Environmental, Ecological, and Paleoanthropological Implications of the Late Pleistocene Mammalian Fauna from Equus Cave, Northern Cape Province, South Africa

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The late Pleistocene deposits of Equus Cave, northern Cape Province, South Africa, have provided more than 30,000 taxonomically identifiable mammal bones from 48 species. Context, associations, and features of the bone assemblage implicate brown hyenas as the main accumulators. The fauna is significant mainly because (1) it supplements previous evidence that regional climate was cooler and possibly also somewhat moister during part(s) of the late Pleistocene, but deviated less from the historic norm than in areas farther south; (2) it shows that Bond's springbok, which became extinct in the early Holocene, differed from the surviving common springbok not only in important morphological respects but also in reproductive pattern; and (3) it sustains earlier suggestions that an abundance of carnivores, a paucity of small hard bones, an increase in the cranial/postcranial ratio with species size, and exclusively attritional mortality profiles are features that tend to differentiate assemblages accumulated by brown hyenas from those accumulated by people. In addition, pending firmer dating, the fragmentary human fossils from Equus Cave may support an exclusively African origin for anatomically modern humans.   © 1991 University of Washington.

INTRODUCTION

Equus Cave, South Africa, has provided one of the largest Pleistocene faunal samples in the world. Geologic context and taxonomic composition imply a late Pleistocene age, while context, taxonomic composition, bone damage, and associated objects indicate that brown hyenas were the main accumulators. So far, only the human remains and statistics on carnivore size have been published (Grine and Klein, 1985; Klein, 1986a). Our purpose here is to summarize the implications of the fauna for (1) late Quaternary environmental change in southern Africa; (2) the ecology and behavior of key species, including especially the brown hyena and the very abundant, ex-

tinct Bond's springbok; and (3) the differences between fossil assemblages accumulated by hyenas and those accumulated by Stone Age people.

THE SETTING OF EQUUS CAVE

Equus Cave (approximately 27°37′S, 24°37′E) is located on the Gaap Escarpment at Norlim (formerly Buxton), near Taung in the northern Cape Province of South Africa (Fig. 1, bottom). The escarpment is a 275-km-long, Precambrian dolomite cuesta that trends SW to NE between 27°07′ and 29°10′S on the southeastern margin of the Kalahari Desert and separates the Gaap Plateau on the northwest from a lowerlying planar surface dipping toward the Vaal
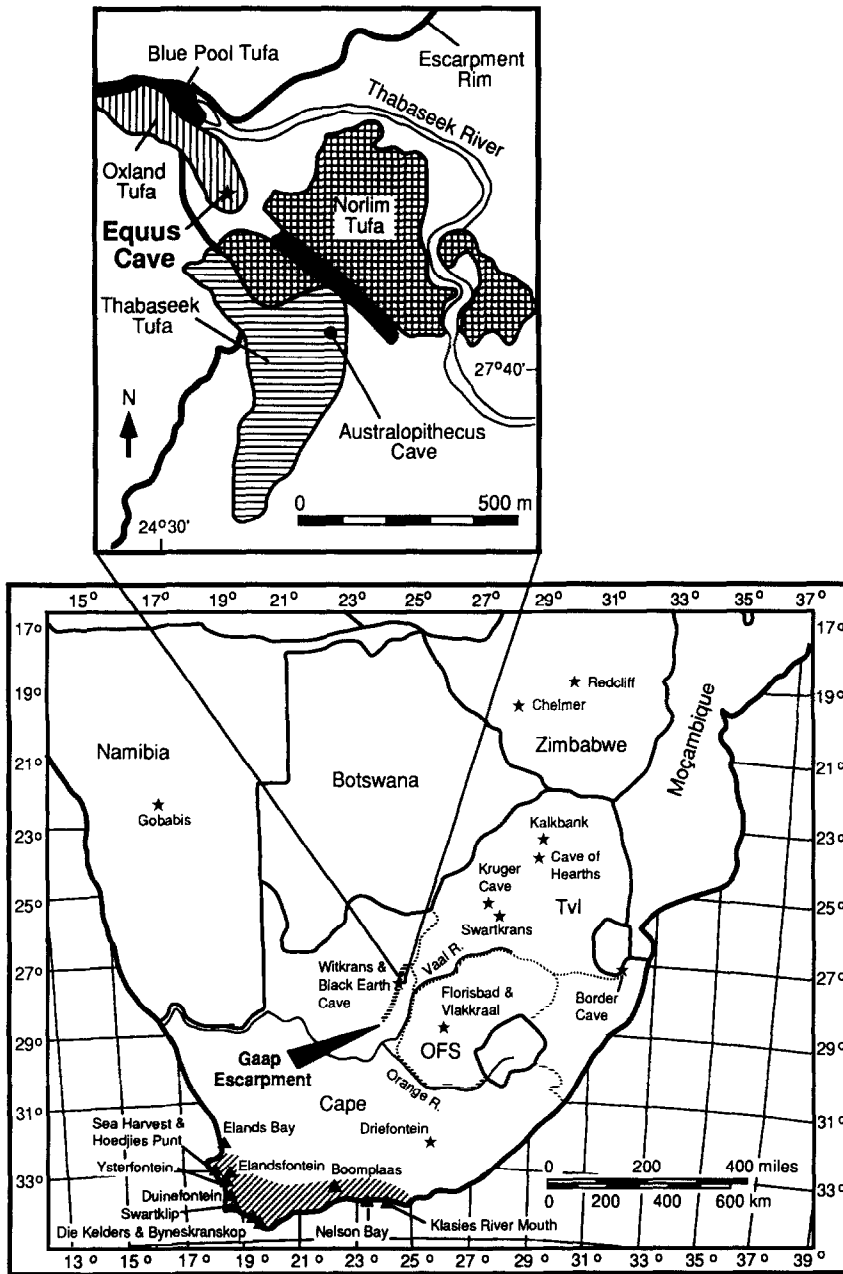
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FIG. 1. Bottom: Map showing the approximate locations of the sites mentioned in the text. Stars designate sites where Bond's springbok has been found, and hatching indicates the southern and southwestern Cape region where it is unknown and probably never occurred. Top: Equus Cave and the various tufa bodies developed at Buxton-Norlim (partly after Butzer, 1974, Fig. 3).

River on the southeast. Its face averages 70–120 m high and is mantled at several places with sheets or lobes of tufa (freshwater limestone). These originated from the evaporation of carbonate-charged spring waters, arguably in times of accelerated spring discharge (Butzer et al., 1978; Butzer, 1984) or under conditions no moister than the present (Partridge, 1985). They are particularly well developed in the

Norlim area, where Peabody (1954) and Butzer (1974, 1984; Butzer et al., 1978) have identified four major generations, known (from oldest to youngest) as the Thabaseek, Norlim, Oxland, and Blue Pool/Channel tufas. The tufa bodies contain caves, including one inside the Thabaseek Tufa that provided the first specimen of *Australopithecus africanus* (Dart, 1925). Equus Cave occurs inside the much younger Oxland Tufa, approximately 500 m northwest of the australopithecine cave (Fig. 1, top).

The climate of the Gaap Escarpment is semiarid, with no water surplus at any season. The winters (May to October) are cool and very dry, while the summers (November to April) are hot and punctuated by short, violent storms that provide 95% of the total yearly rainfall. Precipitation near Equus Cave varies from less than 100 to over 1000 mm per annum with an average of about 425 mm (Climate of South Africa, 1954; U.S. Department of Commerce, 1966–1967). Historically, the regional vegetation was dominated by grasses with scattered acacia thorn trees in a community known as "Kalahari Thornveld" (Acocks, 1953) or perhaps more descriptively as acacia grassland. The indigenous fauna must be reconstructed from scattered early travelers' reports (Skead, 1980), but it is clear that grazers predominated, including especially mountain reedbuck and vaalribbok on the escarpment itself and blue wildebeest, Cape hartebeest, blesbok, roan antelope, common springbok, Burchell's zebra, and warthog on the plains above and below. Browsers were certainly less prominent overall, but giraffes fed on the acacias scattered over the plains, and greater kudu and grey duiker found both browse and cover in patches of bush that were concentrated on and adjacent to the escarpment. The most abundant mixed grazer/browser was steenbok, with eland a distant second. The most plentiful nonungulate herbivores were rock hyrax, springhare, Cape hare, scrub hare, porcupine, and baboon. The principal car-

nivores were lion, leopard, caracal, serval, wild cat, cheetah, brown hyena, spotted hyena. Cape hunting dog, black-backed jackal, and silver fox. The plains ungulates and perhaps also some of the carnivores were probably migratory—during the drier (winter) season, many probably moved away from the Gaap Plateau above the escarpment, perhaps mainly to the valleys of the Vaal River and its tributaries on the undulating plain below.

EXCAVATION, STRATIGRAPHY, AND ANTIQUITY OF THE EQUUS CAVE FILL

Peabody (1954, Fig. 7) was the first to record fossils at Equus Cave, and his mention of an *Equus* tooth gave the site its name. Beaumont and Shackley undertook the first systematic excavations in 1978, and Beaumont extended them in 1982. Commercial quarrying of the tufa had partially destroyed the cave before excavation, and large blocks from the collapsed roof had to be removed from the exposed deposit. A grid of squares 1 m on a side was then laid down (Fig. 2), and the excavation proceeded according to arbitrary 7.5-cm-deep levels or "spits" within four poorly defined natural stratigraphic units, called (from top to bottom) 1A, 1B, 2A, and 2B (Fig. 3).

The uppermost unit, 1A, is a layer of grayish-brown sandy loam up to 50 cm thick, lying unconformably on unit 1B below. Units 1B through 2B comprise a conformable series of mainly reddish-brown, subhorizontal sandy loams with lenses of tufa grit. Unit 2A is differentiated from 1B above and 2B below primarily by an abundance of large, partially corroded tufa (roof) fragments, accompanied by some carbonate cementation of the enclosing sands. In thickness, 1B varies from 30 to 50 cm, 2A from 60 to 70 cm, and 2B from 60 to 80 cm. The origin of the reddish sands is largely, if not entirely, eolian (Shackley, personal communication, 1982).

The entire sequence is rich in animal bones, and 1A also contains typical Later
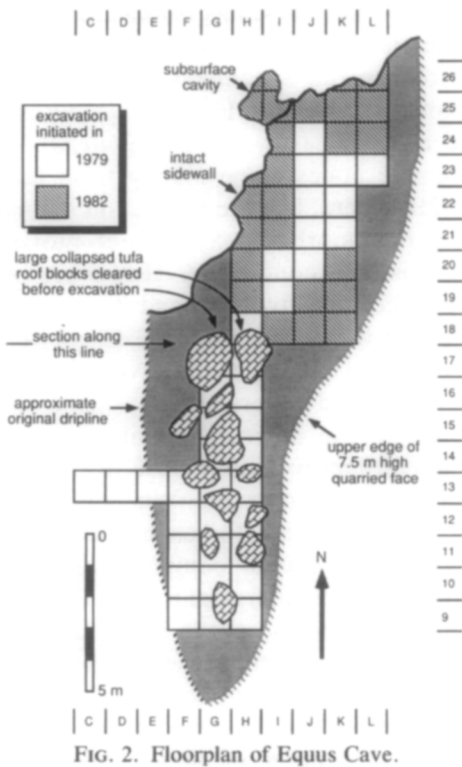
FIG. 2. Floorplan of Equus Cave.

Stone Age bone points. Two radiocarbon dates—2390 ± 60 yr B.P. (Pta-2452) on charcoal from near the middle of 1A and 7480 ± 80 yr B.P. (Pta-2495) on ostrich eggshell from near its base—indicate that 1A dates from the Holocene (Vogel *et al.*, 1986). The geologic antiquity of units 1B through 2B is much less certain. Occasional artifacts of Middle Stone Age (MSA) aspect, particularly in 2B (Beaumont *et al.*,

FIG. 3. Profile along the south wall of strip 18 at Equus Cave.

1984), suggest that 1B–2B are older than 30,000–40,000 yr B.P., the upper limit of the MSA elsewhere in southern Africa (Volman, 1984). However, organic residues extracted from bones in the upper part of 2B have been dated to 16,000 ± 160 yr B.P. by radiocarbon (J. C. Vogel, unpublished data). If this dating is valid, it would imply that the MSA artifacts are derived (washed in). Perhaps equally likely, the dated samples have been contaminated by younger carbon, and the antiquity of the 1B–2B sequence may be indicated more accurately by its geomorphic context.

The position of 1B–2B within the Oxland Tufa show that they postdate the outer portion of this tufa, dated by ionium (^{230}Th) to about 230,000 yr B.P. (Vogel and Partridge, 1984). In addition, Butzer *et al.* (1978) argue that they antedate the development of a manganiferous patina that covers the Blue Pool Tufa I and that is older than 32,700 yr B.P. Butzer (1984) has further suggested that the dissolution and initial filling of Equus Cave reflect the same accelerated spring discharge that produced Blue Pool Tufa I, which began to form perhaps 103,000 yr B.P. according to U-series dating (Vogel and Partridge, 1984). In sum, circumstantial, geomorphic evidence suggests that units 1B–2B were deposited sometime between 103,000 and 32,700 yr B.P., either in the latter part of the last interglaciation (oxygen-isotope stage 5) or in the early to middle part of the last glaciation (isotope stages 4 and 3).

In what follows, we often treat layers 1B, 2A, and 2B as if they were a single unit. This is partly because they are totally conformable and partly because layer-by-layer analyses not presented here suggest no major differences in their faunal contents.

PALYNOLOGY

Equus Cave has provided little pollen, except in hyena coprolites that occur throughout. The pollen spectra from coprolites in unit 1A imply vegetation broadly
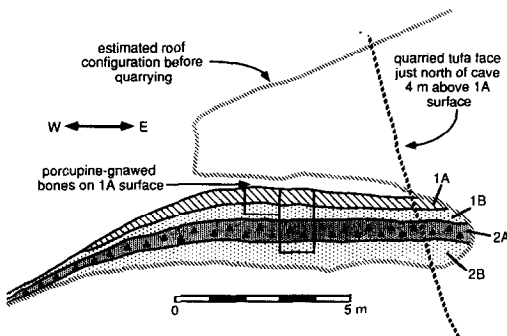
similar to the historic Kalahari Thornveld, while spectra in coprolites from units 1B through 2B indicate far more open vegetation with many fewer trees, particularly relative to grasses and composites (Scott, 1987). Tree pollen is especially rare in coprolites from 2B, where the total spectrum suggests much cooler conditions, up to 4°C below the present average. As discussed below, a cooler climate is also implied by the 1B–2B fauna. The pollen further implies greater effective moisture, though this could reflect simply reduced evaporation under cooler temperatures. The pollen evidence is not helpful in resolving the dating uncertainty, because cooler conditions are in keeping with either the tentative 16,000 yr B.P. date for 2B or with the geomorphic argument bracketing the entire 1B–2B sequence between 103,000 and 32,700 yr B.P. In the latter case, the pollens would mean that 1B–2B accumulated either within the earlier part of the last glaciation, sometime between 75,000 and 32,700 yr B.P. or within the pronounced cool phase (isotope substage 5b) that interrupted the last interglaciation between about 94,000 and 84,000 yr B.P.

GENERAL CONDITION AND COMPOSITION OF THE BONE ASSEMBLAGE

The Equus Cave bones are very friable and highly fragmented, partly from pre-depositional events and partly from profile compaction and postdepositional leaching. Some additional fragmentation occurred during excavation and transport from the site, but many pieces still remain readily identifiable to skeletal part and taxon. The overwhelming majority come from macro-mammals (hedgehog/hyrax-size or larger) on which we focus here. In addition, there are occasional bones from micromammals (small rodents, insectivores, and bats), birds, reptiles, amphibians, and fish. The micromammals and birds will be reported by D. M. Avery and G. Avery, respec-

tively. No specialist has studied the reptile, amphibian, and fish bones, but among them we recognized specimens from snake(s), tortoise(s), monitor lizard (*Varanus* sp.), and crocodile (*Crocodylus niloticus*). The crocodile bones come mainly from layers 1B–2B, where, like the pollen and the macromammals, they may reflect moister-than-historic conditions. However, only five pieces are involved, and it is conceivable that they came from the Harts River, about 8 km away, where crocodiles may have occurred historically.

Among the macromammal bones, we identified approximately 10% or 32,343 to skeletal part and taxon. Whenever possible, besides taxon, for each part we also recorded degree of completeness, side, and/or state of epiphyseal fusion. Following the procedures laid out in Klein and Cruz-Uribe (1984), we then used these data to calculate both the number of identifiable specimens (NISP) for each taxon and the minimum number of individuals (MNI) from which the specimens must have come. Table 1 presents the summary NISPs and MNIs for each taxon, while Figures 4–6 show the proportional representation of each taxon based on its MNI.

Because the bones are highly fragmented and often come from species that are osteologically very similar, many specimens were identifiable only to superspecific categories. The most numerous problematic bones were bovid postcranial fragments, which we could assign only to size categories—small, small-medium, large-medium, and large (see Table 1 caption). The NISPs and MNIs for bovid species are thus based exclusively on cranial elements (teeth and horncores), while those for size categories include both these and all postcranial bones. Other distinctions we often could not make were between Cape fox and bat-eared fox, brown hyena and spotted hyena, wildcat and black-footed cat, and leopard and cheetah. The lumping of bones from each species pair is reflected in the composite categories in Table 1, which include

TABLE 1. The Number of Identifiable Specimens (NISP)/the Minimum Number of Individuals (MNI) per Large Mammal Species and Stratigraphic Unit at Equus Cave

	Undiff. 1	1A	1B	2A	2B	1B–2B
Erinaceus frontalis, hedgehog	—	—	—	2/1	1/1	3/2
Leporidae gen. et sp. indet. hare(s)	22/2	27/3	43/5	52/4	110/9	205/16
Pedetes capensis, springhare	4/1	5/1	17/3	9/1	2/1	28/4
Hystrix africaeaustralis, porcupine	3/1	9/2	13/2	19/2	68/6	100/7
Papio ursinus, chacma baboon	15/3	62/6	39/3	47/4	12/2	98/7
Homo sapiens, people	—	3/1	2/1	3/1	4/1	9/1
Canis mesomelas, black-backed jackal	41/3	262/15	497/15	1122/41	4314/165	5838/217
Vulpes chama, Cape fox	9/2	44/5	55/8	88/13	408/50	543/65
Otocyon megalotis, bat-eared fox	1/1	3/2	8/2	16/2	75/9	99/11
Cape fox/bat-eared fox	26/2	161/5	225/8	419/13	1512/52	2156/67
Lycaon pictus, Cape hunting dog	5/1	—	13/2	25/4	88/11	126/16
Mellivora capensis, honey badger	—	1/1	1/1	8/3	18/4	27/4
Aonyx capensis, clawless otter	—	—	4/2	6/2	35/5	45/8
Genetta sp., genet	—	—	1/1	2/1	4/1	7/2
Atilax paludinosus, water mongoose	—	—	—	—	5/1	5/1
Herpestes ichneumon, Egyptian mongoose	—	5/2	—	—	1/1	1/1
Cynictis penicillata, yellow mongoose	3/1	2/1	12/2	19/2	52/3	83/5
Suricata suricatta, suricate	—	—	—	1/1	—	1/1
Crocuta crocuta, spotted hyena	—	2/1	11/2	29/4	128/13	168/19
Hyaena brunnea, brown hyena	3/1	35/5	58/8	151/11	492/41	701/54
Brown hyena/spotted hyena	4/1	41/6	83/9	214/13	737/47	1034/58
Felis libyca, wildcat	2/2	4/4	9/3	18/4	60/10	87/14
Felis nigripes, black-footed cat	—	1/1	1/1	—	1/1	1/1
Wildcat/black-footed cat	3/2	15/4	42/3	47/4	106/10	195/14
Felis caracal, caracal	1/1	4/1	16/1	86/4	278/8	380/12
Panthera leo, lion	—	—	8/1	15/2	62/4	85/5
Panthera pardus, leopard	—	3/2	6/2	14/2	45/7	65/11
Acinonyx jubatus, cheetah	—	—	1/1	1/1	1/1	3/2
Leopard/cheetah	—	3/2	14/3	27/2	65/7	106/12
Orycteropus after, aardvark	—	1/1	10/3	3/1	5/1	18/3
Procavia capensis, rock hyrax	37/2	121/8	44/6	65/11	120/17	229/32
Equus burchelli, Burchell's zebra	13/2	37/3	163/12	389/14	1341/44	1893/62
Equus capensis, "Cape zebra"	—	—	16/2	41/4	169/9	226/12
Diceros bicornis, black rhinoceros	—	—	2/1	5/2	14/3	21/3
Hippopotamus amphibius, hippo	—	—	—	1/1	4/1	5/1
Phacochoerus aethiopicus, warthog	6/2	21/5	31/5	37/5	115/14	183/23
Giraffa camelopardalis, giraffe	—	—	—	—	1/1	1/1
Taurotragus oryx, eland	—	3/2	2/2	6/1	20/2	20/4
Tragelaphus strepsiceros, greater kudu	—	2/1	9/3	8/3	26/5	43/9
Hippotragus sp. indet., roan or sable antelope	—	3/1	22/7	36/5	51/7	109/13
Kobus leche, lechwe	—	—	10/2	29/4	90/9	129/12
Redunca fulvorufula, mountain reedbuck	15/2	29/6	57/9	109/13	402/44	568/60
Pelea capreolus, vaalribbok	3/2	14/3	17/3	73/10	221/20	316/30
Connochaetes gnou and/or *Alcelaphus buselaphus*, black wildebeest/red hartebeest	12/2	21/4	101/12	209/16	698/64	1008/79
Megalotragus priscus, "giant hartebeest"	—	—	1/1	9/2	18/6	28/8
Damaliscus dorcas, blesbok	6/1	7/2	50/6	240/18	824/69	1121/88
Connochaetes taurinus, blue wildebeest	—	4/2	11/3	44/7	125/16	180/19

TABLE 1—*Continued*

	Undiff. 1	1A	1B	2A	2B	1B–2B
Antidorcas marsupialis,						
common springbok	9/2	36/6	209/25	489/59	1606/163	2304/247
Antidorcas bondi, Bond's springbok	12/3	—	242/21	754/72	2512/201	3508/284
Raphicerus campestris, steenbok	10/2	44/5	97/12	180/21	372/38	649/64
Sylvicapra grimmia, grey duiker	6/2	22/4	15/4	10/2	9/2	34/6
Ovis aries, sheep	—	11/4	—	—	—	—
Syncerus caffer, Cape buffalo	—	1/1	6/1	4/1	23/5	33/6
Bovidae—general						
Small	25/2	98/5	191/12	294/21	680/38	1165/64
Small-medium	59/5	216/15	840/55	2144/151	7699/412	10,683/606
Large-medium	22/3	75/6	388/24	978/40	3622/137	4988/183
Large	—	7/2	20/3	65/4	272/10	357/13

Note. Undiff. 1 comprises bones from parts of the site where layers 1A and 1B could not be distinguished. 1B–2B comprises bones from layers 1B, 2A, and 2B treated as if they were a single layer. For taxa listed together, the NISP and MNI are based on bones that both could and could not be separated between the taxa. The bovid size categories are basically equivalent to those used by other analysts [e.g., Brain (1981), Voigt (1983), and Brink (1988)]. Small bovid bones come exclusively from steenbok; small-medium bones from mountain reedbuck, vaalribbok, common springbok, Bond's springbok, and sheep; large-medium bones from greater kudu, roan/sable antelope, lechwe, black wildebeest/red hartebeest, blesbok, and blue wildebeest; and large bones from eland, "giant hartebeest," and buffalo.

both bones that were specifically identifiable and those that were not.

DATING IMPLICATIONS OF THE FAUNA

The species found in layer 1A all occurred in the region historically and are entirely consistent with the Holocene age implied by ^{14}C dating. Most of the species in layers 1B–2B were also present historically, but there are also three—Cape zebra, giant hartebeest, and Bond's springbok—that were totally extinct in historic times, and one—lechwe—whose nearest occurrence to Equus Cave was in the Okavango delta of Botswana, 700–800 km to the north (Ansell, 1971). The same extinct species and lechwe characterize other comparably modern fossil faunas that span the late Pleistocene interval (last interglaciation and last glaciation) in the South African interior (Klein, 1980, 1984). Discoveries at sites on the southern and western Cape coasts suggest that Cape zebra and giant hartebeest became extinct during the Pleistocene/ Holocene transition, about 12,000–9000 yr

B.P. (Klein, 1984), while excavations at Kruger Cave in the Transvaal indicate that Bond's springbok survived into the early Holocene, approximately 7500 yr B.P. (Brown and Verhagen, 1985). It is uncertain when lechwe last occurred south of the Okavango.

In sum, the fauna could support either the geomorphic evidence that layers 1B–2B accumulated sometime between 103,000 and 32,700 yr B.P. or the tentative radiocarbon date suggesting an age of only about 16,000 yr B.P. A final choice will not affect the paleoenvironmental and ecological inferences we draw below, but it is crucial to understanding the course of late Quaternary environmental change in southern Africa. It is also important from a paleoanthropological perspective. This is because the bones from layers 1B–2B include a fragmentary human mandible and nine isolated human teeth that are thoroughly modern in their morphology (Grine and Klein, 1985). If they are only about 16,000 yr old, their modern morphology is relatively unremark-
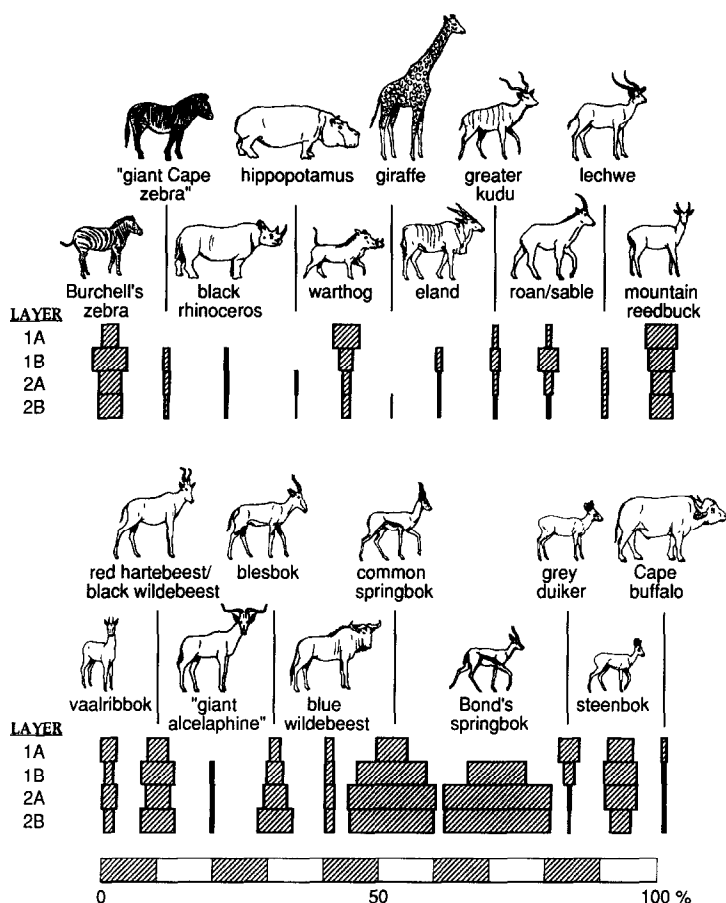
FIG. 4. The proportional representation of each ungulate species in each layer at Equus Cave, based on the minimum number of individuals.

able. If they antedate 32,700 yr B.P., however, they would join the list of fossils implying an exclusively African origin for anatomically modern people (Stringer and Andrews, 1988).

THE BONE COLLECTOR(S)

The only African species that are known to accumulate large numbers of macromammal bones in caves are people, porcupines, and hyenas. At sites that are broadly contemporaneous with Equus Cave, people are commonly implicated by abundant stone artifacts, by remnants of fire places ("hearths"), and by bones cut by stone tools. Porcupines are suggested by numerous bones bearing their distinctive incisor gnaw marks. These are generally deeper

and much more obvious than carnivore tooth marks, and they are readily visible even on relatively weathered or leached bones. In recent porcupine accumulations, indisputable incisor marks commonly occur on more than 60% of the bones (Brain, 1968, 1981; Maguire et al., 1980). Hyenas are indicated by an abundance of coprolites and by a distinctive pattern of bone damage. Especially numerous are shafts that end in ragged, scalloped perimeters where the epiphyses have been bitten away, bones scored or punctured by teeth, and bone chunks that have been corroded by gastric acids (Maguire et al., 1980; Brain, 1981). In layer 1A at Equus Cave, the relative abundance of artifacts, the small number of porcupine gnawed bones (109 = 9%), and the
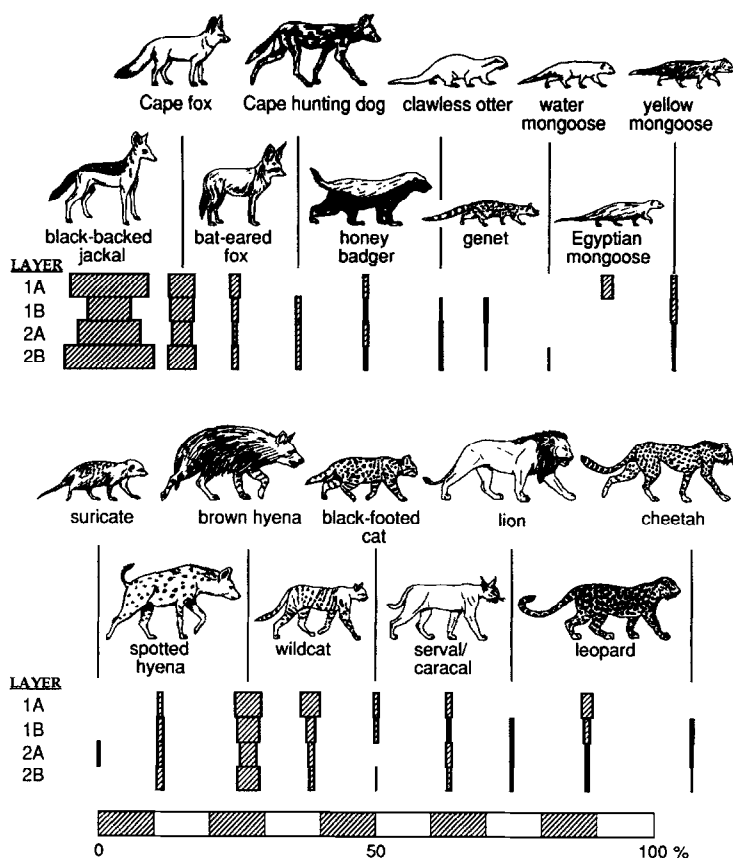
FIG. 5. The proportional representation of each carnivore species in each layer at Equus Cave, based on the minimum number of individuals.

rarity of coprolites suggest that people were the main bone collectors. In contrast, in layers 1B–2B the paucity of artifacts, the absence of cut bones and of "hearths" and other archeological features, the rarity of porcupine-gnawed bones (119 = 0.4%), and the abundance of hyena coprolites imply that hyenas were the principal accumulators. The high degree of fragmentation and leaching has largely obscured potentially diagnostic hyena damage to shaft perimeters and bone surfaces, but tooth-scoring and gastric acid attack are still obvious on 81 (0.3%) and 240 (0.8%) of the specimens, respectively.

During the late Quaternary, two hyena species—the spotted and brown hyenas—occurred in southern Africa, and both are represented at Equus Cave. Both are known to collect bones at lairs. [For the spotted hyena, see Sutcliffe (1970), Kruuk (1972), Bearder (1977), Mills and Mills (1977), and Henschel et al. (1979); for the brown hyena, see Stevenson-Hamilton (1947), Skinner (1976), Mills (1973, 1978a), Mills and Mills (1977), M. Owens and Owens (1978, 1979), D. Owens and Owens (1979), and Avery et al. (1983, 1984)]. However, in Equus Cave layers 1B–2B and in most other southern African fossil hyena lairs the main bone accumulators were probably brown hyenas. This is partly suggested by the small size of the coprolites, which tend to be much larger in spotted hyenas (Skinner and van Aarde, 1981), and partly by the following circumstantial observations:

(1) Brown hyenas carry bones to dens far more often than spotted hyenas do (Kruuk, 1972; Mills, 1978a; Henschel et al.,
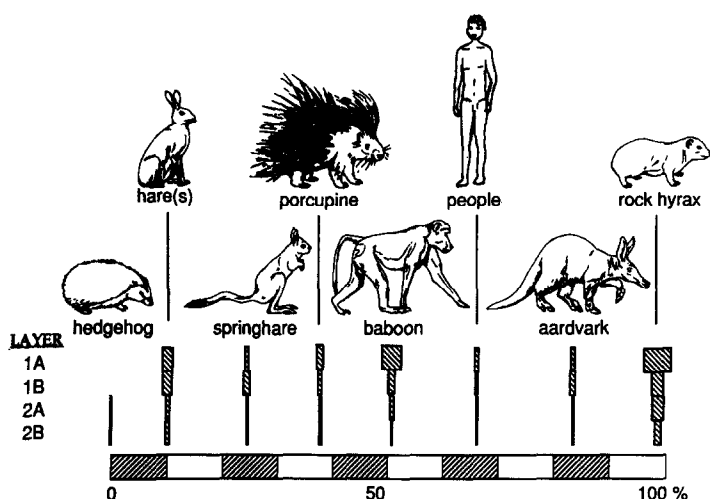
FIG. 6. The proportional representation of nonungulate and noncarnivore mammalian species in each layer at Equus Cave, based on the minimum numbers of individuals.

1979). This is mainly because brown hyenas regularly provision their young at dens (Mills, 1983), while spotted hyenas rarely do (Hill, 1980). The sheer volume of bones at Equus Cave and other South African fossil hyena lairs like Swartklip near Cape Town (Klein, 1975, 1986b) suggests brown hyena provisioning, possibly at communal maternity dens like those observed in the southern Kalahari by Mills (1982, 1983) and in the central Kalahari by M. Owens and D. Owens (1978, 1979).

(2) Where both large and small food animals are available, the less predatory, more solitary brown hyenas feed mostly on creatures springbok-size or smaller, while spotted hyenas feed far more often on larger animals (Skinner, 1976; Mills, 1978b; Tilson and Hamilton, 1984). This dietary difference is reflected in a preponderance of bones from larger animals in and around recent spotted hyena dens (Henschel et al., 1979). The faunas from Equus Cave (Figs. 4–6), Swartklip, and most other southern African fossil hyena dens are heavily dominated by animals in the springbok-or-smaller size range on which brown hyenas more commonly feed.

(3) Unlike spotted hyenas, brown hyenas tend to bring home relatively large numbers of bones from small carnivores

such as jackals and foxes (Mills and Mills, 1977; Mills, 1978a; Brain, 1981). The reason is that their more opportunistic, less predatory foraging and feeding strategy increases the likelihood of contact and conflict with smaller carnivores, above all with jackals whose foraging strategy is very similar. In the abundance of small carnivores, the bone assemblages from Equus Cave layers 1B–2B (Fig. 5) and other southern African fossil hyena sites clearly recall modern brown hyena assemblages.

(4) While both brown hyenas and spotted hyenas are represented in the fossil assemblages, brown hyena remains tend to be much more common, and they come mainly from young cubs (characterized by relatively unworn deciduous dentitions). Juvenile spotted hyenas are rare or absent. The most likely explanation for the difference is that it reflects brown hyena mortality at a maternity den.

(5) Throughout the late Quaternary, as in historic times (Smithers, 1971, 1983), brown hyenas were probably much more common than spotted ones in especially dry parts of southern Africa, including the southern Kalahari fringe where Equus Cave is located. The reason is that drier areas probably contained relatively few of the large ungulates to which the more pred-

atory, frequently social foraging and feeding strategy of the spotted hyena is geared. Potential foods probably had a very patchy distribution and were dominated by small mammals, reptiles, insects, birds eggs, carrion, fruit, berries, and other vegetal items for which the brown hyena's more opportunistic, solitary foraging strategy is better suited. Brown hyenas are also much less water dependent.

In sum, the available evidence, though indirect, distinctly favors brown hyenas as the main bone accumulators in layers 1B–2B at Equus Cave and most other southern African fossil hyena dens.

PALEOENVIRONMENTAL IMPLICATIONS OF THE FAUNA

The previously cited studies of living brown hyenas show that bone assemblages at dens will be biased toward springbok-size ungulates, since brown hyenas commonly consume smaller animals (like hare and springhare) completely, while they rarely feed on larger ones (like zebra and wildebeest). Thus, the extraordinary dominance of springbok-size (small-medium) bovids in the 1B–2B fauna does not mean that these species were equally dominant in life. However, it is certainly significant that within this size class, grazers or mixed grazer/browsers (the springboks, mountain reedbuck, and vaalribbok) far outnumber browsers (grey duiker) (Table 1 and Fig. 4). The same preponderance of grazers marks other size classes, and the implication is that the regional vegetation was dominated by grasses as opposed to bush or scrub. This is entirely consistent with the pollen evidence discussed above.

The fauna also supports pollen evidence that climate was cooler and relatively moister in 1B–2B times. Cooler temperatures are implied by the large average size of the most abundant carnivores—Cape fox, black-backed jackal, otter, spotted hyena, brown hyena, wildcat, and caracal. Modern comparative samples of each species show that individual size tends to in-

crease with decreasing temperature within Africa, in keeping with Bergmann's Rule, and for each species, individuals in layers 1B–2B tend to be significantly larger than historic individuals from the same latitude (Klein, 1986a). The especially numerous black-backed jackals are particularly informative because they show that large individual size characterizes layers 2B, 2A, and 1B both separately and together and that small (roughly historic) size characterizes layer 1A (Klein, 1986a). This conforms entirely to the pollen evidence that in contrast to 1B–2B, 1A accumulated under relatively warm, modern or near-modern conditions.

Moister climate in 1B–2B times is suggested by the presence of lechwe, an antelope that is closely tied to shallowly inundated floodplains or swamps (de Vos and Dowsett, 1966; Smithers, 1983). Historically, there was no comparable water-loving or water-dependent antelope in the South African interior and, as already noted, the lechwe itself occurred no closer than northern Botswana, 700–800 km north of Equus Cave, in the swamps of the Okavango Delta. However, it is also known in fossil form from Black Earth Cave very near Equus Cave (personal observation) and from Vlakkraal, Florisbad, and other late Pleistocene sites in the Orange Free State to the southeast (Gentry, 1978; Brink, 1987, 1988) (Fig. 1). At all these sites its occurrence suggests that standing water was more abundant nearby throughout the year, as a result of reduced evaporation, increased precipitation, or both.

The evidence for environmental change at Equus Cave is clear and consistent. However, like late Pleistocene faunas from other sites in the region, the Equus Cave assemblage does not suggest the kind of wholesale change that occurred farther south, in the southern and southwestern Cape (Klein, 1980, 1983). Here, at late Pleistocene sites like Swartklip and Duinefontein 1, the increase in average carnivore size is significantly greater, and the faunas are dominated by species that are totally

unknown in local Holocene assemblages. These species imply that the local macchia ("fynbos") vegetation of the Holocene was almost entirely replaced by grassveld. The greater degree of change to the south is also reflected in geomorphic evidence (Deacon and Lancaster, 1988), and it probably reflects the greater impact of climatic change farther from the Equator. Firmer dates will be necessary to confirm this hypothesis, and they are also crucial for establishing the course of late Quaternary climatic change in southern Africa. Firmer dates at Equus Cave, for example, could resolve the question of whether the region was drier or moister at the last glacial maximum, 17,000–18,000 yr B.P. At the moment, questionably dated geomorphic evidence can be used to argue either way (Deacon and Lancaster, 1988).

SKELETAL PART REPRESENTATION

The analysis of skeletal part representation at Equus Cave must be based mostly on theoretical considerations, since the published bone assemblages from recent hyena dens are too small for meaningful comparison. Additionally, the fact that they have no postdepositional history limits the extent to which they are directly comparable to any fossil assemblage. However, from observations of extant brown hyenas, we can hypothesize that skeletal part representation would differ significantly among food species of different sizes. This is because brown hyenas are much more likely to obtain smaller species, up to springbok (small-medium bovid) size, as whole carcasses, while they are more likely to obtain larger species only as partial carcasses from which other carnivores have already taken the most desirable parts. Additionally, hyenas are more likely to damage or destroy the bones of smaller species. In relative terms, the cumulative result would be that skeletal part representation in smaller species would be shaped more by selective destruction and in larger species more by selective transport.

This hypothesis might be tested using the method proposed by Grayson (1988) in which the abundance of each skeletal part is plotted first against its density (a measure of its ability to survive hyena feeding) and second against its basic food value (a measure of the likelihood hyenas will encounter it at carcasses). The predicted result is that abundance and density will be more positively correlated in smaller animals and abundance and food value more negatively correlated in larger ones. Figure 7 provides relevant plots for the small-medium and large-medium bovids in layers 1B–2B, based on the MNIs for individual skeletal parts in Table 2, on density estimates taken from Lyman (1984, 1985), and on a food utility index provided by Metcalfe and Jones (1988).

The figure, in fact, suggests there is no meaningful difference between the size classes in either the abundance/density or the abundance/food value correlations. For both classes, there is a strong positive relationship between abundance and density and a somewhat weaker, but still strong negative relationship between abundance and food value. In terms of the hypothesis we offered earlier, this might mean that carcasses of both size classes were equally obtained by scavenging, followed by equally intensive destruction during hyena feeding. However, the result is probably misleading, since in each case, the relatively high negative correlation between abundance and food value may reflect only the tendency for density and food value themselves to be negatively related (Lyman, 1985), while the high positive correlations between abundance and density are probably due mainly to intensive postdepositional leaching. Intensive leaching almost certainly explains why the Equus Cave bones are far more heavily fragmented than those from modern hyena dens or from fossil dens like Swartklip where the bones are much better preserved. It probably also explains why teeth dominate so much more heavily at Equus Cave and why tooth rows (as opposed to

Small-medium bovid MNI = 6.933
(bulk density) + 0.512
Pearson's r = 0.69 (p = 0.0001)
Spearman's r = 0.757 (p = 0.0001)

Small-medium bovid MNI = -0.026
(Food Utility Index) + 4.097
Pearson's r = -0.458 (p = 0.0125)
Spearman's r = -0.514 (p = 0.0065)

Large-medium bovid MNI =
5.597 (bulk density) + 0.501
Pearson's r = 0.623 (p = 0.0003)
Spearman's r = 0.683 (p = 0.0003)

Large-medium bovid MNI = -0.021
(Food Utility Index) + 3.313
Pearson's r = -0.413 (p = 0.0259)
Spearman's r = -0.46 (p = 0.0149)
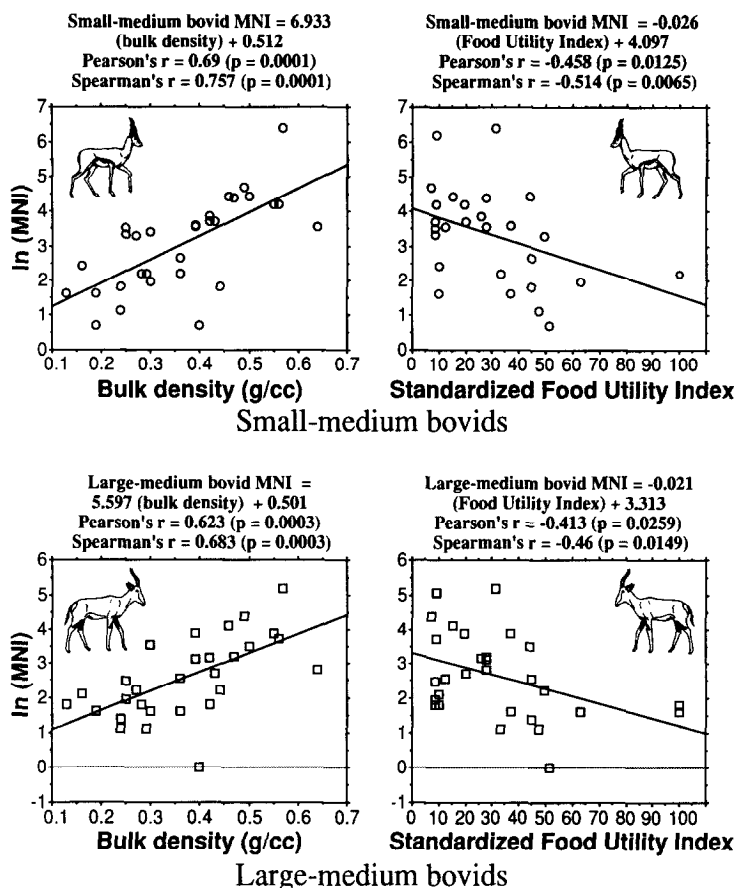
Small-medium bovids

Large-medium bovids

FIG. 7. Left: The relationships between skeletal part density and skeletal part abundance in small-medium and large-medium bovids from Equus Cave layers 1B–2B. Right: The corresponding relationships between food value and skeletal part abundance. To reduce the variability in abundance to approximately the same level as the variability in bulk density and food value, the MNI for each part has been transformed to its natural logarithm. The bulk density estimates (from Lyman, 1984, 1985) and food value estimates (from, Metcalfe and Jones, 1988) were derived from anatomically similar, close relatives of the Equus Cave species.

isolated teeth) are so much rarer than at Swartklip. We have not illustrated this here because of lack of space, but it becomes readily apparent when NISP/MNI ratios like those in Table 2 are compared between Equus Cave and Swartklip. For any given jaw and size class, the NISP/MNI ratios are much higher at Equus Cave.

The powerful postdepositional overlay at Equus Cave has almost certainly swamped the kind of predepositional differences in transport and destruction that Grayson's methodology is designed to detect. This does not mean, however, that there is no useful behavioral information in the pat-terns of skeletal part representation at Equus Cave. We show below that they may still reveal differences between hyena and human actions, when they are compared to patterns of skeletal part representation in comparably leached and fragmented archeological assemblages.

SEASON OF BONE ACCUMULATION

In the southern African interior, grazing ungulates tend to have their young just before or during the November-to-April (summer) rainy season when fresh, highly palatable grasses are most abundant (Mentis, 1972; Smithers, 1983). This is also the pri-

TABLE 2. THE NUMBER OF IDENTIFIABLE SPECIMENS/MINIMUM NUMBER OF INDIVIDUALS THEY REPRESENT FOR EACH SKELETAL PART OF SMALL, SMALL-MEDIUM, LARGE-MEDIUM, AND LARGE BOVIDS IN LAYERS 1B–2B AT EQUUS CAVE

	Small	Small-medium	Large-medium	Large
Frontlet	12/7	7/5	3/2	1/1
Occipital condyle	1/1	15/9	1/1	−/−
Maxilla	217/32	3116/488	1126/161	52/10
Mandible	432/64	3609/606	1365/183	37/7
Hyoid	−/−	3/2	1/1	−/−
Atlas	1/1	12/5	15/6	−/−
Axis	2/2	15/11	10/8	1/1
Cervical vertebrae 3–7	1/1	22/5	25/5	1/1
Thoracic vertebrae	7/2	29/3	19/3	1/1
Lumbar vertebrae	6/2	47/9	12/3	−/−
Sacrum	−/−	7/2	−/−	−/−
Ribs	6/1	32/2	14/1	−/−
Scapula	7/4	35/14	32/13	−/−
Proximal humerus	2/2	13/6	8/4	1/1
Distal humerus	7/5	86/37	147/49	12/7
Proximal radius	11/7	126/47	95/24	11/5
Distal radius	13/7	98/41	35/15	11/6
Proximal ulna	10/6	65/30	89/35	3/3
Carpals	21/6	254/35	118/13	10/4
Proximal metacarpal	9/5	188/68	166/42	14/5
Distal metacarpal	17/8	362/109	304/81	40/13
First phalanges	72/6	475/41	102/6	8/1
Second phalanges	74/11	322/34	93/12	6/2
Third phalanges	87/11	237/28	67/7	2/1
Innominate	20/4	129/27	43/9	−/−
Proximal femur	−/−	25/9	11/5	1/1
Distal femur	2/1	24/9	14/6	−/−
Patella	3/2	7/6	−/−	−/−
Proximal tibia	3/3	18/7	9/5	1/1
Distal tibia	20/11	208/85	100/34	16/7
Calcaneum	20/9	87/35	50/17	20/8
Astragalus	11/8	140/80	53/25	16/9
Naviculo-cuboid	12/6	67/28	44/14	18/7
Cuneiform tarsals	3/2	122/35	76/23	15/8
Proximal metatarsal	33/10	267/68	255/50	14/4
Distal metatarsal	17/8	290/83	262/62	41/13
Proximal sesamoids	−/−	49/4	77/5	1/1
Distal sesamoids	−/−	4/1	35/5	2/1

mary birth season for many of the carnivores, probably reflecting the generally dependable supply of newborn, highly vulnerable herbivores. Recent observations near Kimberley indicate, for example, that common springbok are born mainly in October (Bigalke, 1970), while observations in the Transvaal show that brown hyenas are born between August and November (Skinner, 1976).

The seasonal breeding of many Equus Cave species makes it possible to determine whether bone accumulation was also seasonal. This is because a population of seasonally breeding animals will contain distinct age cohorts, each separated from adjacent cohorts by a gap equal to the interval between birth seasons. In species that give birth only once a year, the average gap between cohorts will be 1 year. The age discontinuities will become fixed in a bone accumulation that formed during a short pe-

riod in any 1 year and also by extension in an accumulation that formed discontinuously at more or less the same period (season) over many years. It is repeated seasonal accumulation that we hypothesize for Equus Cave.

Kurtén (1953) was probably the first to point out that where high-crowned ungulates are abundant, as at Equus Cave, their crown heights may be used to detect fossilized age cohorts. If such cohorts are present, each will be represented by a distinct crown-height mode, separated from adjacent modes by a gap representing the interval each year when individuals in each cohort were wearing their teeth, but could not reach a site because the bone accumulators were absent. The modes should be roughly equidistant and their number should approximate the potential lifespan of individuals within the species. In practice, this approach clearly requires large samples, preferably from species that are very high-crowned and relatively short-lived. In such species, the gap between modes (the average amount of crown height lost between age cohorts) will be relatively large and the number of modes relatively small, facilitating their detection. With these requirements in mind, the springboks are by far the most suitable species for crown-height analysis at Equus Cave.

We examined the crown-height distributions of springbok upper and lower dP4's and M3's. These are abundant in the assemblage and easy to recognize even when isolated. They are also very useful for constructing species age profiles, as discussed in the next section. The lower and upper teeth provided the same basic result, but we present here only the distributions for the more abundant lower teeth. These are shown in Figures 8 and 9, which also illustrate how we measured crown height—from the enamel/dentine junction on the root to the occlusal surface on the buccal side of the most anterior lobe of each tooth.

Figures 8 and 9 (bottom) show that the M_3 distributions of both springbok species

display multiple crown height modes that suggest seasonal bone accumulation. The dP_4 distributions (left center) are supportive, as we explain below. However, only the common springbok can be used to establish the actual season of bone accumulation, because only its birth season was observed historically. Like the season of bone accumulation, the birth season for Bond's springbok must be inferred from the common springbok data. We show below that it probably occurred somewhat after the common springbok birth peak.

Figure 8 (bottom) shows that there are seven discernible crown-height modes in the common springbok M_3 distribution. Since common springbok erupt their M_3's at about 12 months (Rautenbach, 1971), at the very beginning of their second year, we have labeled the mode containing the most lightly worn teeth "II" and the succeeding six modes "III" through "VIII." The teeth in II are the most fragile, which probably explains why they are less numerous than teeth in the later modes. The gaps separating modes III through VIII are roughly equidistant, in keeping with the seasonal hypothesis, but the gap between II and III is much larger. This was expectable, since the rate of wear in freshly erupted teeth is especially rapid (Spinage, 1973; Klein and Cruz-Uribe, 1984). A comparable slowing of wear in old, heavily worn teeth probably largely explains why there is no discernible mode beyond VIII, even though springbok have a maximum longevity of 9 years (Mentis, 1972; Rautenbach, 1971). Equally important, even if wear after VIII were more rapid, the tiny number of individuals in the last potential year of life would always make it difficult to identify a putative ninth mode.

Figure 8 (left center) shows that the common springbok dP_4's exhibit only one crown height mode, whereas two are predictable from the average age of 18 months at which dP_4 is shed. However, the dP_4's in the single discernible mode are all in medium to late wear and most, if not all, prob-
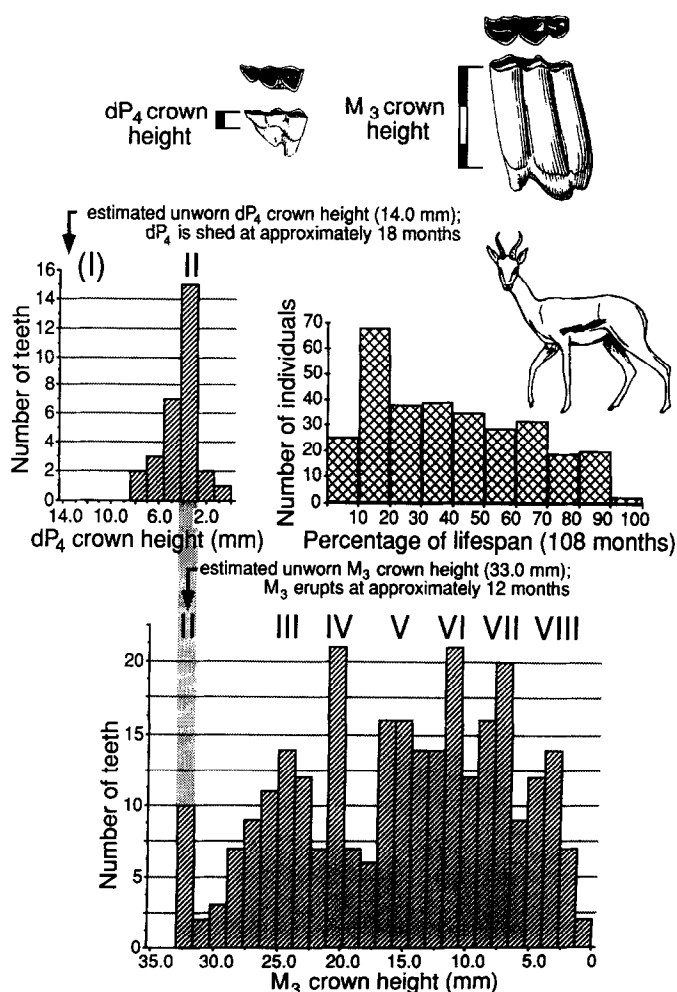
FIG. 8. Left center and bottom: common springbok dP$_4$ and M$_3$ crown heights in Equus Cave layers 1B–2B. Right center: The mortality profile derived from the crown heights.

ably come from individuals in which M$_3$ was in early wear, that is, ones in M$_3$ mode II. Younger, more lightly worn dP$_4$'s that could comprise a second, younger dP$_4$ mode ("I") are totally absent. To some extent their absence probably reflects their extreme fragility, just as the relative fragility of dP$_4$'s in general probably explains why they are much less common than M$_3$'s. However, unworn and lightly worn dP$_4$'s do occur in samples of the other small-medium bovids at Equus Cave, including the much smaller samples of vaalribbok and mountain reedbuck, and we conclude that

lightly worn common springbok dP$_4$'s are absent because they were less available to the collectors. The implication is that bones generally did not accumulate at Equus Cave during the peak springbok birth season.

Determining when they did accumulate is more problematic. Even the highest-crowned common springbok M$_3$'s (in mode II) tend to have lost enough height to suggest they had been in use a minimum of 2–3 months. The implication is that they reached the site at least 14–15 months after the springbok were born. Assuming that the
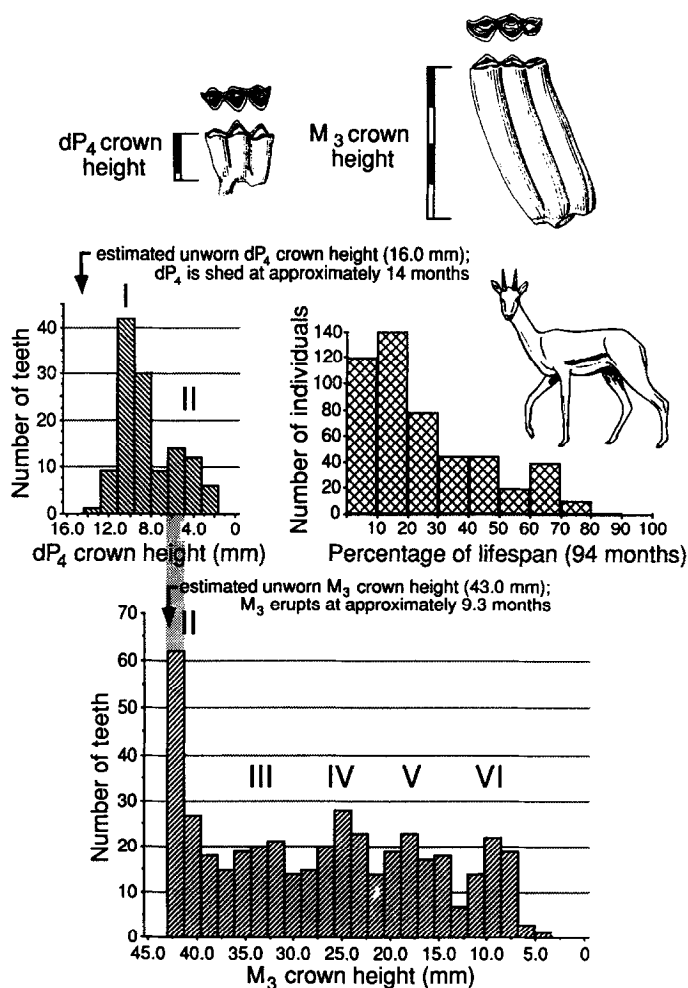
FIG. 9. Left center and bottom: Bond's springbok dP_4 and M_3 crown heights in Equus Cave layers 1B–2B. Right center: The mortality profile derived from the crown heights. Ages of dental eruption and shedding and of maximum life expectancy were estimated from those of similar-sized, extant bovids.

birth occurred in October as it does now, bone accumulation would have begun in the December–February interval.

The remaining ungulate species are represented by too few teeth to provide a reliable seasonal cross-check, but the very abundant black-backed jackals and even the brown hyenas are more helpful. Although jackals are abundant in the fauna (Fig. 5), their deciduous teeth are completely absent, and the youngest individuals have freshly erupted, unworn permanent carnassials. In modern jackals, these ap-

pear about 4–5 months after birth, which occurs mainly between August and September (Lombaard, 1971; Rautenbach, 1982; Ferguson et al., 1983), just before the springbok lambing peak. Assuming that the jackals at Equus Cave were also born mainly in August–September, the youngest ones must have reached the site in December–January, in keeping with the season provisionally established from the springbok.

The brown hyenas are represented by both deciduous and permanent teeth. De-

ciduous teeth predominate and are all lightly worn to approximately the same extent (Fig. 10). We presently have no means to determine just how old the juvenile hyenas were, but if they were born mainly between August and November, like their modern counterparts, the degree of wear appears consistent with a mean time of death beginning in the December–February interval suggested by the common springbok and the jackals. The absence of yet younger hyenas is readily understandable if, as we believe, the Equus Cave accumulation reflects brown hyena provisioning at a maternity den. For various reasons, including the buildup of ectoparasites, brown hyenas rarely occupy a den for more than 2–3 months at a time (Mills, 1982, 1983), and cubs less than 3 months old are only nursed, nor provisioned. Bones are thus unlikely to accumulate at a den with cubs

under 3 months. Multiple litters of older cubs are sometimes provisioned in a single communal den (Owens and Owens, 1979; Mills, 1982), and if this were the case at Equus Cave, it could explain the large volume of bone.

In sum, assuming that the common springbok births peaked in October, it is likely that the bones at Equus Cave accumulated mainly in the summer months, beginning in December. More certainly, the seasonality data imply some significant differences in potential lifespan and breeding cycle between the two springbok species. The smaller number of discernible M_3 modes suggests that Bond's springbok was somewhat shorter-lived, in keeping with its somewhat smaller size. In addition, on average, the wear on the youngest Bond's springbok dP_4's and M_3's is much lighter than on their common springbok counter-
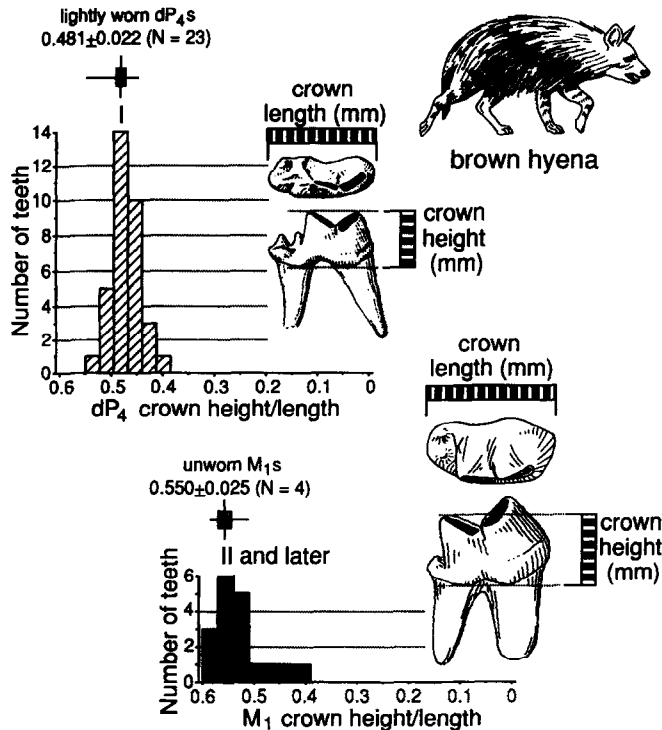

FIG. 10. Crown heights/crown lengths of brown hyena deciduous and permanent lower carnassials in Equus Cave layers 1B–2B. Height was divided by length to reduce the considerable variability in height introduced by size differences among teeth. "I" and "II" designate age cohorts containing individuals in their first and second years of life, respectively.

parts, suggesting that Bond's springbok births peaked later, nearer to the main season of bone accumulation at Equus Cave. This finding complements other indications of differences between the two species. For example, morphological observations by Vrba (1973) and ourselves suggest that Bond's springbok may have been less cursorial and less nomadic than the common springbok. Moreover, the species has a distinctive distribution. It is far more common in late Pleistocene nonarcheological sites like Equus Cave, Florisbad (Brink, 1987, 1988), and Swartkrans Cave Member 5 (Brain, 1981, 1988) than in broadly contemporaneous archeological sites like Witkrans Cave (Clark, 1971), Border Cave (Beaumont, 1980; Klein, 1977), or Redcliff Cave (Cooke, 1978; Cruz-Uribe, 1983), while it is totally unknown at sites in the historic macchia area of the southern and southwestern Cape (Fig. 1). This area, which has provided several large, late Pleistocene assemblages, seems to have been inhabited exclusively by the common springbok (or by the morphologically very similar southern springbok, *Antidorcas australis*.) Hopefully, the developing morphological, behavioral, and distributional characterization of Bond's springbok will ultimately clarify why it failed to survive the early Holocene.

MORTALITY PROFILES

In theory, the carcasses on which brown hyenas feed should include significantly more very young and very old individuals than exist in stable live populations. This is because the very young and the old are disproportionately susceptible to natural mortality, including hyena predation. It follows that the age (mortality) profiles of the food species represented at sites like Equus Cave should contain disproportionately large numbers of very young and older animals. In theory, the peak in very young individuals should be especially obvious, since they not only suffer high mortality, but are very abundant to begin with.

The same crown heights that were used to check for seasonal bone accumulation can be used to construct interpretable age profiles, using the assumptions and relationship between crown height and age described in Klein et al. (1983) and Klein and Cruz-Uribe (1984). Figures 8 and 9 (right center) show that the resulting age profiles for both springboks meet our expectation: older individuals (beyond 40% of maximum potential lifespan) are much better represented than they are in stable, live populations, where they are always outnumbered by those between 20 and 40% of potential lifespan (Klein, 1982, and references therein). The common springbok profile is particularly clear, but the differences between the two profiles are readily attributable to natural differences in population dynamics among species. A higher frequency of twinning could, for example, explain the relatively larger number of Bond's springbok individuals between 20 and 40% of lifespan. To some extent also, the smaller number of older Bond's springbok (beyond 40% of lifespan) may be more apparent than real, since the model used to convert crown heights to ages may be less appropriate for a hyperhypsodont species like Bond's springbok than for a more moderately hypsodont one like the common springbok.

Figures 8 and 9 also show that the springbok mortality profiles do not conform to *a priori* expectations that very young individuals (in the first 10% of potential lifespan) would be especially common. Very young Bond's springbok are relatively more numerous than very young common springbok, in keeping with the probability that Bond's springbok were born during or just before the season when hyenas occupied Equus Cave. However, even for Bond's springbok, very young animals are much less numerous than they would have been in a stable, live population. The same paucity of very young individuals characterizes the mortality profiles of the other small-medium bovids at Equus Cave (which resemble those of the springboks). More generally, very young individuals from smaller

species are consistently underrepresented in all the hyena-derived faunas we have examined, and the reason is almost certainly that their smaller, more fragile skulls were disproportionately destroyed during hyena feeding and subsequent profile compaction and leaching.

In contrast, very young individuals are disproportionately well represented in larger species, such as wildebeest and zebra, and the reason is probably partly that the young skulls of larger species are more durable than those of smaller species. In addition, the skulls of older individuals were probably often too heavy for ready transport to dens. Figure 11 illustrates the high proportion of very young zebra in the Equus Cave sample, but shows also that older adults are disproportionately abundant, just as in the springboks. In sum, we conclude that when the biases introduced

by hyena feeding and transport are considered, the Equus Cave mortality profiles conform to our *a priori* expectations. Most important, in keeping with ecological theory, they imply that the hyenas had relatively limited access to prime-age (reproductively active) adults in the ungulate species on which they fed.

BROWN HYENAS VERSUS PEOPLE AS BONE ACCUMULATORS

Table 3, based on our previous research, outlines five major features that differentiate fossil assemblages attributable to brown hyenas from ones accumulated by stone age people. One of these features—the higher ratio of nearly complete shafts to epiphyses in hyena assemblages—cannot be examined at Equus Cave because the bones were so highly fragmented after burial, but the others are all supported.
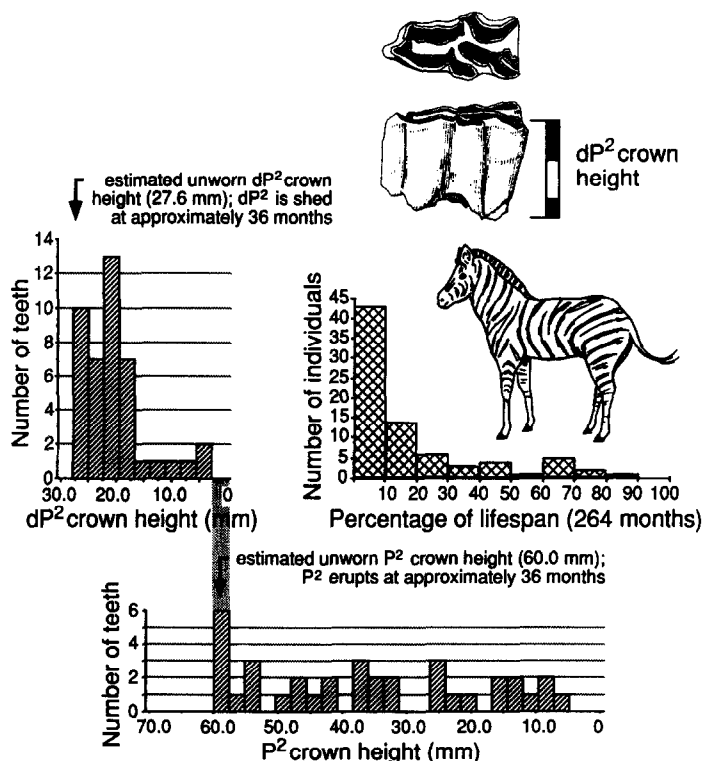

Fig. 11. Left center and bottom: Burchell's zebra dP^2 and P^2 crown heights in Equus Cave layers 1B–2B. Right center: The mortality profile derived from the crown heights. The ages of dental eruption and shedding are from Klingel (1965) and Smuts (1974). Potential lifespan is from Mentis (1972).

TABLE 3. DISTINCTIONS BETWEEN BONE ASSEMBLAGES FROM FOSSIL HYENA DENS AND FROM STONE AGE ARCHEOLOGICAL SITES IN SOUTHERN AFRICA

Feature	Hyena dens	Archeological sites
Cranial/postcranial ratio	Ratio tends to decrease with ungulate size (smaller ungulates better represented by postcranial bones). In addition, large ungulate postcranial bones tend to come from adults, while large ungulate cranial bones derive from juveniles.	Ratio tends either to be independent to ungulate body size or to increase with body size.
Long bone representation	Long bone shafts tend to complete, but missing epiphyses.	Long bone shafts tend to be broken, while epiphyses are still present.
Skeletal part representation	Small, hard bones (carpals, tarsals, sesamoids) always rare.	Small, hard bones always present; will be superabundant if the assemblage is highly fragmented.
Carnivore/ungulate ratio	Carnivores at least 20% of total carnivore + ungulate MNI.	Carnivores often less than 10% of the carnivore + ungulate MNI; never more than 13%
Mortality profiles	Tend to be attritional.	May be catastrophic or attritional, depending on species, technology, and hunting method.

Note. The main fossil hyena samples come from Equus Cave, Swartklip 1, Elandsfontein ("bone circle"), Ysterfontein, Sea Harvest, and Hoedjies Punt. The main archeological samples to which they have been compared are from Klasies River Mouth, Nelson Bay Cave, Boomplaas Cave, Die Kelders Cave 1, Byneskranskop 1, Elands Bay Cave, and Border Cave.

Thus, the abundance of carnivores in layers 1B–2B (30% of the total MNI for carnivores plus ungulates) is comparable to that in other hyena assemblages and far exceeds the level in archeological sites. Similarly, as we indicated in the last section, the ratio of past-prime to prime adults is much higher in the Equus Cave mortality profiles than in stable live populations. Such profiles are generally referred to as "attritional," because they are the expectable end-product of on-going, day-to-day mortality in a natural population. They contrast with "catastrophic" profiles, which result from nonroutine events like great floods, volcanic eruptions, or epidemic diseases. These disasters tend to impact upon all age classes equally and they therefore produce mortality profiles in which the ratio of past-prime to prime adults is the same as in live populations. In our experience, hyena assemblages are characterized exclusively by attritional profiles, while archeological assemblages present a mix of attritional and catastrophic profiles (Klein and Cruz-Uribe, 1984). We attribute the catastrophic profiles in archeological contexts to the uniquely human ability to drive herds of some species over cliffs or into other traps where all individuals can be obtained, regardless of age.

In our previous work on hyena-accumulated faunas (Klein and Cruz-Uribe, 1984, and references therein), we found that the ratio of cranial bones to postcranial bones decreased with species size. In addition, the cranial and postcranial bones of larger species came from different sets of individuals, the cranial bones mainly from juveniles and the postcranial bones mainly from adults. This contrasts with our findings on archeological faunas, and we believe the

difference reflects three observed or expectable aspects of hyena feeding and transport behavior: (1) hyenas commonly destroy the postcranial bones of smaller species but leave the skulls more intact (Richardson, 1980); (2) they commonly destroy soft juvenile postcranial bones regardless of size; and (3) they are often unable to transport the adult skulls of larger species. People are both less destructive and more able to transport large skulls. Using the cranial/postcranial ratios for different-sized bovids and equids in layers 1B–2B, Table 4 shows that Equus Cave conforms to our prediction that the cranial/postcranial ratio would decrease with size. Using comparable data from the Middle and Later Stone Age layers of Boomplaas Cave A (Deacon, 1979), the table also reveals the different trend that we have come to expect in archeological faunas. We chose Boomplaas for comparison because it is our largest archeological sample in which postdepositional destruction is comparable to that at Equus Cave. In all comparisons involving skeletal part numbers, it is obviously important to control for postdepositional effects.

TABLE 4. CRANIAL/POSTCRANIAL RATIOS FOR BOVIDS AND EQUIDS IN THE HYENA-ACCUMULATED ASSEMBLAGE FROM LAYERS 1B–2B AT EQUUS CAVE AND IN THE HUMANLY ACCUMULATED ASSEMBLAGE FROM THE MIDDLE AND LATER STONE AGE LAYERS OF BOOMPLAAS CAVE A

	Cranial MNI	Postcranial MNI	Ratio
Equus Cave			
Small bovid	64	11	5.8
Small-medium bovid	606	109	5.6
Large-medium bovid	183	81	2.3
Large bovid	10	13	0.8
Small zebra	61	39	1.6
Large zebra	5	11	0.5
Boomplaas Cave A			
Small bovid	35	16	2.2
Small-medium bovid	39	12	3.3
Large-medium bovid	52	11	4.7
Large bovid	13	2	6.5
Small zebra	12	2	6.0

Note. At Equus Cave "small zebra" refers to Burchell's zebra, and at Boomplaas Cave A to mountain zebra (*Equus zebra*) and/or Burchell's zebra. "Large zebra" refers to the Cape zebra.

The Equus Cave bones also conform to our prediction that cranial bones of larger species will come mainly from juveniles, while the postcranial bones will come mainly from adults. Burchell's zebra, for example, whose teeth come overwhelmingly from individuals in the first 10% of potential lifespan (Fig. 11) is represented by only 11 unfused epiphyses out of 150 pieces on which degree of fusion can be established. The fused to unfused ratios for such late-fusing bones as the distal radius and proximal calcaneum are 11:3 and 13:3, respectively. By analogy to the domestic horse (Schmid, 1972), the predominant fused specimens in each case must come from individuals significantly older than those that dominate the dental age profile. Unfortunately, the number of Boomplaas larger ungulate postcranial bones on which state of fusion can be reliably determined is too small for meaningful comparison to Equus Cave.

Finally, our previous research indicated that, compared to archeological assemblages, ones accumulated by hyenas tend to be much poorer in carpals, cuneiform tarsals, sesamoids, and phalanges. These are small, dense bones that should survive postdepositional destruction relatively well, and their rarity in fossil hyena assemblages almost certainly reflects the observed hyena tendency to swallow and digest them (Richardson, 1980). Table 2 shows that carpals, cuneiform tarsals, sesamoids, and phalanges are indeed rare at Equus Cave, while Table 5 uses the data on large-medium bovids to show that these elements are more abundant not only at Boomplaas Cave A but also among the comparably leached and fragmented bones of like-sized red deer (*Cervus elaphus*) from the terminal Pleistocene, Magdalenian level 4 at El Juyo Cave, northern Spain (Klein and Cruz-Uribe, 1987).

In sum, to the extent that bone condition allows, Equus Cave confirms our proposed criteria for distinguishing hyena-accumulated from humanly accumulated bone as-

TABLE 5. The Minimum Number of Large-Medium Bovid/Cervid Individuals Represented by
Carpals, Phalanges, Cuneiform Tarsals, Sesamoids, and Mandibular Dentitions in Layers 1B–2B
at Equus Cave, in the MSA and Prepastoralist LSA Layers of Boomplaas Cave A, and in
Magdalenian Layer 4 at El Juyo Cave

	Equus Cave, large-medium bovids	Boomplaas, large-medium bovids	El Juyo layer 4, red deer
Carpals	13 (7%)	5 (10%)	7 (21%)
Phalanges	12 (7%)	10 (19%)	17 (50%)
Cuneiform tarsals	23 (12%)	9 (17%)	16 (47%)
Sesamoids	5 (3%)	9 (17%)	11 (32%)
Mandibular dentition	183 (100%)	52 (100%)	34 (100%)

Note. In each case, the mandibular dentition provided the largest minimum number, which was then used to calculate the percentage representation of the other bones.

semblages. The importance of the hyena diagnostics is that they can be applied to bone assemblages where *a priori* evidence for a hyena-versus-hominid role is controversial. A case in point is the assemblage from the Grey Breccia (Member 3) at the Makapansgat australopithecine site. Dart (1957), Richardson (1980), and others have argued that the pattern of bovid skeletal part representation in the Grey Breccia was probably created by *Australopithecus*. However, Klein (1975) and Brain (1981) have shown that this pattern is at least as likely to result from hyenas, which Maguire (1985; Maguire *et al.*, 1980) believes are implicated by bone damage. The probable hyena collector at Makapansgat is the striped hyena (*Hyaena hyaena*), which is well represented in the Grey Breccia, but which today occurs only in eastern and northern Africa and in southern Asia where its behavioral and ecological resemblance to the brown hyena is well established (Mills, 1978b; Skinner *et al.*, 1980). Maguire's position is clearly supported by those features of the Makapansgat fauna for which data are available—especially (1) the abundance of carnivores, including many juvenile striped hyenas (Collings *et al.*, 1976), (2) the extreme rarity of bovid phalanges (no numbers are available on other small, hard bones) (Dart, 1957), (3) the tendency for the cranial/postcranial ratio to decrease with bovid size (Dart, 1957; Richardson, 1980), and (4) the tendency for larger bovid denti-

tions to come from juveniles (Wells and Cooke, 1956; Vrba, 1987; and Klein, personal observation) while larger bovid postcranial bones come mainly from adults (Dart, 1957).

CONCLUSIONS

In sum, the Equus Cave fauna (1) supports independent evidence from Equus Cave and other sites that the regional environment was equally or more grassy, cooler, and perhaps also somewhat moister during a part of the late Pleistocene, but differed from the historic environment less than late Pleistocene environments differed from their historic counterparts further south; (2) implies that the extinct Bond's springbok differed from the surviving common springbok not only in important morphological respects but also in the timing of its birth peak and possibly other facets of reproductive biology like the frequency of twinning. As the differences become better understood, they may help explain why only the common springbok survived past the early Holocene; and (3) sustains earlier suggestions that an abundance of carnivores, a paucity of small hard bones, an increase in the cranial/postcranial ratio with species size, and exclusively attritional mortality profiles are features that tend to differentiate assemblages accumulated by brown hyenas from ones accumulated by people.

The Equus Cave fauna illustrates the de-

cided advantage of large samples, while simultaneously revealing the disadvantage of imprecise dates. Firmer dates are crucial for establishing the exact pattern of regional late Pleistocene climatic change and equally for determining whether the human remains should be added to those that imply an African origin for anatomically modern people.

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