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Faunal Exploitation Strategies During the Later Pleistocene in Southern Africa

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Summary

Analysis of Late Pleistocene fauna exploitation (~130,000–12,000 years ago) in southern Africa is of global academic relevance. Faunal analyses from southern African sites have led to the development of influential hypotheses on the evolution of modern human hunting methods and subsistence economies.

In the 1970s and 1980s, analysis of faunal remains from the Middle Stone Age site Klasies River informed the hypothesis that Middle Stone Age humans were less effective hunters than ethnographically documented hunter-gatherers. This was based on the underrepresentation of dangerous prey species in the bone assemblages. The development of detailed taphonomic research in the 1990s and 2000s demonstrated that the accumulation of faunal assemblages was the result of complex processes involving both human and nonhuman agents. These studies helped establish that Middle Stone Age hunters were as capable as those in ethnographically documented societies. Since then, important progress has been made in the identification of the weapons systems that were used to hunt animals. Analyses of lithic implements indicate bow-and-arrow use in southern Africa going back to at least 65,000 years ago.

Animal exploitation strategies do change over time. Hunting strategies probably focused on large antelope during the Middle Pleistocene, and the importance of smaller animals increased This change was likely caused by a shift in prey populations that stemmed from a combination of environmental change and perhaps human population pressure.

Late Pleistocene archaeological sites show increasing evidence for intensification; that is, an increase in the amount of food extracted from the environment by more thorough processing of prey, exploitation of new prey types, and development of new exploitation strategies. This pattern is usually linked to animal overexploitation and may be a result of human population expansion or environmental change if decreasing productivity limits the supply of animal prey. Notable examples of this are shellfish middens at coastal sites, the abundance of tortoises, and the presence of large numbers of small mammals that were likely snared instead of pursued.

Keywords

Late Pleistocene, Middle Stone Age, Later Stone Age, faunal analysis, modern human behavior, subsistence behavior, scavenging, coastal foraging, intensification, mass collection

Overview

Late Pleistocene animal exploitation strategies in southern Africa are relevant to archaeological debates globally, especially regarding the evolution of modern human behavior.

Evidence of encounter hunting appears in the archaeological record from the later Middle Pleistocene (from about 500,000 to 123,000 years ago), and most evidence of its organization comes from the Late Pleistocene (130,000–11,700 years ago). This period began with the previous warm period (Last Interglacial, 130,000–115,000 years ago) and covered the Last Ice Age (115,000–11,700 years ago). The Ice Age comprises two very cold intervals—Marine Isotope Stage (MIS) 4 (71,000–57,000 years ago) and MIS 2 (Last Glacial Maximum, 29,000–11,700 years ago)—separated by a more temperate phase. The Late Pleistocene, which ended with the beginning of the current warm period (the Holocene), posed many challenges for human societies in southern Africa. The region experienced rapid climatic changes, including temperature and rainfall fluctuations that led to sometimes arid conditions in large parts of the region.

The Late Pleistocene in southern Africa encompassed the Middle Stone Age (MSA) and the early part of the Later Stone Age (LSA; see the article "Southern African Stone Age"). Southern Africa was inhabited by anatomically modern humans at this time, and the archaeological record shows the early appearance of complex, sophisticated behaviors thought to be characteristic of our species (see the article "Modern Human Behavior").

The scientific consensus in the 1970s and 1980s was that MSA people did not exploit animals as effectively as contemporary hunter-gatherers. Researchers proposed that many of the bones excavated at archaeological sites reflected either scavenging activities or less proficient hunting strategies focused on "easy" prey. However, detailed taphonomic work and information from newly excavated sites has shifted the interpretation of the bone collections. MSA societies are now thought to have hunted as effectively as LSA groups. In the 21st century, research has focused on more detailed questions related to the weapon systems that were used; the adaptation of foraging strategies to changing environments; and "intensification," which refers to the extraction of increasing amounts of food from the environment by adding prey types and new exploitation strategies. This article briefly highlights the history of research and current consensus on some of the major research topics and provides a chronological review of the main developments. Although archaeologically less visible, it must be kept in mind that the exploitation of plant foods was calorically at least as important as faunal exploitation throughout the Late Pleistocene.

History of Subsistence Research

Early Beginnings

Early analyses of MSA stone tools associated with animal bones concentrated on the types of species present at sites and their relative age so that faunal remains could be used as chronological markers (e.g., Goodwin 1928; Cooke 1939; Wells et al. 1942). Nevertheless, the association of stone tools and bones also led to speculation on how humans exploited animals. Broom (1913) established the contemporaneity of human occupation with now-extinct animal species in South Africa. He described materials collected by Martha Johanna Venter during the construction of baths at the Florisbad spring (then called Haagenstad). Among the animal remains were broken bones of giant buffalo (Syncerus antiquus). He interpreted the breakage patterns on these bones as the result of human exploitation

(Broom 1913, 14). Subsequent research has shown that the taphonomic history of these deposits is complex and the assemblage was mainly the result of carnivore activities around the spring (Brink 1987).

The study of human hunting was taken up in earnest by C. K. Brain (1969, 1981). He saw Stone Age faunal remains in the Bushman Rock Shelter as the result of human exploitation of animals and compared them with the fauna of the much older Plio-Pleistocene deposits at Swartkrans and other South African early hominin sites. Brain (1981) showed that the Plio-Pleistocene bone assemblages differed from those accumulated by humans and noted that these early hominin materials were likely accumulated by carnivores.

1970s and 1980s: Hunting Proficiency and the Role of Scavenging

South African archaeozoology was furthered by American scholar Richard Klein, who started working in South Africa in the 1970s. Klein analyzed the faunal assemblages of many important Pleistocene and Holocene sites in the region (e.g., Henshilwood et al. 2001; Klein 1972, 1976, 1977; Klein and Cruz-Uribe 1987, 2000). Led by Klein, South African bone collections from the 1970s were explicitly interpreted in terms of the development of early human behavior.

With the analysis of the bone collections from Klasies River (Klein 1976), Klein developed an influential model on the development of human hunting behavior (Klein 1975). Klasies River contains a stratigraphic sequence of MSA deposits over 20 m thick, with sediments dated to the first half of the Late Pleistocene (~125,000–50,000 years ago; Wurz et al. 2018). The sequence thus provides a long-term perspective on human behavior. A comparison of the species present in the MSA deposits at Klasies River with the LSA bone collections of a nearby site, Nelson Bay Cave, shows interesting differences (see Fig. 1 for site locations). Klein (1976) noticed that the representation of animal species at Klasies River differs from that at Nelson Bay Cave. At Klasies River, eland (Tragelaphus oryx), a large antelope, is well represented, as is blue antelope (Hippotragus leucophaeus), a medium-to-large antelope that went extinct around 1800 CE (Fig. 2) (Faith & Thompson 2013). African buffalo (Syncerus africanus), the now-extinct giant buffalo, and suids (warthog and bushpig) are more common at Nelson Bay Cave (Fig. 2). This prey preference is not absolute. Bones of suids and buffalo have also been excavated at Klasies River.

Eland and blue antelope are considered docile species, which are most likely to flee when attacked. Buffalo and suids, on the other hand, are aggressive and often attack predators (see Klein 1975, 1976; also see Dusseldorp 2010). This choice of docile prey animals in the MSA suggested to Klein (1975, 1976) that that MSA hunters were not as effective as LSA people.

Eland antelope are better represented than the dangerous animals, and the ages of the exploited individuals also differ. Mortality profiles, or ages at which animals die, can tell us much about human hunting strategies (Klein 1982). Generally, two types of mortality profiles occur: attritional and catastrophic patterns. Attritional patterns reflect natural death rates, with most animals dying either when they are very young or very old. We expect to see this type of pattern in a cemetery (hence it is sometimes called a cemetery pattern). This pattern in a faunal assemblage suggests that weaker individuals were preferentially hunted. Catastrophic patterns occur when most remains are of prime-aged adults. This type of pattern ensues when a living population is wiped out by a natural catastrophe, such as a flash flood or volcanic eruption. In a hunted assemblage, it demonstrates that the largest and most dangerous individuals were mainly exploited.

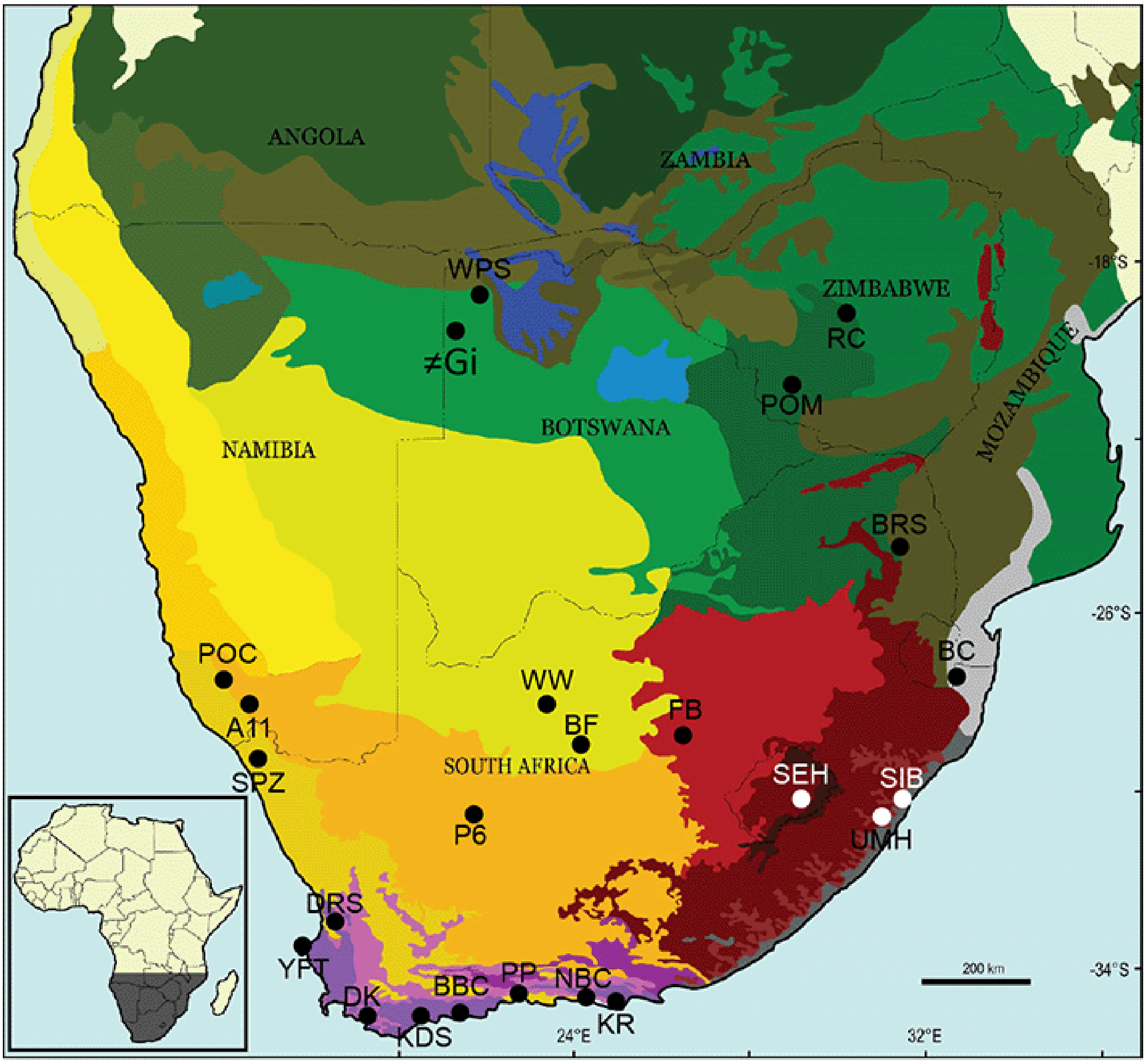

Figure 1*. Map showing the distribution of different biomes in southern Africa with the location of the most important sites mentioned in the text. Biomes: yellow, orange, and light green, arid environments; dark green and blue, savannah; red, grasslands; gray, subtropical forest; blue, Cape floristic region.*

Note: A11, Apollo 11; BBC, Blombos Cave; BC, Border Cave; BF, Bundu Farm; BRS, Bushman Rock Shelter; DK, Die Kelders; DRS, Diepkloof Rock Shelter; FB, Florisbad; KDS, Klipdrift Shelter; KR, Klasies River; NBC, Nelson Bay Cave; P6, Pniel 6; POC, Pockenbank; POM, Pomongwe; PP, Pinnacle Point; RC, Redcliff; SEH, Sehonghong; SIB, Sibudu; SPZ, Spitzkloof; UMH, Umhlatuzana; WPS, White Paintings Shelter; WW, Wonderwerk; YFT, Ysterfontein.

At Klasies River, both these patterns are evident in the large herbivore assemblage. The mortality profiles of eland show a catastrophic pattern, while buffalo profiles are attritional with an abundance of very young individuals (Klein 1976, 83–84). Klein (1983) argues that eland were probably caught in pit traps or possibly driven off nearby cliffs while buffalo were individually stalked, with only the most vulnerable age groups (i.e., the youngest or oldest) caught. The model of more limited hunting proficiency during the MSA compared to the LSA was in the subject of subsequent analyses and remains influential (Klein and Cruz-Uribe 1996, 2000).

Figure 2. *(a) Eland; (b) Blue antelope, the main types of docile prey at Klasies River with catastrophic mortality profiles; (c) buffalo; (d) warthog, the main types of dangerous prey that appeared underrepresented in the Klasies MSA deposits.*

Source: Photographs a, c, and d by Gerrit Dusseldorp; b from Naturalis Biodiversity Centre Leiden, used with permission.

Klasies Pattern and Scavenging

Klein's (1976) analyses also highlighted a peculiar pattern of skeletal element representation (i.e., which bones were recovered during the excavations and which were missing). It turned out that mainly the "axial skeleton" (skull, vertebra, ribs) and the "distal" elements (hand and foot bones) are present. The large leg bones, which represent the meat-bearing limbs, are severely underrepresented. This pattern is especially prominent for the larger antelope species. This skeletal element representation later became known as the "Klasies Pattern" (Bartram and Marean 1999; Marean and Assefa 1999) and is present at many Stone Age archaeofaunal assemblages throughout the world. Klein compared the skeletal part representation of the Klasies fauna to that of ethnoarchaeologically documented assemblages. He concluded that large antelope skulls and vertebra were selected by people and transported to the site, while complete carcasses of small antelope were transported. These bones were then subjected to quite intense destructive processes (Klein 1989).

Lewis Binford focused on this skeletal part representation in his analysis of the bone collections from Klasies River. His work in the 1980s contributed significantly to debates on early human hunting strategies. Binford (1981) argued that animal remains at most early hominin sites in East Africa were not hominin prey as often suggested. Rather, they represented carnivore prey that were later scavenged by hominins. He subsequently applied this argument to the animal remains from Klasies River (Binford 1984).

In his reanalysis, Binford observed that the axial and distal bones can be considered of low “food utility”; that is, their lack of meat indicated that they were not valuable food sources. These are the parts presumed to be eaten last by carnivores and therefore most likely to be available to scavenging people (Binford 1984, 190–191). He argued that the remains of especially the larger antelopes at Klasies River represented scavenged animals, and he proposed that scavenging remained important to modern humans until late in the Pleistocene (Binford 1984, 246). He used his Klasies River analysis to develop an alternative to the “central place foraging” model: “routed foraging.” Under his model, Klasies River functioned perhaps more as a resting place to which animals that needed processing were transported, rather than as a camp (Binford 1984, 260–263). This model has also been applied outside of southern African Late Pleistocene contexts (e.g., Bunn 1994; Langbroek 2012).

Binford’s conclusions proved provocative and spurred intensive criticism and further research at Klasies River and into the MSA. Some important shortcomings to his conclusions were pointed out. First, some of Binford’s reasoning was argued to be faulty; for example he misinterpreted the stratigraphic sequence (e.g., Singer and Wymer 1986; Marean 1986). Second, the data set he studied, which was produced during 1960s excavations, was shown to be seriously biased (Turner 1989). This was confirmed in the course of continued work at the site by Hilary Deacon (e.g., Van Pletzen-Vos et al. 2019; Reynard and Wurz 2020). The study of taphonomy of faunal assemblages was affected by this debate. As a result of this work, from the late 1980s most workers in the field did not seriously consider Late Pleistocene societies in southern Africa to have been heavily dependent on scavenging.

1990s Onward: A Taphonomic Turn

Taphonomic research concerns the analysis of how bone assemblages are formed and which factors influence the preservation of the bones and the composition of the collection throughout the ages from deposition through to excavation and analysis (see the article “Archaeozoology: Methods”). The hunting and scavenging debate, as well as Brain’s (1981) studies of the taphonomy of Plio-Pleistocene hominin sites, provided an important impetus for taphonomic research. During the 1980s and especially the 1990s, taphonomic analyses become increasingly detailed. By the turn of the 21st century, taphonomic analysis to determine the factors responsible for the accumulation and subsequent modifications of bones in archaeological sites had become standard practice for Late Pleistocene excavations.

To evaluate scavenging interpretations, the study of traces of human (e.g., cut and chop marks) and carnivore (e.g., tooth marks) activities becomes important. Microscopic analysis of the assemblages from Klasies River revealed a much greater incidence of human butchery marks than Binford had observed with the naked eye (Fig. 3). This supports more active human involvement with the bones than Binford had supposed (Milo 1998). Moreover, a tip of a stone point embedded in the vertebra of a giant buffalo evokes active hunting of very large animals by the site’s occupants (Fig. 4) (Milo 1998).

***Figure 3**. Cut marks on the lumbar vertebra of a large mammal in the ~100,000-year-old layers from Klasies River.*
Source: Photograph by Amy Lap, used with permission.

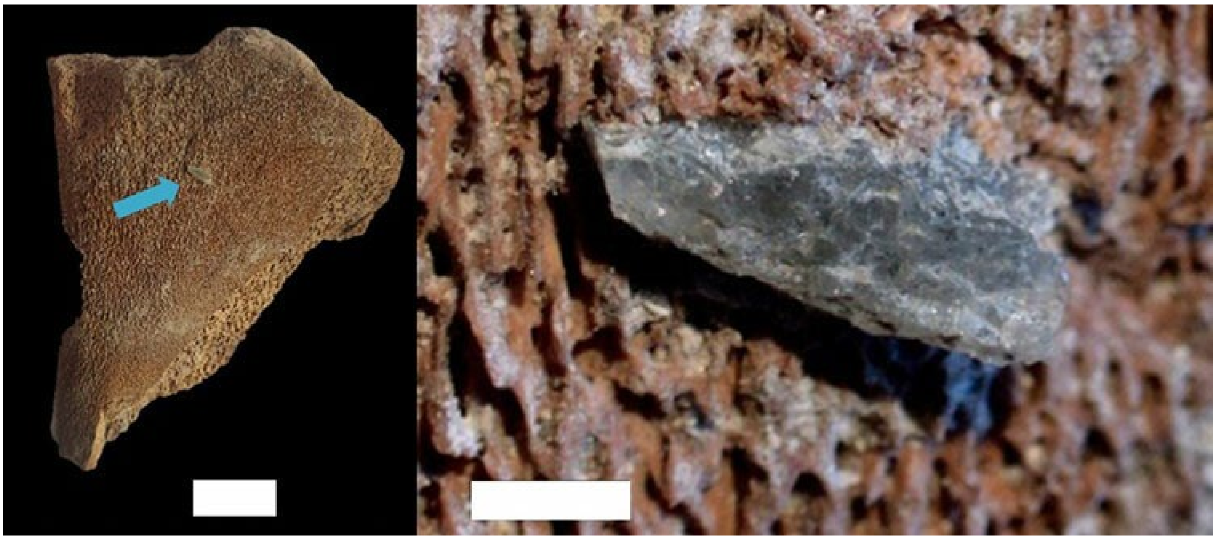

***Figure 4.** Stone tool embedded in a long bone in the 100,000-year-old layers at Klasies River.*
Source: Photograph by Amy Lap, used with permission.

The representation of skeletal elements, the so-called Klasies pattern, has since been observed in many assemblages, including those outside of southern Africa. To understand what processes led to the representation of skeletal elements in the archaeological record, archaeological assemblages were compared with bone assemblages of a known history. Klein compared the Klasies materials with those of Native American villages (Klein 1976, 93–94). Further comparisons were made with assemblages accumulated and affected by carnivores (e.g., Bartram and Villa 1998; Marean and Spencer 1991) and accumulated by hunter-gatherer societies (Bartram and Marean 1999). These studies, together with a reevaluation of the excavation methods of the initial Klasies excavations (Turner 1989), led to a new understanding of the Klasies pattern. The current consensus is that it is likely a result of the combined influence of the chopping open of long bones to consume marrow, followed by the destruction of some elements by carnivores. Chopping open long bones and carnivore activities decrease the identifiability of long bones much more than of small, dense, and nonnutritious bones, such as foot elements and vertebra. If this is combined with selection for identifiable elements by faunal analysts, then a severely biased impression of the bone assemblage and thus human foraging strategies is created (Bartram and Marean 1999).

Further, detailed taphonomic analyses of more recently excavated sites, such as Die Kelders, show that human scavenging cannot explain the skeletal element representation at these sites. By looking specifically at bones that are not easily destroyed, such as carpal and tarsal bones, Marean, Cowling, and Franklin (2000) controlled for the influence of carnivore destruction of some bones in the collections. Within "high-survival" elements (more dense bones), they showed that bones that represent a high food utility are more likely to be transported to the site. The bone assemblage thus represents human exploitation of hunted animals, rather than leftovers from carnivore meals (Marean et al. 2000). Only the smaller animals at the site (antelopes below 23 kg in body weight) were partly brought in by carnivores and not just hunted by MSA people (Marean et al. 2000, but see Armstrong 2016). This "taphonomic turn" thus led to the reversal of received wisdom on human faunal exploitation within thirty years. Instead of concluding that people scavenged larger animals and actively hunted only the smaller species, the consensus has become that people actively hunted larger antelopes and many of the bones of smaller species were contributed by carnivores. Taphonomic analysis thus played a decisive role in the resolution of the hunting versus scavenging debate. It continues to be important in Pleistocene archaeology, as no interpretation of the fauna at sites can be made if the depositional history of the assemblages is not understood.

Hunting and Modern Human Behavior

Modern Homo sapiens and the development of sophisticated behavior have deep roots in the African MSA (e.g., Barham 1998; Deacon 1992, 1995; Wurz 1999). Archaeological evidence from at least 100,000 years ago shows a florescence of artifacts and behavior linked to complex, "modern" cognition. Previously, many models of our species' behavioral evolution proposed a revolutionary development between 50,000 and 40,000 years ago in which the whole suite of characteristically modern behaviors appeared suddenly, including symbolic evidence of group and individual identity (ornaments and art) and complex chemical compounds (e.g., adhesives, pigments). With the increasing realization that the development of modern human behavior took place gradually from the late Middle Pleistocene onward, faunal exploitation was also viewed through the lens of "behavioural modernity" (e.g., McBrearty and Brooks 2000, 506–510; see the articles "Faunal Analysis in African Archaeology" and "Modern Human Behavior" for more details on this subject). The "modernity" debate touches on several aspects of faunal exploitation, including:

- hunting competence of MSA foragers;
- planning to take advantage of brief exploitation opportunities;
- subsistence intensification; and
- production of bone tools.
- Middle Stone Age versus Later Stone Age Hunting Ability

The hypothesis of limited hunting proficiency of MSA people continues to be important. In influential papers, Klein and Cruz-Uribe (1996, 2000) reiterate limited hunting proficiency in the MSA compared to the LSA. An added element is the suggestion of limited temporal planning by MSA societies. Age-at-death estimates of seal remains show that (Holocene) LSA people intensively scavenged one-year-old pups that had just been weaned. These wash up on beaches seasonally, in winter (August–September), which demonstrates that LSA people scheduled their mobility strategies to coincide with periods of resource abundance at specific places in the landscape. In MSA assemblages, the age representation of seals is much wider and comparable to that of brown hyena dens. This may represent randomly timed coastal visits spread throughout the year and thus less effective scheduling of mobility (Klein and Cruz-Uribe 1996, 2000; Klein et al. 1999; but see Dusseldorp and Langejans 2013; Langejans et al. 2012).

This hypothesis was contested by taphonomic studies showing that the Klasies pattern was likely influenced by nonhuman factors affecting the bone assemblages at archaeological sites and increasing evidence of cut marks and active hunting. In their seminal paper on the origins of modern behavior, McBrearty and Brooks (2000) state that there is insufficient evidence to suggest less hunting proficiency during the MSA. Henshilwood and Marean (2003) argue that many of the accepted hallmarks of modern behavior are taphonomically vulnerable. As the time depth and thus the influence of biasing factors has a much greater influence on MSA bone collections than on mainly Holocene LSA bone collections, making comparisons between these assemblages is a problematic approach.

In the 2000s, there was a steady accumulation of evidence and arguments to suggest that differences in the archaeological signature of MSA and LSA foragers cannot be interpreted as the result of changing hunting proficiency. First, when examining a large data set of MSA and LSA bone assemblages, it transpires that eland, buffalo, and suids are not underrepresented (Faith 2008). Moreover, the preferred exploitation of eland over most other animals including suids and buffalo is expected from an economic perspective (Dusseldorp 2010). The most parsimonious interpretation is that MSA people hunted the most attractive prey; not because of a lack of hunting skill but because it is the sensible thing to do. The regular presence of buffalo at their sites demonstrates that they could deal with dangerous animals if needed. Further, the excavation of faunal assemblages under controlled circumstances from other sites such as Blombos Cave, Klipdrift Shelter, and Sibudu (Clark and Plug 2008; Henshilwood et al. 2001; Badenhorst, Van Niekerk, and Henshilwood 2016; Reynard et al. 2016) has yielded increasing evidence for the efficient exploitation of a broad range of mammal species.

Hunting Weapons

Stone tools and surface marks on bones from archaeological sites are used to infer the types of hunting strategies and weapons that were used. Although most of the surface marks on bones reflect butchery and carnivore feeding, some reflect the impact of hunting weapons. In addition to fragment of stone points embedded in giant buffalo bones, hunting lesions on bones have also been found. O’Driscoll and Thompson (2018) dubbed these “projectile impact marks.” Three instances of such marks have been recognized at the Pinnacle Point site. The oldest MSA deposits at the site from around 160,000 years ago contain at least one such mark. Comparison to experimental hunting damage on animal bones suggests that all three recognized marks at Pinnacle Point are characteristic of handheld spears (O’Driscoll and Thompson 2018). The dimensions of MSA point types as well as the edge damage on such points have been interpreted to demonstrate the use of handheld spears from the Middle Pleistocene onward (Villa and Lenoir 2006; Wilkins et al. 2012; Mohapi 2012).

Finely worked bifacial leaf-shaped (lanceolate) points from about 80,000 to 70,000 years ago appear in the archaeological record across southern Africa. This is the type found at the Still Bay technocomplex (see the article "Southern African Stone Age"). These points have a relatively broad base that tapers toward the tip and are generally considered to have been used as spear tips. Their use as arrowheads has also been suggested for similar pieces from pre–Still Bay levels at Sibudu Cave (Rots et al. 2017). The presence of Still Bay points shows the importance of encounter hunting with handheld spears at this time.

New weapon systems appear to have been developed about 70,000 years ago. The Howiesons Poort technocomplex (from ~70,000 to 50,000 years ago) is characterized by microlithic tools: small lithics generally less than 3 cm long (see the article "Howiesons Poort"). These lithics were probably hafted or glued to bone or wooden shafts to make effective spears, knives, scrapers, or complex weapon systems. The most characteristic artefacts of the Howiesons Poort technocomplex are so-called segments. These artefacts are "backed", i.e., one side of the tool is repeatedly struck to produce a blunted edge opposite a sharp edge. These artefacts likely functioned as arrowheads (Fig. 5). Examples from Sibudu Cave and Umhlatuzana Rock Shelter have dimensions consistent with those of ethnographically known arrowheads and show both hafting adhesives and damage likely caused by high-velocity impact (Lombard and Phillipson 2010; also see Lombard 2020). Bow and arrow are thought to be better suited to exploit small-bodied ungulates, and these increase in importance at some sites during this period (see Dusseldorp 2014). Not all dimensions of backed segments may be suitable for arrowheads, and size variation is exhibited between different raw materials (Wadley and Mohapi 2008). However, Lombard (2020) demonstrates that large portion of Howiesons Poort segments fit the dimensions of ethnographically known arrowheads. In addition, some bone points from the Howiesons Poort and especially the LSA are indistinguishable from ethnographically known arrowheads (Backwell, d'Errico, and Wadley 2008; Bradfield et al. 2020; d'Errico et al. 2012).

***Figure 5**. Howiesons Poorts segment in quartz from Sibudu Cave, demonstrating use traces pointing to their use as arrowheads.*
Source: Photographs by Marlize Lombard, used with permission.

The spear thrower apparatus, or atlatl, is not definitively known from the Pleistocene of southern Africa. This weapon system releases javelins of darts at high velocity and allows hunting from distances of around forty m (Churchill 1993). Its use is well attested in the European Upper Palaeolithic and in American and Australian prehistory and ethnography. Although unknown ethnographically from the

African continent, the dimensions of some larger backed segments, as well as some MSA points such as bifacial points from the Still Bay complex, are argued to fall within the range of ethnographically known atlatl darts (Churchill and Rhodes 2009; Schoville et al. 2017; but see Lombard 2020; Lombard and Shea 2021).

A poison applicator from the earliest LSA layers (~40,000 years ago) at Border Cave provides positive evidence for the use of poison. This element of Late Pleistocene weapon systems may be substantially older. Comparative analysis of the dimensions of ethnographic stone arrowheads with poison residue still adhering to them and backed microliths from the MSA shows that assemblages from Sibudu, Rose Cottage Cave, and Pinnacle Point from 70,000 to 58,000 years ago are similar in size and shape to those of ethnographically known poisoned arrowheads (Lombard 2020). The use of poison allowed the exploitation of large-bodied prey with relatively small projectiles. This innovation may therefore have originated in the second half of the MSA.

Intensification

Intensification refers to the investment of more energy in foraging to increase the amount of food extracted from the environment (Morgan 2015). People are assumed to preferentially exploit animals that are more "profitable." In other words, given the amount of time and effort taken to conduct hunting expeditions, foragers often focus on larger prey with more meat. However, if large animals become less common, the chances of coming across this prey diminishes. Therefore, "encounter rates" with such species may be low, and the success rate for hunting them may be even lower. This can lead to the addition of smaller, less meaty species to the diet to ensure a sufficient supply of food (see Dusseldorp 2010, 2012a).

Although the exploitation of large animals in the long run leads to the highest return rates, this comes at the price of an insecure food supply. Ethnographic studies on contemporary hunter-gatherers, for example, demonstrate that hunting success for large game may be as low as 3 percent for the Hadza in East Africa (Hawkes et al. 1991). To mitigate these risks, groups like the San in the Kalahari use snares to hunt small game.

The causes of intensification may vary. Shifting environmental conditions, the changing availability of plants and animals, human population expansions, and technological developments may all result in intensification (Morgan 2015).

Increasing Diet Breadth

Intensification is generally linked to the exploitation of a wider range of species. By adding smaller or more difficult-to-catch animals to the diet, known as expanding the diet breadth (Dusseldorp 2012a), more food becomes available. An example of this is the "broad-spectrum revolution," (Stiner 2001, 6993) which was long thought to immediately precede the development of food production (Stiner 2001). However, the southern African archaeological record shows that diversification has deep roots in the Late Pleistocene.

A distinction between slow-moving and fast-moving small prey has been applied to intensification, on the assumption that small moving prey, such as tortoises and mollusks, are easier to exploit (Stiner, Munro, and Surovell 2000). Tortoise exploitation is attested at Pinnacle Point from the late Middle Pleistocene occupations (~160,000 years ago) onward. Here, few tortoises are represented, and part of the assemblage was likely brought in by predators (Thompson 2010). During the Late Pleistocene, tortoises are present in much larger numbers at some sites. The large tortoise assemblage at Blombos Cave has been subjected to detailed taphonomic analysis, which showed it was accumulated largely by people occupying the site rather than by carnivores (Thompson and Henshilwood 2014b). However, due to their small size, the nutritional value of tortoise was limited (Thompson and Henshilwood 2014a).

Tortoises are slow-growing animals and Stone Age people were more likely to capture the largest tortoises available. Thus, size reduction of tortoise bones through time can provide archaeological evidence of over-exploitation. Examination of tortoise upper leg bone size demonstrates that MSA exploitation remained small scale, compared to that in the (Holocene) LSA. A significant decrease in tortoise size has only been documented in LSA deposits (Klein and Cruz-Uribe 1983, 2000). This could be due to increased exploitation pressure, but it may also be related to environmental factors stimulating slower growth patterns in the warm Holocene compared to the last Ice Age. In sum, tortoise was a reliable prey, present in relatively high numbers around MSA sites, but its exploitation was not intense enough to be reflected in its population structure.

Fast-moving prey such as small mammals and birds is generally considered more difficult to exploit. Although present during the Middle Pleistocene, small mammals, such as small antelope and rock hyrax, are more commonly represented in Late Pleistocene MSA assemblages (Thompson 2010). Rock hyrax (Fig. 6) especially appears to have been heavily exploited at some sites (Badenhorst 2014).

Figure 6. *Rock hyrax at Cape Point Nature Reserve, Western Cape, South Africa.*
Source: Photograph by Gerrit Dusseldorp.

Small solitary animals can be exploited using encounter strategies that were similar to those applied to larger species. Nevertheless, the exploitation of new species often requires behavioral or technological innovations (see e.g., Dusseldorp 2012b). The development of new weapons systems during the Late Pleistocene can thus be viewed as another expression of the development to increase the efficiency of food production from the landscape. Other capture-aiding equipment was also developed.

Snares, Traps, and Nets

Lyn Wadley (2010) proposed the early adoption of snares and traps during the Howiesons Poort at Sibudu. A large, small-mammal assemblage was recovered from these occupations containing a diverse range of small carnivores. Small carnivores are not usually exploited for food, but the use of snares leads to species being randomly captured, which may result in their archaeological presence. Carnivore remains were also recovered from other Howiesons Poort sites, such as Klipdrift Shelter and Diepkloof. At Diepkloof, there is an abundance of cut-marked carnivore bones in the Still Bay and Howiesons Poort layers (Val et al. 2020). These marks are positioned in a way that suggests the carnivores were exploited for their pelts. It is likely that these nocturnal, solitary, and dangerous felines were caught in traps. The representation of nocturnal animals, which are difficult to exploit without domestic dogs, provides an additional argument for the use of snares and traps. Nocturnal species are also well-represented at other MSA sites prior to the Howiesons Poort (e.g., Klasies River, and Blombos Cave). Traps may thus have been used from at least MIS 5 onward (Van Pletzen 2000; Dusseldorp and Langejans 2015).

The abundance of small antelope in the Howiesons Poort of Sibudu Cave, mainly red (Cephalophus natalensis) and blue duiker (Philantomba monticola), suggests the use of net-hunting. With a pursuit hunting strategy, these small solitary animals living in bushy environments are less attractive prey than larger herd-living animals (Dusseldorp 2014). A more efficient way to capture such prey is in communal drives, which guide the animals into nets that have been installed (Clark and Plug 2008). The presence of large numbers of bird remains at Sibudu may also point to the use of nets (Val, de la Peña, and Wadley 2016).

Intensification and evidence of snaring, trapping, and netting may not only reflect environmental change or population pressure; it may also be linked to changing gender roles. In contrast to the hunting of large herbivores, trapping small animals and collecting tortoises is more closely associated with gathering activities such as shell fishing, digging up plant roots, or fruit harvesting (Marlowe 2007; Yellen, 1991). Thompson (2020) has argued that the focus on large herbivore hunting in MSA research has placed more emphasis on the subsistence activities of men, rather than of the community as a whole. Acknowledging the importance not only of large prey but of the shift to exploiting smaller animals that are reliably present from at least the Still Bay period onward may also highlight the increasing role that women played in animal exploitation activities (see Dusseldorp and Langejans 2013).

Aquatic Resources

Aquatic settings provide rich and reliable resources, such as mollusks, fish, and aquatic mammals, as well as an important avenue for intensification. These settings allowed some hunter-gatherer societies to develop high population densities. The exploitation of marine resources is well attested at many of the Late Pleistocene near-coastal sites in South Africa. Marean (2015, 2016) suggests that the predictability and defensibility of these resources may have triggered the development of territoriality and created selective pressure for intensive cooperation in human societies. This in turn may have spurred Homo sapiens' global dispersal.

The archaeological visibility of marine resource exploitation is strongly dependent on Pleistocene climates. During Ice Ages, seawater was trapped in expanding glaciers and ice near the poles and continental sea levels receded. This means that many of the locations where marine foods were exploited during the last Ice Age are submerged. Taking this limitation into account, the MSA archaeological record still provides crucial evidence for the development of coastal foraging strategies by modern humans (Marean 2014; Will, Kandel, and Conard 2019).

The most abundant remains of marine exploitation are mollusks that are present at many coastal and near-coastal sites. The oldest southern African evidence for mollusk foraging occurs at Pinnacle Point (from 160,000 years ago onward; Jerardino and Marean 2010). Some occupation layers at Blombos Cave, Klasies River, Ysterfontein, and Klipdrift contain very large proportions of shellfish, sometimes over 100 kg/m3 of sediment (Langejans et al. 2012; Henshilwood et al. 2014; Marean 2014; Niespolo et al. 2021).

The larger exploited species were found relatively far offshore in the so-called infratidal zone. This zone was only accessible at very low tides. So, to exploit these species, people needed to schedule their mobility to ensure that they were at the coast at spring low tides (Marean 2011; Langejans et al. 2012; De Vynck et al. 2016). Geochemical analysis of the composition of mollusks also suggests that MSA people timed shellfish exploitation seasonally (Loftus et al. 2019).

The mainstay of exploitation in many occupation phases is the brown mussel (Perna perna) living on rocky shores. This species can easily be mass collected (Langejans et al. 2012). Mass collection of prey items is one way in which the efficiency of intensification strategies can be increased (Ugan 2005). In locations such as Pinnacle Point, the shoreline is dominated by sandy beaches that are less productive than rocky shores. Hence, the much lower shellfish densities during the Middle Pleistocene occupations at this site cannot be interpreted as reflecting less sophisticated foraging behavior but rather suggest less emphasis on aquatic foraging.

Yet, although mollusks are abundant at sites, it is important to realize that their large numbers still represent relatively few consumed calories (Kyriacou 2017). The entire shellfish assemblage of the M2 phase at Blombos has been calculated to represent the same caloric contribution as the meat weight of a single bontebok (Clark and Kandel 2013). Therefore, the mainstay of animal exploitation was clearly large herbivores.

Nevertheless, the quantity of shellfish remains at sites cannot be directly equated to the intensity of their exploitation. Their archaeological visibility also depends on other factors. As global temperatures decreased, the importance of shellfish in the deposits, such as those at Klasies River, appears to decrease during the Howiesons Poort period. There are indications that this may represent a difference in archaeological visibility and not in decreased dietary importance. It appears that transport was selective and fewer mollusk remains ended up at what was becoming an inland site. One indication of this is in the transport of giant periwinkle (Turbo sarmaticus), a sea snail consisting of a shell with a "trapdoor" (operculum) closing the opening. Relatively more operculum remains are found from later phases at Klasies River. This means that people left the heavy shell at the beach and only brought the shell meat with the operculum attached to the site (see Dusseldorp and Langejans 2013; Langejans et al. 2012; Thackeray 1988).

After Howiesons Poort, shellfish exploitation decreased and is archaeologically almost invisible. At the coldest part of the last Ice Age, the shore shifted over 100 km seaward. The sites where people ate shellfish at this time became submerged during the Holocene. When global temperatures started rising, the shoreline shifted to its modern position. By about 14,000 years ago, the coast was close enough to its current location for shellfish collection to becomes archaeologically visible again at sites such as Klipdrift Cave and Nelson Bay Cave (Klein and Steele 2013; Loftus et al. 2016; Ryano et al. 2019). At this time, the sea was still much lower than in the Holocene. This is demonstrated by the presence of black mussels at Nelson Bay Cave. This cold-loving species currently lives mainly on South Africa's west coast where the sea is colder. But at the end of the last ice age, it evidently extended its range to the south coast.

Marine mammal bones, mainly from Cape fur seal (Arctocephalus pusillus) (Fig. 7), are also present in the deposits at coastal MSA sites. At Pinnacle Point they occur in modest numbers, but in later sites like Klasies River and Blombos they are the most common single mammal species in some occupation phases (Thompson 2010; Van Pletzen-Vos et al. 2019; Dusseldorp and Langejans 2013; Reynard and Henshilwood 2019). Currently, seal colonies are located mainly at offshore islands, probably in response to human and carnivore hunting. This means that it is difficult to target seals for exploitation except at the time when one-year-old pups are weaned and wash up on the beach (Klein et al. 1999). The representation of seals at MSA sites may reflect a different distribution of seal colonies prior to the retreat of the sea during the last Ice Age. Larger individuals are frequently present. Their frequency, especially of the largest size class, is too high to be explained only as the result of scavenging washed-up individuals (Dusseldorp and Langejans 2013).

Figure 6. *Cape fur seal, Blombosfontein Nature Reserve, Western Cape, South Africa.*
Source: Photograph by Gerrit Dusseldorp.

Cetaceans, whales, and dolphins are represented in very small numbers. These large animals wash up intermittently along the South African coast. They represent a sizable but unpredictable food resource. Although whale meat was likely never a major component of MSA or LSA exploitation strategies, it is likely that their role was more important than suggested by their bones alone. The presence of whale barnacles (barnacle species that only occur on whales) in MSA deposits at Pinnacle Point shows that sometimes whale meat was brought to sites without any bones (Jerardino and Marean 2010).

Fish are rare at Late Pleistocene coastal sites compared to mollusks. However, analysis of fish remains does establish that they were acquired by humans at Klasies River and Blombos Cave, rather than being brought in by birds (Van Niekerk 2011). In highland Lesotho, freshwater fish were first exploited during the Late Pleistocene. At the sites of Sehonghong and Likaoeng, large numbers of fish remains have been found in layers dating to the early part of the LSA. They were likely acquired when people exploited spawning runs up the Gariep and its tributaries (Plug and Mitchell 2008; Pargeter and Dusseldorp 2022). Their exploitation represents the mass collection of a very rich resource and is an important intensification option in inland areas (Stewart and Mitchell 2018).

Subsistence Behavior through Time

The Environmental Context

The southern African environment was a key factor in Stone Age hunting and food-getting strategies. Onshore, the warm Agulhas ocean current travels south down the eastern coast meeting the cold, west coast Benguela current along the southern Cape. The Drakensberg mountain range traverses the north–south spine of the subcontinent, separating the region into a wetter east and dryer west. Rainfall is highly seasonal with most of the country receiving much of its rainfall (>66%) in summer, while a zone along the west coast is characterized by the opposite pattern with most rainfall in winter (Lennard 2019). Vegetation ranges from savannah in the north and northeasterly regions to more forested environs in the east and in areas on the southern coast (refer to Fig 1. for vegetation zones). Grasslands dominate the central Highveld and Lesotho highlands. Much of the interior is arid with sparse rainfall, including the succulent-dominated Karoo, the deserts of Namibia, the Kalahari of the morthern Cape and southern Botswana, and the west Cape coast (Mucina and Rutherford 2011). The Cape Floristic Region—encompassing the southern and southwestern Cape of South Africa—is generally temperate with winter-dominated rainfall in the west becoming more summer-dominated in the east. This Mediterranean-like environment is dominated by fynbos—an evergreen, sclerophyllous shrub—but also encompasses temperate forests in wetter regions and succulent-dominated vegetation in the dryer interior (Bergh et al. 2014).

Palaeoclimatic records show a significantly different environment in the past (Knight 2020). The arid interior of South Africa, for example, was likely wetter for much of the Pleistocene than it was in historic times (e.g., Wilkins et al. 2021). Brink (2016) argued that increased moisture during the Middle Pleistocene is indicated by the presence of lechwe (Kobus leche), hippopotamus (Hippopotamus amphibius), and Bond's springbok (Antidorcas bondi) in the interior of southern Africa and is associated with extensive, >300,000-year-old wetlands. The Cape Floristic Region was also considerably different. The southern Cape sits at the edge of the Agulhas Bank—the wide, shallow continental shelf off the southern African coast. Lower sea levels during Ice Age periods resulted in the exposure of large areas of land in the southern Cape. This additional land was probably dominated by expansive grasslands that attracted herds of grazing herbivores, such as wildebeest (Connochaetes taurinus), hartebeest (Alcelaphus buselaphus), and zebra (Equus quagga) (Cowling et al. 2020; Marean et al. 2020). Thus, during glacial periods with lower sea levels, the grasslands and productive environment of the southern Cape coastal plain would likely have been an ideal region for hunting and foraging.

Late Middle Pleistocene (~500–130,000 Years Ago)

Archaeological evidence for active hunting during the mid-Pleistocene in southern Africa is ambiguous, but this may reflect the scarcity of sites. Stone points recovered from Kathu Pan near Wonderwerk Cave may have been hafted and used as spear tips around 500,000 years ago (Wilkins et al. 2012). This shows that spear hunting began long before the appearance of Homo sapiens.

Except for Pinnacle Point, no well-studied rock-shelter bone collections are available. Instead, most assemblages from this period are from open-air sites, where natural deaths and episodes of human and carnivores activities are very difficult to unravel (Hutson 2018; also see Smith et al. 2019).

The ancient wetland environments of the interior may have acted as animal traps for Middle Pleistocene human hunters. Indeed, many interior sites dated to the mid-Pleistocene occur on the edge of wetlands, pans, or other bodies of water. Tooth marks are prevalent on animal remains from these sites, suggesting they were the result of carnivore kills. Yet, it is also likely that early human hunters exploited these wetland environments to aggressively scavenge prey from these predators or hunt trapped animals.

There is some evidence of an increase in human carcass processing through time across the Middle Pleistocene. Two early MSA open-air sites in the interior—Pniel 6 (>300,000 years ago) and Florisbad "Old Collection" (~260,000)—represent situations where carnivores may have accumulated part of the assemblages, while hominin marks are present in relatively small numbers (Brink 1987; Hutson 2018). At nearby Bundu Farm (300,000–200,000 years ago), hominins may have accumulated the bone collection, which was then scavenged by carnivores (Hutson 2018). At Wonderwerk Cave, in layers dating between 240,000 and 150,000 years ago, large ungulates such as zebra, alcelephines, and kudu are common. While it is difficult to tell how much carnivores contributed to the assemblage, many of the bones are burnt, suggesting that humans played a large role in accumulating these faunal remains. However, stone tools from these layers lack the characteristics of complex hunting equipment evident in the later MSA (Chazan et al. 2020). It is important to note that early human subsistence strategies are much more difficult to evaluate compared to later periods because of the paucity of sites and their very different depositional contexts (open-air versus caves and rock shelters).

Marine Isotope Stage (MIS) 6, an Ice Age or glacial period from about 190,000 to 130,000 years ago, was likely a significant period in modern human evolution. MIS 6 was probably one of the coldest glacial periods in this region. Human groups would have been under substantial stress and were likely small at this time. In the southern Cape, this Ice Age resulted in a vast exposed area of the southern coastal plain as sea levels receded (Marean et al. 2014). Human populations may have focused their foraging strategies on coastal habitats. Given these relatively small populations, archaeological sites dated to MIS 6 are rare and, in the southern Cape, most of the occupational camps from this period are underwater.

Pinnacle Point yielded some of the earliest evidence of shellfish exploitation and ochre processing ~160,000 years ago (Marean et al. 2007). The site also provides clear evidence of active hunting during the later part of the Middle Pleistocene (O'Driscoll and Thompson 2010). This demonstrates that the complex taphonomy of Middle Pleistocene open-air assemblages, which often precludes interpretations of active encounter hunting by humans, does not provide definitive evidence of the absence of encounter hunting.

The fatty marrow from long bones has always been consumed by hominins. Because fatty acids are rare in nature but critical for human sustenance, fat was likely just as important as meat when early humans targeted large game (Speth 2010; Speth and Spielman 1983). Indeed, hammerstone percussion-marked bones show that marrow extraction was common during this period. At Pinnacle Point, the MIS 6 layers show people focused on large bovids, including the processing of long bones for marrow. Smaller bovids the size of the Cape grysbok (Raphicerus melanotis) appear to have been exploited more opportunistically and not systematically (Thompson 2010).

Border Cave, near Eswatini, has yielded important archaeological evidence that may underscore early human subsistence behavior. Burnt bedding from the 200,000-year-old layers and cooked starchy rhizomes dated to 170,000 years ago show that people during this period used fire for food preparation (Wadley et al. 2020a, 2020b). This emphasizes the Middle Stone Age exploitation of varied food sources. The rhizomes are located underground and are inaccessible to many nonhuman animals in the landscape. The cooking of these rhizomes also aids in digestibility. This type of behavior would have laid the groundwork for more complex subsistence strategies and task specialization that became more evident during the later Pleistocene.

Late Pleistocene (~130,000–30,000 Years Ago)

From about 130,000 years ago, people became the main contributors of faunal remains at most archaeological sites and there is more evidence of planned, large herbivore hunting encounters. Debates on the hunting strategies of MSA people often focus on the representation of the very large buffalo and eland. Nevertheless, in many assemblages the mainstay of human exploitation was bovids weighing anywhere from 23 to 296 kg (i.e., kudu, wildebeest, reedbuck, depending on the environmental context of the site) (fig. 8), while in others small animals dominated (Klein 1976; Clark and Kandel 2013; Reynard et al. 2016).

At Florisbad, the more recent “MSA Assemblage”—dated to ~121,000 years ago—appears mainly accumulated by people in contrast to the older assemblages. Given the location at a spring eye, the site was probably used for ambush hunting (Brink 1988). Large herbivores are often prime-aged adults, and cut marks on bones indicate that people had primary access to the meat. While large herbivores were generally the preferred target of encounter hunting, there is some evidence of an increase in smaller bovids at some sites.

At Klasies River, an abundance of large antelope is clear evidence of active hunting by modern humans. Previous interpretations of limited hunting proficiency or scavenging as the main animal exploitation strategies are no longer widely supported. Taphonomic analyses of the ~100,000-year-old layers from the Wurz excavations at Klasies show that carnivore tooth marks are more common on small Raphicerus-sized bovids than on larger eland-sized herbivores (Lap 2020). This suggests that smaller bovids were probably accumulated by both people and carnivores, such as leopards or hyenas. In contrast, larger bovids display more cut marks, which indicates that encounter hunting was an important strategy.

***Figure 8**. Kudu at Isimalingo wetland park, KwaZulu-Natal, South Africa.*
Source: Photograph by Gerrit Dusseldorp.

Blombos Cave was occupied between ~110,000 and 70,000 years ago. An abundance of fauna recovered from the site provides a relatively good understanding of changing hunting patterns (Thompson and Henshilwood 2011, 2014a, 2014b). Larger herbivores are common in the occupations at ~100,000 years ago. Diagnostic impact fractures on lithic flakes in those layers suggests that these tools were used as spear tips and that active, large game hunting was common by this time (Lombard 2007). The relative abundance of percussion-marked bone in these layers also suggests that the extraction of bone marrow was an important strategy.

The Still Bay period (~80,000–70,000 years ago) appears to correspond with an increase in smaller antelope recovered from archaeological sites. The large number of blue duiker in the Still Bay and pre–Still Bay layers (~77,000–71,000 years ago) at Sibudu Cave suggests that game drives or snaring and trapping were used before the Howiesons Poort at that site (Clark 2019). At Blombos Cave, small, Raphicerus-size bovids are more common in the Still Bay than in the preceding ~100,000-year-old layers. By the later Still Bay period, small animals were even more prevalent at Blombos, although the low number of cut marks on small fauna suggests that some of these animals were probably collected by carnivores rather than people (Reynard and Henshilwood 2019). Similarly, from about 100,000 years ago at Pinnacle Point, smaller bovids became more common (Thompson 2010). The prevalence of small animals and nocturnal species at Blombos and Klasies River implies that, in addition to encounter hunting, trapping may have been used to collect prey (Dusseldorp and Langejans 2015). During the Still Bay period, large herbivores remained a key source of food, with some evidence that the meat may have been dried for storage (Reynard and Henshilwood 2019).

The mass exploitation of large antelope (e.g., through game drives and pit traps) was an important feature of human hunting strategies in the Late Pleistocene throughout southern Africa. Evidence of large antelope is common in the >70,000-year layers at sites like Bushman Rock Shelter (Badenhorst and Plug 2012). At Redcliff Cave in Zimbabwe, mortality patterns of large herbivores show that most of the antelope at the site had "catastrophic" mortality patterns, suggesting that many herd game were probably caught by traps or in game drives (Klein 1978; Cruz-Uribe 1983). Redcliff contains archaeological material dated to the "Bambata" and "Tshangula" periods in Zimbabwe. Bambata stone tools (~95,000–30,000 years ago), including unifacial and bifacial points, were often categorized as part of the "Stillbay" stone tool tradition in earlier studies. The Tshangula (~35,000–20,000 years ago) site contains microlithic tools and resembles the Howiesons Poort farther south (Wurz 2021).

The appearance of the Howiesons Poort period between about 70,000 and 50,000 years ago is associated with a significant change in the way Stone Age people exploited animals. The use of microlithic technology shows that people at this time were effective spear and, likely, bow hunters who were able to exploit a wide range of prey. In fact, this period is associated with a prevalence of small, Raphicerus-sized antelope across many southern African sites (Clark and Kandel 2013). Yet, although an abundance of small animals suggests the introduction of mass collection techniques, large herbivores were still a critical source of food. The occurrence of ostrich eggshell containers with similar engraved designs during the Howiesons Poort at Diepkloof Rock Shelter and Klipdrift Shelter is potential evidence that social networks were linked over a vast region (Douze et al. 2018). In fact, these ostrich eggshell containers are a form of water transportation technology (i.e., the ability to transport water across vast distances) that, combined with the pursuit of migratory herds across the landscape may have been key to establishing ties between these groups and extending social networks (Reynard 2021).

Larger herbivores become more common again in the post–Howiesons Poort (or Sibudan; see the article "Sibudan") period some 50,000 years ago. While this probably reflects environmental conditions associated with more open, grassy landscapes, it also shows how effectively people adapted to changing environments. On the whole, occupational intensity at many sites began to decrease at this time, which may relate to more arid or unproductive environments (Faith 2013). Yet, the changing environment and disappearance of microlithic technology during MIS 3 (~60,000–29,000 years ago) does not signal a break in subsistence practices after the Howiesons Poort. There is still evidence of intensification practices at some sites. At the early LSA occupations (~44,000–41,000 years ago) at Border Cave, for example, over 40 percent of animals are bushbuck-sized antelope, suggesting that people there concentrated on a particular species and may well have used mass-collection techniques such as netting or trapping to hunt prey.

Middle Stone Age Adaptation to Extreme Environments

The Late Pleistocene also saw people adapting to extreme environments. A number of MSA sites are known in arid Namibia. Apollo 11 demonstrates pulsed occupation with MSA deposits overlain by Still Bay, Howiesons Poort, Late MSA, and early LSA levels. These occupations were characterized by arid conditions comparable to those that prevailed in the early 21st century. Hiatuses between the deposits likely correspond to more arid phases. Some of the smallest fauna at the site is likely not anthropogenic, but carnivore marks are rare on the bones (Vogelsang et al. 2010). Human exploitation focused heavily on small animals, and hare and rock hyrax are well represented. Larger species are scarce, but klipspringer, springbok, and equids also occur (Thackeray 1979; Vogelsang et al. 2010). The exploitation of hare and hyrax is also evident at Zebrarivier (undated) and Pockenbank (lowest MSA undated, higher units yield radiocarbon dates suggesting calendar ages in MIS 3 [Vogelsang 1998]). Pockenbank has possible evidence of gemsbok, and both sites include remains of equids and klipspringer (Thackeray 1979; Cruz-Uribe and Klein 1983). A similar arid context is represented by Spitzkloof in the semidesert of Namaqualand, which was occupied intermittently from >50.000 years ago. Here, no rock hyrax is in evidence, but small numbers of mostly small antelope and gemsbok are accompanied by large numbers of tortoise (Dewar and Stewart 2012, 2017). Spitzkloof, Pockenbank, and Apollo 11 also yielded large numbers of ostrich eggshell fragments. Although some may have been used to produce jewelry, they were probably exploited for nutrition. At Spitzkloof the Ostrich eggshell assemblages total <200 grams, which is less than the weight of a complete ostrich egg (Dewar 2012 & Stewart). However, over 7 kg is present at Pockenbank and more than 3 kgs at Apollo 11 (Vogelsang 1998). This still represents rather small amounts of food relative to the antelope in the assemblages, but it does indicate a broadening of the resource base.

The Kalahari in northern Botswana also yielded Middle Stone Age archaeological occurrences. ≠Gi (~77,000 ka) occurred in an ephemeral channel during semiarid conditions. The accumulation of large mammals at the site suggests it may have functioned as an ambush hunting stand (Brooks et al. 2006; Helgren and Brooks 1983). White Paintings Shelter in the Tsodilo Hills provides evidence of MSA occupations relatively close to the Okavango Delta. MSA sediments and sediments containing both MSA and LSA materials, which are assumed to be transitional between the two, have yielded fish bones. These were rare in the MSA, but large numbers have been recorded in levels assumed to represent transitional and Pleistocene LSA occupations (Robbins et al. 2000). Nevertheless, refitting analysis of lithic materials at the site demonstrated large-scale vertical movement of artifacts (Staurset and Coulson 2014), which means fish remains in the Middle Stone Age may have percolated downward from Pleistocene LSA deposits.

End and Terminal Pleistocene (~30,000–12,000 Years Ago)

The Last Glacial Maximum during MIS 2 (~29,000–14,000 years ago) was a particularly cold Ice Age period globally and may have corresponded to drier more drought-prone environments in southern Africa. Sites dated to this period on the southern Cape coast are rare—probably because shorelines had retreated extensively and most previously occupied archaeological sites were located on the now-submerged coastal shelf. In the interior, deposits dated to this period are quite sparse, which may reflect lower or less frequent occupations at this time. From about 20,000 years ago, many sites such as Nelson Bay Cave in the southern Cape, Strathalan near the Drakensberg, and Grassridge Rock Shelter in the Eastern Cape show a dominance of large, grazing herbivores. The prevalence of grazers probably reflects more open, grassier environments. However, there was a significant increase in small animals such as tortoise, rock hyrax, and small, Raphicerus-sized antelope at those sites (Klein 1972; Opperman 1987). It is likely that the abundance of small animals there is a result of increased faunal intensification. It is also possible, however, that carnivores occupying sites during periods with lower-intensity human occupation may have contributed to this abundance. Despite the lack of taphonomic analyses of these assemblages, the use of snares, traps, and other remote capture technology probably played a key role in small animal abundance at these sites (Klein 1972).

One of the key differences in archaeofaunas between Pleistocene and Holocene sites is a notable decrease in megafauna in the Holocene. Megaherbivores are large herbivores weighing more than 1,000 kg, such as elephant, hippo, giraffe, and rhino. Unlike other continents, megaherbivores still dominate African environments. Extinct megaherbivores such as the long-horned ("giant") buffalo (Syncerus antiquus), the giant wildebeest (Megalotragus priscus), and the Cape horse (Equus capensis) are quite common in southern African Pleistocene assemblages, but they had disappeared by the mid-Holocene (Klein 1980; Faith 2014). The causes of these extinctions has generated intense debate among scholars. The rapid pace of megaherbivore extinctions over the Pleistocene–Holocene transition raises essential questions over whether humans or environments were the key drivers of these extinctions. The stone tip embedded in a giant buffalo at Klasies shows that early humans were capable of hunting these megafauna over 100,000 years ago (Milo 1998). It has been argued that increases in human hunting efficiency and advanced technology in the LSA contributed significantly to megafaunal extinctions in the Holocene, including in Africa (Klein 1980; Lyons, Smith and Brown 2004). However, African megaherbivore extinctions preferentially affected species that were grazers or preferred grasslands (Faith 2014, 105). The current consensus is that significant rises in temperatures and environment change from the Pleistocene to the Holocene in southern Africa would have played a critical role in the demise of these megafauna (Brink 2016; Faith 2014).

The introduction of LSA technology, such as microliths and fishing tools, likely had a significant impact on foraging behavior at this time. Occupation of high-altitude sites, such as those in Lesotho, suggests the expansion of the territorial ranges of Stone Age people into more arduous environments. The introduction of large numbers of fish at Sehonghong in highland Lesotho around the peak of the last Ice Age demonstrates that efficient exploitation strategies for new resources were being developed at this challenging time (Plug and Mitchell 2008; Pargeter and Dusseldorp 2022). This is reinforced by the presence of large numbers of fish bones during the Late Pleistocene LSA at White Paintings Shelter in Botswana (Robbins et al. 2000).

Plug (1997, 2017) has argued that the types of animals recovered from archaeological sites during the LSA show that people linked their hunting excursions to animal migratory patterns. It is also likely that foragers may have used game drives to focus on specific prey. Holocene "desert kites" (stone-walled structures used to funnel game to specific areas) discovered in the Northern Cape Province and a mass kill site of springbok at the site of SK400 in Namaqualand suggest that herds of springbok may have been targeted (Dewar et al. 2006; Lombard et al. 2021). It is not unreasonable to imagine that this kind of targeting began prior to the Holocene.

***Table 1.** Overview of the Chronological Periods Used and the Main Developments in Faunal Exploitation Strategies Observed*

Period	Ages	Associated exploitation strategies	Key references
Middle Pleistocene: Early Middle Stone Age	~300,000–130,000 years ago; MIS 8–6)	Mainly open-air assemblages Pinnacle point shows primary access by people	Jerardino and Marean 2010; O'Driscoll and Thompson 2018; Wilkins et al. 2012; Thompson et al. 2010

		Handheld spears, possibly stone tipped Beginnings of shellfish exploitation	
Late Pleistocene: Klasies River, Mossel Bay and Still Bay technocomplexes	~130,000–70,000 years ago; MIS 5	More assemblages from rock shelter Primary access by humans (e.g., Klasies River, Blombos Cave) Taphonomic signals often suggest carnivore contribution to small mammal bones in bone assemblages, but small species such as rock hyrax also exploited by people Bow and arrow proposed (e.g., backed pieces at Pinnacle Point, points from Sibudu Cave) Traps used? (nocturnal animals well represented) Intensive marine exploitation	Thompson and Henshilwood 2011; Langejans et al. 2012; Badenhorst et al. 2016; Dusseldorp and Langejans 2015; Wadley 2015; Rots et al. 2017; Van Pletzen-Vos et al. 2019; Lombard 2020
Late Pleistocene: Howiesons Poort technocomplex	~70,000–50,000 years ago; MIS 4	Intensive exploitation of small ungulates (Sibudu) and other small mammals (Hyrax Die Kelders); intensification of butchery (Klipdrift Shelter) Snares and traps proposed Bow-and-arrow hunting (bone points from Sibudu and Klasies River) Intensive marine exploitation (Klipdrift)	Clark and Plug 2008; Clark 2017; Lombard and Phillipson 2010; Wadley 2010; Reynard and Henshilwood 2017; Armstrong 2016; Bradfield et al. 2020
Late Pleistocene: final Middle Stone Age, Post–Howiesons Poort (Sibudan technocomplex)	~60,000–40,000 years ago; MIS 3–2	At some sites increase in large-bodied animal exploitation Continued evidence of pit trap/game drive hunting (Redcliff) In western part of South Africa, decrease in occupation intensity? Lowering of sea level means little information on marine exploitation	Cruz-Uribe 1983; Clark and Plug 2008; Langejans et al. 2012; Langejans, Dusseldorp, and Thackeray 2017; Dusseldorp 2014; Collins 2016; Clark 2017
End Pleistocene: Early Later Stone Age	~40,000–18,000 years ago; MIS 3–2	Few faunal assemblages Large mammal hunting Introduction of freshwater fish, large	Plug and Mitchell 2008; Pargeter and Dusseldorp 2022

		number of remains in some contexts (e.g., Sehonghong, Likoaeng Lesotho)	
Terminal Pleistocene: Robberg	~18,000–12,000 years ago; MIS 2	Hunting terrestrial prey dominant Small animals and tortoises at times intensively exploited (e.g., Elands Bay Cave)	Parkington 1980; Opperman 1987

Note: MIS, marine isotope stage.

Concluding Remarks

Human occupations in southern Africa dating to the Middle Pleistocene are documented mainly in open-air sites with complex taphonomic histories. The late Middle Pleistocene occurrence of Pinnacle Point provides good evidence of active hunting of antelopes, which suggests that active hunting has deep roots in southern Africa.

During the Late Pleistocene, modern human societies in southern Africa used sophisticated subsistence strategies. This included active hunting of large mammals, subsisting at many locations on the rich herbivore guild, and exploiting large numbers of medium- and large-sized herbivores. Technological innovation leading to the introduction of the bow and arrow can also be established. Although small animal remains are present in many assemblages, taphonomic studies of some bone collections shows that they were not always brought in by people. Indications of intensification in the form of the specialized exploitation of small animals are established from at least the Howiesons Poort period. However, the presence of nocturnal solitary animals in earlier deposits suggests that snares, traps, or hunting drives were used earlier, perhaps from the start of the Late Pleistocene onward. A higher degree of intensification of faunal exploitation during the later parts of the Pleistocene LSA than during the Middle Stone Age may point to increased human population size or decreased environmental productivity at this time. Although archaeological attention often focuses on terrestrial mammals, aquatic foods, especially mollusks, were heavily exploited. Other animal classes, such as birds and tortoises, have also been recovered among the food remains. During the Last Glacial Maximum, freshwater fish started to be exploited, possibly as people seasonally targeted spawning runs.

It is tempting to read a slow but steady increase of “menu diversity” into the evidence for animal exploitation strategies during the previous interglacial and the last Ice Age. However, the patchiness of the archaeological record, the complexity of taphonomic histories, and the paucity of sites make this a hazardous undertaking. It is more plausible that an adaptable population added and dropped different foodstuffs as environment, technology, and tastes changed over eons of human existence.

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