AFRICA AND PLEISTOCENE OVERKILL

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A harvest of almost twenty years of radiocarbon dates, the increasing use of pollen analysis in the investigation of Pleistocene faunas, and new information on the faunas themselves, have rejuvenated interest in Pleistocene extinction. The enduring problem which fascinated Darwin, Wallace, Lyell, Owen, Cuvier, and other naturalists in the 18th and 19th centuries can be re-examined in the light of recent findings[1].

In continental North America north of Mexico, thirty-five extinct genera of large mammals and one genus of reptiles characterize Late Pleistocene deposits (see Table 1). Their disappearance is among the criteria often used to define the boundary between Pleistocene and Recent in North America. Only on oceanic islands did Late Pleistocene extinction affect small vertebrates. Some 100 radiocarbon dates in various degrees of association with remains of extinct mammoths, mastodons, sloths, horses, camels, and other large mammals indicate that the extinction occurred at the end of the last episode of continental glaciation. The time at which each species vanished is crucial; it should reveal the pattern in which extinction occurred and, one hopes, its cause. So far, there is no clear-cut case of the extinction of any of the North American genera of the Rancholabrean fauna (listed in Table 1) before 15,000 B.P. or after 6,000 B.P. (see Martin in ref. 1). Within this interval of 9,000 years there is much chronological evidence to suggest that, rather than being uniformly or randomly distributed, the lost genera disappeared suddenly soon after the first arrival of fluted-point hunters who had spread their distinctive stone tools rapidly from coast to coast by roughly 11,000 years ago.

Table 1. North American Pleistocene Megafauna exceeding 50 Kilograms*

Order	Irvingtonian + Blancan extinction	Rancholabrean extinction (last 15,000 years)	Living (1·5–2 million years)
Edentata	*Glyptotherium* *Glyptodon*	*Megalonyx* *Nothrotherium* *Paramylodon* *Eremotherium* *Boreostracon* *Brachyostracon* *Chlamytherium*	
Carnivora	*Borophagus* *Ischyrosmilus* *Chasmaporthetes*	*Arctodus* *Smilodon* *Dinobastis* *Aenocyon* *Tremarctos* †	*Euarctos* *Ursus* *Felis* *Panthera* *Canis*
Proboscidea	*Rhyncotherium* *Stegomastodon*	*Mammut* *Cuvieronius* *Mammuthus*	
Artiodactyla	*Pliauchenia* *Titanotylopus* *Hayoceros* *Platycerabos*	*Platygonus* *Mylohyus* *Camelops* *Tanupolama* *Sangamona* *Cervalces* *Capromeryx* *Stockoceros* *Tetrameryx* *Bootherium* *Symbos* *Euceratherium* *Preptoceras* *Saiga* † *Bos*	*Cervus* *Odocoileus* *Oreamnos* *Ovibos* *Ovis* *Rangifer* *Antilocapra* *Bison* *Alces*
Perissodactyla	*Nannippus* *Plesippus*	*Equus* † *Tapirus* †	
Rodentia		*Castoroides* *Neochoerus* *Hydrochoerus* †	
Reptilia (Testudinata)		*Geochelone* †	
Total	13	36	14

* Adapted from Hibbard *et al.* (ref. 8).
† Living species surviving south of the United States or in Eurasia.

Even in arid America, fossil pollen and other palaeoecological evidence fails to show any obvious defect in range carrying capacity at the time of extinction[1]. A major vegetation shift accompanying climatic warm-up and the retreat of the Wisconsin ice sheet was drawing to a close. But there must have been many earlier and similar shifts in the Pleistocene, and yet there was no major decline in the megafauna during or after the earlier glaciations. The failure to find evidence of environmental upset strengthens the proposal that extinction in the Americas was triggered in some unknown way by the arrival of prehistoric hunters and would not have occurred without this intervention of human beings (see articles by Martin and Edwards in ref. 1).

Among the objections raised by Eiseley and others[2] to the hypothesis that prehistoric man was the single basic cause of New World extinction is the example of Africa. If Early Man was responsible for the destruction of the New World fauna, the argument goes, why did the evolving hominids leave the African fauna intact during their evolutionary development over more than a million years[2]? The impressive diversity of African big game has apparently led some scientists to assume that there could have been no additional extinct Pleistocene fauna associated with the living one. But there was. Hopwood and Hollyfield[3] list 50 extinct genera for the Pleistocene of Africa up until 1950. More than half the extinct African genera are recorded from the latter part of the Pleistocene when they coexisted with virtually all the living genera and with Acheulean hunting cultures (Table 2).

It seems almost unbelievable, but the African game plains presently contain only about 60 per cent of the genera of large mammals encountered in the hand-axe faunas (see Tables 2 and 3). According to Ewer and Cooke[4] "If a modern naturalist were to return to this period he would probably find himself somewhat confused at first. At one moment he would be quite at home, able to identify every mammal he saw; the next, his confidence would be rudely shaken as a totally unfamiliar beast, a sabre-tooth or a giant buffalo, a pig or a giraffid belonging to an extinct genus, met his view." The ecological implications in terms of hypothetical empty niches in the African game plains are intriguing, but are not the subject of this account, which is concerned mainly with matters of chronology.

The list of extinct African genera of large mammals (those estimated to exceed 50 kg adult body weight) in Table 2 was assembled from Cooke's recent, comprehensive review[5]. Although preferable in certain respects, an attempt at a list of species would founder on many unresolved and perhaps unresolvable systematic problems. New fossil genera will undoubtedly be discovered and described, others will be taxonomically submerged, some elements of the Middle Pleistocene fauna may be found to be Late Pleistocene survivors, and certain Villafrancian genera will undoubtedly also be found in younger deposits, but it is nevertheless clear that the African extinction record involves a major reduction comparable with the extinction pattern of the later Pleistocene of other con-

Table 2. African Pleistocene Megafauna†

	Part *A* Villafrancian and Early Middle Pleistocene (1·0–2·0 million years)	Part *B* Late Middle Pleistocene extinction (last 100,000 years)	Part *C* Living genera
Primates	*Gorgopithecus*	*Simopithecus*	*Pan*
	Dinopithecus		*Gorilla*
	Cercopithecoides		*Mandrillus*
	Australopithecus		
	Paranthropus		
	Telanthropus		
	Parapapio		
Carnivora	*Lycyaena*	*Machairodus*	*Actinonyx*
	Meganteron		*Panthera*
	Homotherium		*Hyaena*
			Crocuta
Tubulidentata			*Orycteropus*
Proboscidea	*Anancus*	*Archidiskodon*	*Loxodonta*
	Stegodon	*Gomphotherium*‡	
	Deinotherium		
Perissodactyla	*Metaschizogherium*	*Stylohipparion*	*Equus*
	Serengeticeros	*Eurygnathohippus*	*Diceros*
			Ceratotherium
Artiodactyla			
Suidae	*Potamochoerops*	*Potamochoeroides*	*Potamochoerus*
	Omochoerus	*Mesochoerus*	*Sus*
		Notochoerus	*Phacochoerus*
		Tapinochoerus	*Hylochoerus*
		Stylochoerus	
		Metridiochoerus	
		"*Kolpochoerus*"	
		Orthostonyx	
Hippopotamidae			*Hippopotamus*
			Choeropis
Camelidae		*Camelus**	
Cervidae		*Megaceroides*	*Cervus*
Giraffidae		*Libytherium*	*Giraffa*
			Okapia
Bovidae	*Pultiphagonides*	*Homoioceras*	*Tragelaphus*
	Numidocapra	*Bularchus*	*Boocercus*
		Pelorovis	*Taurotragus*
		Lunatoceras	*Syncerus*
		Megalotragus	*Cephalophus*
		(Gen. nov. 1)	*Kobus*
		(Gen. nov. 2)	*Redunca*
		Makapania	*Hippotragus*
		Phenacotragus	*Oryx*
			Addax
			Damaliscus
			Alcelaphus
			Beatragus
			Connochaetus
			Aepyceros
			Litocranius
			Gazella
			Capra
			Ammotragus
Total	19	26	40

* Living species surviving in Eurasia.
† Adapted from Cooke (ref. 5) and including mammals estimated to exceed 50 kg body weight.
‡ According to Clarke (personal communication) *Gomphotherium* in the Vaal River gravels may be derived from an older outcrop, possibly Pliocene.

tinents. In Africa as in North America, the extraordinary record of generic extinction so late in the Pleistocene has been hard to believe. On the assumption that a large number of extinct genera in a fossil deposit must indicate a considerable age, some palaeontologists have apparently been led to "back date" their faunas. For example, Cornelia, now regarded as belonging to the Middle Pleistocene by Cooke[5], was considered of Pliocene age by van Hoeppen.

The difference in rate of generic extinction between the end and the rest of the Pleistocene deserves further consideration. As already noted, in America 35 genera of large mammals disappear at the end of the Rancholabrean, most of them apparently within the last 12,000 years. In the preceding one or two million years, only 13 genera of large mammals were lost—a difference that can be ascribed only in small part to our less adequate knowledge of the older faunas. In Africa the difference between earlier and later Pleistocene faunas seems less striking until some thought is given to the time involved. In the first 1·5 million years, 19 large mammalian genera were lost but within roughly the last 100,000 years, at least 26 genera have disappeared—a rate at least twenty times greater.

Exactly when did the last wave of extinction occur in Africa? How may it be compared with late Pleistocene extinction in the Americas? At sites such as Olduvai (Bed *IV*), Olorgesailie, Kariandusi, Hopefield, Ismilia, and the Vaal River gravels, most of the list of genera in Part *B*, Table 2, are found in stratigraphic association with Acheulean artefacts. The artefacts are typified by large hand-axes and cleavers. In addition, there are bifacial knives, a variety of stone tools for scraping, boring, and grooving, and heavy duty picks, choppers, scrapers, polyhedral stones (assumed by some to have been thrown as bolas) and other crude bifacial and large flake tools[6]. After this generalized culture of intercontinental distribution, there develop the more specialized Sangoan-Fauresmith-Levallois/Mousterian cultures which lead in Africa into the Middle Stone Age[6]. Of the extinct genera, only three—*Camelus*, *Megaceroides*, and *Homoioceras*—are known to disappear long after the end of the Acheulean in the Middle or Late Stone Age[5]. The first two were never part of the extinct sub-Saharan faunas. In spite of profound ecological changes brought about by the prehistoric spread of agriculture, the adoption of iron weapons and ultimately the intrusion of western civilization itself, no generic extinction is known to have occurred in Africa in the last 1,000 years.

The terminal age for the extinct fauna may be inferred from its association with the hand-axe cultures. Radiocarbon and potassium-argon dating have both been attempted for the Late Acheulean with discordant results[7]. The Late Acheulean must be somewhat older than the 19,000–40,000-year ages on Stillbay obtained repeatedly by radiocarbon dating[6]. On the basis of carbon-14 dates at Kalambo Falls, Clarke[6] places the final Acheulean at about 50,000 B.P. Although the uncertainties of the carbon-14 method require that samples should be virtually free from contamination if finite dates greater than 30,000 years are to be accepted with confidence, the age of 50,000 years assigned to the final Acheulean by Clarke is strongly supported by archaeological evidence by the theoretically more reliable dates of slightly younger cultures.

Table 3. Summary of Mammalian Megafaunal Extinction and Survival*

	Africa	U.S.A. + Canada
(1) Living genera (50 kg)	40	14
(2) Later Pleistocene extinction	26 +	35
(3) Earlier Pleistocene extinction	19	13
(4) Normal Pleistocene megafauna (rows 1 and 2)	66 +	49
(5) Later Pleistocene Extinction intensity (Row 2/Row 4)	39 per cent	71 per cent

* Data from Tables 1 and 2.

Exactly when such distinctive Middle Pleistocene genera as the baboon *Simopithecus*, the horse *Stylohipparion*, the pigs *Notochoerus* and *Tapinochoerus*, the giraffid *Libytherium*, and the giant sheep *Pelorovis* disappeared remains to be determined. Because of problems in fixing dates greater than 40,000 years, the African extinction chronology may never be known with the same precison as the extinction chronology of North America. The most that can be inferred at present is that there is a temporal association of the Middle Pleistocene fauna with the Chellean-Acheulean, together with the fact that the extinct animals (other than *Homoioceras*) have nowhere been found in association with cultures dated at less than 40,000 years by the carbon-14 method.

The fact that faunal upset in North America lagged by tens of thousands of years must be explained in any extinction analysis. At the time the hand-axe fauna disappeared in Africa, North America was experiencing faunal enrichment with the arrival across the Bering Bridge of Eurasian genera of Arcto-Boreal adaptations such as *Rangifer*, *Saiga*, *Oreamnos*, *Ovibos*, *Ovis*, *Bos*, and *Alces*[8].

In contrast with the history of the megafauna, the principal vegetation changes in the Late Pleistocene of

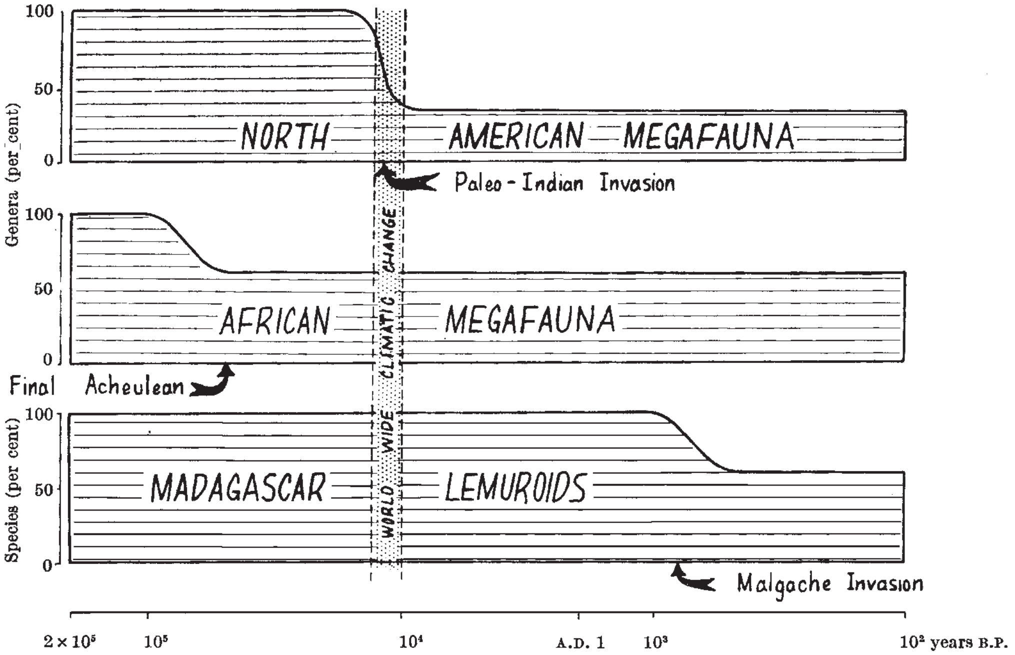

Fig. 1. Extinction chronology showing percentage reduction of Pleistocene animals in three parts of the world. In each case a major cultural change accompanies extinction. Time scale is logarithmic.

Africa and the Americas seem to be comparable in age and in magnitude. There is now substantial evidence for a major upward shift in montane forest and alpine zones about 12,000 years ago[9], at about the same time as the upward movement of montane forest in Andean regions occupied by paramo roughly 20,000 years ago[10]. Those African pollen diagrams which are assigned by carbon-14 dating to the last 20,000 years show a marked shift of many montane species and presumably imply a major change in climate during the late-glacial. One cannot conclude that Africa was sheltered from Pleistocene climatic change.

This point bears directly on the question of Pleistocene extinction. Those who hold that climatic change is the chief cause of faunal extinction in the Americas have claimed that the events of the last glaciation were unique, that climatic stress was greater in the late Wisconsin than at any previous time in the Pleistocene (see Slaughter and Guilday in ref. 1). But the one marked shift in vegetation zones now known from late-glacial pollen records in both Africa and America is accompanied by catastrophic extinction only in America (Fig. 1).

In Africa, as in arid parts of the New World, certain authors have regarded drought as the cause of Late Pleistocene extinction[11]. The drought hypothesis seemed slightly more plausible when the Acheulean of Africa was correlated with the last interglacial and was not recognized as extending into the time of early Würm–Wisconsin glaciation. The drought hypothesis can be questioned on two grounds. First, it is *ad hoc*. If, under an increasingly arid climate, large animals found the local range completely unsuitable, what prevented their emigration, either seasonally or permanently, to a more suitable habitat ? The famous 800-mile annual migration of certain wildebeests from the arid Serengeti Plains to the humid shores of Lake Victoria and back is a case in point[12]. Second, if a unique catastrophic drought or other environmental upset of continental proportions decimated the Pleistocene fauna in both Africa and the Americas, why was the timing not synchronous ? Why did not at least a few genera of large mammals in North America die out during the middle of the Rancholabrean ? Why did not at least a few of the surviving African genera perish in the late-glacial warm-up 11,000 years ago ?

Timing is even more critical in the case of Madagascar. In this island of 588,000 square kilometres separated by an average distance of 410 km of open ocean from Africa, there are, in addition to a highly endemic living fauna, some 16 extinct genera of vertebrates, many extremely common in fossil faunas of the island (Table 4). Precise carbon-14 dating of the deposits has hardly begun, but there is no evidence—either radiometric or stratigraphic—to suggest extinction that might correspond with extinction of the hand-axe fauna in Africa or with the late-glacial faunas of North America (Fig. 1).

Table 4. EXTINCT GENERA OF MADAGASCAR

Aves	Palaeognathae	*Aepyornis* *Mullerornis*
	Anseriformes	*Centrornis* *Chenalopex*
	Falconiformes	*Accipiter*
	Gruiformes	*Triboynx*
Mammalia,	Artiodactyla	*Hippopotamus*
	Muridae	*Majoria*
	Megaladapidae	*Megaladapis*
	Indriidea	*Palaeopropithecus* *Mesopropithecus* *Neopropithecus* *Archaeoindris* *Archaeolemur* *Hadropithecus*
	Tubulidentata	*Plesiorycteropus*

Most of the genera of extinct vertebrates are known from sites associated with artefacts in deposits of late post-glacial age. While the cultural history of the island is poorly known, no trace of Acheulean or Middle Stone Age artefacts has been found. Faunal extinction apparently occurred only within the last thousand years, after Melanesian invasion (see Battistini and Verin in ref. 1).

Thus the chronology of extinction—first in Africa, second in America, finally in Madagascar—and the intensity of extinction—moderate in Africa, heavier in America, and extremely heavy in Madagascar where it affected much smaller species than on the continents—seems clearly related to the spread of human beings to their cultural development, and to the vulnerability of the faunas they encountered (Fig. 1).

There are certain other apparently incongruous features of the later Pleistocene that may be credible if they are examined in terms of the admittedly provocative hypothesis of prehistoric overkill. For example, Pleistocene faunas are renowned for their large size. They are frequently regarded as illustrating the phenomenon of gigantism. The cause of "gigantism" is a matter of speculation, sometimes held to be the result of hypertrophy of the pituitary, a surplus of trace elements, or a response to cooler Pleistocene climates with increases of size in accordance with Bermann's rule. But it may be that the small size of the Pleistocene survivors and not the large size of their predecessors is the unusual condition. If we assume that normal Cenozoic selection pressures favoured large herbivores, it is possible to regard the modern and post-glacial fauna as exhibiting nanism, an artificial dwarfing imposed by selective hunting of prehistoric man. Left to itself, natural selection in a non-hominoid ecosystem would favour redevelopment of the giant species. The advantage of smaller size in the face of human predation presumably lies in the more rapid reproductive rate and the better chance of concealment. Certain morphological features such as the protruding orbit of *Hippopotamus gorgops* suggest a more conspicuous habit for an extinct species.

Without knowing more about the essentially unknowable life histories of the extinct species, it seems impossible to learn why they perished and others survived. But in the case of the lemuroids of Madagascar, Walker (see ref. 1) has made some revealing inferences. Based on morphology and presumed locomotor habits, Walker concludes that 14 species of extinct lemurs, megaladapids, and indriids were relatively large, probably all diurnal, often terrestrial, and relatively sluggish. The 20 living species are smaller, often nocturnal, and can be divided into active arboreal quadrupedal and active arboreal leaping forms. Both living and extinct species are found together in sub-recent deposits of the island. It seems that the habits of the extinct lemurs would have made them excessively vulnerable to human predation. The fact that animals the size of an Alsatian dog or smaller were lost in the wave of extinction sweeping Madagascar may be attributed to the fact that until 1,000 years ago the fauna was protected not only from man but also from advanced carnivores of virtually all kinds.

But where the continents are concerned, why should generic extinction of large mammals be less intense in the later Pleistocene of Africa, with roughly 40 per cent of the fauna lost in the last 100,000 years, than in North America, with roughly 70 per cent lost ? I have pointed out the total lack of any synchronous extinction pattern in Africa and America that may have been related to worldwide climatic change. If prehistoric man was the main factor in Pleistocene megafaunal extinction, one would expect the fauna of the newly invaded continent to be affected more markedly than that of a region in which hominids evolved throughout the Pleistocene, finally developed a variety of tools and, presumably, a variety of hunting techniques. In comparison with Africa, the American fauna must have lacked the simplest behavioural defences against human predators, a point indirectly considered by Darwin and recently re-examined by Jelinek and Edwards (see ref. 1).

For the earlier Pleistocene, it is important to know why generic extinction seems heavier in Africa, the vertebrate faunas of which are not so well known as those of North America (line 3, Table 3) ? Dart has asserted that the depredations of the Australopithecines ". . . were probably insufficient, despite their lengthened life span, to make serious inroads upon the stupendous faunal reserves of Early Pleistocene Africa" (see ref. 4, p. 64). But the number of extinct genera, 19 in the pre-hand-axe Pleistocene megafauna compared with 13 known from the Blancan and Irvingtonian of North America, suggests an excessive loss in Africa; this is certainly true among the larger primates, which include seven extinct genera. Would this loss have occurred in the absence of the Australopithecines ?

Turning to a much younger cultural problem and as a final speculation, I would suggest that the survival of a diverse plains game fauna in Africa south of the Sahara may account for the remarkable lag in Neolithic agriculture in that part of the globe. In the absence of vast herds of large mammals in the flood plain fields, the domestication and widespread adoption of crop plants was possible at an early date in the Near East and the Americas. The destruction of New World large mammals 11,000 years ago not only may have hastened, through necessity, the first casual experiments of Early Man with plant foods, but may also have made available the essential untrampled and ungrazed flood plain habitats where domestication began.

In conclusion, the circumstance of a relatively homogeneous hand-axe culture abundantly distributed throughout Africa and disappearing together with some 26 extinct genera roughly 50,000 years ago is quite provocative. Unbalanced megafaunal extinction is encountered in the fossil record only from that part of the Pleistocene when Stone Age hunters or younger cultures are also known. The extinction pattern matches no known world-wide climatic upset. Only on islands were small genera of animals lost. These facts, together with the evidence of strong selection for smaller size and cryptic habits at the time of extinction, point toward prehistoric overkill as the main cause. Above all, the inference of no extinction in the later Pleistocene of Africa, cited by Eiseley and others[2] as evidence against the hypothesis of culturally caused extinction in the New World, must be rejected in view of the palaeontological record.

The overkill hypothesis is likely to continue to provoke serious and perhaps unanswerable objections. But until a continent or island can be found in which a major wave of Pleistocene megafaunal extinction clearly pre-dates the arrival of human beings, the hypothesis stands unrefuted on chronological grounds.

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