

## Article

# The Evolution of Paleolithic Hunting Weapons: A Response to Declining Prey Size

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**Abstract:** This paper examines the hypothesis that changes in hunting weapons during the Paleolithic were a direct response to a progressive decline in prey size. The study builds upon a unified hypothesis that explains Paleolithic human evolutionary and behavioral/cultural phenomena, including improved cognitive capabilities, as adaptations to mitigate declined energetic returns due to a decline in prey size. Five selected case studies in Africa and Europe were analyzed to test this hypothesis, focusing on the relative presence of megaherbivores (>1000 kg) in the transition between the Acheulean/Early Stone Age and the Middle Paleolithic/Middle Stone Age. The findings indicate a decline in megaherbivores' presence and biomass contribution in the studied transition period associated with the introduction of Levallois technology. We review the evolution of hunting weapons, including wooden-tipped and stone-tipped spears and bows and arrows. Analysis of tip size and breakage patterns indicate a reduction in point size over time, aligning with the declining prey size. We propose that changes in hunting weapons and strategies were driven by the practical and ontological incentives presented by the availability and size of prey. Developing smaller, more precise weapons required increased cognitive capacities, leading to the parallel evolution of human cognitive abilities.

**Keywords:** human evolution; hunting weapons; Levallois; prey size; Paleolithic



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## 1. Introduction

In our previous paper in this journal [1], we proposed a unified hypothesis that explains key evolutionary and behavioral/cultural phenomena and changes in prehistory as adaptations to mitigate declining energetic returns due to prey size decline. Additionally, as research has linked weapon systems complexity to increased cognitive abilities [2–4], we proposed that prey size decline is causally related to brain size growth. This hypothesis also implies a connection between humans' evolutionary pressures and their environment. The decline in prey size would have represented a significant challenge for early humans, pushing them towards increasing adaptability and innovation in their hunting practices. These changes, in turn, would have affected their social structures, cultural practices, and overall survival strategies.

In this paper, we test a sub-hypothesis that the evolution of hunting weapons during the Paleolithic era was a direct response to a progressive decline in prey size. Smaller, precision-focused weapons were required to replace large, strength-based weapons.

The unifying hypothesis assumes there were ecological changes, possibly coupled with human predation, that led to a reduction in the size of commonly hunted animals during the Paleolithic era. To continue their subsistence lifestyle, humans had to adapt their hunting strategies and tools. The sub-hypothesis proposes that larger, heavier weapons, such as thrusting spears, which would have been effective for large prey like megaherbivores, became less useful as their abundance decreased. As a result, there was a shift towards more lethal and precise hunting tools.

These changes in weapon technology also reflect the evolution of human cognitive abilities, including problem-solving, creativity, and the ability to adapt to changing circumstances. Developing smaller, more precise weapons may have required greater skill and planning, leading to parallel cognitive development.

To test the above-mentioned hypothesis, we need to establish the basic premise that prey size declined throughout prehistory in the various regions of the Paleolithic world. We also need to present key prehistoric phenomena that changed in temporal association with the alleged decrease in prey size. We started, with partners, mapping prey size dynamics in the Levant. We used data from 133 stratigraphic layers from 58 archaeological sites throughout the Pleistocene and early Holocene. We identified a statistically significant decline in prey size between each successive cultural entity. It began with an average prey weight of three tons in the Lower Paleolithic Acheulean and ended with an average of 50 kg in the Epi-Paleolithic Natufian [5].

Other studies also found evidence of prey size decline in other areas of the world at different times during the Pleistocene. Faith et al. [6] documented a continuous decline in large and medium-sized species and an increase in small-size herbivores in East Africa throughout the Pleistocene. Yravedra [7] identified a decline in prey size in Spain between successive cultures throughout the Paleoarchaeological record. A decline in prey size megafauna richness between the Middle Paleolithic (M.P.)/Middle Stone Age (MSA) and the Upper Paleolithic (UP)/Later Stone Age (LSA) throughout the world is well documented as The Late Quaternary Megafaunal Extinction, e.g., [8,9]. Thus, scholars generally agree with the decline in prey size found in archaeological sites throughout the Pleistocene. The decline might be differently represented at different localities due to variability in animal taxa and specific environmental and topographic conditions. Thus, changes in animal taxa are to be expected.

While larger taxa were plentiful at the beginning of the Pleistocene, mostly small taxa survived into the Holocene. We will not investigate the causes of this decline. Several studies link it exclusively to stochastic ecological changes [10–12], whereas others argue that over-predation by humans was a major contributor [13–15]. In the Levant, humans were either directly responsible for the decline or made larger species more vulnerable to climate change [5]. However, our hypothesis attempts to explain the implications of size decline, not its causes. It is not dependent on the reasons for this decline.

This paper analyzes selected case studies of several key sites in South Africa, East Africa, Spain, and France. Archaeological records at these sites and groups of sites provide information about trends in prey size over time. We concentrated data collection and analysis on the transition between the Acheulean/Early Stone Age (ESA) and the MP/MSA as prey size declines in the later transition from the MP/MSA to the UP/LSA are better documented in The Late Quaternary Megafaunal Extinction framework [8,9,16,17].

Stone tools are the most conspicuous phenomenon in the prehistoric archaeological record. However, unequivocal evidence for using stone-tipped hunting weapons is found only as early as the MP [18–22], although some claims were put forward for making stone projectiles as early as half a million years ago [23]. We have solid evidence for using stone tools in animal carcass processing as early as stone tool production began three million years ago [24]. Human dependence on stone tools for meat, fat, and marrow characterizes human existence and adaptation throughout the Pleistocene and even later [25–31].

Stone tools were used to shape wood, bone, and antler into tools. However, we believe their primary role was to provide early humans access to animal carcasses' calories. It might be argued that changes in animal availability and prey size were both practical and ontological incentives for developing stone tool technologies throughout the Pleistocene. However, this paper will focus only on hunting tools rather than the entire technological repertoire. We focused on evidence of evolved morphology and complexity in hunting weapons production and use as a key phenomenon in human cultural and biological evolution. Due to the considerable time and cognitive demands of producing and maintaining

complex hunting tools [32,33], it is safe to assume that they would not have evolved merely through ‘cultural drift’ sensu Koerper and Stickel [34].

No archaeological evidence exists for stone-tipped hunting weapons for the first two million years of human evolution. However, there is compelling evidence for hunting large prey, beginning in the Acheulean and possibly earlier, e.g., [35–37].

A wooden spear from Clacton, dated to MIS 11 (427 thousand years ago (ka) [38], and a wooden spear and hunting sticks from Schoningen, dated to MIS 9 (330 ka) [39–42], are the earliest archaeological evidence for hunting weapons. Schoningen spears’ diameter suggests thrusting spears [43]. Nonetheless, they were also interpreted as throwing spears, except for one long spear, which was unanimously considered a thrusting spear. A double-ended short 64.5 cm spear was interpreted as a throwing stick [44]. Persistent hunting was considered to have been the method of choice in the Lower Paleolithic [45]. However, other hunting strategies were proposed for big game hunting in the past and present [46,47]. Recent indigenous hunters sometimes use clubs or spears to kill animals after their collapse at the end of persistent hunting [48]. Wooden spears were probably used for hunting before 400 ka. This was done by other methods [49,50] that may not be employed today due to alternative weapons. Based on the ethnographic record, Churchill [47] associated wooden thrusting spears with disadvantaging (limiting the movement) as a hunting method for very large animals. Persistence hunting can also be considered disadvantaging as the hunt aims to bring the prey to a static state of exhaustion. Milks [51], however, showed that wooden spears were used recently to hunt various animals sizes, both as throwing and thrusting spears.

The undisputed second stage of weapon evolution was wooden spear stone-tipping. The stone-tipping of spears may have begun as early as 500 ka [52]. However, stone tipping became prevalent in archaeological sites during the MP/MSA, beginning at 300 ka [21,53–56].

The third wave of hunting weapons inventions was mechanically projected weaponry systems, such as bows and arrows and spear throwers, and darts, which may have originated 100–64 ka in Africa [57–59] but were only widely used during the UP/Late Stone Age (LSA) [56,60] in Africa and the Old World. Other inventions include the domestication of dogs for use as hunter assistants in the middle to late UP [61–64] and the use of traps to capture small game [65–67].

Unlike stone, antler, and bone points, hunting weapons’ other components are seldom preserved. Therefore, point size and breakage patterns are the most common indicators of hunting tool use. Reduction of point size has been a prominent trend since their appearance in the MP/MSA. Tip cross-sectional area (TCSA) is an accepted measure of tip size [68] though tip cross-sectional perimeter (TCSP) may be a more accurate measure [69]. A reasonable approximation of the TCSA can be obtained by multiplying half the tip’s maximum width by its maximum thickness [43]. American ethnographic data on the average TCSA of tips attached to their shafts show that thrusting spear tips, dart (spear thrower) tips, and arrow tips have declining mean TCSAs of 168, 58, and 33, respectively [43]. Reviewing the South African record [53] found that the TCSA of points declined, beginning at 300 ka until reaching arrow tip size during the MIS 4 glacial (~71 ka). A further decline in TCSA points occurred in Africa in the LSA [70]. In the Levant, TCSA values were stable during the M.P. and declined during the UP, ending at the lowest values in the Neolithic [43] (Tables 2, 4 and 5). In Europe, there was a substantial decline in TCSA values of points between the M.P. and the UP, with no clear trend during the UP [43] (Figure 10).

Shea [43] proposed that projectile weapons were developed to provide an advantage in intraspecific human quarrels over diminishing resources in the UP/LSA. A case of interpersonal violence using a weapon is known from the Late Paleolithic [71], but ethnographic and archaeological evidence suggests prey-directed reasoning. “Each species... has its weapon”, writes Bruce Winterhalder on the Cree of northern Ontario [72] (p. 85), and Churchill [47] shows that different hunting weapons were used with different hunting methods to capture different kinds of prey. In many cases, weapons and methods were associated with prey size though bows and arrows were used for hunting a wide range of

prey sizes [47,73]. To our knowledge, besides Shea's [43] hypothesis, no hypothesis that associates hunting weapons evolution with an ecological driver has ever been proposed.

The chronological evolution of hunting weapons is widely accepted, namely wooden tools in the Lower Paleolithic, stone-tipped spears in the MP/MSA, and bows and atlatls mainly in the UP/LSA. As noted, a decline in megafauna presence in the Late Pleistocene is also accepted. Our testing was influenced by previous studies showing that megaherbivore biomass was high in Acheulean assemblages [5,74,75]. Consequently, we tested whether megaherbivore representation in archaeological sites declined between the LP/ESA/Acheulean and the MP/MSA in tandem with changes in hunting gear and proposed a causal explanation.

## 2. Material and Methods

We selected five multilevel sites with faunal data and long chronological records in the transition between the Lower Paleolithic (LP)/ESA and the MP/MSA. We compared the relative presence of megaherbivores between the two periods. Herbivores weighing more than 1000 kg are considered megaherbivores [76]. Our definition of megaherbivores is slightly different: herbivores weighing more than 1000 kg that do not escape. Owen-Smith [76] (p. 1) names megaherbivores as elephants, rhinos, and hippos "while giraffe slips marginally into the category". We did not include giraffes or *bos/bison*, which may sometimes have had bodyweights exceeding 1000 kg, because they tend to escape, though, for *bos/bison*, this is not always true, especially in the herd's safety. According to Churchill [47], elephants and hippos are hunted by disadvantaging and dispatching with thrusting spears, presumably the oldest hunting weapon, when untipped with stone points. A reduction in the number of megaherbivores in the assemblages suggests the need for new hunting weapons to hunt smaller, fleeing species. It was, therefore, imperative to compare the relative abundance of megaherbivores that did not escape. It should be noted that although megaherbivores usually do not comprise a high percentage of the NISP or the MNI, they may provide a dominant portion of bioenergy. For example, a six to twelve tons elephant could have provided over a hundred times more calories than smaller animals like Impala at 50 kg, so the energetic impact of their decline could have had dire consequences [74,75,77]. To study the significance of the change in megaherbivores' presence, we compared their relative contribution to total biomass in each case.

NISP (number of identified specimens) has been proposed to be superior to MNI (minimum number of individuals) in studies of taxa relative abundance [78,79]. In recent historical reviews of these indexes [80], there was no clear consensus on whether MNI or NISP indexes should be employed. There is scanty literature on using NISP or MNI to compare prey abundance by size instead of taxa. Usually, the prey abundance for a specific taxon is expressed as the relative NISP or MNI of that taxon. Our work shows that for abundance by prey size, MNI is superior to NISP because a markedly higher percentage of bones of smaller animals are brought to a central site [75]. It should be noted that only pre-depositional biases were considered in our actualistic work, so large bones, post-depositional preservation bias, and identification bias can change the conclusion. NISP, however, can be biased to a greater extent by taphonomy than MNI [81].

We used two comparison methods to elucidate megaherbivores' presence trend between the LP/ESA or Acheulean and the MP/MSA. In one method, we used only MNI. In the second, we added a consideration of the relative prey mass to sample the bioenergetic consequences of the change better.

1. **Relative abundance of megaherbivores**—MNI (megaherbivores)/total MNI—This is close to the common abundance index where, instead of one taxon, we include megaherbivores as a group of taxa.
2. **MNI-based relative biomass contribution of megaherbivores.** We multiplied the mass of each megaherbivore species by its MNI, summed it across all megaherbivore species, and divided it by the total biomass. In the case of the Hadza [75], introducing

biomass to the relative MNI index resulted in the closest estimate to the actual relative biomass contribution of the taxon to the total biomass of the assemblage.

In the data, we included only large animals known as prey, i.e., mainly herbivores >20 kg. We excluded avians and small animals such as Testudines, Leporidae, and Carnivora since they would have diluted the megaherbivore percentages and made the differences appear smaller. Animal weights were taken from Smith et al. ([82] in Supplementary Materials).

Many, if not most, Pleistocene zooarchaeological assemblages contain anthropogenic and non-anthropogenic bone accumulations that can rarely be reliably and completely separated. We analyzed the complete assemblages since the availability of prey to humans represented by non-anthropogenic accumulations also provides relevant information, even if biased against megaherbivores if the carnivorous contribution to the assemblage is significant.

Figure 1 shows the location of the studied sites in Africa and Europe and Table 1 list the sites, the reference for the data and the total MNI in each site.



**Figure 1.** Location of sites: 1—Elandsfontein, 2—Duinefontain, 3—Bundu Farm, 4—Pniel, 5—Florisbad, 6—Olorgesailie, 7—Bolomor Cave, 8—Sima del Elefante and Gran Dolina, 9—Orgnac 3.

**Table 1.** List of sites and references.

Country	Site	Period	Total MNI	Reference
South Africa	Elandsfontein	ESA	1140	[83–86]
South Africa	Duinefontain	ESA	225	[87,88]
South Africa	Bundu Farm	Early MSA	29	[89,90]
South Africa	Pniel 6	Early MSA	48	[89,90]
South Africa	Florisbad	Early MSA	29	[91]
East Africa	Ologesailie Member 10	Acheulean	31	[92,93] (Supplementary Materials)
East Africa	Ologesailie BOK layers	Early MSA	45	[92,93] (Supplementary Materials)
Europe, Spain	Bolomor Cave	Ancient MP	92	[94,95]
Europe, Spain	Sima del Elefante	Early Pleistocene	46	[96]
Europe, Spain	Gran Dolina	Early Pleistocene, Late Acheulean	57	[96]
Europe, France	Orgnac 3	Upper Acheulean, Early MP	410	[97,98]

### 3. Results

#### 3.1. Africa

##### 3.1.1. South Africa

Smith et al. [99] published a pan-African meta-study comparing Early Middle Pleistocene (EMP) to Late Middle Pleistocene (LMP) faunal assemblages to determine human behavioral changes in the period when modern humans and the MSA appeared. They concluded that adding cave assemblages to the LMP record is responsible for the apparent decline in prey size between the EMP and LMP.

We used Smith, Ruebens, Gaudzinski-Windheuser, and Steele's [99] site list, which compared EMP to LMP layers in open-air sites. We, however, divided the sites into Acheulean or MSA sites regardless of their temporal position in the EMP or LMP. The Acheulean open-air sites contain six EMP layers from Elandsfontein and two LMP/Acheulean layers from Duinefontein. Two of the MSA layers are from the LMP sites, Pniel 6 Level 3 and Bundu Farm Groups 4–6, and one is from the EMP site of Florisbad. There is doubt about the attribution of Florisbad to the MSA because the lithics were assigned to the MSA as "None of the assemblages contradicts an MSA characterization" [100] (p. 1414). Excluding Florisbad from the comparison would have produced a higher degree of megaherbivores decline in the MSA as the site contains five hippos of a total MNI of 29. It should be noted that the Acheulean Elandsfontein and the early MSA sites are situated in two distinct South African regions, the coastline and the interior, respectively. The environment of Elandsfontein, the main site in the Acheulean group, had an open landscape with a significant woody or bushy component [84] (p. 15). The early MSA sites in the interior were close to a water source in what is described as a drier environment with a more variable climate [89,100]. Based on ecological structure analysis, Haradon [92] (p. 251) attributes grassland continuity to the interior region during the Acheulean–MSA transition.

The MNI/NISP data in the open-air sites show a marked decline in megaherbivores in the MSA from 22% to 10% (Figure 2). Considering biomass, the high biomass contribution of megaherbivores is maintained despite a decline from 58% in the Acheulean to 47% of the total biomass in the Early MSA (Figure 2).

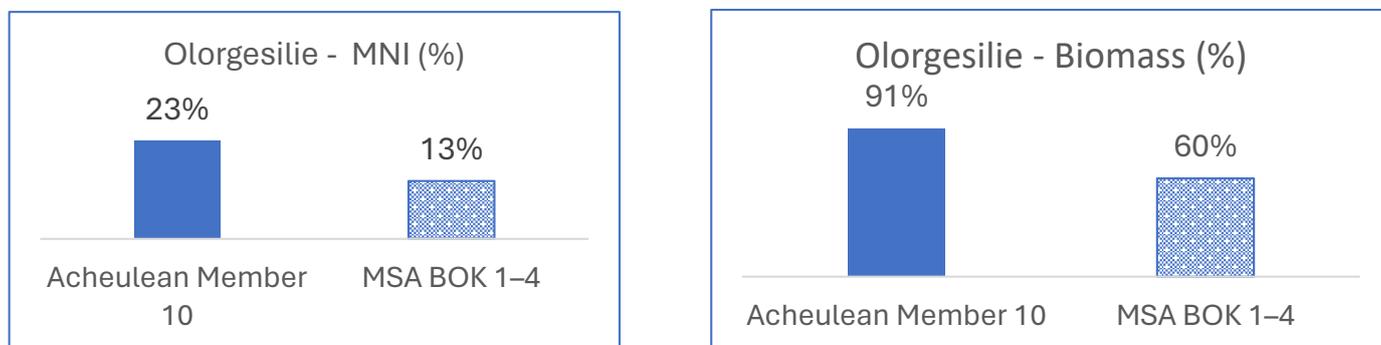


**Figure 2.** Percentage of MNI and Biomass of megaherbivores in the studied South African layers. Megaherbivores abundance declined between the Acheulean and the early MSA. In all the proceeding site charts, the light patterned columns represent the periods when Levallois became a significant technology.

### 3.1.2. East Africa, Olorgesailie

Olorgesailie is the only area with reports of NISP and MNI in East Africa’s Acheulean and MSA layers [92]. Faith et al. [101] identified a reduction in prey size as part of a species turnover in East Africa between 500 and 400 ka. Potts et al. [102] temporally associated the species turnover with the appearance of the MSA and *H. sapiens*. Potts indicate that the fauna of the Olorgesailie BOK MSA layers matches the fauna from open, arid settings.

The decline in the relative presence of megaherbivores is very clear in the two methods. It was very high in the Acheulean at 90% of the biomass, which was like levels that we identified in the Levant Acheulean [5,74], yet, in contrast to the Levant, even after the decline in the MSA, megaherbivores still composed 60% of the biomass (Figure 3).



**Figure 3.** Percentage of MNI and Biomass of megaherbivores in Olorgesailie. Prey size declined between the Acheulean and the early MSA.

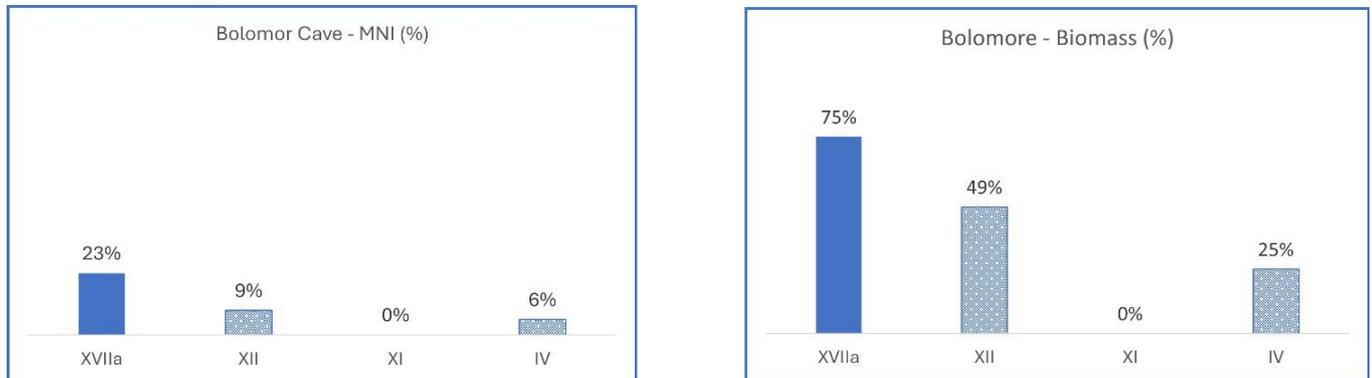
## 3.2. Europe

### 3.2.1. Spain, Bolomor Cave

Bolomor Cave, near Valencia, Spain, presents a late Middle Pleistocene MIS 9 to MIS 5e record. The stratigraphy of the cave consists of 17 levels. We compared Levels XVIIa (dated to MIS 9, 350 ka), XII, XI (dated to MIS 6), and IV (dated to MIS 5e), sampling the full length of the record. Controlled use of fire is evident, beginning in level XIII in MIS 7. The lithic assemblage shows progressing usage of Levallois techniques, although the tools’ morphology was not classic. Pseudo-Levallois points appear in level XII, MIS 6 [103]. Animals associated with open space dominate the cave’s assemblages, indicating a stable open landscape throughout [95].

The decline in megaherbivores is manifested in the two methods and is concurrent with the appearance of points in level XII. There is an increase in megaherbivores’ presence

between levels XI and IV. In any event, MIS 6 and MIS 5e layers (XII, XI, and IV) exhibit a marked decline in megaherbivores' biomass contribution compared to the MIS 9 layer (XVIIa) (Figure 4).

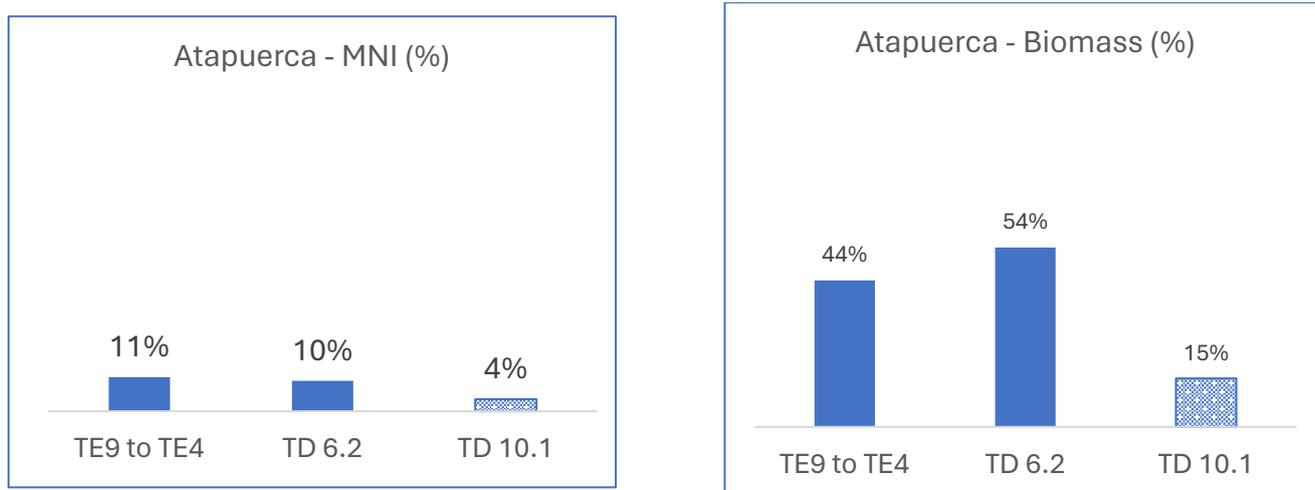


**Figure 4.** Percentage of MNI and Biomass of megaherbivores in Bolomor Cave. Prey size declined through the MIS 9 level (XVIIa) to the MIS 6 level (XII and XI) and MIS 5e level (IV).

### 3.2.2. Spain, Atapuerca

The Atapuerca archaeological complex contains several caves and galleries that provide the deepest perspective on European cultural and faunal trends. We compared layers from three assemblages hundreds of thousands of years apart. Layers TE9 to TE14 of Sima del Elefante cave are dated to the Early Pleistocene, before 1220 ka [104] (Table 1). Remains of *Homo antecessor* were found in TE9. Mode 1 lithic assemblage recovered from TE9, made on raw materials close to the cave. The environment of TE9 to TE14 was defined as “Temperate open woodlands and meadows with lagoons”. Gran Dolina cave is also part of the Atapuerca archaeological complex. Layer TD6.2, dated to  $731 \pm 63$  ka, and layer TD10.1, dated to  $337 \pm 29$ , present significant faunal assemblages [104]. Both levels were interpreted as base camps. The environment of layer 6.2 was interpreted as “open woodland and steppe” and layer 10.1 as “Mediterranean open woodland; thus, the later Gran Dolina layers were not significantly different from the TE9-TE14 layers’ environment. Regarding lithic technology, layer TD6.2 presents Mode 1 technology, like the TE9-14 layers but with a high diversity of knapping strategies and raw material sourcing. Layer TD10.1 presents a transition from mode 2 to mode 3 in centripetal cores tending to Levallois [105].

The two comparison methods show the same pattern. There is a modest difference in megaherbivores presence between the Early Pleistocene TE-TE14 and the early Middle Pleistocene TD6.2, but a significant decline in megaherbivores’ presence and biomass contribution from 44–54% during the Early Pleistocene to 15% during the Middle Pleistocene (Figure 5).



**Figure 5.** Percentage of MNI and Biomass of megaherbivores in Atapuerca. There is not much change in the MNI ratio of megaherbivores decline from the TE9 to TE 14 layers of Sima del Elefante dated to before 1220 ka, to layer TD 6.2 of Grand Dolina, dated to 771 ka. However, there is a marked decline in megaherbivores presence (MNI% and biomass%) between layer TD 6.2 and layer TD 10.1 of Grad Dolina dated to 337 ka.

### 3.2.3. France, Orgnac 3

The Orgnac 3 site is on a plateau near the Rhone River valley (France), on the right-hand bank of the Ardeche River gorges. The site layers cover MIS 10 to MIS 8 occupations, during which the European transition to Levallois-MP culture occurred [97,98]. The earlier 5–7 layers and the 4a and 4b layers were formed in a cave, but the later layers were formed in an open site after the cave roof receded. Levallois core technologies appeared in the middle levels 4a and 4b but became dominant in the MIS 8 layers 3 to 1. The climate in the period of layers 5–7 was humid and temperate at the beginning and became gradually cooler but remained humid with a forested landscape. There was no evidence of Levallois technology in layers 5–7.

The presence and biomass contribution of megaherbivores declined substantially in the MIS 8 levels 1–3, side by side with the emerging dominance of Levallois technology [98]. The climate became cold and dry, and the landscape became open, normally relatively favorable conditions for megaherbivores such as mammoths [106], so climate change cannot explain the decline (Figure 6).



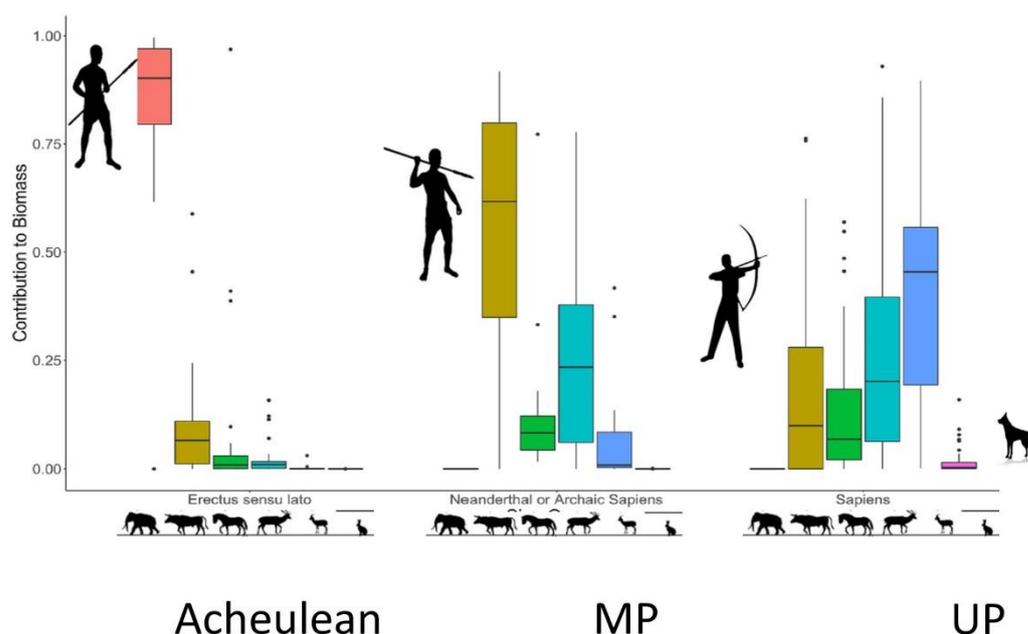
**Figure 6.** Percentage of MNI and Biomass of megaherbivores in Ornac. There is an increase in the presence of megaherbivores between MIS 9 layers 5–7 and layers 4A and B but a marked decline in the ratio of megaherbivores in the MIS 8 layers 1–3, compared to both 5–7 and 4A and B layers.

### 4. Discussion

The results should be considered exploratory because of the small sample size, excluding the Levant [5]. Both methods show that megaherbivores' presence and biomass contribution declined over time in all five cases. There seems to be a clear association between megaherbivore decline and the transition between the Acheulean and the MP/MSA in the cases where the data spanned the Acheulean and the MP/MSA. While the data do not allow examination of the transition between modes of adaptation in the three other cases, Atapuerca, Bolomor Cave, and Orgnac 3, the decline of megaherbivores was associated with an increase in Levallois-like technologies. In the Levant, Levallois technology at the end of the Acheulean was associated with elephant disappearance [107]. In all but one case (Olorgesailie), megaherbivore declines were not directly associated with climate change.

Concerning Africa in general, our findings do not corroborate Smith et al.'s (2019b) [99] assertion that the prey size decline observed during the Middle Pleistocene is an artifact of the increased number of caves used by humans between the early and late Middle Pleistocene. The increase in caves in Smith et al.'s data relates to South Africa and North Africa, so a priori could not apply to open-air sites in East Africa, where in addition to our analysis, prey size decline was evident by faunal turnover [93,101]. Additionally, we showed, via separate analysis of open-air sites in Africa, that a decline occurred in South and East Africa, which cannot be an artifact of a change in site type. It is also noteworthy that Bolomor is a cave, and at certain times, Atapuerca and Orgnac 3 were caves. They all show megaherbivores' presence decline in the Middle Pleistocene. It may well be that the causation in Smith, Ruebens, Gaudzinski-Windheuser, and Steele [99] is reversed. It is not the increased dwelling in caves that presents a faulty picture of prey size decline. It was the decline in megaherbivore reliance in the LMP that allowed humans to dwell in caves more often.

Figure 7 demonstrates the temporal association between the dynamics of prey size and hunting weapons' change, using data from the Levant.



**Figure 7.** The graph is taken from [5]. The prey size decline is made more apparent by considering the prey biomass as documented for the Paleolithic Levant. Megaherbivores dominated the Acheulean prey biomass in the Levant, whereas in the MP, *Bos/bison* size prey (700–1000 kg) dominated the assemblages' biomass. Later, smaller prey like gazelles provided most of the biomass in the UP. Placing the figure of the typical hunting weapon of the period next to the prey size biomass distribution demonstrates the temporal association.

#### 4.1. Energetic Return and Prey Size

Prey size is not the only factor affecting weapon choice [108]. Landscape factors such as hiding opportunities may facilitate a closer approach and improve weapon effectiveness. Small prey was also hunted throughout the Paleolithic, necessitating multiple hunting gears and strategies. Despite this acknowledged variability, this paper discusses the most appropriate hunting weapons for each phase's major dietary source. Furthermore, we follow the logic that the disappearance/decline of larger taxa led to the adoption of more appropriate weapons for smaller animals. For simplicity, the argument is presented dichotomously, although, in real life, nuanced approaches prevail.

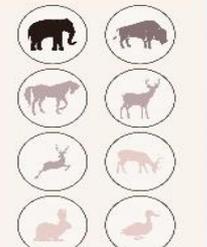
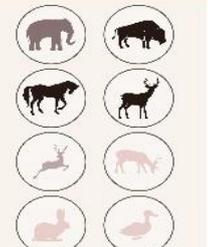
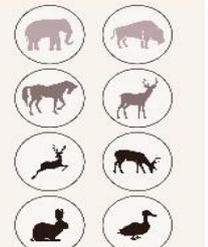
Due to the wider range of weapons available to hunters at the end of the Pleistocene, the hunter could better match prey size and other circumstances of the hunt to maximize energy returns [72,85].

Prior to the MP/MSA, early humans used mostly wooden spears and throwing sticks for hunting. What would be the impact of hunting smaller prey with wooden-tipped spears on total energetic return? The same question about the transition from MP/MSA to UP/LSA and stone-tipped spears must be asked. What would have been the energetic returns of hunting small prey like gazelles with a stone-tipped spear had the bow and arrow not been invented? Studies in the Levant (Figure 7) and in Tanzania [75], as well as other studies [77], indicate that large prey provides most of the animal-sourced subsistence energy, so a decline in its abundance should have presented a significant loss of resources to the hunters. Existing hunting tools could not bridge the gap since they were no longer suitable for smaller and faster game. The energetic return on hunting megaherbivores with wooden-tipped spears should be compared to the return on hunting many more fleeing smaller prey animals to fill the biomass gap with the same wooden-tipped spears. There are no data on net energetic returns for such a comparison. It may have been possible to use wooden-tipped spears to hunt an increased number of smaller prey, but the energetic return is likely to have been insufficient.

To maximize their return under varying landscapes and prey sizes, recent hunter-gatherers had a full arsenal of hunting weapons at their disposal [72]. San hunters in the Kalahari sometimes carried bows, arrows, and spears in their hunting kits, and they used both thrusting and throwing spears [109]. Morin et al. [110]'s conclusion that ethnography-based hunter-gatherers' returns are not associated with prey size is thus not relevant to explaining prehistoric behaviors when hunting technologies were much more limited. After all, bows and arrows were unavailable for over 95% of the Pleistocene, and dogs, pervading Morin et al.'s data, were unavailable for 99% of it.

If anything, Morin, Bird, Winterhalder, and Bird's [110] conclusion of the non-association of net energetic returns with prey sizes confirms our assertion that the innovation of new hunting weapons and new technologies was aimed at mitigating the decline in net energetic returns due to prey size decline [1]. Their conclusion confirms that the mitigation was successful.

Figure 8 provides a graphic description of the main premise of the paper—In each period, the weapons were adapted to energetically efficiently hunting the dominant size prey of that period.

Period	LP/ESA	MP/MSA	UP/LSA
Weapon			
Prey			

**Figure 8.** Each period is depicted with its typical hunting weapons and dominant prey in terms of potential caloric contribution (in darker colors). All sizes of prey were acquired in every period.

#### 4.2. Tipping Spears with Stone Points

At geographically widespread archaeological sites, this paper shows a decline in mega-herbivore abundance between the Acheulean and MP/MSA periods. There is clear evidence for the MP/MSA appearance of hafted stone points (see references in [23]). Therefore, we can determine a temporal correlation between the decline in mega-herbivore presence and the appearance of hafted stone points. There is convincing evidence that hafted points were used in hunting proboscideans in North America and Europe [46,111,112], though their use has not been unanimously accepted [113]. This phenomenon may be explained by the global availability of stone points and hafting technology during the Late Pleistocene and the high relative abundance of proboscideans in new territories. Stone-tipped spears may be more effective than wooden-tipped spears in hunting proboscideans under certain circumstances. Still, in America, stone point size declined with prey size [114,115]. In the transition between MP/MSA and UP, we find a similar association. There was a decline in the size of prey in archaeological sites during this transition [5,8,9], and smaller stone tips appeared to be interpreted as dart tips and arrowheads [56,60]. The association between prey size decline and stone-tipped spears and later spear thrower-darts and bow-and-arrow hunting weapons systems must be explained.

So why would it be advantageous to tip wooden spears with stone points in the MP/MSA when mega-herbivores' share of humans' food resources declined? Many changes in prehistory could be explained by adaptations to hunting smaller prey animals without exceeding a limited energetic budget [1]. Using a stone point instead of a wooden tip should have produced an increased energetic return in MP/MSA hunts of non-mega-herbivores if the hypothesis holds true.

In comparing the energetic cost of hunting mega-herbivores like elephants and large herbivores like bison, it is not clear if, a priori, a search for a mega-herbivore is more time-consuming than a search for a large herbivore. Mega-herbivores may be scarce in numbers, but they are conspicuous in the landscape because they are bigger. They leave noticeable

traces in large spoons, dung piles, and broken branches [76]. Elephants are relatively easy to find, following expected paths to water sources. Many large herbivore species like *bos/bison* and equids are also conspicuous as they are large and tend to live in herds. The ethnographic record shows that stone tipping was used mainly in throwing spears [108], although stone points were used in thrusting spears. However, stone tipping of thrusting spears is not applicable to the Lower Paleolithic. Using a boat or a horse often accompanies ethnographic stone point usage in thrusting spears. This allows the stocking of several spears as the stone points tend to break and thus prevent repeated usage of the thrusting spear. In throwing spears, the stone tip allows skin penetration with a lighter spear. A lighter spear could be thrown from a longer distance, thereby increasing the chances of maintaining surprise and increasing the success rate of hitting the prey. In addition, it would reduce the energetic cost of the first stage of the hunt [108].

The next energy-consuming stage of the hunt is the pursuit, which in the hunt of large herbivores replaces the stage of disadvantaging the megaherbivores [47]. The pursuit stage can be energetically costly [110], and we can assume that the severity of the hunting weapon wound will be inversely associated with the time and distance of pursuit. Testing replicas of projectile points on gelatin, Anderson [116] found that stone points created a wound from 183 percent to 311 percent wider than that produced by a pointed wooden shaft. The same effect could be assumed in stone-tipped spears. The primacy of increased lethality in hunter consideration is supported by an ethnographic review of stone-tipped spears, spear throwers (atlatl), and arrows [108,117]. Tyua hunters of the northern Kalahari state that spears are superior to bows and arrows for killing large animals. They state that spear impact results in immediate death or sufficient blood loss to weaken the animal relatively quickly [109]. Thus, we can infer that spear stone tipping provides a larger interior wound area than wooden spear tips. Weapons kill by bleeding and damaging vital organs [68,118,119]. Thus, increased bleeding from the larger wound should shorten the escape/pursuit stage. Additionally, hyenas and other carnivores are less likely to steal the escaping prey because the pursuit is shorter. Although the breakability of the stone tip is often presented as a negative attribute, it should be considered that leaving the whole tip or a broken part of the tip in the animal tissue may cause greater blood flow as the prey escapes and thus shorten the escape/pursuit. Another consideration for MP/MSA hunters in the attempt to increase the lethality of the spears may have been safety, as the large prey they targeted, like *bos/bison*, could also attack the hunter [108,109,120].

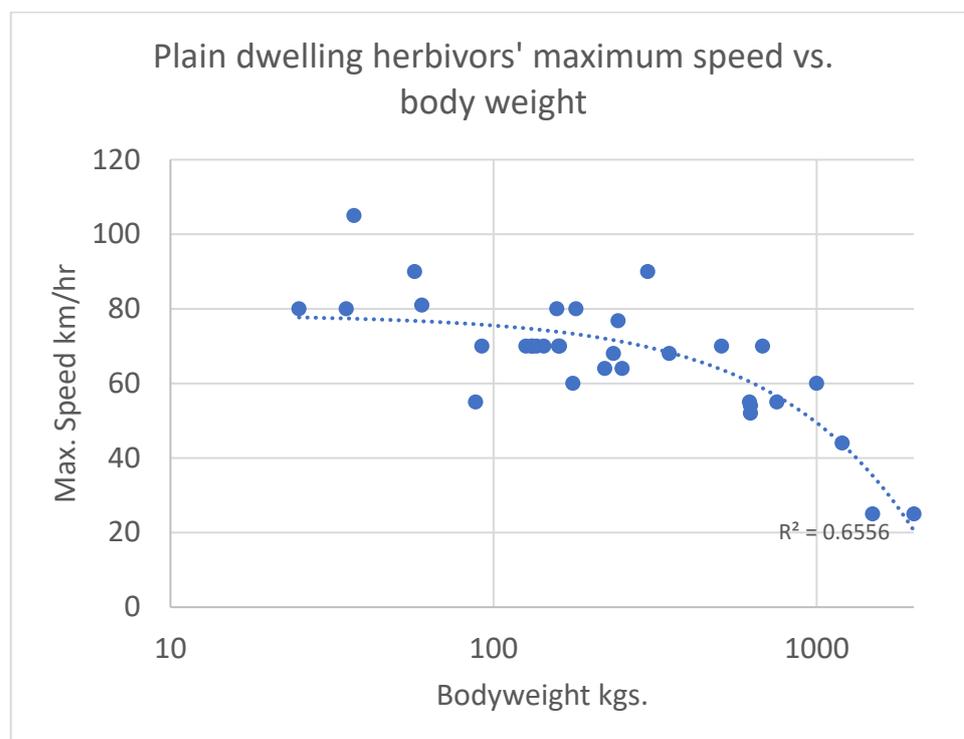
#### 4.3. Developing Complex Weapon Systems

There is strong evidence that prey size declined during UP/LSA as part of the Late Quaternary Megafaunal Extinction, e.g., [5,8]. The widespread usage of bows and arrows as hunting tools likely began in the Upper Paleolithic period [43].

The earliest known evidence of bow and arrow use comes from the South African site of Sibudu Cave, where researchers discovered small, pointed pieces of stone that could have been used as arrowheads, dating back approximately 64,000 years ago [58,121].

The next question is whether there is a causal association between the switch to complex projectile weapons (arrows, darts) and the further decline in prey size between the MP/MSA and the UP/LSA. A review of experimental and ethnographic literature concludes that humans traded wound areas for accuracy by switching to bows and arrows from spears. Small animals are as fast or faster than large escaping animals (Figure 9). For example, the African elephant has a maximum speed of 35 km/h, whereas the Zebra is 70 km/h, and the Impala is 90 km/h [122]. At the same time, the target organs (mostly the heart and lungs [119]) are smaller than those of large animals. At the same time, the depth of penetration and the wound size required to subdue the animal also decline. Arrows travel almost three times faster than spears [68]. The increased arrow speed enables better aiming as the trajectory is flattened (more accurate placement) [68,123]. Thus, the bow provides better accuracy at the cost of a smaller wound area. Hughes [68] mentions two other attributes of bows that increase the probability of hitting prey: the ability to

produce repeated fire and the relative quietness of the arrow delivery, which maintains the element of surprise. Both attributes seem effective in hunting the fastest-flying small prey. To summarize, the main energetic savings from the transition to spear-throwers and bows and arrows may have come, as is the case with the transition from wooden to stone-tipped spears, from the increased success rate and the reduced pursuit cost when hunting small animals.



**Figure 9.** Speed vs. Weight in Plane-dwelling herbivores. Plane-dwelling herbivore becomes quicker as their size decrease but the association levels off at about 100 kg. Based on data from [122].

The domestication of dogs is another technology that can reduce the costs of pursuing small prey. Dog domestication occurred during the UP [124] when prey size continued to decline as megafauna became extinct in the LQME. Ethnographic evidence shows that dogs are predominantly used for hunting small prey [63,109]. During small game hunting, dogs do part of the pursuit and sometimes assist in the search, saving energy.

Studies of the association between prey size and weapons are particularly interesting when projectile points appear briefly. One such case is Sibudu Cave in South Africa. Bows and arrows are interpreted to have appeared in the Howiesons Poort and likely disappeared in the post-Howiesons Poort layers [125], when points were interpreted as spear points [21]. Explanations for the 'regression' from the use of bow and arrow are centered on demographic developments (see references in [125]). However, the decline in prey size in the Howiesons Poort, coupled with the reversal of the decline in post-Howiesons Poort assemblages [126], may also explain the appearance and disappearance of the bow. The bow introduction followed a decline in prey size in North America after 2000 B.P. [127–129]. In spite of the fact that bows were used in the Old World before humans migrated to America, they first appeared here more than ten thousand years after humans arrived. It is likely that the early Paleoindians were exposed to bow technology but did not use it until the size of prey decreased.

The model predicts that the gradual introduction of the light javelin in South Africa during the MSA, as is evident by the decline in TSCA values of the points [53], was associated with a decline in the density of large prey during the MSA. This prediction will have to be tested in the future.

#### 4.4. Prey Size Decline and the Evolution of Cognition

The emergence of a causal brain size—prey size (reversed) association is a key implication of the causal association between prey size decline and the development of novel hunting weapons. Human biological and cultural evolution is closely linked to technological innovations [33,130]. As weapons become more complex, they require more cognitive ability [131,132]. Additionally, tracking prey may also require enhanced cognitive abilities [133,134]. As noted, a key difference in energy expenditure between disadvantaging megaherbivores and ambush hunting smaller prey is that disadvantaging saves pursuit. In contrast, ambush hunting with a spear or bow and arrow is associated with a longer pursuit of the smaller and faster prey (Figure 9). As far as we could ascertain, none of the past literature discusses a unifying ecological driver for weapon technology evolution or the need for enhanced cognitive capability for the tracking stage of smaller prey. We argue that the production of complex weapons and the employment of gradually more advanced tracking behaviors, at the cost of increasing cognitive resources, contributed to energetic savings in the increasingly longer pursuit stages of the hunt. We can thus infer that prey size decline and the resulting need to mitigate the additional energetic expenses imposed by the decline were, at least partly, driving human cognition evolution.

## 5. Conclusions

The findings in this paper contribute to the growing body of evidence that suggests prey sizes declined during the transition between the LP, ESA, and Acheulean. The decline was first associated with the appearance of spear-sized stone points, mostly made by the Levallois method. Later, the prey size decline known as The Late Quaternary Megafaunal Extinction was associated with the invention and adoption of complex projectile systems, trapping devices, and dog domestication. We hypothesized that the employment of the new weapon technology resulted in the mitigation of potential energetic cost increases with the decline in prey size. We expanded on the mechanism for the weapons to improve the energetic return from hunting smaller prey. Additionally, we discussed the emerging causal relationship between prey size decline and cognitive abilities extension. Wider geographical and temporal research is needed to increase the resolution of the association between prey size trends and the evolution of hunting weapons, technologies, and methods.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/quat6030046/s1>. The data that support the findings are available from the corresponding author upon request.

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