

# Paleoenvironmental and Human Behavioral Implications of the Boegoeberg 1 Late Pleistocene Hyena Den, Northern Cape Province, South Africa

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Boegoeberg 1 (BOG1) is located on the Atlantic coast of South Africa, 850 km north of Cape Town. The site is a shallow rock shelter in the side of a sand-choked gully that was emptied by diamond miners. Abundant coprolites, chewed bones, and partially digested bones implicate hyenas as the bone accumulators. The location of the site, quantity of bones, and composition of the fauna imply it was a brown hyena nursery den. The abundance of Cape fur seal bones shows that the hyenas had ready access to the coast. Radiocarbon dates place the site before 37,000 <sup>14</sup>C yr ago, while the large average size of the black-backed jackals and the presence of extralimital ungulates imply cool, moist conditions, probably during the early part of the last glaciation (isotope stage 4 or stage 3 before 37,000 <sup>14</sup>C yr ago) or perhaps during one of the cooler phases (isotope substages 5d or 5b) within the last interglaciation. Comparisons of the BOG1 seal bones to those from regional Middle Stone Age (MSA) and Later Stone Age (LSA) archeological sites suggest (1) that hyena and human seal accumulations can be distinguished by a tendency for vertebrae to be much more common in a hyena accumulation and (2) that hyena

and LSA accumulations can be distinguished by a tendency for hyena-accumulated seals to represent a much wider range of individual seal ages. Differences in the way hyenas and people dismember, transport, and consume seal carcasses probably explain the contrast in skeletal part representation, while differences in season of occupation explain the contrast in seal age representation. Like modern brown hyenas, the BOG1 hyenas probably occupied the coast year-round, while the LSA people focused their coastal visits on the August–October interval when nine-to-eleven-month-old seals were abundant. The MSA sample from Klasies River Mouth Cave 1 resembles BOG1 in seal age composition, suggesting that unlike LSA people, MSA people obtained seals more or less throughout the year. © 1999 University of Washington.

**Key Words:** fossil brown hyenas; Middle Stone Age; Later Stone Age; southern Africa.

## INTRODUCTION

The Boegoeberg 1 fossil hyena den (hereafter BOG1) is located at 28° 46' 6" S, 16° 34' 37" E on the Atlantic Coast of

the Northern Cape Province of South Africa, approximately 850 km north of Cape Town (Fig. 1). The BOG1 fauna offers a rare opportunity to illuminate the Quaternary history of the region, which is poorly known. In addition, the fauna is dominated by fur seals, and it can therefore be used to seek similarities and differences between hyenas and stone age people in fur seal exploitation. Fur seals abound in well-known Middle Stone Age (MSA) and Later Stone Age (LSA) coastal sites to the south and east (Fig. 1), where they have suggested that MSA people occupied the coast year round, while LSA people occupied it only seasonally (Klein, 1989). The BOG1 hyenas almost certainly remained at the coast all year, and the seal sample can thus be used to check the idea that MSA people did likewise. A difference in seasonal transhumanance would support other indications that LSA people hunted and gathered more efficiently. This in turn may explain how they spread to Eurasia, where they replaced the Neanderthals and other archaic humans. It is the paleoenvironmental and human behavioral implications of the BOG1 fauna that we stress here. Two of us (R.G.K. and K.C.U.) take primary responsibility for the behavioral interpretations.

HISTORY OF DISCOVERY AND EXCAVATION

BOG1 was discovered when Alexcor diamond miners bulldozed sand from a gully in schist bedrock and exposed a shallow, fossiliferous shelter in the gully wall. Sand removal also revealed a second nearby shelter (BOG2) containing a stratified shell midden. The mine geologist notified one of us (J.E.P.), who subsequently recovered a small bone sample from BOG1. Unfortunately, the bulldozing had damaged or removed much of the deposit from both shelters, but in November 1994 and April 1996, two of us (D.H. and T.H.) excavated the surviving deposit in both shelters. Both sites were overlain

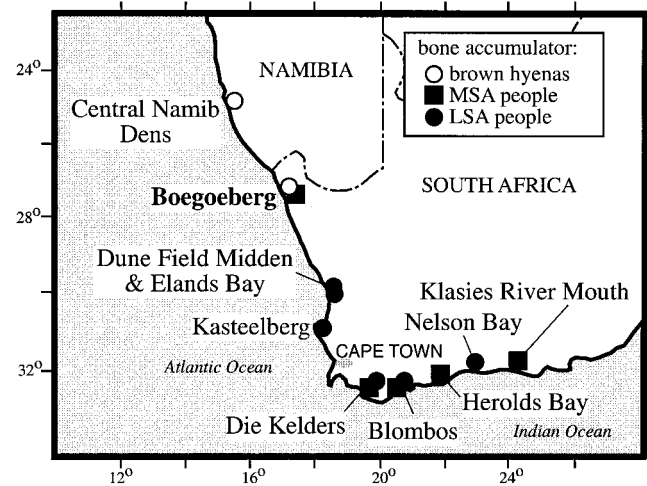


FIG. 1. Approximate locations of BOG1, the Central Namib brown hyena dens, and the South African MSA and LSA sites mentioned in the text.

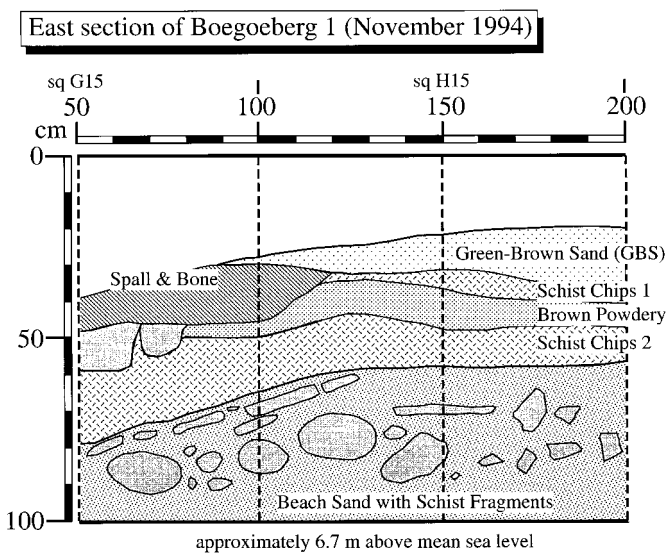


FIG. 2. A schematic section through the deposits at BOG1.

with a grid of meter squares, and each square was subdivided into 16 sectors, 25 cm on a side. All objects were recorded with respect to sector and natural stratigraphic unit. Excavations at BOG1 produced numerous bones, while those in BOG2 provided a few bones, abundant shells, and some characteristic MSA stone artifacts. We focus here on BOG1, but note that BOG2 is one of only seven well-documented MSA shell middens known on South African coasts. We plan to describe it fully when the artifact analysis has been completed.

GEOLOGIC ANTIQUITY

The sedimentary fill at BOG1 comprises two major units, beach sands to a height of roughly 7 m above mean sea level overlain by a mix of alluvial and eolian sands (Fig. 2). Fragments of the schist bedrock occur throughout. Bones are absent in the beach sands but abound in overlying deposits. Excavations exposed five conformable fossiliferous units, differentiated primarily by the quantity and size of the schist fragments and by their state of decomposition. The five units are faunistically identical, and for comparative purposes, we treat them as a single unit below. All five provided abundant eggshell fragments from ostrich (*Struthio camelus*), and three eggshell samples submitted for radiocarbon dating produced the following results (<sup>13</sup>C-corrected and in descending stratigraphic order).

Date in <sup>14</sup> C years B.P.	Unit
37,220 + 5,010, -3,060 (GX-22191)	GBS (Square H15)
33,230 + 2,630, -1,980 (GX-21189)	schist chips 1 (Square H16)
34,990 + 3,110, -2,240 (GX-21190)	brown powdery (Square G15)

The dates are indistinguishable when the large standard errors are considered and should probably be considered min-

ima, since the actual ages could be much greater if the samples were only minutely contaminated by more recent carbon. To some extent, the true age of the deposit is constrained by the fauna (described below), which implies relatively cool, moist conditions. This rules out a full interglacial date within marine oxygen-isotope substage 5e, between roughly 127,000 and 115,000 yr ago, and perhaps also the relatively mild substages 5c and 5a centered on 97,000 and 79,000 yr ago, respectively (Bassinot *et al.*, 1994). The most likely age is probably within substage 5d (centered on 106,000 yr ago), substage 5b (centered on 86,000 yr ago), or stage 4 (between roughly 71,000 and 59,000 yr ago). Even stage 6 (the penultimate glaciation roughly 186,000 to 127,000 yr ago) is possible, but a cool interval after substage 5e is more probable, assuming that the basal beach sands reflect the high sea-level stand associated with substage 5e. Global estimates for this high stand range between 2 and 7 m above present mean sea level (CLIMAP Project Members, 1984), and it is probably represented by a 4-m shoreline observed elsewhere on the west coast of South Africa (Hendey and Volman, 1986).

Ostrich eggshell from BOG2 produced an age of  $44,200 \pm 1200$   $^{14}\text{C}$  yr B.P. (Pta-6956), but the actual age is probably much older, since the fauna implies true interglacial conditions. Arguably, BOG2 formed during one of the milder phases (substage 5e, 5b, or 5a) of the last interglacial, while BOG1 formed during the early or middle part of the succeeding last glaciation. If this is accepted, then BOG1 dates sometime between 71,000 yr ago (the beginning of stage 4) and 37,000  $^{14}\text{C}$  yr ago (the minimum age implied by the  $^{14}\text{C}$  dates.)

### THE FAUNA

Mammals prevail heavily in the BOG1 fauna, followed by birds (mainly bones from jackass penguins, *Spheniscus demersus*, and eggshell fragments from ostrich) and finally by tortoises of undetermined species. There are also rare remains of fish, rock lobster (*Jasus lalandii*), and granite limpets (*Patella granatina*). We argue in the next section that brown hyenas probably accumulated most of the bones and other remains, and we compare the mammal bones to ones from southern African stone age sites. Our purpose is to illuminate similarities and differences in behavior between hyenas and prehistoric people. G. Avery is presently analyzing the bird bones from the same comparative perspective.

Table 1 lists the number of identified specimens (NISP) for each mammal species in each BOG1 unit and the minimum numbers of individuals (MNIs) from which the specimens must have come. Klein and Cruz-Urbe (1984) explain the assumptions and algorithms behind the MNI calculation. In the text below, we provide Linnaean names only for species not listed in Table 1. The table shows that fur seals dominate throughout. Excepting black-backed jackals, other species are notably rare. This may seem an odd result, but it follows directly from the

coastal location of the site and from aspects of brown hyena ecology.

### THE BONE COLLECTOR

The BOG1 sample contains no artifacts or bones damaged by artifacts, but it is rich in hyena coprolites, and it differs from archeological faunas in the presence of conspicuously chewed or digested specimens (Fig. 3). These observations clearly implicate hyenas as the principal bone collectors. Both the brown hyena and the spotted hyena (*Crocuta crocuta*) occurred regionally in historic times, and both occupy similar regions in Namibia today. However, three circumstantial observations suggest that only the brown hyena was involved at BOG1.

First, only the brown hyena is represented in the BOG1 deposit, and two of the three individuals recovered were cubs who are especially likely to have lived (and died) in a den. Second, in similar settings in Namibia, where both brown and spotted hyenas survive today, only brown hyenas occupy the coast (Skinner and van Aarde, 1981). Spotted hyenas remain inland, perhaps because onshore breezes often produce cool, misty conditions they cannot tolerate or because they must drink regularly and the coast provides no surface water. Spotted hyenas were similarly absent or rare along the entire South African west coast historically (Skead, 1980), but brown hyenas were so common that early European travelers and settlers at the Cape of Good Hope called them "strandwolves" (beach wolves). Finally, there is the sheer quantity of bone. Both hyena species collect bones at nursery or maternal dens, but only brown hyenas routinely provision their young (Mills, 1990; Owens and Owens, 1978, 1979; Skinner and van Aarde, 1991). Thus, assuming a relatively rapid rate of bone accumulation, only brown hyenas are likely to produce the kind of dense bone concentrations found at BOG1.

In the absence of artifacts and cut-marked bones, in the abundance of coprolites and chewed bones, and in the dense bone concentration, BOG1 recalls other southern African fossil sites that probably also mark brown hyena nursery dens. The main ones are the late Pleistocene occurrences at Equus Cave, Sea Harvest, Hoedjies Punt 1, the Elandsfontein "Bone Circle," Ysterfontein, Duinefontein 1, and Swartklip 1 (Cruz-Urbe, 1991; Klein *et al.*, 1991), and a late-prehistoric or historic occurrence at Salpeterkop (Avery, 1993). The spotted hyena is rare or absent at each of these sites, and where it does occur (at Equus Cave and Swartklip 1), its bones come entirely from adults. In contrast, the bones of brown hyenas come mainly from cubs, as at BOG1.

Like other presumed brown hyena dens, BOG1 differs from like-aged archeological sites (such as BOG2, Die Kelders Cave 1 (Avery *et al.*, 1997), Blombos Cave (Henshilwood, 1998), Herolds Bay Cave (Brink and Deacon, 1982), and the Klasies River Mouth Caves (Deacon, 1995; Singer and Wymer, 1982)) not only in the absence of artifacts and cut-marked bones but also in the abundance of terrestrial carnivore remains, partic-

**TABLE 1**  
**The Mammalian Species Represented at BOG1**

	GBS		Spall & bone		Schist chips 1		Brown powder		Schist chips 2		All	
	NISPs	MNI	NISPs	MNI	NISPs	MNI	NISPs	MNI	NISPs	MNI	NISPs	MNI
Small hare ( <i>Leporidae</i> gen. et sp. Indet.)	4	1	0	0	3	1	0	0	0	0	7	1
Namaqua dune molerat ( <i>Bathergus janetta</i> )	2	1	1	1	3	1	0	0	0	0	6	1
Black-backed jackal ( <i>Canis mesomelas</i> )	361	12	132	7	104	9	25	3	38	3	630	21
Cape fox ( <i>Vulpes chama</i> )	5	2	5	1	2	1	0	0	1	1	12	3
Bat-eared fox ( <i>Otocyon megalotis</i> )	1	1	0	0	3	1	0	0	0	0	4	1
Cape fox and/or bat-eared fox	8	2	6	1	6	2	0	0	1	1	20	3
Hunting dog ( <i>Lycaon pictus</i> )	2	1	0	0	0	0	0	0	0	0	2	1
Striped polecat ( <i>Ictonyx striatus</i> )	1	1	0	0	0	0	0	0	0	0	1	1
Honey badger ( <i>Mellivora capensis</i> )	1	1	1	1	0	0	5	1	0	0	7	1
Gray mongoose ( <i>Herpestes pulverulentus</i> )	2	1	1	1	1	1	0	0	0	0	4	1
Suricate ( <i>Suricata suricatta</i> )	1	1	0	0	0	0	0	0	0	0	1	1
Gray mongoose and/or suricate	13	3	1	1	1	1	0	0	0	0	15	3
Brown hyena ( <i>Hyaena brunnea</i> )	36	2	11	2	11	1	5	1	3	1	64	3
Wildcat ( <i>Felis libyca</i> )	0	0	0	0	1	1	0	0	0	0	1	1
?Lion (? <i>Panthera leo</i> )	1	1	0	0	0	0	0	0	0	0	1	1
Cape fur seal ( <i>Arctocephalus pusillus</i> )	2190	18	1418	12	688	10	255	3	122	3	4641	32
Black rhinoceros ( <i>Diceros bicornis</i> )	1	1	0	0	0	0	0	0	0	0	1	1
Black rhinoceros and/or white rhinoceros	10	1	8	2	0	0	0	0	0	0	18	2
Gemsbok ( <i>Oryx gazella</i> )	7	1	6	1	2	1	0	0	1	1	17	1
Southern reedbuck ( <i>Redunca arundinum</i> )	4	1	0	0	0	0	0	0	0	0	4	1
Blue wildebeest ( <i>Connochaetes taurinus</i> )	3	1	1	1	0	0	0	0	0	0	4	1
Springbok ( <i>Antidorcas marsupialis</i> )	22	3	7	2	3	1	1	1	1	1	34	4
Steenbok ( <i>Raphicerus campestris</i> )	3	1	0	0	4	1	1	1	0	0	8	1
Bovids, general												
Small (steenbok-size)	3	1	1	1	4	1	1	1	0	0	10	2
Small-medium (springbok-size)	75	4	35	2	23	2	12	1	3	1	152	5
Large-medium (reedbuck/gemsbok/blue wildebeest-size)	33	2	9	1	6	1	4	1	2	1	54	2
Dolphin(s) ( <i>Delphinidae</i> gen. et sp. Indet.)	0	0	3	1	0	0	0	0	0	0	3	1
Whale(s) ( <i>Cetacea</i> gen. et sp. Indet.)	3	1	1	1	1	0	0	0	1	0	6	1

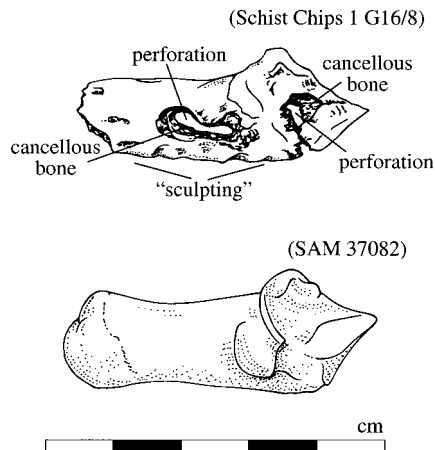
*Note.* The columns show the number of identifiable specimens (NISP) for each species in each stratigraphic unit (top row) and the minimum number of individuals (MNI) from which they must come. The numbers for the individual bovid species are based on dentitions only. The numbers for the bovid size categories are based on all elements.

ularly those of black-backed jackals. The abundance of jackal bones is a consistent marker of hyena activity, and it no doubt reflects the frequent interaction between brown hyenas and jackals at carcasses (Mills, 1990). Jackals that are too slow or too daring become additional food for brown hyenas.

BOG1 differs from other fossil brown hyena sites in the rarity of ungulates and in the remarkable abundance of fur seals. However, the other sites divide between ones that are located far inland and ones that are coastal today but were much farther from the sea when the bones accumulated. Swartklip 1, for example, is now immediately adjacent to False Bay, 30 km southeast of Cape Town, but the granulometry of the sedimentary matrix, the composition of the ungulate assemblage, and the very large size of the jackals (discussed below) imply that the Swartklip bones accumulated under peak-glacial conditions when global sea-level depression displaced the coast up to 50 km seaward. Observations near fur seal colonies on the Namibian coast show that where seals abound, brown

hyenas subsist largely on scavenged seal carcasses (Skinner *et al.*, 1995,1998; Skinner and van Aarde, 1991). They also sometimes kill seal pups, scavenge dead sea birds and occasional dead springbok and gemsbok, and compete with black-backed jackals. Seals remain a key food item even where no permanent seal colonies exist, although in such circumstances scavenged springbok and gemsbok gain in dietary importance (Avery *et al.*, 1984).

Through the courtesy of J.D. Skinner, we examined seal and jackal bones from two recently active Namibian brown hyena nursery dens, and we use them for comparative purposes below. Both dens are shallow rock-shelters similar to BOG1, and one is located 8.2 km from the sea. If this distance is taken to be the maximum over which hyenas will move large numbers of seal bones, BOG1 could not have formed under peak-glacial conditions, when the coastline would have been more distant. However, in the time range we envision for BOG1, sea level considerations eliminate only isotope stage 2, between



**FIG. 3.** (Top) A steenbok calcaneum from BOG1 damaged by hyena gastric acid. Damage includes the development of perforations in the bone, exposure of the cancellous interior, and "sculpting" along the edges. (Bottom) An intact steenbok calcaneum from the comparative collection of the South African Museum (SAM).

roughly 24,000 and 12,000 yr ago, which the radiocarbon dates also categorically preclude. The coastline was mostly, if not always sufficiently, close during the cooler substages of the previous interglaciation (stage 5) and even during the immediately succeeding early or middle last glacial phases to which we have tentatively attached the site.

### THE PALEOENVIRONMENT

The coastal strip including BOG1 receives less than 100 mm of rain per annum, but sea mists ensure sufficient vegetation to support the Namaqua dune molerat, a large burrowing rodent, and small numbers of springbok, gemsbok, and steenbok. Onshore breezes from the cold Benguela Current maintain relatively cool temperatures throughout the year. Mean January temperature (summer) is 16°C; mean July temperature (winter) is 13°C (Schulze, 1986). Cold-water upwelling supplies nutrients that sustain large numbers of fish, and these in turn nourish numerous fur seals, jackass penguins, cormorants (*Phalacrocorax* spp.), and other marine birds. A large fur seal hauling-out colony occurs only 4–5 km from BOG1, and the abundance of seals in the site suggests a similar colony existed nearby when the bones accumulated.

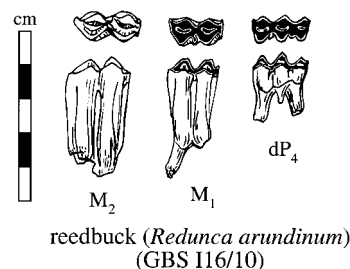
Most of the BOG1 mammals would have been at home in the historic environment, and their relative numbers are historically predictable given the tendency of brown hyenas to focus tightly on fur seals when these are locally abundant. However, the fossil assemblage includes two ungulate species—the blue wildebeest and the southern reedbuck—that were not recorded locally and that could not survive in the historic environment. Both would require much denser vegetation, at least seasonally. The occurrence of reedbuck (Fig. 4) is particularly striking, since it indicates a nearby marsh that historic conditions

could not sustain. The BOG1 bones thus accumulated at a time of greater rainfall, significantly cooler temperatures (reduced evaporation), or both.

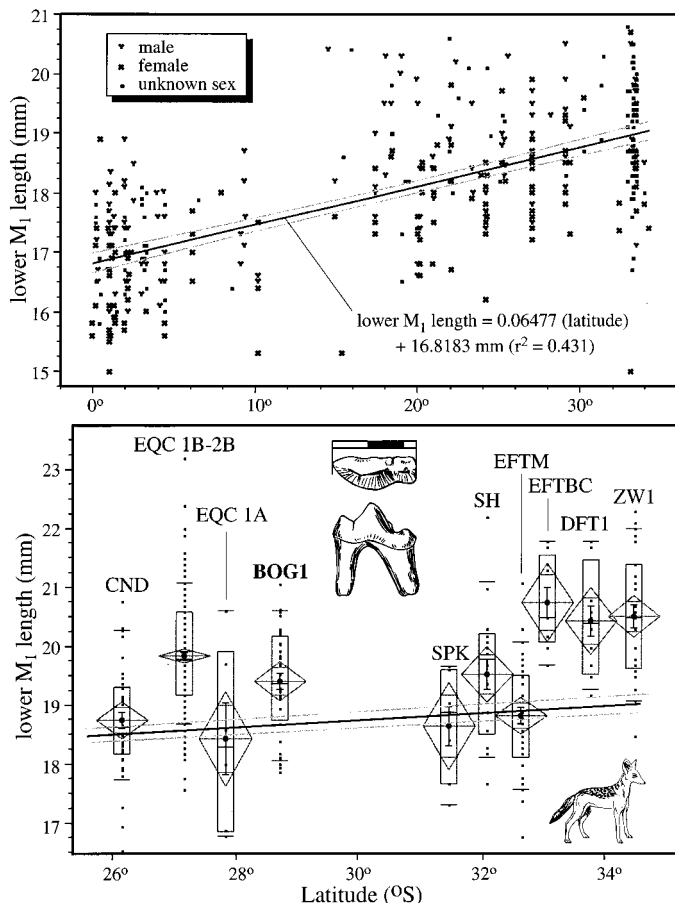
The black-backed jackals can be used to investigate the possibility of cooler temperatures, because in historic populations, average adult size increases with distance from the Equator, in keeping with "Bergmann's Rule," an ecological generalization which states that all other things being equal, larger body size is advantageous in cooler climates. Figure 5 (top) illustrates the positive relationship between jackal size and temperature, using lower carnassial ( $M_1$ ) length as a proxy for individual size and latitude as a proxy for temperature. The sloping line in the center of the figure is the least-squares linear regression of lower carnassial length on latitude. The curves on either side of the regression line are its 95% confidence limits.

We chose the lower carnassial as an index of individual size because it is common in museum comparative collections, is usually the most numerous element in fossil assemblages (due to its robusticity), and is easily identified to jackal species. Thackeray and Kieser (1992) demonstrated that carnassial length and body mass are closely related in black-backed jackals. We employed latitude rather than temperature because we could not obtain reliable temperature estimates for many of the localities that provided our modern jackal sample. The regression shows that lower carnassial length increases significantly with latitude, and the failure of individual specimens to cluster more tightly around the line probably partly reflects the unavoidable use of proxy variables. In part, it also reflects the tendency for male jackals to be significantly larger than females at any given latitude. Regressions calculated for each sex separately are much tighter, but they are not useful for evaluating fossil jackal size, since jackal carnassials cannot be independently assigned to sex.

Figure 5 (bottom) summarizes black-backed jackal lower carnassial length at BOG1 and other hyena dens in a mean-based boxplot format and compares each boxplot to the regression of carnassial length on latitude illustrated in Figure 5 (top). The caption describes the boxplot format. The key element in each plot is the diamond near the center, which marks the 95% confidence limits for the mean. Loosely speaking,



**FIG. 4.** Southern reedbuck lower right deciduous fourth premolar, permanent first molar, and erupting permanent second molar from BOG1. The teeth were found isolated but in immediate proximity to each other (in sector 10 of square I16). They probably come from a single dentition.



**FIG. 5.** (Top) Black-backed jackal lower carnassial length and latitude. (Bottom) Boxplots summarizing black-backed jackal lower carnassial length at BOG1 and other southern African brown hyena dens. The large dot near the center of each plot marks the arithmetic mean, the vertical line bisecting the mean designates the standard error of the mean, the vertical dimension of the diamond around the mean marks the 95% confidence limits for the mean, the open rectangle encloses the middle half of the data (between the 25th and 75th percentiles), the short horizontal line inside the rectangle marks the median (the 50th percentile, usually close to the mean), and the equally short horizontal lines above and below the rectangle set off the upper and lower 10% of the data, respectively.

fossil jackals can be considered “too large” for their latitude if the pertinent 95% confidence limits for a sample do not overlap the 95% confidence limits for the regression line.

The figure shows that jackals were much larger than expected at ZW (Swartklip) 1, DFT (Duinefontein) 1, EFTBC (the Elandsfontein “Bone Circle”), and EQC (Equus Cave) 1B-2B, at each of which the associated fauna, sediments, or both imply peak or near-peak glacial conditions. They were somewhat larger than expected at SH (Sea Harvest), where the associated fauna implies somewhat milder glacial climate, and essentially the same size as modern jackals at CND (Central Namib Dens), EQC1A, EFTM (Elandsfontein Main), and SPK (Salpeterkop), where dating, the associated fauna, or both imply interglacial climate. (The CND jackals are from the

recently active Namibian dens referred to above.) The figure indicates that the BOG1 jackals resembled those from SH in being only moderately “too large” for their latitude. We conclude that BOG1 formed under cooler-than-historic conditions, but probably not under the especially cool climate implied for sites such as ZW1.

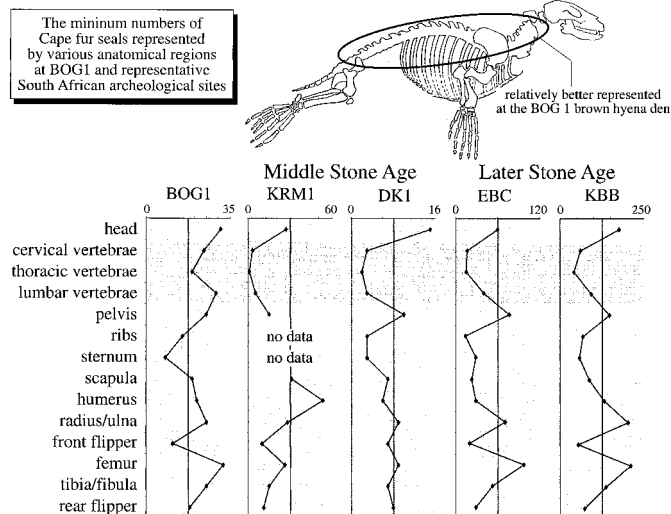
The cool, moist climate, the obvious proximity of the sea, and the radiocarbon dating underlie our assignment of BOG1 to the earlier part of the last glaciation or to one of the cooler phases within the preceding interglaciation. If a more precise date is obtained, BOG1 could become a key datum for testing models of regional Quaternary climatic change.

## SEAL SKELETAL PART REPRESENTATION

The Cape fur seal that dominates BOG1 also abounds at coastal Middle Stone Age (MSA) and Later Stone Age (LSA) archeological sites occupied under interglacial or moderate glacial conditions (Fig. 1). The most important MSA sites are Klasies River Mouth Cave 1 (Deacon, 1995; Klein, 1976; Singer and Wymer, 1982) and Die Kelders Cave 1 (Avery *et al.*, 1997; Grine *et al.*, 1991). The principal LSA sites are Nelson Bay Cave (Inskeep, 1987; Klein, 1972), Die Kelders Cave 1 (Schweitzer, 1979), Kasteelberg A and B (Klein and Cruz-Urbe, 1989; Smith, 1987), Elands Bay Cave (Klein and Cruz-Urbe, 1987; Parkington, 1988), and the Dune Field Midden (Cruz-Urbe and Klein, 1994; Parkington *et al.*, 1992). The two MSA occurrences antedate 60,000 yr ago, while the five LSA occurrences are all younger than 13,000 yr. Archeological sites with seal bones from the intervening 50,000 years are lacking, partly because regional aridity during this interval reduced the visibility of human populations and partly because the coastline was sometimes displaced far seaward, particularly after 30,000 yr ago. Sites related to drowned coastlines are, of course, now inaccessible.

Figure 6 compares seal skeletal part representation among BOG1, the MSA samples from Klasies River Mouth Cave 1 (KRM1) and Die Kelders Cave 1 (DK1), and the LSA samples from Elands Bay Cave (EBC) and Kasteelberg B (KBB). The EBC and KBB samples were chosen to represent the LSA because they are very large, they contrast in age (mostly near 11,000 yr ago at EBC and mostly between 1300 and 880 yr ago at KBB), and they differ sharply in the abundance of carnivore-chewed bones (conspicuous only at KBB, where domestic dogs probably did the chewing). The figure shows that the archeological samples tend to resemble each other and BOG1 in overall composition, including especially a shared tendency for the flippers (podials, metapodials, and phalanges) to be under-represented relative to the principal limb bones. This is readily understandable since the flippers possess little food value and the flipper bones tend to be comparatively small and fragile. Both hyenas and people are thus more likely to leave flippers at carcasses or to destroy the flippers they remove.

In most respects, the BOG1 sample differs from the arche-



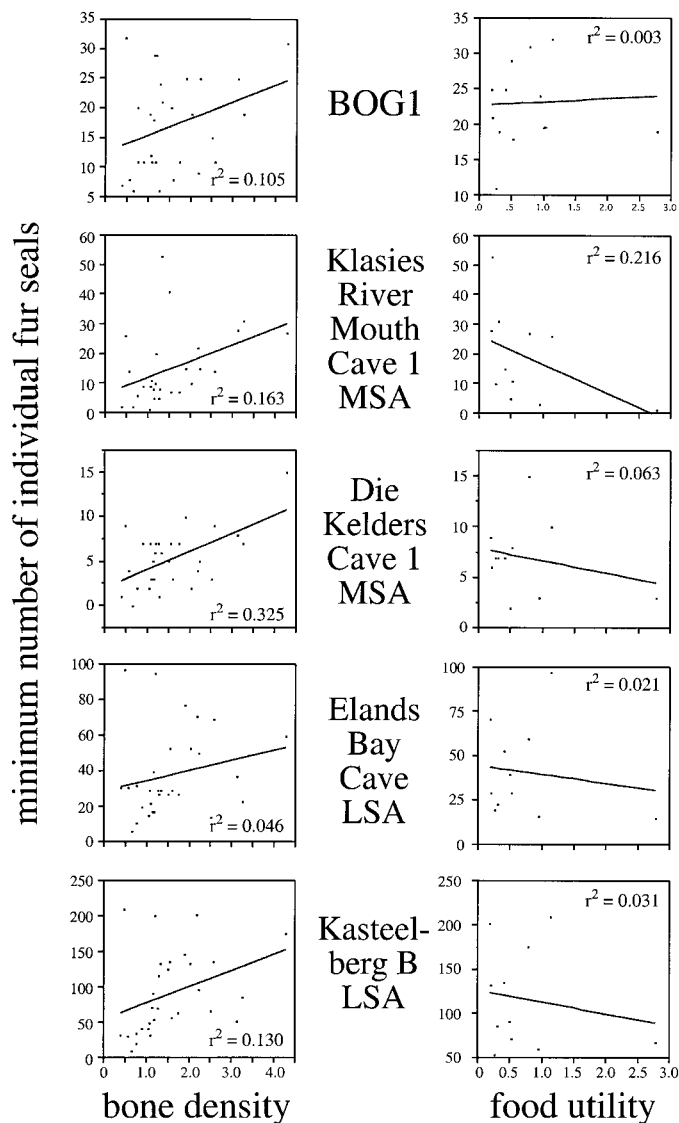
**FIG. 6.** The minimum numbers of Cape fur seals represented by various anatomical regions at BOG1 and at representative South African archeological sites. The horizontal gray bar highlights the position of vertebrae in each sample. Vertebrae are relatively more common at BOG1 than in the archeological samples.

ological samples no more than they differ from one other, with one prominent exception. This is the clear tendency for vertebrae to be more common at BOG1. The reason cannot be relatively great vertebral density in the face of unusually stringent pre- and post-depositional destructive pressures, since density measurements on Cape fur seal bones (Woodborne, 1996) and on bones of phocid seals (Chambers in Lyman, 1994) imply that vertebrae are among the softest bones in the seal skeleton. The fur seal vertebral column, however, is relatively rich in associated flesh and grease (Woodborne, 1996), and the greater abundance of vertebrae at BOG1 could mean that hyenas encountered fresh seal carcasses more often than did stone age people. In support of this possibility, Figure 7 shows that BOG1 resembles the archeological sites in the relationship between skeletal part abundance and bone density or hardness, but it differs from them in a tendency for more nutritious parts (those with greater food utility) to be more common.

However, Figure 7 also shows that hardness and food utility tend to explain relatively little skeletal part variation in any of the samples, probably because their effects have been overridden by other factors, including skeletal part size and shape (apart from density) and the energetic costs of separating, transporting, and consuming various seal parts (apart from their food value). Thus, the greater abundance of vertebrae at BOG1 may simply reflect differences in how hyenas and people usually dismember and transport carcass segments, or it could mean that compared to people, hyenas are more prone to destroy seal limb bones and to leave vertebrae. Seal limb bones lack medullary cavities, but they

are suffused with marrow and grease, which hyenas could extract only by total consumption.

Unfortunately, the BOG1 abundance of vertebrae cannot be checked at the recently active Namibian hyena dens, because field collection emphasized crania and major limb bones. However, if additional modern or fossil dens confirm the BOG1 pattern, the relative rarity of seal vertebrae could be added to the artifacts, hearths, and cut-marked bones which imply that people and not hyenas collected the seals at Klasies River Mouth, Die Kelders, and other archeological sites.



**FIG. 7.** The relationship between the density of different Cape fur seal skeletal parts and their abundance (left) and between the food (flesh and grease) utility of various anatomical regions and their abundance (right). Woodborne (1996) provides the density and food utility estimates. Meat utility values obtained by Savelle *et al.* (1996) for the closely related California sea lion (*Zalophus californianus*) produce a very similar result. Binford (1978) introduced the concept of skeletal part utility as it is used here. Grayson (1988) proposed the analytic protocol on which the figure is based.

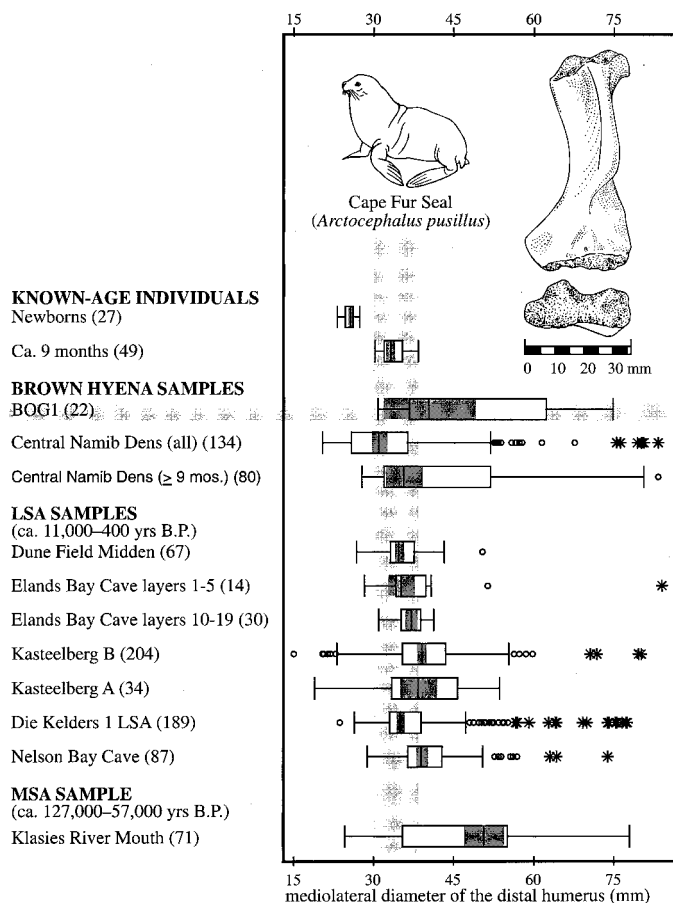
## SEASON OF BONE ACCUMULATION

Fur seal bones have a unique potential to reveal the season(s) when bones accumulated at a fossil site. The reason is that until 1941, when fur seals were first legally protected from human predation, they bred almost exclusively on offshore rocks (David, 1989; Skinner and Smithers, 1990). The vast majority of births occurred within a few weeks in late November and early December, and adults forced the young from the rocks about nine months later. In recent times large numbers of nine-to-eleven-month-old seals then washed up ashore, exhausted or dead. It is the short fur seal birth season and the consequent peak in onshore availability that allow estimates of when fur seal bones reached fossil sites. In cases where the fossil seal ages cluster tightly around nine to eleven months, bone accumulation probably centered tightly on the August–October period of superabundance of nine-to-eleven-month-old seals. Where ages cluster more loosely around nine to eleven months, bone accumulation probably included not only the August–October period but also other times. And where ages fail to cluster near the nine-to-eleven-month average, then accumulation probably fell largely outside that period.

In fur seals, as in most other mammals, juvenile age can be determined from bone size. In most fossil fur seal samples, the most useful bones for estimating age composition are humeri, radii, or femora, because they tend to be relatively well preserved and abundant. We rely here on humeri, because they are the most complete and most readily measurable elements at both BOG1 and the fur-seal-rich archeological sites. Since the humerus measurements are age-dependent, they need not be normally distributed, and we therefore describe them in a boxplot format based on the median.

Figure 8 presents boxplots for the mediolateral diameters (“breadths”) of distal humeri in modern known-age fur seals and in the fur seal samples from BOG1, the Central Namib hyena dens, the MSA layers of Klasies River Mouth Cave 1, and the LSA layers of the Dune Field Midden, Elands Bay Cave, Kasteelberg B, Die Kelders Cave 1, and Nelson Bay Cave. Klasies River Mouth is the only MSA site that has provided enough seal humeri for meaningful comparison to other samples. The key elements in each plot are the median, represented by a vertical line near the middle, the middle half of the data represented by the open box around the median, and the 95% confidence limits for the median, represented by the shaded box. Other elements are described in the figure caption. To aid visual assessment, the vertical gray bar extends the range for known nine-month-olds through the diagram.

Figure 8 shows first that the BOG1 median lies just above the range for nine-month-olds, while the median for the recent Central Namib dens lies just above its lower limit. The small size of the Central Namib median reflects the presence of 54 humeri from newborn seals. The abundance of newborns in the Central Namib sample was expectable, since the dens are immediately adjacent to one of the mainland breeding colonies



**FIG. 8.** Boxplots summarizing the mediolateral diameters (“breadths”) of fur seal humeri in known age individuals and in the bone samples from BOG1, the Central Namib Dens, and South African Middle Stone Age (MSA) and Later Stone Age (LSA) sites. In each plot, the vertical line near the center is the median, the open rectangle encloses the middle half of the data (between the 25<sup>th</sup> and 75<sup>th</sup> percentiles), the hachured rectangle is the 95% confidence interval for the median, and the vertical lines near the ends mark the range of more or less continuous data. Circles and asterisks indicate extreme values (points far removed from the main body of data). Sample sizes are given in parentheses. Samples for which the 95% confidence limits do not overlap can be considered significantly distinct in the conventional statistical sense.

that fur seals have established since 1941. The rarity or absence of newborns in all the remaining samples indicates that no breeding colony existed nearby. Recall that the colony that occurs near BOG1 today is used only for “hauling out” not breeding, and the lack of newborns at BOG1 implies that the ancient colony was similar, or perhaps that there was no colony at all. The consistent shortage of newborns in all the fossil samples implies that the fur seal tendency to breed exclusively offshore has great time depth. Offshore breeding was an effective response to human predation on newborns, since historical observations indicate that indigenous foragers lacked seaworthy watercraft.

Figure 8 shows second that when individuals under nine months of age are eliminated from the Central Namib sample,

median distal humerus breadth and the degree of dispersion around the median increase significantly. The wide dispersion in humerus size reflects the Namib hyenas' presence year-round, including the August–October period when nine-to-eleven month olds are especially common and the remainder of the year when only older animals are available. When the newborn seals are ignored, the Central Namib and BOG1 plots are closely similar, and we conclude that the BOG1 hyenas also occupied the coast year-round.

Figure 8 shows third that the LSA plots exhibit relatively little dispersion (that is, each shows relatively tight packing around the median). Together with the tendency for the LSA medians to lie within or just above the range for known nine-month-olds, the limited dispersion suggests that LSA people focused their coastal visits on the August–October interval when nine-to-eleven-month-old seals were especially abundant. Median variation among the LSA sites probably reflects variability in the precise timing of coastal visits, conditioned, for example, by the need for some LSA people to ensure pasture for their sheep and cattle.

Finally, Figure 8 shows that the LSA plots all differ from the plot for the Klasies River Mouth MSA sample, in which the median is very large and the wide degree of age dispersion recalls BOG1 and the Central Namib dens. A reasonable inference is that the Klasies River Mouth people accumulated seal bones nonseasonally, either continuously or in seasonally unfocused coastal visits. The very large median size of the Klasies River Mouth seals may imply that neither a breeding colony nor a hauling-out colony existed nearby.

The Klasies River Mouth pattern obviously requires corroboration from other MSA sites, but if the pattern is substantiated, it would reflect a significant difference in seasonal movements between MSA and LSA people. This reason could be that unlike LSA people, MSA foragers lacked water containers (documented only for the LSA (Deacon, 1984)), or it could even be that MSA people failed to recognize seasonal variability in fur seal availability. In either case, MSA people were relatively disadvantaged, since seasonal transhumanance allows optimal exploitation of seasonally variable resources, and both ethnohistoric and archeological observations indicate that most South African LSA hunter-gatherers were transhumanant (Deacon, 1984). In the western part of the country, seasonal fluctuations in useful animals and plants suggest that foragers should visit the coast more frequently in winter and turn inland mainly in other seasons (Parkington *et al.*, 1988), and this is the pattern that the LSA seals imply.

If more limited seasonal mobility is confirmed for MSA people, it could be added to the list of MSA/LSA contrasts which suggest to one of us (R.G.K.) that MSA people were relatively ineffective hunter-gatherers (Klein, 1989). The most conspicuous contrast is the tendency for remains of fish, airborne birds, and dangerous terrestrial ungulates to be much rarer in MSA sites. The difference is consistent with the absence of artifactual evidence for fishing and fowling gear and

for projectile weapons, all of which are documented only for the LSA (Deacon, 1984). It is also in keeping with the greater size of tortoises and shellfish in MSA sites, implying lighter MSA predation pressure and thus less dense MSA human populations. The MSA/LSA transition occurred between 50,000 and 40,000 yr ago, and enhanced LSA hunting-gathering ability could help explain the nearly simultaneous expansion of fully modern Africans to Eurasia, where they replaced the Neanderthals and other nonmodern humans.

## SUMMARY AND CONCLUSION

The absence of artifacts and cut-marked bones and the presence of coprolites and chewed or digested bones indicate that hyenas accumulated the bones at BOG1. The most probable accumulator was the brown hyena, which far outnumbered the spotted hyena in similar coastal settings historically. It is also far more likely to have produced the dense bone accumulation found at BOG1, since unlike the spotted hyena, it provisions its young at communal nursery dens.

Radiocarbon dates place the BOG1 accumulation before 37,000  $^{14}\text{C}$  yr ago, while the large size of the black-backed jackals and the presence of extralimital ungulate species imply cool, moist conditions relative to the present. Extreme glacial conditions are ruled out by the abundance of fur seal bones, which indicate that the coast remained nearby, and a time within one of the cooler phases of the last interglaciation (global isotope stage 5) or the earlier part of the last glaciation (between 71,000 and 37,000 yr ago) seems likely.

The BOG1 sample is much richer in fur seal vertebrae than comparable MSA and LSA archeological samples, probably because prehistoric people usually dismembered, transported, or consumed seal carcasses differently than hyenas. The BOG1 sample resembles the large MSA sample from Klasies River Mouth Cave 1 in seal age representation, but it contrasts strongly with LSA samples in this respect. The similarity to the MSA sample suggests that MSA people resembled brown hyenas in their tendency to patrol the coast year-round or in seasonally unfocused visits. In contrast, LSA people seem to have focused their coastal visits on the August–October period, when they could literally harvest nine-to-eleven-month-old seals.

If BOG1 can be dated more precisely, it could become an important datum for reconstructing the pattern of late Quaternary climatic change in southern Africa. Even without a more precise date, it shows how a nonarcheological site can illuminate the behavior of prehistoric people.

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