Rhinoceros from the Middle Stone Age in the Eastern and Western Cape of South Africa

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Abstract

In southern Africa, the Middle Stone Age (MSA), spanning more than 200,000 years, is a critical time period, in which *Homo sapiens* first appears. MSA sites located in the Eastern and Western Cape provinces of South Africa have yielded extensive faunal assemblages accumulated by anatomically modern humans. Many of these faunal assemblages include evidence of rhinoceros. To investigate how rhinoceros were potentially hunted/scavenged, we compare the representation of rhinoceros with that of large bovids and zebras in these faunal assemblages across seven sites in the region. All sites contain individual specimens of rhinoceros; however most faunal assemblages yielded only a few isolated specimens (201 specimens in total, representing 5% of the total sample). Similarly low representation was found for elephant and hippopotamus. In total, 60% of all the remains of rhinoceros accumulated during the MSA were found at a single site, Die Kelders. This indicates that people rarely brought back portions of rhinoceros carcasses containing bones to cave and shelter sites. The low frequency of rhinoceros findings suggests that people either did not regularly hunt or scavenge carcasses of these large ungulates, which are known for their aggressive behaviour; or, due to their large size inhibiting portability, they camped and feasted on rhino carcasses at sites where the animals were killed. In the latter scenario, meat containing a few bones could have been dried and brought to caves.

Résumé

En Afrique australe, l'âge de pierre moyen (MSA), qui s'étend sur plus de 200 000 ans, est une période critique, au cours de laquelle *l'Homo sapiens* apparaît pour la première fois. Les sites MSA situés dans les provinces du Cap oriental et occidental en Afrique du Sud ont produit de vastes assemblages fauniques accumulés par des humains anatomiquement modernes. Beaucoup de ces assemblages fauniques contiennent des preuves de rhinocéros. Pour étudier comment les rhinocéros ont été potentiellement chassés / récupérés, nous comparons la représentation des rhinocéros avec celle des grands bovidés et zèbres dans ces assemblages fauniques sur sept sites de la région. Tous les sites contiennent des spécimens individuels de rhinocéros; cependant, la plupart des assemblages fauniques n'ont donné que quelques spécimens isolés (201 spécimens au total, représentant 5% de l'échantillon total). Une représentation également faible a été trouvée pour les éléphants et les hippopotames. Au total, 60% de tous les restes de rhinocéros accumulés pendant la MSA ont été retrouvés sur un seul site, Die Kelders. Cela indique que les gens rapportaient rarement des parties de carcasses de rhinocéros contenant des os dans des grottes et des abris. La faible fréquence des découvertes de rhinocéros suggère que les gens ne chassaient pas régulièrement ou ne récupéraient pas les carcasses de ces grands ongulés, qui sont connus pour leur comportement agressif; ou, en raison de leur

grande taille empêchant la portabilité, ils campaient et se régalaient de carcasses de rhinocéros sur les sites où les animaux étaient tués. Dans ce dernier scénario, la viande contenant quelques os aurait pu être séchée et amenée dans des grottes.

Introduction

The conservation of rhinoceros (*Diceros bicornis* and *Ceratotherium simum*) remains an ongoing concern in Africa, and numerous studies have focussed on biological and zoological aspects of these large pachyderms (for a summary, see Skinner and Chimimba 2005). In southern Africa, recent studies on rhinoceros increasingly make use of archaeological information to gain an understanding over greater time scales (Boeyens and Van der Ryst 2014). In this paper, we trace the potential exploitation of rhinoceros in South Africa during the Middle Stone Age (MSA), a critical time in the evolution of *Homo sapiens* spanning more than 200,000 years.

Hominins hunted and consumed megafauna throughout the Pleistocene. The nature of hunting by early humans during the MSA in southern Africa has long been debated. Initial research suggested that people of the MSA were mainly scavengers who engaged in limited hunting of small bovids, and that they were less competent than hunters of the Later Stone Age (Klein and Cruz-Uribe 1996). More recently, it has become widely accepted that people were able to successfully hunt large, dangerous prey like the extinct giant buffalo (*Syncerus antiquus*) during the MSA (Milo 1998).

The MSA is a cultural period that persisted from approximately 280 to 50 thousand years ago (kya) in Africa and is associated with the appearance of anatomically modern humans in southern Africa. Various innovations became widespread during the MSA, such as ornaments made from seashells and ostrich eggshells engraved with intricate patterns. These innovations are linked with greater cognitive ability in humans. A number of MSA sites have been excavated in the Eastern and Western Cape of South Africa, providing large archaeological faunal assemblages. Many of these sites are currently located at the coast, but during glacial events, areas now close to the coast were further inland during the MSA (Wadley 2015). At the time, the region mainly comprised extensive plains and marshes, ideal for hunting wild animals. From early historical accounts of both groups in South Africa (San hunter-gatherers and early historical farming communities), pits were often used to hunt pachyderms and buffalo (Andersson 1856:455; Hall 1977). These pits were often located near water sources and once trapped, a large dangerous animal could be dispatched with spears (Hall 1977). The practice of constructing such pits is thought to date back to the MSA (Milo 1998). In coastal areas, people in the MSA also likely scavenged carcasses of beached whales, similarly to historical accounts (Smith and Kinahan 1984); while circumstantial evidence, although ambiguous, suggests that they used snares to obtain meat of smaller animals (Wadley 2015). Many of the faunal assemblages from MSA sites in the Eastern and Western Cape of South Africa have yielded remains of large mammals, including rhinoceroses.

Rhinos are large ungulates, and today two species are found in South Africa. The black rhinoceros (*Diceros bicornis*) weighs between 800 and 1,400 kg and the white rhinoceros (*Ceratotherium simum*) weighs between 1,700 and 2,300 kg (Skinner and Chimimba 2005). The black rhinoceros occurred in the Eastern and Western Cape provinces during the Pleistocene and Holocene. During the Holocene, white rhinoceros were absent from the area (Plug and Badenhorst 2001; Rookmaaker 2008; Skead et al. 2007), but their skeletal remains have been found in various Pleistocene deposits of the Western Cape (Avery 2019) including Sea Harvest (Grine and Klein 1993), Duinefontein 2 (Cruz-Uribe et al. 2003), Hoedjiespunt 1 (Stynder 1997) and Swartklip 1 (Klein 1983).

Methodology

Several MSA faunal assemblages from the Eastern and Western Cape of South Africa have been studied, notably Blombos Cave, Die Kelders Cave, Diepkloof Rock Shelter, Klipdrift Shelter, Pinnacle Point, Ysterfontein Rock Shelter (all in the Western Cape), and Klasies River Main Site (Eastern Cape). These seven sites (Table 1, Fig. 1) fall broadly in the Cape Floristic Region, in which extensive scrublands are

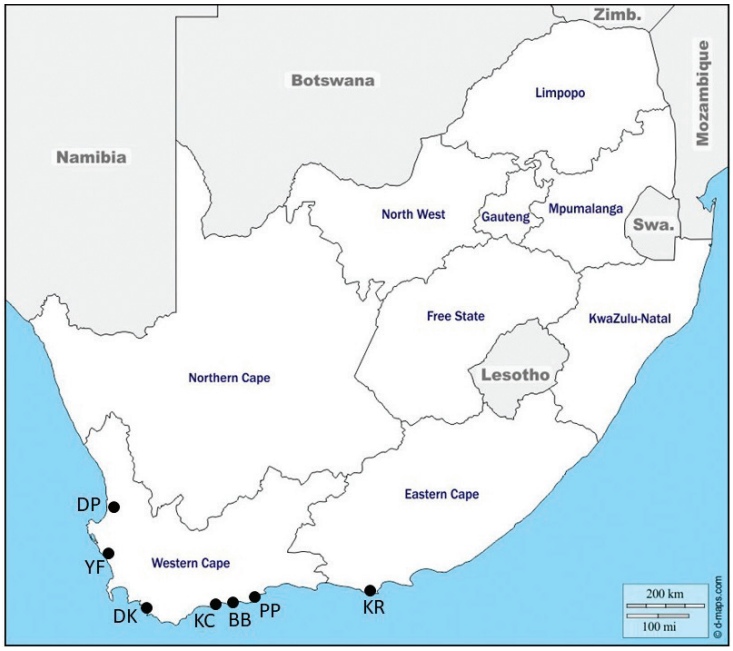

Figure 1. Location of MSA sites in the Eastern and Western Cape of South Africa (Map adapted from: https://d-maps.com/carte.php?num_car=4414&lang=en). YF (Ysterfontein), DK (Die Kelders), BB (Blombos Cave), DP (Diepkloof), PP (Pinnacle Point), KC (Klipdrift Shelter), KR (Klasies River).

Table 1. Faunal assemblages used in this study (also Wadley 2015 for dates)

Sites	Age Ranges (kya)	Reference(s)
Blombos Cave	(101 ± 4) – (73.3 ± 4.4)	Henshilwood et al. 2001; Badenhorst et al. 2016; Reynard and Henshilwood 2019
Die Kelders Cave	(79.7 ± 15.6) – (50.6 ± 4.6)	Klein and Cruz-Uribe 2000
Diepkloof Rock Shelter	107–46	Steele and Klein 2013
Klasies River Main Site Cave 1 and 1A	110–43	Van Pletzen et al. 2019
Klipdrift Shelter	(65.5 ± 4.8) – (59.4 ± 4.6)	Reynard et al. 2016
Pinnacle Point	174–35	Rector and Reed 2010
Ysterfontein Rock Shelter	(132.1 ± 8.0) – (120.6 ± 6.6)	Avery et al. 2008

interspersed with coastal forests, and thus have a relatively similar animal biodiversity (Skinner and Chimimba 2005), making the faunal assemblages suitable for comparative analysis. While there may have been some sporadic carnivore activity at these sites during the MSA, the vast majority of animal remains (from these sites) were collected by humans (Van Pletzen et al. 2019; Badenhorst et al. 2016). We used the faunal assemblages discovered at these sites for this study.

We grouped all rhinoceros remains (recorded as black rhinoceros, white rhinoceros, or indeterminate rhinoceros) from these sites together into a single category. In order to investigate the possible uses made of these large animals, we compared these data to data for large ungulates and zebras. The vast majority of large animal remains were large ungulates. Most of these were apparently hunted and then brought to cave and shelter sites by hominins during the MSA to be butchered and eaten. These large ungulates weigh from several hundred kilograms to more than one tonne. They belong to Bovid Size Class III and IV (Brain 1974). They include red hartebeest (*Alcelaphus buselaphus*), African buffalo (*Syncerus caffer*), giant

buffalo (*Syncerus antiquus*), eland (*Tragelaphus oryx*), kudu (*Tragelaphus strepsiceros*), black wildebeest (*Connochaetes gnou*), giant wildebeest (*Megalotragus priscus*) and waterbuck (*Kobus sp.*). We included all large ungulates identified to the genus or family level (e.g. *Alcelaphinae sp.*, *Alcelaphus/Connochaetes sp.*, etc.) and all those specimens identified as indeterminate Bovid Size Class III and IV (Brain 1974), as well as indeterminate remains described as Large and Very Large Bovids. Also included in this category are zebras (*Equus capensis*, *Equus quagga*, *Equus sp.*). Collectively, we refer to the above group as 'Large Bovids and Equids' (LBE).

The Number of Identified Specimens (NISP) is the preferred quantification method used by most zoo-archaeologists (Lyman 2008). All publications of faunal assemblages reported NISPs, except in the case of Klein's (1976) analysis of Klasies River Mouth, which was excluded from our calculations due to the use of the problematic Minimum Number of Individuals (MNI; Lyman 2008). However, we included the more recent analyses of fauna from the latter site (Van Pletzen et al. 2019; Reynard and Wurz 2020). We assumed all 'cf.' identifications (meaning 'possibly') were correctly assigned to the relevant species.

Results

Assemblages from all seven sites yielded remains of rhinoceros, except for those associated with recent analyses of samples from Klasies River Mouth (Table 2). However, the initial analysis from the latter site yielded remains of rhinoceros (Klein 1976). It can therefore be said that remains of rhinoceros are present in all the faunal assemblages. Overall, remains of rhinoceros only account for 5% of total specimens (i.e. rhinoceros plus LBE), based on analysis of 53 discrete samples from the seven sites shown in Table 1. The highest percentages of rhinoceros remains, are from samples at two sites, Ysterfontein Rock Shelter (44% of the total, from the 'Middle' component, dating to between 120 and 132 kya[1]) and Die Kelders (34% of the total from layer 'MSA 4/5', possibly dating to between 64 and 51 kya). However, the sample for Ysterfontein is small and, overall, the specimens from Die Kelders (n = 121) represent 60% of all rhinoceros remains identified from all MSA assemblages in the Eastern and Western Cape. These finding indicate that, in general, with the exception of Die Kelders (during the period corresponding to layer MSA 4/5) and Ysterfontein, few rhinoceros were brought back to cave sites in the Eastern and Western Cape during the MSA.

Most of the rhinoceros remains (from the MSA assemblages) were identified as black rhinoceros, which was found at Blombos Cave (Henshilwood et al. 2001; Badenhorst et al. 2016;), Ysterfontein (Avery et al. 2008), Klipdrift (Reynard et al. 2016), Pinnacle Point (Rector and Reed 2010), Klasies River (Klein 1976) and Die Kelders (Klein and Cruz-Uribe 2000). Indeterminate rhinoceros were identified at Blombos Cave (Henshilwood et al. 2001; Badenhorst et al. 2016; Reynard and Henshilwood 2019), Diepkloof (Steele and Klein 2013), Ysterfontein (Avery et al. 2008) and Die Kelders (Klein and Cruz-Uribe 2000), while white rhinoceros were found only at Die Kelders (Klein and Cruz-Uribe 2000). None of the studies listed above that identified rhinoceros remains provided details of the skeletal elements used for identification.

Thus, low numbers of rhinoceros remains were found in the MSA faunal assemblages from the Eastern and Western Cape. Similarly low numbers of remains are reported for other megafauna, namely hippopotamus (*Hippopotamus amphibius*) and elephant (*Loxodonta africana*), indicating that few remains of these species were brought back to cave sites by people during the MSA (Table 3). This is a notable result, since both hippopotamus and elephants occurred widely during the Holocene and Pleistocene over southern Africa, including the Eastern and Western Cape (Plug and Badenhorst 2001; Skinner and Chimimba 2005; Avery 2019).

Some additional faunal assemblages from the region were unambiguously collected largely by carnivores, and date to the Middle and Late Pleistocene (Table 4). Three of the assemblages, namely those from Boomplaas Cave, Pinnacle Point PP30 and Herolds Bay, lack remains of rhinoceros; while the largest number of rhinoceros remains in a carnivore assemblage was discovered at Swartklip. Overall, however, the representation of rhinoceros among large fauna in carnivore assemblages is similar to that found in anthropogenic faunal accumulations.

[1]Researchers use a variety of different terms to distinguish layers of remains they excavated, as shown in Table 2.

Table 2. Representation of rhinoceroses and Large Bovid and Equids (LBE), reported as Number of Identified Specimens (NISP), in anthropogenic MSA assemblages from the Eastern and Western Cape

Sites	Layer/Phase	Age (kya)	Rhino	LBE	Total	% rhino
Blombos	M1	(74.9 ± 4.3) – (73.3 ± 4.4)	18	418	436	**4**
	M2	(85 ± 6) – (75 ± 2)	6	203	209	**3**
	M3	(101 ± 4) – (94 ± 4)	5	219	224	**2**
Die Kelders	MSA 4/5	(63.9 ± 4.8) – (50.7 ± 4.7)	85	168	253	**34**
	MSA 6	-	27	576	603	**5**
	MSA 7	(75.3 ± 6.8) – (63.9 ± 7.0)	0	13	13	**0**
	MSA 8	-	0	24	24	**0**
	MSA 9	(79.7 ± 15.6) – (63.0 ± 5·7)	0	23	23	**0**
	MSA 10	-	0	103	103	**0**
	MSA 11	(70.3 ± 5.8) – (59.4 ± 5.0)	0	32	32	**0**
	MSA 12	-	1	178	179	**1**
	MSA 13	(59.8 ± 4.7) – (50.6 ± 4.6)	0	13	13	**0**
	MSA 14	-	4	122	126	**3**
	MSA 15	-	4	68	72	**6**
Diep–kloof	Post-HP	57–46	7	76	83	**8**
	Late-HP	52 ± 5	9	78	87	**10**
	Inter HP	(85 ± 9) – (65 ± 8)	10	33	43	**23**
	MSA–Jack	89 ± 8	1	12	13	**8**
	Early HP	(109 ± 10) – (105 ± 10)	2	27	29	**7**
	Still Bay	109	8	24	32	**25**
	Pre–SB Lynn	100 ± 10	1	5	6	**17**
	MSA–Mike	-	1	7	8	**13**
	Lower MSA	107–100	0	8	8	**0**
Klasies River	MSA II 1A	43.4 ± 3.0, 57.0 ± 4.0	0	68	68	**0**
	HP 1A	63.2 ± 2.7, 65.6 ± 5.3, 53 ± 3	0	77	77	**0**
	Upper	70	0	117	117	**0**
	Top SAS	77	0	44	44	**0**
	Middle SAS	-	0	52	52	**0**
	MSA II U 1 and 1A	100.8 ± 7.5, 85.2 ± 2.1, 77.4 ± 7.0	0	107	107	**0**
	MSA II L 1/1A AA43/Z44	101 ± 12	0	376	376	**0**
	MSA I 1/1A AA43/Z44	106.8 ± 12.6, 108.6 ± 3.4	0	45	45	**0**
	Bottom SAS	126	0	262	262	**0**
	LBS member	110	0	69	69	**0**
Klipdrift	PAY	60.0 ± 4.0	0	7	7	**0**
	PAZ	-	0	12	12	**0**
	PBA/PBB	59.4 ± 4.6	0	50	50	**0**
	PBC	65.5 ± 4.8	2	65	67	**3**
	PBD	64.6 ± 4.2	0	65	65	**0**
	PBE	-	0	8	8	**0**
	PCA	63.5 ± 4.7	0	77	77	**0**

Pinnacle Point	LB SAND 1	90–89	0	3	3	**0**
	DB SAND	102–91	1	12	13	**8**
	LB SAND 2	102–91	0	1	1	**0**
	LBG SAND	134–94	0	14	14	**0**
	4aDB SAND	166–117	0	1	1	**0**
	LBS	112–110	0	0	0	**0**
	FILL	39–35	0	2	2	**0**
	SB SAND	98–96	0	2	2	**0**
	URS	98–91	0	12	12	**0**
	LRS	112–110	0	3	3	**0**
	LC–MSA	174–153	0	7	7	**0**
Ysterfontein	Upper	128.6 ± 6.3	0	17	17	**0**
	Middle	-	4	5	9	**44**
	Lower	(132.1 ± 8.0)–(120.6 ± 6.6)	5	10	15	**33**
Total			**201**	**4020**	**4221**	**5**

Table 3. Numbers of hippopotamus and elephant remains from MSA sites, reported as Number of Identified Specimens (NISP)

Site	Hippopotamus	Elephant	Indeterminate very large mammal
Blombos Cave	5	0	4
Die Kelders Cave	154	0	0
Diepkloof Cave	19	0	0
Klasies River Mouth	28	0*	0
Klipdrift Shelter	0	0	1
Pinnacle Point Cave	0	0	0
Ysterfontein Rock Shelter	0	0	0
Total	206	0	5

*Hippopotamus and elephant remains were present in previous study sample (Klein 1976).

Table 4. Representation of rhinoceroses and Large Bovid and Equids (LBE) in carnivore accumulated assemblages from the Eastern and Western Cape. Numbers were reported as Number of Identified Specimens (NISP), except at Herolds Bay, where Brink and Deacon (1982) reported Minimum Number of Individuals (MNI)

Site	Rhino	LBE	% rhino	Reference
Sea Harvest	10	311	3	Grine and Klein 1993
Boomplaas	0	125	0	Faith 2013
Herolds Bay	0	17	0	Brink and Deacon 1982
Pinnacle Point PP30	0	189	0	Rector and Reed 2010
Elandsfontein Bone Circle	2	350	1	Klein 1983
Duinefontein 2	53	1902	3	Cruz-Uribe et al. 2003
Hoedjiespunt 1	5	698	1	Stynder 1997
Swartklip 1	63	362	15	Klein 1983
Total	**133**	**3937**	**3**	

Discussion and Conclusion

The presence of large bovid and equid remains in MSA faunal assemblages, in combination with the presence of hunting tools, suggest hominins in southern Africa during this period had the skill and ability to hunt or trap large, dangerous prey (Milo 1998; Van Pletzen et al. 2019). Yet, despite their hunting capabilities, and the availability of large quantities of meat on the carcass of a single rhinoceros, bone remains of these large animals are not common at MSA sites in the Eastern and Western Cape.

Three potential reasons could be offered for the low frequency of rhinoceros remains in the MSA samples. First, it is possible that people did not hunt rhinoceros during the MSA. Given the abundance of other easily accessible resources, such as shellfish and tortoises (Klein and Cruz-Uribe 2000; Steele and Klein 2013), people may have been disinclined to exploit large mammals that were potentially dangerous to hunt or trap. Historical descriptions of hunter-gatherers mention that some preyed on rhinoceroses (Alexander 1838; Andersson 1856), but this does not necessarily imply that this happened during the MSA. Despite the important cultural and symbolic meaning of rhinoceros among early historical farming communities in southern Africa (e.g. drawing parallels in rhino behaviour to leadership qualities, using figurines during initiation schools, ascribing a complex folk taxonomy, utilizing remains of these pachyderms in rainmaking rituals), remains of these animals are also meagre at late Holocene farming sites (Boeyens and Van der Ryst 2014). Some early historical accounts from southern Africa report that the meat of black rhinoceros has an acrid and bitter flavour (Delegorgue 1997; Andersson 1856:395). However, this is unconvincing as an explanation for the consistently low representation of these large mammals in faunal assemblages from the MSA. The meat of white rhinoceros reportedly contains substantial fat and has an agreeable taste (Andersson 1856:395), yet white rhinoceroses are even more poorly represented in the faunal assemblages than black rhinoceroses.

A second possible explanation for the low number of rhinoceros remains is that people hunted these animals, but that few skeletal remains were brought back to cave sites. Rhinoceroses are very large mammals with heavy bones, and it is unlikely that an entire carcass would have been brought back to camp sites. Even transporting portions of dismembered limbs would have been challenging owing to the weight of meat and bones. Larger animals were often butchered at kill sites, and only some parts returned to camp sites (Klein 1976). Black and white rhinoceroses are creatures of habit, and repeatedly use the same paths to and from water sources (Skinner and Chimimba 2005), making it possible to hunt them using pits and traps. If feasting took place at camp sites where the animals were slaughtered, then few if any remains of these animals would have been transported back to cave sites. While the excess meat may have been dried and then brought back to caves, this meat would have contained few, if any bones.

Thirdly, the low numbers of rhinoceros at these sites may be a result of a low abundance or complete absence of rhinoceros across the landscape during the MSA. A low abundance would have resulted in low encounter rates, limiting the possibilities for people to hunt or scavenge these large herbivores. Notwithstanding the complexities of using modern census data from national parks and reserves, it may be presumed that rhinoceros generally occur in low numbers compared to other large ungulates (Table 5). However, travellers during the early historical period frequently encountered rhinoceros (Harris 1840; Andersson 1856), suggesting that their low natural population numbers, compared to large bovids and

Table 5. Census data from two large game reserves in southern Africa, showing the representation of rhinoceroses and other large ungulates

Nature Reserve	Number of rhinoceros	Numbe of LBE	% Rhinoceros	Reference
Kruger National Park (South Africa)	11,129	67,640	14	Ferreira et al. 2017; Sanparks.org. 2020
Etosha National Park (Namibia)	20	66,600	<1	Odendaal et al. 1964

zebras, are an unlikely explanation for scarcity of remains at MSA sites. While it is possible that at times rhinoceroses were completely absent from the area, the presence of specimens in deposits indicates that they were present in the region during the MSA.

Potentially, analyses of the skeletal parts and taphonomy of rhinoceros remains from MSA sites could provide clues as to their role in the past. However, obtaining such data, which are not generally available in the literature, would require re-analysis of faunal assemblages containing thousands of specimens. Moreover, this type of analyses might not provide conclusive results, for a number of reasons. The skeletons of rhinoceros are particularly porous (Alexander and Pond 1992), so that their remains are likely to be severely affected by post-depositional processes. Remains of rhinoceros could therefore be under-represented in the archaeological faunal assemblages due to taphonomic factors, but the extent of this cannot be determined by studies of skeletal parts. It should be borne in mind that skeletal part profiles of animal remains in faunal samples only reflect the identified component. However, most faunal assemblages are dominated by unidentified specimens, which simply cannot be identified as they lack morphological features (Badenhorst and Plug 2011). The consequence of this for zoo-archaeology is that skeletal part profiles are biased and provide information on only a small component of the overall assemblage. Taphonomic modifications like evidence for butchering are generally rare on archaeological bones from the MSA, even on remains of hunted animals.

Data on the species of rhinoceroses hunted is insufficient to draw any firm conclusions. However, it is notable that while white rhinoceroses are found at Die Kelders in the lowermost layers MSA 14 and MSA 15 (Klein and Cruz-Uribe 2000), black rhinoceroses occur in the upper layers of the same site, namely MSA 4/5 and 6 (Klein and Cruz-Uribe 2000). White rhinoceroses are exclusively grazers, whereas the black rhinoceroses are browsers. Thus, while the dating of Die Kelders is problematic (Wadley 2015), this data suggests a change in vegetation type from open to bushy environments, leading to a change in the species composition around the site over time.

People evidently had the skills to hunt large ungulates during the MSA in the Eastern and Western Cape of South Africa. Despite this, few remains of rhinoceros are present in MSA faunal assemblages. It is possible that people either did not hunt rhinoceros on a regular basis, or that they camped and consumed the meat at carcass sites. In this case, if they brought meat back to caves and shelter sites, the meat contained few if any bones.

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References

Alexander JE. 1838. Report on an expedition of discovery, through the countries of the Great Namáquas, Boschmans, and the Hill Damáras, in South Africa. *Journal of the Royal Geographical Society of London* 8:1–28.

Alexander RM, Pond CM. 1992. Locomotion and bone strength of the white rhinoceros, *Ceratotherium simum*. *Journal of Zoology* 227 (1):63–69. https://doi.org/10.1111/j.1469-7998.1992.tb04344.x

Andersson CJ. 1856. *Lake Ngami. Explorations and discoveries during four years' wanderings in the wilds of southwestern Africa*. Harper, New York.

Avery MD. 2019. *A fossil history of southern African land mammals*. Cambridge, Cambridge University Press.

Avery G, Halkett D, Orton J, Steele T, Tusenius M, Klein R. 2008. The Ysterfontein 1 Middle Stone Age

rock shelter and the evolution of coastal foraging. *South African Archaeological Society Goodwin Series* 10:66–89.

Badenhorst S, Plug I. 2011. Unidentified specimens in zooarchaeology. *Palaeontologia Africana* 46:89–92.

Badenhorst S, Van Niekerk KL, Henshilwood CS. 2016. Large mammal remains from the 100 ka Middle Stone Age layers of Blombos Cave, South Africa. *South African Archaeological Bulletin* 71:46–52.

Boeyens JCA, Van der Ryst MM. 2014. The cultural and symbolic significance of the African rhinoceros: a review of the traditional beliefs, perceptions and practices of agropastoralist societies in southern Africa. *Southern African Humanities* 26 (1):21–55.

Brain CK. 1974. Some suggested procedures in the analysis of bone accumulations from southern African Quaternary sites. *Annals of the Transvaal Museum* 29 (1):1–8.

Brink JS, Deacon HJ. 1982. A study of a last interglacial shell midden and bone accumulation at Herolds Bay, Cape Province, South Africa. *Palaeoecology of Africa and the Surrounding Islands* 15: 31–39.

Cruz-Uribe K., Klein RG, Avery G, Avery DM, Halkett D, Hart T, Milo RG, Sampson C G, Volman TP. 2003. Excavation of buried late Acheulean (mid-Quaternary) land surfaces at Duinefontein 2, Western Cape Province, South Africa. *Journal of Archaeological Science* 30:559–575.

Delegorgue A. 1997. *Travels in Southern Africa*, vol. 2. Durban: Killie Campbell Africana Library, and Pietermaritzburg: University of Natal Press. [Translated from the original French of 1847.]

Faith JT. 2013. Taphonomic and palaeoecological change in the large mammal sequence from Boomplaas Cave, Western Cape, South Africa. *Journal of Human Evolution* 65:715–730.

Ferreira SM, Bissett C, Cowell CR, Gaylard A, Greaver C, Hayes J, Hofmeyr M, Moolman-Van der Vyver L, Zimmermann D. 2017. The status of rhinoceroses in South African national parks. *Koedoe* 59 (1):1–11.

Grine FE, Klein RG. 1993. Late Pleistocene human remains from the Sea Harvest site, Saldanha Bay, South Africa. *South African Journal of Science* 89:145–152.

Hall M. 1977. Shakan pitfall traps: hunting technique in the Zulu kingdom. *Annals of the Natal Museum* 23 (1):1–12.

Harris WC. 1840. *Portraits of the game and wild animals of Southern Africa*. W. Pickering, London.

Henshilwood CS, Sealy JC, Yates R, Cruz-Uribe K, Goldberg P, Grine FE, Klein RG, Poggenpoel C, Van Niekerk K, Watts I. 2001. Blombos Cave, southern Cape, South Africa: preliminary report on the 1992–1999 excavations of the Middle Stone Age levels. *Journal of Archaeological Science* 28 (4):421–448. https://doi.org/10.1006/jasc.2000.0638

Klein RG. 1976. The mammalian fauna of the Klasies River Mouth sites, Cape Province, South Africa. *South African Archaeological Bulletin* 31: 75–98. https://doi.org/10.2307/3887730

Klein, RG. 1983. Palaeoenvironmental implications of Quaternary large mammals in the Fynbos Biome. *South African National Scientific Programmes Reports* 75:116–138.

Klein RG, Cruz-Uribe K. 1996. Exploitation of large bovids and seals at Middle and Later Stone Age sites in South Africa. *Journal of Human Evolution* 31:315–334. https://doi.org/10.1006/jhev.1996.0064

Klein RG, Cruz-Uribe K. 2000. Middle and later Stone Age large mammal and tortoise remains from Die Kelders Cave 1, Western Cape Province, South Africa. *Journal of Human Evolution* 38 (1):169–195. https://doi.org/10.1006/jhev.1999.0355

Lyman RL. 2008. *Quantitative Paleozoology*. Cambridge University Press, Cambridge.

Milo RG. 1998. Evidence for hominid predation at Klasies River Mouth, South Africa, and its implications for the behaviour of early modern humans. *Journal of Archaeological Science* 25 (2): 99–133. https://doi.org/10.1006/jasc.1997.0233

Odendaal FH, Van Eck HJ, Snyman HW, Bruwer JP, Van S, Quin PJ, Claasen CJ. 1964. *Verslag van die kommissie van ondersoek na aangeleenthede van Suidwes-Afrika / Report of the commission of enquiry into South West Africa affairs*. Government Printer, Pretoria.

Plug I, Badenhorst S. 2001. *The distribution of macromammals in Southern Africa over the past 30 000 Years*. Transvaal Museum Monograph 12. Transvaal Museum, Pretoria.

Rector AL, Reed KE. 2010. Middle and late Pleistocene faunas of Pinnacle Point and their

palaeoecological implications. *Journal of Human Evolution* 59:340–357. https://doi.org/10.1016/j.jhevol.2010.07.002

Reynard JP, Discamps E, Badenhorst S, Van Niekerk K, Henshilwood CS. 2016. Subsistence strategies in the southern Cape during the Howiesons Poort: Taphonomic and zooarchaeological analyses of Klipdrift Shelter, South Africa. *Quaternary International* 404:2–19. https://doi.org/10.1016/j.quaint.2015.07.041

Reynard JP, Henshilwood CS. 2019. Environment versus behaviour: Zooarchaeological and taphonomic analyses of fauna from the Still Bay layers at Blombos Cave, South Africa. *Quaternary International* 500:159–171. https://doi.org/10.1016/j.quaint.2018.10.040

Reynard JP, Wurz S. 2020. The palaeoecology of Klasies River, South Africa: an analysis of the large mammal remains from the 1984–1995 excavations of Cave 1 and 1A. *Quaternary Science Reviews* 237:106–301.

Rookmaaker LC. 2008. *Encounters with the African rhinoceros: A chronological survey of bibliographical and iconographical sources on rhinoceroses in southern Africa from 1795 to 1875. Reconstructing views on classification and changes in distribution*. Schuling Verlag, Munster.

Sanparks.org. 2020. South African National Parks–Sanparks–Official Website–Accommodation, Activities, Prices, Reservations. Available at: <https://www.sanparks.org/parks/kruger/conservation/scientific/ff/biodiversity_statistics.php> [Accessed 18 August 2020].

Skead CJ, Boshoff AF, Kerley GIH, Lloyd PH. 2007. *Historical incidence of the larger land mammals in the broader Eastern Cape, 2nd ed*. Nelson Mandela Metropolitan University, Port Elizabeth.

Skinner JD, Chimimba CT. 2005. *The mammals of the southern African sub-region*. Cambridge University Press, Cambridge.

Smith AB, Kinahan J. 1984. The invisible whale. *World Archaeology* 16 (1): 89–97. https://doi.org/10.1080/00438243.1984.9979918

Steele TE, Klein RG. 2013. The Middle and Later Stone Age faunal remains from Diepkloof Rock Shelter, Western Cape, South Africa. *Journal of Archaeological Science* 40 (9):3453–3462. https://doi.org/10.1016/j.jas.2013.01.001

Stynder DD. 1997. The use of faunal evidence to reconstruct site history at Hoedjiespunt 1 (HDP1), Western Cape. MSc dissertation. University of Cape Town, Cape Town.

Van Pletzen LV, Brink J, Reynard JP, Wurz S. 2019. Revisiting Klasies River: A Report on the Large Mammal Remains from the Deacon Excavations of Klasies River Main Site, South Africa. *South African Archaeological Bulletin* 74:127–137.

Wadley L. 2010. Were snares and traps used in the Middle Stone Age and does it matter? A review and a case study from Sibudu, South Africa. *Journal of Human Evolution* 58 (2):179–192. https://doi.org/10.1016/j.jhevol.2009.10.004

Wadley L. 2015. Those marvellous millennia: The Middle Stone Age of southern Africa. *Azania: Archaeological Research in Africa* 50 (2):155–226. https://doi.org/10.1080/0067270X.2015.1039236