Megafaunal Extinctions: The Conservation Message from 11,000 Years B.P.

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Abstract: *At the end of the Pleistocene, the Americas, northern Eurasia, and Australia experienced a vast decline in large mammal diversity, while Africa and tropical Asia were hardly affected. The elimination of the megaherbivores (animals weighing > 1000 kg), probably by human predation, removed the vegetation impact of these species. The resultant reduction in habitat mosaic diversity and in forage quality probably precipitated the extinctions of lesser large mammalian species. Surviving megaherbivores in the form of elephants and rhinoceroses are currently being exterminated from many African conservation areas. African savanna ecosystems could prove more resistant to species losses than north temperate ecosystems, because geomorphic factors plus low and erratic rainfall enhance spatial heterogeneity and vegetation quality independently of large herbivore impact. Nevertheless, the history of the Hluhluwe Game Reserve in South Africa suggests that certain African ecosystems may become susceptible to an inexorable decline in populations of some large herbivores following the extermination of elephants. If elephants and rhinoceroses cannot be conserved, active habitat manipulation will be needed to retain a diverse fauna of large mammals in such regions.*

Resumen: *A fines del Pleistoceno, las Américas, el norte de Eurasia y Australia experimentaron una amplia disminución de diversidad en mamíferos grandes, mientras que Africa y Asia Tropical casi no fueron afectados. La eliminación de megahervíboros (animales que pesan más de 1,000 kg), probablemente por depredación humana, removió el impacto a la vegetación por parte de dichas especies.*

La resultante reducción en la diversidad de mosaicos de habitat y de la calidad de forraje probablemente precipitó la extinción de especies de mamíferos de menor tamaño. Los megahervíboros sobrevivientes, en forma de elefantes y a los rinocerontes, están siendo hoy, exterminados en muchas áreas de conservación africanas.

Los ecosistemas de savana africanos podrían ser más resistentes a la pérdida de especies que los ecosistemas templados del Norte, debido a que factores geomórficos y de precipitación baja e irregular promueven la heterogeneidad espacial y la calidad de la vegetación, independientemente del impacto de hervíboros grandes.

Sin embargo, la historia de Hluhluwe Game Reserve en Sudáfrica indica que algunos ecosistemas africanos podrían llegar a ser suceptibles a una decadencia inexorable en poblaciones de algunos hervíboros grandes, siguiendo la exterminación de elefantes.

Si no se puede conservar a los elefantes y rinocerontes, será necesario desarrollar un manejo activo de habitat para conservar una fauna diversa de mamíferos grandes en esa región.

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Introduction

At the end of the Pleistocene, c. 11,000 years B.P., a major loss in biotic diversity occurred over much of the globe. Over 60 percent of genera of large mammalian herbivores became extinct throughout North and South America, Europe, and northern Asia. Australia lost 40 percent of its large herbivore genera a few thousand years earlier. The extinctions of herbivores were associated with the disappearance of mammalian carnivores dependent upon the herbivores as prey, together with large scavenging birds. However, the species richness of small mammals, other birds, and insects was hardly affected. Africa and tropical Asia incurred only minor extinctions at this time, and have retained relatively intact the Pleistocene richness of their large mammal fauna (see Martin & Klein 1984).

Elsewhere I proposed that the extermination of the megaherbivores (species attaining an adult body mass > 1000 kg) by human hunters played a pivotal role in the extinctions of other large mammalian species during the late Pleistocene (Owen-Smith 1987). Elephants and rhinoceroses are currently being reduced to precariously low numbers in many African conservation areas by human killing, as a consequence of the high prices fetched by ivory and rhinoceros horn. I now consider the implications of this Pleistocene scenario for the conservation of Africa's large mammals, should elephants and rhinoceroses disappear from many of its national parks and other protected areas.

The Keystone Herbivore Scenario

Two alternative hypotheses have previously been invoked to explain the late Pleistocene extinctions of large mammals. One hypothesis emphasizes the consequences of climatic change and the associated vegetation transformations for habitat conditions, the other direct impact of predation by immigrant human hunters upon a naive prey community. Paleontologists have been almost equally divided in their support of these two hypotheses. The problem for proponents of climatic causation has been to explain why no similar wave of extinctions occurred at previous glacial-interglacial transitions. The problem for proponents of the human overkill hypothesis has been to account for the disappearance not only of those large mammals that were obvious prey of human hunters, but of a wide range of other species as well (see various papers in Martin & Klein 1984).

The "keystone herbivore" hypothesis (Owen-Smith 1987) invokes the elimination of megaherbivores by human predation as an important contributory cause of the habitat changes that occurred between the Pleistocene and the Holocene. Species over 1000 kg in body mass show maximum rates of population growth of 7–10 percent per annum. Hence their populations decline inexorably should losses due to human predation exceed this threshold.

Modern African elephants push over, break, or uproot trees, altering vegetation physiognomy and hence habitat conditions for other animal species. Trees killed by elephants are replaced by regenerating shrubs or grasses that offer more accessible foliage for consumption by smaller herbivores. The leaves of rapidly growing woody plants are less strongly defended chemically than those of the slower-growing trees they replace (Coley et al. 1985). Rates of nutrient recycling are also accelerated (Botkin et al. 1981). Grazing pressure from white rhinoceroses and hippopotamuses transforms medium-tall grasslands into a mosaic of short and tall grass patches. Short, creeping grasses are generally less fibrous and more nutrient rich than taller grasses. As a result of such vegetation changes, food quality is improved for smaller, more selective grazers. Animal species dependent upon a dense cover of woody vegetation or tall grasses for predator evasion may persist in areas of low impact. The mosaic diversity of habitats created by megaherbivore impacts on vegetation may be of crucial importance in promoting the coexistence of a wide diversity of other large herbivore species (see Owen-Smith 1988).

The fossil pollen record suggests that vegetation during the Pleistocene formed an open parkland with conifers, broadleaf hardwoods, grasses, and forbs intermingled over much of North America (Wright 1984). North of this in the periglacial region was a vast arid grassland stretching through Alaska into Siberia. The patchy diversity of this former vegetation has been replaced by the more uniform zonation of forests, prairie grasslands, and shrub tundra of today (Guthrie 1984). This transformation could be a consequence not so much of climatic change (which largely brings about latitudinal shifts in vegetation zones), but of the elimination of megaherbivore disturbance. Grazing megaherbivores in the form of mammoths, certain gomphotheres, and ground sloths, together with browsers such as mastodonts, other gomphotheres, and ground sloths disappeared from North America around the time of the appearance of artifacts documenting the arrival of skilled human hunters (Martin 1984).

Nevertheless, areas of open, diverse, nutrient-rich vegetation persist independently of megaherbivore impact in association with geomorphic disturbances. In northern Canada, grazing wood bison still occur in a predominantly coniferous forest region where deltaic and lacustrine sediments have promoted localized grasslands and meadows. With the disappearance of megaherbivores, medium-sized grazers may have become restricted to the spatially localized areas of such geomorphic features. These animals may have been un-able to penetrate the surrounding closed forests to follow the movement of vegetation zones that was the result of climatic amelioration. During previous glacial-interglacial transitions, populations of such species could have tracked suitable habitat conditions by following corridors of open nutrient-rich vegetation created by megaherbivores. Sedentary species would have been more vulnerable to sustained human predation than wide-ranging populations. Notably, the open country ungulates that have survived to the present day in North America and northern Eurasia tend either to migrate over large areas (e.g. bison, caribou, and saiga), or to move seasonally along altitudinal gradients (e.g., mountain sheep and elk). Browsing ungulates incurred fewer extinctions than grazing ungulates (Guthrie 1984).

Hence the keystone herbivore hypothesis suggests the following sequence of events. First, the arrival, in Europe and then the Americas, of human hunters skilled at killing very large mammals. Second, vegetation changes resulting from the elimination of megaherbivores, causing a reduction in patch diversity as well as a decline in general forage quality. Third, localization of populations of the more sedentary large herbivores to regions of geomorphic disturbance. Finally, such localized populations become vulnerable to habitat changes brought about by shifting climatic zones, and perhaps also become more susceptible to human predation.

African Savanna Ecosystems

Africa retains some 35 genera of large terrestrial herbivores, a vastly greater richness than that of any other region of the world today. This biogeographic contrast is due solely to the fact that Africa has kept its Pleistocene diversity, whereas other continents lost theirs. Paleontological records indicate about 54 genera of large herbivores in South America during the Pleistocene, and about 40 genera in North America. Europe was somewhat less diverse with only 20 genera, perhaps because of the barriers to north-south migration posed by the Alps and other mountain ranges during glacial-interglacial transitions. Australia was always relatively impoverished.

Africa differs from other continents geomorphologically in its extensive high-altitude interior plateau. This factor causes steep rainfall gradients and strongly seasonal climates, and hence promotes a greater expanse of savanna relative to forest than occurs on other continents. Furthermore, because of the uplifting and rifting that this plateau has undergone, an extensive area is underlaid by nutrient-rich volcanic deposits. Such regions include the East African plateau bordering the rift, where the most spectacular abundance of large herbivores persists today, as well as much of southern Africa, particularly those areas subjected to surface (basaltic) or fissure (doleritic) laval outpourings at the time of the breakup of Gondwanaland. Furthermore, the seasonal climates and relatively low rainfall over much of the plateau favor retention of soil nutrients against leaching.

African savanna ecosystems have been characterized as being highly resilient in response to disturbance (Walker & Noy-Meir 1982). Nevertheless, under conditions of sustained heavy grazing, with consequent suppression of fires, they may become transformed into persistent woody thickets (Walker et al. 1981).

The greater part of the savanna biome of Africa is made up of mesic dystrophic broadleaf ("miombo") woodlands, growing on nutrient-impoverished sandy soils derived from basement granitic rocks (Huntley 1982). In this region herbivore populations are typically concentrated around the grassy drainage depressions ("dambos") that dissect the plateau. These woodlands of *Brachystegia*, *Combretum*, or *Colophospermum* species are subject to drastic modification when elephants become concentrated within them. Closed canopy woodlands with an understory of relatively low, shade-tolerant grasses may be changed into open or shrubby woodlands with tall grasses up to 2 m in height, within less than a decade (Thompson 1975; Cumming 1981). Such tall fibrous grasslands may be even less attractive to grazing ungulates than the shaded understory grasses they replace. Nevertheless, grazing and trampling by megaherbivores as well as by buffalo herds, in combination with frequent fires, may result in a relatively high herbivore biomass. The Garamba Park in northern Zaire appears to contain an example of such a situation. This region, despite being underlain by basement gneiss, supported (until recently) a high abundance of elephant, buffalo, and white rhino in an open grassland environment (Bourliere 1965).

The vast concentrations of wildebeest and other migratory grazers in the Serengeti region of Tanzania and in southern Kenya are quite independent of megaherbivores for their nutrient-rich forage. The short-grass grasslands on the eastern plains are promoted by a surface layer of mineral-rich volcanic ash derived from the nearby rift volcanos, plus a claypan layer restricting water infiltration, and hence rooting depth for woody plants (Sinclair 1979). The wildebeest concentrations are furthermore able to graze down the taller grass of the wetter granitic areas into which they migrate seasonally. Nevertheless, the soils in this higher rainfall region are susceptible to invasion by *Acacia* trees in the absence of frequent fires. With fire incidence diminished due to the grazing impact of the wildebeest concentrations, the relatively small elephant population in the region may be playing an important role in checking woody plant invasion through their consumption of seedlings (Dublin 1984).

The arid eutrophic thorn savannas of northern Kenya and adjoining regions, and of southwest Africa, are also relatively little dependent upon megaherbivores for their open character and nutrient-rich grazing. Low rainfall alone limits woody plant density and favors soil nutrient retention. Nevertheless, certain regions of intermediate aridity may become dense shrub thickets in the absence of elephant disturbance. A notable example is Tsavo East in Kenya, where elephants transformed *Commiphora* thickets into open steppe. There is evidence from earlier patterns of human occupation that the region was formerly relatively open, suggesting that the thickets resulted from the extermination of elephants during the ivory trading era of the sixteenth to eighteenth centuries (Thorbahn 1984).

While the white rhinos persisting in the Umfolozi Game Reserve in South Africa show a strong preference for short grasses for most of the year, during the dry season they expand their grazing into surrounding regions of medium-height *Themeda triandra*–dominated grasslands. The result is the creation of a mosaic of short and tall grass patches in a region with moderate (700 mm) rainfall (Owen-Smith 1988). White rhinos formerly ranged far more widely through savanna Africa than their restricted distribution in historic times. They may have played an important role in diversifying medium-tall grasslands following the opening up of the tree stratum by elephants. Hippopotamuses have a similar impact on grassland structure, although their grazing effects are restricted to a relatively narrow fringe bordering the rivers or lakes that serve as their daytime refuges. Earlier in the Pleistocene, prior to about 130,000 years B.P., the effects of these two grazing megaherbivores were supplemented by a second species of elephant, *Elephas recki,* evidently specialized for a grass diet.

Because of the depression of elephant populations throughout most of Africa during the ivory trading era of the sixteenth to eighteenth centuries (Spinage 1973), few African ecosystems exhibit today the full impact elephants can have on woody plant communities. Even in areas where elephants apparently attained saturation densities (e.g., Tsavo in Kenya and Luangwa in Zambia), this situation did not persist for long before illegal hunting decimated the elephant populations. No African ecosystem today exhibits the combined impact of a browsing megaherbivore and a grazing megaherbivore both at saturation densities.

Conservationists have commonly perceived the vegetation "damage" caused by elephants, white rhinoceroses, or hippos to be adverse for other species. Hence both in southern Africa and in Uganda the responsible agencies have mounted culling operations to restrict or reduce populations of megaherbivores. However, declines among other ungulates in response to the vegetation changes brought about by megaherbivores have rarely been documented. In the Tsavo East region of Kenya, browsers, including black rhinoceros, declined in abundance following the opening up of shrub thickets by elephants, but black rhino losses were probably due mainly to increased exposure to poachers. In compensation, grazing ungulates such as oryx and zebra increased (Parker 1983). In contrast, in the Addo Park in South Africa, the entry of elephants into an area of previously undisturbed shrub thicket has led to increased numbers of smaller browsers such as eland and kudu, necessitating culling of the latter (Hall-Martin, personal communication). In the Umfolozi Reserve in South Africa, the expansion of the white rhinoceros population was associated with increases by other grazing ungulates, in particular wildebeest and zebra, although two species dependent on tall grass cover, reedbuck and waterbuck, declined.

Nevertheless, where dispersal is blocked by fencing or deterred by human disturbance, elephant destruction of trees coupled with fires suppressing regeneration may change vegetation so much that habitat diversity is reduced. This appears to have taken place at the Murchison Falls (Kabalega) National Park in Uganda (Laws et al. 1975). Today, however, only the elephant population in the Chobe National Park and environs in northern Botswana, plus the smaller ones in the Amboseli and Mara regions in Kenya, remain little affected by either management culling or illegal hunting. Destruction of the woodland fringing the Chobe River and elsewhere is a source of great concern among conservationists, but among large mammal species only bushbuck, a species occupying riverine thickets, appears to be adversely affected.

A Possible African Example

One southern Africa conservation area may illustrate what could happen to ungulate populations following the disappearance of megaherbivores. This is the Hluhluwe Game Reserve in Natal, which is connected to the Umfolozi Reserve by a corridor of unallocated land permitting wildlife movements over an area of 950 km^2. Hluhluwe differs from Umfolozi in receiving considerably more rain (960 mm at Hilltop camp) and in being more hilly. Both areas are underlaid by sedimentary shale and sandstone of the Karoo System, with doleritic intrusions. Elephants were eliminated from the region by hunters between 1850 and 1890 (Vincent 1970). From the 1930s on, when the first records were made, management authority has mounted a losing battle to halt the steady encroachment of forest and thicket into areas shown on early photographs to have been open grassland. Attempts to use fire and manual bush-clearing have failed to halt this trend, because herbivores grazed down the grasses appearing in any opened areas, thereby reducing fire intensity (Brooks & Macdonald 1983).

Populations of open country grazers such as wildebeest, zebra, waterbuck, and reedbuck reached peak levels during the early 1960s, but thereafter declined drastically (Fig. 1). Reedbuck have become locally extinct within the boundaries of the Hluhluwe Reserve, as have two initially uncommon small antelope species, steenbok and klipspringer. Among large grazers buffalo have maintained their numbers, while white rhino have steadily increased. Among browsers, bushbuck, kudu, and black rhino populations have declined, while impala and nyala have increased dramatically. Interestingly, impala did not occur historically in the area, being introduced from elsewhere during the 1930s, while nyala were rare and supplemented by introductions at the same time. The current prevalence of these two thicket-inhabiting species is a testimony to the degree of habitat transformation that has occurred.

The causes of the vegetation change at Hluhluwe are not simple to interpret, since many factors have been at work. The open, grassy conditions of the 1930s were maintained largely by frequent fires, a legacy of the former human inhabitants of the region. Herbivore populations increased to very high numbers partly due to the absence of lion, cheetah, and wild dog among large predators, although leopard and hyena remained common. The result was widespread overgrazing, which was exacerbated by drought conditions prevailing around 1950 and again during the late 1960s. The drainage

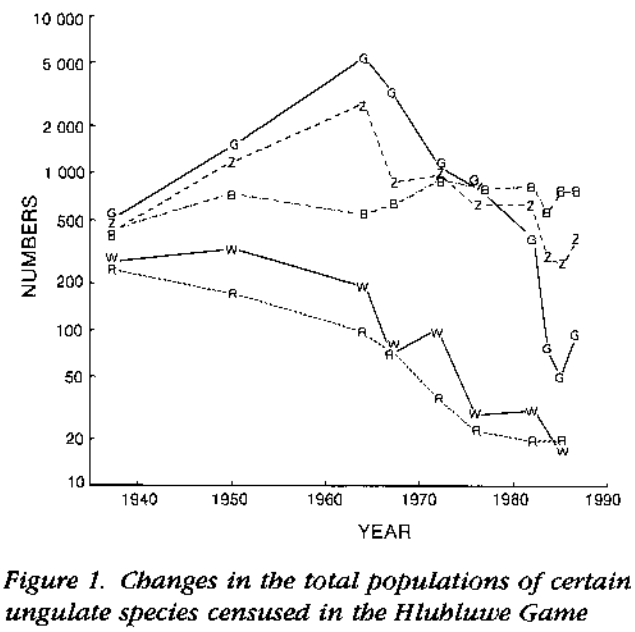

Figure 1. Changes in the total populations of certain ungulate species censused in the Hluhluwe Game Reserve plus adjoining northern section of the corridor. Population changes prior to 1982 from Brooks & Macdonald (1983). Subsequent population changes supplied by Trevor Sandwith (personal communication), from unpublished Natal Parks Board records. G = blue wildebeest, Z = plains zebra, B = African buffalo, W = waterbuck, R = reedbuck.

sump grasslands favored by reedbuck and, to a lesser degree, waterbuck, were adversely affected by gully erosion, which was largely a consequence of the high grazing pressure. Management culling of large ungulates was initiated during the 1950s and intensified during the 1960s. Large numbers of wildebeest were removed together with moderate numbers of zebra. The only removals of waterbuck were 72 animals taken out in 1970, while no reedbuck were removed. Culling of wildebeest and zebra was greatly curtailed during the 1970s, without halting their population declines (Fig. 1). Large-scale emigrations of wildebeest, zebra, and other species into Umfolozi Game Reserve took place during the 1960s, and may have continued thereafter in response to animal culling and the more favorable habitat conditions in Umfolozi. During the 1970s lions recolonized Hluhluwe Game Reserve, while cheetahs and African hunting dogs were reintroduced, so that increased predation must have exerted some further impact on ungulate populations (Brooks & Macdonald 1983).

The general interpretation has been that the increase in woody vegetation resulted from the overgrazing episode. However, two points need to be made. The first is that droughts and associated overgrazing are recurrent phenomena in African savannas. The second is that, once the trend towards woody vegetation was underway, it proved impossible to reverse it by any form of management intervention. The difference in the present circumstances in Hluhluwe Game Reserve, compared with the former situation, is that there have not, until very recently, been any elephants to exert a reverse impact on woody plants.

The management authority, the Natal Parks Board, has accepted the futility of their past attempts to control the expansion of woody vegetation in the Hluhluwe Reserve. In 1981 they took the step of reintroducing elephants into Hluhluwe, and in 1985 also into Umfolozi. At the time of writing nearly 100 elephants occur in the region. The experimental test of the keystone herbivore hypothesis in this particular region is underway, although it is likely to be decades before the outcome is clear.

Discussion

African savanna ecosystems may indeed be less susceptible to macrofaunal collapse than other continents because of basic features of physical geography, which promote extensive areas of diverse, nutrient-enriched vegetation. The one area in Africa where there seems to be clear evidence of adverse effects on ungulate diversity following the disappearance of elephants, Hluhluwe Game Reserve, is associated with relatively high rainfall and hence somewhat leached soils. Conditions of high rainfall and low soil nutrient status are more widespread in the low-lying tropical continents of South America and, to a lesser degree, of southern Asia, than in Africa. The regions of South America where semiarid eutrophic conditions prevail, the caatinga of northeast Brazil and the chaco of northern Argentina, are today closed thorny thickets rather than open savanna (Bucher 1982, 1987). In the middle latitudes of North America and Europe, high effective precipitation (reduced evapotranspiration due to low temperatures) is associated with relatively nutrient-rich soils due to the absence of leaching. Furthermore, soils are derived largely from fertile wind-blown loess, partly as a consequence of the continental glaciers to the north during the Ice Ages. Such regions tend to support closed forests in the absence of disturbance, except in the interior of the land masses where rainfall is diminished.

The Serengeti National Park, and other parks on the East African plateau in proximity to rift vulcanism, are unlikely to lose their large mammal diversity as a consequence of megaherbivore disappearance. In South Africa, the Kruger National Park has retained a high diversity of ungulates despite past near-extermination of elephants and rhinos and a current management policy that places a ceiling on the maximum number of elephants. Nevertheless, wildebeest and zebra numbers are vastly lower here than they are in Serengeti, and persistently small populations of certain antelope species are a source of concern to managers (notably roan and sable antelope, and tsessebe, species typically associated with granitic landscapes; Pienaar 1974). Other parks in miombo woodland regions have retained a diversity of ungulates despite relatively low numbers of elephants—for example, Kafue National Park in Zambia and Kasungu National Park in Malawi (Bell 1981). In these parks herbivore numbers are relatively low overall, with animal biomass concentrated on floodplains or around grassy dambo depressions.

Where herbivore numbers are low, repeated fires may maintain a relatively open vegetation physiognomy. Nevertheless, elephant numbers were high in some of these parks in the relatively recent past (little more than a century ago), and it may be only a matter of time before adverse woodland thickening takes effect. Perhaps the only agents able to reverse such a habitat change, by persistent disruption of the woody canopy allowing penetration of grasses, hence fire, are elephants or similarly large browsers (in the absence of humans).

However, persistent elephant disturbance coupled with fires may lead ultimately to the disappearance of the tree component of savanna vegetation, reducing habitat diversity. Locally severe grazing by white rhinos, hippos, and in the past mammoths and other primarily grass-feeding megaherbivores, may create fire-free zones where woody seedlings can become established, as well as a mosaic of different grassland forms. Thus the combined influence of grazing and browsing megaherbivores may be needed to produce a structurally diverse savanna that persists in the absence of fire. Medium-sized grazers like wildebeest and buffalo may have a similar effect where they occur in large concentrated herds. How far the trend towards closed woody communities progresses depends on factors such as rainfall and grazing pressure. Even in the absence of elephants, areas too far from water for sustained grazing pressure may show open savanna conditions maintained by fire.

The importance of megaherbivore impacts on vegetation for biotic diversity is not restricted to savanna regions. In dense evergreen forest in central Africa, elephants promote favorable habitat conditions for gorillas and a range of forest ungulates by creating, maintaining, and enlarging treefall gaps and clearings (Carroll 1988).

Conclusions

The consequences of megaherbivore elimination for faunal diversity in African ecosystems remain uncertain and speculative. Monitoring the consequences of the elephant introductions in the Hluhluwe and Umfolozi reserves, and of leaving elephants unculled in Chobe National Park and other areas where elephant populations tend towards saturation densities, could provide experimental tests of the keystone herbivore hypothesis; but it will be some time before results are forthcoming, and other events may intervene. The fact of the collapse in large mammal diversity elsewhere in the world at the end of the Pleistocene remains, and neither climatic change nor human overkill scenarios have satisfactorily explained the features of this extinction episode. In the face of this uncertainty, how should we proceed with our conservation actions?

Should we allow megaherbivore extermination to proceed in Africa as an alternative replicated experiment to test the keystone herbivore hypothesis—as seems to be happening inevitably due to the ineffectiveness of past conservation actions? It seems that a more cautious standpoint, based on the philosophy of minimum regret, would be advisable.

First, strenuous efforts should be directed toward maintaining populations of elephants and rhinos where they still persist despite the pressures of illegal hunting. These megaherbivores may have far more important functions than just serving as standard-bearers for the ecosystems they inhabit. The ability of savanna ecosystems to maintain large, viable populations of many other species may in the long term depend on the interactive impacts of these very large animals on vegetation physiognomy.

Second, where megaherbivores are absent, a laissez-faire management policy allowing "nature" to take its course cannot be upheld, since habitat changes may follow quite different trajectories from those of earlier times. For instance, without elephants frequent hot fires may be essential to maintain the open state of woodlands. Where woody saplings have become established, manual or mechanical thinning may be needed to replace former elephant breakage and thereby hasten the progression towards mature, open woodland. To restore open savanna conditions after closed woodlands have formed and suppressed the intensity of fires, more drastic intervention may be needed. For example, bush removal is currently being carried out in certain private nature reserves bordering the Kruger National Park, apparently with some success. This bush clearing is restricted to the seepling zone in granitic landscapes, where it was predicted that clearing would recreate the soil waterlogging that had formerly maintained an open grassy zone, prior to overgrazing. Experiments involving the use of chemical herbicides and fire following manual cutting of trees are currently in progress in Hluhluwe Game Reserve, and show improved success in opening up thickets now that grazing pressure has been reduced.

In other situations management culling aimed at limiting the vegetation impact of expanding megaherbivore populations may be misdirected. The opening up of woodlands by elephants, or of tall grass cover by white rhinos, could promote increased rather than reduced faunal diversity. A suggestive example can perhaps be drawn from the Kruger Park, where the roan antelope population has failed to increase beyond 250–300 animals, despite research efforts and veterinary intervention. Roan are known to favor relatively open vegetation in Kruger, as well as elsewhere in Africa. Such habitat conditions are currently restricted in their occurrence in the Kruger Park. Allowing elephants to exert their full woodland clearing impact in regions of the park where roan occur might enhance the population status of the roan remnant. In the Umfolozi Reserve, regions where white rhino grazing pressure had maintained short grass conditions provided an important habitat refuge for other grazing ungulates during a period of high rainfall (Walker et al. 1987).

In the long term, the greatest threat to current conservation efforts lies in the climatic changes that are inevitable, and may even be under way due to anthropic influences on carbon dioxide, ozone, and other atmospheric constituents. The ability of populations of large mammals to adjust their distributions in response to shifting habitat conditions is currently being drastically restricted by the impermeable boundaries generally set around conservation areas. Far from being sentimental anachronisms, megaherbivores such as elephants and rhinoceroses may be essential agents in modifying vegetation patterns to maintain suitable habitat conditions for other threatened species, against the forces of climatic change. If actions aimed at halting the losses of elephants and rhinos prove futile, the problems of preserving the full richness of the large mammal fauna that has persisted to the present day in many African parks and wildlife reserves may prove ultimately insuperable.

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