

man. If one adopts all Dr Leakey's suggestions for updating or factually improving the African list of extinct mammals, the net effect is trivial—an increase in the number of living large genera from forty to forty-one, an increase in later Pleistocene extinction from more than twenty-six to more than twenty-nine genera, a decrease in earlier Pleistocene extinction from nineteen to eighteen genera, and an overall change in the amount of later Pleistocene megafaunal extinction in Africa, as computed in Table 3, ref. 2, from thirty-nine to forty-one per cent. I do not see how the omission of the genera Leakey adds to the Early Pleistocene group "... puts the whole picture out of balance"¹.

As the richest single stratified fossil deposit representing the time interval in question the Olduvai record deserves special consideration. Leakey³ reports twenty-one extinct genera of large mammals, presumably all from the living floors or camp sites of prehistoric man at Olduvai, five last recorded in the Upper Villafrancian, six in the Early Middle Pleistocene in strata associated with Chellean tools and ten surviving to the time of Bed IV, the unit associated with Acheulean artefacts of the late Middle Pleistocene (Table 1). Evidence of Acheulean association elsewhere indicates that at least four of the Bed II extinct genera from Olduvai, namely *Mesochoeerus*, *Orthostonyx*, *Phenacotragus*, and a machairoidont, may be considered contemporaries of the hand-axe fauna of Bed IV. Because Leakey reports that less is known about the fauna of Bed IV than about that of Bed I and II (ref. 3), they may yet be found. Clearly, generic extinction during the time of the hand-axe hunters far outstrips extinction during any earlier interval yet known in the African Pleistocene. How is it to be interpreted?

Table 1. LAST OCCURRENCES OF EXTINCT LARGE MAMMALS (> 50 KG) FROM OLDUVAI GORGE²

Upper Villafrancian (Olduvan Culture)		Middle Pleistocene	
Bed I		Bed II Upper (Chellean)	
CHALICOTHERIIDAE		MACHAIRODONTINAE†	
	<i>Ancylotherium</i> *		<i>gen. indet.</i>
SUIDAE	<i>Ectopotamochoerus</i>	SUIDAE	<i>Mesochoeerus</i> †
	<i>Promesochoeerus</i>		<i>Orthostonyx</i> †
	<i>Pronotochoerus</i> *	BOVIDAE	<i>Pultiphagoides</i> *
Bed II Lower			<i>Phenacotragus</i> †
DEINOTHERIIDAE:			<i>Pelorovis</i>
	<i>Deinotherium</i>	Bed IV (Acheulean)	
		CEROPITHECIDAE	<i>Simopithecus</i>
		EQUIDAE	<i>Stylohipparion</i>
		SUIDAE	<i>Notochoerus</i>
			<i>Tapinochoerus</i>
			<i>Afrochoerus</i>
		GIRAFFIDAE	<i>Libytherium</i>
		BOVIDAE	<i>Thaleroceros</i> *
			<i>Parmularius</i>
			<i>Xenocephalus</i> ²
			<i>Bularchus</i>

* Rare (three individuals or less).
† Acheulean association elsewhere.

Dr Leakey regards drought as the cause of African extinction^{1,3,4}. If so, it was the first catastrophic drought to strike the African fauna, and while one must believe it affected the entire continent, it was unique to Africa, an event that left no obvious mark on the megafauna of the time in other areas including Madagascar.

In his book on Olduvai, Leakey takes a restrained position on the palaeoclimatic meaning of extinct mammals³: "... it is not generally recognized that many of the larger mammals are remarkably adaptable... While zebra and giraffe are most commonly found in savannah and open plains with scattered thorn bush, they can also be found well within tropical forest zones such as those bordering Lake Manyara. These few examples serve to show how unwise it is to regard the usual habitat of large mammals as necessarily constant. If the habitat of large living mammals, belonging to a single species, varies so widely it is clear that the presence of extinct fossil species—even if related to the living forms—cannot be used as a basis for deducing ecological or climatic conditions." Thus in attributing the extinction of large

mammals of Bed IV to drought, Leakey ignores both his own advice and also the present distribution of East African mammals. Five of the largest species, elephant, hippopotamus, black rhino, giraffe, and buffalo, all occupy (or did in historic time) the desertic shores of Lake Rudolph, a region of under 250 mm rainfall, one of the driest parts of equatorial Africa.

I do not wish to deny the likelihood of droughts at any time during or after deposition at Olduvai. The point is that at Olduvai as elsewhere in the world a major episode of Late Pleistocene megafaunal extinction coincides with the prehistoric development of big game hunters. Unless a continent or island can be found in which a major wave of megafaunal extinction occurs other than soon after the arrival of man, or his cultural development as a stone age hunter, the possibility of overkill, will persist as a challenging "least improbable hypothesis".

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Received March 6; revised April 3, 1967.

¹ Leakey, L. S. B., *Nature*, **212**, 1615 (1966).

² Martin, P. S., *Nature*, **212**, 339 (1966).

³ Leakey, L. S. B., *Olduvai Gorge 1951-1961* (Cambridge Univ. Press, 1965).

⁴ Leakey, L. S. B., *The Ecology of Man in the Tropical Environment* (I.U.C.N. Publ. No. 4, Morges, Switzerland, 1964).

It does not seem worth devoting more time, or space, to discussing that part of my argument with Dr Paul Martin, on the subject of Pleistocene overkill, which deals with percentages of genera that may have become extinct at a given point of time, or that have survived to the present day. My reasons for saying this are as follows: (a) there is too little agreement as to what constitutes a genus; (b) that even since the publication of the earlier notes by Martin and myself last year, *Bulcharus* has been made a synonym of *Pelorovis*, and it has been suggested that *Tapinochoerus* is generically identical with *Orthostonyx*. It must also be noted that the majority of anthropologists now treat *Telanthropus* as belonging to the genus of *Homo* and the others as *Australopithecus*. No one accepts it as a distinct genus. Similarly, *Australopithecus*, *Paranthropus* and *Zinjanthropus* are now all genus *Australopithecus*.

Then again, few zoologists agree on the subject of the generic classification of living genera in Africa. Some would list zebra as *Hippotigris*, not *Equus*, and the wild ass of Somaliland as *Asinus*—some would list *Theropithecus* as a distinct genus from *Papio*, others would not. Some would divide wildebeeste into two genera—*Gorgon* and *Connochaetes*—and so on. It thus seems clear that any arguments based on statistics and percentages of wholly unsure genera are of little value.

Dr Martin completely ignores the last paragraph of my communication¹ of December 31 in his present reply. I believe it is quite unscientific to invoke "overkill" by Acheulean hunters to explain the extinction of some forty or more genera at the end of the Middle Pleistocene when the much more numerous and much better equipped hunters who succeeded Acheulean man, during the Upper Pleistocene and post-Pleistocene time, had so little effect on the remaining fifty or more genera. I refer, of course, to the hunters of the Middle Stone Age, the Upper Palaeolithic, the Mesolithic, the Neolithic and also the Iron Age hunters. On the basis of Dr Martin's arguments, these people should have exterminated nearly all the genera which survived into the Upper Pleistocene. In fact we know that they did not.

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Received April 27, 1967.

¹ Leakey, L. S. B., *Nature*, **212**, 1615 (1966).