of surviving megaherbivores, plus various species of whale, decline progressively through human hunting, today largely for artifacts rather than meat. Populations of these and many other large mammals are isolated within the remnant habitats protected within designated wildlife parks. Global climatic change looms imminent. We may perceive the central involvement of humans in the sixth great extinction episode, but can we do much about it?

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