8. Late Pleistocene Subsistence Strategies and Resource Intensification in Africa

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Keywords Middle Stone Age • Later Stone Age • modern humans • Late Pleistocene • subsistence • hunting • ecology • intensification • diet breadth • prey choice

Abstract Studies in southern Africa, western Europe, and the Mediterranean Basin have documented changes in subsistence strategies and technologies during the Late Pleistocene, and have often related them to differences between the Middle and Upper Paleolithic of Europe and the Middle and Later Stone Age of Africa. However, few explicit comparisons have been made between these geographic regions to create a global view of the evolution of human diet. In this paper, we begin by documenting the state of our knowledge in coastal South Africa, where Middle Stone Age paleoecology is best documented. The lines of evidence that we consider here follow those identified by previous researchers: large game exploitation as indicated by prey mortality profiles and processing intensity; changes in the relative abundance and increasing diversity of species included in the diet, especially the addition of small, fast game such as hares, birds, and fish relative to small, slow game such as shellfish and tortoises; and changes in shellfish size reflecting intensity of collection. We then expand the discussion to include all of Africa, highlighting similarities and differences in the record and the areas that require further research. Two of the major limitations to this research are the lack of zooarchaeological assemblages that span the "transition" from the Middle to Later Stone Age (60,000 to 20,000 years ago) and the lack of zooarchaeological data from most regions of Africa. Finally, we consider how the documented subsistence changes relate to demographic changes, the modern human expansion out of Africa, and models of modern human origins.

Introduction

Many researchers investigating changes in human diet during the Late to Terminal Pleistocene have concentrated on Europe and the eastern Mediterranean, with the focus usually on the "transition" from the Middle Paleolithic, associated with Neanderthals, to the Upper Paleolithic, associated with modern humans. Initially, most investigations focused on larger game exploitation, but few differences have been found (Grayson and Delpech, 2003; Steele, 2003; Stiner, 2005a). The key difference may have been an increase in the rate or degree of hunting success, but currently it is not possible to directly measure this with archaeological records. The most significant documented shift is the appearance of small, quick, difficult to catch game, such as fish, birds, hares and small carnivores, in Upper Paleolithic assemblages. In contrast, these prey species are rare or absent in earlier time periods (Straus, 1977; Chase, 1986; Stiner, 2001; Costamagno and Laroulandie, 2004; Laroulandie, 2004; Pérez Ripoll, 2004; Stiner, 2005a). This difference is further supported by the isotopic signatures preserved in Neanderthal and modern human bones, which

J.-J. Hublin and M.P. Richards (eds.), *The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence,* 113–126.
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indicate that some modern humans had a more diverse diet than Neanderthals (Richards et al., 2001). Additional changes during the Terminal Pleistocene, just before the advent of agriculture and domestication in the Near East, include the addition of more small game, a decrease in the ages of the large ungulates that were hunted, and an increase in how intensively these ungulates were exploited for resources such as marrow and grease (Munro, 2004; Davis, 2005).

However, paleontological and genetic data point to Africa as the place where modern humans originated, either during the Middle Stone Age (MSA, whose makers were Neanderthal contemporaries/near-modern humans living about 250,000 to 50,000 years ago) or at its end with the "transition" the to Later Stone Age (LSA associated with fully modern humans from 50,000 years ago to ethnohistoric times). It was only with the beginning of the LSA that modern humans spread from Africa, eventually replacing the Neanderthals in Eurasia. This means that the Middle to Upper Paleolithic, or the Neanderthal to modern human "transition" in Eurasia was not an *in situ* "transition." To understand the origins of modern human subsistence, we must examine the African record.

The modern human expansion out of Africa would have involved increases in human population sizes, and probably also in local population densities. This increasing population size comes at or after the "transition" from the MSA to LSA, and therefore followed technological changes that allowed modern humans to extract more resources from the environment. Following optimal foraging theory (Stephens and Krebs, 1986), this increased demand could be reflected in the archaeological record in a variety of ways (Munro, 2004). Modern humans could have increased their exploitation of existing high-ranked prey resources, assumed here to be ungulates, by obtaining more of these individuals. If they could, hunters would have first targeted prime-aged animals, because these animals maximize the caloric return for energy spent hunting them. Then, if there was strong hunting pressure on these prime individuals, which could happen if the technological changes of the LSA increased the hunting success rate of modern humans, the typical ages of the animals in the prey herds would have declined; so that by necessity, more young individuals would be taken. The modern humans could also have processed each animal more intensively to extract more calories and nutrients in the forms of marrow and grease. Additionally, decreasing abundance of high-ranked prey due to over-exploitation could cause people to increase their exploitation of existing low-ranked resources, here assumed to be small animals. As a result, small game would become more abundant in the diet, and the median size of slow-growing and long-lived mollusks and tortoises would decline as exploitation increased. Finally, the expanding populations may have added new low-ranked species to the diet. The addition of these previously low-ranked species to the LSA diet could also be the result of technological changes that made it possible or more efficient to capture these resources, and therefore, they would have been included in the diet.

Extensive research in southern Africa has identified a number of differences in human subsistence between the MSA and the LSA, including increased exploitation of dangerous game, such as buffalo and wild pigs; increased exploitation of young seals; increased exploitation of marine mollusks, tortoises, and airborne birds; as well as the addition of fish to the diet (Klein, 1975; Klein and Cruz-Uribe, 1983, 1996; Klein, 1998; Klein et al., 1999, 2004; Steele and Klein, 2005/2006).

However, despite the abundance of publications discussing the Eurasian and African changes in human diet during the Late Pleistocene, only a few formal comparisons of the two records have been made (e.g., Marean and Assefa, 1999; Marean, 2005). Our goal here is to begin making these comparisons. Specifically, we analyze the southern African record using similar methods to those typically employed by researchers working in Eurasia (e.g., Stiner and Munro, 2002; Munro, 2004; Stiner, 2005b). We highlight similarities and differences between the records and suggest areas that require further research. In doing so, we hope to encourage a more global view of the evolution of human diet.

Samples

The faunal remains from nine sites found along the coast of South Africa are considered here (Fig. 8.1, Table 8.1). We chose these sites b ecause they have provided the best-documented assemblages available, and most of them were included in earlier investigations into MSA and LSA ecology. Although there is some inconsistency in reporting, the assemblages have been excavated and analyzed by related teams of researchers, making the data comparable between assemblages. The recovery and recording of small animals, such as hare (*Lepus* sp.) and dune molerat (*Bathyergus suillus*) dental remains indicates that excavation and analytical procedures were sufficient for consideration of small game exploitation.

The assemblages span two environmental zones. This is important because it increases the ecological variability under consideration, making it more likely that any identified patterns reflect human behavior and not climatic or environmental variation. The ocean waters off the western coast of South Africa are cool and nutrient-rich, while the land experiences long, warm, dry summers and short, cool, wet winters, limiting the available land resources. In contrast, the waters off the southern coast are more variable, and the land receives rainfall during the summer months and in larger amounts than on the western coast. As a result, the southern coast has a richer terrestrial environment, and these environmental differences are also reflected in the animal community. Overall, the contrast between western coast and southern coast faunal assemblages is present throughout the Late Pleistocene and Holocene, indicating that this environmental variation has great time depth, but the boundary between the two environmental zones has fluctuated with the glacial cycles.

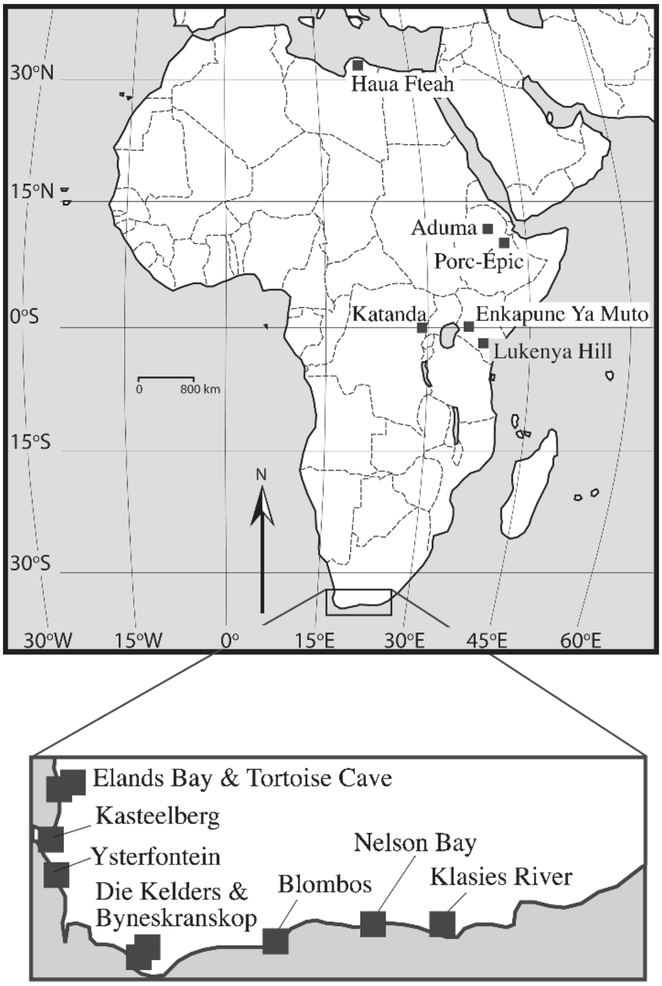

FIG. 8.1. Map of the sites discussed in the text. Table 8.1 lists the references for each sample that provided the data presented here.

Increased Exploitation of Existing High Ranked Prey Resources

Previous studies of large game exploitation in South Africa have investigated the relative species abundances of some the largest prey, as well as the associated mortality profiles. Eland (*Taurotragus oryx*) were more common in MSA assemblages (KRM, DK1, and BBC), while Cape buffalo (*Syncerus caffer*) and bushpig (*Potamochoerus larvatus*) were more abundant in LSA assemblages (NBC and BNK1) (Klein, 1994; Klein and Cruz-Uribe, 2000). This pattern holds across two geographic areas and multiple environmental regimes (Fig. 8.2). Cape buffalo and bushpig are among the most difficult to capture of those animals identified in the assemblages because of their strong predator-defense capabilities. Their greater abundance in the LSA assemblages could reflect the introduction of projectile technology, which allowed hunters to strike from a safer distance. When the mortality profiles for the bovids are compared, the profiles for Cape buffalo from KRM MSA and NBC LSA are similar to what might be expected from attritional mortality factors like predation and endemic disease, which disproportionately affect the weakest members of the population – the youngest and oldest. The mortality profiles constructed for eland from KRM MSA and DK1 MSA more closely resemble what would be expected if individuals of different ages were being taken in proportion to their live abundance (Klein, 1978, 1994; Klein and Cruz-Uribe, 1996). These patterns were found to be consistent across two techniques of mortality profile analysis: histograms of age-at-death estimates and boxplots of tooth crown heights (see Steele, 2005 for a detailed comparison of the methods). Unfortunately, small sample sizes do not allow for an examination of eland mortality profiles from LSA assemblages.

Following analyses conducted in the Mediterranean Basin, mortality profiles were further investigated via triangular graphs, which plot the percentages of juveniles, prime, and old individuals in a faunal sample (Stiner, 1990). The method was modified to add 95% confidence limits to the triangular graphs (Steele and Weaver, 2002; Steele, 2005). When plotted this way, the eland samples from three MSA assemblages are statistically indistinguishable from each other, and show an abundance of prime individuals; however attritional hunting cannot be ruled out with statistical confidence for DK1 MSA (Fig. 8.3a; Tables 8.2 and 8.3). When Cape buffalo and giant or long-horned buffalo (*Pelorovis antiquus*) are added to the graph, they are also statistically indistinguishable from each other and indicate attritional or juvenile dominated mortality. In addition, with the exception of the DK1 MSA eland sample, the eland profiles are significantly different from the

TABLE 8.1. References that provided the data used in this paper.

Site	Abbreviation	References
Blombos Cave	BBC	Henshilwood et al., 2001
Byneskranskop 1	BNK1	Klein, 1981; Schweitzer and Wilson, 1982
Die Kelders 1	DK1	Schweitzer 1979; Klein and Cruz-Uribe, 2000; Avery, 1990; G. Avery, 2003, personal communication
Elands Bay Cave	EBC	Klein and Cruz-Uribe, 1987; Avery, 1987; Avery, 1990
Kasteelberg	KBA, B	Klein and Cruz-Uribe, 1989
Klasies River Main	KRM1, 1A, 5	Klein, 1976b; Singer and Wymer, 1982; G. Avery, 2003, personal communication
Nelson Bay Cave	NBC	Klein, 1972a, b; Avery, 1990
Tortoise Cave	TC	Klein and Cruz-Uribe, 1987
Ysterfontein 1	YFT1	Klein et al., 2004; Halkett et al., 2003; G. Avery, 2006, personal communication, continuing research

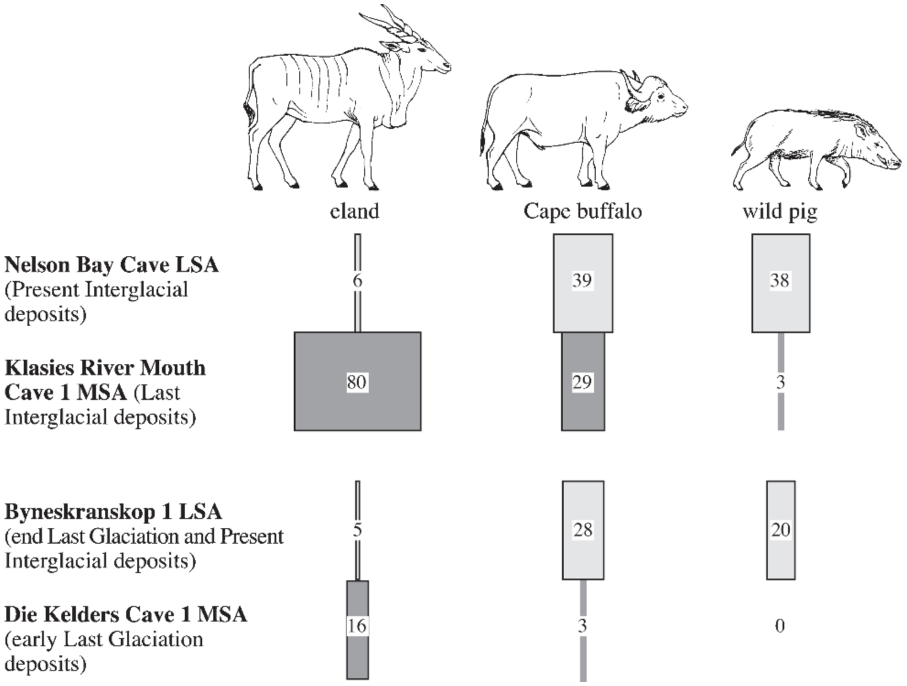

FIG. 8.2. Top: The minimum numbers of eland, Cape buffalo, and bushpig in samples from the Last Interglacial deposits of KRM Cave 1 and in the Present Interglacial deposits of nearby NBC. Bottom: The minimum number of individuals from the same species in the early Last Glaciation deposits of DK1 and in the end Last Glacial/Present Interglacial deposits of nearby BNK1. The relatively greater abundance of buffalo and bushpig at NBC and BNK1 probably reflects the more sophisticated technology of local LSA hunters over their MSA predecessors.

buffalo profiles. These results are consistent with earlier studies based on histograms and boxplots.

We examined a few additional species to further investigate the question of MSA and LSA hunting patterns, and the possibility that large game experienced over-exploitation with the "transition" from the MSA to the LSA. The mortality profiles of the extinct blue antelope (*Hippotragus leucophaeus*) from KRM MSA and NBC LSA show a similar pattern to the buffalo from the same sites (Fig. 8.3b). The samples are statistically indistinguishable from each other and most similar to what is expected for attritional hunting, although the hunting of more prime individuals cannot be excluded, particularly for NBC LSA.

All of the bovids we have discussed so far are large bodied (large-medium or large body-size classes), so they would provide the most calories and potentially be the most highly ranked in a forager's diet. Their slower reproductive rates also mean that they should be sensitive indicators to over-exploitation. However, when comparisons are available, we find no differences in mortality profiles between the MSA and LSA samples. Rather, the differences we do find are between species. During the MSA, eland may have been individually hunted in equal proportion to their abundance on the landscape or entire herds may have been taken at once (as would occur during a drive), creating a catastrophic mortality profile. In contrast, the buffalo and blue antelope samples consistently fall into the attritional zone, indicating that they were probably hunted singly, and only the most vulnerable individuals were taken during both the MSA and LSA. Advances in LSA technology, such as projectile weapons, should have allowed hunters to successfully hunt buffalo more frequently, but because they were taking only the most vulnerable individuals, the age structure of the living population would not have been affected, and hunting was sustainable. The abundance of juvenile remains in the buffalo and blue antelope samples suggests that these animals were not the result of scavenging, because the initial predator would be expected to consume juvenile carcasses more or less completely. These results contrast with those from the Mediterranean Basin where very few samples fall within the attritional zone and none within the juvenile dominated zone. Additionally, old individuals dominate a few Mediterranean Basin samples but no MSA or LSA samples (Stiner, 1990).

To further examine predator-prey dynamics, we investigated the mortality profiles of steenbok (*Raphicerus campestris*) and grysbok (*R. melanotis*), small bovids that are much more abundant in the faunal assemblages than the species discussed above (Fig. 8.3c). The two MSA samples we consider contain only grysbok, while the LSA samples contain a mix of grysbok and steenbok (which are distinguishable skeletally mainly by their horncores and the shape of the inferior margin of the mandible (Klein, 1976a)). The steenbok/grysbok mortality profiles show a variety of distributions. The two MSA assemblages are significantly different from each other, with KRM having more prime adults and DK1 having more juveniles. The DK1 LSA, BNK LSA, and EBC LSA samples are all similar to the DK1 MSA sample, and fall within the zone for attritional mortality on the graph. These results are somewhat surprising given the expectation that neither MSA nor LSA people should have had problems capturing these small-bodied bovids. There are a few possible explanations. First, steenbok and grysbok are fast-breeding (continuously through the year with minor birth peaks) and short-lived species with relatively low-crowned teeth (Klein, 1976a; Skinner and Chimimba, 2005). Juveniles are abundant and old individuals are naturally rare in these populations, so it may not be possible to distinguish attritional and catastrophic shaped mortality profiles unless samples are very large. Furthermore, reliably separating the few old individuals from prime adults can be difficult in species with low-crowned teeth. As a result, the variation identified here may have a number of causes, and larger sample sizes and more data on the age structures of living *Raphicerus* populations and on age estimation techniques are necessary for fuller examination. Stiner (2005b: 207–208) offers an alternate explanation for some samples that fall within the attritional zone of the triangular graph. These samples may reflect hunting pressure, because the age structure of the herd has been altered so that a larger proportion of juveniles is present than expected in a typical living structure, and there are fewer old individuals. In this case, the proportion of old individuals in the sample can help distinguish attritional mortality from hunting pressure, because more old individuals should be present in the attritional profile. A final explanation is that some of the specimens, especially those in select DK1 MSA samples, were not the result of human hunting at all, but were in fact brought into the cave by large raptors (Klein and Cruz-Uribe, 2000).

Modern humans may have extracted more calories from large game by processing carcasses more intensely. Unfortunately, few studies on MSA and LSA faunal assemblages have directly addressed this issue, perhaps because marrow processing has been securely documented in earlier Plio-Pleistocene faunal assemblages (Blumenschine, 1995; de Heinzelin et al., 1999). For the MSA of South Africa, only a few samples of the DK1 MSA fauna have been coded for traits characteristic of marrow extraction, including fracture outlines and angles and percussion marks, and the samples show evidence for marrow extraction (Marean et al., 2000). Only one similar analysis has been conducted on an LSA sample, and it also concludes that the bones had been exploited for marrow (Dewar et al., 2006). To the best of our knowledge, no LSA assemblage has been examined for evidence of boiling for grease extraction (as in Outram, 2001; Munro and Bar-Oz, 2005). Further research will hopefully shed more light on this issue.

In sum, the primary contrast between MSA and LSA large game exploitation is in relative species abundance. The variation in mortality profiles appears to be more species-specific and not directly related to differences in technology. Advances in technology may have allowed LSA hunters to more frequently take buffalo and pigs, but not so frequently that the age structures of the herds were impacted.

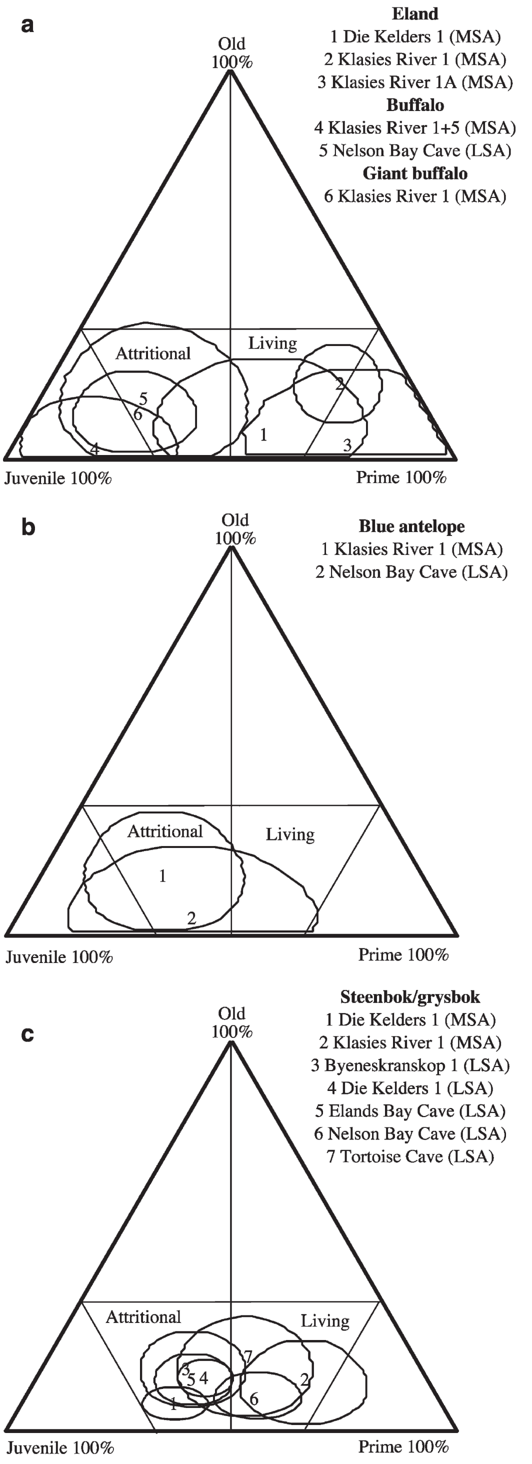

FIG. 8.3. Modified triangular graphs showing the percentage of young, prime, and old individuals in each sample, along with the 95% confidence interval around each point (Steele and Weaver, 2002). (**a**) MSA eland hunters were able to hunt many adult eland, while both MSA and LSA hunters could only take the youngest and oldest buffalo. (**b**) Both MSA and LSA people hunted only the youngest and oldest blue antelope. (**c**) There is a wide variety in the ages of steenbok and grysbok that were taken by MSA and LSA hunters. Together, these graphs show that prey age selection is more closely related to species than to technology.

TABLE 8.2. Data used to calculate mortality profiles on the modified triangular graph (Steele and Weaver, 2002). Young = number of dp4s with measurable crown heights; Prime = number of measurable m3s with crown heights less than 50% worn; and Old = number of measurable m3s with crown heights more than 50% worn (following Klein et al., 2007). The degree of wear on each m3 was assessed by dividing each crown height by maximum unworn m3 crown height (mm) for that species: eland = 47.1[a], buffalo = 53.0[b], giant buffalo = 70.2[b], blue antelope = 40.0[b], and steenbok/grysbok = 14.7[a].

Species	Site	Industry	Young	Prime	Old	Total
Eland	DK1	MSA	8	11	2	21
Eland	KRM1	MSA	15	59	17	91
Eland	KRM1A	MSA	3	11	1	15
Buffalo	KRM1 + 5	MSA	18	4	1	23
Buffalo	NBC	LSA	12	5	3	20
Giant buffalo	KRM1	MSA	29	10	5	44
Blue antelope	KRM1	MSA	15	7	4	26
Blue antelope	NBC	LSA	9	6	1	16
Steenbok/grysbok	BNK1	LSA	40	26	12	78
Steenbok/grysbok	DK1	LSA	140	106	37	283
Steenbok/grysbok	DK1	MSA	119	68	13	200
Steenbok/grysbok	EBC	LSA	75	50	18	143
Steenbok/grysbok	KRM1	MSA	12	26	5	43
Steenbok/grysbok	NBC	LSA	48	62	10	120
Steenbok/grysbok	TC	LSA	20	23	8	51

[a] Unworn m3 crown height taken from original data.

[b] Unworn m3 crown height taken from Klein (1978).

TABLE 8.3. The minimum number of individuals (MNI) used to calculate the relative abundances presented in Figs. 8.3 and 8.4. Presence and absence of other taxa are also provided.

	DK1	KRM	BBC	NBC	EBC	KBA	KBB	BNK1	DK1	KRM	BBC	YFT1
	LSA	LSA	LSA	LSA	LSA	LSA	LSA	LSA	MSA	MSA	MSA	MSA
Small game sub-total	2,811	2	108	148	6,361	99	2,217	2,943	8,848	100	943	109
Hares	5	0	4	3	61	1	4	10	392	2	9	4
Cape dune molerat	1,766	0	60	0	334	1	5	95	3,646	0	34	33
Hyrax	28	2	12	145	86	0	0	9	170	98	37	0
Tortoise[a]	1,012	0	32	0	5,880	97	2,208	2,829	4,640	0	863	72
Carnivore sub-total	140	35	9	204	329	32	182	41	98	184	28	21
Cape fur seal	108	28	4	160	216	24	133	10	38	134	7	11
Other carnivores	32	7	5	44	113	8	49	31	60	50	21	10
Ungulate sub-total	330	59	238	369	481	43	102	237	444	634	66	33
Bird sub-total[b]	99	56		509	445	Rare	Rare	Y	66	174		28
Penguin	16	6	?	106	65				26	124	?	12
Airborne marine birds	73	50	?	443	380				40	50	?	16
Ostrich egg shell	Y	?	?	Y	?	?	?	Y	?	Y	Y	Y
Mollusks	Y	Y	Y	Y	Y	Y	Y	Y	Y[c]	Y	Y	Y
Fish	Y	Y	Y	Y	Y	Rare	Rare	Y	N	Rare	Y	N

[a] Number of identifiable humeri.

[b] Freshwater and terrestrial birds are not considered here because the data are not available for all sites.

[c] Poorly preserved.

Increased Exploitation of Existing but Low Ranked Resources

Following the work conducted around the Mediterranean, we next investigate the relative abundance of prey taxa, because foragers can extract more calories from the environment by increasing their exploitation of lower-ranked resources that are already part of their diet. This is done either when the higher ranked resources became harder to find, or when technological changes make the lower ranked resources more profitable. In the case of coastal South Africa, significant new technologies are found in the LSA that were not present in the MSA, and so technological change can be implicated in many of the dietary changes. We follow Munro (2004), and begin by comparing the proportions of ungulates, carnivores, and small game in a number of MSA and LSA assemblages (Fig. 8.4). As with Mediterranean Basin samples (Stiner and Munro, 2002), this analysis shows little patterning, although KRM LSA and MSA and NBC show a low abundance of small game. We note that Cape fur seals (*Arctocephalus pusillus*) are commonly classified as Carnivora (Skinner and Chimimba, 2005; Wilson and Reeder, 2005) and therefore are included as carnivores here, but their ecology is very different from other members of this order; they were frequently exploited for human subsistence, unlike other members of this order. This underscores the importance of examining prey ecologically, not always taxonomically.

To further examine relative abundances in more detail, we calculated the reciprocal of Simpson's Index (as described in Stiner, 2005b: 167) to examine the evenness in the representation of genera in the samples (approximately 60 genera are represented between the samples; 40 more than in the Mediterranean Basin series). Evenness is consistently low in all samples (<4.2), except that again the KRM LSA, KRM MSA, and NBC differ (8.7, 12.6 and 9.0 respectively). Furthermore, there is no significant trend through time ($r^2 = 0.15$, $p = 0.22$) or between the MSA and LSA medians (Wilcoxon 1-way Test, ChiSquare Approximation $p = 0.61$). The KRM and NBC samples are distinctive because they lack tortoises, which are extremely abundant in all the other samples. These sites are further east on the South African coast than the other samples considered here, and are located in an environment that must not have ever been favorable for tortoises.

Much of the recent research into changing diets in the Middle and Upper Paleolithic has emphasized the importance of small game, and especially the need to consider small game in terms of its ease of capture and reproductive potential instead of taxonomic classification (Stiner et al., 2000; Stiner and Munro, 2002; Munro, 2004). These studies have contrasted the exploitation of slow versus quick game, namely tortoises and mollusks versus hares and game birds, although other taxa are included. Middle Paleolithic samples contain primarily slow, easy-to-capture prey, and quick game do not become more abundant until the Upper Paleolithic, increasing into the Epipaleolithic (Stiner et al., 1999, 2000; Stiner and Munro, 2002; Stiner, 2005a, b).

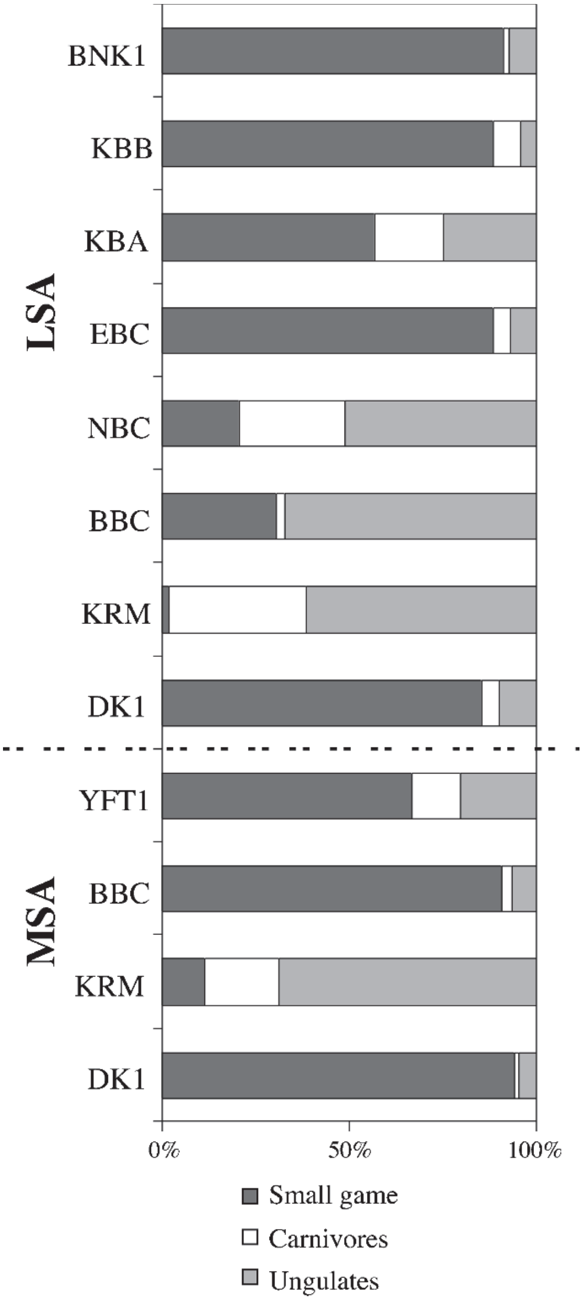

Fig. 8.4. Relative abundance of ungulates (bovids, equids, rhinos, suids), carnivores (small and large, seals), and small game (hare, molerat, hyrax, tortoise) in MSA and LSA assemblages. Birds are not included here because data are not available for all assemblages. All abundance indices are based on MNI counts. Abbreviations for sites follow Table 8.1.

As with the large game in South Africa, comparable comparisons are not straightforward. Slow, easy to capture resources include tortoises (*Chersina angulata*), mollusks, and ostrich (*Struthio camelus*) eggs. However, these remains are inconsistently quantified, making comparisons difficult. Tortoise abundance may be compared using either the minimum number of humeri or femora, or the number of identified specimens (which can be artificially inflated because of the high fragmentation potential of the carapace and plastron). Mollusks are weighed and where possible, non-duplicated parts (mussel hinges and limpet apices) are counted for minimum numbers of individuals. Ostrich eggshell can be quantified by weight or by counting the number of fragments, but some pieces of eggshell may enter the site as water canteens, blanks for making beads, or already-made beads. Nevertheless, if these data are consistently reported across samples, comparisons can be made.

Small, quick game also create some complications. Hare are rare in both MSA and LSA faunal assemblages (<1.5% in the samples considered here), although their consistent but sparse presence indicates that they existed on the landscape, at least in small numbers, when environments were suitable. Hyraxes (*Procavia capensis*) and dune molerats are also present in the majority of assemblages considered here, often in high numbers. Like hares, they probably should be considered quick, hard-to-capture game, given their ability to rapidly return to their shelters or burrows. The more important question, however, is ensuring that the hares, hyraxes, and molerats were brought into the sites as human food and not by non-human predators, especially raptors. Klein and Cruz-Uribe (2000) concluded that the extremely high abundance of molerats in the MSA at DK1 (over 90% of the fauna) was a result of eagle owl hunting, not human exploitation. However, in the same study, they showed that humans probably collected the molerats in the LSA layers, because unlike the MSA specimens, some of these were burnt or had cut-marks. Henshilwood (1997) documented another example of humans consuming molerats in the LSA layers at BBC, identified by a distinct burning pattern on their premaxillas, mandibles and incisors; he supported this inference with ethnographic examples. Because of these factors, detailed taphonomic studies are needed to determine the dominant mode of accumulation for each sample. Unfortunately, these detailed analyses have not yet been documented for the majority of samples considered here, but the general pattern appears to be that molerats were more frequently exploited for food in the LSA than they were in the MSA, supporting the proposal that quick game were more frequently taken in the LSA than in the MSA.

Cruz-Uribe and Klein (1998) determined that skeletal part representation can be useful for distinguishing hares and hyraxes accumulated by humans from those accumulated by eagles, because eagle roost assemblages often contain an abundance of hind-limb elements from these small animals. When they examined hare and hyrax skeletal part representation in many of the archaeological sites considered here, they concluded that humans, not raptors, were responsible for introducing the majority of these small animals into the sites. When they further examined the ages of the hyraxes in the samples, they documented that MSA samples (KRM and DK1) contained few young hyraxes compared to the LSA samples (NBC and DK1). They argued that this difference could reflect differences in hunting technology, which allowed LSA foragers to more readily capture quick game.

The final type of quick game is birds. These can be divided into three groups along the South African coast: marine, freshwater, and terrestrial, although marine birds (primarily cormorants [*Phalacrocorax* sp.] and gannets [*Morus capensis*]) provide the majority of specimens (Avery, 1987). However, the South African coast has one species that deserves special consideration – African or jackass penguins (*Spheniscus demersus*). These flightless birds are probably easier to take than their airborne cousins, but unless they are scavenged, they are not gatherable like tortoises. Because they do not fall neatly into a particular category, we consider them separately here. The ethnohistoric record provides a few descriptions of techniques for capturing coastal birds: young penguins on the beach were chased and captured, juvenile cormorants were clubbed, and gulls were shot with bows and arrows (Avery, 1984 in Avery, 1987). In inland regions snares, bows and arrows, and sticks were used (Steyn, 1971 in Avery, 1987).

We start by comparing slow, easy-to-capture game to quick game, with penguins in their own category. Because of the taphonomic and quantification issues described above, our comparison includes tortoises, penguins, and airborne marine birds, plus hares and hyraxes only for assemblages where marine bird abundances are available (Fig. 8.5a). When present, tortoises dominate all assemblages, masking any difference between the MSA and LSA, so relative abundances of tortoises versus fast game do not seem to be informative. All of these samples also contain varying abundances of mollusks (although they were too poorly preserved in DK1 MSA to quantify), and if they were included, slow game would further dominate the assemblages. Therefore, we must examine the other components in more detail. A comparison of just penguins to airborne marine birds reveals that the LSA samples all contain significantly more airborne marine birds than penguins (Fig. 8.5b). These differences could reflect different seasons of site occupation (Avery and Underhill, 1986; Avery, 1987), but because they are consistent between so many assemblages, we think they are more likely to reflect differing subsistence behaviors. Furthermore, only LSA sites contain artifacts similar to ethnohistoric fowling gear. Although Avery (1987) argues that these could actually be fishing implements, this further supports the case for an increased exploitation of airborne birds in the LSA. Comparisons are not available for inland sites, and inland sites contain fewer birds overall (Avery, 1987).

Despite the consistently high abundance of tortoises and mollusks in most assemblages, these taxa may still reveal evidence for increased human exploitation. These animals have slow and continuous growth, and a relatively extended time until sexual maturity; therefore, under intense exploitation the median body size of the available animals will decline (Klein and Cruz-Uribe, 1983; Stiner et al., 2000; Mannino and Thomas, 2002; Steele and Klein, 2008). In the Late Pleistocene Mediterranean Basin, tortoise (*Testudo graeca*) size may decline from the Middle to Upper Paleolithic, and limpet (*Patella caerula*) size declines within the Upper Paleolithic (Stiner et al., 1999, 2000; Stiner, 2005b). In South Africa, smaller LSA mollusks (relative to their MSA counterparts) have been clearly documented for both the western (limpets [*Cymbula* sp. and *Scutellastra* sp.]) and southern (Cape Turban shells [*Turbo sarmaticus*]) coasts, indicating more intense mollusk exploitation in the LSA (Fig. 8.6) (Voigt, 1982; Parkington, 2003; Steele and Klein, 2005/2006, 2008). Because of the large number of samples considered from a variety of environments, climate is probably not the causal factor, making it more likely that higher human population

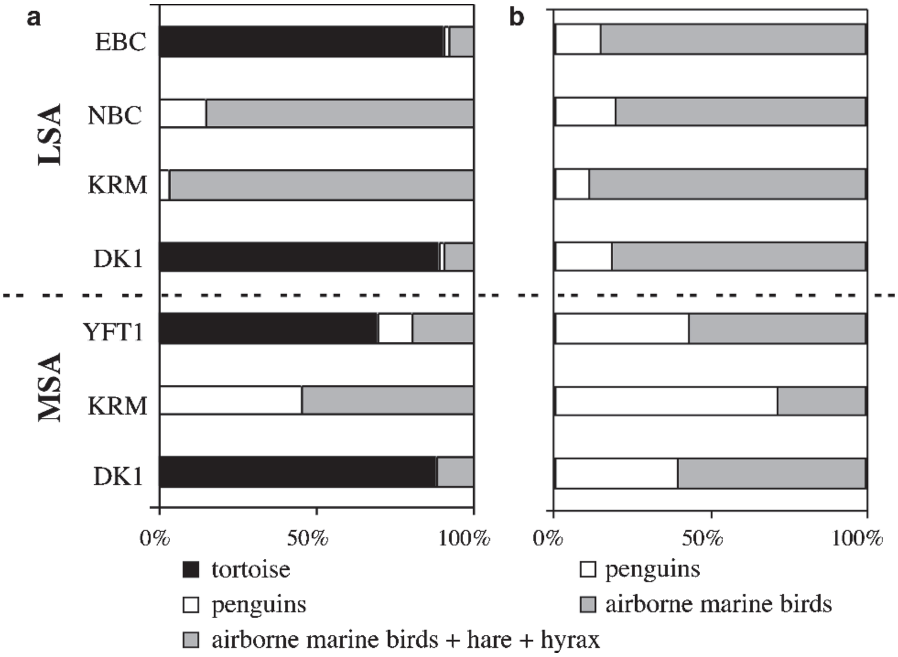

Fig. 8.5. (**a**) Relative abundance of slow (tortoise, penguins) versus quick (airborne marine birds, hare, hyrax) prey and (**b**) penguins versus airborne marine birds. LSA samples contain a significantly larger abundance of airborne marine birds compared to penguins (Likelihood Ratio or *G*-test of Independence [Sokal and Rohlf, 1995: 731–732] on pair-wise comparisons: YFT1 MSA/EBC LSA $p = 0.0087$, KRM MSA/NBC LSA $p < 0.0001$, KRM MSA/KRM LSA $p < 0.0001$, DK1 MSA/DK1 LSA $p = 0.0030$). Abbreviations for sites follow Table 8.1.

densities, and hence the collecting of more mollusks, caused the diminution. Declines in median tortoise sizes, as determined by the maximum breadth of distal humeri, from the MSA to LSA samples are not as clear as in the mollusks, but in general LSA tortoises are smaller than MSA ones (Klein and Cruz-Uribe, 1983; Steele and Klein, 2005/2006).

Exploitation of New Prey

Intensifying human groups may add new species to their diets to obtain more calories from the environment. Along the coast of South Africa, we see the inclusion of many more marine components in the LSA diet (Klein et al., 2004; Steele and Klein, 2008). The most significant addition to the LSA diet that is rarely seen in the MSA is large numbers of coastal fish. As with fowling implements, only LSA assemblages have provided artifacts that resemble recent fishing equipment, such as fish gorges. On the west coast, rock lobsters (*Jasus islandii*) were also added to the diet in the LSA (Buchanan, 1988; Jerardino et al., 2001; Orton et al., 2005). While a variety of mollusks were gathered during the MSA, exploitation concentrated on a few species, especially limpets and black mussels (*Choromytilus meridionalis*). In contrast, in the LSA, other taxa, including sand mussels (*Donax serra*) and whelks (*Burnupena* sp.), were regularly gathered, occasionally in large quantities (Buchanan et al., 1978; Klein et al., 2004, current research). This higher diversity of mollusks in the LSA samples reflects the LSA people's wider diet breadth, which was probably necessary to support their larger population sizes. It is unknown if LSA technological changes made it more efficient to gather a higher diversity of mollusks, but these advances almost certainly were critical for supporting larger human population sizes.

Discussion

Our results indicate that there were significant changes in subsistence between the MSA and LSA, and that LSA foragers consumed a wider variety of resources. We propose that this increased diet breadth was able to support larger and more dense human populations, and that these changes must have occurred close in time to when modern humans were expanding out of Africa.

However, there is one major limitation to our analysis: the MSA samples included here all accumulated more than 60,000 years ago, while the LSA samples are all younger than 20,000 years old. Unfortunately, coastal South Africa experienced extreme aridity in the midst of the Last Glaciation (OIS 3), and as a result, local human populations were very sparse during this time. Therefore, it may not be possible to fully test our proposals using the coastal record from South Africa. We must turn to other parts of Africa where climatic conditions were more favorable to human occupation during this time.

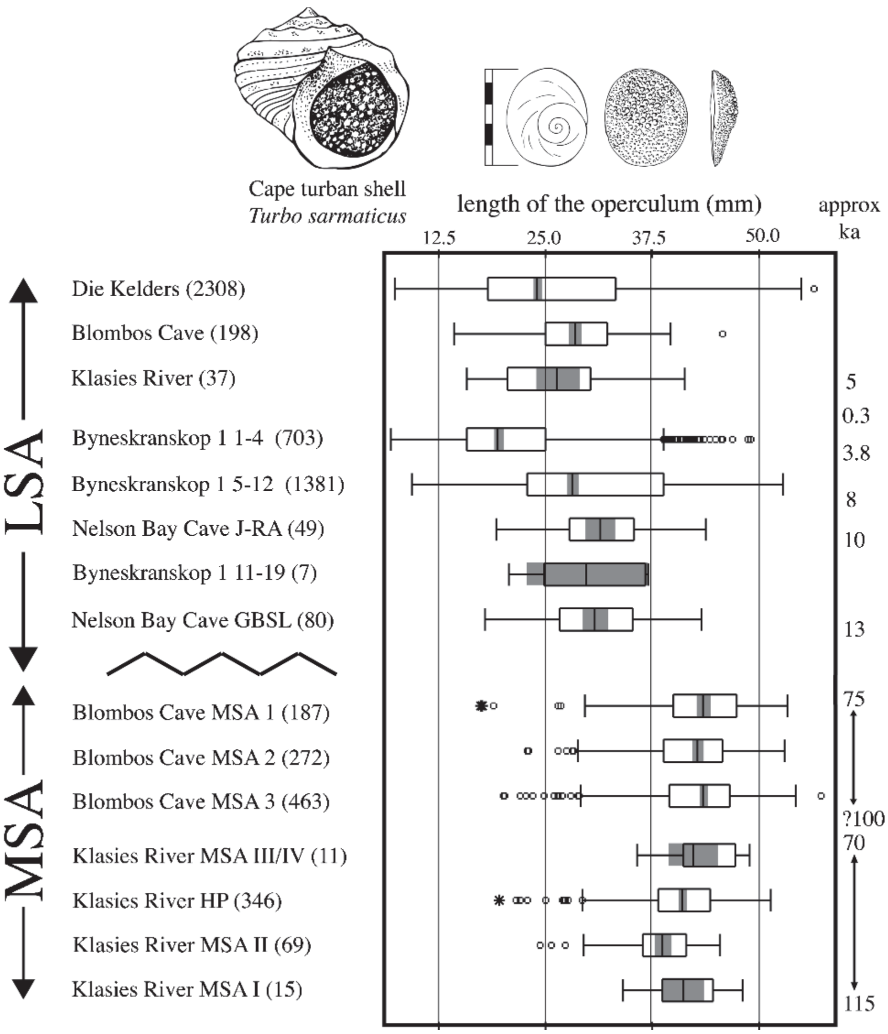

FIG. 8.6. Box plots summarizing the maximum diameter of Cape turban shell opercula from successive units of many of the sites considered here. The number in parentheses after each sample name is the number of specimens in that sample. The sample median is indicated by the vertical line near the center of each plot; the 95% confidence limits for the median is indicated by the shaded rectangle around each median; and the number of measured shells is shown in parentheses. Medians whose 95% confidence limits do not overlap are significantly different. The numbers along the right margin designate the approximate ages of the samples in thousands of years before present. The LSA opercula tend to be significantly smaller than the MSA ones, suggesting that LSA people were more intensively collecting turban shells, likely because LSA people were living at higher population densities than MSA people.

After southern Africa, northern Africa has been subject to the most archaeological investigations into Late Pleistocene deposits. Unfortunately, despite this attention, little is known about the details of the subsistence strategies. This region also probably suffered from the same aridity as southern Africa, and therefore human populations were probably equally sparse during the interval of interest. Bone preservation is generally poor in the northeast corner of the continent, so only a few faunal analyses have been possible, and they have necessarily been limited. The western part of the region contains more cave and rockshelter deposits, so bone preservation and relative chronological control is better. However, much of the work done in this area has been paleontological and biochronological in nature. Although some preliminary work has been done (Thomas, 1981; Amani, 1991; Aouraghe, 2004), more detailed zooarchaeological studies are needed. One exception is Klein and Scott's (1986) re-analysis of the fauna from Haua Fteah and a few nearby sites from Cyrenaican, Libya, which span from the Middle Paleolithic to historic times. However, their analysis was hampered by a lack of stratigraphical control over the assemblages, because the excavation was conducted in spits that crossed natural stratigraphic levels. Nonetheless, they discuss mollusk remains from this site and others from coastal northwestern Africa, tortoises that were present in variable numbers through the sequence, and abundances of large mammals that varied with climate. Unfortunately, sample sizes were not large enough to examine variation in mollusk or tortoise body size through time. Birds were preserved throughout the sequence, along with ostrich eggshells. Although bird bones are sparse in the Middle Paleolithic levels, some dove (*Columba* sp.) and partridge (*Alectoris barbara*) bones were burnt (6% of the total), indicating that humans occasionally exploited them (MacDonald, 1997).

Because of the extreme aridity at the northern and southern ends of the African continent during the Last Glaciation, the most likely place to find faunal assemblages that span the MSA to LSA "transition" is in East Africa. However, until recently, few zooarchaeological studies have been conducted, in part because few suitable assemblages from the relevant sites are known. One exception is Porc-Epic, Ethiopia, where Assefa (2006) recently completed a detailed analysis of the MSA faunal remains. The fauna supports the interpretation of accumulation during the Last Glaciation because more grazers are present in the MSA assemblage than in the historic fauna, indicating a drier, more open environment. The sample size of dental remains is too small for mortality profile analysis, but the high frequency of green fractures and of incomplete shaft circumferences, especially on the larger bovid remains, shows extensive marrow extraction. However, the assemblage also shows a high degree of carnivore tooth-marks relative to cut-marks, but Assefa (2006) argues that the overall pattern still indicates first access by hominids, not by carnivores. For small, quick game, both hare and hyrax are present in the assemblage; slow game are either not present or not considered. Many of the hare and hyrax bones had butchery marks and traces of burning, but the skeletal parts found in the assemblage were similar to those that Cruz-Uribe and Klein (1998) documented in eagle assemblages, causing Assefa (2006) to conclude that both humans and raptors played a role in accumulating these small animals. Unfortunately, no studies on nearby LSA remains are available for further comparison. Elsewhere in Ethiopia, preliminary work at sites in Aduma, Middle Awash Valley, suggest that MSA people exploited large, easily predated catfish (*Clarias* sp.) (Yellen et al., 2005). Catfish (*Clarias* sp. and *Synodontis* sp.) may also have been exploited at Katanda, Upper Semliki Valley, Democratic Republic of the Congo (Brooks et al., 1995).

The contrasts between MSA and LSA faunal assemblages are greater than the variation found among MSA assemblages. This indicates that significant dietary changes occurred with the "transition" from the MSA to LSA, and had a major role in the expansion of modern humans out of Africa. Specialists agree that humans were fully modern in their behavior with the "transition" from the MSA to the LSA, but they disagree on whether the behavioral shift occurred gradually within the MSA (Gradual Accumulation Model) or abruptly at its end (Abrupt and Late Model) (Henshilwood and Marean, 2003; Steele and Klein, 2005/2006). Our results argue that intensification did not occur until the LSA, and could not occur until the changes in LSA technology took place. Therefore, modern human behavior more likely arose at the beginning of the LSA and not during the MSA. However, this proposal remains to be tested with more assemblages spanning the geographic and temporal gaps in the African Late Pleistocene archaeological record.

Conclusions

There are many subsistence differences between MSA and LSA foragers of coastal South Africa. LSA people more intensively extracted resources from the environment. These results are broadly consistent with those found in the Mediterranean Basin contrasting Middle Paleolithic and Upper Paleolithic foragers, although the specifics are different. Prey mortality profiles remain consistent between the MSA and LSA, and they vary more with species than with technology. However, relative species abundances are different between MSA and LSA assemblages. LSA people exploited more bushpigs and buffalo, while MSA people took more eland. LSA people consumed more molerats, young hyraxes, and airborne birds. They added fish and rock lobster to their diet, as well as regularly consumed a wider variety of mollusks. Finally, the median mollusk size is smaller in LSA samples than in their MSA counterparts, indicating that more LSA people were more heavily exploiting mollusks. All of these lines of evidence point to a larger diet breadth for LSA foragers, which supported larger human population densities. The challenge for understanding modern human origins is finding faunal assemblages from throughout the African continent that span the 60,000 to 20,000 year gap in coastal South African assemblages, so that we can more closely document the subsistence changes that co-occur with the expansion of modern humans out of Africa.

Acknowledgments. We would like to thank Jean-Jacques Hublin and Mike Richards for inviting us to participate in this symposium, funded by the Max Planck Society, and Allison Cleveland for patiently handling the manuscript. Tim Weaver and conference participants provided helpful comments.

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