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# Middle and Later Stone Age large mammal and tortoise remains from Die Kelders Cave 1, Western Cape Province, South Africa

Die Kelders Cave 1, South Africa, has provided more than 150,000 taxonomically identifiable mammal and tortoise bones from Middle Stone Age (MSA) and Later Stone Age (LSA) deposits. Cape dune molerats dominate the mammal sample, and they appear to have been accumulated mainly by people during the LSA occupation and mainly by eagle owls in the MSA. In sharp contrast to the LSA fauna, the MSA sample contains extralimital ungulates that imply relatively moist, grassy conditions. The large mean size of the MSA molerats also points to greater humidity, while the large size of the gray mongooses implies cooler temperatures. The sum supports luminescence and ESR dates that place the MSA occupation within the early part of the Last Glaciation (global isotope stage 4). The Die Kelders ungulate bones support those from Klasies River Mouth in suggesting that MSA people obtained dangerous terrestrial prey much less frequently than their LSA successors, probably because MSA people lacked the bow and arrow and other projectile weapons. The Die Kelders tortoise bones constrain the extent of climatic change, since their abundance indicates that warm, dry days remained common, at least seasonally. The tortoises tend to be much larger in the MSA layers than in the LSA ones, suggesting that MSA people collected tortoises less intensively, probably because MSA populations were relatively sparse.

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## Introduction

The African Middle Stone Age (MSA) was coeval with the European Middle Paleolithic (Mousterian) between roughly 250 ka ago and 50–40 ka ago. It also closely resembled the Middle Paleolithic in every detectable archeological respect, including basic stone flaking technology, the relatively small number of readily distinguishable stone artefact types, the rarity or absence of bone artefacts, the lack of unequivocal art or bodily ornaments, and a remarkable degree of artefactual homogeneity through time and space. From a strictly archeological perspective, the MSA and the Middle Paleolithic are distinguished mainly by geographic distance and scholarly tradition, yet MSA and Middle Paleolithic people were physically very different (Stringer & Gamble, 1993; Stringer, 1996). A sparse, but growing fossil record shows that MSA people were anatomically modern or near-modern, and they surely included the ancestors of living humans. In contrast, Middle Paleolithic people were Neanderthals, who were probably extinguished when anatomically modern humans spread from Africa to Europe beginning 50–40 ka ago. The spread coincides with a sharp increase in the variety of standardized stone artefact types, a great proliferation of artefacts in bone, ivory, and related substances, an artistic florescence, and a dramatic acceleration in

artefact-assemblage variation through time and space.

Most authorities agree that the behavioral shift helps explain how modern humans could replace the Neanderthals, but they disagree sharply on what produced the shift (Appenzeller, 1998; Holden, 1998). Some, for example, Bar-Yosef (1998), Marean and Assefa (1999), and Soffer (1994), believe that the underlying cause was a profound social, demographic, or technological transformation among people who had long been capable of modern human behavior. This idea may be correct, but there is no evidence for such a transformation independent of the behavioral effect it is supposed to have produced, and there is no explanation of why the transformation occurred when it did. It thus seems more parsimonious to postulate that the behavioral shift followed on a genetically based neurological change that promoted the modern ability to innovate, beginning in Africa roughly 50 ka ago. This notion assumes only the last in the kind of selectively advantageous, spontaneous mutations that must underlie the obvious correspondence between neural and behavioral change earlier in human evolution. The behavioral shift that occurred 50–40 ka ago was arguably much more dramatic than any previous one, but the evidence for much older neural change derives from increases in average endocranial capacity, and most, if not all human populations had achieved essentially modern capacity long before 50–40 ka ago. Thus, a neural change that prompted modern human behavior 50–40 ka ago could have involved only brain organization, and fossil skulls do not reveal this unambiguously. Unfortunately then, for the moment, the neural hypothesis depends entirely on parsimony.

There is the further problem that the behavioral shift occurred in an interval between 60 and 40 ka ago that few African archeological sites record. Southern and northern Africa have provided almost no sites of this age, probably because African low-mid latitudes became very arid at the start of this global-isotope stage 3 roughly 57 ka ago, and regional human populations crashed. More archeologically visible, if perhaps still sparse, populations survived only in equatorial eastern Africa, and it is thus to eastern Africa that we should probably look for modern behavioral origins. The archeological evidence remains meager, but Enkapune Ya Muto in Kenya has produced bodily ornaments that antedate any well-documented European ones. They comprise ostrich eggshell beads that are more than 40 ka old (Ambrose, 1998).

However, even if southern Africans before 60 ka ago were not directly ancestral to living humans, human fossils from the Klasies River Mouth caves (Rightmire & Deacon, 1991), Die Kelders Cave 1 (Avery et al., 1997; Grine et al., 1991; Grine, 1999), and other southern African sites still pinpoint Africa as the cradle of modern morphology, and southern Africa has provided most of what we know about MSA behavior. Southern African assemblages underscore the MSA artefact characterization we offered above (Volman, 1984; Thackeray, 1992, 1999), and the associated animal remains have provided most of what we know about MSA subsistence and ecology.

Southern Africa is also the main source of information on the Later Stone Age (LSA) complex that succeeded the MSA. LSA sites contain a wide variety of highly standardized stone and bone artefacts, numerous art objects, etc., and the material record implies no significant behavioral difference between LSA populations and historically observed stone age hunter-gatherers. Comparisons between LSA and MSA faunal remains can thus illuminate the extent to which MSA economies resembled historic ones. Comparisons to date suggest that MSA people hunted and gathered relatively ineffectively (Klein & Cruz-Uribe, 1996a), but there is the limitation that the known MSA faunal

assemblages all antedate 60 ka, while LSA sites with large samples span only the past 20 ka. It is therefore not certain that more advanced hunting-gathering marked the beginning of the LSA between 50 and 40 ka ago. If this can be assumed, however, it would further explain how anatomically modern Africans spread to Europe.

Among the MSA sites that preserve faunal remains, the Klasies River Mouth caves (KRM) (Klein, 1976; Singer & Wymer, 1982) and Die Kelders Cave 1 (DK1) (this paper) have provided by far the largest samples. The MSA deposits at KRM date between roughly 127 and 57 ka ago (Deacon & Shuurman, 1992), while luminescence and ESR dates (Feathers & Bush, 2000; Schwarcz & Rink, 2000) and paleoenvironmental evidence presented here bracket the DK1 MSA Layers within global isotope stage 4, between roughly 71 and 57 ka ago. Our purpose here is to summarize the implications of the DK1 fauna for MSA environment and subsistence. For comparative purposes, we also describe the LSA fauna. We have presented some of this information briefly before, based on excavations in 1969–73 (Grine *et al.*, 1991) and in 1992–93 (Avery *et al.*, 1997). Here, we provide a single comprehensive account, based on the combined samples from 1969–95.

## An overview of the fauna

The DK1 fauna comprises micromammals (<0·75 kg adult weight), macromammals (≥0·75 kg adult weight), birds, reptiles, fish, and shellfish. Micromammal bones, mainly from tiny rodents and insectivores, occur primarily in the MSA sequence. They tend to abound in layers where other faunal remains and artefacts are rare, suggesting that barn owls (*Tyto alba*) or Cape eagle owls (*Bubo capensis*) were the principal accumulators. A mongoose or some other small carnivore may also have played a role. The 1992–1995 micromammal samples have not been analyzed, but the 1969–1973 samples imply the same environmental conditions that we infer from the macromammals below (Avery, 1982).

Macromammal bones are common throughout the DK1 sequence. We focus here on the specimens that we could readily identify to skeletal element and taxon, and we emphasize their utility for reconstructing prehistoric environment and ecology. Our most basic conclusions are that the MSA people lived under relatively cool, moist conditions and that they exploited terrestrial mammals less effectively than their LSA successors.

Bird bones also occur throughout the sequence, but they are far more numerous in the LSA layers, and the species frequencies also differ between the LSA and MSA. Cape gannet (*Morus capensis*) and cormorants (especially the Cape cormorant, *Phalacrocorax capensis*) heavily dominate the LSA, while the jackass penguin (*Spheniscus demersus*) is significantly more common in the MSA (Avery, 1990). An elevated frequency of penguins also distinguishes the MSA deposits at KRM, and MSA layers everywhere lack any trace of the bow and arrow, of snares, or of other technology that historic stone age people used to catch birds. Vestiges of this technology are known only from the LSA (Deacon, 1984), and the combined faunal remains and artefacts imply that MSA foragers much less often obtained birds that could fly.

Reptile bones are also common throughout the sequence. A small, unanalyzed minority come from snakes, probably mostly the mole snake (*Pseudoapsis cana*). A far larger number represent the angulate tortoise (*Chersina angulata*), which is still abundant nearby. Pieces of carapace and plastron dominate, but they tend to be highly fragmented, especially in the MSA layers, and for analytic purposes limb bones are more useful. Measurements we present below

show that the MSA tortoises tended to be significantly larger than the LSA ones. Since tortoise collection does not require sophisticated technology, the most parsimonious explanation is that the MSA people preyed less intensively on tortoises, probably because MSA human populations were relatively sparse.

Fish bones occur only in the LSA deposits, where they are extremely abundant (Schweitzer, 1979). The sample includes at least eight coastal species, but it is heavily dominated by the Hottentot fish (*Pachymetopon blochii*). Individuals of all sizes are well represented, suggesting that fishing involved both baited lines and nets. The DK1 MSA layers have provided no fish bones, and other regional MSA sites have produced only occasional large specimens that could come from scavenged washups. Only LSA sites contain fish gorges, net sinkers, and other likely fishing gear (Deacon, 1984), and the sum suggests that MSA people hardly exploited fish at all.

Shells occur in both the LSA and MSA deposits, but the MSA specimens are poorly preserved and difficult to identify. Assuming fundamental similarity to the MSA shells from KRM (Voigt, 1982; Thackeray, 1988) and from current excavations at Blombos Cave (Henshilwood, 1998), MSA people at DK1 collected the same intertidal mussels, whelks, limpets, topshells and so forth that abound in the LSA deposits (Schweitzer, 1979). At KRM, Blombos Cave, and other regional MSA sites, shells of various species tend to be much larger than those in LSA layers that formed under similar environmental conditions. Like tortoises, shellfish can be gathered with very simple technology, and larger MSA shellfish size again implies relatively small MSA human populations.

In sum, like the faunal evidence from other MSA sites, the DK1 data suggest that MSA people hunted and gathered less efficiently than their LSA successors.

## Macromammal taxonomic abundance

The LSA and MSA macromammal samples from all seasons now include, respectively, 51,571 and 174,816 bones that we could identify to skeletal part and taxon. Table 1 presents the number of identifiable specimens (NISPs) per taxon per stratigraphic unit together with the minimum numbers of individual animals (MNIs) from which the bones must come. Klein & Cruz-Uribe (1984) and Cruz-Uribe & Klein (1986) outline the assumptions and algorithms used to compute the MNIs. Figure 1 uses the MNIs to show the relative abundance of the main taxa in each DK1 layer described by Tankard and Schweitzer (1976) and Marean *et al.* (2000*b*). To aid interpretation, the figure also includes the macromammal MNIs from the nearby LSA site of Byneskranskop Cave 1 (BNK1) (Schweitzer & Wilson, 1982). BNK1 enjoys the same climatic and vegetational setting as DK1, but its fill dates mainly from the 11 ka immediately preceding the LSA occupation of DK1. It therefore helps to fill in the nearly 60-ka-long gap between the DK1 MSA and LSA layers.

Like most African archeological sites, DK1 has provided numerous highly fragmented bovid bones that are difficult to separate among closely related, like-sized species. Table 1 thus lists NISPs and MNIs for individual bovid species based strictly on specifically identifiable dentitions and horn-cores, and NISPs and MNIs for five bovid size classes based on all skeletal elements. The size classes are more or less conventional and they correspond closely to the categories used by other analysts [for example, Vrba (1980); Brain (1981); Voigt (1983), and Plug (1985, 1990, 1993). In regard to the DK1 and BNK1 faunas (Linnean names in Table 1), small bovids include Cape grysbok, steenbok, and klipspringer; small-medium bovids include bushbuck, mountain reedbuck, vaalribbok,

springbok, and sheep; large-medium bovids include greater kudu, blue antelope, southern reedbuck, Cape hartebeest, bontebok, and black wildebeest; large bovids include eland, Cape buffalo, and cattle; and very large bovids include the extinct long-horned buffalo.

## Historical and environmental implications of the macromammal species

Table 1 and Figure 1 show that the Cape dune molerat, a large burrowing rodent, dominates the MSA and LSA macromammal samples. The dune molerat is very common near Die Kelders today, and its persistence through the entire sequence (including the terminal Pleistocene/Holocene LSA deposits at BNK1) indicates fundamental continuity in suitable sandy soils and associated food plants near DK1.

The manner in which the dune molerats were introduced is debatable, and we suggest below that they were accumulated mainly by people in the LSA and mainly by Cape eagle owls in the MSA. An important eagle owl contribution seems particularly likely in those MSA layers where dune molerats comprise more than 90% of the fauna (Figure 1). Based on historic observations (Avery, 1990), Cape eagle owls could also have introduced many of the hares, rock hyraxes, and even some of the small antelopes that are the next most common species in the MSA layers.

The LSA faunal sample comprises nearly all the macromammal species that were recorded near DK1 historically, and none that was not. In addition, the proportional representation of various species broadly recalls historic accounts of their relative abundance, and the fauna thus provides no indication that the LSA environment differed significantly from the historic one. This could have been anticipated, since the

LSA deposits accumulated only between 2000 and 1500 years ago.

DK1 was the first site to show that sheep were introduced to southern Africa roughly 1900 years ago (Schweitzer & Scott, 1973; Schweitzer, 1974; Henshilwood, 1996), and a side chamber known as Sampa's Cave may even have been a sheep pen. In this light, it is notable that the LSA fauna lacks firm evidence for cattle, which the historic Khoikhoi herder-foragers kept in large numbers (Elphick, 1977; Deacon, 1984; Smith, 1990, 1992). A neonate bovine dentition is the best candidate, but it cannot be unequivocally separated from Cape buffalo, and the possibility remains that the DK1 people had only sheep. Taken with evidence from the Kasteelberg open-air middens and other like-aged regional LSA sites, the implication may be that cattle reached the southern tip of Africa only 1300 years ago (Smith, 1990, 1992; Sealy & Yates, 1994), 600 years after sheep and 100–200 years after LSA people ceased to visit DK1 routinely.

In sharp contrast to the LSA fauna, the MSA sample contains several species that did not occur near DK1 historically and that are unknown in any regional fauna post-dating 10 ka ago. The extralimital species include the quagga, black wildebeest, and springbok, which were widespread in the South African interior into the nineteenth century; the southern reedbuck, whose nearest historic occurrence was in marshy areas far to the east and north (Skead, 1980; Skinner & Smithers, 1990); and the Cape zebra and the long-horned buffalo, which apparently vanished from southern Africa about 10 ka ago (Klein, 1984). The extralimital forms are all grazers that could not have prospered in the sclerophyllous scrub and bush (fynbos) that dominated the DK1 region historically. Their presence thus implies grassier vegetation, probably as a result of reduced evaporation, greater rainfall, or both. The southern reedbuck also indicates sufficient moisture to maintain a

Table 1   The macromammal taxa represented in the LSA and MSA layers of Die Kelders Cave 1 (NISPs=the number of identifiable specimens; MNIs=the minimum number of individuals the specimens must represent)

| | LSA | | MSA 4/5 | | MSA 6 | | MSA 7 | | MSA 8 | | MSA 9 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | NISPs | MNIs | NISPs | MNIs | NISPs | MNIs | NISPs | MNIs | NISPs | MNIs | NISPs | MNIs |
| Hedgehog (*Erinaceus frontalis*) | | | 27 | 7 | 38 | 5 | 1 | 1 | | | 1 | 1 |
| Hares (*Lepus* spp.) | 40 | 5 | 2500 | 72 | 11,694 | 227 | 247 | 9 | 727 | 22 | 107 | 5 |
| Cape dune molerat (*Bathyergus suillus*) | 30,549 | 1766 | 9117 | 244 | 20,267 | 443 | 8438 | 255 | 105,974 | 2464 | 3911 | 89 |
| Porcupine (*Hystrix africaeaustralis*) | 10 | 2 | 9 | 1 | 15 | 2 | | | | | 1 | 1 |
| Chacma baboon (*Papio ursinus*) | 113 | 5 | | | | | | | | | | |
| Human (*Homo sapiens*) | 73 | 3 | 3 | 1 | 18 | 2 | | | 2 | 1 | | |
| Black-backed jackal (*Canis mesomelas*) | 18 | 1 | 7 | 1 | 2 | 1 | | | | | | |
| Cape fox (*Vulpes chama*) | 2 | 1 | | | | | | | | | | |
| Cape hunting dog (*Lycaon pictus*) | | | | | | | | | | | | |
| Striped polecat (*Ictonyx striatus*) | 59 | 5 | 6 | 1 | | | | | | | | |
| Honey badger (*Mellivora capensis*) | 23 | 3 | 37 | 2 | 55 | 2 | 2 | 1 | 3 | 1 | 1 | 1 |
| Genet cat (*Genetta* sp(p).) | 50 | 3 | 1 | 1 | 6 | 2 | | | | | | |
| Water mongoose (*Atilax paludinosus*) | | | 1 | 1 | | | 1 | 1 | | | | |
| Indeterminate mongoose (Viverridae indet.) | 4 | 1 | | | 1 | 1 | | | | | | |
| Egyptian mongoose (*Herpestes ichneumon*) | 1 | 1 | 5 | 1 | 4 | 1 | | | | | | |
| Gray mongoose (*Herpestes pulverulentus*) | 32 | 5 | 24 | 3 | 187 | 9 | | | | | | |
| Brown hyena (*Hyaena brunnea*) | | | | | 3 | 1 | 1 | 1 | | | | |
| Wild cat (*Felis libyca*) | 51 | 4 | 11 | 1 | 11 | 2 | | | | | | |
| Carcal or serval (*Felis caracal* or *F. serval*) | 38 | 3 | 5 | 1 | 6 | 1 | | | | | 2 | 1 |
| Lion (*Panthera leo*) | | | | | 1 | 1 | | | | | | |
| Leopard (*Panthera pardus*) | 32 | 3 | | | | | | | | | | |
| Cape fur seal (*Arctocephalus pusillus*) | 12,153 | 108 | 169 | 4 | 619 | 12 | 7 | 1 | 16 | 2 | 82 | 2 |
| Southern elephant seal (*Mirounga leonina*) | 2 | 2 | | | | | | | | | | |
| Rock hyrax (*Procavia capensis*) | 503 | 28 | 352 | 21 | 1964 | 103 | 54 | 4 | 95 | 5 | 49 | 5 |
| African elephant (*Loxodonta africana*) | 22 | 1 | | | | | | | | | | |
| Cape zebra (*Equus capensis*) | | | 1 | 1 | | | | | | | | |

| Taxon | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quagga (*Equus quagga*) | | | | | 2 | 1 | | | | | | |
| Black rhinoceros (*Diceros bicornis*) | 8 | 1 | 85 | 2 | 26 | 2 | | | | | | |
| White rhinoceros (*Ceratotherium simum*) | | | | | | | | | | | | |
| White, black and indet. rhinoceros (Rhinocerotidae) | 8 | 1 | 85 | 2 | 27 | 2 | | | | | | |
| Hippopotamus (*Hippopotamus amphibius*) | 2 | 1 | 6 | 1 | 139 | 3 | 2 | 1 | 3 | 1 | 2 | 1 |
| Bushpig (*Potamochoerus porcus*) | 1 | 1 | | | | | | | | | | |
| Eland (*Taurotragus oryx*) | | | 48 | 3 | 171 | 10 | 1 | 1 | 1 | 1 | 7 | 2 |
| Bushbuck (*Tragelaphus scriptus*) | 1 | 1 | | | | | | | | | | |
| Greater kudu (*Tragelaphus strepsiceros*) | | | 2 | 1 | 4 | 1 | | | | | | |
| Blue antelope (*Hippotragus leucophaeus*) | 1 | 1 | 3 | 1 | 39 | 5 | 3 | 1 | 1 | 1 | | |
| Southern reedbuck (*Redunca arundinum*) | | | 10 | 3 | 48 | 3 | | | 2 | 1 | | |
| Mountain reedbuck (*Redunca fulvorufula*) | | | 1 | 1 | 2 | 1 | | | | | | |
| Vaalribbok (*Pelea capreolus*) | 3 | 1 | 27 | 5 | 167 | 11 | 1 | 1 | 3 | 1 | 3 | 1 |
| Bontebok (*Damaliscus dorcas*) | | | 2 | 1 | 1 | 1 | | | 1 | 1 | | |
| Cape hartebeest (*Alcelaphus buselaphus*) | 1 | 1 | | | | | | | | | | |
| Black wildebeest (*Connochaetes gnou*) | | | 24 | 3 | 55 | 4 | 5 | 1 | 2 | 1 | 1 | 1 |
| Springbok (*Antidorcas australis*) | | | 4 | 2 | 15 | 3 | 2 | 1 | 3 | 1 | 5 | 1 |
| Klipspringer (*Oreotragus oreotragus*) | 8 | 2 | 68 | 4 | 192 | 6 | 1 | 1 | 5 | 1 | | |
| Steenbok (*Raphicerus campestris*) | 73 | 27 | | | | | | | | | | |
| Cape grysbok (*Raphicerus melanotis*) | 246 | 105 | 16 | 10 | 51 | 15 | | | 5 | 3 | | |
| Steenbok and/or grysbok (*Raphicerus* spp.) | 2634 | 157 | 642 | 25 | 6066 | 151 | 124 | 5 | 232 | 9 | 45 | 3 |
| Cape buffalo (*Syncerus caffer*) | 52 | 5 | 7 | 1 | 6 | 2 | 1 | 1 | | | 1 | 1 |
| Long-horned buffalo (*Pelorovis antiquus*) | | | 4 | 1 | 22 | 2 | | | 3 | 1 | | |
| Buffalos and/or cattle (Bovini) | 68 | 5 | 11 | 1 | 32 | 3 | 1 | 1 | 3 | 1 | 2 | 1 |
| Sheep (*Ovis aries*) | 943 | 21 | | | | | | | | | | |
| Bovids—general | | | | | | | | | | | | |
|   Small | 3949 | 158 | 1497 | 25 | 11,999 | 156 | 270 | 6 | 730 | 16 | 112 | 4 |
|   Small–medium | 1018 | 21 | 234 | 5 | 1321 | 16 | 14 | 1 | 73 | 4 | 49 | 2 |
|   Large–medium | 68 | 3 | 220 | 5 | 669 | 10 | 17 | 2 | 30 | 2 | 11 | 1 |
|   Large | 611 | 6 | 139 | 3 | 489 | 11 | 5 | 1 | 19 | 1 | 22 | 2 |
|   Very large | | | 4 | 1 | 30 | 2 | 2 | 1 | 3 | 1 | | |
| Dolphins (Delphinidae indet.) | 53 | 2 | | | 4 | 1 | | | 3 | 1 | | |
| Whales (Cetacea indet.) | 8 | 1 | | | 8 | 1 | | | | | | |

*Continued*

DIE KELDERS 1 FAUNA

**Table 1** *(Continued)*

| | MSA 10 | | MSA 11 | | MSA 12 | | MSA 13 | | MSA 14 | | MSA 15 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | NISPs | MNIs | NISPs | MNIs | NISPs | MNIs | NISPs | MNIs | NISPs | MNIs | NISPs | MNIs |
| Hedgehog (*Erinaceus frontalis*) | 1 | **1** | | | | | | | 1 | **1** | | |
| Hares (*Lepus* spp.) | 80 | **3** | 13 | **2** | 49 | **3** | 31 | **3** | 634 | **18** | 46 | **3** |
| Cape dune molerat (*Bathyergus suillus*) | 1208 | **30** | 300 | **8** | 268 | **12** | 185 | **6** | 382 | **10** | 117 | **6** |
| Porcupine (*Hystrix africaeaustralis*) | | | | | | | | | | | | |
| Chacma baboon (*Papio ursinus*) | | | | | 1 | **1** | | | 1 | **1** | | |
| Human (*Homo sapiens*) | 1 | **1** | | | | | | | 3 | **1** | | |
| Black-backed jackal (*Canis mesomelas*) | 1 | **1** | | | | | | | | | | |
| Cape fox (*Vulpes chama*) | | | | | | | | | | | | |
| Cape hunting dog (*Lycaon pictus*) | | | | | | | | | 1 | **1** | | |
| Striped polecat (*Ictonyx striatus*) | | | | | | | | | 2 | **1** | | |
| Honey badger (*Mellivora capensis*) | | | | | | | | | | | | |
| Genet cat (*Genetta* sp(p).) | | | | | | | 2 | **1** | | | | |
| Water mongoose (*Atilax paludinosus*) | | | | | | | | | | | | |
| Indeterminate mongoose (Viverridae indet.) | | | | | | | | | | | | |
| Egyptian mongoose (*Herpestes ichneumon*) | | | | | | | | | | | | |
| Gray mongoose (*Herpestes pulverulentus*) | | | | | 4 | **1** | | | 10 | **2** | | |
| Brown hyena (*Hyaena brunnea*) | 1 | | | | 3 | **1** | 1 | **1** | | | | |
| Wild cat (*Felis libyca*) | | | | | | | 1 | **1** | 1 | **1** | | |
| Carcal or serval (*Felis caracal* or *F. serval*) | | | | | | | | | | | | |
| Lion (*Panthera leo*) | | | | | | | | | | | | |
| Leopard (*Panthera pardus*) | | | | | | | | | | | | |
| Cape fur seal (*Arctocephalus pusillus*) | 254 | **4** | 29 | **2** | 58 | **2** | 20 | **1** | 66 | **3** | 9 | **2** |
| Southern elephant seal (*Mirounga leonina*) | | | | | | | | | | | | |
| Rock hyrax (*Procavia capensis*) | 43 | **5** | 6 | **1** | 53 | **5** | 15 | **2** | 112 | **7** | 10 | **2** |
| African elephant (*Loxodonta africana*) | | | | | | | | | | | | |
| Cape zebra (*Equus capensis*) | | | | | | | | | | | | |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quagga (*Equus quagga*) | | | | | | | | | | | | |
| Black rhinoceros (*Diceros bicornis*) | | | | | | 1 | **1** | 2 | **1** | | |
| White rhinoceros (*Ceratotherium simum*) | | | | | | 1 | **1** | 1 | **1** | | |
| White, black and indet. rhinoceros (Rhinocerotidae) | | | | 1 | **1** | 4 | **2** | 4 | **1** | | |
| Hippopotamus (*Hippopotamus amphibius*) | | | | | | 2 | **1** | | | | |
| Bushpig (*Potamochoerus porcus*) | | | | | | | | | | | |
| Eland (*Taurotragus oryx*) | 17 | **2** | 16 | **1** | 68 | **7** | 1 | **1** | 40 | **3** | 15 | **1** |
| Bushbuck (*Tragelaphus scriptus*) | | | | | | | | | | | |
| Greater kudu (*Tragelaphus strepsiceros*) | | | | 3 | **1** | | | | | | |
| Blue antelope (*Hippotragus leucophaeus*) | 1 | **1** | | | 1 | **1** | | | | | |
| Southern reedbuck (*Redunca arundinum*) | 1 | **1** | | | 2 | **1** | | | 3 | **1** | |
| Mountain reedbuck (*Redunca fulvorufula*) | | | | 1 | **1** | | | | | | |
| Vaalribbok (*Pelea capreolus*) | | | | | | | | 1 | **1** | | |
| Bontebok (*Damaliscus dorcas*) | | | | | | | | | | | |
| Cape hartebeest (*Alcelaphus buselaphus*) | | | | | | | | | | | |
| Black wildebeest (*Connochaetes gnou*) | 5 | **1** | | | 1 | **1** | | | 4 | **1** | |
| Springbok (*Antidorcas australis*) | 5 | **2** | | | | | | | 2 | **1** | |
| Klipspringer (*Oreotragus oreotragus*) | | | 1 | **1** | 3 | **1** | | | 3 | **1** | 2 | **1** |
| Steenbok (*Raphicerus campestris*) | | | | | | | | | | | |
| Cape grysbok (*Raphicerus melanotis*) | 2 | **2** | 1 | **1** | 1 | **1** | | | 3 | **2** | |
| Steenbok and/or grysbok (*Raphicerus* spp.) | 79 | **3** | 12 | **2** | 86 | **3** | 26 | **2** | 215 | **10** | 3 | **1** |
| Cape buffalo (*Syncerus caffer*) | | | | | | | | | | | |
| Long-horned buffalo (*Pelorovis antiquus*) | | | | | | | | 2 | **1** | | |
| Buffalos and/or cattle (Bovini) | | | | 1 | **1** | 2 | **1** | 2 | **1** | | |
| Sheep (*Ovis aries*) | | | | | | | | | | | |
| Bovids—general | | | | | | | | | | | |
|   Small | 123 | **3** | 37 | **2** | 151 | **4** | 61 | **2** | 465 | **10** | 57 | **3** |
|   Small–medium | 75 | **2** | 11 | **1** | 31 | **2** | 13 | **2** | 43 | **3** | 4 | **1** |
|   Large–medium | 63 | **2** | 6 | **1** | 45 | **2** | 8 | **1** | 38 | **2** | 8 | **1** |
|   Large | 35 | **2** | 26 | **2** | 132 | **7** | 5 | **1** | 79 | **3** | 58 | **1** |
|   Very large | | | | | | | | 4 | **1** | | |
| Dolphins (Delphinidae indet.) | 1 | **1** | | | | | | | 1 | **1** | |
| Whales (Cetacea indet.) | | | | | | | | | | | |
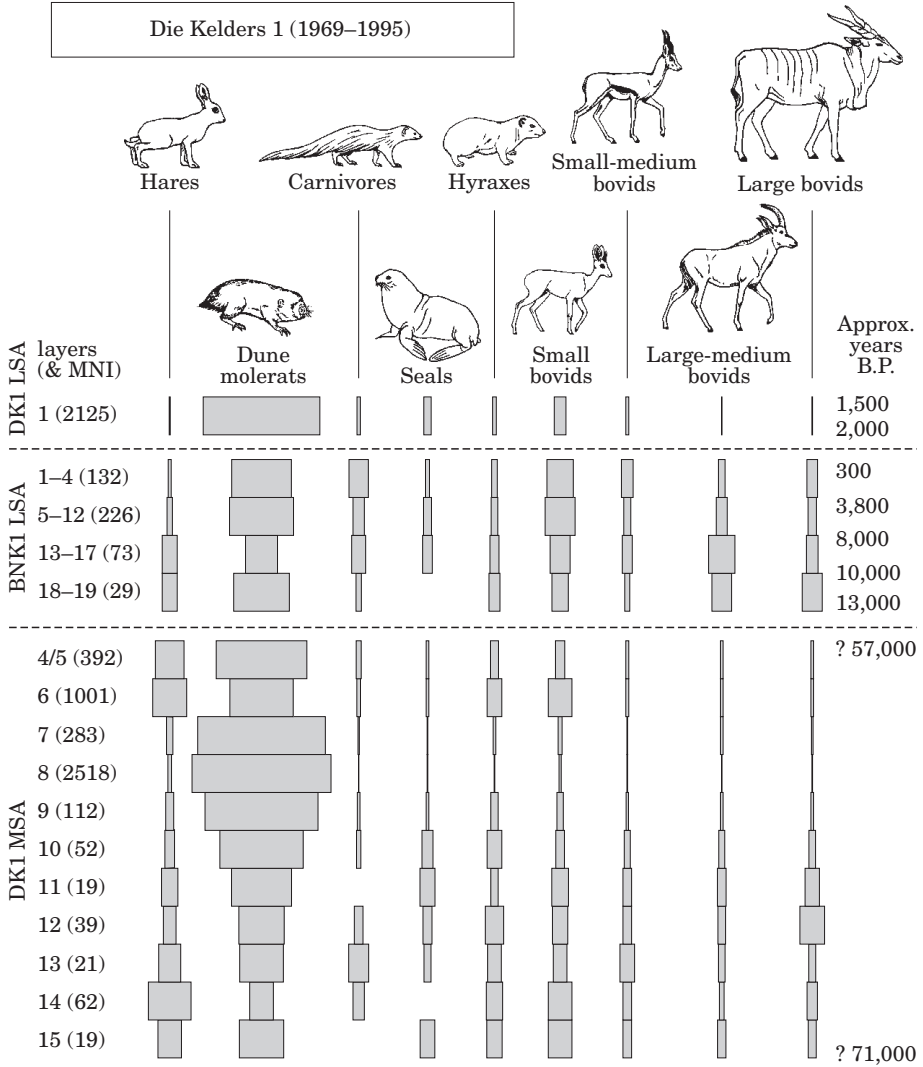
Figure 1. The relative abundance of the main taxa in the MSA and LSA layers of Die Kelders Cave 1 and in the LSA layers of Byneskranskop Cave 1. The horizontal bars are proportional to the minimum number of individuals (MNI) by which each taxon or quasi-taxon is represented in each layer of each site.

marsh or other large body of standing freshwater where none existed historically. In general then, the macromammal species are consistent with sedimentological indications for relatively cool, moist conditions during the MSA occupation (Tankard & Schweitzer, 1976). The microfauna supports the same inference, but it also suggests relatively lower humidity near the beginning

and end of the MSA sequence (Avery, 1982). Reduced moisture could explain the tendency for hares to be most numerous near the bottom and top (Figure 1), and it may also be signaled by a reduction in mean molerat size near the top (next section).

Faunas with the same historically absent grazing or moisture-living species found at DK1 have also been found at Nelson Bay

Cave, Boomplaas Cave A, BNK1, Swartklip 1, Elands Bay Cave, and other regional archeological and fossil sites (Klein, 1983). In each case, direct dating or geologic context indicates a glacial age, mainly within the Last Glaciation (defined as global isotope stages 4 through 2, roughly between 71 and 12 ka ago). At Nelson Bay, Swartklip 1, and other sites where the grazing species dominate heavily, direct dating, sedimentologic observations, or both indicate peak glacial conditions. These were associated with a drop in sea level that displaced the coastline up to 80 km seawards. As a result, peak glacial deposits totally lack marine creatures, including fur seals and shore birds. Their persistence at DK1 implies that the MSA occupation occurred under milder glacial conditions. Luminescence and ESR dates in fact show that the DK1 MSA deposits formed during the early part of the Last Glaciation (=isotope stage 4), when the coastline was probably mainly within 5–8 km of the site (van Andel, 1989; van Andel & Tzedakis, 1996).

It is now well-known that glacial intervals tended to be drier than interglacial ones, mainly because of reduced evaporation from cooler oceans. However, the precipitation history of individual regions also depended on changes in oceanic and atmospheric circulation patterns. Faunal and sedimentological evidence from sites like DK1 suggests that the southwestern corner of Africa was relatively moist in the early part of the Last Glaciation (stage 4, between roughly 71 and 57 ka ago), generally very dry in the middle part (between about 57 and 24 ka ago), and variably moist in the late part (stage 2, from 24 to 12 ka ago). It is the aridity in the middle part that sparked the population decline and reduced archeological visibility to which we referred above. The early Holocene, between roughly 9 and 6 ka ago was also relatively dry, and only the late Holocene, after 6–5 ka ago, was as moist or moister than the present.

## Average adult mammal size and past climate

Fossil adult size can illuminate the ancient environment in mammal species where mean adult size in living populations has been related to geographic variation in temperature, precipitation, or some other key environmental variable. The fossil sample must of course be large enough to allow a reliable estimate of fossil mean size. At DK1, the three species that best match the basic requirements are the gray mongoose, the Cape dune molerat, and the rock hyrax.

Within the gray mongoose's historic range, adult size tends to increase as average temperature decreases (Klein, 1986), in keeping with the ecological generalization known as Bergmann's Rule. Figure 2 illustrates the size–temperature relationship, with upper carnassial length as a proxy for size and latitude as a proxy for temperature. The figure also includes a boxplot summarizing DK1 MSA upper carnassial length. The key elements in the plot are the mean, represented by a horizontal line near the center, and the 95% confidence limits for the mean represented by the surrounding diamond. The plot shows that the MSA carnassials tended to be significantly longer than the regression predicts for the latitude of DK1. This supports other faunal and sedimentological indications that the MSA deposits formed under relatively cool conditions. Unfortunately, gray mongooses are too rare in the LSA sample to estimate their mean size.

In the Cape dune molerat, adult size varies with rainfall rather than with temperature (Klein, 1991). Figure 3 illustrates the size–rainfall relationship, based on the mediolateral diameter of the fused distal humerus as a proxy for individual size and on rainfall estimates produced by the program *GENRAIN*. *GENRAIN*, written by Walter Zucchini of the University of Cape Town, includes data on historic rainfall
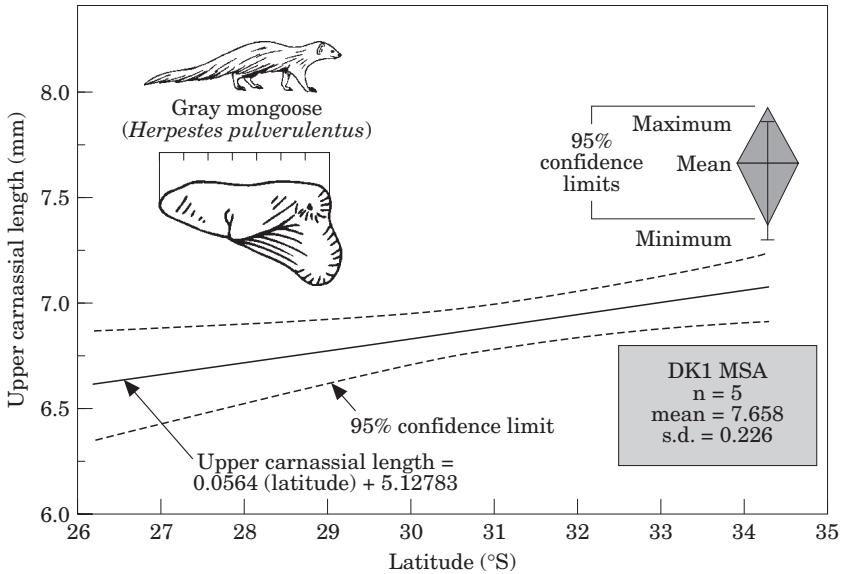
Figure 2. A least squares linear regression of gray mongoose upper carnassial (P⁴) length on latitude, based on 69 modern mongooses, and a boxplot describing upper carnassial length in the MSA layers of Die Kelders Cave 1.

across South Africa. It uses the latitude and longitude of any given locale to predict the mean annual rainfall over an interval of any length. We used it to estimate annual rainfall over a 10-year period for each modern molerat locale. Since the locales are not evenly distributed through all possible rainfall regimes and the mean annual rainfall for each locale is itself only an estimate, the regression line in Figure 3 must only approximate the real relationship between molerat size and rainfall. However, using the same fundamental boxplot format as Figure 2, the figure not only reveals the positive association between molerat size and rainfall, it also shows that on average the DK1 MSA molerats were much larger than the historic rainfall (roughly 550 mm per annum) predicts. This strongly supports other faunal and sedimentologic evidence for moist climate when MSA people occupied DK1.

The figure also shows the DK1 LSA molerats tended to be significantly smaller than their MSA counterparts. However, on average, they may still have exceeded the mean size anticipated from present-day rainfall, and the difference could imply somewhat higher rainfall when the LSA sample accumulated between 2000 and 1500 years ago. Alternatively, it might simply reflect imperfections in the historic dataset used to calculate the size-and-rainfall relationship.

Figure 4 illustrates mean molerat size for successive stratigraphic units within the composite DK1 and BNK1 sequences. The circles at the bottom of the diagram summarize the information in the means diamonds (95% confidence limits). Means associated with circles that do not overlap differ in the conventional statistical sense. The greater the distance between circles, the greater the probability of a real (versus chance) difference. The figure demonstrates once again the remarkably large size of the MSA molerats, but it also shows that they tend to become smaller towards the top of the sequence.

The molerat size data thus support microfaunal indications for somewhat drier
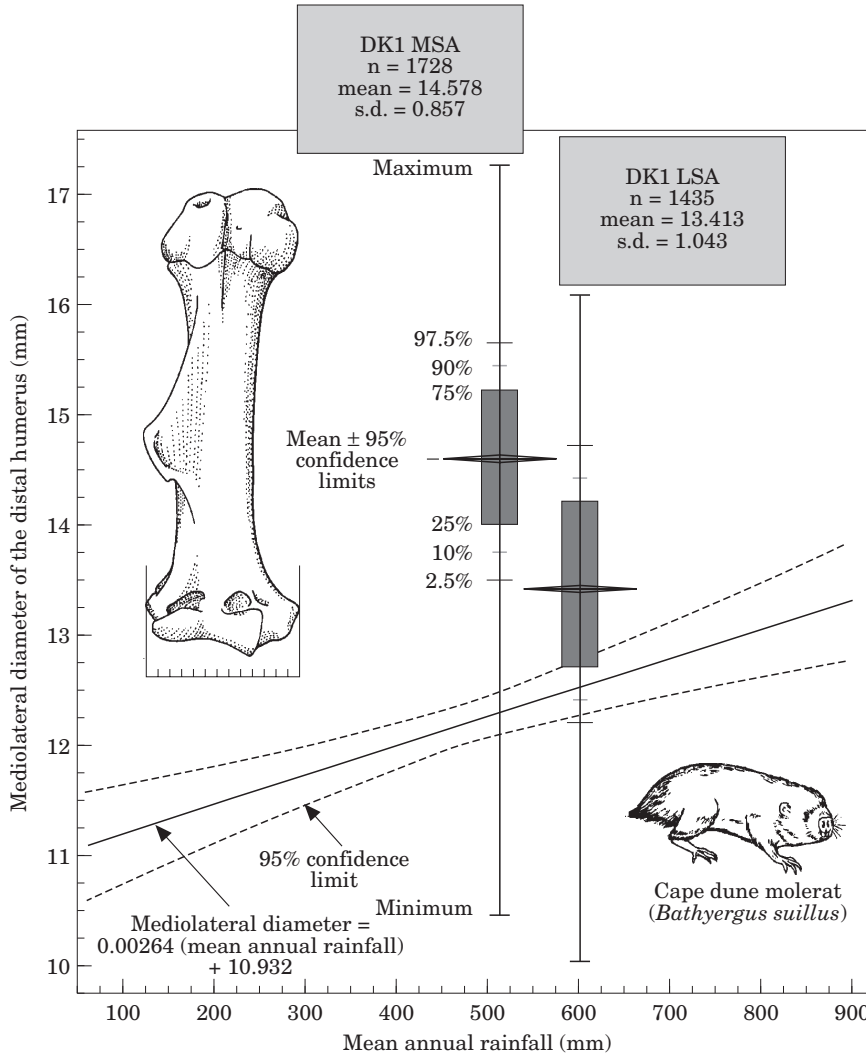
Figure 3. A least squares linear regression of dune molerat distal humerus breadth on rainfall, based on 144 modern dune molerats, and boxplots summarizing distal humerus breadth in dune molerat samples from the LSA and MSA layers of Die Kelders Cave 1.

climate near the top of the MSA sequence. The molerat samples from the lowermost layers (9–15) had to be lumped for statistical summarization, but larger samples may one day show that the climate was also relatively drier near the bottom. The figure indicates that the smallest molerats, implying the driest conditions in the composite sequence, come from the early Holocene layers 12–5 at BNK 1. In this instance, relatively small size is in keeping with other indications that early Holocene climate was regionally dry. On the west coast of South Africa, and in the interior, it may have been so dry that human populations declined almost as much as they did in the middle of the Last Glaciation (Deacon & Thackeray, 1984).

The rock hyrax resembles the dune molerat in that mean adult size varies with rainfall rather than with temperature, but
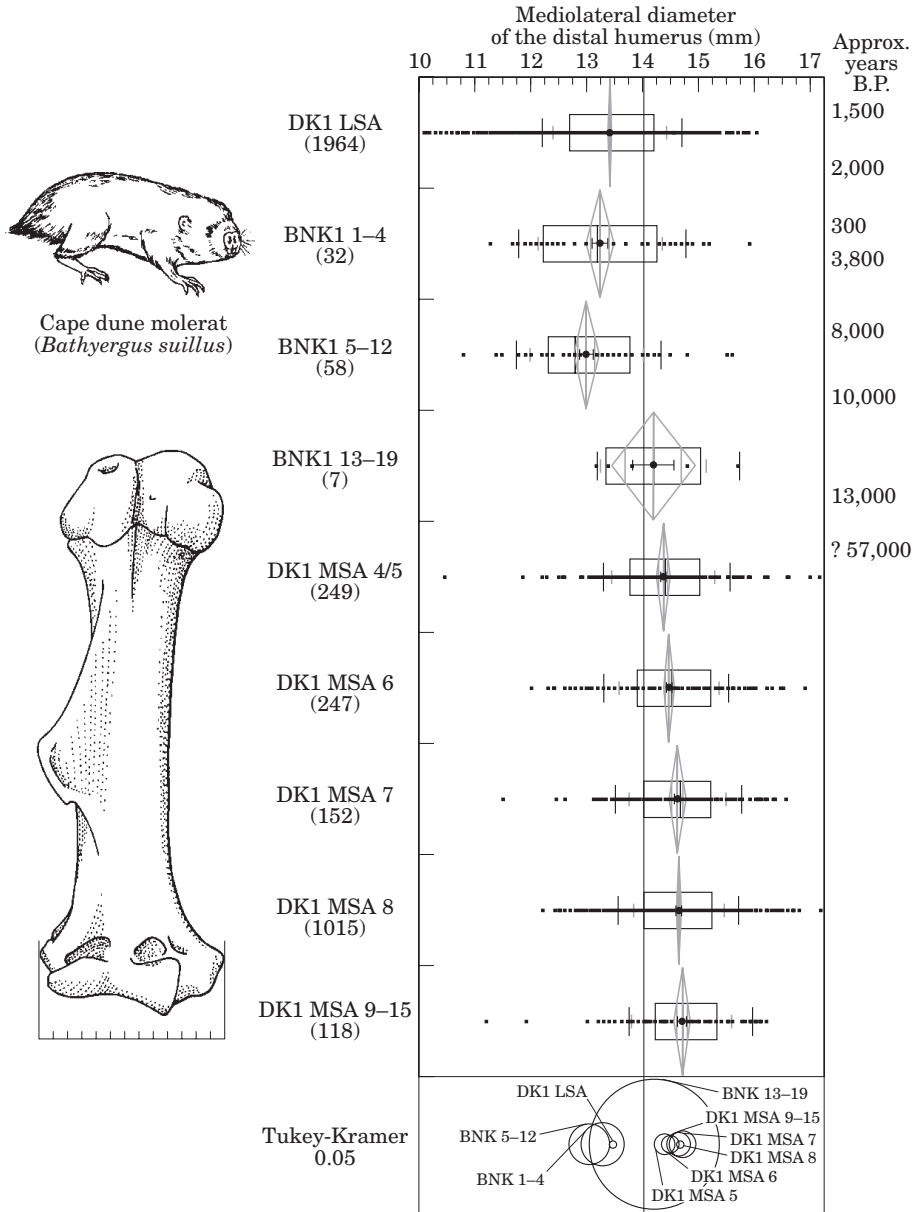
Figure 4. Boxplots summarizing dune molerat distal humerus breadth in successive stratigraphic units at Die Kelders Cave 1 and Byneskranskop Cave 1. The most essential features of each boxplot are the mean, indicated by the vertical line near the center and the 95% confidence limits for the mean, indicated by the surrounding diamond. In conventional statistical terms, two sample means differ significantly when their associated diamonds fail to overlap.

the relationship is not linear. Average hyrax size peaks at a rainfall of about 700 mm per annum and it declines both below and above this figure (Klein & Cruz-Uribe, 1996b). The curvilinear relationship emerged from an analysis of thousands of hyrax crania
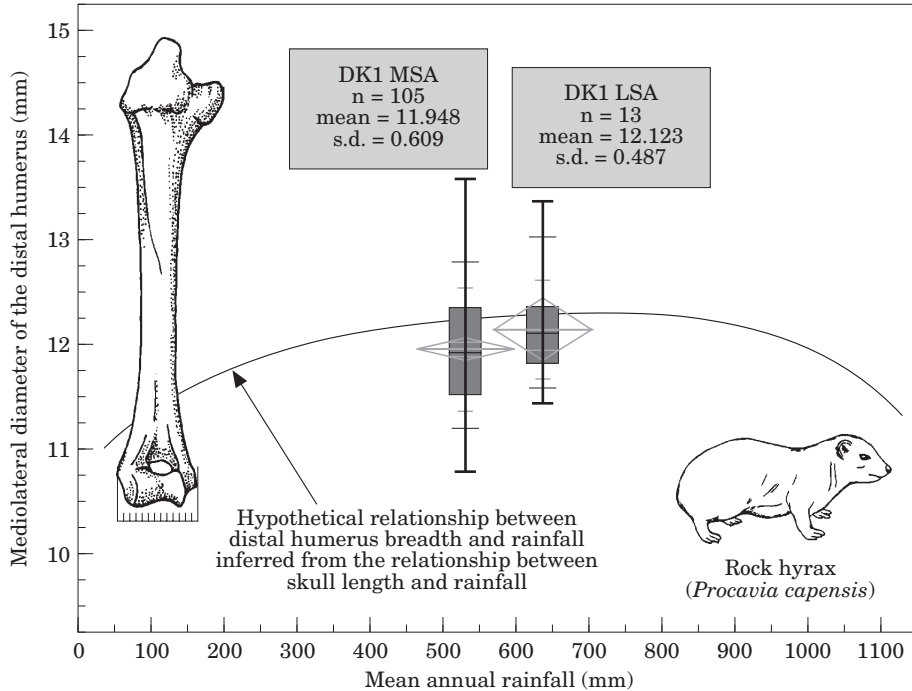
Figure 5. The approximate curvilinear relationship between rock hyrax distal humerus breadth and rainfall, and boxplots summarizing distal humerus breadth in the LSA and MSA samples from Die Kelders Cave 1. The caption to Figure 4 outlines the boxplot format.

from eagle roosts scattered across southern Africa, but the eagles unfortunately consumed most of the hyrax limb bones, and limb bones—not crania—dominate all archeological hyrax samples, including those from DK1. Distal humeri are particularly common in the fossil samples, and Figure 5 presents a pseudoregression of distal humerus breadth on rainfall assuming that the regression would have the same shape as the regression of cranial length on rainfall. The figure also includes boxplots that summarize hyrax distal humerus size in the DK1 LSA and MSA samples. The plots reveal no significant size difference between the two samples, and the lack might appear to undermine the inference that the MSA climate was much wetter. However, with the curvilinear nature of the size–rainfall relationship in mind, the boxplots might instead mean that MSA rainfall was about

as far above the 700 mm optimum as LSA rainfall was below it.

## Behavioral implications of the macromammals

At KRM, the MSA fauna is notable for an abundance of eland, which far outnumbers Cape buffalo, bushpig, and other species that were probably far more common near the site (Klein, 1976). In sharp contrast, LSA faunas that accumulated under similar environmental conditions contain many fewer eland relative to other species. Since eland respond to hunters far less aggressively than buffalo or bushpig, a reasonable explanation is not that LSA people hunted eland less, but that their enhanced technology allowed them to pursue other, more aggressive and more common species much more. The increase in meat yields would have been
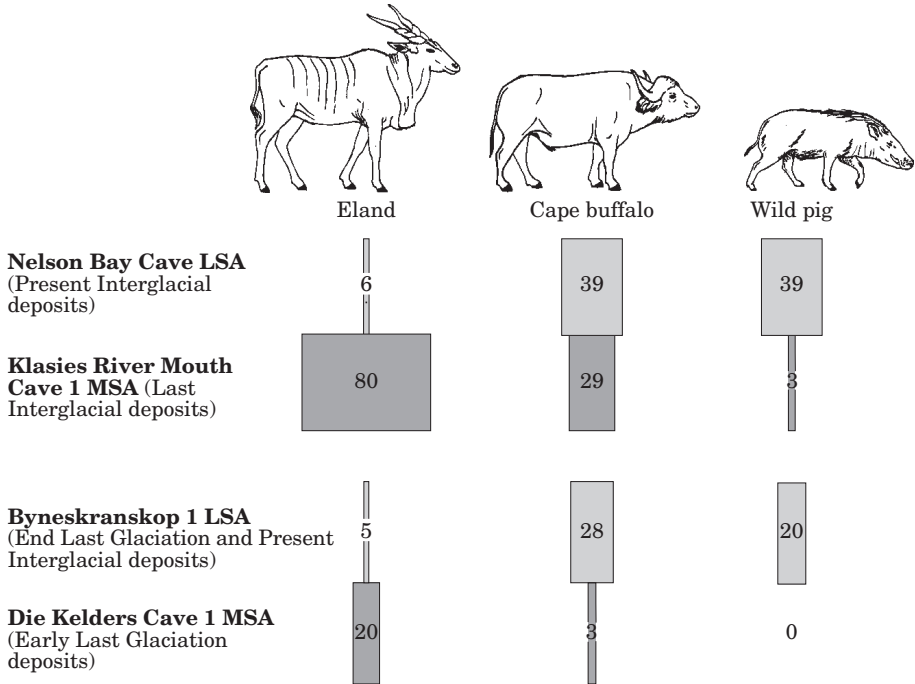
Figure 6. Top: The minimum numbers of eland, Cape buffalo, and bushpig in samples from the Last Interglacial deposits of Klasies River Mouth Cave 1 and in the Present Interglacial deposits of nearby Nelson Bay Cave. Bottom: The minimum number of individuals from the same species in the early Last Glacial deposits of Die Kelders Cave 1 and in the end-Last Glacial/Present Interglacial deposits of nearby Byneskranskop Cave 1.

significant, and this could help explain why LSA populations appear to have been much denser. Eland appear similarly abundant relative to other large ungulates in the DK1 MSA sample and they are much less numerous in the LSA sample from nearby BNK1 (Figure 6). However, the contrast provides only indirect support for inferior MSA hunting ability, because the DK1 large ungulate subsample is relatively small and the BNK1 LSA sample formed under mostly different (terminal glacial but mainly present interglacial) climatic conditions.

Among other behavioral issues that the DK1 fauna could address are the season(s) of the year when the site was occupied and the ways in which various species were obtained (for example, by stalking, trapping, or driving). Seasonality is most readily established from species in which females

tend to give birth more or less simultaneously. With regard to DK1, historic observations indicate that the most appropriate species are large grazing ungulates, like the hartebeest, wildebeest, and Cape buffalo, and the Cape fur seal. If each of these species were obtained only seasonally, individual death ages would form discrete clusters, separated by gaps reflecting a repeated period(s) each year when carcasses could not reach the site, because people were absent. Unfortunately, the detection of discrete age cohorts requires very large samples, and even KRM has produced too few large bovid bones. The more abundant small bovids, like the Cape grysbok and steenbok, are unsuitable, because they tend to breed throughout the year.

At DK1, only the LSA deposits have provided enough fur seal bones for age–cohort

detection. Metric comparisons to humeri, mandibles, and other bones from known age individuals show that the LSA seals were overwhelmingly about 9–11 months old (Klein & Cruz-Uribe, 1996a). Essentially the same peak in 9–11-month-olds characterizes all coastal LSA sites where fur seals are well represented, and the implication is that LSA people focused their coastal visits on the August–September interval when 9-month-old seals are ejected from their offshore birth rookeries and frequently wash up on mainland beaches, exhausted or dead. In contrast, the large KRM MSA seal sample contains many more subadult and adult seals, and the wide KRM age distribution resembles that in modern Namibian brown hyena dens (Klein & Cruz-Uribe, 1996a). The brown hyenas occupy the coast year round, and the implication may be that MSA people did likewise. MSA seasonal movement may have been constrained by technological limitations, including a lack of water containers. So far, these are evidenced only for the LSA (Deacon, 1984).

In general, sample demography provides the most direct indication of how prehistoric people obtained a species. A fundamental assumption is that both sexes and all ages were available, but that species behavior or technology led people to obtain individuals of one sex or of particular ages disproportionately. At DK1, the fur seals meet the availability requirement most poorly, since individuals spend most of their time on off-shore rookeries or at sea where local stone age people could not reach them. Terrestrial ungulates are less problematic, and their sex-age profiles can be very informative. It is usually difficult to determine ungulate sex from the skeletal parts that survive in fossil assemblages, but age is closely reflected in dental wear, and teeth are generally abundant. Wear can be assessed subjectively, but for the high-crowned ungulates that dominate DK1 and most other African samples, dental crown

heights provide a more objective and readily replicable measure of age. This is particularly true, since subjective wear assessment is extremely difficult for isolated teeth, and these prevail in many fossil samples, including that from DK1.

For species in which the relationship between crown height and age has been established, ages can be estimated from crown heights and then plotted for comparison to the two related theoretical age profiles that characterize all stable populations of large mammals. The two profiles differ most conspicuously in the representation of prime-age (reproductively active) adults, between roughly 10% and 40% of potential lifespan. In the first theoretical profile, which mirrors the structure of a live herd, prime-age adults are very abundant relative to old (post-prime) individuals. In the second, which reflects the age structure of those individuals who must die to maintain the live profile, prime-age adults are much rarer relative to older ones.

The two theoretical profiles apply to all populations, but their specific shapes differ from population to population, and truly enormous samples are necessary to distinguish them in rapidly breeding species. This is because these species tend to contain an extremely small number of old (vs. prime-age) individuals. Unfortunately, the grysbok and steenbok that dominate the DK1 ungulate samples fall in the fast-breeding category, and the samples are not large enough to determine whether the observed profiles more closely resemble one or the other theoretical standard. In fact, they need not resemble either, since human behavior or local ecological conditions can produce site-specific deviations.

With regard to large, relatively slow-breeding ungulates at DK1, the LSA sheep and the MSA eland have provided sufficient specimens for demographic evaluation. For the sheep, it is possible to determine both age and sex, since bone preservation is
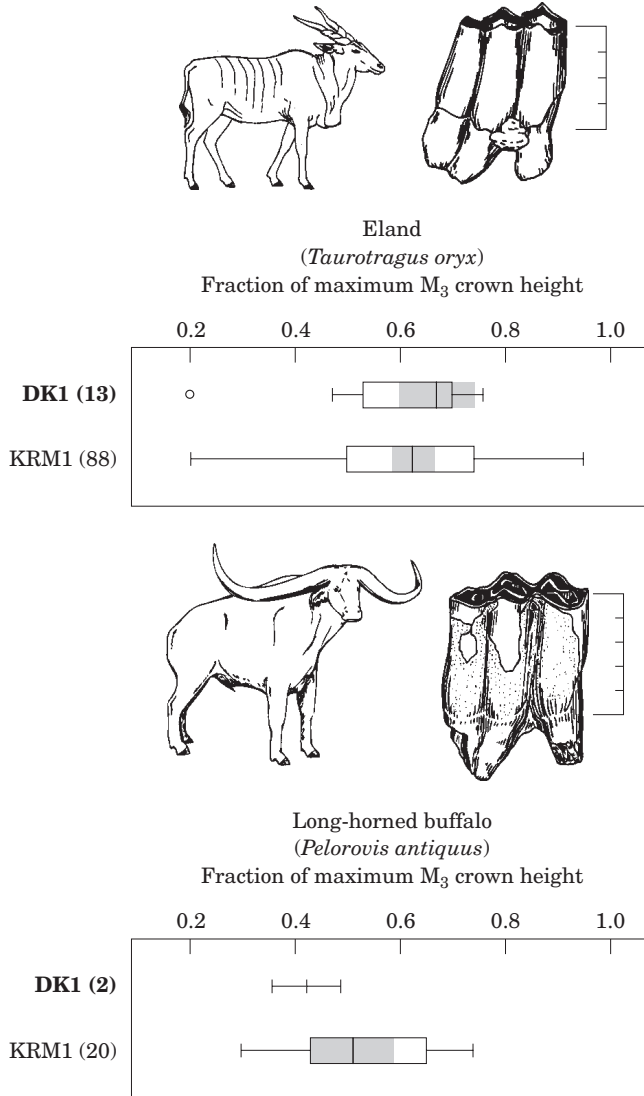
Eland
(*Taurotragus oryx*)
Fraction of maximum $M_3$ crown height





Long-horned buffalo
(*Pelorovis antiquus*)
Fraction of maximum $M_3$ crown height



Figure 7. Boxplots summarizing long-horned buffalo and eland $M_3$ crown heights at the MSA deposits of Die Kelders 1 and Klasies River Mouth. Key elements are the median, indicated by the vertical line near the middle of each plot; the middle half of the data, indicated by the open box; and the 95% confidence limits for the median, indicated by the shaded box. In conventional statistical terms, two sample medians differ significantly when their 95% confidence limits fail to overlap.

excellent in the LSA layers, and the sample includes the part of the skull that bears the horns (absent in females). Mortality analysis based on the presence or absence of horns and on dental wear shows that the sheep comprise mainly very young males and old females (Schweitzer, 1974, 1979). This is the pattern that would be expected from flock management, that is, if the people were herders rather than rustlers.

Sex is indeterminate for the MSA eland sample, but Figure 7 summarizes average age based on crown heights of the lower third molar ($M_3$) at DK1 and at KRM. The

individual crown heights have been divided by maximum possible (unworn) crown height to allow direct comparisons to crown heights of long-horned buffaloes at both sites. Unlike linear dimensions that are unaffected by age, crown heights need not be normally distributed, and the figure thus employs a boxplot format centered on the median. The vertical line near the center of each boxplot is the median, the open rectangle encloses the middle half of the data between the 25th and 75th percentiles, the shaded rectangle is the 95% confidence interval for the median, and the vertical lines at the ends mark the range of more or less continuous data. Circles indicate outliers (points that are far removed from the main body of data). The number of specimens in each sample is given in parentheses. Samples for which the 95% confidence limits do not overlap differ significantly in the conventional statistical sense.

In high-crowned ungulates, $M_3$s that are less than half worn generally represent prime-age (reproductively active) individuals (Klein, 1982), and Figure 7 shows that on this basis, prime-age individuals probably dominate the eland samples from both DK1 and KRM. The most economic explanation is that MSA people obtained eland mainly by driving herds over cliffs or into traps that occur near both sites. Driving would net prime-age individuals in rough proportion to their live abundance, but it probably occurred rarely, because the people probably rarely found eland herds in the appropriate position. In fact, if the people could have driven eland more or less at will, the persistent, routine loss of prime-age adults would have propelled the eland to extinction. There is no indication at either DK1 or KRM that eland became less abundant with time.

Figure 7 also shows that the long-horned buffalo $M_3$s from KRM tend to be significantly more worn than those of eland, and the implication is that the buffalo sample comprises a significantly higher proportion of post-prime individuals. The difference is consistent with the much greater danger that prime-age buffalo would present to hunters on foot, especially if they lacked projectile weapons like the bow and arrow. Post-prime buffalo, with dulled special senses, would be much more vulnerable. Arguably, the KRM people did not hunt post-prime buffalo at all, but scavenged their carcasses, since it is these (vs. those of prime adults) that would be most common in the veld. The DK1 buffalo sample is too small for secure assessment, but it could reflect the same basic emphasis on post-prime individuals as at KRM.

Following Binford (1984), the extent to which the DK1 people hunted or scavenged ungulates might be determined from the pattern of skeletal part representation. Binford noted that in the MSA layers at KRM, relative to smaller ungulates (like grysbok and bushbuck), much larger ones (like eland and buffalo) tend to be more poorly represented by proximal limb bones and better represented by bones of the feet and skull. Proximal limb bones (humeri, radioulnae, femora, and tibiae) are relatively rich in meat, marrow, and grease, and Binford therefore suggested that the relatively small number of large bovid specimens meant that the KRM people did not hunt large bovids routinely. Instead, they mainly scavenged carcasses from which other predators had already removed the most desirable parts.

At KRM, the relative shortage of large ungulate proximal limb bones is based on epiphyseal counts, and the difference from the small ungulates is statistically significant. At DK1, the MSA epiphyses suggest a similar difference between small and large ungulates, but the large ungulates are too rare to demonstrate statistical significance. In addition, meticulous refitting of large ungulate shaft fragments indicates that at DK1 the shortage of large ungulate proximal

limb bones may result from a reliance on epiphyseal counts alone. When the refitted shafts are counted, proximal limb bones become more common (Marean, 1998; Bertram & Marean, 1999; Marean *et al.*, 2000*a*), and the pattern of skeletal part representation is consistent with active hunting.

## The Cape Dune molerat: human or nonhuman accumulator?

The Cape dune molerat occurs in virtually every archeological site within its historic range, but it is especially abundant at DK1. Figure 1 shows that dune molerats exceed 90% of the fauna throughout most of the MSA sequence, and in the very middle (Level 8), their frequency reaches 100 individuals per square meter. It is of course possible that MSA people simply concentrated on a species that had become exceptionally abundant near the site, but it is at least equally plausible that the extraordinary abundances of molerats reflects specialized predation by Cape eagle owls. These are known to focus on colonial species (like molerats), they sometimes roost in caves, and they can take animals up to 1·5 kg in weight (Avery, 1990). Adult dune molerats average less than 1 kg (Skinner & Smithers, 1990).

Indications that eagle owls may have contributed to the fauna would include: (1) surficial damage to dune molerat or other small mammal bones; (2) the pattern of skeletal part representation; and (3) a tendency for dune molerat bones to vary in frequency independently of bones of tortoises, seals, and other species that owls could not have introduced.

A damage analysis would be particularly telling if it revealed etching by eagle owl gastric acids. Unfortunately, most etching might be visible only under very high magnification (Andrews, 1990), and a thorough microscope study would probably require

many months. In the absence of microscopic observations, we note that few dune molerat bones exhibit conspicuous macroscopic damage, but ones that appear to have been polished and diminished by digestion occur only in the MSA sample (Figure 8), while obviously burnt or cutmarked specimens occur only in the LSA assemblage. At least tentatively, the difference suggests that non-human accumulation was more important in the MSA.

Overall, the principal dune molerat parts in both the LSA and the MSA are maxillae (detached from brain cases), mandibles, and complete limb bones. This is the basic pattern of small mammal skeletal part representation that modern Cape eagle owls produce (Avery, 1990), but human butchering and selective postdepositional destruction might also create it. Broadly the same pattern characterizes all the dune molerat samples we have studied (mostly from LSA contexts, except at DK1 and Blombos Cave).

For the moment, perhaps the most persuasive observation concerns a contrast between the LSA and the MSA in the ways that dune molerat numbers covary with those of other species. In 1992–95, the excavators recorded numerous microstratigraphic units (Marean *et al.*, 2000*b*), and as we sorted, we noted that dune-molerat-rich LSA microstratigraphic units generally also contained many other bones, while dune-molerat-rich MSA units tended to contain little else. This was true even within MSA layers like 4/5 where dune molerats were less dominant. To check this observation more rigorously, we undertook principal components analysis of the NISPs for dune molerats and for the four next most common taxa—tortoises, seals, hyraxes, and ungulates—in the microstratigraphic units for the LSA (244) and for MSA 4/5 (121). As the NISP for tortoises, we used the sum of the two most durable and conspicuous limb bones, the humerus and the femur.
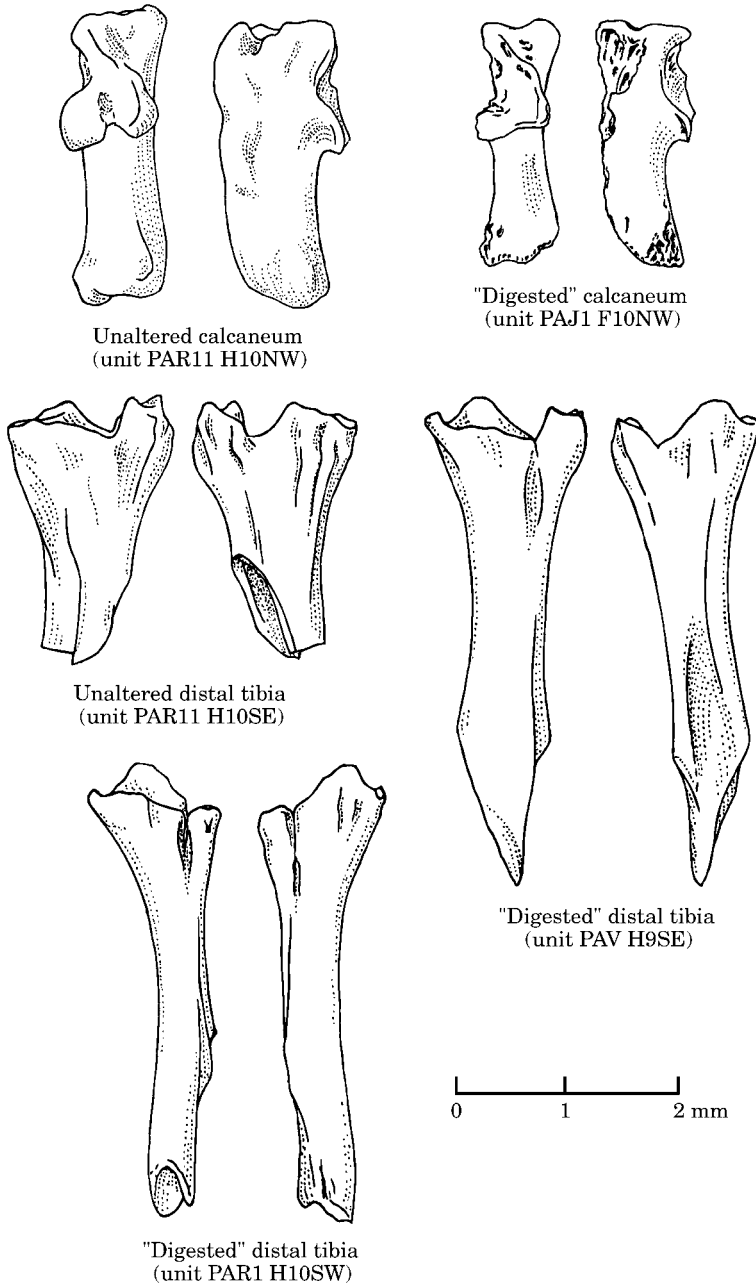
Unaltered calcaneum
(unit PAR11 H10NW)

"Digested" calcaneum
(unit PAJ1 F10NW)

Unaltered distal tibia
(unit PAR11 H10SE)

"Digested" distal tibia
(unit PAV H9SE)

"Digested" distal tibia
(unit PAR1 H10SW)

0    1    2 mm

Figure 8. Unaltered and partially digested dune molerat calcanea and distal tibiae from Die Kelders Cave 1 Layer 4/5.

Table 2 summarizes the result. It presents rotated, two-component solutions for the LSA and for MSA 4/5 that respectively explain 85% and 89% of the variation in the underlying NISP matrices. Component loadings (that is, correlations between taxa

**Table 2 Principal-components analyses of the frequencies of tortoises, dune molerats, seals, hyraxes, and ungulates in LSA and MSA 4/5 microstratigraphic units at Die Kelders Cave 1**

Varimax-rotated two-component solutions

| Later Stone Age | 1 | 2 |
|---|---|---|
| Tortoises | 0·28202650 | **0·9418222** |
| Dune molerats | **0·8066411** | 0·4180354 |
| Seals | **0·8446142** | 0·3935373 |
| Hyraxes | **0·8761193** | 0·1228026 |
| Ungulates | **0·8050441** | 0·4197212 |
| | | |
| Middle Stone Age | 1 | 2 |
| Tortoises | **0·9125912** | 0·2909968 |
| Dune molerats | 0·20644030 | **0·9636924** |
| Seals | **0·9263548** | 0·0573729 |
| Hyraxes | **0·7625713** | 0·4281602 |
| Ungulates | **0·9292754** | 0·2931393 |

**Table 3 Principal-components analyses of the frequencies of tortoises, hares, dune molerats, seals, hyraxes, ungulates, and stone artifacts in MSA 4/5 microstratigraphic units at Die Kelders Cave 1**

Varimax-rotated two-component solutions

| Middle Stone Age | 1 | 2 |
|---|---|---|
| Tortoises | **0·9245325** | 0·3154593 |
| Hares | **0·7914802** | 0·5714823 |
| Dune molerats | 0·1965972 | **0·9673891** |
| Seals | **0·9567955** | 0·0502254 |
| Hyraxes | **0·7246102** | 0·4360712 |
| Ungulates | **0·9154638** | 0·3249951 |
| Larger artifacts | **0·8146751** | 0·2904989 |

and components) that exceed 0·71 are bold-faced, because they imply that the component accounts for at least 50% (0·71 × 0·71) of interunit variation in the NISPs of the associated taxon. Taxa whose loadings exceed 0·71 on the same component can reasonably be assumed to covary from unit to unit within either the LSA or MSA 4/5.

The table shows that the LSA dune molerats covary with the seals, hyraxes, and ungulates, but the MSA 4/5 molerats covary weakly or not at all with other taxa. This result supports our hypothesis that the LSA molerats were introduced mainly by the same human agency that introduced most other mammals, while the MSA molerats were introduced mainly by a separate nonhuman agency.

In further support, we present Table 3, which contains a rotated, two-component solution for an MSA 4/5 frequency matrix involving the same five taxa listed in Table 2 plus hares (too infrequent for analysis in the LSA microstratigraphic units) and stone artefacts greater than 2 mm in diameter (numbers kindly provided by A. I. Thackeray). The dune molerats remain largely isolated on their own component,

separate from the artefacts, which load highly on the same component as the tortoises, hares, seals, hyraxes, and ungulates. This is the expected result if the artefact markers were largely responsible for all taxa but the molerats. We note, however, a tendency for other small mammals (hares and hyraxes) to associate somewhat more weakly with the artefacts and somewhat more strongly with the dune molerats. This may imply that a nonhuman agency was also partly responsible for the other small mammals.

Table 2 further suggests a difference between the LSA and MSA 4/5 in tortoise accumulation. Since people almost certainly introduced most of the tortoises in both units, the difference would have to reflect a change in human behavior. Speculatively, we suggest either a change in the season(s) of the year when the site was occupied or perhaps a difference in the division of human labor by age and sex.

## The angulate tortoises

The persistence of angulate tortoises throughout the DK1 MSA sequence shows that warm, dry days must have remained seasonally common, despite the general tendency towards cooler, moister climate.

Overall, angulate tortoises rival dune molerats in numbers, although in the MSA layers, tortoise and molerat frequencies vary inversely. In the middle of the MSA sequence (Layers 7 and 8), where molerats are superabundant, the tortoise sample is small even when specimens from adjacent layers are lumped. To estimate tortoise numbers at DK1 and in most other fossil samples, we have relied mainly on the humerus and the femur, because these are the most durable and most readily identifiable tortoise elements. They are also suitable for measurements that reflect the size of live individuals, and our prior work has revealed significant intersample variation in average tortoise size. It is average size and its human demographic implications that we stress here.

Unlike dune molerats (and other mammals), tortoises are ever growing, and the median is thus more appropriate than the mean as an index of average size. Figure 9 thus summarizes the mediolateral diameters of DK1 and BNK1 tortoise distal humeri using the same median-based (nonparametric) boxplot format as Figure 7. The key elements again are the median, represented by the vertical line near the center of each plot, the open rectangle which encloses the middle half of the data between the 25th and 75th percentiles, the shaded rectangle which marks the 95% confidence interval for the median, and the horizontal line which designates the range of continuous data. Circles or star bursts indicate outliers. The number of specimens in each sample is given in parentheses. Recall that samples for which the 95% confidence limits do not overlap differ significantly in the conventional statistical sense.

The figure shows that on average, the MSA tortoises tend to be significantly larger than the LSA specimens, although there is also significant variation within the composite BNK1/DK1 LSA sequence. It might be argued that larger tortoise size reflects

more favorable circumstances for tortoise growth, but the largest specimens at both DK1 and BNK1 accumulated under relatively cool, moist conditions that are not likely to have affected tortoises positively. The most plausible alternative is that large MSA tortoise size reflects relatively limited human predation, probably because MSA human populations were relatively sparse. In this light, it is notable that on average, the smallest tortoises in the sequence come from the youngest LSA deposits, after 2000 years ago when local people had added sheepherding to hunting-gathering. It is unlikely that local people would have adopted sheep herding unless it allowed larger human populations.

The MSA tortoises from Blombos Cave also tend to be large (unpublished measurements), and they bolster a human behavioral (versus climatic) explanation for large tortoise size, since the Blombos deposits are believed to have formed mainly under warm interglacial conditions. In sum, large MSA tortoise size supports other evidence that the people were less effective hunter-gatherers than their LSA successors.

### Summary and conclusion

The large Die Kelders MSA and LSA faunal samples bear on the paleoenvironment, on the agents of bone accumulation, and on ancient human behavior. In regard to paleoenvironment, the abundance of Cape dune molerats and of angulate tortoises throughout the combined MSA and LSA sequence indicates a degree of environmental continuity with the present. The taxonomic composition of the LSA fauna, which includes only species that existed nearby historically, underscores basic similarity between the LSA and the present environments. In contrast, the MSA sample includes two totally extinct species (Cape zebra and long-horned buffalo) and four historically extant, extralimital forms
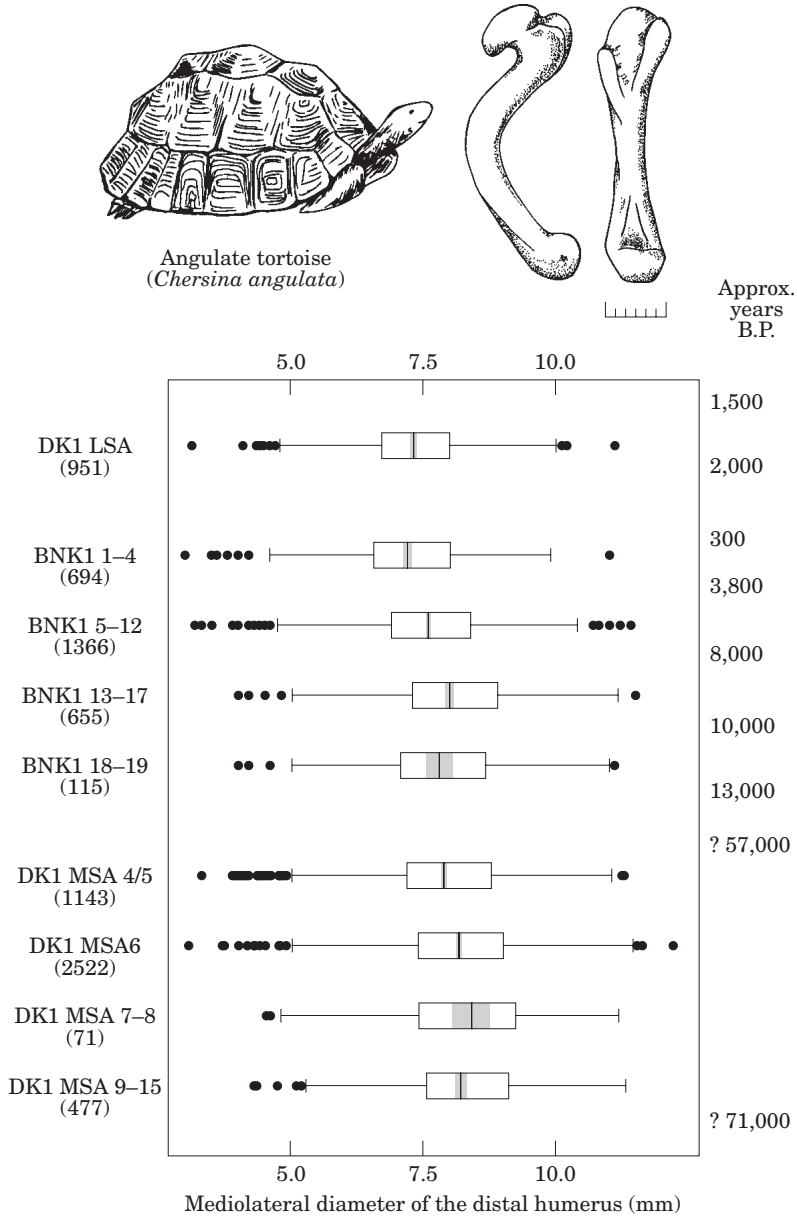
Figure 9. Boxplots summarizing the mediolateral diameter of angulate tortoise distal humeri in fossil samples from Die Kelders Cave 1 and Byneskranskop Cave 1. The caption to Figure 1 outlines key features of the boxplot format.

(quagga, black wildebeest, springbok, and southern reedbuck) that together imply somewhat wetter, grassier conditions during the MSA occupation. The large average size of the MSA dune molerats also indicates moist surroundings, while the large size of the MSA gray mongooses suggests relatively cool temperatures. The sum is fully consistent with micromammalian and sedimentologic observations for cooler, moister MSA

climate and with ESR and luminescence dates that place the MSA sequence within global isotope stage 4, roughly between 71 and 57 ka ago.

In regard to agents of accumulation, contrasts between the MSA and LSA samples in bone damage and in the way that molerat bones, bones of other animals, and artefacts covary suggest that people accumulated most of the LSA molerats, while Cape eagle owls accumulated most of the MSA specimens. Eagle owls could also have been responsible for the hares, hyraxes and even many of the small antelopes in the MSA deposits. Arguably, MSA people were primarily responsible only for the bones of birds (mainly penguins), larger ungulates, and seals. In effect then, during the MSA occupation, Die Kelders may have been as much an eagle owl site as a human one.

In regard to human behavior, the DK1 faunal samples recall those from other sites which suggest that MSA people hunted and gathered less effectively than their LSA successors. In particular, bones from fish and airborne birds (as opposed to penguins) abound only in the LSA sample; the MSA sample is relatively poor in bones of buffalo and other especially dangerous terrestrial prey and relatively rich in eland, even though eland were probably rare nearby; and tortoises tend to be much larger in the MSA than in the LSA, suggesting that MSA people collected tortoises less intensively, probably because MSA populations were less dense. The faunal differences reinforce the artefactual record which suggests that only LSA people possessed fishing and fowling gear and only they had projectile weapons with which hunters could attack dangerous prey from a safe distance.

The faunal and artefactual contrasts between the MSA and the LSA help explain why anatomically modern or near-modern MSA people failed to spread from Africa before 60 ka ago. It was only when anatomically modern Africans became behaviorally modern that they developed a competitive advantage over their Eurasian contemporaries. The issue now is to determine when and how the behavioral advance occurred. East African evidence provisionally suggests it occurred abruptly at or shortly after 50 ka ago. Unfortunately, few southern African sites record the crucial period, and much fresh research in eastern Africa is necessary to test our proposal that it witnessed an abrupt advance in hunting-gathering ability.

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