

12. SUPERSIZE DOES MATTER: THE IMPORTANCE OF LARGE PREY IN PALAEOLITHIC SUBSISTENCE AND A METHOD FOR MEASURING ITS SIGNIFICANCE IN ZOOARCHAEOLOGICAL ASSEMBLAGES

Miki Ben-Dor^{1,*}, Ran Barkai^{1,*}

¹Department of Archaeology, Tel Aviv University, P.O.B 39040, Tel Aviv, Israel 6997801

*bendor.michael@gmail.com, barkaran205@gmail.com, barkaran@tauex.tau.ac.il

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ABSTRACT

Humans consumed megaherbivores, including proboscideans, throughout the Pleistocene. However, there is a high potential for underappreciation of their relative importance to humans' economy due to their potential relative underrepresentation in Palaeolithic archaeological sites. Relying on our previous work, we discuss the critical importance of large animals in human prehistory. We review four factors that made megaherbivores critically important to humans: high ecological biomass density, lower complexity of acquisition, higher net energetic return, and high fat content. We propose a model that intends to overcome the potential underrepresentation bias by multiplying the MNI (Minimum Number of Individuals) of each animal species by its weight and only then determining the relative biomass abundances. The next step of the model is the accumulation of the relative biomass abundance, beginning with the largest animal. This step enables a comparison of various assemblages

in the relative complexity of acquisition, the level of net energetic return, and the level of fat content in the prey. We successfully test the method on an actualistic case of 61 hunts of the Hadza, where the true number and the MNI are known. We then apply the method to three comparisons between two successive cultural periods each, in the Levant, East Africa and Southern France. We find that there is indeed great potential for the underrepresentation of megaherbivores in the analysis of Palaeolithic faunal assemblages. Since the largest animal in our actualistic study was a giraffe, we propose a future avenue of research for better correction of the underrepresentation of elephants, which often have partial to no representation in central base sites.

1.2.1 INTRODUCTION

Humans and animals shared habitats across the Old and New Worlds throughout the long presence of the human race upon the earth. Before



the advent of agriculture, humans were heavily dependent on animals for their survival, as is clearly shown by the dominance in prehistoric archaeological sites of bones and stone tools, both bearing marks of anthropogenic exploitation of animals for food. Animal resources were essential, first and foremost, in supplying humans with the daily caloric intake and nutritional needs, but also in providing materials for utensils, construction, clothing, and hunting gear.

The Pleistocene global-scale extinctions of many of the large terrestrial mammals that humans used to consume have been a major ecological phenomenon (Barnosky et al., 2004; Sandom et al., 2014; Potts et al., 2018; Smith et al., 2018, 2019a; Faith et al., 2019). The extinction of the larger animals continued into the Holocene (Dirzo et al., 2014). The role of humans in the extinction is highly debated, yet, discussion of the implications of the extinctions on humans are less prominent in the literature.

This paper aims to propose a hypothesis outlining the potential importance of large animals, particularly megaherbivores and proboscideans, in humans' subsistence during the Pleistocene and the implications of their extinction and disappearance. We propose a method of measuring the significance of large game in faunal assemblages and identify cases of probable stress to humans, caused by the disappearance and extinction of megaherbivores. Likewise, we argue that these extinctions led to changes in vegetal and faunal relative biomass, as well as in large prey's relative abundance (Johnson, 2009; Bakker et al., 2016; Faith et al., 2019), and thus necessitated appropriate changes in human behavior and modes of adaptation (Ben-Dor, 2018: chapter 5.3; Ben-Dor and Barkai, 2020).

A bias might occur between the surviving archaeological evidence on-site and the actual original fauna retrieved and processed by early humans, as archaeological faunal assemblages are affected by many parameters, such as body part transportation, distance from the kill sites and preservation issues. In order to confront such a bias, we ana-

lyze an actualistic ethnographic case study in an attempt to discern the degree of bias against the expected proper representation of large prey in Palaeolithic faunal assemblages. We then propose and test a methodology to partially reduce the bias. We apply the method to three archaeological case studies where sufficient data exist to compare two consecutive Palaeolithic cultural phases in the same region and draw conclusions regarding human behavior in the face of changing faunal availability and representation, based on our hypothesis. We conclude by highlighting the underrepresentation of proboscideans in Palaeolithic assemblages, as inferred from the model and propose future research to better account for this.

Typically, a lower percentage of megaherbivores' complete body parts are transported to a central place, due to their higher weight and the probable long distances from the place of acquisition to the central place (Bunn et al., 1988; O'Connell et al., 1990). The butchery of a large game at the kill site and the transportation of soft tissue and fat to the central place will yield almost no identifiable archaeological signature at the locale of consumption [regarding elephants, see Lewis (this volume) and Yasuoka (this volume)]. Upon examining the evidence for Middle Palaeolithic diets, Morin et al. (2016) conclude that taphonomic and transport considerations may lead to underestimation of the contribution of large animals to the diet, especially megaherbivores. In Europe, there appears to be a significant mismatch between the considerable importance of mammoths in the Middle and Upper Palaeolithic diet, according to stable isotope analysis (Bocherens et al., 2005, 2013; Bocherens, 2011; Wißing et al., 2019; Bocherens and Drucker, this volume) compared with zooarchaeological analysis (e.g., Grayson and Delpech, 2002). Bocherens proposes that the mismatch between the zooarchaeological and isotopic dietary determinations may be due to taphonomic biases and site specialization (Bocherens, 2011: p. 73). Another explanation "could be linked to transport decisions: filleted meat of very large herbivores could have been transported to the camp and therefore

did not leave as many bone remnants as those of less bulky prey species” (Bocherens, 2009: p. 247). The underrepresentation of megaherbivore bones in faunal assemblages may lead to an underappreciation of their economic importance to humans in the Palaeolithic and of the potential effect of humans on the extinction of megaherbivores and other large animals.

White (1953) proposed that to estimate the relative dietary contribution of species, the Minimum Number of Individuals (MNI) in an assemblage be multiplied by their consumable meat content to arrive at a biomass abundance index. However, biomass indexing of faunal assemblages is rarely performed in the analysis of Pleistocene faunal assemblages. Even in the rare cases, when biomass abundance index is calculated (e.g., Crader, 1984; Patou-Mathis, 2005), the animals are not sorted by size, so it is difficult to appreciate the contribution of large mammals versus smaller ones. Moreover, these studies usually do not address the behavioral and economic implications of the relative contribution of large prey [but see Guil-Guerrero (2017) regarding omega-3 fatty acids content of the diet]. Thus, a hypothesis regarding the reasons for the importance of acquiring large prey in the Palaeolithic can advance our ability to draw concrete adaptive predictions from identified changes in prey size composition in faunal assemblages. Testing and applying the hypothesis can lead to a better understanding of the role megaherbivores played in the cultural and biological history of humanity.

12.2 THE IMPORTANCE OF MEGAHERBIVORES IN PALAEOLOGIC SUBSISTENCE

Humans had access to large prey during most of the Pleistocene. Recent analyses of the archeozoological and palaeontological East African record portray *Homo erectus* as a habitual hunter of large prey (Domínguez-Rodrigo and Pickering, 2017; Roach et al., 2018). Preference for large prey an-

imals during the Pleistocene is a conventional interpretation of archaeological assemblages (Isaac, 1984; Bunn and Ezzo, 1993; Bunn, 2006; Surovell and Waguespack, 2009; Domínguez-Rodrigo et al., 2014a). Large animals, including proboscideans, are a common feature in early African Pleistocene sites (Klein, 1988; Bunn and Ezzo, 1993; Domínguez-Rodrigo et al., 2014a, b) and early sites outside Africa, such as Ubeidiya, Latame, Gesher Benot Ya’aqov, Holon and Revadim in the Levant (Bar-Yosef and Belmaker, 2011; Ben-Dor et al., 2011), Dmanisi in Georgia (Gabunia et al., 2000; Bar-Yosef and Belmaker, 2011; Carotenuto et al., 2016), Marathousa 1 in Greece (Panagopoulou et al., 2018), Tarragona and Orce in Spain (Mosquera et al., 2015; Espigares et al., 2019), sites in central Spain (Yravedra et al., 2017), and Castel di Guido and La Polledrara in Italy (Saccà, 2012; Santucci et al., 2016), to mention only some of the most prominent Lower Palaeolithic sites. Moreover, it is evident that large animals, including proboscideans, continued to be an important component of archaeological sites worldwide throughout the Pleistocene (e.g., Zhang et al., 2010; Wojtal and Wilczyński, 2015; Pitulko et al., 2016; Yravedra et al., 2017; Demay et al., this volume; Rosell and Blasco, this volume).

Faurby et al. (2020) added a palaeontological angle to the hypothesis that humans preferred large prey. They hypothesized that, beginning in the Early Pleistocene, carnivorous activity of humans affected the diversity of other large carnivores. Werdelin and Lewis (2013) suggested that 1.5 million years ago, humans became members of the large carnivore guild, specializing in the acquisition of large herbivores, as evident by the extinction of sabretooth predators along with some hyenas [but see Faith et al. (2018) and reply to Faith et al. by Faurby et al. (2020)]. Additional support for humans’ preference for large prey can be gained from the pattern of the extinction of large but not small animals in association with humans’ introduction to previously unoccupied regions (Johnson et al., 2016; Saltré et al., 2016; Smith et al., 2019a), although other researchers emphasize the

role of climate in these extinctions (Grayson and Meltzer, 2015). However, there is little argument that on islands, humans were responsible for the extinction of large animals (Duncan et al., 2002; Burney et al., 2003; Stuart, 2015; Cooke et al., 2017).

Although small animals were also acquired by humans in the Palaeolithic (Blasco and Fernández Peris, 2012; Blasco et al., 2016), an increase in the archaeological presence of smaller prey animals is evident in the Upper Palaeolithic in Eurasia, together with signs of increased plant food consumption (Stiner, 2002; Bar-Yosef, 2014). These changes are, intriguingly, temporo-spatially associated with the late Quaternary megafauna extinction (Barnosky et al., 2004).

A preference for large animals is also apparent in recent hunter-gatherers as they consistently accord the highest-ranking to larger prey (Broughton et al., 2011; Tanner, this volume). Based on their analysis of the Hadza men's hunting and sharing patterns, Hawkes et al. (2001) also noticed the preferential targeting of large prey. However, they attributed the preference to male costly signaling or "show-off" in order to attract mates. Speth (2010) reached a similar conclusion, associating big game hunting with male costly signaling rather than economics. Analyzing later data from the Hadza, Wood and Marlowe (2013) concluded instead that food economics rather than "show-off" was at the base of the Hadza men's hunting preferences, and Domínguez-Rodrigo et al. (2014a) reached a similar conclusion in a Palaeolithic context.

There are several reasons why larger, especially very large, animals are attractive to humans as prey, as we will discuss below.

12.2.1 WHY HUMANS PREFERRED TO ACQUIRE LARGE PREY

We propose that four factors made megaherbivores a primal target of human predation. The first is the high relative biomass density of megaherbivores. The second factor is their tendency to not escape

from predators. The third is the higher net energetic return that is gained from their acquisition, and the fourth is their relatively high fat content. All these aspects may be inter-related. For example, high biomass is the cause of their higher energetic return and of not needing to escape from predators (Owen-Smith and Mills, 2008). Not needing to escape may enable the accumulation of higher fat content (Owen-Smith, 2002: p. 143).

We have to comment here on a paper by Lupo and Schmitt (2016) that claims that very large animals, like giraffes and elephants, are ranked among the lowest in terms of net energetic return (7th and 8th out of 8 animals in their table 4), because of their high acquisition and processing costs, and thus are acquired only in the framework of costly male signaling. It should be noted that their analysis is based entirely on general ethnographic data without actualistic or experimental support of a single complete case. The parameters they have used, namely, pursuit costs and hunting failure rates, are extremely sensitive to ecological conditions that, as previously discussed, were markedly different during the Pleistocene. Other parameters, like the need for preserving meat by smoking, are also assumed rather than evidenced or measured. For example, they consider all the 2.2 million calories of the elephant as subject to the costs of preservation and smoking. However, around 50% of the caloric estimation they present, or a million calories of the elephant energetic resources, are in the form of fat (Ben-Dor et al., 2011; Guil-Guerrero et al., 2018), which does not require smoking for preservation, for the most part. Likewise, a Pleistocene elephant was more likely to supply double the calories estimated in their paper (Ben-Dor et al. 2011), thus providing the hunting group with essential calories and fatty acids for weeks (Guil-Guerrero et al., 2018) and thus a surely prized food package (see Ichikawa, this volume; Lewis, this volume; Yasuoka, this volume). We recently argued that the Hadza and the San, and arguably most recent hunter-gatherer groups, were adapted technologically and behaviorally to hunt small game rather than

megaherbivores, due to the massive global decline in megaherbivore richness and biomass density during the later phases of the Pleistocene and the Holocene (Ben-Dor and Barkai, 2020). We concluded that the ethnographic quantitative subsistence analogies with the Pleistocene are not viable, due to major differences in megaherbivore availability and related environmental consequences. The only recent groups that were referenced in Lupo and Schmitt (2016) as hunting elephants live in the densest jungles of Central Africa, an extremely unrepresentative environment for hunter-gatherers in the deep past or recent past, especially when it comes to Pleistocene acquisition of elephants that occupied diverse but mostly open environments. Thus, we question the relevance of their analysis with regard to hunter-gatherers occupying non-forested areas. Moreover, according to our analysis of an actualistic case here, the giraffe, the lowest ranking animal in Lupo and Schmitt's analysis, contributed more than 50% of the weight of the Hadza's animal-based diet (see Fig. 12.5). In fact, the lowest-ranking animals in the Lupo and Schmitt analysis are the largest animals (eland, giraffe, elephant), and the highest-ranking are the smallest animals (bush duiker, springhare, steenbok, bat-eared fox). The Hadza seem to behave exactly in opposition to this ranking in that around 90% of their hunting weight originates from the largest animals (giraffe, buffalo, eland, zebra; Fig. 12.5). This trend of large prey dominance in the Hadza meat acquisition is confirmed by Marlowe (2010: fig. 8.7), who also rejects the "hunting as costly signaling" hypothesis based on the data he collected (Marlowe, 2010: pp. 215–216). The last point in this regard has to do with the view that recent hunter-gatherers of the Congo basin are purposefully making efforts to remain egalitarian and keep personal autonomy, even though elephant hunting might be used to gain personal benefits that might undergo the social cohesion of the group (Lewis, this volume; Yasuoka, this volume). This view of the Baka Pygmies elephant hunters of Central Africa is in strict opposition with the costly signaling argument

suggested by Lupo and Schmitt (2016). It presents a socio-cultural mechanism of making use of the dietary benefits of hunting and consuming elephants while maintaining an egalitarian way of life (Yasuoka, this volume).

RELATIVE BIOMASS OF VERY LARGE HERBIVORES |

The late Quaternary extinction (Baranosky et al., 2004) and the further extinction of large species during the Holocene (Braje and Erlandson, 2013) make present biomass density distribution studies inapplicable to Palaeolithic ecological analogies (Faith et al., 2019).

Still, even present studies of large herbivores' density (reviewed in Silva and Downing, 1995) find that the largest herbivore species sustain higher densities than predicted by general power-function relationships between density and body mass. Silva and Downing (1995: pp. 711–712) speculate that the relative higher densities of large herbivores are due to lower rates of predation, ability to exploit low-quality resources and plant cell walls, and domination of inter-specific aggression. They conclude, "...thus, the largest mammals may be able to extract more energy from the environment, which permits them to sustain higher densities than simple allometry predicts".

Elephants still dominate the biomass of herbivores in several African nature reserves forming up to 80–89% of the herbivores' biomass (Leuthold and Leuthold, 1976: tab. 4; Milligan et al., 1982; White, 1994; Valeix et al., 2007). In some game-reserves, where elephants and other megaherbivores are protected from predation by humans, they are so "embarrassingly successful" as one researcher (Owen-Smith, 1988: p. 2) put it, that there is often a need to reduce their population by culling in order to avoid vegetal and faunal changes that are detrimental to the existence of other species. This phenomenon naturally also raises the possibility of a role for humans in top-down control of megaherbivores' populations in the past.

Reconstructing the biomass density of herbivores in Africa one thousand years ago, Hempson et al. (2015: p. 1056) estimate the "nonruminants"

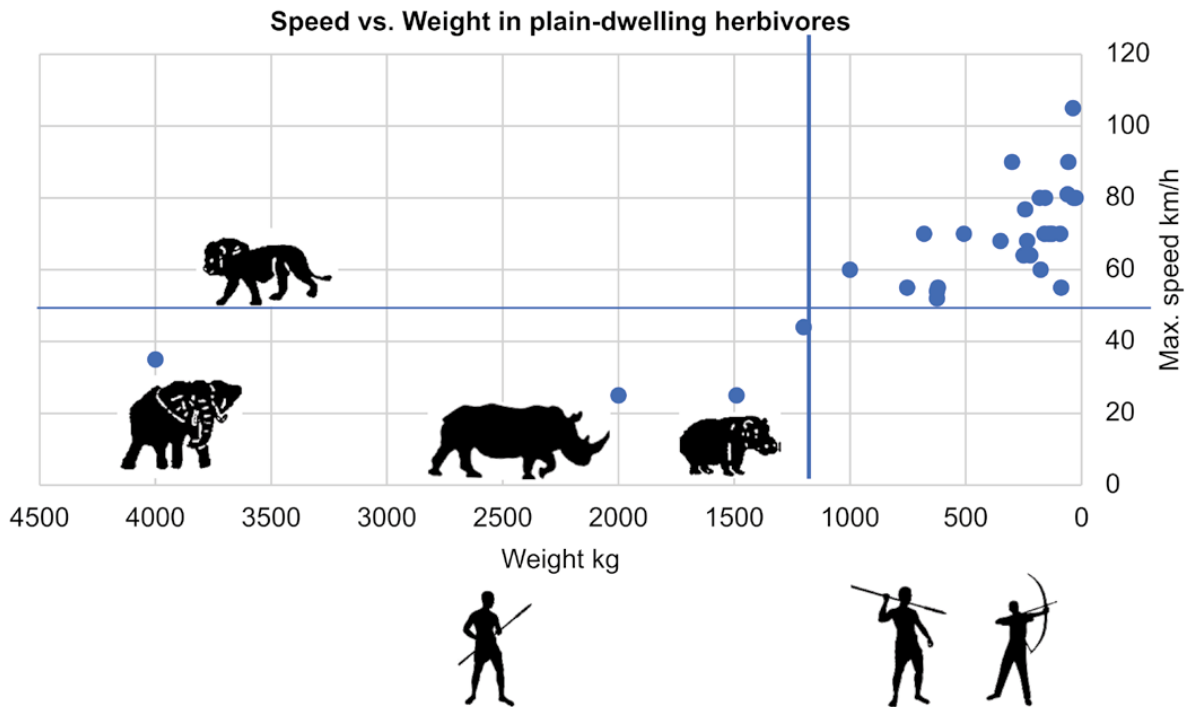


Figure 12.1: Speed vs. weight in plain-dwelling herbivores.

group, which contains mainly megaherbivores, to have had a biomass density of 37 to 10,646 kg/km². “Water-dependent grazers,” the second densest group, which includes a larger number of medium-sized animals such as wildebeest, achieve only some one-sixth of the biomass density of the “non-ruminants” group (0–1553 kg/km²). They predict that elephants, in particular, provided an exceptional amount of herbivore biomass. Elephants were particularly widespread in different ecological regions of Africa, possibly due to their ability to feed on low-quality forage and a broader variety of stages of vegetation, which improves resource partitioning. Hempson et al. (2015: p. 1056) predict that one thousand years ago, “elephants dominate African herbivore biomass, often having biomasses equivalent to those of all other [herbivores] species combined”.

It is well accepted that the productivity of carnivores is a function of the abundance of herbivores (Leonard and Robertson, 1997). Therefore, it only makes economic sense that a predator capable of hunting megaherbivores, which were proba-

bly mainly humans (Agam and Barkai, 2018), will spend a significant amount of his energetic budget exploiting this high biomass density. The dominant share of large herbivores of the total potential prey biomass also has economic implications in that, relative to their biomass, large herbivores are encountered in higher frequencies. Additionally, because of their size, megaherbivores are conspicuous in the landscape and leave large traces of their presence in the form of spoor and excrements. They are also water-dependent (Hempson et al., 2015), so they can be expected to periodically frequent known water sources. In summary, megaherbivores are found in great numbers and are relatively easy to trace and locate. We, however, do not claim that megaherbivores were the dominant herbivores always and everywhere. Throughout the Pleistocene, there are regions and periods with evidence for the varying presence of megaherbivores. We do claim, however, that as megaherbivores represent an unprecedented amount of fat and protein, it was always the preferred prey whenever available. When unavailable, humans had to invest more effort in

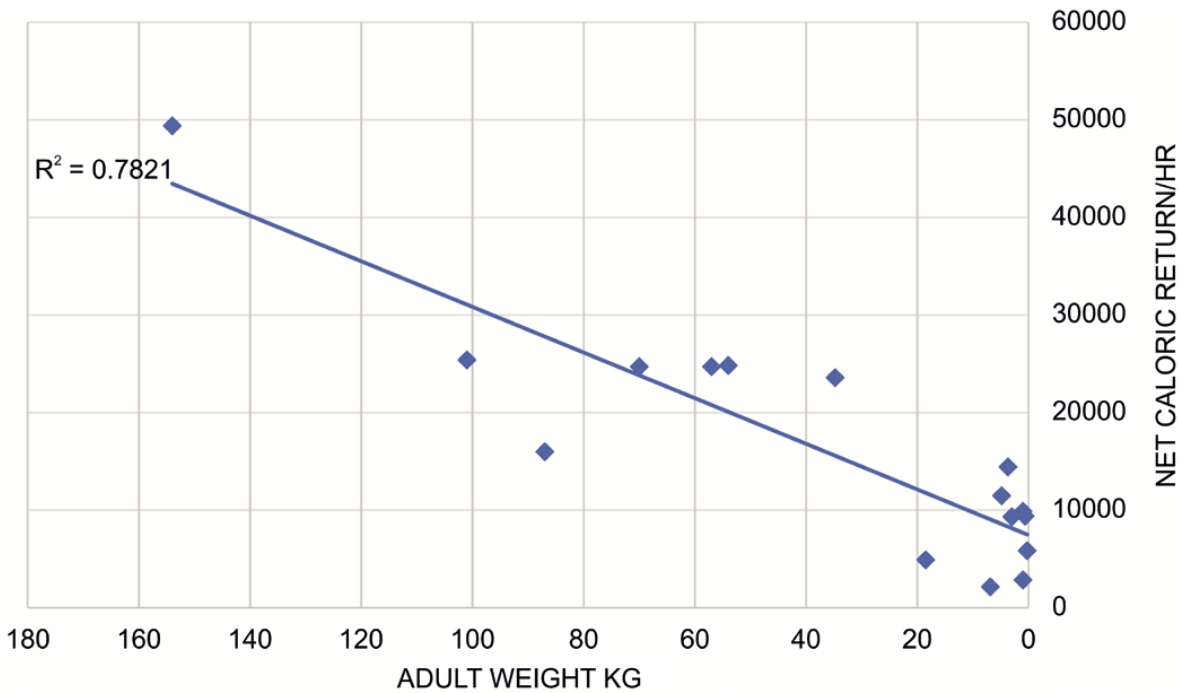


Figure 12.2: Net caloric return/hour by animal weight (Kelly, 2013: tabs. 3–4).

supplying the necessary caloric intake by pursuing smaller game and other resources.

NOT ESCAPING – EASIER TRACKING AND LESS COMPLEX HUNTING TOOLS | Figure 12.1 draws the maximum speed of plain-dwelling herbivores in relation to their size. As shown below, megaherbivores —namely elephants, rhinos, and hippos— do not rely on escape as a predator protection strategy, as evident by their low maximum speed compared to that of a lion (Hirt et al., 2017: appendix). Unlike ungulates, megaherbivores lack specific predation risk alarm signals (Owen-Smith, 1988: p. 132). Presently, when humans approach, they tend to stand still and may flee or charge when humans get closer (Owen-Smith, 1988: pp. 127–128). This behavior has several implications that make their acquisition by humans relatively energetically profitable and technologically less complex than hunting smaller, fleeing prey, though arguably requiring great personal courage and associated with increased personal risk.

The chart depicts plain-dwelling herbivores’

maximum speed as a function of their weight. It also shows (based on Churchill, 1993) that more complex technologies are used for the acquisition of smaller and faster game, namely thrusting spear for non-escaping megaherbivores, throwing spears (with stone tips) for medium size-medium weight animals, and bow and arrow for smaller and faster herbivores.

The smaller and faster the animal is, the more complex the technology that is used in its acquisition (Churchill, 1993). Generally, fast escaping animals are hunted with projectile weapons. In contrast, there are quite a few methods of hunting elephants that require little technological sophistication. Most of the hunting methods of megaherbivores aim at limiting the mobility of the prey, for example, by digging a pit or driving it to a mud trap, at which time dispatching requires only a wooden thrusting spear (Churchill, 1993; Agam and Barkai, 2018). Both the easier locating and tracking of the megaherbivores and the relatively less complicated tools that are used presumably have bioenergetic profitability implications to their acquisition.

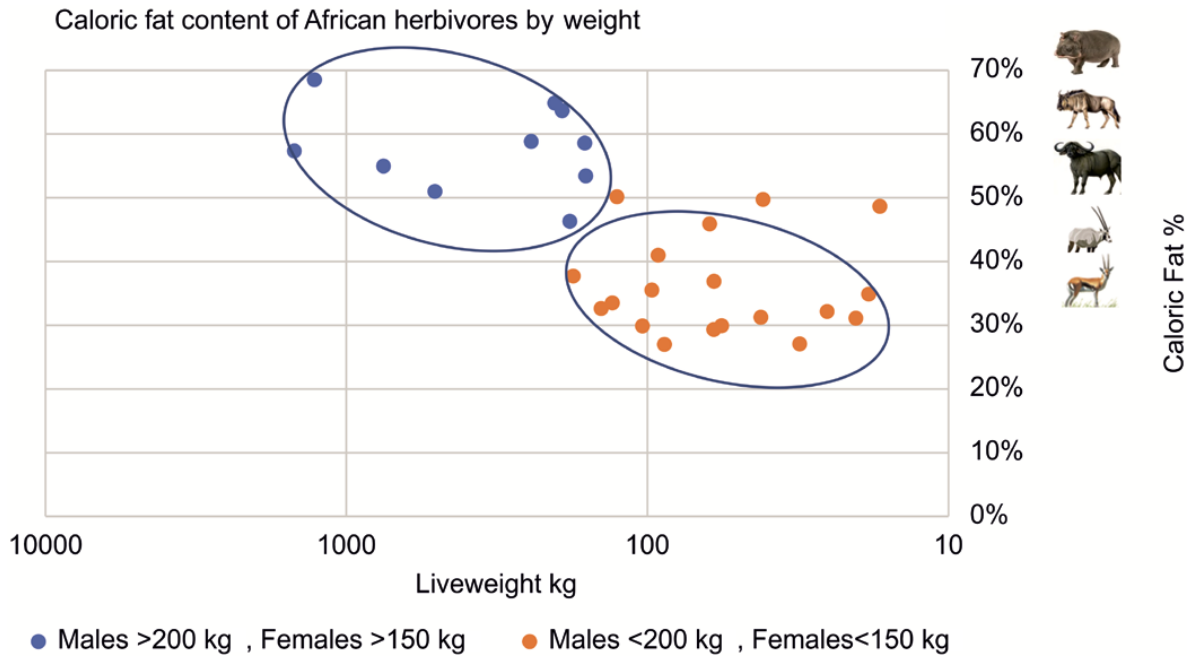


Figure 12.3: The caloric fat content of African herbivores by weight, based on Ledger (1968).

LARGER ANIMALS PROVIDE HIGHER ENERGETIC RETURN | Ethnographic data (Kelly, 2013: tab. 3-4) show that large animals offer higher net energetic returns (Fig. 12.2). Although there are no data for megaherbivores, as these large animals were mostly unavailable for recent hunter-gatherers, the association between size and net energetic return is quite robust.

Ethnographic research shows that large animals rank higher than smaller animals because they provide higher energetic returns (Ugan, 2005: tab. 1; Stiner and Kuhn, 2009: tab. 11.1; Broughton et al., 2011: tab. 1). According to the data in Kelly (2013: tabs. 3-4), medium-sized animals provide a net caloric return of some 25–50,000 calories/hour. In comparison, small animals provide one-fifth to one-half of the net caloric return. Plant food returns are similar to those of very small animals. Seeds, the most nutritious plant food, return 191–13,437 kcal/hr, berries 250–4,018 kcal/hr, and tubers 267–6,252 kcal/hr. Following classic optimal foraging theory (see review in Lupo, 2007), we argue that striving to optimize energetic return, humans will prefer the acquisition of ani-

mals, and especially large animals, over plants. Of course, local environmental conditions such as mass extinctions of large herbivores, and seasonal and local abundance of particular plants, may create occasions where plants dominate the diet. However, we have argued that these types of situations had a higher likelihood of occurring relatively recently at the end of the Pleistocene and during the Holocene in areas where the vegetal to faunal biomass ratio had changed dramatically after large herbivores extinctions (Ben-Dor and Barkai, 2020; Ben-Dor et al., in review).

In summary, we believe that bioenergetic considerations weigh heavily in favor of the importance of large herbivores to the human economy during the Pleistocene.

LARGER PREY CONTAINS HIGHER BODY FAT

| We hypothesized that dietary animal fat played a crucial role in human survival during the Pleistocene (Ben-Dor et al., 2011, 2016; Ben-Dor, 2018: chapter 7). Protein consumption in humans is limited to around 35–50% of the daily calories, due to the limited ability of the liver and kidney to remove

larger quantities of the toxic nitrogen by-product of their metabolism (Speth, 1989). This limitation means that 50–65% of the calories should come from fat or carbohydrates. Elephants contain enormous amounts of fat, about one million calories in the fat of a single mammoth (Guil-Guerrero et al., 2018), and most probably an even higher number of fat calories in the much larger Pleistocene elephants (Ben-Dor et al. 2011). More calories can be gained by accessing the proboscideans' bone marrow (Boschian et al., 2019). Pitts and Bullard (1967) were the first to find that larger mammals contain relatively more fat than smaller animals. An analysis of a dataset of nineteen African herbivore species (Ledger, 1968) confirmed this phenomenon (Ben-Dor et al., 2011) (see Fig. 12.3 and data in Ben-Dor, 2020).

In the Ledger (1968) dataset, male herbivores weighing over 200 kg and female herbivores weighing over 150 kg contain, on average, 44% more body fat, relative to body weight, than smaller animals.

Equally important, since humans mostly occupied seasonal environments, large herbivores maintain a high level of fat during periods of low forage (Lindstedt and Boyce, 1985), probably due to their ability to exploit low-quality forage and lower metabolic rate to body size ratio (Owen-Smith, 2002: p. 88). Since periods of low availability of forage are usually also periods of low plant food availability for humans, large herbivores' fat availability at these periods may become even more critical to humans' survival (Tanner, this volume). Recently, delayed consumption of marrow in the form of preserved fallow deer's bones was identified at Qesem Cave (420 to 200 ka), likely highlighting the criticality of preserving fat for dry seasons (Blasco et al., 2019).

The criticality of the availability of fat, and, consequently, that of large prey, is a function of the relative availability of plants and the relative energetic costs of their exploitation. A multidisciplinary reconstruction of the human trophic level during the Pleistocene (Ben-Dor, 2018: chapter 5.5; Ben-Dor et al., in review) found that humans

were highly carnivorous during most of the Pleistocene, declining in trophic level towards the end of the Pleistocene, hand in hand with the late Quaternary megafauna extinction and the concomitant increase in relative vegetation density (Johnson, 2009; Bakker et al., 2016; Faith et al., 2019). Ethnographic reports of low trophic levels in groups like the Hadza of Tanzania and the Ju/'hoansi (!Kung) that are sometimes used to support low trophic level during the Pleistocene were shown to be better analogies to the very end of the Pleistocene, representing adaptations to prey-size declines (Ben-Dor, 2018: chapter 5.3; Ben-Dor and Barkai, 2020). There is insufficient space here to describe the 27 pieces of evidence that the Ben-Dor (2018) and the Ben-Dor et al. (in review) reconstruction of the human trophic level includes, but a short review may be in order. The majority of the evidence (18 items) come from human biology and include genetic, metabolic, and morphological adaptations to a high trophic level that are unique to humans. In some cases, like the high acidity of the human stomach (Beasley et al., 2015), the adipocytes morphology (Pond and Mattacks, 1985), the short weaning period (Psouni et al., 2012), the authors themselves classified humans among carnivores. Genetic information provided signs for adaptation to a higher plant consumption at the end of the Pleistocene. Most of the archaeological evidence (8 items) also supported a high trophic level, leading with stable isotopes data, and fat-oriented large and prime adult prey selection, and exploitation of bone fat at great energetic expense. Other archaeological items like the pattern of stone tools prevalence also pointed to increased plant food utilization towards the end of the Pleistocene. Finally, palaeontological evidence of the type we cite in this paper and analogies with the zoological record regarding carnivores also support carnivorous trophic level during the Pleistocene. Of note, in connection with the subject of this paper, is the fact that all carnivores that acquire large prey are hypercarnivores, obtaining most of their calories from animals (Wroe et al., 2005; Van Valkenburgh et al., 2016).

SPECIES	COMMON NAME	NUMBER	MNI	MAU	AVERAGE WEIGHT (KG)	REFERENCE
<i>Giraffa camelopardalis</i>	giraffe	11	8	39.6	1010	3
<i>Syncerus caffer</i>	buffalo	2	2	19.8	753	1
<i>Taurotragus oryx</i>	eland	2	2	13.0	508	1
<i>Equus burchelli</i>	zebra	15	14	168.7	235	2
<i>Connochaetes taurinus</i>	wildebeest	3	3	26.8	181	1
<i>Alcelaphus buselaphus</i>	hartebeest	2	2	24.0	135	1
<i>Phacochoerus aethiopicus</i>	warthog	6	6	83.6	74	1
<i>Aepyceros melampus</i>	impala	19	19	198.0	50	1
<i>Papio cynocephalus</i>	baboon	1	1	15.0	19	3
Total		61	57	588.5		

Table 12.1: The Hadza sample - Basic data. References for weights. 1, Ledger (1968); 2, Hirt et al. (2017); 3, Skinner and Chimimba (2005: pp. 616–620).

12.3 A METHOD TO CORRECT THE UNDER-REPRESENTATION OF LARGE ANIMALS IN PALAEOLOGIC ARCHAEOLOGICAL ASSEMBLAGES

In an attempt to measure and test ways to correct the potential under-representation of large animals in the zooarchaeological faunal analysis, we analyzed an actualistic ethnographic case study. In this case study, the true quantities of the acquired animals are known, thus enabling a comparison between the various abundance indexes. The common abundance indexes are based on either Minimum Number of Individuals (MNI (species) divided by MNI (total)) or Number of Identified Specimens (NISP (species) divided by NISP (total)) (Lyman, 2018). Neither indexes, however, take into account a possible transport bias of larger animals' heavier bones and probably an even higher bias in the transportation of megaherbivores' bones. Moreover, the weight and caloric content of the different prey animals is not accounted for. For example, in three out of three elephant kills and butchering sites of the Efe in the Ituri forest, observed by Fisher Jr (2001), the entire group moved to temporary camp adjacent to the kill site, and no bones were carried beyond the temporary camp, while large quantities of fat and meat stripped from the bones were transported elsewhere. Total

omissions and reduced transport of large animals are bound to bias the indexes to overestimate the abundance of small animals and underestimate the abundance of large animals in the acquired faunal assemblages.

In 1986, two research groups measured multiple variables that were associated with the Hadza's hunting of large prey. O'Connell et al. (1988) initially analyzed 49 cases and later (O'Connell et al., 1990) reanalyzed these cases, plus five additional ones, to a total of 54 cases. Bunn et al. (1988) analyzed 29 additional cases. The purpose of their analysis was primarily to draw analogies that will aid in differentiating kill and butchering sites from central place type archaeological sites. Later, Monahan (1998) combined both groups' data in a reanalysis of his own. The increase in sample size comes at the cost of combining results from two separate geographical backgrounds. However, we feel that since the same group is studied at the same time (1985–6) in the group's territory, the averaging effect of combining the group may even be advantageous rather than deleterious. We used the data from Monahan (1998: tab. 2). The table lists 61 animals for which the meat and skeletal elements were transported away from the Hadza kill and butchery sites to a central place (camp). Immature animals and scavenged animals that were partially exploited were eliminated from Mo-

ANIMAL	AVERAGE WEIGHT (KG)	TRUE			ASSEMBLAGE			
		NUMBER	%NUMBER	%BIOMASS	%MNI	%MAU	%BIOMASS (MNI)	%BIOMASS (MAU)
giraffe	1010	11	18 %	57 %	14 %	7 %	50 %	32 %
buffalo	753	2	3 %	8 %	4 %	3 %	9 %	12 %
eland	508	2	3 %	5 %	4 %	2 %	6 %	5 %
zebra	235	15	25 %	18 %	25 %	29 %	20 %	32 %
wildebeest	181	3	5 %	3 %	5 %	5 %	3 %	4 %
hartebeest	135	2	3 %	1 %	4 %	4 %	2 %	3 %
warthog	74	6	10 %	2 %	11 %	14 %	3 %	5 %
impala	50	19	31 %	5 %	33 %	34 %	6 %	8 %
baboon	19	1	2 %	0 %	2 %	3 %	0 %	0 %

Table 12.2: The Hadza sample - Comparison of true, MNI and MAU abundance indexes.

nahan’s data. Bunn’s group used MNE (Minimum Number of Elements), and O’Connell’s group used MAU (Minimum Number of Units) to report the skeletal elements that were transported to the base camp. We transformed Bunn’s group’s MNE to MAU based on data regarding the number of elements in animals at the bottom of Monahan’s table 2. A summary of the data appears in Table 12.1.

Although other researchers use an estimate of the consumable meat to calculate the dietary contribution (White, 1953), we used the total liveweight since our main aim here is to correct a bias in transporting body parts, including bones, and there is no evidence that the consumable meat weight is a better predictor of this bias. Also, according to our hypothesis, large animals are preferred mainly because of the high total weight and size that confers various advantages in locating and acquiring them.

In Table 12.2, we compared the widely used MNI- and NISP- (MAU- in our case) based abundance indexes (Lyman, 2018) to indexes that account for the animal weight (relative MNI or NISP multiplied by animal weight). The indexes were compared to the “true value”. The true value was based on the relative number of each animal multiplied by its weight. For example, the true potentially consumable biomass contribution of

the giraffe is 57% of the total weight. Eleven giraffes were obtained out of a total of 61 animals. Since each giraffe weigh 1010 kg, their weight contribution was $11 \times 1010 = 11,110$ kg. The total weight of the assemblage was 19,383 kg, hence $11,110/19,383 = 0.57 = 57\%$.

The table demonstrates that MNI is constantly closer to the true abundance than MAU (NISP), especially of the larger and smaller species where the relative under- and over-representation of MAU-based indexes are high. For example, giraffes form 18% of the total true number of animals and 14% of the total MNI, while they constitute only 7% of the total MAUs. Since the largest animals in this sample contain several times the weight of smaller animals, the use of MNI is critical to the correction of the relative biomass bias.

Regarding biomass, it can be seen from Table 12.2 that there is a major underestimation of the large animals’ potentially consumable biomass share if the regular MNI or NISP abundance indexes are used. This bias stems mainly from the fact that no bones were brought back to camp from three out of the eleven giraffes consumed, so they were not counted in the MNI. As we saw (Fisher Jr, 2001), when larger animals such as elephants are acquired, the consumption of the meat and fat will sometimes take place at the kill site, so the number of times that zero bones were transported

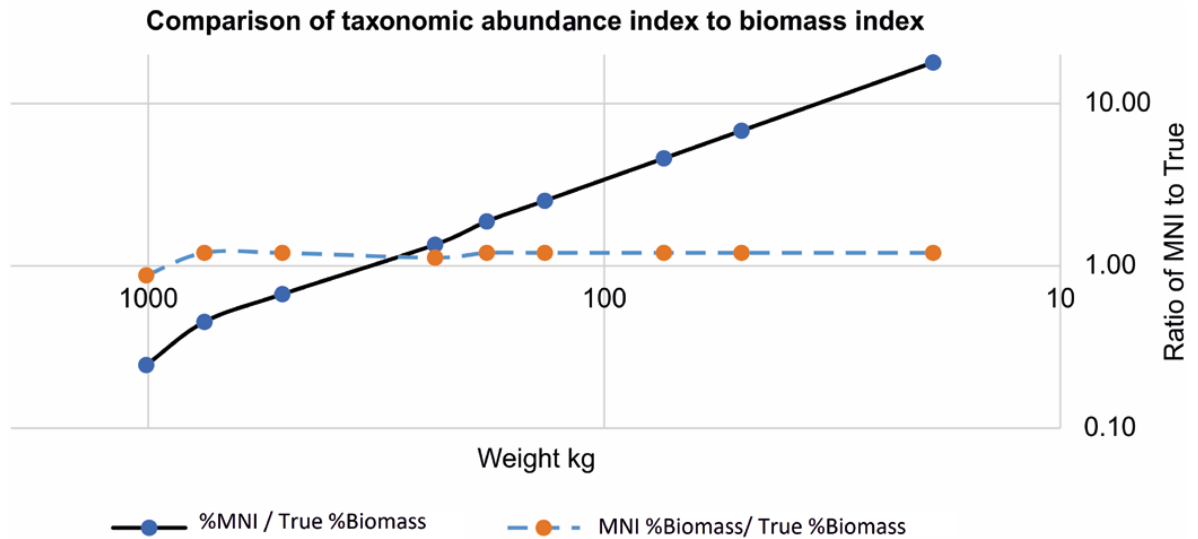


Figure 12.4: Comparison of taxonomic abundance index to weight-adjusted index.

to the central place will be high and so will the bias. The bias is also very apparent in small animals. The 19-impala contributed only 5% to the true potential consumable biomass while their MNI abundance index was 33%.

As expected (Lyman, 2018), the NISP (MAU) index performed even worse than the MNI-based index when it came to predicting relative dietary importance (biomass). In Table 12.2, for giraffes, the true biomass index (57%) is only 14% higher than the MNI biomass index (50%), while it is 78% higher than the NISP biomass index (32%). These results make reliance on NISP data a distant second-best to MNI. At least according to the Hadza sample, the potential for substantial remaining underestimation of the relative biomass of large animals should be taken into account when using NISP data.

A marked improvement took place when the MNI abundance index was multiplied by the animal weight. The “Weight adjusted MNI index” (the “MNI biomass index”) predicts a 50% share for the giraffe compared to a true value of 57%. This stems from the fact that the initial bias in transportation is a function of the weight of the animal. As can be seen both in Bunn et al. (1988) and O’Connell et al. (1988) data, the

relative number of elements that are transported is affected by the weight of the animal and the distance of the kill site from base camp, which is also, stochastically, a function of the weight of the animals.

In Figure 12.4, we show the relative predictive strength, compared to the true values, of the commonly used MNI abundance index and the one proposed here that standardizes the MNI abundance index by the animal weight (MNI biomass index). We do that by dividing the MNI abundance index and the MNI-based biomass index values by the true value for each species. For example, the MNI abundance index for impala is 33%, and the MNI biomass index is 6%, whereas the true biomass contribution of the impala is 5%. We calculate 6.6 times (33% divided by 5%) overestimation relative to the MNI abundance index, compared in the dotted line to 1.2 times (6% divided by 5%) overestimation in the MNI biomass index compared to the true value. The straight log/log line of the relation between the MNI-based taxonomic index (%MNI) and the true values indicates a strong correlation between animal weight and bone transportation. The slope changes at the giraffe, which may point to there being a threshold animal size in which the trans-

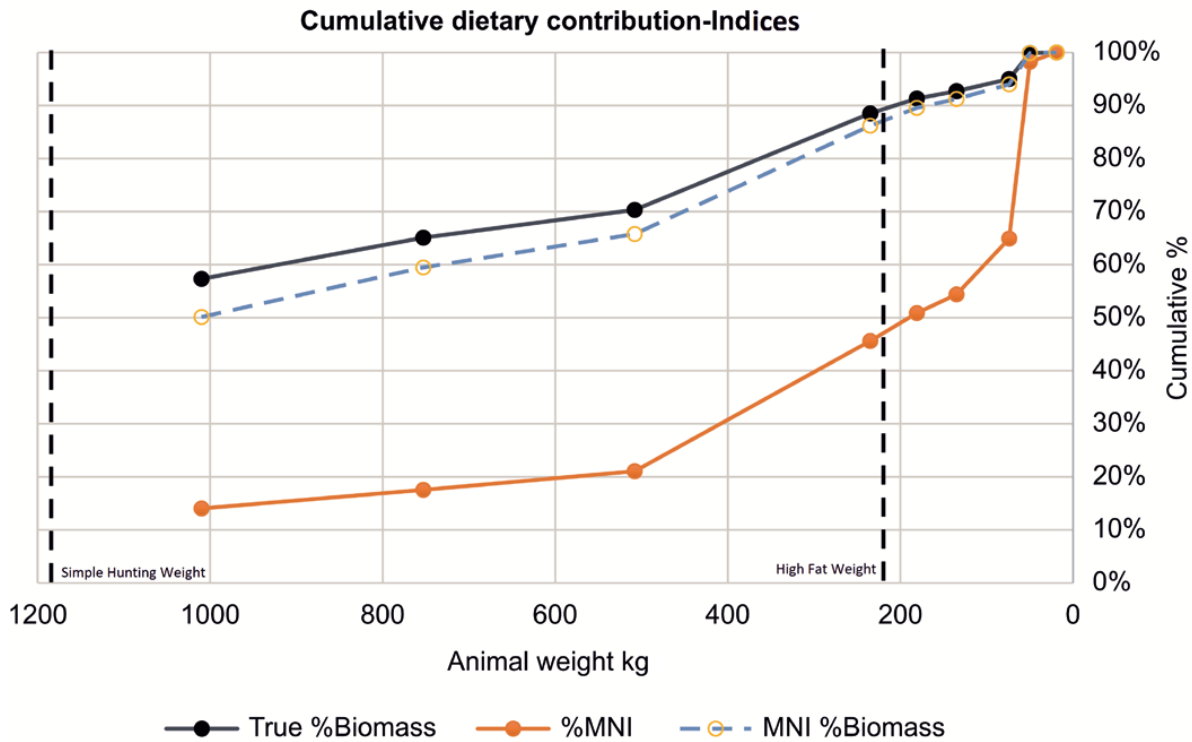


Figure 12.5: Cumulative potentially consumable biomass contribution by weight. (the dotted vertical lines denote weights of animals that are relatively less complex to hunt (See section „Not escaping – Easier tracking and less complex hunting tools”) and animals with relatively high fat content (See section „Larger prey contains higher body fat”).

port of bones to the central place is diminished at a faster rate. In the giraffe, the largest animal, the MNI index underestimation drops from 76% in the MNI abundance index to 13% in the MNI biomass index. Since $Y = 1$ in the chart is the true value ($\%MNI * Weight = \%Number * Weight$), the flat line close to 1, after the addition of weight standardization to the straight MNI abundance index, shows that the multiplication by weight leads to a significant improvement of the prediction of the relative dietary importance of the various species.

12.3.1 CUMULATIVE PRESENTATION OF THE BIOMASS ABUNDANCE INDEX

Having a hypothesis regarding the dietary importance of large prey animals and an index that arguably provides better predictions of their relative dietary importance, we can now compose a

model that will allow us to infer the significance of prey availability on human behaviors, based on Palaeolithic faunal assemblages. Firstly, we would like to know what percentage of the diet was supplied by animals that could be obtained with relatively less complex technological means. Based on the maximum speed chart (Fig. 12.1), these are animals that weigh over 1200 kg and that do not tend to escape. The second point of interest is what percentage was supplied by animals with relatively high-fat content, which, according to our calculations, weigh over approximately 150 kg for females and approximately 200 kg for males (Fig. 12.3). We would also like to know what portion of high net return animals contributed to the diet, assuming, as per section “Larger animals provide higher energetic return”, that larger animals provide a higher return than small animals. For that purpose, we calculate the cumulative values of the biomass index, beginning with the largest animal (Fig. 12.5).

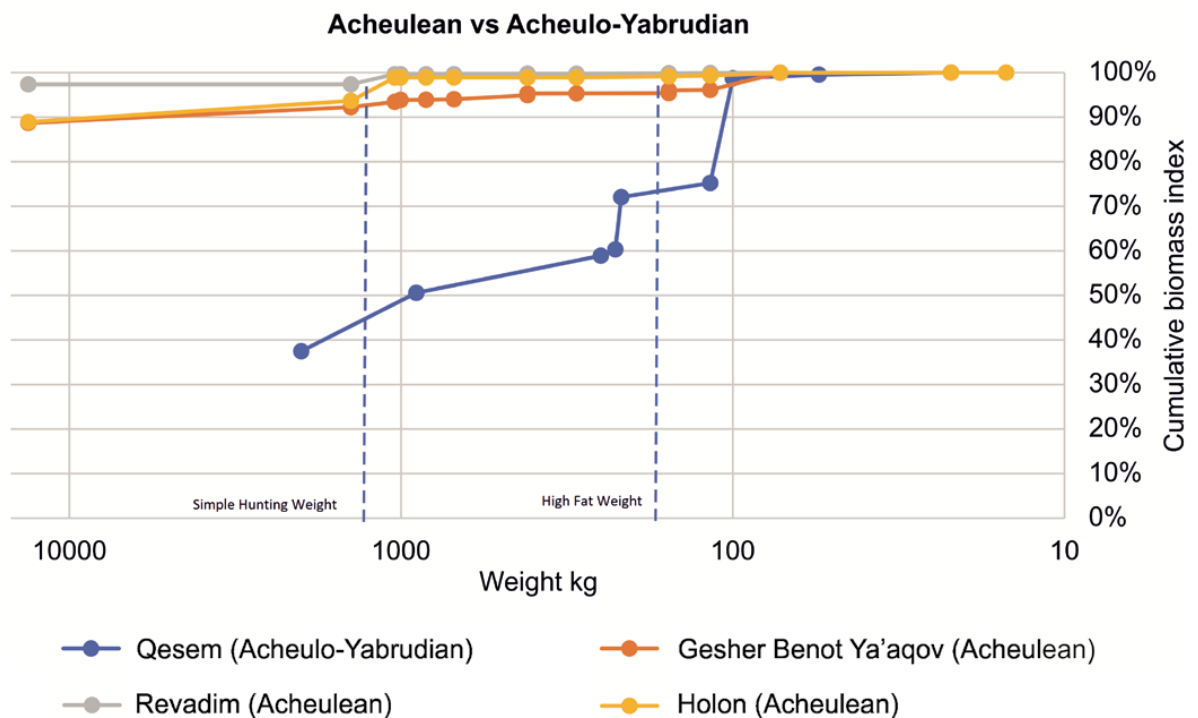


Figure 12.6: The Levant - Acheulean sites (Gesher Benot Ya'aqov, Revadim, Holon) vs. Acheulo-Yabrudian site (Qesem Cave). The dotted vertical lines denote weights of animals that are relatively less complex to hunt (See section „Not escaping – Easier tracking and less complex hunting tools”) and animals with relatively high fat content (See section „Larger prey contains higher body fat”).

Assuming that the data includes a representative sample of the Hadza animal-based diet, it can be concluded that the true contribution of animals that do not escape (heavier than 1200 kg) to the animal portion of the diet is nil (Section “Not escaping – Easier tracking and less complex hunting tools”). The giraffe’s maximum speed is 60 km/h (Hirt et al., 2017: appendix), faster than a lion, so it is built to escape. We can thus predict that the Hadza had to use projectile technology suitable for the acquisition of escaping prey. Since giraffes form over 50% of the potentially consumable biomass, we can conclude that the Hadza would have had a hard time obtaining a significant quantity of meat without projectile technology. With the addition of animals that weigh close to 200 kg, the Hadza reach 90% of the animal portion of the diet. We can thus determine that most of the animal portion of their diet is obtained from animals that provide a relatively high net caloric return (Section “Larger animals provide higher energetic return”)

and contain a relatively high level of fat (Section “Larger prey contains higher body fat”).

12.4 APPLICATIONS OF THE MODEL

12.4.1 SOUTHERN LEVANT - COMPARING ACHEULEAN TO ACHEULO-YABRUDIAN SITES

There is a clear difference in the composition of prey by size between the three Lower Palaeolithic Acheulean sites (Gesher Benot Ya'aqov, Holon and Revadim) and the terminal Lower Palaeolithic Acheulo-Yabrudian Qesem Cave (Fig. 12.6). In the Acheulean, nearly 100% of the animal-based diet came from megaherbivores, specifically from *Palaeoloxodon antiquus*, that presumably do not escape and supply a high level of fat. However, in the Acheulo-Yabrudian, only 39% of the animal-based diet came from

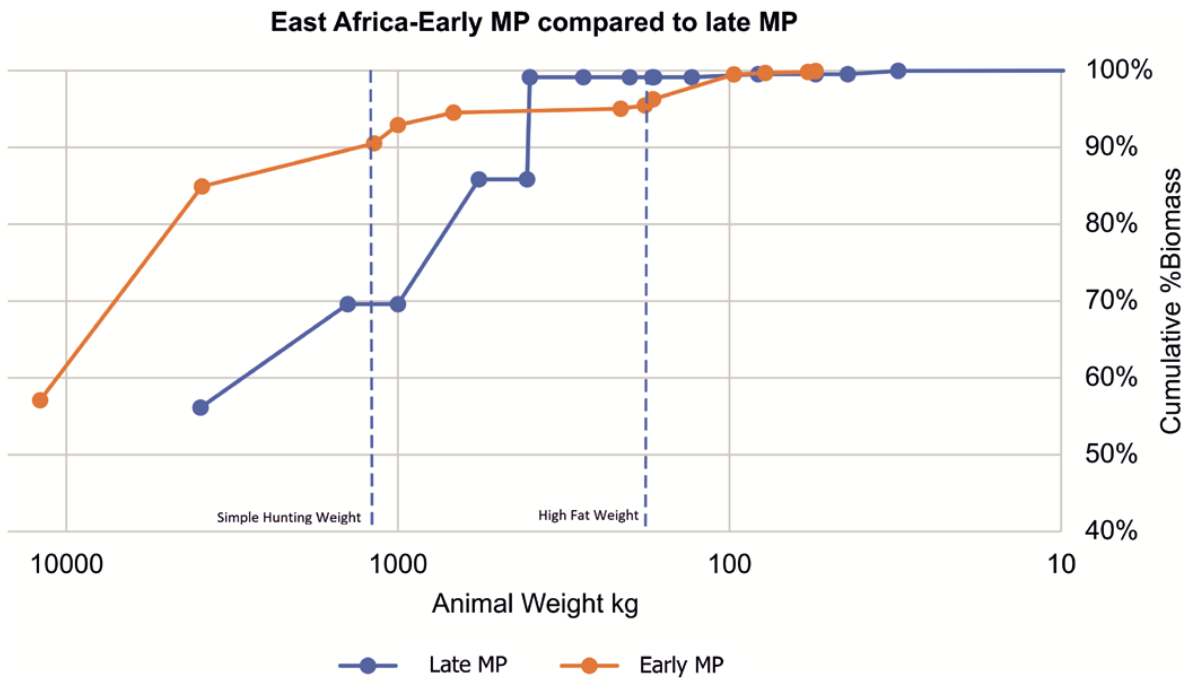


Figure 12.7: East Africa - early Middle Pleistocene vs. late Middle Pleistocene. The dotted vertical lines denote weights of animals that are relatively less complex to hunt (See section: „Not escaping – Easier tracking and less complex hunting tools”) and animals with relatively high fat content (See section: „Larger prey contains higher body fat”).

animals heavier than 1200 kg that do not escape (rhino, in this case). Moreover, only 70% of the cumulative weight of the animals from Qesem Cave came from high fat-containing animals (above ~200 kg). The 30% contribution of small animals, specifically fallow deer (23%), to the diet is substantial. The need to efficiently hunt a much larger portion (61%) of escaping animals and process a high number of the smaller animals, compared to the Acheulean, may explain the dramatic cultural differences and possibly physiological differences between the Acheulean and the Acheulo-Yabrudian humans and culture (Ben-Dor et al., 2011; Barkai and Gopher, 2013; Barkai et al., 2017). One caveat in this comparison is that the Acheulean sites are open-air sites, and the Acheulo-Yabrudian site is a cave site that may contain smaller-sized animals on average, regardless of culture or region (Smith et al., 2019b). Also, both periods are compared based on NISP data. As we saw in the Hadza case, it is probable that the use of NISP results in a lower

correction of the biomass index bias, which in this case would be more significant in the case of Qesem Cave, extending the difference between the two periods beyond the true value.

12.4.2 EAST AFRICA - EARLY MIDDLE PLEISTOCENE COMPARED TO LATE MIDDLE PLEISTOCENE

The early Middle Pleistocene (MP) is represented in the data by Olorgesailie Member 10 and the late MP by Olorgesailie BOK 1E, 2 and 4, and by Omo Kibish 1 (data in Ben-Dor, 2020, extracted from Smith et al., 2019b), all by MNI. In the late MP, 70% of the diet was obtained from non-escaping animals that are relatively less complex to locate and hunt, compared to 93% in the early MP. Here, we should note that in the early MP, *Palaeoloxodon recki* was the elephant species in the assemblage, while it was the smaller (and possibly less naive?) *Loxodonta africana* in the late MP.

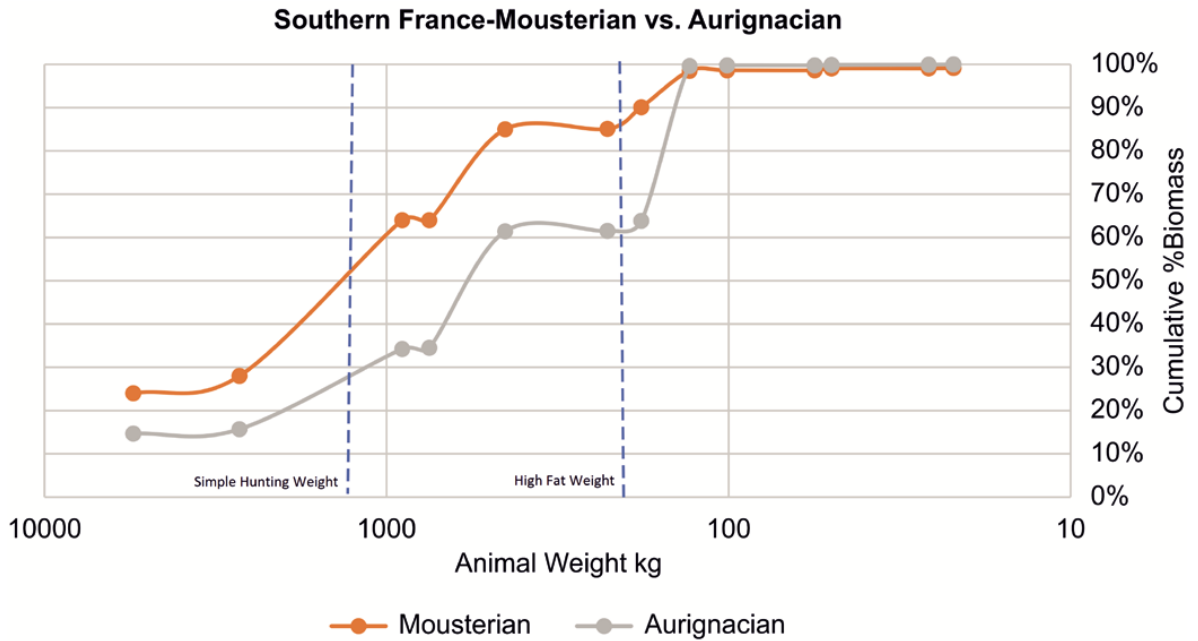


Figure 12.8: Southern France - The Mousterian vs. the Aurignacian. The dotted vertical lines denote weights of animals that are relatively less complex to hunt (See section: „Not escaping – Easier tracking and less complex hunting tools“) and animals with relatively high fat content (See section: „Larger prey contains higher body fat“).

There is a cultural change with the appearance of the Middle Stone Age in East Africa at the late MP. Potts et al. (2018) and others (Faith et al., 2012; Owen et al., 2018) noticed a general decline in herbivores' sizes with a faunal turnover at the end of the early MP, which is reflected in the right shift of the curves between the early MP and late MP in Figure 12.7. It is possible that the need to hunt escaping animals and a new elephant species was part of the trigger for the cultural change from the Acheulean to the Middle Stone Age, as it has arguably been the case in the Levant's transition from the Acheulean to the Acheulo-Yabrudian. In both, the early and late MP, the high-fat line at 200 kg shows that close to 100% of the weight of the prey were of high fat content.

12.4.3 SOUTHERN FRANCE – THE MOUSTERIAN COMPARED TO THE AURIGNACIAN

Analysis of a database that includes the NISP record of 169 Middle Palaeolithic Mousterian lay-

ers and 41 Upper Palaeolithic Aurignacian layers (Grayson and Delpech, 2002) shows (Fig. 12.8) that on both counts, dealing with non-escaping animals (>1200 kg) and obtaining animals with a high-fat content (>200 kg), the Anatomically Modern Humans (AMH) of the Aurignacian had a harder time. Hunting non-escaping animals only provided some 15% of their animal-based diet, compared to some 30% for the Neanderthals of the Mousterian. In terms of obtaining animals with high fat content, some 60% of the Aurignacian hunted biomass was obtained from animals with higher levels of body fat, while Neanderthals obtained some 90% of their animal-based diet from high fat containing animals (>200 kg). These differences can shed light on possible physiological and cultural adaptations that allowed modern humans to succeed in handling both these handicaps. It can be hypothesized that lighter bodyweight and advanced agility allowed AMH to acquire smaller escaping animals at reduced locomotion costs (Stuedel-Numbers and Tilkens, 2004). Use of projectile hunting tools, which are used mainly on smaller prey, is also sometimes mentioned as a

differentiating capability, although there are signs that Neanderthals may have also used some projectile tools (Hardy et al., 2013). There are even some scholars who claim that AMH were anatomically adapted to the use of projectile tools (Churchill and Rhodes, 2009).

It should be mentioned that most of the sites in the database are cave sites, and one would expect the bias against the representation of proboscideans to be higher than in open sites (see discussion). Moreover, as discussed, the NISP (rather than MNI) data of this dataset may still leave substantial room for underestimation of large animals biomass contribution.

12.5 DISCUSSION

We hypothesized that the criticality of large prey to humans, coupled with a decline in prey size during the Pleistocene, has led to behavioral and possibly also physiological adaptations that we described here and in the cited papers. Underrecognition of the true relative abundance of large prey animals in archaeological sites may blind us to the importance of large prey animals in general, and to specific trends in large prey prevalence that could drive the hypothesized adaptations. We have described a method to correct some of the underrepresentation of large prey in archaeological sites. However, the method may still leave much room for the underrepresentation of very large prey animals, such as proboscideans, since they may be significantly underrepresented in the MNI and even more so in the NISP. For example, in the Hadza sample (Table 12.1), 27% of the giraffes are not included in the MNI because not a single bone of 3 out of the 11 giraffes was brought to the central place. In contrast, only one smaller animal out of 50 (2%) is not represented in the MNI of the assemblage. It seems that there is a certain bodyweight/distance threshold above which bones become too heavy to transport, or the meat and fat contribution becomes so high for a given group size, that there is less incentive to bring bones to the central place.

Alternatively, in the case of large herbivores, bones might be striped of meat and fat at the hunting station and be left there, so no hard evidence for the transport of a huge amount of calories would be represented at the central place. If true for a giraffe, it is undoubtedly true for proboscideans, which weigh about six times more than a giraffe and, in the past, were up to ten times heavier.

12.5.1 UNDERREPRESENTATION OF PROBOSCIDEANS

Theoretically, one can think of a method to account for “missing” individuals that rely on the relative biomass density in a given environment. If we accept that humans prefer large prey, we also have to account for a preference for the acquisition of a higher proportion of large prey, say proboscideans, than their relative biomass density in the environment. To estimate the level of preference, we tried to determine the relationship between the relative natural biomass of giraffes in East Africa and their relative biomass in the Hadza assemblage. We reviewed the East African record of biomass density of six nature reserves (Leuthold and Leuthold, 1976), presenting more than four species from the Hadza sample and calculated an average biomass density of 13% for giraffe in relation to the other animals in the Hadza sample (minimum 2%, maximum 36%) (calculations in Ben-Dor, 2020). Since the biomass density of giraffe in the Hadza sample is 57% (Table 12.2, %biomass), we can infer a strong “preference factor” of (57% divided by 13%) of 4.4 times (maximum 32, minimum 1.6) compared to the relative natural biomass density. So, theoretically, if we can estimate the relative biomass density of proboscideans, as was done by Hempson et al. (2015), and estimate the preference factor for proboscideans, we may be able to estimate the relative acquired proboscidean biomass in the absence of bones. There are many limitations to the applicability of the Hadza sample to actual cases. Firstly, the data from nature reserves may not be representative of the biomass distribution in the

Hadza territory. Also, it is known that the Hadza do not hunt proboscideans despite their occasional presence in their territory (Marlowe, 2010). The considerations of which specific species to hunt may be many and varied. For example, contrary to giraffes, we have calculated the preference factor for the buffalo to be strongly negative at 0.2 (8% of the biomass in Table 12.2 divided by an average of 46% in nature reserves). One potential explanation for not hunting elephants and rarely hunting buffalo can be a reliance of the Hadza on the bow and poisoned arrows in hunting. Bow and arrow may not have the capability of deterring potential charges from elephants and buffalo (Owen-Smith, 1988) and might be relatively inefficient in such a hunt. In contrast, giraffes typically do not charge (Owen-Smith, 1988: p. 126). As we pointed out, hunting of elephants and other large animals is typically performed using other tools/weapons and different methods (Churchill, 1993; Agam and Barkai, 2018). In summary, it seems that a method that uses relative biomass densities to account for missing proboscideans needs more study before it can be applied. However, general considerations regarding the underrepresentation of proboscideans that take into account their relative biomass and an assumption of preference for the acquisition of large prey may still be of value.

For example, the relative natural biomass density method may be helpful in generally assessing the likelihood of the three applications of the assemblage biomass model in section 12.4 regarding proboscideans. We start with the estimate of Hempson et al. (2015) of >50% relative natural biomass of proboscideans among herbivores in Africa a thousand years ago and take as a guide a cautious preference for proboscideans as for the minimum preference factor (1.6) that we found for the giraffe based on the biomass in the African nature reserves. Thus, we would expect the proboscideans to compose >50% times 1.6 = >80% of the relative biomass in the assemblages. The Levant Acheulean sample at close to 90% proboscideans (section 12.4.1) seems to be in line with the natural biomass density method, while the East Afri-

can late Middle Pleistocene sample at slightly less than 60% (section 12.4.2) seems moderately lower than expected. The analysis of Southern France (Section 12.5.3) points to a possible substantial under-representation of proboscideans at 15–25% of the biomass in both the Mousterian and the Aurignacian, much below 80%.

We emphasize that the lack of localized historical data limits the use of the natural biomass method in predicting past relative acquired biomass predictions. The introduction of the method here is meant only to generate questions and hypotheses and interest in the prediction of natural biomass data of the kind that Hempson et al. (2015) performed.

12.6 CONCLUSIONS

The abundance of fossilized bones in prehistoric archaeological sites shows that the acquisition of animals, including very large animals, was an essential activity of humans. We described several reasons for the critical importance of large herbivores as prey. The question that we tried to answer here was how we could determine the relative importance of large and very large animals in archaeological assemblages. The answer to this question, in general and in particular situations, may have critical implications for understanding human behavior and evolution. We presented arguments for the position that the acquisition of large prey was more energetically efficient and less technically complex than the acquisition of small prey animals. We showed evidence that large animals have relatively higher biomass density in the environment, and, maybe most importantly, pack relatively more fat than smaller animals.

Using an actualistic database, we have presented a case for a need for species biomass adjustment of, preferably, MNI- or else, NISP-based abundance indexes in Palaeolithic assemblages, when the relative economic importance of species is investigated. We have also presented a method for the presentation of biomass abundance results, in

a way that will allow estimation of the need for less or more complex hunting tools and technics and the availability of relatively fat animals in order to overcome the limit on protein metabolism. Three demonstrative comparisons of two Palaeolithic faunal assemblages each from different regions and periods were performed using the method. We also made an initial proposal of a method that may be more suitable for the prediction of the relative consumption of proboscideans, where, in many cases, no bones are transported from the kill or butchery sites.

We believe that the importance of this type of analysis will become more apparent as the crucial implications to humans of the massive extinction of large prey animals during the Pleistocene are beginning to come to light.

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