Nutritional values of tortoises relative to ungulates from the Middle Stone Age levels at Blombos Cave, South Africa: Implications for foraging and social behaviour

Jessica C. Thompson\textsuperscript{a,*}, Christopher S. Henshilwood\textsuperscript{b,c}

\textsuperscript{a} School of Social Science, Archaeology Program, Michie Building (9), University of Queensland, Brisbane, QLD 4072, Australia
\textsuperscript{b} Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa
\textsuperscript{c} Institute for Archaeology, History, Culture and Religion, University of Bergen, Norway

\textbf{ABSTRACT}

The site of Blombos Cave (BBC), Western Cape, South Africa has been a strong contributor to establishing the antiquity of important aspects of modern human behaviour, such as early symbolism and technological complexity. However, many linkages between Middle Stone Age (MSA) behaviour and the subsistence record remain to be investigated. Understanding the contribution of small fauna such as tortoises to the human diet is necessary for identifying shifts in overall foraging strategies as well as the collecting and processing behaviour of individuals unable to participate in large-game hunting. This study uses published data to estimate the number of calories present in tortoises as well as ungulates of different body size classes common at South African sites. A single tortoise (\textit{Chersina angulata}) provides approximately 3332 kJ (796 kcal) of calories in its edible tissues, which is between 20 and 30\% of the daily energetic requirements for an active adult (estimated between 9360 kJ [3327 kcal] and 14,580 kJ [3485 kcal] per day). Because they are easy to process, this would have made tortoises a highly-ranked resource, but their slow growth and reproduction makes them susceptible to over-exploitation. Zoarchaeological abundance data show that during the ca. 75 ka (thousands of years) upper Still Bay M1 phase at BBC, tortoises contributed twice as many calories to the diet relative to ungulates than they did during the ca. 100 ka lower M3 phase. However, in spite of the abundance of their fossils, their absolute caloric contribution relative to ungulates remained modest in both phases. At the end of the site’s MSA occupation history, human subsistence strategies shifted to emphasise high-return large hunted mammals, which likely precipitated changes in the social roles of hunters and gatherers during the Still Bay.

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\textbf{Introduction}

Research on the African Middle Stone Age (MSA) is often embedded within larger questions of the origins of modern human behaviour. The MSA commenced by ca. 285,000 years ago in East Africa and the Horn (Tryon and McBrearty, 2002; Tryon and McBrearty, 2006; Morgan and Renne, 2008). In South Africa, technological elements of the MSA appear as early as ca. 500 ka (thousands of years ago) (Porat et al., 2010; Wilkins and Chazan, 2012; Wilkins et al., 2012), and disappear as recently as 20 ka (Clark, 1999). In central and southern Africa, deposits dating especially to the final 100 ka of the MSA have yielded evidence for the emergence of important behaviours shared by all modern hunter-gatherers. These include symbolism, social complexity, technological complexity using a variety of raw materials, and flexible foraging strategies (Wurz, 1999; McBrearty and Brooks, 2000; Barham, 2001; Deacon, 2001; Wadley, 2001; Henshilwood et al., 2002; Henshilwood and Marean, 2003; d’Errico et al., 2005; Henshilwood, 2007; Marean et al., 2007; d’Errico et al., 2008; Brown et al., 2009; Henshilwood et al., 2009; Texier et al., 2010; Watts, 2010; Henshilwood et al., 2011; Henshilwood and Dubreuil, 2011; Wadley et al., 2011; Brown et al., 2012; d’Errico et al., 2012; McCall and Thomas, 2012; Nash et al., 2013; Vanhaeren et al., 2013).

A widely-discussed aspect of modern human origins has been how important changes in human behaviour may have been reflected in or perhaps facilitated by changes in diet, subsistence, and...
foraging efficiency. Some researchers initially argued that MSA people exploited resources less effectively and were less capable hunters than their Later Stone Age (LSA) successors (Binford, 1981, 1984; Klein, 1994, 1995; Klein and Cruz-Uribe, 1996; Klein, 1998, 2000; Klein et al., 2004; Avery et al., 2008; Klein, 2009; Weaver et al., 2011). More recent work has indicated that MSA people had an unrestricted hunting ability (Milo, 1998; Marean et al., 2000; Faith, 2008; Dusseldorp, 2010; Thompson, 2010a; Thompson and Henshilwood, 2011). Such work has also examined the possibility that small ungulate trapping and snaring reflected technological subsistence solutions as complex as those used by modern people (Clark and Plug, 2008; Wadley, 2010; Clark, 2011).

Much of this research has emphasised the dietary contributions of ungulates, although small fauna such as tortoises are also commonly — sometimes more commonly — preserved. Because tortoises would have provided protein, fat, and other ‘animal’ resources in a ‘collectable’ package, their fossils should provide insight into the subsistence behaviour of individuals within MSA groups that had limited hunting ability (e.g., pregnant, lactating, or menstruating women, children, the elderly, or the infirm). 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 highlight changes in resource use within the MSA, allowing productive questions about human demography, prey choice, and adaptability to be explored.

This study quantifies the relative dietary contributions of tortoises and ungulates at the site of Blombos Cave (BBC), Western Cape, South Africa (Fig. 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 nutritional literature provide the basis for establishing how the two faunal groups were ranked in the diet, and zooarchaeological data show how they were actually exploited. This provides a platform for investigation of overall foraging strategies, site occupation intensity, and the role of both hunters and gatherers within the MSA.

**Blombos Cave**

Blombos Cave is located on the southern coast of South Africa, approximately 300 km east of Cape Town (Fig. 1). Excavations between 1992 and 2009 uncovered a stratified sequence of LSA and MSA deposits (Henshilwood et al., 2001a, 2009). The MSA levels at BBC are divided into four phases: M1, upper M2, lower M2, and M3. These have been dated using thermoluminescence (TL), optically stimulated luminescence (OSL), electron spin resonance (ESR) and thorium/uranium to between ca. 75 to >130 ka (Jones, 2001; Henshilwood et al., 2002; Tribolo, 2003; Jacobs et al., 2003a,b; Jacobs et al., 2006; Tribolo et al., 2006; Henshilwood et al., 2011; Jacobs et al., 2013). Summaries of the chronology of the BBC deposits, their associated ages, material culture, and site layout are provided in Table 1 and Fig. 2.

The taxonomic composition of the BBC MSA faunal remains has been previously reported by Henshilwood et al. (2001a) and taphonomic work has been reported by Thompson and Henshilwood (2011). Bovids dominate the large mammal sample, with small size 1 ungulates such as grysbok/steenbok (Raphicerus spp.) very common in the M3 and Upper/Lower M2 phases but with more representation of larger ungulates in the M1 phase. Across ungulate body size classes, MSA people are implicated as the primary accumulators, with perhaps slightly less human input of small

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**Figure 1.** Modern distribution of *Chersina angulata* (Hofmeyr, 2009), showing location of Blombos Cave and other sites mentioned in the text. BBC — Blombos Cave, DRS — Diepkloof Rock Shelter, YSF1 — Ysterfontein 1 (YFT1), DK1 — Die Kelders Cave 1, BNK1 — Byneskranskop 1, BPA — Boomplaas Cave, PP13B — Pinnacle Point 13B, KRM — Klasies River Mouth. Topographic data are SRTM data.
Table 1  
Summary of ages (a) and material culture (b) associated with the BBC stratigraphy.

<table>
<thead>
<tr>
<th>Phase</th>
<th>Age (ka)</th>
<th>Method</th>
<th>Details</th>
<th>Material culture citations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sterile Sand</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BBC M1</td>
<td>68 ± 4</td>
<td>OSL</td>
<td>Demonstrates separation between LSA and MSA layers</td>
<td>Henshilwood et al., 2002; Jacobs et al., 2003a,b; Jacobs et al., 2006</td>
</tr>
<tr>
<td></td>
<td>73 ± 3</td>
<td>OSL</td>
<td>Pressure-flaked bifacial foliate points made mainly on heat-treated silcrete</td>
<td>Henshilwood and Sealy, 1997; Henshilwood et al., 2001a; d’Errico and Henshilwood, 2007</td>
</tr>
<tr>
<td></td>
<td>67 ± 7</td>
<td>TL</td>
<td>Formal and informal tools</td>
<td>Henshilwood et al., 2002; Henshilwood et al., 2009; Henshilwood et al., 2011</td>
</tr>
<tr>
<td></td>
<td>81 ± 10</td>
<td>OSL</td>
<td>None</td>
<td>Henshilwood et al., 2001b</td>
</tr>
<tr>
<td></td>
<td>77 ± 8</td>
<td>OSL</td>
<td>Sold specimens</td>
<td>Henshilwood et al., 2001b; Henshilwood et al., 2009</td>
</tr>
<tr>
<td></td>
<td>68 ± 6</td>
<td>TL</td>
<td>Taphonomic histories.</td>
<td>Henshilwood et al., 2004; d’Errico et al., 2005; Henshilwood et al., 2009; Vanhaeren et al., 2013</td>
</tr>
<tr>
<td></td>
<td>82 ± 4</td>
<td>OSL</td>
<td>Works as prey items</td>
<td>As above</td>
</tr>
<tr>
<td></td>
<td>81 ± 4</td>
<td>TL</td>
<td>Works as prey items</td>
<td>Henshilwood et al., 2009; Henshilwood et al., 2011</td>
</tr>
<tr>
<td></td>
<td>76 ± 5</td>
<td>OSL</td>
<td>Works as prey items</td>
<td>Henshilwood et al., 2009</td>
</tr>
<tr>
<td>BBC M2 Upper</td>
<td>94 ± 3</td>
<td>OSL</td>
<td>Ochre-processing workshop and first recorded use of a container and a pigmented compound</td>
<td>Henshilwood et al., 2001b (hearts and ochre); Henshilwood 2009; Henshilwood et al., 2011 (ochre workshop); Henshilwood, 2012</td>
</tr>
<tr>
<td>BBC M3</td>
<td></td>
<td>U/Th</td>
<td>Ochre</td>
<td>Henshilwood et al., 2001b (hearts and ochre); Henshilwood 2009; Henshilwood et al., 2011 (ochre workshop); Henshilwood, 2012</td>
</tr>
<tr>
<td>BBC M2 Lower</td>
<td>85 ± 6</td>
<td>U/Th</td>
<td>Ochre</td>
<td>Henshilwood et al., 2009</td>
</tr>
<tr>
<td></td>
<td>76 ± 7</td>
<td>OSL</td>
<td>Ochre</td>
<td>Henshilwood et al., 2009</td>
</tr>
<tr>
<td></td>
<td>97 ± 4</td>
<td>OSL</td>
<td>Ochre</td>
<td>Henshilwood et al., 2009</td>
</tr>
<tr>
<td></td>
<td>101 ± 4</td>
<td>OSL</td>
<td>Ochre</td>
<td>Henshilwood et al., 2009</td>
</tr>
<tr>
<td></td>
<td>&gt;92</td>
<td>OSL</td>
<td>Ochre</td>
<td>Henshilwood et al., 2009</td>
</tr>
</tbody>
</table>

Tortoises as prey items

In South Africa, tortoise remains are found in archaeological deposits ranging from Middle Pleistocene to historic sites (Cruz-Uribe and Schrire, 1991; Klein et al., 1999). They are common in both MSA and LSA sites in the Western Cape, for example reaching densities of 49–304 individuals/m³ at the LSA site of Byneskranskop (BNK) and 3–18 individuals/m³ at the LSA/MSA site of Die Kelders Cave 1 (DK1) (Cruz-Uribe and Schrire, 1991). Several MSA sites in the Western Cape of South Africa, such as Ysterfontein 1 (YFT1), Diepkloof Rock Shelter (DRS), Boomplaas Cave (BPA), DK1, and BBC have produced large tortoise assemblages where, in many cases, they outnumber other faunal classes in terms of number of identified specimens (Klein and Cruz-Uribe, 2000; Henshilwood et al., 2001a; Klein et al., 2004; Faith, 2011; Steele and Klein, 2013).

The nutritional values of small faunal components have been estimated for several Holocene sites in South Africa (Buchanan, 1986, 1988), and tortoises were argued to have been an important terrestrial component to the early Holocene diet. However, in the MSA their analysis has been restricted mainly to their demographic, rather than subsistence, implications. Specifically, decreasing tortoise and shellfish sizes from the Middle to Later Stone Age in South Africa have been used to argue for increased predation pressure from growing human populations (Klein, 1978; Klein and Cruz-Uribe, 2000; Klein et al., 2004).

Decreasing tortoise size from the Middle to Upper Palaeolithic has also been argued to indicate increasing human populations in the Mediterranean region (Stiner et al., 1999, 2000), which shares many environmental similarities with the southwest coast of South Africa (Cowling et al., 1996). Here, tortoises are also a consistent component of faunal assemblages from the Middle Pleistocene to the Holocene (Blasco et al., 1986; Stiner et al., 2000; Speth and Tchernov, 2002; Blasco, 2008; Blasco and Fernández Peris, 2012a). However, in the Mediterranean Basin the subsistence implications...
of tortoise exploitation have also been examined in detail, especially through use of optimal foraging theory and diet breadth models (Stiner et al., 1999, 2000; Stiner, 2001; Stiner and Munro, 2002; Munro and Atici, 2009; Blasco and Fernández Peris, 2012a,b).

Under a diet-breadth model, prey are ranked according to their net return, which is their caloric value minus the energetic costs of their acquisition and processing, or search and handling costs (Winterhalder and Smith, 2000; Bird and O’Connell, 2006). From this perspective, resources are included in the diet depending on their ranking. Those with higher returns are always taken on encounter, while lower-ranked resources may be bypassed. Expansion in diet breadth occurs when people begin to exploit lower-ranked resources, often because encounter rates with more highly ranked resources have become unsustainably low. In the Mediterranean Basin, diet breadth was narrow during the Middle Palaeolithic, although tortoises were consistently taken. Diet breadth expanded in pulses toward the end of the Middle Palaeolithic and into the Upper and Epi-Palaeolithic, which has been interpreted as further evidence for increased human population sizes beginning at the end of the Middle Palaeolithic (Stiner et al., 1999, 2000).

There has often been an assumption that prey body size is the main determining factor in hunter decision-making, with animals of a larger body size being most highly ranked (Bayham, 1979; Broughton, 1994ab; Dusseldorp, 2010). Madsen and Schmitt (1998) have challenged the simplicity of this assumption by suggesting that mass collecting of small prey can result in return rates comparable with those of large fauna, although Ugan (2005) has found that individual handling costs of processing small birds and mammals remain high regardless of the mode of collection. Models of prey returns and energetic costs of transport have shown that large mammals will always provide greater returns than small fauna even if long transport distances are involved, except when the smaller resource has very low processing costs (Grimstead, 2010). Bird et al. (2009) has shown that in some environments body size is positively correlated with prey mobility, but inversely correlated with pursuit success and is therefore not always an appropriate archaeological measure of prey ranking. Hockett and Haws (2003, 2009) have further suggested that dietary diversity is nutritionally advantageous in its own right and thus diet-breadth models are not universally applicable.

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

These issues are examined archaeologically at BBC through combined analyses of tortoise and ungulate remains. Here, the ranking of the two faunal subsets relative to one another in the MSA diet is investigated by first establishing their respective caloric returns. The intensity of their exploitation is then inferred at BBC by combining the nutritional data and zooarchaeological abundance data. Against the backdrop of modern human origins research, the relative importance of ‘hunted’ and ‘collected’ fauna in the MSA is then discussed within this quantitative framework.
Materials and methods

The BBC archaeological collections are curated at the Iziko South African Museum in Cape Town and the data in this research were collected there. Taphonomic, taxonomic, and skeletal element abundance (SEA) data were collected from the M1 phase (the uppermost layers, CA/NA), with additional SEA data collected from the M3 sample (also the uppermost layers of this phase, CH/CI). A modern skeletal collection was used to identify each specimen >1 cm in the maximum dimension to taxonomic affinity, element, and side to the greatest extent possible. Skeletal element abundances were evaluated using the Number of Identified Specimens (NISP) and the Minimum Number of Elements (MNE); the highest count on the latter provided the Minimum Number of Individuals (MNI). Because identifiable tortoise elements fragment in consistent portions and at consistent landmarks compared with mammals, the fraction-summation approach was a time-effective and accurate means of estimating the MNE and MNI (Marean et al., 2001), and was used for both limb and shell elements. The total NISP sufficiently identifiable to be used for MNE calculation was 3562 from M1 and 727 from M3 (Table 2), available from a total analysed sample of 8657 and 1029, respectively.

The ungulate sample was drawn from analysis of all large mammal postcranial fragments (>4.5 kg live body weight [LBW]).
exceeding 2 mm in the maximum dimension that had been recovered during the 2000, 2002, and 2004 excavation seasons, for a total NISP of 3879 from M1 and 1256 from M3 (Thompson and Henshilwood, 2011). The subsample sufficiently identifiable to element, side, and body size to be used in MNE estimates comprised a NISP of 440 (M1) and 110 (M3). Because the tortoises were so numerous, analysis could only be done for a smaller area of deposit than was possible for the mammals; approximately 4.3 times less for M1 and 3.1 times less for M3. If the sample of large mammal data was restricted for analysis to only the same excavated contexts from which tortoise data were available, then the NISP appropriate for MNE analysis was 259 and 60 for M1 and M3, respectively. Data for both sample sizes are provided in Table 3.

In faunal assemblages, MNE data quickly demonstrate an MNI of one because it only takes a single specimen to represent an individual animal. In highly fragmented assemblages, the MNE and MNI thereafter increase slowly relative to total NISP because it is more difficult to prove fragments are not from the same individual (Lyman, 2008). In less fragmented assemblages, or at sufficient sample sizes, NISP and MNE increase in tandem (Grayson and Frey, 2004). The ungulate assemblage from BBC is highly fragmented (Thompson and Henshilwood, 2011), but for tortoises the NISP: MNE ratio is nearly 1:1 (Thompson and Henshilwood, 2014). Therefore, MNI data from a smaller sample of deposit are more likely to over-represent ungulates relative to tortoises than would be the case with a larger sample. Assuming a random distribution of faunal remains across the site, the numbers of tortoises should increase as a factor of the amount of deposit sampled. This is supported by the high numbers of conjoining tortoise elements and their close spatial proximity, indicating that the remains of single individuals are not widely distributed across the site. To take full advantage of the available sample of large mammal data, the number of tortoises that should be present in the same amount of deposit was therefore also estimated by multiplying the tortoise MNI by 4.3 for M1 and 3.1 for M3.

Mammal specimens identifiable to individual element were drawn into the geographic information systems (GIS) image-analysis program developed by Marean et al. (2001). The MNE was estimated from these GIS images on the principle of overlaps: where two fragments overlap on a given element they cannot be from the same element (Marean et al., 2001). The advantages and drawbacks to this method are discussed in Lyman (2008) and Thompson and Henshilwood (2011).

Data were collated from the literature for key macronutrient (fat and protein) estimates for tortoises and for size 1, 2, 3, and 4 ungulates, following the bovid body size categories of Brain (1981). This provided a basis for understanding relative resource rankings. Given the body of data suggesting that MSA hunters were fully competent, it was assumed that complete (un-scavenged) carcasses were available to the group, and that each ungulate MNI represents a complete individual. The caloric estimates were multiplied by the MNI for their respective ungulate body size classes and the tortoise MNI within each phase to obtain a quantitative assessment of how many calories each faunal subset would have contributed to the diet, and thus its actual significance regardless of ranking. This facilitated discussions of the implications of changing contributions by hunters and gatherers within the group. Finally, published data for the daily nutritional requirements of hunter-gatherers were used to estimate the minimum number of people who could have been sustained for different periods of time at the site by the individuals identified in the BBC faunal assemblage.
Table 3
NISP and MNE counts for the identifiable ungulate sample that underlie the MNI estimates.

<table>
<thead>
<tr>
<th>Ungulate Size</th>
<th>BBC M1</th>
<th>BBC M3</th>
<th>BBC M1</th>
<th>BBC M3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NISP</td>
<td>MNE</td>
<td>Sample</td>
<td>NISP</td>
</tr>
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<td>2</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Cervical Vertebra</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Thoracic Vertebra</td>
<td>9</td>
<td>16</td>
<td>7</td>
<td>5</td>
</tr>
<tr>
<td>Lumbar Vertebra</td>
<td>2</td>
<td>5</td>
<td>7</td>
<td>5</td>
</tr>
<tr>
<td>Sacrum</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Rib</td>
<td>3</td>
<td>9</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Scapula</td>
<td>16</td>
<td>5</td>
<td>9</td>
<td>4</td>
</tr>
<tr>
<td>Humerus</td>
<td>16</td>
<td>5</td>
<td>11</td>
<td>3</td>
</tr>
<tr>
<td>Radius</td>
<td>14</td>
<td>3</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Ulna</td>
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<td>2</td>
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<td>1</td>
</tr>
<tr>
<td>Metacarpal</td>
<td>10</td>
<td>2</td>
<td>1</td>
<td>5</td>
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<td>10</td>
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<td>Femur</td>
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<td>Tibia</td>
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<td>Sacrum</td>
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<tr>
<td>Metatarsal</td>
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<td>0</td>
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</tr>
</tbody>
</table>

Data are provided for both the entire available ungulate sample and the subsample that was drawn from the same area of deposit as the tortoise data.
ungulate and tortoise remains in order to understand site occupation intensity and predation intensity.

**Results**

**Tortoise taxonomy, ecology, and macronutrient estimates**

The angulate tortoise (*Chersina angulata*) comprised more than 99.9% of the portion of the sample that could be identified to the family level or below. *Chersina* is a small to medium tortoise that does not exceed 250–300 mm in maximum length (*Branch, 1984; van Heezik et al., 1994; Hofmeyr, 2009*). It is currently distributed throughout the southwestern portion of South Africa and into southwestern Namibia (Fig. 1). Although monotypic, west and southern coast specimens are genetically distinct (*Daniels et al., 2007; McCall and Thomas, 2012*). They occur preferentially away from the interiors of both countries, but tolerate a broad range of habitats and are found in all of the major floral biomes of South Africa (*Boycott and Bourquin, 1988; Hofmeyr, 2009; Joshua et al., 2010*).

The species is monotypic and sexually dimorphic, with little phenotypic variation across its geographic distribution (*Van Den Berg and Baard, 1984*) and with males slightly larger than females (*Berry and Shine, 1980; Branch, 1984*). Populations normally contain a preponderance of adults (*Branch, 1984*). Males are significantly more active than females during the summer and spring (*Ramsay et al., 2002; Keswick et al., 2006*), when most fighting and courtship occurs.

The majority of complete skeletal elements from BBC were from adult tortoises, based on both their size and bone surface texture. In a study of body composition of four different species of tortoise, the shell weight comprised 31.3% ± 8.1% (15.9–48.9%; *n = 52*) of total body weight (*Kienzle et al., 2006*). The mean fat content found by *Kienzle et al. (2006)* was 2.7% ± 2.2% of dried matter (compared with aquatic turtles, with a mean fat content of 12.0 ± 4.6%, *n = 31*). A much earlier study found that in a sample of five gopher tortoises (*Gopherus polyphemus*) fat content was on average 13.4% of overall dried matter weight (*Pearse et al., 1925*), while more recent analysis of body composition of captive spur-thighed tortoises (*Testudo graeca*) found that lipid concentrations change throughout the lifespan (*Lapid et al., 2005*), reaching an equilibrium of around 7% when tortoises achieve a total body weight of approximately 170 g. Although none of the tortoise studies have specifically been on *Chersina*, an estimate of 7% is used here because the study by *Lapid et al. (2005)* had the most consistent experimental conditions. Within the body itself, tortoises therefore appeared to be lean sources of meat with fat proportions similar to or only slightly higher than those of wild game (*Crawford et al., 1970; Skinner and Louw, 1996; Crawford et al., 2010*).

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

Modern adult male *Chersina* are larger than females (*Branch, 1984*), with mean body weights (with shells) of 907 g for males and 815 g for females (*van Heezik et al., 1994*). Using the estimate of shell weight to body weight from *Kienzle et al. (2008)*, the average body mass without shell of an adult male tortoise should be approximately 623 g, and that of an average adult female approximately 560 g. Using the percentage body composition given by *Lapid et al. (2005)*, a male *Chersina* would yield 109 g of protein and 44 g of fat and an average female would yield 98 g of protein and 39 g of fat. This can be converted into kilojoules (kJ) or kilocalories (kcal) and quantitatively compared to the nutritive returns of ungulates commonly available to MSA hunters on the southern African coast.

It is significant to note that the caloric estimates for *Chersina* compiled from these data (3332 kJ/796 kcal) are a close match to the value of 3738 kJ/890 kcal reported for turtles exploited by hunter-gatherers in the Amazon Basin (*Hill et al., 1984*), and almost identical to the yield (3470 kJ/829 kcal) that would be calculated using caloric return data from the Australian turtle *Chelodina rugosa* (*Brand et al., 1983*). The figure calculated here updates that estimated by *Buchanan (1986)*, who used substantially lower estimates for edible body weight in *Chersina* than what current quantitative data would suggest for tortoises in general.

Carcass composition data are available for a variety of African ungulates, many of which are still consumed today as commercial game species (*Ferreira and Hoffman, 2001; Hoffman and Ferreira, 2004; van Zyl and Ferreira, 2004; Hoffman et al., 2005; Hoffman and Wiklund, 2006; Hoffman, 2008; Hoffman et al., 2009, 2010*). The nutritional quality of ungulates depends on their age, sex, health, and the region from which they derive. Table 4 provides a generalised comparison of the nutritional composition and caloric yields of adult *Chersina* to a smaller and a larger size 2 bovid.

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

The carcass composition analysis is used as an approximation of the percentages of available protein and fat in the edible tissues of a wild African ungulate. Females were found to have between 50 and 77% more proportional body fat than males (*van Zyl and Ferreira, 2004*). Because in the zooarchaeological record is it not normally possible to know the sex ratio of ungulates represented in the deposits, an average of males and females was used in calculating the total caloric contribution of the two macronutrients. Table 6 gives a summary of estimated macronutrient and caloric values for the four bovid size classes commonly found at African archaeological sites.

**Nutritional returns of tortoises relative to ungulates**

According to the 1985 Joint FAO—WHO—UNU Expert Consultation, one tortoise would comprise just over one-third of the requirements for an adult human female rural field worker (9360 kJ/2237 kcal) and meet about one-quarter of the energetic

<table>
<thead>
<tr>
<th>Table 4 Nutritional information from Chersina compared with smaller and larger size 2 Ungulates.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Chersina angulata</strong></td>
</tr>
<tr>
<td><strong>Male</strong></td>
</tr>
<tr>
<td>Mean live body weight (g)</td>
</tr>
<tr>
<td>Mean carcass weight (g)</td>
</tr>
<tr>
<td>Protein (g) per carcass</td>
</tr>
<tr>
<td>Fat (g) per carcass</td>
</tr>
<tr>
<td>kl from protein per carcass*</td>
</tr>
<tr>
<td>kl from fat per carcass**</td>
</tr>
<tr>
<td>Total kcal/kl of LWB</td>
</tr>
<tr>
<td>Total kcal/carcass</td>
</tr>
</tbody>
</table>

*1 g protein = 17 kJ.
**1 g fat = 38 kJ.

Data from *van Zyl and Ferreira (2004)*, because the springbok (*Antidorcas marsupialis*) and the blesbok (*Damaliscus dorcas*) are the smallest and largest species for which whole carcass data were measured in the same study and in equivalent ways by the same authors.
requirements of an adult human male engaged in heavy labour (14,580 kJ/3484 kcal). According to Sebastian et al. (2002), it would also meet just under one-third of the estimated caloric requirements for a hunter-gatherer (12,552 kJ/3000 kcal) and just under half the amount of their estimated daily protein intake (234–258 g depending on the relative proportions of animal and plant products in the diet). Although subsisting entirely on tortoises is unfeasible in the long-term (Speth, 2010), they would provide a useful daily source of protein and calories.

Net return estimates are essential for converting these simple caloric data into resource ranking data (Bird and O’Connell, 2006). Comprehensive search and handling times are provided by Hawkes et al. (1982), Hill et al. (1987), and summarised in Bright et al. (2002) for a variety of resource types available to South American Amazon and North American Great Basin hunter-gatherers. Absolute net returns for individual ungulate size classes are difficult to reconstruct archaeologically because: 1) zooarchaeological body size data represent a broad range of live body weights (Brain, 1981); 2) handling costs are dependent on available hunting/capture technology, which has to be inferred (Bright et al., 2002; Dusseldorp, 2012); and 3) transport costs vary depending on the size of the animal, distance to camp, number of carriers, and other archaeologically unknowable factors (Monahan, 1998; Lupó, 2006). However, the available resource return data can be used as a guide to estimate net and relative returns of ungulates and tortoises.

In the Amazon, total search and handling costs for a highly-ranked ungulate (the red brocket deer, Mazama americana, ~30 kg LBW) were summarised as returning 114,600 kJ (27,300 kcal) per handling hour (Hawkes et al., 1982). In contrast, mainly because of much-increased search costs, the next-ranked prey (the paca, Cuniculus paca, ~7.5 kg LBW) had a return of 29,249 kJ (6964 kcal)/hour. The estimate for the deer compares favourably with estimates for the American pronghorn antelope (Antilocapra americana, ~40 kg LBW) and mountain sheep (Ovis canadensis ~70 kg LBW), both at 131,500 kJ (31,450 kcal)/hour (Bright et al., 2002). Some data on handling costs of different-sized African ungulates are also available from the Hadza of East Africa, indicating that a size 4 animal takes approximately twice as long to field process as a size 2 animal (Lupó, 2006), even though the size 4 animal may have more than twice the body mass. This is in line with the general observation that smaller fauna demand higher handling costs relative to their returns (Bright et al., 2002; Ugan, 2005; Grimstead, 2010).

Quantitative data on tortoise handling times are lacking, but estimates can be made using other slow-moving prey such as armadillos (Dasypus novemcintus), which on encounter require about 12 min of handling when taken above ground (Hill et al., 1987). Using the tortoise caloric estimate from Table 6 of 3323 kJ/794 kcal, minimum on-encounter returns for tortoises should be at least 16,600 kJ (3967 kcal)/handling hour. The main processing costs for tortoises are in the cooking and shell breakage, which do not involve any complex technology (Klein and Cruz-Uribe, 2000). Thus, tortoise handling times are likely to be even lower than armadillos, perhaps by half, with high returns up to 33,000 kJ (8000 kcal)/handling hour. This places them well above the net returns reported for all plant foods and small-bodied animal foods in both the Amazon and Great Basin. They should therefore have been one of the highest-ranked ‘collectable’ terrestrial resources on the South African landscape and should have always been taken on encounter in spite of their small body sizes.

**Diet at Blombos Cave**

Tortoises amounted to about 4% (in M1) and 2% (M3) of the total calories from large mammal and tortoise resources combined (Table 7). As discussed, in small, fragmented samples, large-bodied fauna are likely to be over-represented relative to small-bodied fauna. Therefore, an estimate was also made by increasing...
The faunal evidence indicates that from M3 times to the Still Bay at BBC, there was a shift in overall subsistence strategy from one emphasising collectable resources (including ‘trappable’ small ungulates) to one that placed heavier emphasis on higher-return, hunted large mammal resources. This is supported by the abundance of Still Bay points and bone points in the M1 phase that show the investment of substantial effort in the manufacture and maintenance of hunting technology (Henshilwood et al., 2001b; d’Errico and Henshilwood, 2007; Villa et al., 2009). Small-bodied Neotragine ungulates do not live in large groups and are not suitable for monotonous mass drives, but may be obtained as part of more generalised communal net-hunting drives (Tanno, 1976; Bailey and Henshilwood, 2007; Villa et al., 2009). The returns from this activity are believed to be extremely low, at between 879 and 2238 kJ (210–535 kcal)/handling hour (Ugan, 2005). Overall returns should be higher if small ungulates were instead captured in traps as has been suggested at Sibudu Cave (Wadley, 2010), or individually hunted, but still much lower than hunting large-bodied ungulates. At the same time that shifts were occurring in ungulate exploitation, shellfish gathering was lessened by increased distance to the coast, making tortoise collecting a more important resource for the gatherers in the group.

Sustained predation by humans has been suggested in both South African and Mediterranean contexts to have led to size diminution in tortoises, followed by increased emphasis on alternate resources (Klein and Cruz-Uribe, 1983, 2000; Stiner et al., 1999, 2000; Stiner, 2006; Steele and Klein, 2013). This is mainly because tortoises reproduce slowly (Stiner and Kuhn, 2009). Chersina are no exception, laying only one egg every six months to a year (Branch, 1984). Despite low fecundity, a model of population increase has

tortoise numbers as a factor of the amount of sampled deposit to match the larger available ungulate sample (4.3 times larger for M1 and 3.1 times larger for M3). In this case, tortoises amounted to 12% (in M1) and 5% (in M3) of the total calories. Both estimates show that tortoises were a small but persistent component to the diet. If small mammals and shellfish were also eaten, then the total contribution from tortoises to the animal portion of the diet would become even smaller, in spite of their large quantities of remains in terms of NISP.

The MNI data also provide an estimate of the minimum number of nutrition-days available from tortoises and ungulates at BBC. Table 7 uses the daily calorific requirement for a hunter-gatherer of 12,552 kJ/3000 kcal and the calorie estimates from the larger sample of deposit to estimate scenarios of a diet of animal products only, a 55% animal-to-plant diet, and a 35% animal-to-plant diet (in M1) and 5% (in M3) of the total calories. Both estimates show that tortoises were a small but persistent component to the diet. If small mammals and shellfish were also eaten, then the total contribution from tortoises to the animal portion of the diet would become even smaller, in spite of their large quantities of remains in terms of NISP.

### Table 7

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

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

### Table 8

Estimates of the number of days different-sized groups could have been resident at BBC and sustained by the tortoise and ungulate resources represented in the deposits.

<table>
<thead>
<tr>
<th>Phase</th>
<th>No. of days</th>
<th>1 Person</th>
<th>5 People</th>
<th>10 People</th>
<th>15 People</th>
<th>20 People</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M1</td>
<td>M3</td>
<td>M1</td>
<td>M3</td>
<td>M1</td>
<td>M3</td>
</tr>
<tr>
<td>Meat only</td>
<td>Mammal</td>
<td>634</td>
<td>217</td>
<td>127</td>
<td>43</td>
<td>63</td>
</tr>
<tr>
<td></td>
<td>Tortoise</td>
<td>84</td>
<td>12</td>
<td>17</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>All</td>
<td>718</td>
<td>229</td>
<td>144</td>
<td>46</td>
<td>72</td>
</tr>
<tr>
<td>55% Animal energy</td>
<td>Mammal</td>
<td>1787</td>
<td>613</td>
<td>357</td>
<td>123</td>
<td>179</td>
</tr>
<tr>
<td></td>
<td>Tortoise</td>
<td>238</td>
<td>32</td>
<td>48</td>
<td>6</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>All</td>
<td>2025</td>
<td>645</td>
<td>405</td>
<td>129</td>
<td>202</td>
</tr>
<tr>
<td>35% Animal energy</td>
<td>Mammal</td>
<td>2445</td>
<td>839</td>
<td>489</td>
<td>168</td>
<td>245</td>
</tr>
<tr>
<td></td>
<td>Tortoise</td>
<td>326</td>
<td>44</td>
<td>65</td>
<td>9</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>All</td>
<td>2771</td>
<td>883</td>
<td>554</td>
<td>177</td>
<td>277</td>
</tr>
</tbody>
</table>
indicated that *Chersina* can achieve rapid population increase — up to a 600× increase within 75 years in the face of minimal predation (van Heezik et al., 1994). This has also been found to be the case in other tortoise species, even with natural predation taken into account (Hailey, 2000; Marlowe, 2005), and chelonian population sizes and biomasses are normally much higher in a given area than mammalian vertebrates (Verson, 1982). Therefore, while tortoise populations would be unable to handle sustained long-term predation in a given area, they could rebound consistently if exploitation occurred in pulses of a half-century or more.

Population density estimates of introduced angulate tortoises on Dassen Island range from 31 to 34 tortoises/ha (van Heezik et al., 1994), and on mainland pasture in the Eastern Cape between 21 and 38 tortoises/ha (Branch, 1984). These are much different from the estimates of 6.68 tortoises/ha in mixed Fynbos scrub (Stuart and Meakin, 1983), and 0.12 tortoises/ha in the Thicket Biome of the Eastern Cape (Mason et al., 2000). Thus, the sustainability of tortoise populations — and the reliance of human groups on this resource — would be determined by both human population sizes and existing local ecological conditions. Given the rebound potential of *Chersina* populations around BBC, ephemeral occupations at the timescales represented in the deposits should not have affected them. Therefore, their greater abundances but smaller sizes during the M1 phase suggest a relatively short, intensive period of site use. The data also show that just prior to site abandonment, MSA people at BBC experienced declines in the returns from two of their major collectable animal resources: first shellfish, with increasing distance to the coastline, then later tortoises, with decreasing encounter rates and smaller sizes. The combination of environmental change and exploitation of key local resources first led to increased emphasis on hunting and hunting technology and later complete site abandonment.

At the nearby site of Pinnacle Point 13B (PP13B), changing abundances of shellfish track changes in sea levels (Marean et al., 2007; Jerardino, 2010), showing another example of how human subsistence changed in concert with coastlines at a single site during the MSA. Although there were few tortoises overall at PP13B, tortoise remains were also approximately twice as abundant relative to large mammals during MIS 6 — a cool to cold period — than they were during MIS 5 — a cool to very warm period (Thompson, 2010a). Data from BBC and PP13B together suggest that during warmer periods where sea levels were closer, MSA people on the southwestern coast collected many shellfish and few tortoises. As sea levels retreated, tortoises were more often substituted as a source of collectable protein.

The low incidences of tortoises at coastal MSA sites further east from BBC, such as PP13B (Thompson, 2010a) and KRM (Klasies River Mouth) (Klein and Cruz-Uribe, 1987) indicate that tortoises were not common in these areas during the MSA. This is because tortoises were a high-ranked resource and should have been taken on encounter, and encounter rates would have had to have been extremely low or encounter rates with more productive resources extremely high to drive them out of the diet completely (Byers and Ugan, 2005). These patterns are explicable in terms of optimal foraging theory, but the consequences of shifting subsistence strategies would have also had social implications for the MSA groups experiencing them.

**Hunters and gatherers in the archaeological record at BBC**

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

In spite of the nutritive composition of gathered animal resources, and even in societies where gathered foods are abundant and reliable, the contributions of hunters are often considered more valuable both nutritionally and in terms of status than the contributions of gatherers (Hawkes et al., 1982; Kaplan and Hill, 1985a; Hill et al., 1987; Hawkes and Bliege Bird, 2002; Leisa et al., 2003; Marlowe, 2004). There can also be substantial variability in how the returns of large-game hunting are distributed amongst the total group (Hawkes, 1993; Patton, 2005). Because of the additional burdens of pregnancy and lactation, the caloric requirements of hunter-gatherer women can approach those of men (Hill et al., 1984), and pregnant and lactating women require approximately seven to ten additional grams of protein per day (Consultation, 1985). These two categories, as well as young children, have additional need for many micronutrients as well (Ladipo, 2000; Osendarp et al., 2007). Many of these, such as iron, vitamin B12, niacin, and zinc are not concentrated in animal products (Williams, 2007). Therefore, these are the population subsets least able to participate in big-game hunting.

The amount of group coordination required to hunt and process large ungulates presents an immediate, visible, and high output of both investment and return, but a high potential failure rate. In modern hunter-gatherers, hunting is a task that falls most commonly to adult men (Brown, 1970; Lee, 1979; Jochim, 1988; Hawkes et al., 1991; Hurtado et al., 1992; Brightman, 1996; Bird, 1999; Bliege Bird et al., 2001). A review of the ethnographic literature with a particular focus on South Africa has shown that women also provide a great deal of meat resources through less-prestigious activities such as snaring, trapping, and collecting of shellfish (Wadley, 1998). For at least some hunter-gatherer groups, provisioning from older, post-reproductive females is one of the most important sources of nutrition for a family unit (Hawkes et al., 1998; Hill and Hurtado, 2009).

It is difficult to know when the division of subsistence labour may have started in human prehistory (Kuhn and Stiner, 2006), or how it may have been manifested in past societies (Waguespack, 2005). However, because of the biological limitations of reproduction and ageing, it is certain that not all group members would have been able to participate in the increased emphasis on big-game hunting that is inferred for Still Bay times. Although collected resources may be shared amongst the group, women and children in modern societies have been shown to have access to a greater percentage of collected resources than men (Kaplan and Hill, 1985b). Exploitation of tortoises by these individuals would have provided an advantageous dietary supplement in terms of protein, fat, and micronutrients at a relatively low cost. If hunters were economically rather than socially motivated, then tortoises should also have been taken by them, because they should not have ignored prey with such high returns unless encounter rates with large ungulates were extremely high (Byers and Ugan, 2005). However, because large mammal hunting requires greater mobility than collecting, and because tortoises can be processed quickly by individual people, the evidence of these encounters was likely not as often preserved at BBC as the evidence of encounters by collectives with closer foraging radii.

Klein and Cruz-Uribe (2000:190) have also suggested that tortoises offer a window into the changing contributions of hunters and gatherers. They conclude that the changes in body size observed in tortoises at DK1 may indicate “...either a change in the
season(s) of the year when the site was occupied or perhaps a
difference in the division of human labour by age and sex.” Here, we
argue that the change in tortoise size is attributable to increased
exploitation by gatherers during Still Bay times, when shellfish
became less accessible and more able-bodied members of the
group became more invested in big-game hunting. In addition to
increased evidence for hunting technology in the Still Bay, these
deposits have the most abundant evidence for symbolic and/or
ritual behaviour in the form of worked and incised ochre, and shell
beads. Changes in subsistence contributions via hunting and col-
lecting resulted in some division of subsistence labour, regardless of
if it was strictly along gender lines as seen in modern groups. Dif-
ferential access to resources within the group may have followed,
producing a restructuring of social roles reproduced within the
material culture record at BBC.

Summary and conclusions

Modern human origins research in South Africa now allows the
diversity and chronology of MSA lifeways to be explored at an
unprecedented level of detail, revealing variability within a time
period that had previously appeared to be somewhat static
(Lombard and Clark, 2008; Wadley, 2010; Thompson, 2010b; Wurz,
2012). It has also resulted in the recovery of large, well-dated faunal
assemblages associated with some of the earliest or most
convincing examples of modern behavioural complexity (Marean
et al., 2007; Clark and Plug, 2008; Wadley, 2010; Thompson,
2010a; Clark, 2011; Thompson and Henshilwood, 2011; Dusseldorp,
2012; Steele and Klein, 2013). Within this body of
work there has been differential emphasis on the significance of
big-game hunting ability, although recent research has begun to
also explore small ungulate acquisition (Clark and Plug, 2008;
Wadley, 2010). This theme of ungulate research extends even to
diet breadth models, which remain restricted to
within larger mammal taxa rather than considering the suite of other faunal
remains that are often found in the same deposits as the ungulates
(Dusseldorp, 2012). Part of the problem is taphonomic because
plants from this time period are mainly represented by the charred
remnants of fuel or bedding, rather than subsistence resources
(Wadley et al., 2011; Cartwright, 2013; Miller et al., 2013). A new
approach is taken here: to examine ungulate and tortoise data
together from the same deposits so that both ‘hunted’ and
‘collected’ resource types can be explored in the contexts of human
subsistence and social behaviour.

Chersina angulata, the angulate tortoise, comprises the vast
majority of tortoise remains. Quantitative estimates of the nutritive
returns for Chersina relative to ungulates of body size classes
commonly recovered from MSA sites show that it takes approxi-
mately nine tortoises to comprise the nutritive value of a single
size 1 ungulate, and over 500 to comprise the nutritive value of a single
size 4 ungulate. During the M1 (Still Bay) phase, tortoises accounted
for approximately twice the relative amount of calories as in the M3
phase. However, in spite of their abundances in terms of NISP their
actual caloric contribution to both phases was relatively small.

During Still Bay times, large ungulates were more commonly
taken than small ungulates, and shellfish were not as easily
accessible because of retreating coastlines. This, along with the
accompanying material culture, shows a shift in subsistence to
emphasise high-return resources rather than those that are easily
snared, collected, or trapped. Because tortoises are easy to process,
they remain a highly-ranked resource and the frequency of their
gathering increased during Still Bay times as access to shellfish
decreased. Populations of Chersina are quickly impacted by intense
predation but can rebound on half-century timescales, so the
decreasing mean size of tortoises during the final MSA occupation
phase suggests that site occupation was relatively brief and intense
rather than prolonged and ephemeral (Henshilwood et al., 2001a).

Henshilwood et al. (2001a:438) state that “Among herbivores
on which people could depend, the most abundant was probably the
angulate tortoise”. Tortoises were a ‘baseline’ source of essential
macro- and micronutrients, especially important for individuals in
the group who may not have had regular access to hunted re-
sources when big-game hunting was a focus within the group’s
subsistence regime. Regardless of whether a fully modern gendered
division of labour was in place in the MSA, access to collectable
animal resources would have been particularly advantageous for
pregnant and lactating women, children, and the elderly or infirm.
This study has quantitatively confirmed that tortoises were a
highly-ranked and reliable part of the resource landscape over
time, but also shows that their role changed within the overall
subsistence approach as big-game hunting became more important
during Still Bay times. Human behaviour in the MSA was flexible,
responding to changes in the environment and resource base
through adoption of new foraging strategies, innovation of sub-
sistence technologies, and restructuring of social roles.

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