

1
2
3
4 Nutritional values of tortoises relative to ungulates from the Middle Stone Age
5 levels at Blombos Cave, South Africa: Implications for foraging and social behaviour
6
7
8

9
10 Jessica C. Thompson^{a*} and Christopher S. Henshilwood^{b, c}
11

12
13 ^aSchool of Social Science, Archaeology Program, Michie Building (9), University of
14 Queensland, Brisbane, QLD 4072, Australia; jessica.thompson@uq.edu.au
15
16
17

18
19 ^bEvolutionary Studies Institute, , University of the Witwatersrand, Johannesburg, South
20 Africa; christopher.henshilwood@wits.ac.za
21
22

23
24 ^cInstitute for Archaeology, History, Culture and Religion, University of Bergen, Norway
25
26
27

28
29 *Corresponding author Tel. +61 7 3365 2765; Fax +61 7 3365 1544
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52

53 **Keywords:** Blombos; *Chersina angulata*; Middle Stone Age; Gatherers; Foragers;
54 Nutrition
55
56
57

58
59 **Running Title:** Nutritional value of tortoises and foraging implications at Blombos Cave
60
61
62
63
64
65

4 **Abstract**
5

6 The site of Blombos Cave (BBC), Western Cape, South Africa has been a strong
7 contributor to establishing the antiquity of important aspects of modern human behaviour,
8 such as early symbolism and technological complexity. However, many linkages between
9 MSA behaviour and the subsistence record remain to be investigated. Understanding the
10 contribution of small fauna such as tortoises to the human diet is necessary for identifying
11 shifts in overall foraging strategies as well as the collecting and processing behaviour of
12 individuals unable to participate in large-game hunting. This study uses published data to
13 estimate the number of calories present in tortoises as well as ungulates of different body
14 size classes common at South African sites. A single tortoise (*Chersina angulata*)
15 provides approximately 3332 kJ (796 kcal) of calories in its edible tissues, which is
16 between 20 – 30% of the daily energetic requirements for an active adult (estimated
17 between 9360 kJ [3327 kcal] and 14,580 kJ [3485 kcal] per day). Because they are easy
18 to process, this would have made tortoises a highly-ranked resource, but their slow
19 growth and reproduction makes them susceptible to over-exploitation. Zooarchaeological
20 abundance data show that during the ca. 75 ka upper Still Bay M1 phase at BBC tortoises
21 contributed twice as many calories to the diet relative to ungulates than they did during
22 the ca. 100 ka lower M3 phase. However, in spite of the abundance of their fossils, their
23 absolute caloric contribution relative to ungulates remained modest in both phases. At the
24 end of the site's MSA occupation history human subsistence strategies shifted to
25 emphasise high-return hunted mammals, which likely precipitated changes in the social
26 roles of hunters and gatherers during the Still Bay.
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

4 **Introduction**
5

6
7 Research on the African Middle Stone Age (MSA) is often embedded within
8
9 larger questions of the origins of modern human behaviour. The MSA commenced by ca.
10
11 285,000 years ago (ka) in East Africa and the Horn (Morgan and Renne, 2008; Tryon and
12
13 McBrearty, 2002; Tryon and McBrearty, 2006). In South Africa technological elements
14
15 of the MSA appear early as ca. 500 ka (Porat et al., 2010; Wilkins and Chazan, 2012;
16
17 Wilkins et al., 2012), and disappear as recently as 20 ka (Clark, 1999). In central and
18
19 southern Africa, deposits dating especially to the final 100 ka of the MSA have yielded
20
21 evidence for the emergence of important behaviours shared by all modern hunter-
22
23 gatherers. These include symbolism, social complexity, technological complexity using a
24
25 variety of raw materials, and flexible foraging strategies (Barham, 2001; Brown et al.,
26
27 2009; Brown et al., 2012; d'Errico et al., 2012; d'Errico et al., 2005; d'Errico et al., 2008;
28
29 Deacon, 2001; Henshilwood, 2007; Henshilwood et al., 2009; Henshilwood et al., 2002;
30
31 Henshilwood et al., 2011; Henshilwood and Dubreuil, 2011; Henshilwood and Marean,
32
33 2003; Marean et al., 2007; McBrearty and Brooks, 2000; McCall and Thomas, 2012;
34
35 Nash et al., 2013; Texier et al., 2010; Vanhaeren et al., 2013; Wadley, 2001; Wadley et
36
37 al., 2011; Watts, 2010; Wurz, 1999).
38
39
40
41
42
43
44

45
46 A widely-discussed aspect of modern human origins has been how important
47
48 changes in human behaviour may have been reflected in or perhaps facilitated by changes
49
50 in diet, subsistence, and foraging efficiency. Some researchers initially argued that MSA
51
52 people exploited resources less effectively and were less capable hunters than their Later
53
54 Stone Age (LSA) successors (Avery et al., 2008; Binford, 1981; 1984; Klein, 1994;
55
56 Klein, 1995; Klein, 1998; Klein, 2000; Klein, 2009; Klein et al., 2004a; Klein and Cruz-
57
58
59
60
61
62
63
64
65

4 Uribe, 1996; Weaver et al., 2011). More recent work has indicated MSA people had an
5 unrestricted hunting ability (Dusseldorp, 2010; Faith, 2008; Marean et al., 2000; Milo,
6 1998; Thompson, 2010a; Thompson and Henshilwood, 2011). Such work has also
7 examined the possibility that small ungulate trapping and snaring reflected technological
8 subsistence solutions as complex as those used by modern people (Clark, 2011; Clark and
9 Plug, 2008; Wadley, 2010).

10
11
12
13
14
15
16
17
18
19 Much of this research has emphasised the dietary contributions of ungulates,
20 although small fauna such as tortoises are also commonly – sometimes more commonly –
21 preserved. Because tortoises would have provided protein, fat, and other ‘animal’
22 resources in a ‘collectable’ package, their fossils should provide insight into the
23 subsistence behaviour of individuals within MSA groups that had limited hunting ability
24 (e.g. pregnant, lactating, or menstruating women, children, the elderly, or the infirm).
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

Wadley (2010:189) has noted that “it is a mistake to make generalizations about hunting strategies in the MSA”, and the same may be applied to faunal exploitation in a broader sense. The variable abundances of tortoises within and between sites highlights changes in resource use within the MSA, allowing productive questions about human demography, prey choice, and adaptability to be explored.

66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
92
93
94
95
96
97
98
99
100

This study quantifies the relative dietary contributions of tortoises and ungulates at the site of Blombos Cave (BBC), Western Cape, South Africa (Figure 1). The site has played a prominent role in establishing that complex material culture and the expression of symbolic behaviour was present in Africa by at least 100 ka (Henshilwood, 2009; Henshilwood and Dubreuil, 2011), and its faunal data speak to subsistence strategies during a period of emerging behavioural complexity. Optimal foraging theory and

4 nutritional literature provide the basis for establishing how the two faunal groups were
5 ranked in the diet, and zooarchaeological data show how they were actually exploited.
6
7 This provides a platform for investigation of overall foraging strategies, site occupation
8 intensity, and the role of both hunters *and* gatherers within the MSA.
9

10
11
12
13
14 < Figure 1 >
15

16 **Background**

17 *Blombos Cave*

18
19
20
21 BBC is located on the southern coast of South Africa, approximately 300km east
22 of Cape Town (Figure 1). Excavations between 1992 and 2009 uncovered a stratified
23 sequence of LSA and MSA deposits (Henshilwood et al., 2009; Henshilwood et al.,
24 2001b). The MSA levels at Blombos Cave are divided into four phases, M1, upper M2,
25 lower M2 and M3. These have been dated using thermoluminescence (TL), optically
26 stimulated luminescence (OSL), electron spin resonance (ESR) and thorium/uranium to
27 between ca. 75 to > 130 ka (Henshilwood et al., 2002; Henshilwood et al., 2011; Jacobs
28 et al., 2003a; Jacobs et al., 2006; Jacobs et al., 2013; Jacobs et al., 2003b; Jones, 2001;
29 Tribolo, 2003; Tribolo et al., 2006). Summaries of the chronology of the BBC deposits,
30 their associated ages, and material culture, and site layout are provided in Table 1 and
31 Figure 2.
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47

48 < Table 1 >
49

50
51 The taxonomic composition of the BBC MSA faunal remains has been previously
52 reported by Henshilwood et al. (2001b) and taphonomic work has been reported by
53 Thompson and Henshilwood (2011). Bovids dominate the large mammal sample, with
54 small size 1 ungulates such as grysbok/steenbok (*Raphicerus* spp.) very common in the
55
56
57
58
59
60
61
62
63
64
65

4 M3 and Upper/Lower M2 phases but with more representation of larger ungulates in the
5
6 M1 phase. Across ungulate body size classes, MSA people are implicated as the primary
7
8 accumulators, with perhaps slightly less human input of small ungulates in the lowermost
9
10 M3 phase (Thompson and Henshilwood, 2011).
11
12

13
14 < Figure 2 >
15

16 Bone surface modification of the M1 sample showed that MSA people were also
17
18 the main accumulators and modifiers of the tortoises (Thompson and Henshilwood, in
19
20 revision), with human modification present on all element types (Figure 3).
21
22

23
24 < Figure 3 >
25

26 Burning patterns in this phase also demonstrated that tortoises were processed by
27
28 being cooked carapace side down in their shells (Figure 4), which is an efficient mode of
29
30 processing argued to have occurred in both the Old and New Worlds from the Middle
31
32 Pleistocene to the present (Blasco, 2008; Flannery and Wheeler, 1986; Sampson, 2000;
33
34 Schneider and Everson, 1989; Speth and Tchernov, 2002; Stahl and Oyuela-Caycedo,
35
36 2007; Thompson, 2010a; Werner, 1990). Skeletal element abundances suggested that
37
38 humans were also the primary accumulators for the M3 sample, as raptors do not tend to
39
40 deposit large quantities of carapace and plastron elements (Sampson, 2000). Thus the
41
42 ungulates and tortoises are considered to be comparable to one another in terms of their
43
44 taphonomic histories.
45
46
47
48
49

50
51 < Figure 4 >
52

53 *Tortoises as prey items* 54

55 In South Africa, tortoise remains are found in archaeological deposits ranging
56
57 from Middle Pleistocene to historic sites (Cruz-Urbe and Schrire, 1991; Klein et al.,
58
59
60
61
62
63
64
65

4 1999). They are common in both MSA and LSA sites in the Western Cape, for example
5 reaching densities of 49-304 individuals/m³ at the LSA site of Byneskranskop (BNK) and
6
7 3–18 individuals/m³ at the LSA/MSA site of Die Kelders Cave 1 (DK1) (Cruz-Uribe and
8
9 Schrire, 1991). Several MSA sites in the Western Cape of South Africa, such as
10
11 Ysterfontein 1 (YFT1), Diepkloof Rock Shelter (DRS), Boomplaas Cave (BPA), DK1,
12
13 and BBC have produced large tortoise assemblages, where in many cases they outnumber
14
15 other faunal classes in terms of number of identified specimens (Faith, 2011;
16
17 Henshilwood et al., 2001b; Klein et al., 2004b; Klein and Cruz-Uribe, 2000; Steele and
18
19 Klein, 2013).
20
21
22
23
24
25

26 The nutritional values of small faunal components have been estimated for several
27
28 Holocene sites in South Africa (Buchanan, 1986; 1988), and tortoises were argued to
29
30 have been an important terrestrial component to the early Holocene diet. However, in the
31
32 MSA their analysis has been restricted mainly to their demographic, rather than
33
34 subsistence, implications. Specifically, decreasing tortoise and shellfish sizes from the
35
36 Middle to Later Stone Age in South Africa have been used to argue for increased
37
38 predation pressure from growing human populations (Klein, 1978; Klein et al., 2004a;
39
40 Klein and Cruz-Uribe, 2000).
41
42
43
44
45

46 Decreasing tortoise size from the Middle to Upper Palaeolithic has also been
47
48 argued to indicate increasing human populations in the Mediterranean region (Stiner et
49
50 al., 2000; Stiner et al., 1999), which shares many environmental similarities with the
51
52 southwest coast of South Africa (Cowling et al., 1996). Here, tortoises are also a
53
54 consistent component of faunal assemblages from the Middle Pleistocene to the Holocene
55
56 (Blasco et al., 1986; Blasco, 2008; Blasco and Fernández Peris, 2012b; Speth and
57
58
59
60
61
62
63
64
65

4 Tchernov, 2002; Stiner et al., 2000). However, in the Mediterranean Basin the
5
6 subsistence implications of tortoise exploitation have also been examined in detail,
7
8 especially through use of optimal foraging theory and diet breadth models (Blasco and
9
10 Fernández Peris, 2012a; b; Munro and Atici, 2009; Stiner, 2001; Stiner and Munro, 2002;
11
12 Stiner et al., 2000; Stiner et al., 1999).
13
14

15
16 Under a diet-breadth model prey are ranked according to their net return, which is
17
18 their caloric value minus the energetic costs of their acquisition and processing, or search
19
20 and handling costs (Bird and O'Connell, 2006; Winterhalder and Smith, 2000). Resources
21
22 are included in the diet depending on their ranking. Those with higher returns are always
23
24 taken on encounter, while lower-ranked resources may be bypassed. Expansion in diet
25
26 breadth occurs when people begin to exploit lower-ranked resources, often because
27
28 encounter rates with more highly ranked resources have become unsustainably low. In
29
30 the Mediterranean Basin diet breadth was narrow during the Middle Palaeolithic,
31
32 although tortoises were consistently taken. Diet breadth expanded in pulses toward the
33
34 end of the Middle Palaeolithic and into the Upper and Epi-Palaeolithic, which has been
35
36 interpreted as further evidence for increased human population sizes beginning at the end
37
38 of the Middle Palaeolithic (Stiner et al., 2000; Stiner et al., 1999).
39
40
41
42
43
44

45
46 There has often been an assumption that prey body size is the main determining
47
48 factor in hunter decision-making, with animals of a larger body size being most highly
49
50 ranked (Bayham, 1979; Broughton, 1994a; Broughton, 1994b; Dusseldorp, 2010).
51

52
53 Madsen and Schmitt (1998) have challenged the simplicity of this assumption by
54
55 suggesting that mass collecting of small prey can result in return rates comparable to
56
57 those of large fauna, although Ugan (2005) has found that individual handling costs of
58
59
60
61
62
63
64
65

4 processing small birds and mammals remain high regardless of the mode of collection.
5

6 Models of prey returns and energetic costs of transport have shown that large mammals
7
8 will always provide greater returns than small fauna even if long transport distances are
9
10 involved – except when the resource has very low processing costs (Grimstead, 2010).
11
12

13 Bird et al. (2009) has shown that in some environments body size is positively correlated
14
15 with prey mobility, but inversely correlated with pursuit success – and is therefore not
16
17 always an appropriate archaeological measure of prey ranking. Hockett and Haws (2003;
18
19 2009) have further suggested that dietary diversity is nutritionally advantageous in its
20
21 own right and thus diet-breadth models are not universally applicable.
22
23
24

25
26 Within this body of literature tortoises occupy a special place: they are small in
27
28 body size but slow-moving, their acquisition is not risky, and their processing costs
29
30 require minimal technology and effort. Tortoises have other unique and useful properties
31
32 relative to other animal resources. After being eaten, their shells can be used as
33
34 containers, musical instruments, or decorations (e.g. Henshilwood, 2008). The animal
35
36 itself can also be stored while alive and therefore kept fresh and easily transported. All
37
38 these factors should have made them highly ranked, and they should have always been
39
40 taken on encounter (Stiner et al., 2000). However, prey that are ‘slow-moving’ are also
41
42 often ‘slow-growing’ (Stiner and Kuhn, 2009; Stiner et al., 2000; Stiner et al., 1999).
43
44
45 Therefore, it is unlikely that tortoise populations could have sustained intensive, long-
46
47 term human predation.
48
49
50
51

52
53 These issues are examined archaeologically at BBC through combined analyses of
54
55 tortoise and ungulate remains. Here, the ranking of the two faunal subsets relative to one
56
57 another in the MSA diet is investigated by first establishing their respective caloric
58
59
60
61
62
63
64
65

4 returns. The intensity of their exploitation is then inferred at BBC by combining the
5 nutritional data and zooarchaeological abundance data. Against the backdrop of modern
6 human origins research the relative importance of ‘hunted’ and ‘collected’ fauna in the
7 MSA is then discussed within this quantitative framework.
8
9
10
11
12
13
14

15 **Materials and methods**

16
17
18
19 The BBC archaeological collections are curated at the Iziko South African
20 Museum in Cape Town and the data in this research were collected there. Taphonomic,
21 taxonomic, and skeletal element abundance (SEA) data were collected from the M1
22 phase (the uppermost layers, CA/NA), with additional SEA data collected from the M3
23 sample (also the uppermost layers of this phase, CH/CI). A modern skeletal collection
24 was used to identify each specimen > 1cm in the maximum dimension to taxonomic
25 affinity, element, and side to the greatest extent possible. Skeletal element abundances
26 were evaluated using the Number of Identified Specimens (NISP) and the Minimum
27 Number of Elements (MNE); the highest count on the latter provided the Minimum
28 Number of Individuals (MNI). Because identifiable tortoise elements fragment in
29 consistent portions and at consistent landmarks compared to mammals, the fraction-
30 summation approach was a time-effective and accurate means of estimating the MNE and
31 MNI (Marean et al., 2001), and was used for both limb and shell elements. The total
32 NISP sufficiently identifiable to be used for MNE calculation was 3562 from M1 and 727
33 from M3, (Table 2), available from a total analysed sample of 8657 and 1029,
34 respectively.
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56

57 < Table 2 >
58
59
60
61
62
63
64
65

4 The ungulate sample was drawn from analysis of all large mammal postcranial
5 fragments (> 4.5 kg live weight) exceeding 2 mm in the maximum dimension that had
6 been recovered during the 2000, 2002, and 2004 excavation seasons, for a total NISP of
7 3879 from M1 and 1256 from M3 (Thompson and Henshilwood, 2011). The subsample
8 sufficiently identifiable to element, side, and body size to be used in MNE estimates
9 comprised a NISP of 440 (M1) and 110 (M3). Because the tortoises were so numerous,
10 analysis could only be done for a smaller area of deposit than was possible for the
11 mammals – approximately 4.3 times less for M1 and 3.1 times less for M3. If the sample
12 of large mammal data was restricted for analysis to only the same excavated contexts
13 from which tortoise data were available, then the NISP appropriate for MNE analysis was
14 259 and 60 for M1 and M3, respectively. Data for both sample sizes are provided in
15 Table 3.
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32

33 < Table 3 >
34
35

36 In faunal assemblages, MNE data quickly demonstrate an MNI of one because it
37 only takes a single specimen to represent an individual animal. In highly fragmented
38 assemblages, the MNE and MNI thereafter increase slowly relative to total NISP because
39 it is more difficult to prove fragments are not from the same individual (Lyman, 2008). In
40 less fragmented assemblages, or at sufficient sample sizes, NISP and MNE increase in
41 tandem (Grayson and Frey, 2004). The ungulate assemblage from BBC is highly
42 fragmented (Thompson and Henshilwood, 2011), but for tortoises the NISP: MNE ratio is
43 nearly 1:1 (Thompson and Henshilwood, in revision). Therefore, MNI data from a
44 smaller sample of deposit are likely to over-represent ungulates relative to tortoises than
45 would be the case with a larger sample. Assuming a random distribution of faunal
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

4 remains across the site, the numbers of tortoises should increase as a factor of the amount
5
6 of deposit sampled. This is supported by the high numbers of conjoining tortoise
7
8 elements and their close spatial proximity, indicating that the remains of single
9
10 individuals are not widely distributed across the site. To take full advantage of the
11
12 available sample of large mammal data, the number of tortoises that should be present in
13
14 the same amount of deposit was therefore also estimated by multiplying the tortoise MNI
15
16 by 4.3 for M1 and 3.1 for M3.
17
18
19
20

21 Mammal specimens identifiable to individual element were drawn into the GIS
22
23 image-analysis program developed by Marean et al. (2001). The MNE was estimated
24
25 from these GIS images on the principle of overlaps: where two fragments overlap on a
26
27 given element they cannot be from the same element (Marean et al., 2001). The
28
29 advantages and drawbacks to this method are discussed in Thompson and Henshilwood
30
31 (2011) and Lyman (2008).
32
33
34
35

36 Data were collated from the literature for key macronutrient (fat and protein)
37
38 estimates for tortoises and for size 1, 2, 3, and 4 ungulates, following the bovid body size
39
40 categories of Brain (1981). This provided the basis for understanding relative resource
41
42 rankings. Given the body of data suggesting that MSA hunters were fully competent, it
43
44 was assumed that complete (un-scavenged) carcasses were available to the group, and
45
46 that each ungulate MNI represents a complete individual. The caloric estimates were
47
48 multiplied by the MNI for their respective ungulate body size classes and the tortoise
49
50 MNI within each phase to obtain a quantitative assessment of how many calories each
51
52 faunal subset would have contributed to the diet, and thus its actual significance
53
54 regardless of ranking. This facilitated discussions of the implications of changing
55
56
57
58
59
60
61
62
63
64
65

4 contributions by hunters and gatherers within the group. Finally, published data for the
5 daily nutritional requirements of hunter-gatherers were used to estimate the minimum
6 number of people who could have been sustained for different periods of time at the site
7 by the ungulate and tortoise remains in order to understand site occupation intensity and
8 predation intensity.
9
10
11
12
13
14
15
16
17
18

19 **Results**

20 *Tortoise taxonomy, ecology, and macronutrient estimates*

21
22
23 The angulate tortoise (*Chersina angulata*) comprised more than 99.9% of the
24 portion of the sample that could be identified to the family level or below. *Chersina* is a
25 small to medium tortoise that does not exceed 250-300mm in maximum length (Branch,
26 1984; Hofmeyr, 2009; van Heezik et al., 1994). It is currently distributed throughout the
27 southwestern portion of South Africa and into southwestern Namibia (**Error! Reference
28 source not found.**). Although monotypic, west and southern coast specimens are
29 genetically distinct (Daniels et al., 2007; McCall and Thomas, 2012). They occur
30 preferentially away from the interiors of both countries, but tolerate a broad range of
31 habitats and are found in all of the major floral biomes of South Africa (Boycott and
32 Bourquin, 1988; Hofmeyr, 2009; Joshua et al., 2010).
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47

48 The species is monotypic and sexually dimorphic, with little phenotypic variation
49 across its geographic distribution (Van Den Berg and Baard, 1994) and with males
50 slightly larger than females (Berry and Shine, 1980; Branch, 1984). Populations normally
51 contain a preponderance of adults (Branch, 1984). Males are significantly more active
52
53
54
55
56
57
58
59
60
61
62
63
64
65

4 than females during the summer and spring (Keswick et al., 2006; Ramsay et al., 2002),
5
6 when most fighting and courtship occurs.
7

8
9 The majority of complete skeletal elements from BBC were from adult tortoises,
10 based on both their size and bone surface texture. In a study of body composition of four
11 different species of tortoise, the shell weight comprised 31.3% +/- 8.1% (15.9–48.9; n =
12
13 52) of total body weight (Kienzle et al., 2006). The mean fat content found by Kienzle et
14 al. (2006) was 2.7% +/- 2.2% of dried matter (compared to aquatic turtles, with a mean
15 fat content of 12.0 +/- 4.6, n = 31). A much earlier study found that in a sample of five
16 gopher tortoises (*Gopherus polyphemus*) fat content was on average 13.4% of overall
17 dried matter weight (Pearse et al., 1925), while more recent analysis of body composition
18 of captive spur-thighed tortoises (*Testudo graeca*) found that lipid concentrations change
19 throughout the lifespan (Lapid et al., 2005), reaching an equilibrium of around 7% when
20 tortoises achieve a total body weight of approximately 170g. Although none of the
21 tortoise studies have specifically been on *Chersina*, an estimate of 7% is used here
22 because the study by Lapid et al. (2005) had the most consistent experimental conditions.
23 Within the body itself, tortoises therefore appeared to be lean sources of meat with fat
24 proportions similar to those of wild game (Crawford et al., 1970; Crawford et al., 2010;
25 Skinner and Louw, 1996).
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47

48 *Caloric estimates for tortoise yields relative to ungulates* 49

50 Modern adult male *Chersina* are larger than females (Branch, 1984), with mean
51 body weights (with shells) of 907g for males and 815g for females (van Heezik et al.,
52 1994). Using the estimate of shell weight to body weight from Kienzle et al. (2006), the
53 average body mass without shell of an adult male tortoise should be approximately 623g,
54
55
56
57
58
59
60
61
62
63
64
65

4 and that of an average adult female approximately 560g. Using the percentage body
5
6 composition given by Lapid et al. (2005), a male *Chersina* would yield 109g of protein
7
8 and 44g of fat and an average female would yield 98g of protein and 39g of fat. This can
9
10 be converted into kilojoules (kJ) or kilocalories (kcal) and quantitatively understood
11
12 relative to the body masses of ungulates commonly available to MSA hunters on the
13
14 southern African coast.
15
16
17

18
19 It is significant to note that the caloric estimates for *Chersina* compiled from these
20
21 data (3332 kJ/796 kcal) are a close match to the value of 3738 kJ/890 kcal reported for
22
23 turtles exploited by hunter-gatherers in the Amazon basin (Hill et al., 1984), and almost
24
25 identical to the yield (3470 kJ/829 kcal) that would be calculated using caloric return data
26
27 from the Australian turtle *Chelodina rugosa* (Brand et al., 1983). The figure calculated
28
29 here updates that estimated by Buchanan (1986:110), who used substantially lower
30
31 estimates for edible body weight in *Chersina* than what current quantitative data would
32
33 suggest for tortoises in general.
34
35
36
37

38 Carcass composition data are available for a variety of African ungulates – many
39
40 of which are still consumed today as commercial game species (Ferreira and Hoffman,
41
42 2001; Hoffman, 2008; Hoffman and Ferreira, 2004; Hoffman et al., 2005; Hoffman et al.,
43
44 2009; Hoffman et al., 2010; Hoffman and Wiklund, 2006; van Zyl and Ferreira, 2004).
45
46 The nutritional quality of ungulates depends on their age, sex, health, and the region from
47
48 which they derive. Table 4 provides a generalised comparison of the nutritional
49
50 composition and caloric yields of adult *Chersina* to a smaller and a larger size 2 bovid.
51
52
53
54

55 <Table 4 >
56
57
58
59
60
61
62
63
64
65

1 *Nutritional value of tortoises and foraging implications at Blombos Cave*
2
3

4 Most modern carcass composition studies are designed to inform modern butchers
5 and Western consumers, and therefore do not include products desirable to hunter-
6 gatherers such as the fatty organs and bone marrow. Additional data were therefore
7 drawn from Blumenschine and Madrigal (1993) and Blumenschine and Caro (1986) to
8 estimate flesh weights (including the organs) and marrow yields (Table 5).
9
10
11
12
13
14
15

16 < Table 5 >
17
18

19 The carcass composition analysis is used as an approximation of the percentages
20 of available protein and fat in the edible tissues of a wild African ungulate. Females were
21 found to have between 50 – 77% more proportional body fat than males (van Zyl and
22 Ferreira, 2004). Because in the zooarchaeological record is it not normally possible to
23 know the sex ratio of ungulates represented in the deposits, an average of males and
24 females was used in calculating the total caloric contribution of the two macronutrients.
25 Table 6 gives a summary of estimated macronutrient and caloric values for the four bovid
26 size classes commonly found at African archaeological sites.
27
28
29
30
31
32
33
34
35
36
37

38 < Table 6 >
39
40

41 *Nutritional returns of tortoises relative to ungulates*
42

43 According to the 1985 Joint FAO-WHO-UNU Expert Consultation one tortoise
44 would comprise just over a third of the requirements for an adult human female rural
45 field worker (9360 kJ/2237 kcal) and meet about a quarter of the energetic requirements
46 of an adult human male engaged in heavy labour (14,580 kJ/3484 kcal). According to
47 Sebastian et al. (2002), it would also meet just under a third of the average estimated
48 caloric requirements for a hunter-gatherer (12,552 kJ/3000 kcal) and just under half the
49 amount of their estimated daily protein intake (234-258g depending on the relative
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

4 proportions of animal and plant products in the diet). Although subsisting entirely on
5 tortoises is unfeasible in the long-term (Speth, 2010), they would provide a useful daily
6
7 source of protein and calories.
8
9

10
11 Net return estimates are essential for converting these simple caloric data into
12 resource ranking data (Bird and O'Connell, 2006). Comprehensive search and handling
13 times are provided by Hawkes et al. (1982), Hill (1987), and summarised in Bright et al.
14 (2002) for a variety of resource types available to South American Amazon and North
15 American Great Basin hunter-gatherers. Absolute net returns for individual ungulate size
16 classes are difficult to reconstruct archaeologically because: 1) zooarchaeological body
17 size data represent a broad range of live body weights (Brain, 1981); 2) handling costs are
18 dependent on available hunting/capture technology, which has to be inferred (Bright et
19 al., 2002; Dusseldorp, 2012); and 3) transport costs vary depending on the size of the
20 animal, distance to camp, number of carriers, and other archaeologically unknowable
21 factors (Lupo, 2006; Monahan, 1998). However, the available resource return data can be
22 used as a guide to estimate net and relative returns of ungulates and tortoises.
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40

41 In the Amazon, total search and handling costs for a highly-ranked ungulate (the
42 red brocket deer, *Mazama americana*, ~30 kg LBW) were summarised as returning
43 114,600 kJ (27,300 kcal) per handling hour (Hawkes et al., 1982). In contrast, mainly
44 because of much-increased search costs, the next-ranked prey (the paca, *Cuniculus paca*,
45 ~7.5 kg LBW) had a return of 29,249 kJ (6964 kcal)/hour. The estimate for the deer
46 compares favourably with estimates for the American pronghorn antelope (*Antilocapra*
47 *Americana*, ~40 kg LBW) and mountain sheep (*Ovis canadensis* ~70 kg LBW), both at
48 131,500 kJ (31,450 kcal)/hour (Bright et al., 2002). Some data on handling costs of
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1 *Nutritional value of tortoises and foraging implications at Blombos Cave*
2
3

4 different-sized African ungulates are also available from the Hadza of East Africa,
5
6 indicating that a size 4 animal takes approximately twice as long to field process as a size
7
8 2 animal (Lupo, 2006), even though the size 4 animal may have more than twice the body
9
10 mass. This is in line with the general observation that smaller fauna demand higher
11
12 handling costs relative to their returns (Bright et al., 2002; Grimstead, 2010; Ugan, 2005).
13
14

15
16 Quantitative data on tortoise handling times are lacking, but estimates can be
17
18 made using other slow-moving prey such as armadillos (*Dasypus novemcinctus*), which on
19
20 encounter require about 12 minutes of handling when taken above ground (Hill et al.,
21
22 1987). Using the tortoise caloric estimate from Table 6 of 3323 kJ/794 kcal, minimum
23
24 on-encounter returns for tortoises should be at least 16,600 kJ (3967 kcal)/handling hour.
25
26 The main processing costs for tortoises are in the cooking and shell breakage, which do
27
28 not involve any complex technology (Klein and Cruz-Urbe, 2000). Thus, tortoise
29
30 handling times are likely to be even lower than armadillos, perhaps by half, with high
31
32 returns up to 33,000 kJ (8000 kcal)/handling hour. This places them well above the net
33
34 returns reported for all plant foods and small-bodied animal foods in both the Amazon
35
36 and Great Basin. They should therefore have been one of the highest-ranked 'collectable'
37
38 terrestrial resources on the South African landscape and should have always been taken
39
40 on encounter in spite of their small body sizes.
41
42
43
44
45
46
47

48 *Diet at Blombos Cave*
49

50
51 Tortoises amounted to about 4% (in M1) and 2% (M3) of the total calories from
52
53 large mammal and tortoise resources combined (Table 7). As discussed, in small,
54
55 fragmented samples large-bodied fauna are likely to be over-represented relative to
56
57 small-bodied fauna. Therefore, an estimate was also made by increasing tortoise numbers
58
59
60
61
62
63
64
65

4 as a factor of the amount of sampled deposit to match the larger available ungulate
5 sample (4.3 times larger for M1 and 3.1 times larger for M3). In this case, tortoises
6
7 amounted to 12% (in M1) and 5% (in M3) of the total calories. Both estimates show that
8
9 tortoises were a small but persistent component to the diet. If small mammals and
10
11 shellfish were also eaten, then the total contribution from tortoises to the animal portion
12
13 of the diet would become even smaller – in spite of their large quantities of remains in
14
15 terms of NISP.
16
17
18
19
20

21 < Table 7 >
22

23
24 The MNI data also provide an estimate of the minimum number of nutrition-days
25 available from tortoises and ungulates at BBC. Table 8 uses the daily caloric requirement
26 for a hunter-gatherer of 12,552 kJ/3000 kcal and the calorie estimates from the larger
27 sample of deposit to estimate scenarios of a diet of animal products only, a 55% animal-
28 to-plant diet, and a 35% animal-to-plant diet (Sebastian et al., 2002). Clearly, an all-
29 animal product diet is neither reasonable nor sustainable in the long term (Speth and
30
31 Spielmann, 1983; Speth, 2010), but it does provide a *minimum* number of nutrition-days
32
33 represented at the site. In spite of the fact that the data only sample approximately 20%
34
35 (for M1) and 5% (for M3) of the deposit present, the relatively small number of nutrition-
36
37 days speaks to either a very short, punctuated period or periods of occupation or a very
38
39 prolonged and highly ephemeral and opportunistic use of the cave. Similar possibilities
40
41 were suggested by analysis of the larger mammal taphonomy (Thompson and
42
43 Henshilwood, 2011).
44
45
46
47
48
49
50
51
52

53 < Table 8 >
54
55

56 **Discussion** 57 58 59 60 61 62 63 64 65

1 *Nutritional value of tortoises and foraging implications at Blombos Cave*
2
3

4 *Subsistence shifts during the Still Bay*
5

6 The chronology of the MSA at BBC shows that occupation phases corresponded
7 to high sea-level stands (Fisher et al., 2010; Henshilwood, 2008; Jacobs et al., 2006). The
8 minimum distance to the coastline has been estimated at between 1.45 and 2.33 km from
9 the site during all its occupation phases (Fisher et al., 2010). However, the top part of the
10 Still Bay, from which the M1 sample derived, was occupied at a time when the coast was
11 furthest and conditions were moving into a colder phase just prior to site abandonment.
12 This was also the phase in which representation of gregarious, large-bodied ungulates
13 with larger home ranges increased relative to monogamous, territorial, small-bodied
14 ungulates (Henshilwood et al., 2001b; Thompson and Henshilwood, 2011). At this time
15 shellfish were also at their lowest abundances per m³ of deposit (Henshilwood et al.,
16 2001b), and the relative dietary contribution of tortoises was approximately double what
17 it had been during warmer M3 times.
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35

36 The faunal evidence indicates that from M3 times to the Still Bay at BBC there
37 was a shift in overall subsistence strategy from one emphasising collectable resources
38 (including 'trappable' small ungulates) to one that placed heavier emphasis on higher-
39 return, hunted large mammal resources. This is supported by the abundance of Still Bay
40 points and bone points in the M1 phase that show the investment of substantial effort in
41 the manufacture and maintenance of hunting technology (d'Errico and Henshilwood,
42 2007; Henshilwood et al., 2001a; Villa et al., 2009). Small-bodied Neotragine ungulates
43 do not live in large groups and are not suitable for monotaxic mass drives, but may be
44 obtained as part of more generalised communal net-hunting drives (Bailey and Auger,
45 1989; Lupo and Schmitt, 2002; Tanno, 1976). The returns from this activity are
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

4 considered to be extremely low, at between 879 – 2238 kJ (210 – 535 kcal)/handling hour
5
6 (Ugan, 2005). Overall returns should be higher if small ungulates were instead captured
7
8 in traps as has been suggested at Sibudu Cave (Wadley, 2010), or individually hunted,
9
10 but still much lower than hunting large-bodied ungulates. At the same time that shifts
11
12 were occurring in ungulate exploitation, shellfish gathering was lessened by increased
13
14 distance to the coast, making tortoise collecting a more important resource for the
15
16 gatherers in the group.
17
18
19
20

21 Sustained predation by humans has been suggested in both South African and
22
23 Mediterranean contexts to have led to size diminution in tortoises, followed by increased
24
25 emphasis on alternate resources (Klein and Cruz-Uribe, 1983; 2000; Steele and Klein,
26
27 2013; Stiner, 2006; Stiner et al., 2000; Stiner et al., 1999). This is mainly because
28
29 tortoises reproduce slowly (Stiner and Kuhn, 2009). *Chersina* are no exception, laying
30
31 only one egg every six months to a year (Branch, 1984). Despite low fecundity, a model
32
33 of population increase has indicated that *Chersina* can achieve rapid population increase
34
35 – up to a 600x increase within 75 years in the face of minimal predation (van Heezik et
36
37 al., 1994). This has also been found to be the case in other tortoise species, even with
38
39 natural predation taken into account (Hailey, 2000; Marlowe, 2005), and chelonian
40
41 population sizes and biomasses in are normally much higher in a given area than
42
43 mammalian vertebrates (Iverson, 1982). Therefore, tortoise populations would be unable
44
45 to handle sustained long-term predation in a given area but could rebound consistently if
46
47 exploitation occurred in pulses of a half-century or more.
48
49
50
51
52
53
54

55 Population density estimates of introduced angulate tortoises on Dassen Island
56
57 range from 31 – 34 tortoises/ha (van Heezik et al., 1994), and on mainland pasture in the
58
59
60
61
62
63
64
65

1 *Nutritional value of tortoises and foraging implications at Blombos Cave*
2
3

4 Eastern Cape between 21-38 tortoises/ha (Branch, 1984). These are much different from
5
6 the estimates of 6.68 tortoises/ha in mixed Fynbos scrub (Stuart and Meakin, 1983), and
7
8 0.12 tortoises/ha in the Thicket Biome of the Eastern Cape (Mason et al., 2000). Thus, the
9
10 sustainability of tortoise populations – and the reliance of human groups on this resource
11
12 – would be determined by both human population sizes and existing local ecological
13
14 conditions. Given the rebound potential of *Chersina* populations around BBC, ephemeral
15
16 occupations at the timescales represented in the deposits should not have affected them.
17
18 Therefore, their greater abundances but smaller sizes during the M1 phase suggest a
19
20 relatively short, intensive period of site use. The data also show that just prior to site
21
22 abandonment MSA people at BBC experienced declines in the returns from two of their
23
24 major collectable animal resources: first shellfish, with increasing distance to the
25
26 coastline, then later tortoises, with decreasing encounter rates and smaller sizes. The
27
28 combination of environmental change and exploitation of key local resources first led to
29
30 increased emphasis on hunting and hunting technology and later complete site
31
32 abandonment. The
33
34
35
36
37
38
39

40 At the nearby site of PP13B changing abundances of shellfish track changes in
41
42 sea levels (Jerardino, 2010; Marean et al., 2007), showing another example of how
43
44 human subsistence changed in concert with coastlines at a single site during the MSA.
45
46 Although there were few tortoises overall at PP13B, tortoise remains were also
47
48 approximately twice as abundant relative to large mammals during MIS 6 – a cool to cold
49
50 period – than they were during MIS 5 – a cool to very warm period (Thompson, 2010a).
51
52 Data from BBC and PP13B together suggest that during warmer periods where sea levels
53
54 were closer, MSA people on the southwestern coast collected many shellfish and few
55
56
57
58
59
60
61
62
63
64
65

1 *Nutritional value of tortoises and foraging implications at Blombos Cave*
2
3

4 tortoises. As sea levels retreated tortoises were more often substituted as a source of
5
6 collectable protein.
7

8
9 The low incidences of tortoises at coastal MSA sites further east from BBC, such
10
11 as PP13B (Thompson, 2010a) and KRM (Klein and Cruz-Urbe, 1987) indicate that
12
13 tortoises were not common in these areas during the MSA. This is because tortoises were
14
15 a high-ranked resource and should have been taken on encounter, and encounter rates
16
17 would have had to have been extremely low or encounter rates with more productive
18
19 resources extremely high to drive them out of the diet completely (Byers and Ugan,
20
21 2005). These patterns are explicable in terms of optimal foraging theory, but the
22
23 consequences of shifting subsistence strategies would have also had social implications
24
25 for the MSA groups experiencing them.
26
27
28
29
30

31
32 *Hunters and gatherers in the archaeological record at BBC*
33

34
35 Animal resources provide protein, fat, and many essential micronutrients that are
36
37 not readily concentrated in plants (Cordain et al., 2000b), and which have been important
38
39 in the hunter-gatherer diet over the course of human evolution (Cordain et al., 2000a;
40
41 Cordain et al., 2001; Hockett and Haws, 2003; Milton, 2000; Milton, 2003). The most
42
43 visible source of animal products both ethnographically and archaeologically is from
44
45 hunted large mammals, but essential micro- and macronutrients concentrated in animal
46
47 resources are also present in what are often considered ‘gathered’ foods: small mammals,
48
49 fish, shellfish, tortoises, and insects (Bird et al., 2009).
50
51
52
53

54
55 In spite of the nutritive composition of gathered animal resources, and even in
56
57 societies where gathered foods are abundant and reliable, the contributions of hunters are
58
59 often considered more valuable both nutritionally and in terms of status than the
60
61
62
63
64
65

4 contributions of gatherers (Hawkes and Bleige Bird, 2002; Hawkes et al., 1982; Hill et
5 al., 1987; Kaplan and Hill, 1985b; Leisa et al., 2003; Marlowe, 2004). There can also be
6
7 substantial variability in how the returns of large-game hunting are distributed amongst
8
9 the total group (Hawkes, 1993; Patton, 2005). Because of the additional burdens of
10
11 pregnancy and lactation, the caloric requirements of hunter-gatherer women can approach
12
13 those of men (Hill *et al.* 1984), and pregnant and lactating women require approximately
14
15 7 – 10 additional grams of protein per day (Consultation, 1985). These two categories, as
16
17 well as young children, have additional need for many micronutrients as well (Ladipo,
18
19 2000; Osendarp et al., 2007). Many of these, such as iron, vitamin B12, niacin, and zinc
20
21 are concentrated in animal products (Williams, 2007). However, these are the population
22
23 subsets least able to participate in big-game hunting.
24
25
26
27
28
29
30

31 The amount of group coordination required to hunt and process large ungulates
32
33 presents an immediate, visible, and high output of both investment and return, but a high
34
35 potential failure rate. In modern hunter-gatherers hunting is a task that falls most
36
37 commonly to adult men (Bird, 1999; Bliege Bird et al., 2001; Brightman, 1996; Brown,
38
39 1970; Hawkes et al., 1991; Hurtado et al., 1992; Jochim, 1988; Lee, 1979). A review of
40
41 the ethnographic literature with a particular focus on South Africa has shown that women
42
43 also provide a great deal of meat resources through less-prestigious activities such as
44
45 snaring, trapping, and collecting of shellfish (Wadley, 1998). For at least some hunter-
46
47 gatherer groups, provisioning from older, post-reproductive females is one of the most
48
49 important sources of nutrition for a family unit (Hawkes et al., 1998; Hill and Hurtado,
50
51 2009).
52
53
54
55
56
57
58
59
60
61
62
63
64
65

4 It is difficult to know when the division of subsistence labour may have started in
5 human prehistory (Kuhn and Stiner, 2006), or how it may have been manifested in past
6 societies (Waguespack, 2005). However, because of the biological limitations of
7 reproduction and ageing, it is certain that not all group members would have been able to
8 participate in the increased emphasis on big-game hunting that is inferred for Still Bay
9 times. Although collected resources may be shared amongst the group, women and
10 children in modern societies have been shown to have access to a greater percentage of
11 collected resources than men (Kaplan and Hill, 1985a). Exploitation of tortoises by these
12 individuals would have provided an advantageous dietary supplement in terms of protein,
13 fat, and micronutrients at a relatively low cost. If hunters were economically rather than
14 socially motivated, then tortoises should also have been taken by them, because they
15 should not have ignored prey with such high returns unless encounter rates with large
16 ungulates were extremely high (Byers and Ugan, 2005). However, because large mammal
17 hunting requires greater mobility than collecting, and because tortoises can be processed
18 quickly by individual people, the evidence of these encounters was likely not as often
19 preserved at BBC as the evidence of encounters by collectors with closer foraging radii.
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42

43 Klein and Cruz-Urbe (2000:190) have also suggested that tortoises offer a
44 window into the changing contributions of hunters and gatherers. They conclude that the
45 changes in body size observed in tortoises at DK1 may indicate "...either a change in the
46 season(s) of the year when the site was occupied or perhaps a difference in the division of
47 human labor by age and sex." Here, we argue that the change in tortoise size is
48 attributable to increased exploitation by gatherers during Still Bay times, when shellfish
49 became less accessible and more able-bodied members of the group became more
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

4 invested in big-game hunting. In addition to increased evidence for hunting technology in
5 the Still Bay, these deposits have the most abundant evidence for symbolic and/or ritual
6 behaviour in the form of worked and incised ochre, and shell beads. Changes in
7 subsistence contributions via hunting and collecting resulted in some division of
8 subsistence labour, regardless of if it was strictly along gender lines as seen in modern
9 groups. Differential access to resources within the group may have followed, producing a
10 restructuring of social roles reproduced within the material culture record at BBC.
11
12
13
14
15
16
17
18
19
20
21
22

23 **Summary and Conclusions**

24
25
26 Modern human origins research in South Africa now allows the diversity and
27 chronology of MSA lifeways to be explored at an unprecedented level of detail, revealing
28 variability within a time period that had previously appeared to be somewhat static
29 (Lombard and Clark, 2008; Thompson, 2010b; Wadley, 2010; Wurz, 2012). It has also
30 resulted in the recovery of large, well-dated faunal assemblages associated with some of
31 the earliest or most convincing examples of modern behavioural complexity (Clark,
32 2011; Clark and Plug, 2008; Dusseldorp, 2012; Marean et al., 2007; Steele and Klein;
33 Thompson, 2010a; Thompson and Henshilwood, 2011; Wadley, 2010). Within this body
34 of work there has been differential emphasis on the significance of big-game hunting
35 ability, although recent research has begun to also explore small ungulate acquisition
36 (Clark and Plug, 2008; Wadley, 2010). This theme of ungulate research extends even to
37 diet breadth models, which remain restricted to *within* larger mammal taxa rather than
38 considering the suite of other faunal remains that are often found in the same deposits as
39 the ungulates (Dusseldorp, 2012). Part of the problem is taphonomic because plants from
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

2
3
4 this time period are mainly represented by the charred remnants of fuel or bedding, rather
5
6 than subsistence resources (Cartwright, 2013; Miller et al., 2013; Wadley et al., 2011). A
7
8 new approach is taken here: to examine ungulate and tortoise data together from the same
9
10 deposits so that both ‘hunted’ and ‘collected’ resource types can be explored in the
11
12 contexts of human subsistence and social behaviour.
13
14

15
16 *Chersina angulata*, the angulate tortoise, comprises the vast majority of tortoise
17
18 remains. Quantitative estimates of the nutritive returns for *Chersina* relative to ungulates
19
20 of body size classes commonly recovered from MSA sites show that it takes
21
22 approximately 9 tortoises to comprise the nutritive return of a size 1 ungulate, and over
23
24 500 to comprise the nutritive value of a size 4 ungulate. During the M1 (Still Bay) phase
25
26 tortoises accounted for approximately twice the relative amount of calories as in the M3
27
28 phase. However, in spite of their abundances in terms of NISP their actual caloric
29
30 contribution to both phases was relatively small.
31
32

33
34
35
36 During Still Bay times large ungulates were more commonly taken than small
37
38 ungulates, and shellfish were not as easily accessible because of retreating coastlines.
39
40 This, along with the accompanying material culture, shows a shift in subsistence to
41
42 emphasise high-return resources rather than those that are easily snared, collected, or
43
44 trapped. Because tortoises are easy to process, they remain a highly-ranked resource and
45
46 the frequency of their gathering increased during Still Bay times as access to shellfish
47
48 declined. Populations of *Chersina* are quickly impacted by intense predation but can
49
50 rebound on half-century timescales, so the decreasing mean size of tortoises during the
51
52 final MSA occupation phase suggests that site occupation was relatively brief and intense
53
54 rather than prolonged and ephemeral (Henshilwood et al., 2001b).
55
56
57
58
59
60
61
62
63
64
65

4 Henshilwood et al. (2001b:438) state that “Among herbivores on which people
5 could depend, the most abundant was probably the angulate tortoise”. Tortoises were a
6
7 ‘baseline’ source of essential macro- and micronutrients especially important for
8
9 individuals in the group who may not have had regular access to hunted resources when
10
11 big-game hunting was a focus within the group’s subsistence regime. Regardless of if a
12
13 fully modern gendered division of labour was in place in the MSA, access to collectable
14
15 animal resources would have been particularly advantageous for pregnant and lactating
16
17 women, children, and the elderly or infirm. This study has quantitatively confirmed that
18
19 tortoises were a highly-ranked and reliable part of the resource landscape over time, but
20
21 also shows that their role changed within the overall subsistence approach as big-game
22
23 hunting became more important during Still Bay times. Human behaviour in the MSA
24
25 was flexible, responding to changes in the environment and resource base through
26
27 adoption of new foraging strategies, innovation of subsistence technologies, and
28
29 restructuring of social roles.
30
31
32
33
34
35
36
37
38
39
40

41 **Acknowledgements**

42 JCT is indebted to Sven Ouzman and Petro Keene at the Iziko South African
43
44 Museum in Cape Town for facilitating access to the Blombos tortoise collection.
45
46 Wilhelmina Seconna kindly provided daily access to the archaeological collections and
47
48 Denise Hamerton provided access to the tortoise comparative material, as well as
49
50 laboratory space for measuring modern tortoises. Guy Thomas was an invaluable lab
51
52 assistant, and very good at refitting tortoises. Simon van Noort provided access to the
53
54 microscope used to take the photographs of surface modification. The tortoise research
55
56
57
58
59
60
61
62
63
64
65

1 *Nutritional value of tortoises and foraging implications at Blombos Cave*
2
3

4 was funded by a University of Queensland postdoctoral research fellowship. Large
5
6 mammal data were collected with the aid of National Science Foundation (NSF)
7
8 Dissertation Improvement Grant number 0620317, an NSF Graduate Research
9
10 Fellowship, a Fulbright Fellowship to South Africa, and funding from the School of
11
12 Human Evolution and Social Change at Arizona State University. Access to the
13
14 mammalian assemblage was facilitated by Graham Avery and Royden Yates in the initial
15
16 stages of research, and later by Sarah Wurz. Royden Yates must also be thanked for his
17
18 initial idea that “tortoises were the McDonald’s of the MSA”. Financial support was
19
20 provided to CSH by a European Research Council Advanced Grant, TRACSYMBOLS
21
22 No. 249587, awarded under the FP7 programme at the University of Bergen, Norway and
23
24 by a National Research Foundation/Department of Science and Technology funded Chair
25
26 at the University of the Witwatersrand, South Africa. Andrew Ugan, two anonymous
27
28 reviewers, and the Associate Editor of the *Journal of Human Evolution* provided
29
30 extremely detailed and helpful advice for improving the original submission.
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

4 **References Cited**
5

6 Avery, G., Halkett, D., Orton, J., Steele, T., Klein, R.G., 2008. The Ysterfontein 1 Middle
7 Stone Age rock shelter and the evolution of coastal foraging. *South African*
8 *Archaeological Society Goodwin Series* 10, 66-89.
9

10
11 Bailey, R.C., Aunger, R., Jr., 1989. Net hunters vs. archers: variation in women's
12 subsistence strategies in the Ituri forest. *Hum Ecol* 17, 273-297.
13

14
15 Barham, L., 2001. Central Africa and the emergence of regional identity in the Middle
16 Pleistocene, in: Barham, L., Robson-Brown, K. (Eds.), *Human roots: Africa and Asia in*
17 *the Middle Pleistocene*. Western Academic Press, Bristol.
18

19
20 Bayham, F.E., 1979. Factors influencing the Archaic pattern of animal exploitation. *The*
21 *Kiva* 44, 219-235.
22

23
24 Berry, J., Shine, R., 1980. Sexual size dimorphism and sexual selection in turtles (order
25 testudines). *Oecologia* 44, 185-191.
26

27
28 Binford, L.R., 1981. *Bones: Ancient Men and Modern Myths*. Academic Press, New
29 York.
30

31
32 Binford, L.R., 1984. *The faunal remains from Klasies River Mouth*. Academic Press,
33 New York.
34

35
36 Bird, D.W., Bird, R.B., Codding, B.F., 2009. In Pursuit of Mobile Prey: Martu Hunting
37 Strategies and Archaeofaunal Interpretation. *Am. Antiq.* 74, 3-29.
38

39
40 Bird, D.W., O'Connell, J.F., 2006. Behavioral Ecology and Archaeology. *Journal of*
41 *Archaeological Research* 14, 143-188.
42

43
44 Bird, R., 1999. Cooperation and conflict: The behavioral ecology of the sexual division
45 of labor. *Evol. Anthropol.* 8, 65-75.
46

47
48 Blasco, M., Crespillo, E., Sanchez, J.M., 1986. The growth dynamics of *Testudo graeca*
49 *L.* (Reptilia: Testudinidae) and other data on its populations in the Iberian Peninsula.
50 *Israel Journal of Zoology* 34, 139-147.
51

52
53 Blasco, R., 2008. Human consumption of tortoises at Level IV of Bolomor Cave
54 (Valencia, Spain). *J. Archaeol. Sci.* 35, 2839-2848.
55

56
57 Blasco, R., Fernández Peris, J., 2012a. Small and large game: Human use of diverse
58 faunal resources at Level IV of Bolomor Cave (Valencia, Spain). *Comptes Rendus*
59 *Palevol* 11, 265-282.
60
61
62
63
64
65

1 *Nutritional value of tortoises and foraging implications at Blombos Cave*
2
3

4 Blasco, R., Fernández Peris, J., 2012b. A uniquely broad spectrum diet during the Middle
5 Pleistocene at Bolomor Cave (Valencia, Spain). *Quaternary International* 252, 16-31.
6

7
8 Bliege Bird, R.L., Smith, E.A., Bird, D.W., 2001. The hunting handicap: costly signaling
9 in male foraging strategies. *Behavioral Ecology and Sociobiology* 50, 9-19.
10

11 Blumenschine, R.J., Caro, T., 1986. Unit flesh weights of some East African bovids.
12 *African Journal of Ecology* 24, 273-286.
13

14
15 Blumenschine, R.J., Madrigal, T.C., 1993. Variability in long bone marrow yields of East
16 African Ungulates and its zooarchaeological implications. *J. Archaeol. Sci.*, 555-587.
17

18
19 Boycott, R.C., Bourquin, O., 1988. *The South African Tortoise Book*. Southern Book
20 Publishers, Johannesburg.
21

22 Brain, C.K., 1981. *The Hunters or the Hunted? An Introduction to African Cave*
23 *Taphonomy*. University of Chicago Press, Chicago.
24

25
26 Branch, W.R., 1984. Preliminary Observations on the Ecology of the Angulate Tortoise
27 (*Chersina angulata*) in the Eastern Cape Province, South Africa. *Amphibia-Reptilia* 5, 43-
28 55.
29

30
31 Brand, J.C., McDonnell, J., Lee, A., Cherikoff, V., Truswell, A.S., Rae, C., 1983. The
32 nutritional composition of Australian Aboriginal bushfoods. *Food Technology in*
33 *Australia* 35, 293-298.
34

35
36 Bright, J., Ugan, A., Hunsaker, L., 2002. The Effect of Handling Time on Subsistence
37 Technology. *World Archaeology* 34, 164-181.
38

39
40 Brightman, R., 1996. The sexual division of foraging labor: biology, taboo, and gender
41 politics. *Comparative Studies in Society and History* 38, 687-729.
42

43 Broughton, J.M., 1994a. Declines in mammalian foraging efficiency during the late
44 Holocene, San Francisco Bay, California. *J. Anthropol. Archaeol.* 13, 371-401.
45

46
47 Broughton, J.M., 1994b. Late Holocene resource intensification in the Sacramento
48 Valley, California: the vertebrate evidence. *J. Archaeol. Sci.* 21, 501-514.
49

50
51 Brown, J.K., 1970. A note on the division of labor by sex. *American Anthropologist* 72,
52 1073-1078.
53

54
55 Brown, K.S., Marean, C.W., Herries, A.I.R., Jacobs, Z., Tribolo, C., Braun, D., Roberts,
56 D.L., Meyer, M.C., Bernatchez, J., 2009. Fire as an Engineering Tool of Early Modern
57 Humans. *Science* 325, 859-862.
58
59
60
61
62
63
64
65

1 *Nutritional value of tortoises and foraging implications at Blombos Cave*
2
3

4 Brown, K.S., Marean, C.W., Jacobs, Z., Schoville, B.J., Oestmo, S., Fisher, E.C.,
5 Bernatchez, J., Karkanas, P., Matthews, T., 2012. An early and enduring advanced
6 technology originating 71,000 years ago in South Africa. *Nature* 491, 590-593.
7

8
9 Buchanan, W., 1986. *Sea shells ashore: a study of the role of shellfish in prehistoric diet*
10 *and lifestyle at Eland's Bay, Southwestern Cape, South Africa.* University of Cape Town.
11

12 Buchanan, W., 1988. *Shellfish in Prehistoric Diet: Elands Bay, SW Cape Coast, South*
13 *Africa.* British Archaeological Reports International Series, Oxford.
14

15
16 Byers, D.A., Ugan, A., 2005. Should we expect large game specialization in the late
17 Pleistocene? An optimal foraging perspective on early Paleoindian prey choice. *J.*
18 *Archaeol. Sci.* 32, 1624-1640.
19

20
21 Cartwright, C.R., 2013. Identifying the woody resources of Diepkloof Rock Shelter
22 (South Africa) using scanning electron microscopy of the MSA wood charcoal
23 assemblages. *J. Archaeol. Sci.* 40, 3463–3474.
24

25
26 Clark, A.M.B., 1999. Late Pleistocene technology at Rose Cottage Cave: a search for
27 modern behavior in an MSA context. *African Archaeological Review* 16, 93-119.
28

29
30 Clark, J.L., 2011. The evolution of human culture during the later Pleistocene: Using
31 fauna to test models on the emergence and nature of “modern” human behavior. *J.*
32 *Anthrop. Archaeol.* 30, 273-291.
33

34
35 Clark, J.L., Plug, I., 2008. Animal exploitation strategies during the South African Middle
36 Stone Age: Howiesons Poort and post-Howiesons Poort fauna from Sibudu Cave. *J.*
37 *Hum. Evol.* 54, 886-898.
38

39
40 Consultation, J.F.W.U.E., 1985. Energy and Protein Requirements, in: Protection, A.a.C.
41 (Ed.). World Health Organization, Geneva.
42

43
44 Cordain, L., Miller, J.B., Eaton, S.B., Mann, N., 2000a. Macronutrient estimations in
45 hunter-gatherer diets. *The American Journal of Clinical Nutrition* 72, 1589-1590.
46

47
48 Cordain, L., Miller, J.B., Eaton, S.B., Mann, N., Holt, S.H., Speth, J.D., 2000b. Plant-
49 animal subsistence ratios and macronutrient energy estimations in worldwide hunter-
50 gatherer diets. *The American Journal of Clinical Nutrition* 71, 682-692.
51

52
53 Cordain, L., Watkind, B.A., Mann, N.J., 2001. Fatty Acid Composition and Energy
54 Density of Foods Available to African Hominids: Evolutionary Implications for Human
55 Brain Development, in: A.P., S., K.N., P. (Eds.), *Nutrition and Fitness: Metabolic Studies*
56 *in Health and Disease.* Karger, Basel, pp. 144–161.
57
58
59
60
61
62
63
64
65

4 Cowling, R.M., Rundel, P.W., Lamont, B.B., Kalin Arroyo, M., Arianoutsou, M., 1996.
5 Plant diversity in Mediterranean-climate regions. *Trends in Ecology & Evolution* 11,
6 362-366.
7

8
9 Crawford, M.A., Gale, M.M., Woodford, M.H., Casped, N.M., 1970. Comparative
10 studies on fatty acid composition of wild and domestic meats. *International Journal of*
11 *Biochemistry* 1, 295-305.
12

13
14 Crawford, M.A., Wang, Y., Lehane, C., Ghebremeskel, K., 2010. Fatty Acid Ratios in
15 Free-Living and Domestic Animals, in: Watson, R.R., De Meester, F., Zibadi, S. (Eds.),
16 *Modern Dietary Fat Intakes in Disease Promotion*. Humana Press, pp. 95-108.
17

18
19 Cruz-Uribe, K., Schrire, C., 1991. Analysis of Faunal Remains from Oudepost I, an Early
20 Outpost of the Dutch East India Company, Cape Province. *The South African*
21 *Archaeological Bulletin* 46, 92-106.
22

23
24 d'Errico, F., Backwell, L.R., Wadley, L., 2012. Identifying regional variability in Middle
25 Stone Age bone technology: The case of Sibudu Cave. *J. Archaeol. Sci.* 39, 2479-2495.
26

27
28 d'Errico, F., Henshilwood, C., Vanhaeren, M., van Niekerk, K., 2005. *Nassarius*
29 *kraussianus* shell beads from Blombos Cave: evidence for symbolic behaviour in the
30 Middle Stone Age. *J. Hum. Evol.* 48, 3-24.
31

32
33 d'Errico, F., Henshilwood, C.S., 2007. Additional evidence for bone technology in the
34 southern African Middle Stone Age. *J. Hum. Evol.* 52, 142-163.
35

36
37 d'Errico, F., Vanhaeren, M., Wadley, L., 2008. Possible shell beads from the Middle
38 Stone Age layers of Sibudu Cave, South Africa. *J. Archaeol. Sci.* 35, 2675-2685.
39

40
41 Daniels, S.R., Hofmeyr, M.D., Henen, B.T., Crandall, K.A., 2007. Living with the
42 genetic signature of Miocene induced change: Evidence from the phylogeographic
43 structure of the endemic angulate tortoise *Chersina angulata*. *Molecular Phylogenetics*
44 *and Evolution* 45, 915-926.
45

46
47 Deacon, H.J., 2001. Modern human emergence: an African archaeological perspective,
48 in: Tobias, P.V., Raath, M.A., Maggi-Cecchi, J., Doyle, G.A. (Eds.), *Humanity from*
49 *African naissance to coming millennia: colloquia in human biology and*
50 *paleoanthropology*. University of Florence Press, Florence, pp. 217-226.
51

52
53 Dusseldorp, G.L., 2010. Prey choice during the South African Middle Stone Age:
54 avoiding dangerous prey or maximising returns? *African Archaeological Review* 27, 107-
55 133.
56

57
58 Dusseldorp, G.L., 2012. Tracking the influence of technological change on Middle Stone
59 Age hunting strategies in South Africa. *Quaternary International* 270, 70-79.
60
61
62
63
64
65

1 *Nutritional value of tortoises and foraging implications at Blombos Cave*
2
3

4 Faith, J.T., 2008. Eland, buffalo, and wild pigs: were Middle Stone Age humans
5 ineffective hunters? *J. Hum. Evol.* 55, 24-36.
6

7
8 Faith, J.T., 2011. Late Quaternary megafaunal extinctions in southern Africa's Cape
9 Floral Region. The George Washington University, Washington DC.
10

11 Ferreira, A.V., Hoffman, L.C., 2001. Body and carcass composition of the common
12 duiker. *South African Journal of Wildlife Research* 31, 63 -66.
13

14
15 Fisher, E.C., Bar-Matthews, M., Jerardino, A., Marean, C.W., 2010. Middle and Late
16 Pleistocene paleoscape modeling along the southern coast of South Africa. *Quaternary*
17 *Science Reviews* 29, 1382-1398.
18

19
20 Flannery, K.V., Wheeler, J.C., 1986. Animal food remains from preceramic Guila
21 Naquitz, in: Flannery, K.V. (Ed.), Flannery, K.V. (Ed.), Guila' Naquitz. *Archaic*
22 *Foraging and Early Agriculture in Oaxaca, Mexico*. Academic Press, Orlando, pp. 285–
23 295.
24

25
26 Grayson, D.K., Frey, C.J., 2004. Measuring skeletal part representation in archaeological
27 faunas. *J. Taphonomy* 2, 27-42.
28

29
30 Grimstead, D.N., 2010. Ethnographic and Modeled Costs of Long-Distance, Big-Game
31 Hunting. *Am. Antiq.* 75, 61-80.
32

33
34 Hailey, A., 2000. Implications of high intrinsic growth rate of a tortoise population for
35 conservation. *Animal Conservation* 3, 185-189.
36

37
38 Hawkes, K., 1993. Why hunter-gatherers work: an ancient version of the problem with
39 public goods. *Curr. Anthropol.* 34, 341-362.
40

41
42 Hawkes, K., Bleige Bird, R.L., 2002. Showing off, handicap signaling, and the evolution
43 of men's work. *Evol. Anthropol.* 11, 58-67.
44

45
46 Hawkes, K., Hill, K., O'Connell, J.F., 1982. Why hunters gather: optimal foraging and
47 the Ache of eastern Paraguay. *American Ethnologist* 9, 379-398.
48

49
50 Hawkes, K., O'Connell, J.F., Blurton-Jones, N.G., 1991. Hunting income patterns among
51 Hadza: big game, common goods, foraging goals and the evolution of the human diet.
52 *Philosophical Transactions of the Royal Society of London* 334, 243-251.
53

54
55 Hawkes, K., O'Connell, J.F., Blurton-Jones, N.G., Alvarez, H., Charnov, E.L., 1998.
56 Grandmothering, menopause, and the evolution of human life histories. *Proceedings of*
57 *the National Academy of Sciences, USA* 95, 1336-1339.
58

59
60 Henshilwood, C.S., 2007. Fully symbolic sapiens behavior: innovation in the Middle
61 Stone Age at Blombos Cave, South Africa, in: Stringer, C., Mellars, P. (Eds.), *Rethinking*
62
63
64
65

4 the Human Revolution: New Behavioral and Biological Perspectives on the Origins of
5 Modern Humans. University of Cambridge Press, Cambridge, pp. 123-132.
6

7
8 Henshilwood, C.S., 2008. Winds of change: palaeoenvironments, material culture and
9 human behaviour in the Late Pleistocene (c. 77 – 48 ka) in the Western Cape Province,
10 South Africa. South African Archaeological Society Goodwin Series 10, 1-17.
11

12
13 Henshilwood, C.S., 2009. The origins of symbolism, spirituality & shamans: exploring
14 Middle Stone Age material culture in South Africa, in: Renfrew, C., Morley, I. (Eds.),
15 *Becoming human: innovation in prehistoric material and spiritual cultures*. Cambridge
16 University Press, Cambridge, pp. 29-49.
17

18
19 Henshilwood, C.S., D'Errico, F., Marean, C.W., Milo, R.G., Yates, R.J., 2001a. An early
20 bone tool industry from the Middle Stone Age, Blombos Cave, South Africa:
21 implications for the origins of modern human behaviour, symbolism and language. *J.*
22 *Hum. Evol.* 41, 631-678.
23

24
25 Henshilwood, C.S., d'Errico, F., Watts, I., 2009. Engraved ochres from the Middle Stone
26 Age levels at Blombos Cave, South Africa. *J. Hum. Evol.* 57, 27-47.
27

28
29 Henshilwood, C.S., D'Errico, F., Yates, R., Jacobs, Z., Tribolo, C., Duller, G.A.T.,
30 Mercier, N., Sealy, J.C., Valladas, H., Watts, I., Wintle, A.G., 2002. Emergence of
31 modern human behavior: Middle Stone Age engravings from South Africa. *Science* 295,
32 1278-1280.
33

34
35 Henshilwood, C.S., d'Errico, F., van Niekerk, K.L., Coquinot, Y., Jacobs, Z., Lauritzen,
36 S.-E., Menu, M., García-Moreno, R., 2011. A 100,000-Year-Old Ochre-Processing
37 Workshop at Blombos Cave, South Africa. *Science* 334, 219-222.
38

39
40 Henshilwood, C.S., Dubreuil, B., 2011. The Still Bay and Howiesons Poort, 77 - 59 ka:
41 Perspective-taking and the evolution of the modern human mind during the African
42 Middle Stone Age. *Curr. Anthropol.* 52, 361-400.
43

44
45 Henshilwood, C.S., Marean, C.W., 2003. The origin of modern human behavior: Critique
46 of the models and their test implications. *Curr. Anthropol.* 44, 627-651.
47

48
49 Henshilwood, C.S., Sealy, J.C., Yates, R.J., Cruz-Uribe, K., Goldberg, P., Grine, F.E.,
50 Klein, R.G., Poggenpoel, C., van Niekerk, K., Watts, I., 2001b. Blombos Cave, southern
51 Cape, South Africa: Preliminary report on the 1992-1999 excavations of the Middle
52 Stone Age levels. *J. Archaeol. Sci.* 28, 421-448.
53

54
55 Hill, K., Hawkes, K., Hurtado, M., Kaplan, H., 1984. Seasonal variance in the diet of
56 Ache hunter-gatherers in eastern Paraguay. *Hum Ecol* 12, 101-135.
57

58
59 Hill, K., Hurtado, A.M., 2009. Cooperative breeding in South American hunter-
60 gatherers. *Proceedings of the Royal Society B: Biological Sciences* 276, 3863-3870.
61
62
63
64
65

5 Hill, K., Kaplan, H., Hawkes, K., Hurtado, A.M., 1987. Foraging decisions among Ache
6 hunter-gatherers: new data and implications for optimal foraging models. *Ethology and*
7 *Sociobiology* 8, 1-36.
8
9

10 Hockett, B., Haws, J., 2003. Nutritional ecology and diachronic trends in Paleolithic diet
11 and health. *Evolutionary Anthropology: Issues, News, and Reviews* 12, 211-216.
12
13

14 Hockett, B.S., Haws, J.A., 2009. Continuity in animal resource diversity in the Late
15 Pleistocene human diet of Central Portugal. *Before Farming* 2, 1-14.
16
17

18 Hoffman, L.C., 2008. The yield and nutritional value of meat from African ungulates,
19 camelidae, rodents, ratites and reptiles. *Meat Science* 80, 94-100.
20
21

22 Hoffman, L.C., Ferreira, A.V., 2004. Chemical composition of two muscles of the
23 common duiker (*Sylvicapra grimmia*). *Journal of the Science of Food and Agriculture* 84,
24 1541-1544.
25
26

27 Hoffman, L.C., Kritzing, B., Ferreira, A.V., 2005. The effects of sex and region on the
28 carcass yield and m longissimus lumborum proximate composition of impala. *Journal of*
29 *the Science of Food and Agriculture* 85, 391–398.
30
31

32 Hoffman, L.C., Mostert, A.C., Kidd, M., Laubscher, L.L., 2009. Meat quality of kudu
33 (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*): Carcass yield, physical
34 quality and chemical composition of kudu and impala Longissimus dorsi muscle as
35 affected by gender and age. *Meat Science* 83, 788-795.
36
37

38 Hoffman, L.C., Smit, K., Muller, N., 2010. Chemical characteristics of red hartebeest
39 (*Alcelaphus buselaphus caama*) meat. *South African Journal of Animal Science* 40, 221-
40
41

42 Hoffman, L.C., Wiklund, E., 2006. Game and venison – meat for the modern consumer.
43 *Meat Science* 74, 197-208.
44
45

46 Hofmeyr, M.D., 2009. *Chersina angulata* (Schweigger 1812) - angulate tortoise, South
47 African bowsprit tortoise, in: Rhodin, A.G.J., Pritchard, P.C.H., van Dijk, P.P., Sumure,
48 R.A., Buhlmann, K.A., Iverson, J.B., Mittermeier, R.A. (Eds.), *Conservation Biology of*
49 *Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and*
50 *Freshwater Turtle Specialist Group Chelonian Research Foundation*, pp. 030.031-
51 030.036.
52
53

54 Hurtado, A.M., Hill, K., Kaplan, H., Hurtado, I., 1992. Trade-offs between female food
55 acquisition and child care among Hiwi and Ache foragers. *Human Nature* 3, 185-216.
56
57

58 Iverson, J.B., 1982. Biomass in turtle populations: a neglected subject. *Oecologia* 55, 69-
59 76.
60
61
62
63
64
65

1 *Nutritional value of tortoises and foraging implications at Blombos Cave*
2
3

4 Jacobs, Z., Duller, G.A.T., Wintle, A.G., 2003a. Optical dating of dune sand from
5 Blombos Cave, South Africa: II--single grain data. *J. Hum. Evol.* 44, 613-625.
6

7
8 Jacobs, Z., Duller, G.A.T., Wintle, A.G., Henshilwood, C.S., 2006. Extending the
9 chronology of deposits at Blombos Cave, South Africa, back to 140 ka using optical
10 dating of single and multiple grains of quartz. *J. Hum. Evol.* 51, 255-273.
11

12
13 Jacobs, Z., Hayes, E.H., Roberts, R.G., Galbraith, R.F., Henshilwood, C.S., 2013. An
14 improved OSL chronology for the Still Bay layers at Blombos Cave, South Africa:
15 further tests of single-grain dating procedures and a re-evaluation of the timing of the
16 Still Bay industry across southern Africa. *J. Archaeol. Sci.* 40, 579-594.
17

18
19 Jacobs, Z., Wintle, A.G., Duller, G.A.T., 2003b. Optical dating of dune sand from
20 Blombos Cave, South Africa: I--multiple grain data. *J. Hum. Evol.* 44, 599-612.
21

22
23 Jerardino, A., 2010. Shellfish gathering, marine paleoecology and modern human
24 behavior: perspectives from cave PP13B, Pinnacle Point, South Africa. *J. Hum. Evol.* 59,
25 412-424.
26

27
28 Jochim, M., 1988. Optimal foraging and the division of labor. *American Anthropologist*
29 90, 130-136.
30

31
32 Jones, H.L., 2001. Electron spin resonance dating of tooth enamel at three Palaeolithic
33 sites. McMaster University, Ontario.
34

35
36 Joshua, Q.I., Hofmeyr, M.D., Henen, B.T., 2010. Seasonal and Site Variation in Angulate
37 Tortoise Diet and Activity. *Journal of Herpetology* 44, 124-134.
38

39
40 Kaplan, H., Hill, K., 1985a. Food sharing among Ache foragers: tests of explanatory
41 hypotheses. *Curr. Anthropol.* 26, 223-246.
42

43
44 Kaplan, H., Hill, K., 1985b. Hunting ability and reproductive success among male Ache
45 foragers: preliminary results. *Curr. Anthropol.* 26, 131-133.
46

47
48 Keswick, T., Henen, B.T., Hofmeyr, M.D., 2006. Sexual disparity in activity patterns and
49 time budgets of angulate tortoises (*Chersina angulata*) on Dassen Island, South Africa.
50 *African Zoology* 41, 224-233.
51

52
53 Kienzle, E., Kopsch, G., Koelle, P., Clauss, M., 2006. Chemical Composition of Turtles
54 and Tortoises. *Journal of Nutrition* 136, 2053S-2054S.
55

56
57 Klein, R.G., 1978. Stone age predation on large african bovids. *J. Archaeol. Sci.* 5, 195-
58 217.
59
60
61
62
63
64
65

4 Klein, R.G., 1994. The problem of modern human origins, in: Nitecki, M.H., Nitecki,
5 D.V. (Eds.), *Origins of Anatomically Modern Humans*. Plenum Press, New York, pp. 3-
6 17.
7

8
9 Klein, R.G., 1995. Anatomy, behavior, and modern human origins. *Journal of World*
10 *Prehistory* 9, 167-198.
11

12 Klein, R.G., 1998. Why anatomically modern people did not disperse from Africa
13 100,000 years ago, in: Akazawa, T., Aoki, K., Bar-Yosef, O. (Eds.), *Neandertals and*
14 *Modern Humans in Western Asia*. Plenum Press, New York, pp. 509-522.
15
16

17 Klein, R.G., 2000. Archeology and the evolution of human behavior. *Evol. Anthropol.* 9,
18 17-36.
19

20
21 Klein, R.G., 2009. *The Human Career*, 3rd edition ed. University of Chicago Press,
22 Chicago.
23

24 Klein, R.G., Avery, G., Cruz-Uribe, K., Halkett, D., Hart, T., Milo, R.G., Volman, T.P.,
25 1999. Duinefontein 2: an Acheulean Site in the Western Cape Province of South Africa.
26 *J. Hum. Evol.* 37, 153-190.
27
28

29 Klein, R.G., Avery, G., Cruz-Uribe, K., Halkett, D., Parkington, J.E., Steele, T., Volman,
30 T.P., Yates, R., 2004a. The Ysterfontein 1 Middle Stone Age site, South Africa, and early
31 human exploitation of coastal resources. *Proc. Natl. Acad. Sci.* 101, 5708-5715.
32
33

34 Klein, R.G., Avery, G., Halkett, D., Parkington, J., Steele, T., Volman, T.P., Yates, R.,
35 2004b. The Ysterfontein 1 Middle Stone Age site, South Africa, and early human
36 exploitation of coastal resources. *Proc. Natl. Acad. Sci.* 101, 5718-5715.
37
38

39 Klein, R.G., Cruz-Uribe, K., 1983. Stone age population numbers and average tortoise
40 size at Byneskranskop Cave 1 and Die Kelders Cave 1, Southern Cape Province, South
41 Africa. *S. Afr. Archaeol. Bull.* 38, 26-30.
42
43

44 Klein, R.G., Cruz-Uribe, K., 1987. Large mammal and tortoise bones from Eland's Bay
45 Cave and nearby sites, Western Cape Province, South Africa, in: Klein, R.G., Cruz-
46 Uribe, K., Parkington, J., Hall, M. (Eds.), *Papers in the Prehistory of the Western Cape,*
47 *South Africa*. BAR International Series, Oxford, pp. 132-164.
48
49

50 Klein, R.G., Cruz-Uribe, K., 1996. Exploitation of large bovids and seals at Middle and
51 Later Stone Age sites in South Africa. *J. Hum. Evol.* 31, 315-334.
52
53

54 Klein, R.G., Cruz-Uribe, K., 2000. Middle and Later Stone Age large mammal and
55 tortoise remains from Die Kelders Cave 1, Western Cape Province, South Africa. *J. Hum.*
56 *Evol.* 38, 169-196.
57
58

59 Kuhn, S.L., Stiner, M.C., 2006. What's a mother to do? *Curr. Anthropol.* 47, 953-980.
60
61
62
63
64
65

5 Ladipo, O.A., 2000. Nutrition in pregnancy: mineral and vitamin supplements. The
6 American Journal of Clinical Nutrition 72, 280s-290s.
7

8
9 Lapid, R.H., Nir, I., Robinzon, B., 2005. Growth and body composition in captive
10 Testudo graeca terrestris fed with a high-energy diet. Applied Herpetology 2, 201-209.
11

12 Lee, R.B., 1979. The !Kung San: Men, Women, and Work in a Foraging Society.
13 Cambridge, Cambridge University Press.
14

15
16 Leisa, M.G.A., Hofmeyr, M.D., D'Amato, M., 2003. Genetic variation in three *Chersina*
17 *angulata* (angulate tortoise) populations along the west coast of South Africa. African
18 Zoology 38, 109–117.
19

20
21 Lombard, M., Clark, J.L., 2008. Variability and Change in Middle Stone Age Hunting
22 Behaviour: Aspects from the Lithic and Faunal Records, in: Badenhorst, S., Mitchell, P.,
23 Driver, J.C. (Eds.), Animals and People: Archaeozoological Papers in Honour of Ina
24 Plug. Archaeopress, Oxford, pp. 46-56.
25

26
27 Lupo, K., 2006. What Explains the Carcass Field Processing and Transport Decisions of
28 Contemporary Hunter-Gatherers? Measures of Economic Anatomy and
29 Zooarchaeological Skeletal Part Representation. Journal of Archaeological Method and
30 Theory 13, 19-66.
31

32
33 Lupo, K.D., Schmitt, D.N., 2002. Upper Paleolithic net-hunting, small prey exploitation,
34 and women's work effort: a view from the ethnographic and ethnoarchaeological record
35 of the Congo basin. Journal of Archaeological Method and Theory 9, 147-179.
36

37
38 Lyman, R.L., 2008. Quantitative Paleozoology. Cambridge University Press,
39 Cambridge/New York.
40

41
42 Madsen, D.B., Schmitt, D.N., 1998. Mass Collecting and the Diet Breadth Model: A
43 Great Basin Example. J. Archaeol. Sci. 25, 445-455.
44

45
46 Marean, C.W., Abe, Y., Frey, C.J., Randall, R.C., 2000. Zooarchaeological and
47 taphonomic analysis of the Die Kelders Cave 1 Layers 10 and 11 Middle Stone Age
48 larger mammal fauna. J. Hum. Evol. 38, 197-233.
49

50
51 Marean, C.W., Abe, Y., Nilssen, P.J., Stone, E.C., 2001. Estimating the minimum
52 number of skeletal elements (MNE) in zooarchaeology: a review and a new image-
53 analysis GIS approach. Am. Antiq. 66, 333-348.
54

55
56 Marean, C.W., Bar-Matthews, M., Bernatchez, J., Fisher, E., Goldberg, P., Herries,
57 A.I.R., Jacobs, Z., Jerardino, A., Karkanas, P., Minichillo, T., Nilssen, P.J., Thompson,
58 E., Watts, I., Williams, H.M., 2007. Early human use of marine resources and pigment in
59 South Africa during the Middle Pleistocene. Nature 449, 905-908.
60
61
62
63
64
65

5 Marlowe, F., 2004. Mate preferences among Hadza hunter-gatherers. *Human Nature* 15,
6 365-376.
7

8
9 Marlowe, F.W., 2005. Hunter-gatherers and human evolution. *Evolutionary*
10 *Anthropology: Issues, News, and Reviews* 14, 54-67.
11

12 Mason, M.C., Kerley, G.I.H., Weathreby, C.A., Branch, W.R., 2000. Angulate and
13 leopard tortoises in the Thicket Biome, Eastern Cape, South Africa: populations and
14 biomass estimates. *African Journal of Ecology* 38, 147-153>.
15
16

17
18 McBrearty, S., Brooks, A.S., 2000. The revolution that wasn't: A new interpretation of
19 the origin of modern human behavior. *J. Hum. Evol.* 39, 453-563.
20

21 McCall, G., Thomas, J., 2012. Still Bay and Howiesons Poort Foraging Strategies:
22 Recent Research and Models of Culture Change. *African Archaeological Review* 29, 7-
23 50.
24

25
26 Miller, C.E., Goldberg, P., Berna, F., 2013. Geoarchaeological investigations at
27 Diepkloof Rock Shelter, Western Cape, South Africa. *J. Archaeol. Sci.* 40, 3432–3452.
28

29
30 Milo, R.G., 1998. Evidence for hominid predation at Klasies River Mouth, South Africa,
31 and its implications for the behavior of early modern humans. *J. Archaeol. Sci.* 25, 99-
32 133.
33

34
35 Milton, K., 2000. Hunter-gatherer diets—a different perspective. *The American Journal*
36 *of Clinical Nutrition* 71, 665-667.
37

38
39 Milton, K., 2003. The critical role played by animal source foods in human (*Homo*)
40 evolution. *Journal of Nutrition* 133, 3886S-3892S.
41

42 Monahan, C.M., 1998. The Hadza Carcass Transport Debate Revisited and its
43 Archaeological Implications. *J. Archaeol. Sci.* 25, 405-424.
44

45
46 Morgan, L.E., Renne, P.R., 2008. Diachronous dawn of Africa's Middle Stone Age: New
47 $^{40}\text{Ar}/^{39}\text{Ar}$ ages from the Ethiopian Rift. *Geology* 36, 967-970.
48

49
50 Munro, N.D., Atici, L., 2009. Human subsistence change in the Late Pleistocene
51 Mediterranean Basin: The status of research on faunal intensification, diversification &
52 specialisation. *Before Farming* 1, 1-6.
53

54
55 Nash, D.J., Coulson, S., Staurset, S., Ullyott, J.S., Babutsi, M., Hopkinson, L., Smith,
56 M.P., 2013. Provenancing of silcrete raw materials indicates long-distance transport to
57 Tsodilo Hills, Botswana, during the Middle Stone Age. *J. Hum. Evol.* 64, 280–288.
58
59
60
61
62
63
64
65

4 Osendarp, S.J., Baghurst, K.I., Bryan, J., Calvaresi, E., Hughes, D., Hussaini, M.,
5 Karyadi, S.J., van Klinken, B.J., van der Knaap, H.C., Lukito, W., Mikarsa, W., Transler,
6 C., Wilson, C., 2007. Effect of a 12-mo micronutrient intervention on learning and
7 memory in well-nourished and marginally nourished school-aged children: 2 parallel,
8 randomized, placebo-controlled studies in Australia and Indonesia. *The American Journal*
9 *of Clinical Nutrition* 86, 1082-1093.
10
11

12 Patton, J.Q., 2005. Meat sharing for coalitional support. *Evolution and Human Behavior*
13 26, 137-157.
14

15
16 Pearse, A.S., Lepkovsky, S., Hintze, L., 1925. The growth and chemical composition of
17 three species of turtles fed on rations of pure foods. *Journal of Morphology* 41, 191-216.
18
19

20 Porat, N., Chazan, M., Grün, R., Aubert, M., Eisenmann, V., Horwitz, L.K., 2010. New
21 radiometric ages for the Fauresmith industry from Kathu Pan, southern Africa:
22 Implications for the Earlier to Middle Stone Age transition. *J. Archaeol. Sci.* 37, 269-283.
23
24

25 Ramsay, S.L., Hofmeyr, M.D., Quinton, I.J., 2002. Activity Patterns of the Angulate
26 Tortoise (*Chersina angulata*) on Dassen Island, South Africa. *Journal of Herpetology* 36,
27 161-169.
28
29

30 Sampson, C.G., 2000. Taphonomy of tortoises deposited by birds and Bushmen. *J.*
31 *Archaeol. Sci.* 27, 779-788.
32

33 Schneider, J.S., Everson, G.D., 1989. The Desert Tortoise (*Xerobates agassizii*) in the
34 Prehistory of the Southwestern Great Basin and Adjacent Areas. *Journal of California*
35 *and Great Basin Anthropology* 11, 175-202.
36
37

38 Sebastian, A., Frassetto, L.A., Sellmeyer, D.E., Merriam, R.L., Morris, R.C., 2002.
39 Estimation of the net acid load of the diet of ancestral preagricultural *Homo sapiens* and
40 their hominid ancestors. *The American Journal of Clinical Nutrition* 76, 1308-1316.
41
42

43 Skinner, J.D., Louw, G.N., 1996. The springbok *Antidorcas marsupialis* (Zimmerman
44 1780). *Transvaal Museum Monographs* 10, 1-50.
45
46

47 Speth, J., Spielmann, K.A., 1983. Energy source, protein metabolism, and hunter-gatherer
48 subsistence strategies. *J. Anthropol. Archaeol.* 2, 1-31.
49

50 Speth, J.D., 2010. *The Other Side of Protein, The Paleoanthropology and Archaeology of*
51 *Big-Game Hunting.* Springer New York, pp. 45-85.
52
53

54 Speth, J.D., Tchernov, E., 2002. Middle Paleolithic tortoise use at Kebara Cave (Israel).
55 *J. Archaeol. Sci.* 29, 471-483.
56
57

58 Stahl, P.W., Oyuela-Caycedo, A., 2007. Early prehistoric sedentism and seasonal animal
59 exploitation in the Caribbean lowlands of Colombia. *J. Anthropol. Archaeol.* 26, 329-349.
60
61
62
63
64
65

5 Steele, T.E., Klein, R.G., 2013. The Middle and Later Stone Age faunal remains from
6 Diepkloof Rock Shelter, Western Cape, South Africa. *J. Archaeol. Sci.* 40, 3453–3462.
7

8
9 Stiner, M.C., 2001. Thirty years on the "Broad Spectrum Revolution" and paleolithic
10 demography. *Proc. Natl. Acad. Sci.* 98, 6993-6996.
11

12 Stiner, M.C., 2006. Middle Paleolithic subsistence ecology in the Mediterranean Region,
13 Transitions before the transition. Springer, pp. 213-231.
14

15
16 Stiner, M.C., Kuhn, S.L., 2009. Paleolithic Diet and the Division of Labor in
17 Mediterranean Eurasia, in: Hublin, J.-J., Richards, M.P. (Eds.), *The Evolution of*
18 *Hominin Diets*. Springer Netherlands, pp. 157-169.
19

20
21 Stiner, M.C., Munro, N.D., 2002. Approaches to prehistoric diet breadth, demography,
22 and prey ranking systems in time and space. *Journal of Archaeological Method and*
23 *Theory* 9, 181-214.
24

25
26 Stiner, M.C., Munro, N.D., Surovell, T.A., 2000. The tortoise and the hare: small-game
27 use, the broad-spectrum revolution, and Paleolithic demography. *Curr. Anthropol.* 41, 39-
28 73.
29

30
31 Stiner, M.C., Munro, N.D., Surovell, T.A., Tchernov, E., Bar-Yosef, O., 1999. Paleolithic
32 population growth pulses evidenced by small animal exploitation. *Science* 283, 190-194.
33

34
35 Stuart, C.L., Meakin, P.R., 1983. A note on the effect of fire on a population of Angulate
36 tortoises, *Chersina angulata* (Cryptodira: Testudinidae), with an estimate of biomass.
37 *The Journal of the Herpetological Association of Africa* 29, 7-8.
38

39
40 Tanno, T., 1976. The Mbuti net-hunters in the Ituri forest, eastern Zaire: Their hunting
41 activities and band composition. *Kyoto University African Studies* 10, 101-135.
42

43
44 Texier, J.P., Porraz, G., Parkington, J., Rigaud, J.-P., Poggenpoel, C., Miller, C., Tribolo,
45 C., Cartwright, C., Coudenneau, A., Klein, R., Steele, T., Vernai, C., 2010. A Howiesons
46 Poort tradition of engraving ostrich eggshell containers dated to 60,000 years ago at
47 Diepkloof Rock Shelter, South Africa. *Proc. Natl. Acad. Sci.* 107, 6180–6185.
48

49
50 Thompson, J.C., 2010a. Taphonomic analysis of the faunal assemblage from Pinnacle
51 Point Cave 13B, Western Cape, South Africa. *J. Hum. Evol.* 59, 321-339.
52

53
54 Thompson, J.C., 2010b. Variability in Middle Stone Age faunal exploitation and use of
55 the physical and social landscapes in the southwestern Cape, South Africa, in: Delagnes,
56 A., Conard, N. (Eds.), *Settlement Dynamics of the Middle Paleolithic and Middle Stone*
57 *Age III*. Kerns Verlag, Tübingen, pp. 11-38.
58
59
60
61
62
63
64
65

1 *Nutritional value of tortoises and foraging implications at Blombos Cave*
2
3

4 Thompson, J.C., Henshilwood, C., in revision. Tortoise taphonomy and tortoise butchery
5 patterns at Blombos Cave, South Africa. *J. Archaeol. Sci.* in revision.
6

7
8 Thompson, J.C., Henshilwood, C.S., 2011. Taphonomic analysis of the Middle Stone
9 Age larger mammal faunal assemblage from Blombos Cave, southern Cape, South
10 Africa. *J. Hum. Evol.* 60, 746-767.
11

12
13 Tribolo, C., 2003. Apports des méthodes de la luminescence à la chronologie de techno-
14 faciès du Middle Stone Age associés aux premiers Hommes modernes d’Afrique du Sud.
15 Université Bordeaux-1, Bordeaux.
16

17
18 Tribolo, C., Mercier, N., Selo, M., Valladas, H., Joron, J.-L., Reyss, J.-L., Henshilwood,
19 C.S., Sealy, J.C., Yates, R., 2006. TL dating of burnt lithics from Blombos Cave (South
20 Africa): further evidence for the antiquity of modern human behavior. *Archaeometry* 48,
21 341-357.
22

23
24 Tryon, C.A., McBrearty, S., 2002. Tephrostratigraphy and the Acheulian to Middle Stone
25 Age transition in the Kapthurin Formation, Kenya. *J. Hum. Evol.* 42, 211-236.
26

27
28 Tryon, C.A., McBrearty, S., 2006. Tephrostratigraphy of the Bedded Tuff Member
29 (Kapthurin Formation, Kenya) and the nature of archaeological change in the later middle
30 Pleistocene. *Quaternary Research* 65, 492-507.
31

32
33 Ugan, A., 2005. Does size matter? Body size, mass collecting, and their implications for
34 understanding prehistoric foraging behavior. *Am. Antiq.* 70, 75-89.
35

36
37 Van Den Berg, P., Baard, E.H.W., 1994. Regional variation in morphometric characters
38 in the angulate tortoise, *Chersina angulata*, from South Africa. *The Journal of the*
39 *Herpetological Association of Africa* 43, 28-32.
40

41
42 van Heezik, Y.M., Cooper, J., Seddon, P.J., 1994. Population Characteristics and
43 Morphometrics of Angulate Tortoises on Dassen Island, South Africa. *Journal of*
44 *Herpetology* 28, 447-453.
45

46
47 van Zyl, L., Ferreira, A.V., 2004. Physical and chemical carcass composition of
48 springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus dorcas phillipsi*) and impala
49 (*Aepyceros melampus*). *Small Ruminant Research* 53, 103-109.
50

51
52 Vanhaeren, M., d’Errico, F., van Niekerk, K.L., Henshilwood, C.S., Erasmus, R.M.,
53 2013. Thinking strings: Additional evidence for personal ornament use in the Middle
54 Stone Age at Blombos Cave, South Africa. *J. Hum. Evol.*
55

56
57 Villa, P., Soressi, M., Henshilwood, C.S., Mourre, V., 2009. The Still Bay points of
58 Blombos Cave (South Africa). *J. Archaeol. Sci.* 36, 441-460.
59
60
61
62
63
64
65

1 *Nutritional value of tortoises and foraging implications at Blombos Cave*
2
3

4 Wadley, L., 1998. Invisible meat providers: Women in the Stone Age of South Africa, in:
5 Kent, S. (Ed.), *Gender in African Prehistory*. AltaMira Press, Walnut Creek, CA, pp. 69-
6 82.
7

8
9 Wadley, L., 2001. What is cultural modernity? A general view and a South African
10 perspective from Rose Cottage Cave. *Cambridge Archaeological Journal* 11, 201-221.
11

12
13 Wadley, L., 2010. Were snares and traps used in the Middle Stone Age and does it
14 matter? A review and a case study from Sibudu, South Africa. *J. Hum. Evol.* 58, 179-192.
15

16
17 Wadley, L., Sievers, C., Bamford, M., Goldberg, P., Berna, F., Miller, C., 2011. Middle
18 Stone Age Bedding Construction and Settlement Patterns at Sibudu, South Africa.
19 *Science* 334, 1388-1391.
20

21
22 Waguespack, N.M., 2005. The Organization of Male and Female Labor in Foraging
23 Societies: Implications for Early Paleoindian Archaeology. *American Anthropologist*
24 107, 666-676.
25

26
27 Watts, I., 2010. The pigments from Pinnacle Point Cave 13B, Western Cape, South
28 Africa. *J. Hum. Evol.* 59, 392-411.
29

30
31 Weaver, T.D., Steele, T., Klein, R., 2011. The abundance of eland, buffalo, and wild pigs
32 in Middle and Later Stone Age sites. *J. Hum. Evol.* 60, 309-314.
33

34
35 Werner, D., 1990. *Amazon Journey. An Anthropologist's Year among Brazil's*
36 *Mekranoti Indians*. Prentice Hall, Englewood Cliffs.
37

38
39 Wilkins, J., Chazan, M., 2012. Blade production 500 thousand years ago at Kathu Pan 1,
40 South Africa: support for a multiple origins hypothesis for early Middle Pleistocene blade
41 technologies. *J. Archaeol. Sci.* 39, 1883-1900.
42

43
44 Wilkins, J., Schoville, B.J., Brown, K.S., Chazan, M., 2012. Evidence for early hafted
45 hunting technology. *Science* 338, 942-946.
46

47
48 Williams, P., 2007. Nutritional composition of red meat. *Nutrition & Dietetics* 64, S113-
49 S119.
50

51
52 Winterhalder, B., Smith, E.A., 2000. Analyzing adaptive strategies: human behavioral
53 ecology at twenty-five. *Evol. Anthropol.* 9, 51-72.
54

55
56 Wurz, S., 1999. The Howiesons Poort backed artefacts from Klasies River: an argument
57 for symbolic behavior. *S. Afr. Archaeol. Bull.* 54, 38-50.
58

59
60 Wurz, S., 2012. The significance of MIS 5 shell middens on the Cape coast: A lithic
61 perspective from Klasies River and Ysterfontein 1. *Quaternary International* 270, 61-69.
62
63
64
65

8 **Figure Captions**
9

10
11 **Figure 1** Modern distribution of *Chersina angulata* (Hofmeyr 2009), showing location of
12 Blombos Cave and other sites mentioned in the text. Topographic data are SRTM data.
13
14

15
16
17 **Figure 2** Layout and stratigraphy of Blombos Cave. Layers sampled for tortoise analysis
18 and tortoise NISP are indicated.
19
20

21
22 **Figure 3** Human modification on tortoise elements with enlargements of areas of interest
23 at right: a) two cut marks on a limb; b) a scrape mark on the interior of the carapace, with
24 the boundaries indicated by arrows; c and d) percussion marks on the exterior of the
25 carapace with arrows indicating microstriation patches within smoothed areas where the
26 bone surface has been compressed and the texture modified by contact with the
27 percussor.
28
29
30
31
32

33
34 **Figure 4** The distribution and intensity of burning patterns on the shell showing
35 preferential burning on the carapace and around the edges of the plastron and indicating
36 cooking carapace side down while the tortoise was complete.
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

4 **Table Captions**
5

6
7 **Table 1** Summary of ages and material culture associated with the BBC stratigraphy.
8
9

10 **Table 2** NISP and MNE counts for the identifiable tortoise sample that underlie the MNI
11 estimates.
12
13

14
15 **Table 3** NISP and MNE counts for the identifiable ungulate sample that underlie the
16 MNI estimates. Data are provided for both the entire available ungulate sample and the
17 subsample that was drawn from the same area of deposit as the tortoise data.
18
19
20
21

22
23 **Table 4** Nutritional information from *Chersina* compared to a smaller and larger size 2
24 ungulates. Data from van Zyl and Ferreira (2004), because the springbok (*Antidorcas*
25 *marsupialis*) and the blesbok (*Damaliscus dorcas*) are the smallest and largest
26 species for which whole carcass data were measured in the same study and in
27 equivalent ways by the same authors.
28
29
30
31

32
33 **Table 5** Combined data for percentages of protein, fat, and edible versus non-edible body
34 tissues in whole carcasses. Data from Blumenschine and Caro (1986) and van Zyl and
35 Ferreira (2004).
36
37
38
39

40
41 **Table 6** Composite estimates of calories per individual in each average bovid adult body
42 size class compared to a single average adult tortoise. Protein values derived as follows:
43
44 Size 1 = common duiker (*Sylvicapra grimmia*) (Hoffman and Ferreira, 2004); Size 2 =
45 springbok (*Antidorcas marsupialis*) (van Zyl and Ferreira, 2004); Size 3 = red hartebeest
46 (*Alcelaphus buselaphus*) (Hoffman et al., 2010); Size 4 = averages of size 1-3 estimates
47 because no specific protein contents for eland (*Taurotragus oryx*) or buffalo (*Syncerus*
48 *caffer*) are available. Fat values derived as follows: Size 1 = common duiker (Hoffman
49 and Wiklund, 2006); Size 2 = springbok (van Zyl and Ferreira, 2004); Size 3 = average of
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1 *Nutritional value of tortoises and foraging implications at Blombos Cave*
2
3

4 kudu (*Tragelaphus strepsiceros*), red hartebeest, and black wildebeest (*Connochaetes*
5 *gnou*) + 1% to account for all specimens being male (Hoffman and Wiklund, 2006)
6
7 reported by Hoffman and Wiklund (2006). Size 4 = averages of size 1-3 estimates.
8
9

10
11
12
13 **Table 7** Total caloric value of complete ungulates and tortoises based on MNI
14 representation at BBC.
15
16

17
18
19 **Table 8** Estimates of the number of days different-sized groups could have been resident
20 at BBC and sustained by the tortoise and ungulate resources represented in the deposits.
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

Phase	Age (ka)	Method	Dating Citations/Notes
Sterile Sand	69 ± 5	OSL	Henshilwood, et al., 2002, Jacobs, et al., 2003a, Jacobs, et al., 2006, Jacobs, et al., 2003b
	70 ± 5		
BBC M1	72.7 ± 3.1	OSL	Jacobs, et al., 2003a, Jacobs, et al., 2003b
	74 ± 5	TL	Tribolo, et al., 2006
	78 ± 6		
BBC M2 Upper	76.8 ± 3.1	OSL	Jacobs, et al., 2006; Possible <i>terminus post quem</i> for Still Bay levels?
Still Bay overall	ca. 75 – 72	OSL	Jacobs, et al., 2013; Possible <i>terminus post quem</i> for Still Bay levels?
BBC M2 Lower	84.6 ± 5.8	OSL	Henshilwood, et al., 2011, Jacobs, et al., 2006
	78.9 ± 5.9		Jacobs, et al., 2013
	78.8 ± 5.6		
BBC M3	ca. 100 to > 130	OSL	Henshilwood, 2012, Henshilwood, 2009, Henshilwood, et al., 2011, Henshilwood, et al., 2001b (a)

Phase	Material Culture	Details	Material Culture Citations
Sterile Sand	None	Demonstrates separation between LSA and MSA layers	N/A
BBC M1	Still Bay points	Pressure-flaked bifacial foliate points made mainly on heat-treated silcrete	Mourre, et al., 2010, Villa, et al., 2009
	Worked bone tools	Formal and informal tools	d'Errico and Henshilwood, 2007, Henshilwood, et al., 2001a; Henshilwood & Sealy, 1997
	Engraved ochres	Pieces show clear engraved patterns	Henshilwood, et al., 2009, Henshilwood, et al., 2002
	Perforated <i>Nassarius kraussianus</i> shell beads with wear facets	Show differences in style of beading over time	d'Errico, et al., 2005, Henshilwood, et al., 2004, Henshilwood, 2009, Vanhaeren, et al., 2013
BBC M2 Upper	Still Bay points, worked bone tools, shell beads		As above

BBC M3	Basin shaped hearths and ochre, some engraved; Two <i>Haliotis midae</i> (abalone) shells with pigment mixture containing ground ochre, burnt bone, charcoal, ground quartz and associated with grindstones and hammerstones	Ochre-processing workshop and first recorded use of a container and a pigmented compound	Henshilwood, 2012, Henshilwood, 2009, Henshilwood, et al., 2011, Henshilwood, et al., 2001b (hearths and ochre); Henshilwood, et al., 2011 (ochre workshop)
--------	--	--	---

(b)

Table 2.docx

		BBC M1		BBC M3				BBC M1		BBC M3	
		NISP	MNE	NISP	MNE			NISP	MNE	NISP	MNE
TORTOISE CARAPACE AND PLASTRON	Neural	277	23	62	10	TORTOISE LIMBS AND GIRDLES	Scapula	51	19	31	12
	Costal	900	31	145	6		Procoracoid	28	12	19	8
	Marginal	1118	53	186	8		Ilium	39	18	17	4
	Nuchal	66	46	24	12		Ischium	28	14	7	5
	Suprapygal	37	31	0	0		Pubis	49	19	30	4
	Pygal	56	52	11	7		Humerus	51	24	32	14
	Epiplastron	154	65	12	6		Radius	20	9	21	0
	Entoplastron	77	74	5	5		Ulna	18	9	12	0
	Hyoplastron	174	66	19	5		Femur	45	20	22	10
	Hypoplastron	180	51	21	6		Tibia	29	14	26	13
Xiphiplastron	145	62	15	5	Fibula	20	10	10	4		

	BBC M1				BBC M3				BBC M1				BBC M3			
	NI	M	NIS	MN	NI	M	NIS	MN	NI	M	NIS	MN	NI	M	NIS	MN
	SP	N	P	E	SP	N	P	E	SP	N	P	E	SP	N	P	E
	Al	Al	mpl	mpl	Al	Al	mpl	mpl	Al	Al	mpl	mpl	Al	Al	mpl	mpl
Atlas	2	2	0	0	4	3	1	1	0	0	0	0	0	0	0	0
Axis	3	3	1	1	0	0	0	0	0	0	1	1	0	0	0	0
Cervical Vertebra	3	5	4	3	2	2	0	0	1	6	3	1	0	1	0	0
Thoracic Vertebra	9	16	7	5	5	7	6	4	3	3	1	1	0	1	1	1
Lumbar Vertebra	2	5	7	5	4	4	3	2	0	2	0	0	0	1	1	1
Sacrum	0	4	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Rib	3	9	18	2	3	3	5	1	2	5	14	1	0	2	9	1
Scapula	16	5	9	4	4	1	0	0	5	3	2	1	2	1	1	1
Humerus	16	5	11	3	8	4	3	2	18	3	9	3	1	1	1	1
Radius	14	3	7	2	6	2	1	1	8	2	3	2	1	1	0	0
Ulna	2	2	0	0	1	0	0	0	6	2	3	2	1	0	0	0
Metacarpal	10	2	2	1	5	2	0	0	5	2	1	1	0	0	0	0
Innominate	11	5	2	1	10	5	3	3	8	3	2	1	1	1	0	0
Femur	12	3	5	1	8	1	4	1	8	3	4	1	1	0	0	0
Tibia	17	3	12	1	5	4	3	1	20	4	12	4	2	1	0	0
Metatarsal	11	3	4	2	6	3	1	1	10	5	5	2	2	1	0	0

	BBC M1				BBC M3				BBC M1				BBC M3			
	NI	M	NIS	MN	NI	M	NIS	MN	NI	M	NIS	MN	NI	M	NIS	MN
	SP	N	P	E	SP	N	P	E	SP	N	P	E	SP	N	P	E
	Al	Al	mpl	mpl	Al	Al	mpl	mpl	Al	Al	mpl	mpl	Al	Al	mpl	mpl
Atlas	1	2	1	1	0	0	0	0	1	1	1	1	0	0	0	0
Axis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cervical Vertebra	0	11	8	3	0	1	1	1	2	2	2	0	0	0	0	0
Thoracic Vertebra	9	14	12	10	1	2	1	1	0	1	0	0	0	1	0	0
Lumbar Vertebra	1	3	2	1	1	1	1	0	4	3	3	1	0	0	0	0
Sacrum	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Rib	1	8	16	2	0	2	2	1	1	4	9	3	1	1	2	1
Scapula	0	0	0	0	0	0	0	0	2	1	2	0	2	1	0	0
Humerus	31	6	10	3	1	0	1	0	4	2	1	1	1	0	1	0
Radius	11	3	3	2	2	1	1	1	2	1	0	0	1	1	0	0
Ulna	3	2	2	1	0	0	0	0	3	2	1	1	0	0	0	0
Metacarpal	14	4	2	1	1	1	1	1	4	2	0	0	1	1	0	0
Innominate	17	3	9	2	0	0	0	0	2	1	2	0	1	0	0	0
Femur	24	8	4	1	3	1	2	1	5	2	2	1	2	1	1	0
Tibia	37	5	10	3	5	2	3	1	14	3	3	0	3	1	0	1
Metatarsal	10	3	0	0	0	0	0	0	12	3	5	2	1	1	0	0

Table 4.docx

	<i>Chersina angulata</i>		<i>Antidorcas marsupialis</i>		<i>Damaliscus dorcas</i>	
	male	female	male	female	male	female
Mean live body weight (g)	907	815	33700	27100	50400	56200
Mean carcass weight (g)	623	560	19400	15300	24900	28600
Protein (g) per carcass	109	98	4695	3504	5802	6778
Fat (g) per carcass	44	39	164	280	261	610
kJ from protein per carcass	1853	1665	79812	59563	98629	115229
kJ from fat per carcass	1657	1489	6244	10651	9921	23181
Total kJ/g of LWB	4	4	3	3	2	2
Total kJ/carcass	3510	3154	86056	70214	108550	138411
Total kcal/carcass	838	753	20554	16770	25927	33059

*1g protein = 17 kJ

**1g fat = 38 kJ

Table 5.docx

	M	F	M	F	M	F	M	F	M	F	M	F
Live Body Weight (LBW) in kg	16.3	23.7	33.7	27.1	42.6	64.9	57.6	N/A	50.4	56.2	158.3	N/A
%Weight Viscera	15.6	26.1	-	-	19.7	22.6	19.8	-	-	-	26.8	-
%Weight Bone	28.9	24.5	-	-	19.8	19.1	24.1	-	-	-	21.7	-
%Weight Skin	5.2	5.8	-	-	6.1	6.5	6.3	-	-	-	8.6	-
%Weight Flesh	50.4	43.6	-	-	54.4	51.9	49.7	-	-	-	42.9	-
%Weight Marrow	-	0.3	-	-	0.1	0.4	0.3	-	-	-	0.2	-
%Edible Weight	-	43.9	-	-	54.5	52.3	50.0	-	-	-	43.1	-
Carcass Weight as %LBW*	-	-	64.9	62.7	-	-	63.9	66.1	62.6	62.9	-	-
Carcass %protein	-	-	24.2	22.9	-	-	22.1	22.6	23.3	23.7	-	-
Carcass %fat	-	-	3.5	8.0	-	-	1.3	5.8	4.5	9.0	-	-

* Carcass weight is equal to LBW - head, viscera, skin, blood, and feet; in this study cold carcass weight was used, which can be somewhat less than warm carcass weight

	<i>Chersina</i>	Size 1	Size 2	Size 3	Size 4
Live Body Weight (LBW) (g)	861	12750	61000	143500	656000
% Edible Tissue	68.7%	43.9%	50.0%	43.1%	50.0%
Edible Body Weight (EBW) (g)	591	5597	30500	61849	328000
% Protein	17.5%	25.8%	22.4%	23.5%	23.9%
% Fat	7.0%	3.1%	3.6%	3.4%	3.7%
g Protein in EBW	103	1444	6817	14534	78392
g Fat in EBW	41	174	1083	2103	12136
kJ Protein in EBW	1759	24550	115885	247085	1332664
kJ Fat in EBW	1573	6594	41145	79908	461168
kJ per Individual (edible tissues)	3,332	31,143	157,029	326,993	1,793,832
kcal per Individual (edible tissues)	796	7,438	37,506	78,101	428,449
# Tortoises per Ungulate	N/A	9	47	98	538

Smaller sample - both tortoise and ungulate data available

	M1			M3			
	MNI	Total kJ	Total kcal	MNI	Total kJ	Total kcal	
Size 1	4	124,572	29,774	3	93,429	22,330	
Size 2	4	628,117	150,124	1	157,029	37,531	
Size 3	3	980,979	234,460	1	326,993	78,153	
Size 4	2	3,587,664	857,472	1	1,793,832	428,736	
Mammal							
Total	13	5,746,955	1,373,555	6	2,047,065	489,260	
Tortoise							
Total	73	243,359	58,164	14	47,076	11,251	(a)

Larger sample - ungulate data available and tortoise data extrapolated by volume of deposit

	M1			M3			
	MNI	Total kJ	Total kcal	MNI	Total kJ	Total kcal	
Size 1	5	155,715	37,217	4	124,572	29,774	
Size 2	5	785,146	187,654	1	157,029	37,531	
Size 3	5	1,634,965	390,766	2	653,986	156,306	
Size 4	3	5,381,496	1,286,208	1	1,793,832	428,736	
Mammal							
Total	18	7,957,323	1,901,846	8	2,729,420	652,347	
Tortoise							
Total	318	1,060,113	253,373	43	144,591	34,558	(b)

Table 8.docx

		1 Person		5 People		10 People		15 People		20 People	
Phase		No of days	No of days	No of days	No of days	No of days	No of days	No of days	No of days	No of days	No of days
		M1	M3	M1	M3	M1	M3	M1	M3	M1	M3
Meat Only	Mam	634	217	127	43	63	22	42	14	32	11
	Tort	84	12	17	2	8	1	6	1	4	1
	All	718	229	144	46	72	23	48	15	36	11
Energy	Mam	1787	613	357	123	179	61	119	41	89	31
	Tort	238	32	48	6	24	3	16	2	12	2
	All	2025	645	405	129	202	65	135	43	101	32
Energy	Mam	2445	839	489	168	245	84	163	56	122	42
	Tort	326	44	65	9	33	4	22	3	16	2
	All	2771	883	554	177	277	88	185	59	139	44

Figure 1
[Click here to download high resolution image](#)

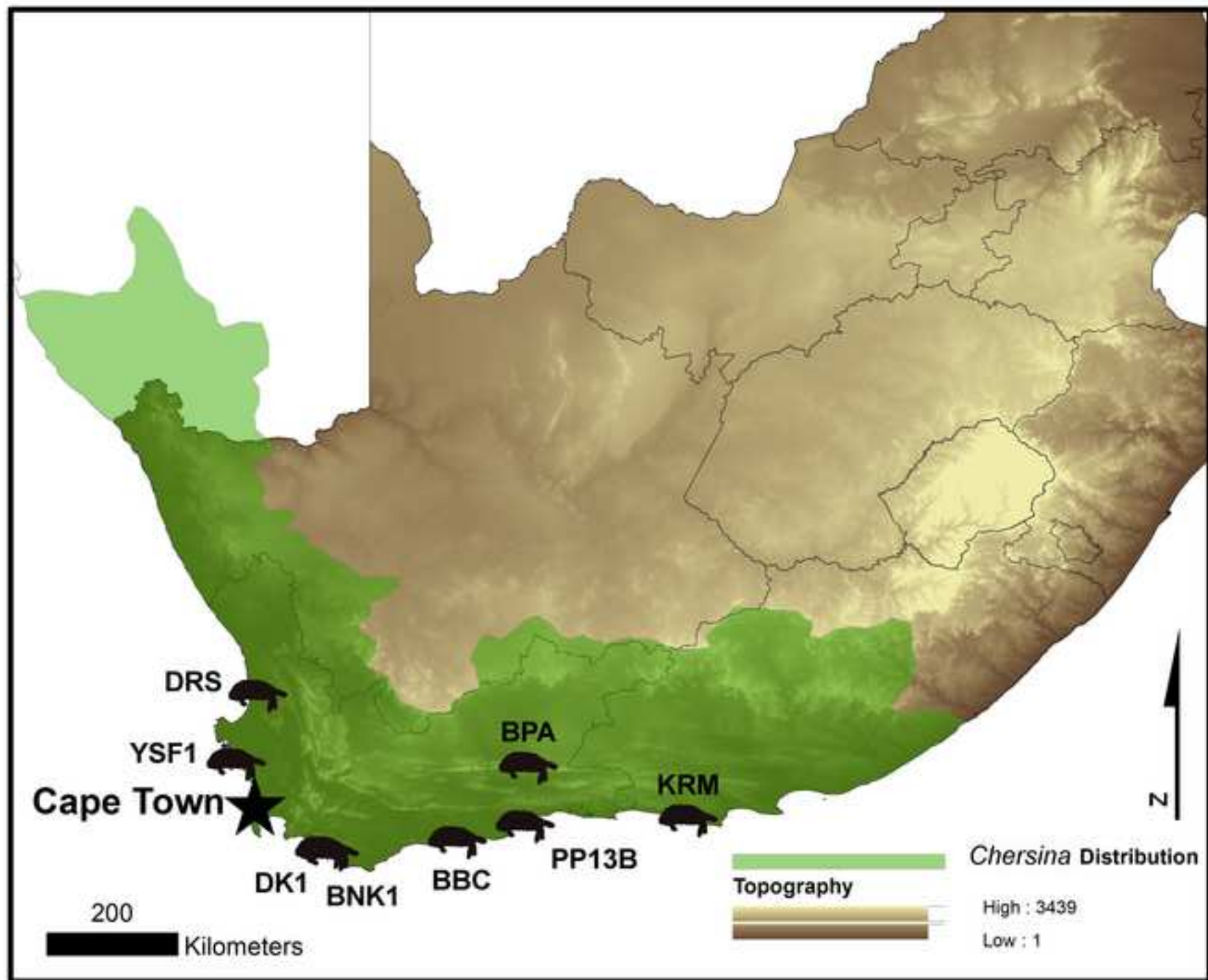


Figure 2
[Click here to download high resolution image](#)

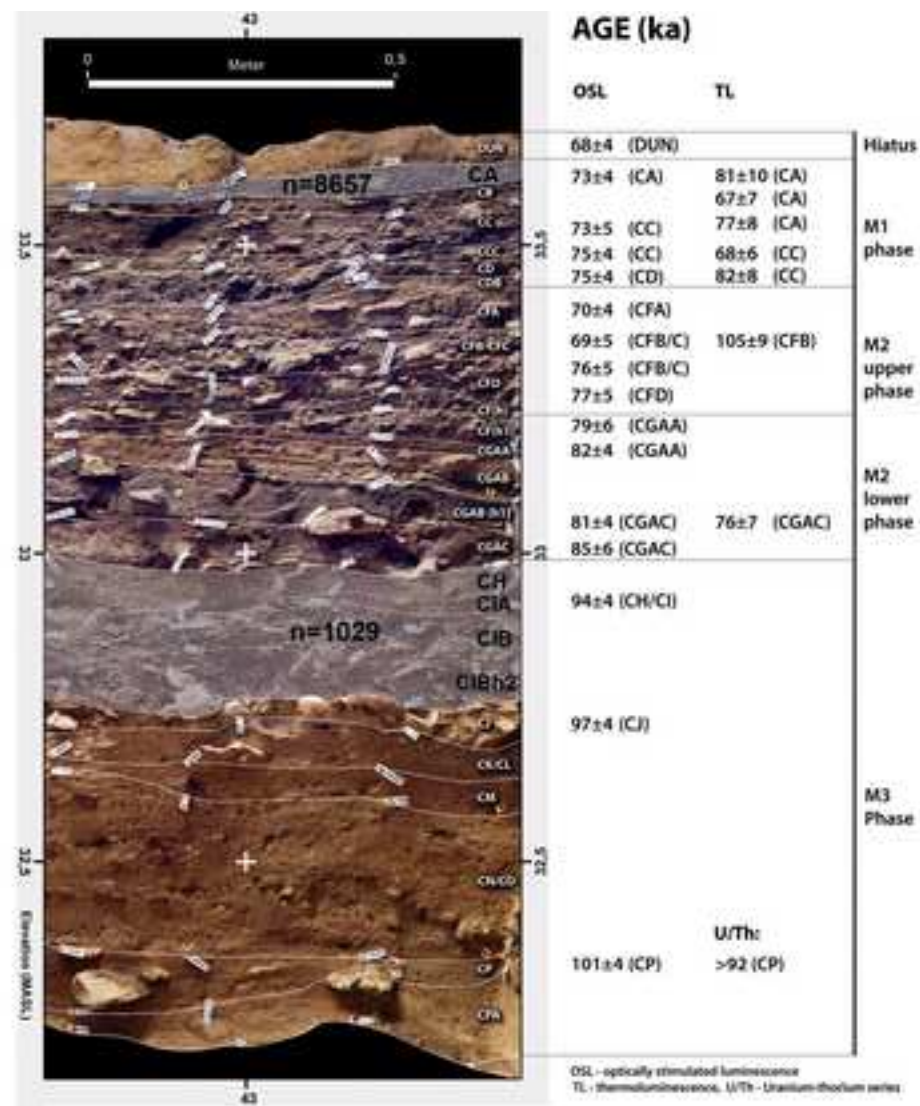
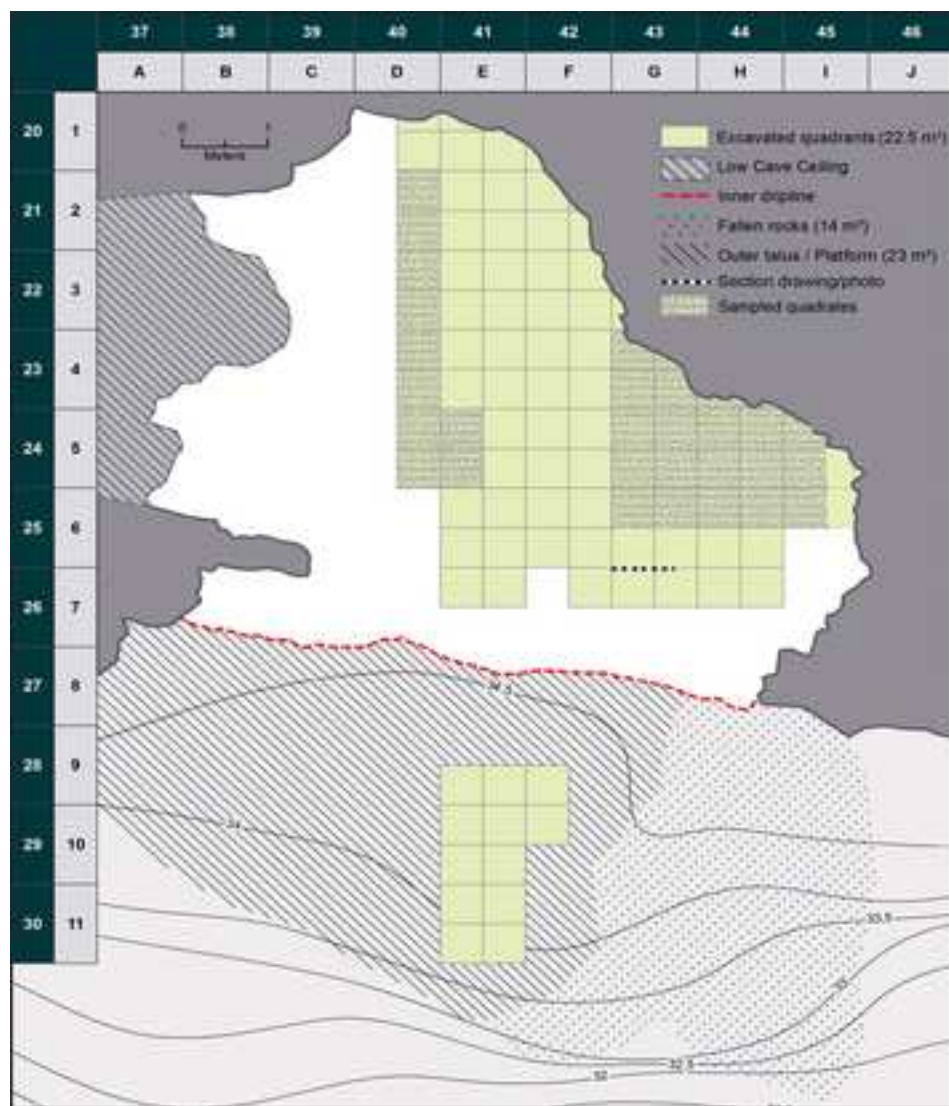


Figure 3
[Click here to download high resolution image](#)

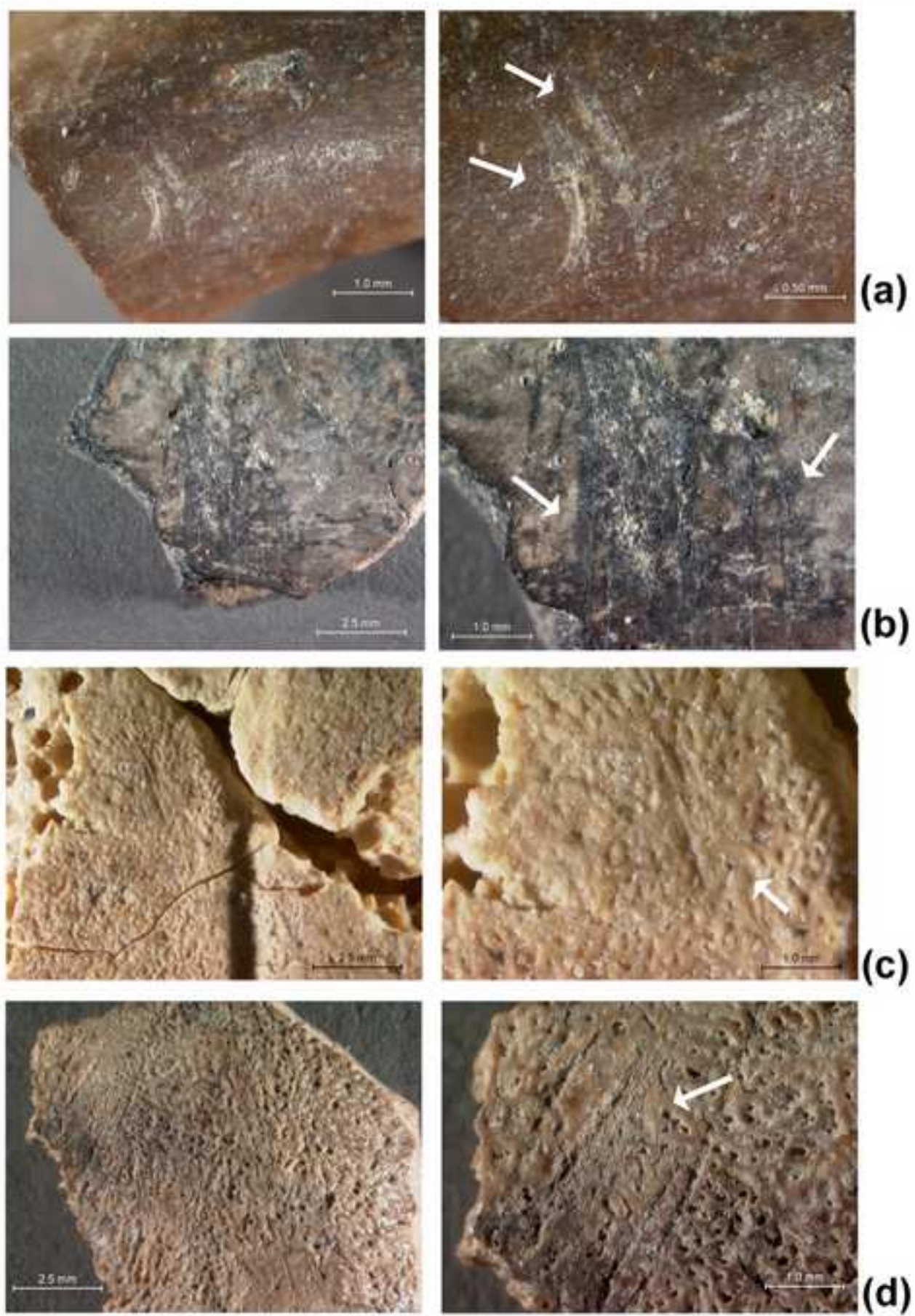


Figure 4
[Click here to download high resolution image](#)

