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Article

Declining Prey Size in the Southern African Pleistocene: Evaluating the Human Impact

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Abstract: Megafauna extinctions are known from the Late Quaternary. This study analyzes trends in prey size from 184 contexts across 49 archaeological sites in southern Africa to assess changes in prey size during the Pleistocene, including the pre-Late Quaternary transition between the Early Stone Age (ESA) and the Middle Stone Age (MSA). Very large prey (>950kg) accounted for over 34% of the biomass in the ESA, declining to 22% in MSA and 11% in LSA, with a compensatory increase in the contribution of smaller (<295 kg) prey that increased from 7% in the ESA to 37% in the MSA and to 48% in the LSA. These trends persisted even when only non-cave sites were considered. We also hypothesize that targeting fat in prey because of a constraint on protein consumption by humans could have been a causal factor in the decline.

Keywords: paleolithic; Southern Africa; prey size; hunting; extinctions

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Introduction

Accumulating evidence suggests biased large prey species' population declines and extinctions before the well-studied Late Quaternary Megafauna Extinction (LQE) (Barnosky et al., 2004).

Here, we present the results of a study of prey size trends in Pleistocene southern Africa based on an analysis of 184 layers from 49 archaeological sites covering the entire Pleistocene. The central position of Africa in human evolution and the relative scarcity of late ESA and early MSA sites in eastern Africa make this study of particular importance.

Establishing 62 million years of terrestrial herbivores' mean body size increase, Smith et al. (2018) observed that by the beginning of the Late Pleistocene, the mean body mass of terrestrial mammals in Africa was half that found on other large continents. They remarked that human coexistence with large herbivores on the continent could be a cause for the decline. In East Africa, Faith et al. (2019) identified a Pliocene-Pleistocene herbivores' size decline, which began with the extinction of large browsers seven million years ago. The decline of C3 vegetation could explain the decline. However, about a million years ago, a significant decrease in the richness of large grazer species occurred despite an increase in C_4 biomass. Concurrently, there was a marked increase in the presence of size 2 species (weighing between 18-80 kilograms) starting around 1.8 million years ago and continuing throughout the rest of the Pleistocene. Similar trends were identified by (Bibi and Cantalapiedra, 2023).

Confirming the trend, Potts et al. (2020) and Faith et al. (2012) identified a faunal turnover in eastern Africa between approximately 780,000 and 320,000 years ago, during which smaller species gradually supplanted larger ones just before the Middle Stone Age (MSA) and *Homo sapiens* appearance. In the Southern Levant, an analysis of 133 stratigraphic layers across 58 Pleistocene and Early Holocene archaeological sites revealed a decline in the weighted mean body mass of prey in archaeological sites. This trend commenced during the Acheulean and continued throughout the Paleolithic period. No associated climatic fluctuations could be identified as triggers for these faunal size declines (Dembitzer et al., 2021). In a recent study, a trend of megaherbivore prevalence decline in five multi-cultural test cases in Africa, Spain, and France was identified in tandem with the appearance of the Middle Paleolithic and the Levallois method much before the LQE (Ben-Dor and Barkai, 2023).

While no in-depth pre-Late Pleistocene study concerning prey size trends has been published for Europe, preliminary observations have suggested a congruous decline at the Acheulean/Middle Paleolithic transition in the Iberian Peninsula (Yravedra, 2001; Rodríguez et al., 2011).

To sum up, there are significant indications for human prey size decline before the LQE.

Methodology

There could be extended periods of regional density declines prior to actual extinctions or extirpations of species (Dembitzer et al., 2021; Lomolino, 2023). We, therefore, attempted to identify general trends of prey animal representation in the archaeological record rather than species extinctions.

Archaeological sites contain zoological evidence in the form of fossilized bones that were brought to site by humans and other predators. Identification of human agency in these situations is partial as consumption of very large prey like elephants usually leave no cut marks on the bones (Haynes and Klimowicz, 2015). We therefore used the assemblages as paleontological data for trends in the availability of prey for predation, be it from humans or other predators. We do assume in our analysis that humans preferred to hunt larger prey when it was available Ben-Dor and Barkai, 2020).

To ensure the comprehensiveness of the analysis, we checked the list of sites against two lists of southern African sites: one encompassing 450 dated lithic assemblages that demarcate the durations of the Earlier Stone Age (ESA), Middle Stone Age (MSA) and Later Stone Age (LSA) and their respective technocomplexes (Lombard et al., 2022), and another comprising 211 sites with faunal remains, including both archaeological and paleontological contexts (Avery, 2019).

Table 1. Revised chrono-stratigraphic Stone Age sequence for southern Africa after Lombard et al. (2022).

Technocomplex	2012 suggested durations	Revised age estimates		
		Median age	Mean age±SD	Most probable duration
LATER STONE AGE				
ceramic final Later Stone Age	<2 ka	AD 774	AD 795± 698	AD 1493-97
final Later Stone Age	0.1-4 ka	546 BC	658 BC±1290	AD 632-1948 BC
Wilton	4-8 ka	4387 BC	4260 BC±1574	2686-5834 BC
Oakhurst	7-12 ka	8814 BC	8797 BC±2042	6755-10839 BC
Robberg	12-18 ka	13 705 BC	14 584 BC±3389	11 195-17 973 BC
early Later Stone Age	18-40 ka	25 998 BC	28 474 BC±8780	19 694-37 254 BC
MIDDLE STONE AGE				
final Middle Stone Age	20-40 ka	37.7 ka	38.8 ±8.9 ka	29.9-47.7 ka
post-Howiesons Poort	45-58 ka	55.1 ka	53±6.6 ka	46.4-59.6 ka

Howiesons Poort	58-66 ka	62.4 ka	62.9±11.4 ka	51.5-74.3 ka
Still Bay	70-77 ka	75.2 ka	78.1±10.7 ka	67.4-88.8 ka
Mossel Bay	77-105 ka	88.2 ka	87.9±10.5 ka	77.4-98.4 ka
early Middle Stone Age	130-300 ka	206.5 ka	196.5±70 ka	126.5-266.5 ka
EARLIER STONE AGE				
Fauresmith	200-600 ka	305 ka	352.6± 118.9 ka	233.7-471.5 ka
Acheulean	300 ka-1.5 Ma	770 ka	834.2± 402.6	431.6 ka-1.23 Ma
Oldowan	1.5-2 Ma	1.61 Ma	1.63 Ma± 546.5 ka	1.08-2.18 Ma

This cross-referencing process identified 61 archaeological sites containing 329 stratigraphic layers or excavated spits for which NISP (Number of Identified Specimens) data were available. We excluded contexts with a total NISP count of less than 30 since, in the averaging method, each layer gets equal weight, and we strived to eliminate random accumulations. This elimination resulted in the inclusion of 184 layers/spits from 49 sites in the analysis (see Supplementary Material). Due to the relatively limited availability of MNI (Minimum Number of Individuals) data, we did not perform a detailed analysis of this aspect of the dataset.

Table 2. Dataset description.

Period	**N sites**	**N layers**	**Avg. NISP/layer**
LSA	21	56	550
MSA	26	113	933
ESA	8	15	1459

It should be noted that there is only data from 15 layers from 8 sites in the ESA. However, the NISP per site is high at 1459 compared to 933 in the MSA and 550 in the LSA.

To classify the animal species within appropriate size classes, we employed average weight data and referred to the Bovids size class system (Clark and Plug, 2008). The size classes were as follows: Bov 1 <23 kg; Bov 2 23-84 kg; Bov 3 85-295 kg; Bov 4 296-950 kg; Bov 5 >950 kg. We used size classes average weight to calculate faunal biomass because faunal size class are commonly reported for southern African sites. The approach allowed the incorporation of the commonly found data on size classes alone, not identified to species or genus level, expanding the scope of the analysis.

We calculated the relative presence of each size class within each context by dividing the total NISPs for the size class by the total NISPs of the context (layer/spit). Then, we calculated the average for each period by averaging the relative presence of each size class in all the contexts for the period. The model assumes that each context represents a distinct behavioral pattern rather than providing an absolute measure of the number of animals accumulated within the layer.

To assess the statistical significance of the declines in the relative presence of larger-size classes and the increase in the relative presence of smaller-size classes during the ESA-MSA transition and the MSA-LSA transition, we conducted t-tests for each size class after normalizing the dataset.

To further comprehend the implications of the declines in prey size, it is necessary to consider the relative energy derived from different size classes. For this purpose, we developed a biomass multiplier for the various size classes, which involved the following steps:

1. We calculated the average weight within each size class.
2. Taking the average weight of size class 1 as the reference, we divided the average weight of each size class by the average weight of size class 1 to determine the multiplier.
3. The average relative presence of each size class within each period was multiplied by the corresponding relative size multiplier.
4. To obtain the ratio of each size class within the period, we divided the result from step 3 by the sum of the multiplied size classes for that period.

Table 3. Size classes - size ranges, average weights, and biomass multipliers for each size class:.

Size Class	**Size Range (min kg)**	**Size Range (max kg)**	**Average Weight**	**Biomass Multiplier**
1	5	23	14	1
2	23	84	53.5	3.8
3	85	295	190	13.6
4	295	950	622.5	44.5
5	950	5000	2975	212.5

By considering the relative biomass contribution of each size class, we can estimate the relative energy that could be obtained from the prey of different sizes. This step may provide a more comprehensive understanding of the implications for humans of the observed changes in the relative presence of different size classes.

We restricted the calculation to biomass and not the caloric content of the prey because the caloric content is strongly associated with the fat content of the animal, which fluctuates widely between seasons, genders, and age groups (Owen-Smith, 2002). These parameters are not available in the dataset.

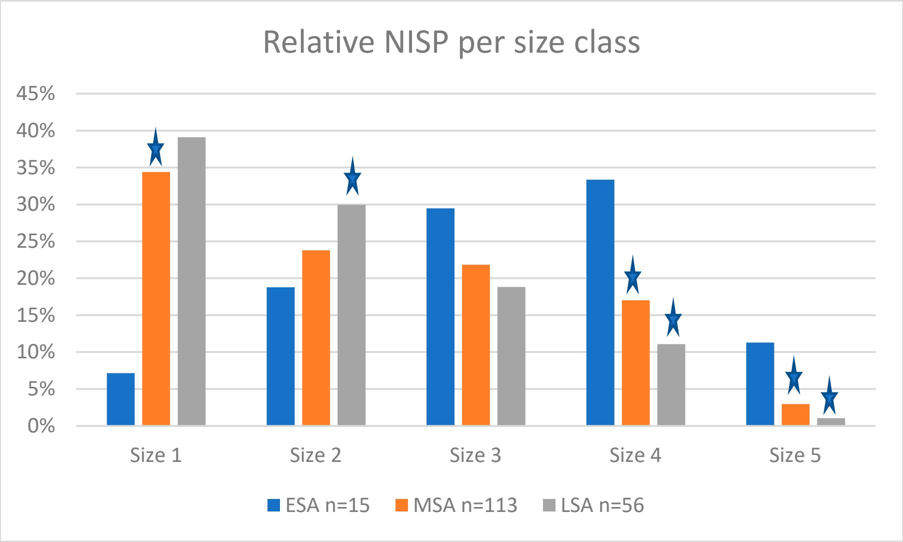
Results

NISP data t-tests indicate statistically significant prey large size declines and small size inclines at archaeological sites between the ESA and MSA and between the MSA and LSA (Figure 1).

For the transition from the ESA to the MSA, we found statistically significant declines in size classes 5 and 4 and a non-significant decline in size 3, indicating a decrease in the relative presence of larger prey animals. Additionally, there was a significant increase in the size class 1 and a non-significant increase in size 2 presence, indicating an increase in the representation of smaller prey animals during this transition.

The same trend continued between the MSA and the LSA. There was a statistically significant decline in size classes 5 and 4, a significant increase in the relative presence of size class 2, and a non-significant increase in size 1.

These changes in prey size distribution provide valuable insights into potential shifts in hunting strategies, resource availability, and human-animal interactions across these archaeological phases.



T Test

	Size 1	Size 2	Size 3	Size 4	Size 5
ESA-MSA	**0.0%**	19%	17%	**2%**	**2%**
MSA-LSA	8%	**1%**	11%	**0%**	**0%**

Figure 1. Relative NISP per size class. * denotes significant change from the previous period.

Biomass Contribution Analysis

The application of the biomass contribution analysis reveals the significant impact of the decline in size 5 (>950 kgs) prey on the overall biomass distribution throughout the periods. This trend is consistently observed in both the transition to the MSA and later to the LSA. In the MSA, the decline in size 5 compared to the ESA was compensated by a relative increase in size 4 and the smaller sizes 1 and 2, while size 3 remained at the same share of the biomass. In the LSA, however, a further decline in size 5 was compensated for by an increase in the share of sizes 1-3, but the share of size 4 persisted, indicating a further tendency to rely on smaller prey (Figure 2).

It is important to highlight that although the two largest size groups consistently accounted for most of the biomass throughout the Pleistocene, their combined share diminished throughout the Periods. In the ESA, size classes 5 and 4 collectively contributed 71% of the biomass, which decreased to 65% in the MSA and further declined to 51% in the LSA. Despite their declining proportion, these findings underscore the significant role played by larger prey animals in terms of biomass throughout all three archaeological periods. The results also underscore the increasing contribution of biomass of the small sizes 1 and 2 (5-84 kgs) in the LSA, from 7% of the biomass in the ESA to 21% in the LSA.

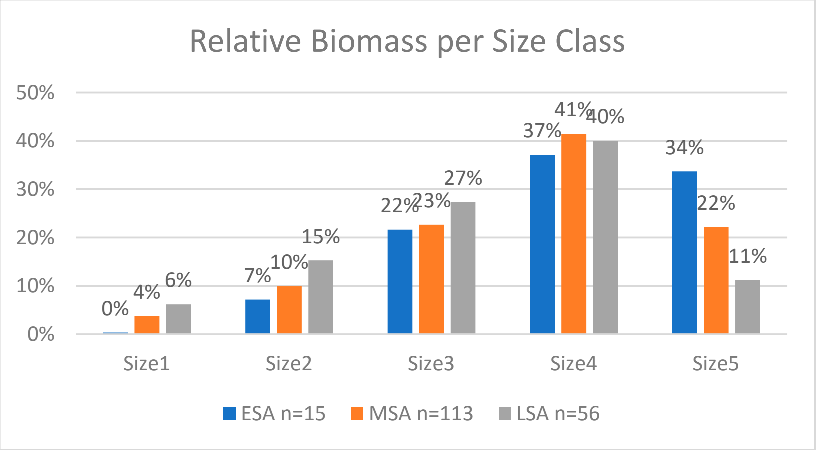


Figure 2. Relative biomass by prey size class.

Discussion

The cumulative pattern observed in these records is influenced by preference and availability. There is evidence for humans' historical preference for large prey based both on ethnographic (Jochim, 1981; Redford, 1992; Bodmer et al., 1997; Bennett et al., 2002; Jerozolimski and Peres, 2003; Hill et al., 2019; Ripple et al., 2019)and archaeological (Bunn and Ezzo, 1993; Hawkes et al., 2001; Bunn, 2006; Surovell and Waguespack, 2009; Speth, 2010; Broughton et al., 2011; Wood and Marlowe, 2013; Dominguez-Rodrigo et al., 2014; Ben-Dor and Barkai, 2020; Linares Matás and Yravedra, 2022). Thus, a decline in prey size in archaeological sites may have reflected a decrease in the availability of such prey.

The results suggest a trend of declining prey size in southern Africa in the transitions between the ESA, the MSA, and the LSA.

It is noteworthy that there is a substantial disparity between the NISP-based analysis and the biomass-based analysis. The cumulative NISPs of size classes 1 and 2 account for a significant proportion (58% in MSA and 69% in LSA) of the total NISPs, whereas the cumulative biomass contribution is much lower (7% in MSA and 13% in LSA). This divergence between the relative quantity of small prey and its biomass contribution is not unique to human predation. Studies on lion predation in the Kruger National Park (Owen-Smith & Mills, 2008) have demonstrated a similar pattern, where the relative number of small prey kills significantly outweighs their biomass contribution. The inclusion of the analysis of the biomass contribution, though more roughly estimated, adds insight as it represents the parameter that drove the prey acquisition – the need for energy. The analysis emphasizes the relative importance of the successive declines in the contribution of the very large (>950) prey between the periods. Both declines in the MSA and the LSA were statistically significant, based on the NISP data, and the fact that the decline is also found in the larger dataset of the MSA and the LSA places a higher probability on the correctness of the earlier decline between the ESA and the MSA despite the ESA's relatively smaller number of contexts and sites.

The data shed light on the changing dynamics of prey availability and exploitation strategies. The decline in very large prey and the subsequent compensatory increase in smaller prey may indicate shifts in hunting technology (e.g., Lombard, 2021). According to ethnographic data (Churchill, 1993), hunting very large prey fundamentally differs from hunting smaller prey. Megaherbivores like elephants and rhinos do not tend to escape in the face of a threat and are usually hunted by limiting their mobility, by a pit trap, for example, and subsequent dispatching by thrusting spears. Smaller prey tends to escape and is hunted by first hitting it with a sharp point to cause bleeding and then tracking the wounded prey. This difference may explain the evolution of hunting weapons (Ben-Dor and Barkai, 2023) with the decline in prey size from the earliest evidence for a hunting weapon in the form of a wooden-tipped spear (Bridgland et al., 1999) (in Europe) through stone-tipped spears in the MSA (Wilkins et al., 2012) to projectile weapons near the end of the MSA and during the LSA (Lombard, 2020).

For example, in the southern African context, previous research by Clark and Plug (2008) identified a decrease in prey size at Sibudu Cave during the Howiesons Poort phase (Table 1), which was associated with climate change (Clark, 2013). They found 68% of NISPs from size class 1, compared to 21% in the post-Howiesons Poort phase. The introduction of the bow and arrow (e.g., Lombard, 2011; Backwell et al., 2018), and possibly also snares (Wadley, 2010) at Sibudu Cave during the Howiesons Poort could be seen as an adaptation to the increased relative availability of small prey.

To further explore the changing prey size pattern in southern Africa, we compared the trends of relative biomass contribution of the size groups in southern Africa and the Levant (Dembitzer et al., 2021) (Figs. 3 and 4, respectively). The most conspicuous phenomenon in the Levant is the disappearance of elephants by the end of the Acheulean, while in southern Africa, elephants are found in archaeological sites throughout the Pleistocene, although, as the data show, in declining rates. The size grouping and the periods dealt with are slightly different in the Levant paper; however, a clear difference emerges between the regions. In the Levant, there is a clear trend of the dominance of one size group in each period and the replacement of the dominant size group by the next smaller one in each successive period. By the UP and the Epipaleolithic (EP), the smallest size groups contributed two-thirds of the biomass in this region. In southern Africa, however, the decline in the largest size class's contribution is more gradual compared to the Levant, and the core of the contribution remains in size classes 4 and 3 (85-950 kgs), which compose more than half of the biomass, in the ESA, MSA, and LSA.

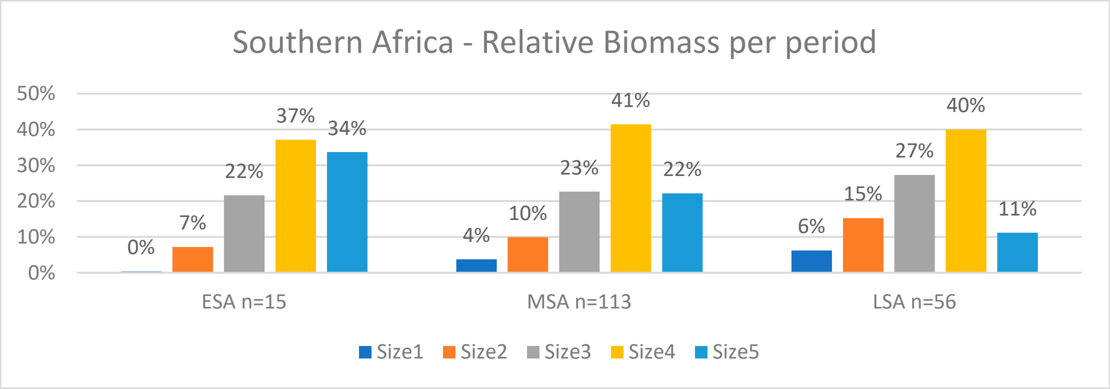


Figure 3. Southern Africa – Relative Biomass per period.

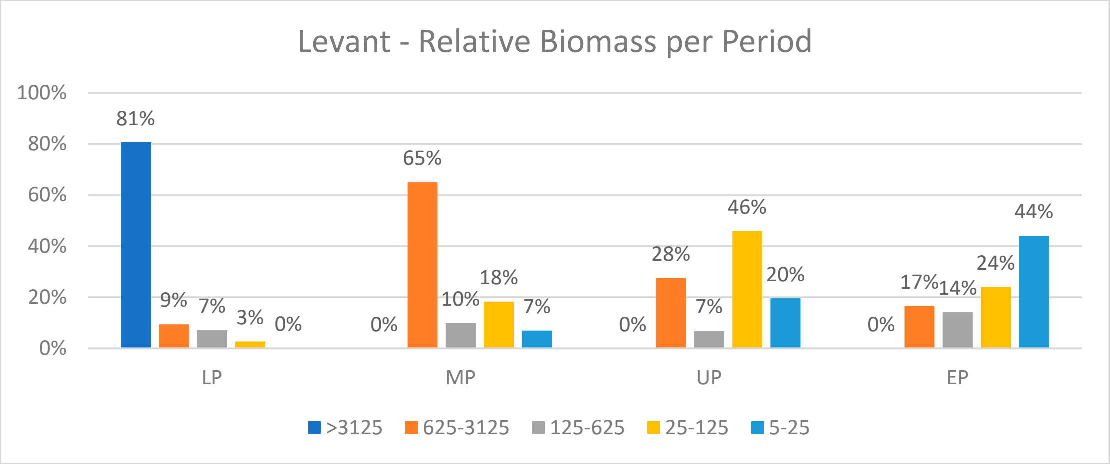
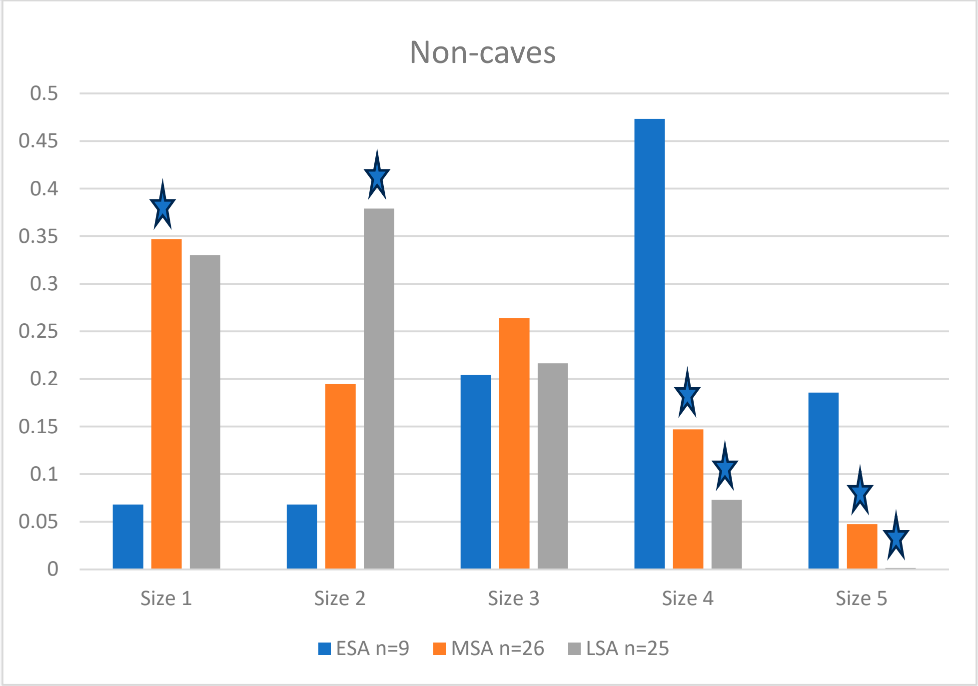


Figure 4. The Levant – Relative biomass per period.

This difference in large prey availability could be attributed to South Africa's large geographic landmass compared to the southern Levant, a small cul de sac. Also, sub-Saharan Africa, or the Afrotropic, is one of the most biodiverse regions globally, with only the southern American neotropics having a greater species diversity. In sub-Saharan Africa, southern Africa has the greatest carrying capacity (Kier et al., 2005; Mutke and Barthlott, 2005).

Smith et al. (2019b), who explored subsistence patterns in Africa during the Middle Pleistocene, also found a decline in prey size in Africa during the period. They concluded that the decline they identified was only an artifact of the dominance of cave sites during the MSA, to which smaller prey body parts were transported compared to the ESA. However, based on our analysis, prey size decline also occurred in non-cave sites in the MSA (Figure 5), with significant t-test results for a decline in size classes 4 and 5 and an increase in size classes 1 and 2 between the ESA and the MSA – and the trend continues through the LSA. It is quite likely that the cause and effect are opposite to what Smith et al. (2019b) assumed, i.e., that the dominance of cave sites in the MSA is a result of the decline in the share of size 5 prey, which was previously more often consumed at the open killing sites.



T test non-cave

	Size 1	**Size 2**	**Size 3**	**Size 4**	**Size 5**
ESA-MSA	**0.0%**	**0.1%**	16.3%	**0.0%**	**0.4%**
MSA-LSA	42.7%	**0.0%**	23.7%	**0.4%**	**0.1%**

Figure 5. Relative NISP by size class in non-cave sites.

Climate and Prey size Decline

A general trend of increasing aridity, accompanied by heightened climatic variability, has been observed in both East Africa (Trauth et al., 2010; Faith, 2014; Potts and Faith, 2015) and Southern Africa (Ziegler et al., 2013; Caley et al., 2018; Scott and Neumann, 2018; Mackay et al., 2022) during the Pleistocene. These climatic shifts have been implicated in human speciation and cultural transformations throughout the Pleistocene (Gosling et al., 2022). Specifically, Potts et al. (2018)

describe a notable correlation between a drying trend, herbivores' size reduction, and events of speciation and cultural change. In eastern Africa, this correlation is evidenced by a faunal turnover in which smaller species supplant larger, extinct species. This turnover is temporally and spatially associated with increased climatic variability, the emergence of *Homo sapiens*, and the appearance of the Middle Stone Age (MSA) in East Africa. A possible human-climate shared responsibility for the size decline is raised by Potts et al. (2020), who propose that human predation could have contributed to the turnover, with the advent of MSA stone points likely serving as an adaptive response to the necessity of hunting smaller prey.

To conclude that climate influenced prey size decline, especially the pronounced decline in size 5 prey identified here, one must explain why a climate change would preferentially affect size 5 prey. Reconstructing herbivore distribution in Africa, Hempson et al. (2015) found that elephants exhibited a lack of response to vegetation composition due to their ability to utilize low-quality forage. However, water dependency can be a limiting factor for the groups of mostly large nonruminants (e.g., elephants and rhinos) and large water-dependent browsers. This analysis may point to a potential biased climate change effect of declining large prey when water bodies' numbers and levels decline.

There is ongoing debate about the extent of climate change during the transition from the ESA to the MSA in southern Africa, and regions within southern Africa are differently influenced by climatic change (Wurz, 2014). However, recent indications point to a relatively wet period at the early MSA (Mis 8-6) from Wonderwerk Cave, Kathu Pan, Bundu Farm, and Florisbad (Lukich and Ecker, 2022). Moreover, the stability in the relative biomass share of size 4 (Figure 2), which also includes water-dependent species, points to a weaker influence of this factor if, indeed, drying reduced the distribution of water bodies.

The transition to the LSA occurred during MIS 3, marked by fluctuating climatic conditions that included moist and cool periods (Lukich and Ecker, 2022). However, in the southern Cape, it was associated with hyperaridity and a hiatus in some sites (Wurz, 2013).

To sum up, climate reconstruction of the entire southern African region is a work in progress, but at the moment, there is no strong evidence for a major drying up of water bodies in the transition between the ESA and the MSA and the MSA and the LSA, and thus we could not conclude that there was a climatic reason for the identified decline.

In the Levant, no association was found between the size decline and climatic indicators pointing to a possible anthropogenic contribution to the decline (Dembitzer et al., 2021). Further research of prey size dynamics during the pre-LQE in Europe and the rest of Asia may provide a better picture of human-prey size historical relationships and a more definitive answer regarding the climatic versus anthropogenic contribution to the changes.

Was Human Predation a Factor in the Decline in Prey Size?

Identifying prey size declines at various times and places throughout prehistory, as we detailed in the introduction, and the finding of this research naturally raises the question of human contribution to the decline. A large body of research advocates anthropogenic cause for the LQE (e.g., Koch and Barnosky, 2006; Sandom et al., 2014; Smith et al., 2019a; Taylor Lemoine et al., 2023), but that conclusion is not unanimously accepted (e.g., Wroe et al., 2013; Grayson and Meltzer, 2015; Meltzer, 2020).

Martin (1966) was the first to offer the hypothesis regarding declines in earlier periods. However, it was not until much later that it was followed by Smith et al. (2018), who suggested that a decline in Africa's pre-Late Pleistocene presence of large mammals was noticed in the form of half the expected mean body size of terrestrial mammals at the beginning of the Late Pleistocene (125 ka) compared to other large continents and that the long coexistence of humans and mammals on the continent could provide an explanation for the decline.

Faith et al. (2020) accepted *Homo sapiens'* contribution to the herbivores' size decline in Africa, presumably beginning around 300 ka but objected to relating any contribution on the part of previous Homo species. Interestingly, Faith et al. (2019) identified a significant decline in the richness of large grazer species a million years ago despite an increase in C_4 biomass, but they attributed the decline to abiotic causes. The decline in prey size in the Levant between the Lower Paleolithic and the Middle Paleolithic was not accompanied by climate change, leading to a possibility of anthropogenic cause (Dembitzer et al., 2021).

For proponents of the anthropogenic contribution to megafaunal extinction, a key question is why and how humans exerted additional predation pressure compared to other predators, leading to the continuous biased population declines of the largest megafaunal species. We propose a driver of this size bias throughout the Paleolithic period – the human quest for fat to mitigate a protein metabolism constraint.

Speth and Spielmann (1983) hypothesized that due to limitations in utilizing protein as an energy source (Rudman et al., 1973; Bilsborough and Mann, 2006), humans can become dependent on a relatively high level of fat consumption. This dependency may have led humans to target prey with high-fat reserves preferentially. Consequently, large species, having high-fat reserves, were a preferred target of human predation. Another unique human pattern, targeting the fatter reproductive segment of prime adults in prey species (Stiner, 1990), could have made the species' populations less stable, exposing them to extinction or population decline risks. Furthermore, the human pursuit of fat led to preferential transportation of fatty parts and wasteful prey exploitation at higher rates and more sensitive seasons to the prey's population growth than established predators.

Plenty of evidence from ethnographic sources shows that prey's fat content was a major choice criterion (Lee, 1969; Tindale, 1972; Jochim, 1981; Coote and Shelton, 1992; Speth, 2010; Kelly, 2013; Tanner, 2014). Kelly (2013) sums the evidence in his authoritative volume 'The Lifeways of Hunter-Gatherers.' in a section on the pivotal role of fat (p. 71) and concludes (p. 74): "It may, therefore, be fat rather than protein that drives the desire for meat in many foraging societies."

Below, we describe how fat-directed hunting could have affected the stability of the human prey population.

Hunting Very Large Prey

Larger mammals have been found to buffer a higher relative amount of fat compared to smaller mammals (Pitts and Bullard, 1967; Calder, 1984) and tend to maintain relatively high levels of fat during periods of nutritional stress (Lindstedt and Boyce, 1985; Owen-Smith, 2002) when fat becomes scarcer. Based on a dataset of the body composition of 257 wild East African common prey animals (Ledger, 1968), large prey mammals were found to contain significantly more body fat, relative to their body weight, than smaller animals (Ben-Dor et al., 2011).

Very large terrestrial animals have survival benefits because of their lower predation risk and because they can utilize low-quality forage and are relatively energetically efficient in relation to their body size (Lindstedt and Boyce, 1985; Owen-Smith, 2002). On the other hand, they are less tolerant if there is predation risk because of their low initial population densities and slower life histories (Cardillo et al., 2005).

Preferential Hunting of Prime Adults

There are plenty of archaeological sites worldwide and throughout the Middle and Late Pleistocene where preferential hunting of prime adults was identified (Stiner, 1990; Enloe, 1997; Hoffecker, 1999; Adler, 2006; Burke, 2006; Clark and Plug, 2008; Gaudzinski-Windheuser and Niven, 2009; Prendergast et al., 2009; Gaudzinski-Windheuser and Roebroeks, 2011; Stiner et al., 2011; Speth, 2012; Rodríguez-Hidalgo et al., 2015; Bunn, 2019).

Humans' preference for targeting prime-adult prey represents an ecologically unprecedented behavior, as they are the only known predators to preferentially focus on the reproductive core of a population (Stiner, 2012).

Prime adult males and females are typically in the middle of their reproductive roles (rut and pregnancy) when their fat content is maximal. By targeting these healthy and mature individuals in

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the quest for fat, human hunters might have significantly reduced the number of offspring born and limited the genetic diversity within a population, leading to their population declines or extinctions.

The Biased Transportation of Fatty Body Parts

Partial consumption, also known as wasteful consumption, where predators exploit only a portion of their acquired prey, is observed across a wide range of mammal and non-mammal predators. This phenomenon is often associated with increased prey density (Kruuk, 1972; Miller et al., 1985; Court, 1996; Stirling and Guravich, 1998; Fantinou et al., 2008).

Partial transportation of butchered prey body parts is a common human behavior, and in several cases, fat-biased transportation has been shown (Morin, 2012; Morin and Ready, 2013). Speth (1983) first identified the human need for fat to supply the non-protein component of the diet when finding preferential transportation of fatty body parts in a bison kill site in New Mexico.

Agam and Barkai (2016) suggest that the high fat content in proboscideans' heads was a primary reason for their preferential transport to central locations. For example, in the difficult-to-access Bolomor Cave, elephant heads were transported to the cave with great effort in MIS 9 to MIS 6 (Blasco and Fernández Peris, 2012). In Gesher Not Ya'acov, 780 thousand years ago, an elephant head was positioned and damaged in such a way as to suggest deliberate breakage for brain extraction (Goren-Inbar et al., 1994). Additionally, recent research has uncovered deliberate accumulation and preservation of fallow deer metapodials, indicative of medium-term marrow storage, at Qesem Cave around 400,000 to 200,000 years ago (Blasco et al., 2019).

A Possible Combined Fat-Targeting and Climatic Influence as a Cause of Prey Size Decline and Evolutionary and Cultural Changes

Here, we described how fat-targeting of prey may create population growth pressure. We accept that climate change could have also caused prey population changes and speciation. It is conceivable that, in certain circumstances, fat-targeting increases a species' sensitivity to population effects of abiotic factors. For example, Potts and Faith (2015) identified nine periods of high climatic variability associated with human evolutionary and cultural changes, and it is possible that climatic and fat-targeting prey population effects combined to cause the observable change in the prey populations and the resultant evolutionary and cultural change.

Conclusions

A study examining the zooarchaeological record of 184 stratigraphic layers in South Africa identified a decline in prey size between the Earlier Stone Age (ESA) and the Middle Stone Age (MSA), as well as between the MSA and the Later Stone Age (LSA). A biomass analysis of the decline found that the most significant contribution was the decline in large (>950 kgs) megaherbivores throughout the transitions between the ESA, the MSA, and the LSA. This finding aligns with previous observations of prey size decline in East Africa and the Levant during the Middle to Late Pleistocene and the global Late Quaternary Megafauna Extinction. By extending the recognition of these patterns to South Africa, the study contributes to understanding the broader impacts of prey size declines on human evolution and behavioral adaptations.

Despite a known continent-wide pattern of drying and increased climatic variability in Africa, in the present climatic reconstruction record of southern Africa, we could not identify climatic indicators such as a reduction in the number and water level of water bodies that could explain the marked declines in size 5 prey biomass contributions in the MSA and the LSA. We proposed that fat-targeting dictated prey choice and exploitation patterns that could impose population pressure on prey in general and large and medium-sized prey in particular, leading to the observed pattern of gradual prey size decline. Identifying the decline further supports our hypothesis of the need to adapt to prey size decline as a primal selecting agent in human physiological and cultural evolution. Since *Homo neanderthalensis* was subject to a similar protein constraint as humans (Ben-Dor et al., 2016),

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further studies of prey size dynamics, especially in Europe, may further contribute to the testing of the hypothesis.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org.

Data Availability: The database of this paper can be found in an Excel file in Medeley.com DOI:10.17632/2z9v7b9vp3.1.

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