Holocene large mammal mass death assemblage from South Africa

Lucinda Backwell [a, b, c, *], Christine Steininger [b, c], Johann Neveling [d],
Fernando Abdala [e, b, c], Lucy Pereira [b], Elver Mayer [f], Lloyd Rossouw [g],
Paloma de la Peña [b, c], James Brink [h, i]

[a] Instituto Superior de Estudios Sociales (ISES-CONICET), Saavedra 254, San Miguel de Tucumán, CP4000, Tucumán, Argentina
[b] Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, WITS, 2050, Johannesburg, South Africa
[c] DST-NRF Centre of Excellence in Palaeosciences, University of the Witwatersrand, Private Bag 3, WITS, 2050, Johannesburg, South Africa
[d] Council for Geoscience, 280 Pretoria St, Silverton, Pretoria, 0184, South Africa
[e] Facultad de Ciencias Naturales e Instituto Miguel Lillo - Universidad Nacional de Tucumán (CONICET), Miguel Lillo 251, San Miguel de Tucumán, T4000JFE, Argentina
[f] Programa de Pós-Graduação em Geociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves 9500, Porto Alegre, RS, 91501-970, Brazil
[g] National Museum, P.O. Box 266, Bloemfontein, 9300, South Africa
[h] Florisbad Quaternary Research Department at the National Museum, P.O. Box 266, Bloemfontein, 9300, South Africa
[i] Centre for Environmental Management of the University of the Free State, P.O. Box 339, Bloemfontein, 9300, South Africa

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ABSTRACT

A fossilised large mammal bonebed was discovered eroding out of a gully in the Free State of South Africa. The bonebed is ~1.5 m below the modern land surface, and extends over an area 35 × 13 m. Surface scatters of stone tools occur in a 1 km radius of the site, and a large fire place associated with spirally fractured burnt bone is preserved to one side. The purpose of this research was to excavate and taphonomically analyse the faunal sample to elicit the cause of death, and radiocarbon date it to establish when it happened. The bonebed is represented by black wildebeest, including juvenile and adult individuals. Faunal remains are randomly oriented and many are complete. Weathering stage 1 on most of the bones together with the articulation pattern suggest that the carcasses were exposed for more than a year and less than three before being buried by hillslope sediment. Two-thirds of those fractured record a spiral breakage pattern. There are a few trample marks on bones and evidence of some termite activity. No stone tools were found in the section of bonebed we excavated, and there is no evidence of manmade or carnivore damage on the fauna. Calcrete nodules in the underlying deposits and phytoliths representative of desertification throughout the sedimentary sequence suggest that the animals died under drought conditions between 3840 ± 40 and 3500 ± 40 cal BP, and that human activity at the site was marginal.

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1. Introduction

The Heelbo fossil bonebed was discovered in 2003 by Lucy Pereira, a palaeontologist who was excavating dinosaur remains in red beds on a hill above the site. Following the definition of Haynes (1988), Heelbo is a mass death site, being a relatively circumscribed locus where a group of animals of one or more taxa died over a brief time span due to a single agency of death. A herd of animals might die together in one instance, but another might die off one at a time over a few months during severe drought. Both are considered mass deaths because causes of death were non-repeated and uninterrupted. Some sites are the scene of recurring mass deaths, with long intervals separating the mortality episodes, and these too are considered as mass death assemblages. Possible causes of mass accumulations of carcasses include tectonic activity (Lyman, 1989), ice (Oliver and Graham, 1994), cold, gases, bogging down in mud, and miring in quick sand or tidal silts, crude oil and asphalt (Weigelt, 1989; Rogers et al., 2007). Fluctuations in salinity and

* Corresponding author. Instituto Superior de Estudios Sociales (ISES–CONICET), Saavedra 254, San Miguel de Tucumán, CP4000, Tucumán, Argentina.
E-mail addresses: lucinda.backwell@wits.ac.za (L. Backwell), christine.steininger@wits.ac.za (C. Steininger), jneveling@geoscience.org.za (J. Neveling), nestor.abdala@wits.ac.za (F. Abdala), palaeopereira@gmail.com (L. Pereira), elvermayer@gmail.com (E. Mayer), lloyd@nasmus.co.za (L. Rossouw), jbrink@nasmus.co.za (J. Brink).

drought (Child, 1972; Shipman, 1975; Haynes, 1988; Weigelt, 1989; Brumfitt et al., 2013), grass and forest fires (Waibel, 1921; Weigelt, 1989), drowning (Dechant-Boaz, 1982; Capaldo and Peters, 1995), flooding (Weigelt, 1989) and hunting (Frison, 1991) are all recognised modes of mass mortality. While the Heelbo bonebed reflects the mass death of large mammals, the cause is less clear.

The Evolution of Terrestrial Ecosystems Program (ETE) bonebed database reflects that more than half of the bonebeds documented occur in North America, with 19% found in Europe and 5% in Africa (Behrensmeyer, 2007). A quarter of bonebed formation is reportedly though hydraulic sorting, 18% is through flood drowning, 15% drought, 8% burrowing, 6% miring, and a few ash fall, poison, storm and predation. Interested in the origin and evolution of the Heelbo site, we set out to find a best fit scenario for the taphonomic pattern recorded in the fauna. The purpose of this research was to excavate and analyse part of the bonebed to reconstruct the site formation process. Our goals were to identify the taxa and ontogenetic stages represented, study the bone preservation, modification and orientation, and compare results with published literature on mass death assemblages, an actualistic study conducted with an eland carcass in a nearby donga, and the results of four large mammal bone modification experiments. Our aims were to radiocarbon date the bonebed to establish when deposition took place, and whether the fossil horizons in a second cutting upslope represent the same event(s). Phytolith samples were taken throughout the sedimentary unit containing the bonebed to reconstruct the palaeoenvironment, and associated lithics analysed to better understand the contribution of humans to the site formation process. The geological age of the Heelbo occurrence could initially be established in approximate terms without radiocarbon dating, based on the size of the black wildebeest limb bones. These indicated that the Heelbo black wildebeest remains were equal to or smaller than those found in the last event of body size reduction in black wildebeest recorded for the mid-Holocene (Brink, 2005). Throughout their evolutionary history black wildebeest have experienced a reduction in body size, which culminated in the mid-Holocene. It was thus immediately apparent that the black wildebeest remains from the Heelbo assemblage have modern dimensions and were probably no older than mid-Holocene in age.

1.1. Regional setting

Heelbo is a palaeontological site on the farm Spion Kop 932 (S 28 28.039′ E 27 49.058′), near the town of Senekal in the eastern Free State Province of South Africa (Fig. 1a). The landscape here (Fig. 1b) is characterized by scenic flat-top mountains of the Karoo Supergroup. Colluvial fans - fine textured, stratified hillslope sediments - drape many of the mountain foot-slopes and grade down slope into the floodplains of local rivers (Botha and Partridge, 2000). The host rock for the sedimentary fans is siltstone and sandstone of the Elliot Formation, which makes up the larger part of the hill above the site. Many of the fans are dissected by mature and continuous gully networks with V-shaped profiles in the proximal slope, and combined V- and U-shaped profiles in the medial and distal sections. Gully formation is linked to the sodium adsorption ratio (SARs) and high soil clay content, which facilitates swelling and shrinking (Evans, 2015). The gully cuttings reveal a sequence of buried palaeosols within a colluvial succession. Situated a few metres from a dry river bed, the bonebed described here is ~1.5 m below the modern land surface, and extends over an area 35 × 13 m (Fig. 1c). Skeletal remains exposed in the section appeared mostly to be those of black wildebeest, and they were rapidly being destroyed by erosion (Fig. 1d). The sedimentary fans, as with those in other mountainous dry regions, have experienced climatically-controlled histories of erosion, sedimentation and pedogenesis. It is proposed that

sedimentation occurred during arid climatic intervals, when decreased vegetation cover provided little surface protection and resulted in increased hillslope sediment being deposited. In contrast, when vegetation cover was restored during humid intervals, the land surface stabilized and the uppermost gravely sands weathered to form clay-like soils (Marker, 1998; Botha and Partridge, 2000; Clarke et al., 2003; Grab et al., 2005; Tooth et al., 2001).

At an elevation of approximately 1670 m above sea level, this semi-arid region receives between 600 and 700 mm of summer rainfall per annum, with marked seasonal contrasts in temperature, varying from −11 °C to 38 °C, with an average of 17 °C. The site is located in a Moist Cool Highveld Grassland Biome, characterized by the presence of many grasses and a few species of dicotyledonous forbs. Redgrass *Themeda triandra* predominates (Low and Rebelo, 1996), but when overgrazed, Weeping Lovegrass *Eragrostis curvula* is dominant. In addition, invasion of other elements such as karroid and woody dwarf shrubs occurs when the vegetation is in poor condition. The site also falls within the Basutolian Ecozone (De Vos, 1975), which in historical times supported large herbivores, mostly grazers, including black wildebeest, red hartebeest, blesbok, gemsbok and quagga, and mixed feeders such as springbok and grey rhebok (Klein, 1984). A review of late Pleistocene and Holocene large mammal distributions in southern Africa shows that most fossil faunas are dominated by the same species that predominated historically, with the addition of six specialised grazers that became extinct at the end of the Late Pleistocene and early Holocene (Klein, 1980; Skinner and Smithers, 1991; Plug and Badenhorst, 2001; Brink, 2005, 2016).

2. Materials and methods

2.1. Excavation and dating

Activities reported on here were conducted during five winter field seasons between 2005 and 2009. In the first field season we excavated a 4 × 2 m area (Fig. 2a) that sampled the top of the bonebed (Fig. 2b). The faunal remains were adjacent to a hearth (Fig. 2c) and a flaked core (Fig. 2d). The following year a 6 × 4 m area was opened along the bonebed section downslope (Figs. 2a and 3a, b) where three fossiliferous horizons were preserved. The bonebed appeared as one unit in some places, and as three horizons in another section that showed a few centimetres of sediment between three layers of bones. Mud cracks were evident in the associated sediment (Fig. 3c) and calcrete nodules were observed in the deposits underlying the bonebed (Fig. 3d). Three samples were collected for radiocarbon dating. Each sample comprised a package of fossil bones from a localized area representing the upper-most, middle and lowest horizons of bones. At the same time phytolith samples were collected from the top to the bottom of the sedimentary unit exposed in the section. A second faunal assemblage was discovered eroding out of a cirque at the base of the hill (S 28°28.211′ E 27°49.160′). This locality is referred to as Fernando's donga (Fig. 3e and f), and is 1,692 km upslope from the current excavation in the same cutting (Fig. 2a). The unit here is 4.15 m thick, and records four bonebeds containing the remains of red hartebeest (*Alcelaphus buselaphus*), black wildebeest (*Connochaetes gnou*), leopard (*Panthera pardus*), jackal (*Canis mesomelas*) and warthog (*Phacochoerus africanus*) (Figure A supplementary online), with each layer separated by approximately 1 m of sediment (Fig. 3f). Four lots of bone samples were collected from the four horizons and all were sent to Beta analytic, USA for dating. We also collected Later Stone Age (Figure B supplementary online) and Middle Stone Age flakes and cores (Figure C supplementary online) in about a 1 km radius of the site, and visited a Later Stone Age rock shelter on an adjacent farm, where there is a painting of what
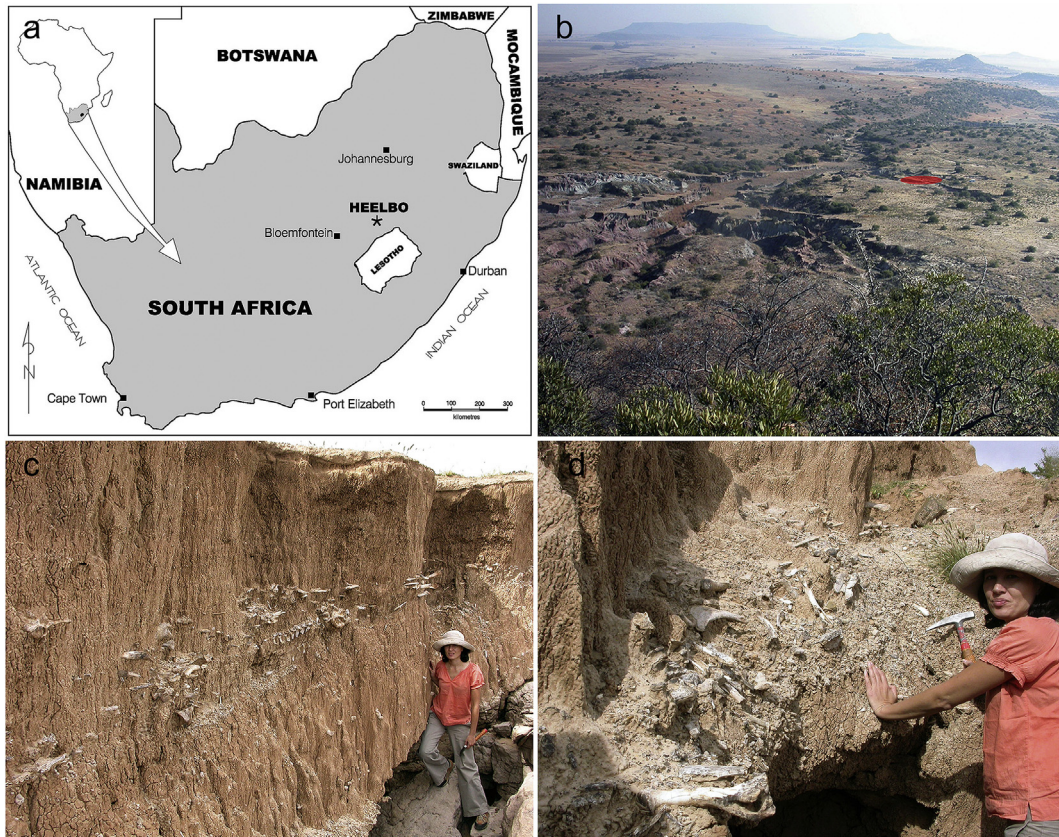
Fig. 1. a. Map of South Africa showing the location of Heelbo. b. View of the landscape from the hill above the site (in red). Note the white vehicle for scale. c. Section of the bonebed exposed in a cutting. d. Christine Steininger shows where the faunal remains are being destroyed by erosion and weathering. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
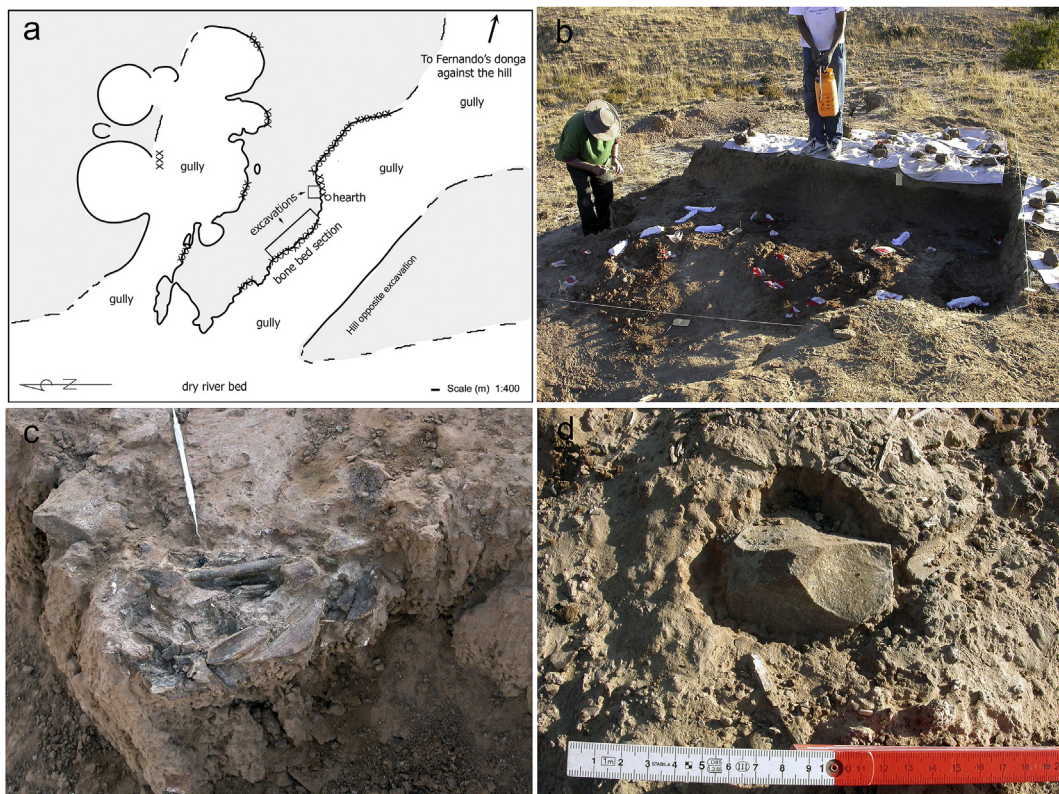

Fig. 2. a. Plotted outline of the sedimentary deposit with gullies/cuttings on both sides and the dry river bed below. The crosses represent bones eroding out of the section. Note the positions of the excavations, with the first small one shown in (b). The faunal remains are next to a hearth (c) and flaked core (d).

Fig. 3. a. Main excavation area that extended for 6 m along a section of the bonebed, and by 4 m in (b). c. Mud cracks associated with the eroding bonebed, and calcrete nodules and rhizoids in the underlying deposits (d). 1-3 mark the spots where samples were taken for radiocarbon dating. e. Fernando's donga in a cirque at the base of the hill where four fossiliferous horizons are separated by approximately 1 m each (f).

appears to be a human figure running behind a wildebeest (Figure D supplementary online).

During excavations, a diluted Paraloid® solution was applied to bone surfaces to preserve integrity and surface structure, and many pieces were jacketed with plaster before lifting. Excavations were conducted with hammers and screwdrivers, brushes and trowels. The calcretised sediment required that a weak acetic acid solution in the form of vinegar was sprayed on areas surrounding fossils. Any sediment removed was systematically sieved using 5 and 2 mm mesh. All skeletal remains were plotted *in situ* using a Nikon total station theodolite. Readings were taken on each end of the long axis of most elements to record orientation. We also plotted the outline of the donga and surface contour of the gulley adjacent to the excavation. A photographic and hand-written record was made of all excavation activities. Planimetric views of the bones per square metre were photographed using a Nikon Coolpix P1 digital camera before lifting.

Each element was photographed on two sides using a Canon G16 digital camera. The following data were captured on

mandibles, scapulae, long bones and pelves: taxon, age, skeletal element and side, weathering stage and fracture pattern(s). The need to consolidate the bones as they became exposed during excavation resulted in many specimens being covered by a layer of Paraloid®, which prevented systematic data collection on surface modifications. Nevertheless, specimens exhibiting clear traces of surface damage were photographed at between 8 and 52x magnification under reflected light using an Olympus SZX9 stereomicroscope fitted with a Nikon Coolpix 990 digital camera. All excavated material is curated with the prefix HB at the Florisbad Quaternary Research Station, National Museum, Bloemfontein.

2.2. Comparative material

On our first day in the field the farm manager informed us that an eland had died from falling into a donga and breaking its femur eight days earlier. We asked if we could study its decomposition and dispersal and he agreed, and moved it to a gulley near to the mass death site. The eland would provide a model by which to

Table 1
Adult male wildebeest used in bone modification experiments, and housed at the Evolutionary Studies Institute, University of the Witwatersrand.

Accession number	Sort code	Common name	Genus	Species	Farm	District	Country	Year	Experiment description
BP4/1292	1284	Blue Wildebeest	*Connochaetes*	*taurinus*	Dqae Qare	Ghanzi	Botswana	2009	Butchered by 6 men using unmodified chert flakes. Bone breakage using stone hammer and anvil following brief heating on a fire.
BP/4/1293	1285	Blue Wildebeest	*Connochaetes*	*taurinus*	Dqae Qare	Ghanzi	Botswana	2010	Butchered and broken while fresh by 6 men using unmodified chert flakes, hammer and anvil.
BP/4/1294	1286	Blue Wildebeest	*Connochaetes*	*taurinus*	Dqae Qare	Ghanzi	Botswana	2010	Scavenged by 11 wild dogs, followed by 2 men using chert flakes, hammer and anvil.
BP/4/1291	1283	Black Wildebeest	*Connochaetes*	*gnou*	Ngonyama Lion Lodge	Krugersdorp	South Africa	2011	Trampled by 31 cows in a sandy enclosure after 6 months exposure in a cage on a nearby farm.

gauge the taphonomic history of a large mammal in this environment. Metal poles were knocked into the ground next to the eland bones as they became dispersed on the landscape. These were painted white, named pole 1, 2, 3 etc. In order to study the rate and nature of sedimentation at the site, where it occurs and whether it is associated with wet or dry phases, we measured the length of the poles after eight, 25, 32 and 48 months.

Four bone modification experiments were conducted with wildebeest carcasses in an attempt to replicate human activities that may have been conducted at Heelbo, namely butchery of carcasses using stone tools, bone breakage with hammer stones and anvils for marrow extraction before and after heating, scavenging by a pack of 11 wild dogs followed by four humans, and, in lieu of wildebeest, trampling by a herd of 31 cows in an enclosure (Table 1). Additional reference material came from a large collection of bones modified by a wide range of known geological and biological agents (naturalistic and experimental), and published literature on mass death assemblages (e.g. Child, 1972; Shipman, 1975; Haynes, 1988, 1993; Rogers, 1990; Weigelt, 1989; Frison, 1991; Capaldo and Peters, 1995; Dudley et al., 2001; Behrensmeyer, 2007).

3. Results and discussion

3.1. Radiocarbon age estimates

Radiocarbon dating of the fossils exposed in the excavated section provides ages of 3840 ± 40 cal BP for the uppermost, 3700 ± 40 cal BP for the middle and 3500 ± 40 cal BP for the lowest bones in the bonebed (Table 2), confirming the expected mid-Holocene age based on the size of the black wildebeest limb bones (Brink, 2005). Each

age is significantly different from the others, indicating that they represent different events. The age estimates show reversals that may be due to collapse of a heap of skeletal remains into each other in a gulley, or erosion channels in the underlying matrix that caused sedimentary collapse and hence faunal mixing. Both scenarios are plausible based on observations made on the eland carcass, and recent erosion underneath sedimentary units where they contact bedrock. Based on three dating samples, bone accumulation took place at least three times in the space of 300 years. Heelbo Layer 1 overlaps temporally with Fernando 2 (3940 ± 40 cal BP) and 3 (3970 ± 40 cal BP) respectively. If one considers the excavated bonebed as corresponding broadly with Fernando's donga, then five depositional events are recorded between the two sites, spanning 1650 years (4520 ± 40 BP to 2870 40 cal BP), with the youngest and oldest ages coming from Fernando's donga.

Luminescence dating of bone from the top of the bonebed provides an age of 3500 +- 180 BP (Evans, 2015). The underlying deposit has an OSL age of 4450 ± 820 BP, which overlaps in age with Fernando 4 (4520 ± 40 cal BP). Age estimates for the Heelbo bonebed and Fernando's donga faunal horizons (Table 2) indicate a protracted arid phase around 4520 cal BP. A case of long-term aridity is supported by the presence of calcrete nodules and rhizoids in deposits underlying the bonebed. Interpreting the Heelbo bonebed as the consequence of mid-late Holocene drought is supported by phytolith data, which indicate desertification throughout the sedimentary unit (Fig. 4).

3.2. Palaeoclimate

Mid-Holocene drought at Heelbo is in broad agreement with other southern African climate proxies (see Mitchell, 1997;

Table 2
Radiocarbon age determinations for bone samples from the top, middle and bottom of the bone bed, and from four layers preserved in Fernando's donga 1,692 km upslope. Material pretreatment included bone collagen extraction with alkali.

| Laboratory number	Sample name	Service	Measured age	13C/12C	Conventional age	2 Sigma calibration BP using SHcal13; relative area under probability distribution in parantheses
Beta - 250271	HEELBO LAYER1	AMS-Standard delivery	3510 ± 40 BP	$-4.9°/oo$	3840 ± 40 BP	4404–4367 (0.033), 4356–4324 (0.035), 4316–4313 (0.001), 4300–4077 (0.885), 4037–3995 (0.045)
Beta - 248398	HEELBO LAYER2	AMS-Standard delivery	3390 ± 40 BP	$-6.0°/oo$	3700 ± 40 BP	4142–4126 (0.019), 4093–3857 (0.981)
Beta - 248399	HEELBO LAYER3	AMS-Standard delivery	3190 ± 40 BP	$-5.8°/oo$	3500 ± 40 BP	3841–3607 (1.000)
Beta - 250267	FERNANDO1	AMS-Standard delivery	2550 ± 40 BP	$-5.5°/oo$	2870 ± 40 BP	3068–2841 (0.971), 2826–2797 (0.029)
Beta - 250268	FERNANDO2	AMS-Standard delivery	3630 ± 40 BP	$-6.4°/oo$	3940 ± 40 BP	4436–4222 (0.936), 4205–4157 (0.064)
Beta - 250269	FERNANDO3	AMS-Standard delivery	3650 ± 40 BP	$-5.5°/oo$	3970 ± 40 BP	4517–4465 (0.090), 4449–4235 (0.910)
Beta - 250270	FERNANDO4	AMS-Standard delivery	4200 ± 40 BP	$-5.3°/oo$	4520 ± 40 BP	5301–4969 (1.000)
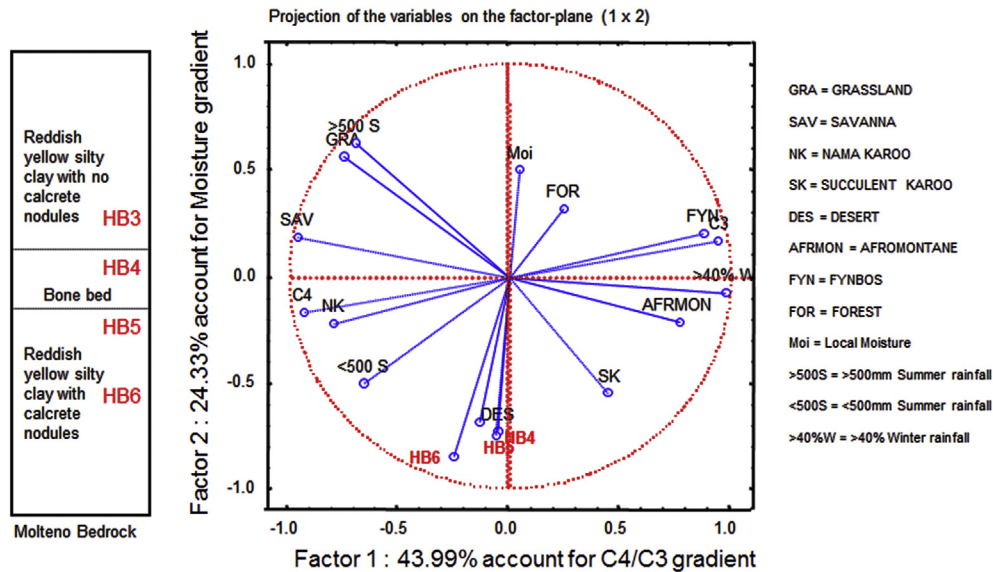
Fig. 4. Ratio (%) of 11 grass silica short cell morphotypes represented by the distribution of 271 grass species in South Africa. The Heelbo phytolith morphotypes plot with those found in deserts, indicating desertification throughout the sequence, in a region that is now a Moist Cool Highveld Grassland Biome.

Burrough and Thomas, 2013 for a review). The pollen record of higher altitude sites in the Drakensberg region and the Free State suggest a long Early Holocene drought phase (Neumann et al., 2014; Norström et al., 2009), echoed in pollen from the eastern Karoo, which indicates a major drought episode from 6500 to 5500 BP (Bousman, 1991; Mitchell, 1997). The same is reflected in charcoal from the north-eastern Cape (Tusenius, 1989) and Swaziland, which shows drier conditions from 6000 to 4000 BP (Prior and Price-Williams, 1985). Pollen data show a rapid shift to an open, arid karroid grassland at Wonderwerk Cave in the northern Cape Province at approximately 5000 BP (Van Zinderen Bakker, 1982), evidencing a major drought in the eastern Karoo from 5000 to 4000 BP. A minor drought episode is inferred from pollen and stable carbon isotope evidence on its eastern margin c. 3200 BP (Bousman, 1991). Periodically wetter conditions for the mid-late Holocene (c. 5000-1000 BP) are suggested by radiocarbon dates for peat accumulation at Tlaeeng Pass in the Lesotho highlands (Hanvey and Marker, 1994), and higher rainfall from 3200 to 2400 BP is inferred from increased spring activity in the Northern Cape (Thomas and Shaw, 1991 in Mitchell, 1997). Burrough and Thomas (2013) report that pollen assemblages from Braamhoek wetland exhibit a marked drying between 6 and 5 ka and moister conditions after 2 ka (Norström et al., 2009). Lacustrine stromatolites show relatively arid conditions between 4 and 3 ka, while lower ð13C between 3 and 1.2 ka indicates a return to wetter conditions (Brook et al., 2010). High grass and Asteraceae pollen counts at Wonderkrater record a cool, grassy environment 3—2 ka, in contrast to a bushy environment in response to warm wet conditions, from 1.2 to 0.6 ka (Scott et al., 2003).

3.3. Faunal analysis

The faunal remains have no impact marks or impact notches associated with human use of stone tools in carcass processing, nor are there cut- or scrape marks of the type created through butchery using stone flakes. Apart from the flaked core associated with the hearth, no stone tools were found in association with the bonebed. The only clear traces of surface modification are a few trampling marks (Fig. 5a and b) and some termite activity (Fig. 5c and d). In his study of elephant bones at die-off locales, Haynes (1988) estimates

that about 40% of bones on the ground were incised by trampling, and that very few of the specimens were heavily scratched, with most specimens bearing isolated incisions made by single grains. Tunnels made by modern termites were retrieved from Layers 1 and 2, and a specimen from Layer 2 recorded modern examples of boring (Fig. 6). Carnivore tooth pits and marks are absent, as is evidence of their typical gnawing on epiphyses and the posterior portions of mandibles. Haynes (1988) notes that many of the elephant bones in his study were still greasy after three years of post-mortem exposure, and therefore made attractive meals for hyaenas. The lack of hyaena damage on the Heelbo remains, in keeping with the low degree of weathering (Table 4), suggests that they were buried relatively soon after death. One specimen records traces of porcupine gnawing. None of the bones is burnt. Many of the bones are coated with a manganese deposit that sometimes follows the pattern of rootlets.

Faunal remains are curated by layer, and are presented as such in plates, with elements grouped by type. See SUPPLEMENTARY Figures E—K for faunal remains from Layers 1—3. Evidence of mixing as per the age estimates limits the value of comparison between layers. We nonetheless explore the bonebed from a taphonomic perspective by treating it as three layers, which may otherwise be taken as upper, middle and lower parts. The Heelbo faunal assemblage comprises 849 taxonomically and anatomically identifiable specimens, plus several fragments of different skeletal elements, including flakes. The elements we analysed in detail (mandibles, scapulae, long bones and pelves) all represent black wildebeest (*Connochaetes gnou*) (Table 3). We also found a single red hartebeest mandible (*Alcelaphus buceaphus*) in the first year in Layer 1 next to the hearth. The bonebed described here is therefore classified as a monotaxic large mammal mass death assemblage. A minimum number of 27 individuals are represented in the excavated fauna based on nine complete left radii and 18 distal portions of this element from the left side. A minimum number of 11 individuals are represented in Layer 1 (based on left humeri or left metatarsals), 12 in Layer 2 (based on left radii) and 9 in Layer 3 (based on right humeri or left radii or left metacarpals). Elements from the left side are more abundant in each layer, with a total of 257 as opposed to 210. This suggests that most of the animals died on their left side, an unexplained phenomenon also reported by
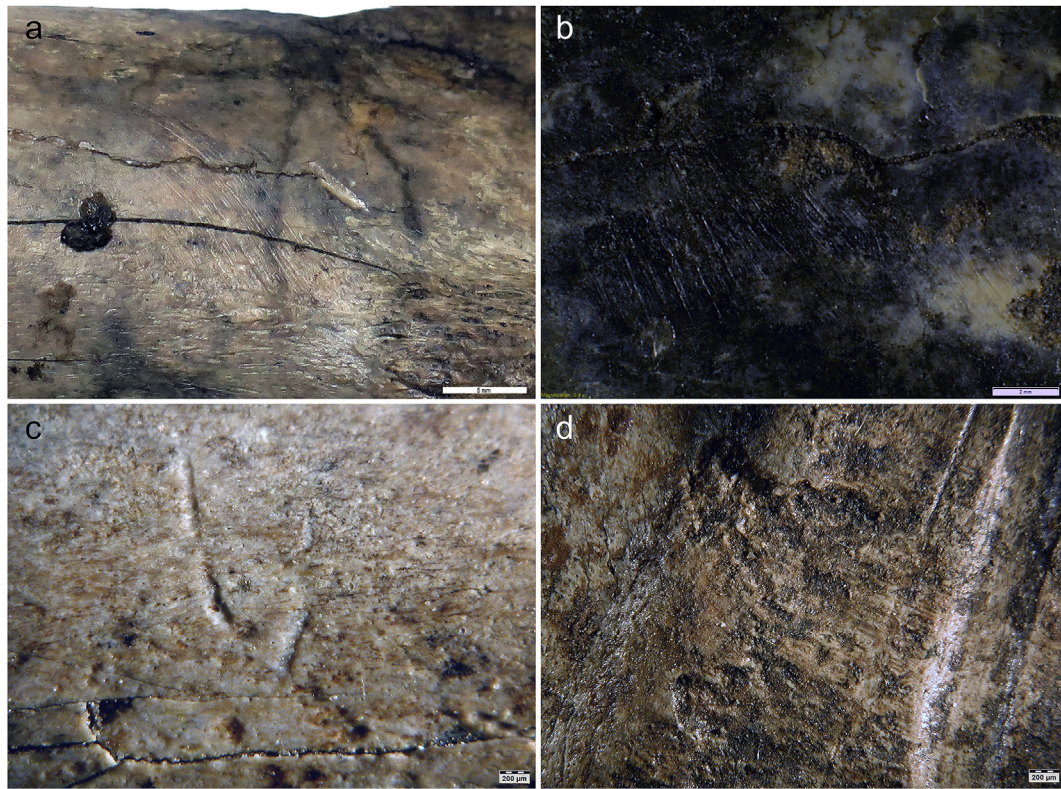
Fig. 5. Trample marks recorded on a distal radius (HB1707) from Layer 2, and a distal humerus (HB1897) from Layer 3. Insect mandible marks on a tibia (HB1814) and an unknown specimen. Scale in a = 10 mm, b = 2 mm, c = 200 μm, d = 500 um.

Haynes (1988) for elephants in southern Africa.

If we look at the number of identifiable skeletal specimens per layer (Table 3), Layer 1 records almost half of the specimens and Layers 2 and 3 record almost the same amount. However, the numbers are variable for all elements for the three layers and are not necessarily more abundant in Layer 1. All elements are well represented and well preserved in Layer 1, including many complete long and flat (scapula, mandibular ramus) bones (SUPPLEMENTARY Figures E—F), with the exception of ribs and fibulae/malleolare. The same is true for Layers 2 and 3, though most ascending rami are absent from Layer 3. Pelves are not well preserved in Layer 1, unlike Layer 2, where three are nearly complete. Relative to the other layers, a high number of cranial and foot bones are preserved in Layer 1. Articulated axial elements occur in all layers, while articulated limbs occur only in Layer 1. The Heelbo skeletal part representation is not like that of a current-sorted assemblage, which typically shows a scarcity of ribs, vertebrae, sacra and phalanges compared with rami, metapodials and tibiae (Voorhies, 1969). As was the case with the eland, running water in channels may have winnowed some elements, for example ribs, metatarsal shafts, radius shafts and carpals, which are represented by one specimen each, and these come from Layer 1. We had expected skeletal remains to be evenly spread across the site, but excavations revealed that the fossil deposit stopped abruptly about 2 m in from the section, and occupied a shallow gully or channel. As such the skeletons would have obstructed sheet-wash from the hill and according to the eland study would have been partially buried with the next rain. Given that the skeletal remains are not evenly spread across the site, it is difficult to estimate the number of animals in the buried assemblage. We guess approximately 70 individuals remain out of thousands, which have since eroded away.

The skeletal part representation at Heelbo does not match that of the so-called "schlepp effect" coined by Perkins and Daly (1968), which posits that an absence of juvenile individuals in an assemblage and low percentage (17%) of cranial remains and proximal limb bones relative to a high number (83%) of foot bones in adults occurs owing to killing of large animals some distance from the occupation site, with the meat carried or dragged back to the site in hides with the feet attached. Fifty-eight identifiable juvenile elements are recorded in the Heelbo assemblage. The juvenile to adult specimen ratio is eight juveniles to 154 adults in Layer 1, 21 juveniles to 142 adults in Layer 2, and 29 juveniles to 94 adults in Layer 3. Juvenile cranial elements, humeri and femori are abundant.

Mixing between layers is evident in the extremely low number of distal metacarpals recorded in Layer 1, as opposed to the very high number of them in Layer 2 (Fig. 7), likewise for scapulae and proximal ulnae. The same may be true for some elements in Layer 2 that settled in Layer 3, such as complete metatarsals and proximal humeri. While some elements migrated down, it is noteworthy that Layer 1 was the only layer to record, albeit in low numbers, humerus, radius and metatarsal shafts. Layer 1 also records a lot of complete and proximal metatarsals relative to the other layers. Four specimens from Layer 1 show clear signs of healed breaks and pathology, with bone deposition and remodelling recorded on a rib, humerus, distal radius and metatarsal (SUPPLEMENTARY Figure L).

Of the 402 fractured bones in the assemblage, two thirds record a spiral breakage pattern. Spiral fractures refer here to helical breaks made when the bone was relatively fresh (Johnson, 1985). When analysed by layer, 63% occur in Layer 1, 70% in Layer 2 and 67% in Layer 3. The number of freshly broken bones appears evenly spread through the layers, with approximately half of the bones in each layer recording a weathered break (Table 4). Only one specimen exhibited a combination of both. Broken bones are often not separated from each other, as one might expect from human
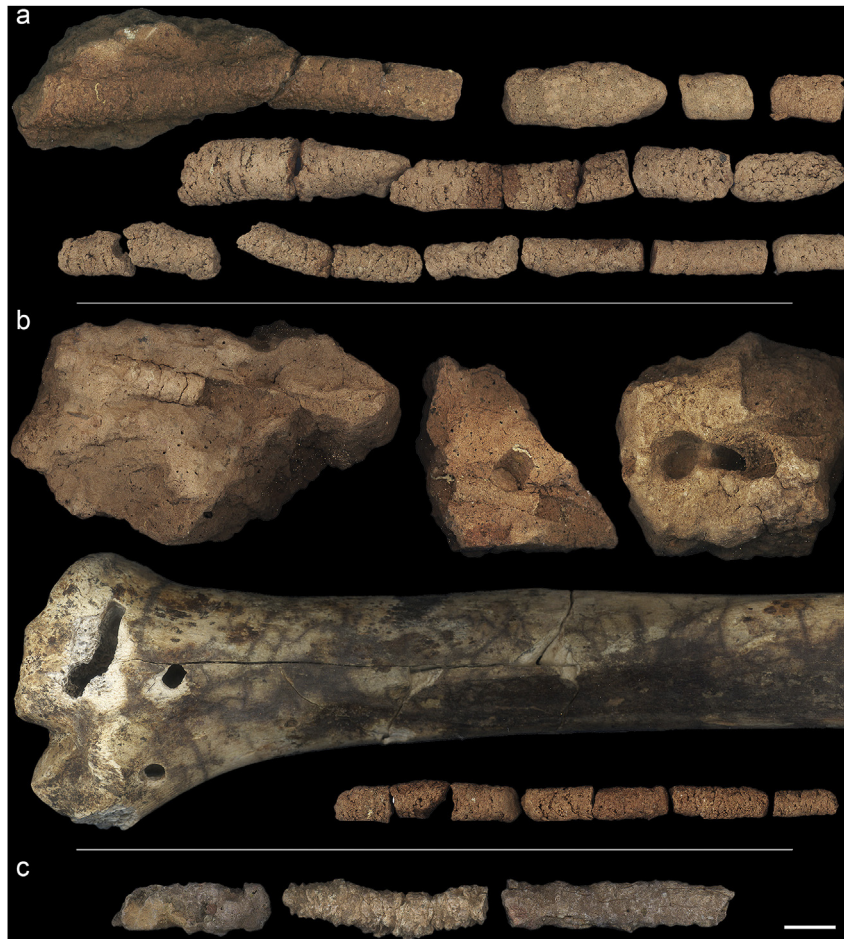
Fig. 6. Evidence of termite activity in the deposit in the form of modern termite tunnels in Layers 1 (a) and 2 (b), and traces of post-fossilisation boring in the matrix and on a distal radius (HB1814) from Layer 2 (b). c. Fossilised tunnels collected from the surface in the gulley adjacent to the excavation.

Table 3
Number of identifiable specimens for selected skeletal elements by layer.

Element	Layer 1	Layer 2	Layer 3	Total
Carpal/Tarsal	61	14	16	91
Femur	14	20	12	46
Fibula	0	0	0	0
Humerus	26	13	20	59
Mandible	24	21	12	57
Metacarpal	12	25	18	55
Metatarsal	25	12	9	46
Pelvis	18	14	11	43
Phalanx	24	14	6	44
Radius	25	29	20	74
Rib	1	0	0	1
Scapula	8	15	3	26
Skull	10	0	0	10
Tibia	18	20	7	45
Ulna	8	14	7	29
Vertebra	115	42	66	223
	389	253	207	849

Carpal/tarsal includes talus, calcaneus and other pes and manus elements.

activity, instead, freshly broken bones remain in anatomical proximity, a feature that may be explained in terms of trampling rather than marrow extraction. Haynes (1988) reports how many elephant bones that have naturally weathered (up to 36 months) will still fracture spirally when stepped on by elephants. In a few cases he recorded spirally fractured long bones broken by trampling while the bones were still partly enclosed in connective tissue or skin. In addition to being spirally fractured, the bones exhibited notches and flake scars identical to those made by humans using hammer stones. During later phases of extended die-offs around water sources, a very high proportion of limb bones were spirally fractured through trampling. The breakage pattern observed on mandibles in the Heelbo sample, namely broken anterior and distal portions, is comparable in all three layers, and similar to that shown in Behrensmeyer (1984) from the Amboseli National Park in Kenya, caused by trampling. Many of the humeri and metapodials are complete in all layers, while tibiae and femora are often broken (SUPPLEMENTARY Figures C, D, F, H). Layers 1 and 2 record a relatively high number of spirally fractured flakes compared to Layer 3 which has only seven. Layer 1 preserves the highest number of flakes at 74, while there are 16 in Layer 2, and all of them have spiral fracture patterns.

Comparison with experimentally modified wildebeest carcasses (Table 1) shows that the fracture pattern caused by bone breakage using hammer stones and anvils following brief heating on a fire is different from that observed in the Heelbo fauna. Heated bones behave like heavily weathered ones, fracturing longitudinally in a jagged or shredded manner. (SUPPLEMENTARY Figure M). Only five flakes were produced during breakage. The Heelbo assemblage pattern is more like the wildebeest experiment that concerned scavenging by wild dogs and humans using chert flakes, hammer stones and anvils (SUPPLEMENTARY Figure N), in that the long
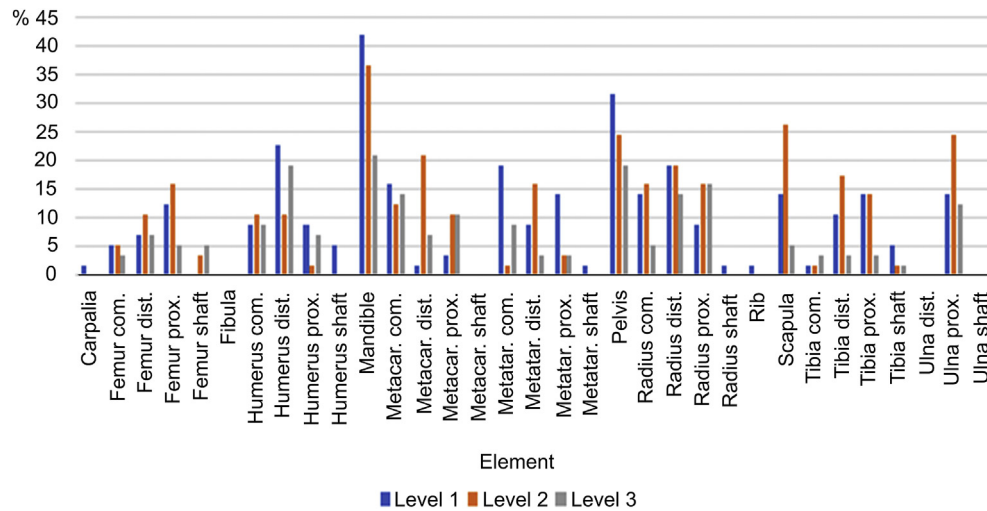
Fig. 7. Plot showing percentage of elements represented in Layers 1, 2 and 3.

Table 4
Number of green and weathered fractures recorded in the Heelbo faunal assemblage, and weathering stages observed by layer.

	Layer 1	Layer 2	Layer 3	Total
Green fracture	107	108	52	267
Weathered fracture	63	46	25	134
Mixed fracture	0	0	1	1
Total	170	154	78	402
Weathering stage 0	31	5	3	39
Weathering stage 1	148	106	77	331
Weathering stage 2	19	56	35	110
Weathering stage 3	7	10	9	26

bones in both are spirally fractured, with 32 green flakes in the experiment. The same is true for the butchery and fresh bone breakage experiment, which also records spiral fractures, and 26 green flakes. The wildebeest trampling experiment produced very few broken bones, and these have spiral and weathered fractures and 18 green flakes (SUPPLEMENTARY Figure P). This blend of features is most like the pattern observed in the Heelbo assemblage, most probably because the wildebeest used in the experiment had been exposed to the elements for six months and showed weathering stage 1. With a sample size of one, the trampling experiment conducted here cannot be taken as a suitable proxy for wildebeest trampling because unlike herds of wildebeest that mass and migrate in their thousands, the 31 cows observed in this study were reluctant to trample the carcass. They stopped short of it and smelled it and then avoided it, even when encouraged to move about the enclosure to stand on it. A long bone became lodged in the cleft of one of the cow's hooves and it walked around looking as if it was snow skiing, with little effect to the cow or bone. The cows did not break many bones, so unlike the Heelbo fauna, the trampled femora and tibiae are unbroken. We are not sure to what extent trampling of a carcass by a herd of wildebeest would be different from that of a herd of cows, but postulate that there would be a higher frequency of breaks caused by wildebeest, given that their hooves are quite pointed relative to the splayed ones of cows. When cow distal phalanges contact the ground, they cover a large flat area over which they exert equal pressure, unlike the pointed hooves of wildebeest, which place high loading forces on a small area at the tip. We expect that there would be different breakage patterns in response to the different types of loading forces (Behrensmeyer

et al., 1989; Johnson, 1989; Marshall, 1989; Shipman, 1989). The one constant that the experiment records is classic examples of trample marks, defined as numerous superficial marks that are closely spaced, intersecting, and of variable curvature, length and breadth (Andrews and Cook, 1985; Fisher, 1995), which in this case were localized sets of shallow, subparallel scratches (Fiorillo, 1989), of the type recorded in the Heelbo faunal collection (Fig. 5a and b).

Articulated segments of vertebrae of different individuals in the Heelbo assemblage show that they assume variable death postures, including curled in a circular shape, flexed with the neck arched backward and straight (Fig. 8). According to Weigelt (1989), death due to mud or quicksand is common in arid depositional environments, and in such instances, and without exception, the feet are stuck deep in what was mud, while the remainder of the skeleton lies higher up. Dying animals also tend to turn their heads toward the pelvis so that the nose points backward, and consequently the skeleton takes on a circular shape. The opposite is linked to desiccation, resulting in the neck being pulled backwards. While some of the Heelbo vertebral series curve inward, the distal limbs were not stuck in mud, and lay on the same horizontal plane as the remainder of the skeleton. Other vertebral series were flexed. Rather than interpreting the death postures as postmorten indicators of palaeoenvironment, we consider them to most likely correspond to "death throes", described by Faux and Padian (2007) as perimortem muscle spasms resulting from various afflictions of the central nervous system. Opisthotonic postures are assumed in life and preserved in death, and a lack of nourishment or essential nutrients are amongst the causes given. There appears to be no distinct orientation in the long bones in all three layers (Fig. 9), suggesting that the animals were buried relatively rapidly in the sedimentary load of alluvial fans, with little or no secondary movement by water once decomposed. Fig. 9 shows the random orientation of bones in all three layers, suggesting that all the animals in the assemblage shared a similar taphonomic history.

Our long-term study of an eland carcass (Fig. 10a) showed that the skeleton remained virtually intact for eight months, after which the hide shrivelled to expose most of the bones (Fig. 10c), which generally exhibited weathering stage 1 (Fig. 10d), which corresponds to <3 years exposure since death (Behrensmeyer, 1978). The study showed that this stage of weathering may be attained in eight months, or one summer, and that it was accompanied by mummification (Fig. 10d). Most skeletal remains in the Heelbo assemblage record weathering stage 1 (Table 4). According to Hill

Fig. 8. Articulated vertebral series showing variable death postures, with examples of inward-curled in Layer 1 (a), straight in Layer 2 (b), flexed in Layer 3 (c, d, e) and straight in Layer 3 (f).

and Behrensmeyer (1984) most disarticulation is over before weathering stage 4 is reached (6—15 years). Some joints, such as the scapula-trunk, are detached before a year has elapsed. Elements preserved in articulation in the Heelbo assemblage (SUPPLEMENTARY Figures E, G, H, I, J) represent joints that disarticulate relatively late (axis-cervical vertebra (3); cervical vertebrae (3) to (7); thoracic vertebra (13)-lumbar vertebra (1); lumbar vertebrae; lumbar vertebra (6) to sacrum; sacrum-innominate; proximal phalanx-distal phalanx), suggesting that the carcasses were exposed for at least one year, and less than three, before being buried. After two years, part of the axial skeleton of the eland was buried by sediment, and many elements had become quite widely dispersed by animals (Fig. 10e), mostly rooikat (*Caracal caracal*) and jackal (*Canis mesomelas*), identified by spoor that had preserved in surrounding sediments. Elements that were not buried had moved (Fig. 10f), and some showed breakage through trampling by antelope (Fig. 10g), which left their spoor when grazing on shrubs that had sprouted around the carcass. The first metal pole knocked into the ground for the eland study was next to the head, which lay on its left side, facing upslope in the base of a gulley. Pole 1 records

rapid sedimentation, with 15 mm deposited after one year, which was due to the carcass having obstructed a water channel. In so doing the left half of the skeleton was buried and remains so. These results are in agreement with age estimates for Fernando 2 (3940 40 cal BP) and 3 (3970 40 cal BP), which show that 1 m of sedimentation built up in only 30 years. Table 5 provides annual measurements of metal poles inserted where the eland bones dispersed. Metal poles inserted where bones were found on the ground surface upslope, and in a channel downslope recorded erosion. While rain and consequent sheet-wash causes rapid sedimentation that facilitates fossilisation, water is equally damaging in cutting gullies and eroding fossil deposits.

3.4. Integrating the Heelbo evidence

Mass death through drought is reportedly a common occurrence, with scores of animals dying from starvation caused by lack of grazing, as well as thirst owing to dried up water sources or increased salinity (Shipman, 1975; Weigelt, 1989). The animals generally contract kidney inflammation and thus die from a
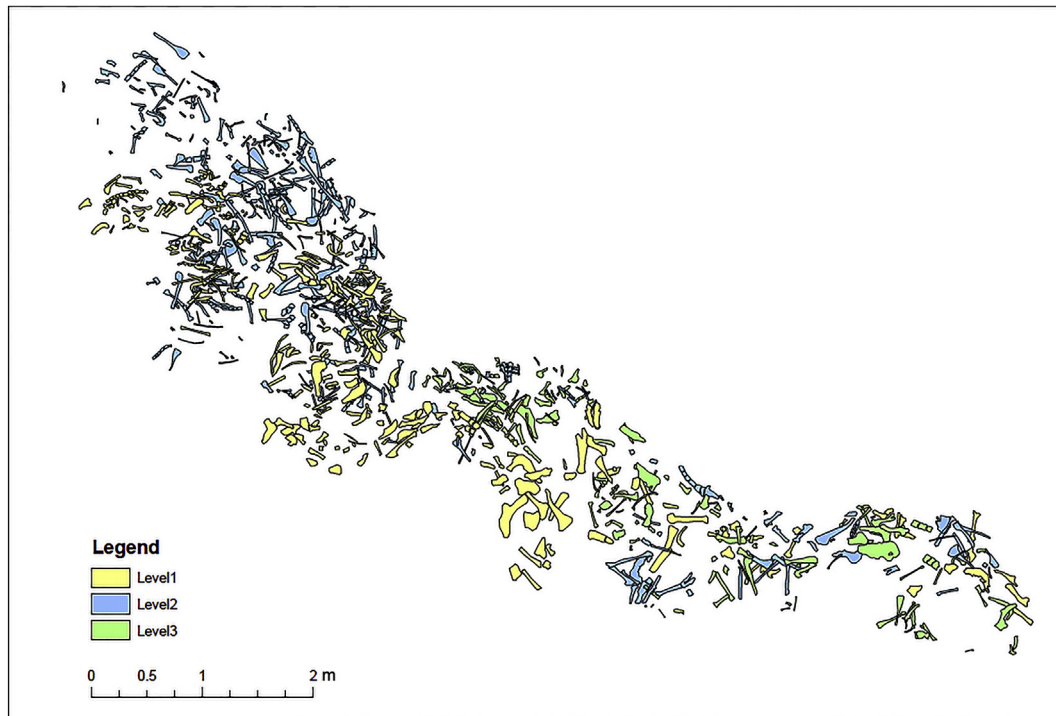
Fig. 9. Planimetric view of excavated elements from Layers 1–3. The bones are randomly oriented in all three layers.

combination of factors. Child (1972) presents observations on a wildebeest die-off that took place in Botswana. The first indications of the impending die-off were congregating wildebeest and hartebeest in their dry season range near perennial water sources. In spite of the unlimited meat available, very few carcasses were touched, even by vultures. Calves were the first age class to die, and a significantly higher proportion of the deaths were male. Haynes (1988) observed modern elephant deaths in Zimbabwe near dried up waterholes, including 45 elephants, six buffalo, two zebras, one lion, one hyaena and five birds. During the Ethiopian drought of 1973, Shipman observed many animals dying of starvation near major water sources. She also found that hyaenas, which habitually consume bones, altered their habits to eating soft tissue instead, resulting in virtually undisturbed skeletons. Under-utilisation of elements by mammalian and avian scavengers was also noted by Behrensmeyer and Dechant-Boaz (1980) during drought conditions at the Amboseli National Park in Kenya. Based on her observations, Shipman (1975) proposed a number of palaeontological criteria for the recognition of fossil assemblages resulting from drought: (1) many animals may be buried close to major water sources, having died from starvation rather than thirst. (2) The age distribution of individuals is catastrophic. (3) Many individuals are preserved partially or fully articulated because carnivores have not disturbed the bones, and desiccated soft tissues have helped to keep joints intact. (4) Animals of disparate habitat preference are found in association, and most species are highly water dependent. (5) Aquatic or semi-aquatic animals die concentrated in small areas. (6) Animals such as crocodiles and lungfish die during aestivation. The geological criteria are as follows: (1) fine-grained strata associated with the fossils show mud-cracks, (2) evaporites and caliche are commonly associated with the fossils but are uncommon in other strata of the deposit, and (3) overlying sediments indicate rapid deposition.

Apart from the aquatic animals, the Heelbo assemblage and site bear all of the features of a drought. The taphonomy evokes a scenario in which animals would congregate at the dried-up river bed during droughts, milling around and trampling skeletal remains that had likely met a similar fate. Our eland study demonstrated partial mummification of limbs eight months post mortem, and how trampling occurred on exposed and partially buried bones owing to grazers feeding on the foliage that had sprouted around the carcass. Our trampling experiment produced flakes and breakage patterns (mandible, pelvis, scapula and radius) that can all be matched in the Heelbo sample. A similar site formation process is proposed for the Langebaanweg bonebed (Brumfitt et al., 2013), which is interpreted as a spring-fed waterhole along a river where animals would mass during droughts. The lack of impact marks on the Langebaanweg faunal remains suggests trampling of partially mummified carcasses by large animals. A comparable trampling scenario is possible for the Heelbo faunal assemblage, which records many spiral breaks, evidence of trample marks on some specimens, and a noteworthy absence of other types of damage.

Mass death sites due to hunting by humans in the form of game drives are characterized by their location, typically a Great Plains landscape or open grassland dissected by gullies, and situated on a migration route to and from water (Frison, 1991 and references therein). North American bison drive sites comprise large bonebeds, between 60 and 120 intact carcasses, and multiple events are common due to strategic use of a topographic feature. Assemblages exhibit spirally fractured long bones that result from animals being crippled in the fall. Bones may record filleting marks, but few cut marks because of the abundance of meat and stripping method used to remove muscle from bone. Projectile points are scarce at many sites. Following these criteria, in which evidence of human activity is elusive, Later Stone Age people may well have been the cause of the mass deaths at Heelbo. Weigelt (1989) explains that causing a herd to panic and stampede is an effective form of hunting because in the course of the stampede there is confusion and the animals break bones, get stuck, fall off high places and exhaust themselves. Setting a grass fire for this purpose is reported

Fig. 10. a. Eland carcass placed in a gulley near to the mass death site a few days after death in August 2005. b. Flies and maggots were abundant in a wound on the hind limb. c. After eight months the hide had shrivelled, and most soft tissue had gone. d. Most of the bones were exposed and showed weathering stage 1. Distal limbs were mummified and the hide recorded traces of consumption by maggots. Skeletal remains were widely scattered (e). The ellipse indicates the original position of the carcass, where part of the axial skeleton was buried by sediment. After two years elements that were not buried had moved (f), and some had been trampled (g). Note the hoof imprint to the right of the 10 cm scale bar.

in Africa by Waibel (1921), and it is said to cause such confusion that animals are easy to slaughter. The Heelbo site and faunal assemblage have all the features of a game drive or panic-induced stampede, in which herds of animals were driven into the dongas. The spiral fractures on long bones and flakes recorded on the modern wildebeest skeletons that were experimentally broken when fresh can all be matched in the Heelbo fauna, which records similar breakage patterns in each layer. In addition, the eland study

demonstrated how falling into a donga resulted in a spirally fractured femur, which crippled it and led to its death. In addition to driving the wildebeest, human activity at the site may have been in the capacity of scavenger, to exploit partially decomposed carcasses for marrow. If this was the case the spiral breakage patterns in the Heelbo assemblage indicate that marrow was harvested from relatively fresh bone, and not following heating on a fire to liquify it. We cannot rule out the possibility that humans were responsible

Table 5
Eland carcass peg measurements (height in cm) over four years.

Peg	Location	start 1-Aug-05	8 months 2-Apr-06	25 months 6-Jun-06	32 months 24-Sep-06	48 months 2-Sep-07	sedimentation	erosion
1	donga depression	35	22.5	20.0	18.6	18.2	16.8	
2	donga depression	–	39.9	37.5	35.0	33.2	6.7	
3	donga depression	–	40.1	39.1	38.6	38.8	1.3	
4	donga depression	–	32.1	31.5	30.6	30.3	1.8	
5	land surface	–	31.5	31.5	31.0	30.9	0.6	
6	land surface	–	20.5	20.6	20.5	20.5	0.0	
7	land surface	–	33.8	34.3	34.0	34.6		0.8
8	land surface	–	35.0	34.5	34.5	34.6	0.4	
9	land surface	–	36.9	38.0	38.5	39.1		2.2
10	channel	–	65.9	64.4	66.5	65.9	0.0	
11	channel	–	65.0	64.1	61.4	65.4		0.4

for the accumulation and modification of the Heelbo assemblage, but are dissatisfied that an absence of evidence is used to build a case in favour of humans. No stone tools were found in the excavated deposit and lithics scattered around the site were found to be the result of knapping activities conducted on the hill, which have been dispersed by sheetwash. An absence of impact marks and cutmarks in the Heelbo assemblage, together with the presence of pig, jackal and rooikat in Fernando's donga, mediate against the likelihood that humans were the cause of repeated mass deaths at the site. While many bison jump sites are documented in North America, only one mass kill site is reported for Africa, namely SK400, a Later Stone Age site from the west coast in South Africa (Dewar et al., 2006), where 123 springbok (*Antidorcas marsupialis*) are thought to have been driven into a trap where they were dispatched by hunters. As with Heelbo, there is a catastrophic mortality profile, the faunal remains are dominated by one species, with a small proportion of jackal represented, and in this case seal, and long bones are spirally fractured. Unlike the Heelbo remains, the SK400 assemblage is fragmented and some bones are burnt. The post-Neolithic Tell Kuran bonebed in the Levant, with a minimum of 93 Persian gazelle and a few other species, is also interpreted as a game drive site (Bar-Oz et al., 2011). Like Heelbo, both immature and adult animals are represented, bones are little weathered, unburnt, spirally fractured and bear few traces of carnivore damage. Unlike Heelbo, the vast majority of bones represented are first, second and third phalanges, and they record butchery marks.

Mass death due to flooding results in long narrow lenses of bones in clays, or tangled clusters of bones from many species. Flume experiments have demonstrated that certain bones come to rest in preferred orientations, with long bones tending to orientate parallel to the current, as do pelves, with the ilia pointing downstream (Voorhies, 1969; Coard and Dennell, 1995). Bones also display different transport potential, e.g. bones common to the transport group from three studies include the atlas, cervical and lumbar vertebrae, sacrum and metatarsals, and the transport potential of bones are generally enhanced when articulated. Bones common to the non-transport group and thus typically represented in flood deposits include the mandible, scapula, ulna, radius and tibia (Voorhies, 1969; Boaz and Behrensmeyer, 1976; Coard and Dennell, 1995). While flash flooding caused by cloudburst may have trapped the animals in the erosion gulley, it could not have drowned them because the catchment area for the gulley and local valley is limited to a fan with a radius of less than 500 m, which means that insufficient water is generated to cause a flood. Analysis shows that the Heelbo fauna is randomly oriented and does not follow the pattern observed in flume experiments. Bones are not tangled or clustered in lenses, and do not represent the remains of many species, features characteristic of flood deaths. Death by drowning produces dense bone deposits over large surface areas adjacent to lakes and rivers. Signature criteria include fairly high concentrations of relatively complete specimens from a single species, a predominance of adults and absence of immature individuals, presence of intact elements of all types, assemblages dominated by axial elements and long bones, and an absence of compact bones. Unlike droughts, drownings represent an important scavenging opportunity for a wide variety of consumers (Capaldo and Peters, 1995; Dechant-Boaz, 1982). The pattern described for death by drowning does not match that of the Heelbo assemblage because compact bones are well represented in each layer and the bones have not been scavenged.

Death due to cold caused by an abrupt drop in temperature has resulted in many modern carcass assemblages, and like many of the natural catastrophic events, mass death may be the cumulative result of multiple factors, for example sudden cold following a long period of drought (Weigelt, 1989). Resulting skeletons would be little modified, and this mode of death may account for the Heelbo assemblage. Finally, death caused by disease is seemingly common, and under disease conditions animals die dispersed over a large area (Weigelt, 1989), and the possibility that this happened at Heelbo cannot be ruled out.

4. Conclusion

Based on a number of taphonomic features - including mixed age profile and stages of preservation, partially articulated individuals and bones showing no evidence of cutmarks or carnivore damage - together with calcrete nodules in the underlying deposit, and phytolith data that show desert conditions throughout the sequence, it is hypothesized that the animals in the Heelbo bonebed died under drought conditions that spanned 300 years (3840 ± 40−3500 ± 40 cal BP). If age estimates for Fernando's donga are included, then regional drought is recorded for 1650 years (4520 ± 40−2870 ± 40 cal BP). The additional taxa (leopard, jackal, pig) found in Fernando's donga support a hypothesis of widespread drought. In this scenario, the bonebed represents herds of water-dependent wildebeest congregating to drink at a dried-up water source. Here they died, and before being relatively quickly covered by sediment were trampled, by each other as herds massed. Sections of the bonebed that recorded three layers of bones are mixed, and represent heaps of skeletons that accumulated and collapsed in a gully. While it may be argued that humans were responsible for the mass death assemblage, there is no compelling evidence on the fauna to support it, and lithics around the site originate from the hill and have been dispersed by sheetwash. As such, the hearth associated with burnt and percussed bones is best explained as an isolated occurrence.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.quaint.2017.11.055.

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