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The causal association between megafaunal extinction and Neandertal extinction in Western Europe – Application of the Obligatory Dietary Fat Bioenergetic Model

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1 ABSTRACT

It is currently assumed that Neandertals evolved gradually over at least 400,000 years in Europe. Neadertals disappeared from the fossil record in Western Europe (Spain, France) some 40,000 years ago (40 Kya). Anatomically modern humans (AMH) started to occupy parts of Europe 43,000 – 45,000 years ago, a few thousand years before the disappearance of the Neandertals although no contemporaneous or alternate occupations of the same sites have been discovered.

The reason for the extinction of the Neandertals in Western Europe, and especially the question of whether AMH played an active role in their demise, is one of the most controversial issues in prehistoric research (Villa and Roebroeks, 2014), and "*remains an enigma, even after more than 150 years of research*" (Bradtmöller et al., 2012). Indeed, Smith (2013) identifies the debate as "*one of the longest, most contentious in science*."

This thesis aims to present and test a hypothesis that the megafaunal extinction that began some 50 Kya in Western Europe played a significant role in the extinction of the Neandertals.

A natural decrease in plant food availability during the long and harsh MIS 3 winters in Western Europe lead to the conclusion that Neandertals relied to a significant extent on animal-sourced food, especially during winters. A physiological ceiling on their protein consumption, coupled with the limited availability of plant food, must have forced Neandertals to depend on the acquisition and consumption of a substantial amount of animal fat. This obligatory amount of fat could only be supplied by acquiring large animals which contain, relatively, a higher proportion of calories from fat than smaller animals and even more so during harsh winters. When large animals diminished, a chronic energetic stress developed which could have caused the extinction of the Neandertals.

The identification of shortage of fat as an environmental stress that could significantly affect Neandertals' survival relies on insights gained from The Obligatory Dietary Fat Bioenergetic Model (ODFBM). Bioenergetic models have been used since the early 1980s to explain human evolutionary phenomena, including the Neandertals' extinction. The ODFBM model is unique in that it uses the three individual macronutrients as parameters in the model. The model relies on the well-accepted fact that humans are much more limited in the amount of protein that they can metabolize to energy in

comparison with other carnivores. The model takes into account the energetic requirements of the studied human and the physiological ceiling on protein consumption to arrive at an obligatory ratio of non-protein caloric sources. Assuming that plant food was scarce during MIS 3 winters, the model determined the obligatory dietary fat ratio of Neandertals to be 75% to 85% of the calories. The last step in the model compares the obligatory dietary fat ratio with the ratio in available prey as it is represented in the archaeological record of the relevant regions. Larger animals have relatively higher fat content. I argue that Neandertals were dependent on calories gained from large animals, with the focus on fat as a major supplier of calories. It is therefore concluded that a diminution of large animals, in the face of such a high obligatory dietary fat requirement, had resulted in energetic stress due to the need to obtain the same amount of fat from a disproportionally higher number of smaller animals. Conversely, it could be that AMH’s lighter weight and longer legs made him better suited, energetically, to obtain and metabolize the required number of calories from smaller prey.

The body of the thesis is devoted to validating the assumptions that were used in the model’s calculations.

The reconstruction of the Neandertal diet begins with an analysis of general patterns in the human diet throughout the Paleolithic. In line with the requirements of the model, the main effort is aimed at determining whether a pattern of the plant-animal ratio can be discerned in the Paleolithic diet that caused humans to exceed the protein constraint and dictate an obligatory consumption of fat.

Most of the attempts to discern a plant-animal ratio in past human diets have relied to a great extent on the ethnographic record. The ethnographic record of two of the most extensively researched hunter-gatherer (HG) groups, the Hadza and the San, is reviewed for suitability as an analog for the Paleolithic HG. The review finds that the plant-animal ratios of recent groups have been significantly affected by a reduction in the prevalence of megafauna and other large animals which dramatically altered the risk-reward ratio of hunting. Also, hunting of smaller animals and gathering were made more efficient by the replacement of stone tools with metal tools, the use of dogs, cooking utensils and other artifacts that were not available to Paleolithic humans. For example, the availability of iron arrow tips saves the time that acquiring, maintaining and replacing stone arrow tips would have required. This time saving could be used to track and hunt smaller animals which have a lower caloric return per hour than larger animals.

Ecologically, the area in which these groups live has gone and is still going through a major faunal and vegetation disturbance which have started some 50 thousand years ago, late in the Pleistocene, as part of the Late Quaternary Megafauna Extinction and possibly even earlier. The result is that the Hadza, for example, no longer hunt elephants, rhinos, and hippos, the three largest animals that they used to hunt.

The archaeological record can only be considered as a partial source of the plant-animal ratio in the Paleolithic diet since plant remains are preserved poorly compared to animal remains. The human body, however, should contain genetic and physiological information that may point to evolutionary adaptations to cope with a particular dietary pattern. A review of some such presumed adaptations, as well as paleontological and other types of archaeological information, has provided significant evidence for adaptation to a high degree of carnivory during most of human evolution. Signs of increasing plant consumption appear in *Homo sapiens* although its diet apparently remained highly carnivorous until well into the Upper Paleolithic (UP). The archaeological and genetic record indicates that a further increase in the share of plants in the diet took place during the UP and beyond.

Such a description of the diet during human evolution provides further credence to the notion that the Neandertal diet was also highly carnivorous. A specific reconstruction of the Neandertal diet concludes that indeed they were top predators although plants were consumed regularly and possibly in higher proportion in more southern regions.

Due to the protein ceiling, highly carnivorous diets entailed a dependency on the acquisition of a significant amount of fat. The archaeological and ethnographical records were reviewed for evidence of such a dependency. The review of the ethnographical record, this time for a pattern of behavior rather than quantitative ratios, showed a strong emphasis on fat acquisition as a major parameter in prey selection, to the extent that hunted animals with low fat content are sometimes abandoned. Several archaeological patterns of animal acquisition and exploitation were identified as emanating from the need to obtain fat. Targeting ‘prime adults,' preferential transportation of fatty parts, exploitation of marrow and bone grease, and preference of large animals were all identified as such patterns both in Neandertals and in other *Homo* species.

Specifically, a strong association between animal size and fat content was established through a detailed analysis of a sizeable database of recent African animals.

Lastly, three archaeological faunal databases covering Western Europe during MIS 3 were analyzed together with 13 individual multi-cultural sites to identify trends in large prey exploitation beginning 50 Kya. The analysis confirmed a significant reduction in the acquisition of the largest prey between 50 Kya to 40 Kya. This trend continued after the Neandertals' extinction.

In summary, application of the Obligatory Dietary Fat Bioenergetic Model to the case of the Neandertals' extinction provided evidence that the demise of Neandertals was a result of energetic stress that developed in Western Europe beginning 50 Kya due to the diminishing of large animals.

LIST OF ABBREVIATIONS:

AMH	Anatomically Modern Human
Au	Aurignacian
BE	Behavioral Ecology
BMR	Basal Metabolic Rate
BP	Before Present
BW	Body Weight
Cal BP	Calibrated years Before Present
CNC	Cultural Niche Construction
CP	Chatelperronian
DPA	Dietary Plant : Animal ratio
FAT	Animal Fat
F/T	Fat to Total calories
HG	Hunter-Gatherers
Kya	Thousand years ago
LGM	Last Glacial Maximum
LSA	Late Stone Age
MIS	Marine Isotope Stage
MNI	Minimum Number of Individuals
MMBM	MNI based Mean Body Mass
MP	Middle Paleolithic
MSA	Middle Stone Age
MTA	Mousterian of Acheulian Tradition
Mya	Million years ago
NC	Niche Construction
NISP	Number of Identified Specimens
NMBM	NISP based Mean Body Mass
OAF	Obligatory Animal Fat

ODFBM	Obligatory Dietary Fat Bioenergetic Model
OFT	Optimal Foraging Theory
PLA	Plant foods consumption
PRO	Animal Protein Consumption
TAC	Total Animal Calories
TDEE	Total Daily Energy Expenditure
USO	Underground Storage Organs

2 INTRODUCTION

It is currently assumed that Neandertals evolved gradually over at least 400,000 years in Europe (Bermúdez de Castro et al., 2017), considered their exclusive 'core area' (Churchill, 2014:2.1), with periodic presence as far as Holland in the north, Russia in the east and the Levant in the south. They produced various Levallois-based lithic industries but also, at times, Quina, laminar and discoid reduction systems. Approximately 40,000 years ago (40 Kya) (Higham et al., 2014), they became extinct. Contemporaneously or sometime after, anatomically modern humans (AMH) began to occupy West European territories that were previously occupied by the Neandertals, including those that were previously exclusively settled by them, in present-day France and Spain.

The reason for the extinction of the Neandertals in Western Europe, and especially the question of whether AMH played an active competitive role in their demise, "*is one of the most discussed issues in paleoanthropology"* (Hublin, 2017) or, in other words, one of the most controversial issues in prehistoric research (Villa and Roebroeks, 2014) and "*remains an enigma, even after more than 150 years of research*" (Bradtmöller et al., 2012). In a wider perspective, Smith (2013) identifies the debate as "*one of the longest, most contentious in science*."

This thesis will present and test a hypothesis that the extinction of the Neandertals happened, at least in large part, as a result of diminishing populations of very large prey species in Western Europe, beginning some 50 Kya (Barnosky et al., 2004; Stewart, 2007). It will argue that acquisition of very large prey species was of critical importance to Neandertals, as they provided relatively large quantities of animal fat, and also lost less fat during winter. That dependency was a result of the presumed limited ability of the Neandertals to metabolize protein to energy coupled with high energetic requirements due to their size and locomotion costs (Froehle and Churchill, 2009). The dependency became more acute during harsh winters due to diminished plant resources. Large animals contain a significantly higher proportion of fat than smaller animals (Pitts and Bullard, 1967; Ben-Dor et al., 2011). Large animals also lose a lower proportion of their fat than smaller animals during conditions of limited availability of grazing and browsing resources such as dry summers, extreme cold weather and extended periods of snow cover (Lindstedt and Boyce, 1985). Presumably, then, a decrease in the size of available prey animals would have resulted in a significant energetic deficit because of the need to acquire a disproportionately larger number of smaller animals with little fat. A significant and ongoing energetic deficit in Neandertals could lead, among other things, to a decline in fertility and their eventual demise.

The hypothesis can be framed within the paradigm of Behavioral Ecology (BE). This evolutionary-based paradigm, as it applies to humans, assumes that humans adopt a set of optimal behaviors that are aimed at acquiring maximum fitness. Regarding obtaining food, the theory claims that people strive to obtain maximum nutritional resources with minimum energetic expenditure (Bird and O'Connell, 2006; Borgerhoff Mulder and Schacht, 2012). Testing of the hypothesis will be carried out using a simple bioenergetic model, developed to explain the disappearance of *H. erectus* from the Levant 400 Kya - The Obligatory Dietary Fat Bioenergetic Model (Ben-Dor et al., 2011). Bioenergetic models use the determination of Total Daily Energy Expenditure (TDEE) of the studied subjects to predict elements of their behavior (e.g., Froehle and Churchill, 2009). Unique to the proposed model is the separate consideration of each of the three dietary macronutrients, namely carbohydrates, protein, and fat. This separation enables the determination of the subject's obligatory ratio of animal-sourced fat from total calories. In this way stress, due to gaps between fat requirements and fat content in available prey, can be identified.

2.1 THE NEANDERTAL – BACKGROUND

The Neandertal was defined taxonomically either as a separate species named *Homo neanderthalensis* or a sub-species of *Homo sapiens* named *Homo sapiens neanderthalensis*, depending on how morphologically distinct from modern humans they are considered, and what evolutionary model is assumed (Smith, 2013 and references therein).

Neandertal-like morphological features may have appeared at least 800 Kya (Bermúdez de Castro et al., 2017). The dating of the split of Neandertals from the common ancestor with *H. sapiens* is the subject of a number of recent genetic studies. Estimates range from 400 Kya (Noonan et al., 2006), 270 - 440 Kya (Green et al., 2010) and 340 – 540 Kya (Endicott et al., 2010). Two, more recent, studies provide an identical estimate for a later Neandertal - AMH split at 550-765 Kya (Prüfer et al., 2014; Meyer et al., 2016)).

Recent genetic studies confirm that humans and Neanderthals did interbreed. However it is not clear where and when this happened (Green et al., 2010; Kuhlwilm et al., 2016). Currently, the estimate of an average of 1.6%-2.1% Neandertal contribution to recent Eurasians (Prüfer et al., 2014) is the figure mentioned in discussions of Neandertal-modern human admixture (Smith et al., 2017). AMH fossils from Altai contain approximately 2%, while the Prstera cu Oase early modern genome, dated to 37-42 Kya, contains 6-9% Neandertal genre (see discussion in (Smith et al., 2017). In any event, evidence for successful interbreeding with *H. sapiens* casts doubt on their definition as a separate species in the strict biological sense. Other researchers claim that the evident degree of interbreeding calls for a reframing of the discussion of the Neandertal disappearance to ‘assimilation’ or “genetic swamping” rather than ‘extinction’ (Zilhão, 2006a; Villa and Roebroeks, 2014; Smith et al., 2017). However, using the term ‘assimilation’ in the context of an attempt to explain the disappearance of the Neandertal may suggest an exclusion of other significant factors that may have contributed to the eventual assimilation. The hypothesis presented here claims a significant role for external environmental conditions as a cause for the disappearance of the Neandertal, so the term ‘assimilation’ is not suitable for describing Neandertal disappearance with the framework of this work. This assertion does not preclude the possibility of a combined model, in which Neandertal populations diminished due to external stressful conditions and towards the end of the process assimilated into the AMH population.

Clear Neandertal-like features appear in the Sima de los Huesos (Atapuerca, Spain) human fossils dated at 430 Kya (Arsuaga et al., 2014). Genetic analysis strongly supports this morphological affinity (Meyer et al., 2014). This evidence for ancestral roots in Western Europe also supports the identification of this area as the ‘core area’ of the Neandertal. The full suite of Neandertal morphological features may have appeared approximately 230 Kya (Smith, 2013). The maximal geographic range of the Neandertals outside their ‘core area’ can only be safely determined based on fossils, as their cultural assemblages (during Middle Paleolithic times) are mostly indistinguishable from those of *H. sapiens* (Churchill, 2014). Neandertals were identified as far east as the Altai Mountains of southern Siberia or even North China (Li et al., 2018) and probably as far north as the Polar Urals near the Arctic Circle but not in

Africa (Smith, 2013 and references therein). Their southernmost appearance is found in the Levant (Shea, 2008), where alternate and concomitant occupations with *H. sapiens* might have occurred throughout the Middle Paleolithic Mousterian cultural complex (Hershkovitz et al., 2015).

No Neandertal fossils are found in the subsequent Upper Paleolithic (UP) cultures (Benazzi et al., 2015) in Europe and the rest of the Old World.

2.2 CLIMATE

The Middle Paleolithic (MP) period started between 300 Kya and 200 Kya in different parts of the Old world (Adler et al., 2014). Neandertals occupied diverse ecosystems, from temperate interstadial Mediterranean to extremely cold tundra-like glacial continental European (Davies and Gollop, 2003). The MP was dominated by long glacial periods and by fluctuating climate patterns from Marine Isotope Stage (MIS) 8 to MIS 3 (VanAndel and Tzedakis, 1996). Only 8% of the MP period can be characterized as interglacial (Gaudzinski-Windheuser and Roebroeks, 2011). It is accepted that large parts of Europe were Tundra-like during most of the MP (Finlayson and Carrion, 2007 after Voisin, 2005; Gaudzinski-Windheuser and Roebroeks, 2011). Tundra can be found today at the northernmost edges of Eurasia and North America and is characterized by flora such as mosses, grasses, lichens, sedges, and shrubs (Bliss et al., 1981). Despite the general cooling trend at MIS 3, regional variability is found in the response of the faunal communities to the changing climate (Discamps and Royer, 2017).

In the Near East, Enzel et al. (2008) and Frumkin et al. (2011) found the last glacial period (110-11.7 Kya), the period during part of which Neandertals occupied this area, to be more humid than expected. Some researchers indicate, however, that wetter winters were associated in the Near East with increased summer aridity (Myers et al., 1998; Rohling et al., 2013 and references therein) and even extended extreme aridity events within the recent glacial period (Torfstein et al., 2013). In any event, in the Near East, summers continued to be dry throughout the MP (Enzel et al., 2008) and therefore lower in available plant resources for humans and animals alike.

2.3 ANATOMY

In general, Neandertals were more 'robust' than AMH (e.g., Harvati, 2010; Churchill, 2014), being heavier despite being shorter. Their weight is estimated at 77kg for males and ~66kg for females, compared to ~58 kg and ~49 kg for AMH respectively (McHenry, 2009a; but see Heyes and MacDonald, 2015). The weight difference is attributed to a thickening of the bone and high muscularity that points to a "*life way in which strength, power, and the ability to master demanding tasks...were a necessity*" (Smith, 2013). The increased weight should have resulted in increased energy budget compared to AMH (e.g., Sorensen and Leonard, 2001). Shorter distal limbs together with a protracted nose, a relatively wide pelvis, and a 'bell' shaped thorax have been interpreted by some researchers as adaptations to a cold climate (Ruff, 1994; Smith, 2013 and references therein; but see below Ben-Dor et al., 2016). Shorter legs relative to body weight and reduced lumbar lordosis may have resulted in an increased ability to carry heavy loads at the cost of less energy-efficient locomotion than AMH (Steudel-Numbers and Tilkens, 2004; Been et al., 2012; Been et al., 2014).

Their relatively low cranial vault (Smith, 2013) held a brain that was similar in size to that of AMH but different in shape as well as organization, which together with larger orbits points to an increased visual processing capacity (Pearce et al., 2013). Other points of cranial differences included a reduced chin, protracted nose and molar dentition similar in size to modern humans (Harvati, 2010) so smaller in relation to bodyweight.

It is hypothesized later in this thesis that the 'bell' shaped thorax of the Neandertal (Garcia-Martinez et al., 2014; Bastir et al., 2015) was, at least in part, an adaptation to a high protein diet in order to compensate for the shortage of fat and carbohydrates during cold and snowy winters in Europe and dry summers in the more southern areas of their settlement(Ben-Dor et al., 2016). The other characteristics of Neandertals' anatomy that increase their total energetic expenditure (TDEE), including body weight, shorter legs, and reduced lumber lordosis, are also relevant to the presented model.

2.4 DIET

This subject will be explored in depth in Chapters 5 and 6. It is accepted that meat from large mammals formed a large part of the Neandertal diet (Hockett and Haws, 2005; Gaudzinski-Windheuser and Niven, 2009; Salazar-Garcia et al., 2013). In recent years, evidence for the cooking and consumption of plants has emerged (Hardy and Moncel, 2011), based on plant residues in Neandertals' dental plaque, taken from fossils originating in various sites in Europe and Asia (Hardy et al., 2012; Salazar-Garcia et al., 2013; Henry et al., 2014). A general trend of increased reliance on plant food in a north to south axis has been identified (El Zaatari et al., 2011).

The emerging picture seems to be in agreement with Salazar-Garcia et al. (2013), who stated that although there are strong indications that the Neandertal diet included plant-sourced foods during glacial periods, at certain times, and in certain areas, it is highly likely that Neandertals became adapted to live for a significant number of months per year, at least during winters, on a diet that included mostly protein and fat.

2.5 EXTINCTION

As stated, the Neandertals' extinction is one of the most prolific research fields in prehistoric archaeology. A large number of hypotheses concerning the process of replacement of the Neandertals by AMH have been put forward by researchers in various scientific fields. This review will cover the most debated hypotheses. A significant portion of the discussion about extinction centers on whether it was primarily environmental change or exclusion competition by AMH that brought about the Neandertals' extinction and eventual replacement. This work will concentrate on the reasons for the extinction, however possible reasons for why AMH were able to become entrenched in regions that were previously exclusively occupied by Neandertals will only be discussed in general terms.

2.5.1 Dating the extinction

The Neandertal lived in the Levant, according to recent estimates, between 80 and 55 Kya (Been et al., 2017).The latest Neandertal fossil in the Levant is dated to 53±8 Kya (Rink et al., 2001). The latest report of Neandertals' presence in Europe is from Gorham's Cave, Gibraltar, circa 28 Kya (Finlayson et al., 2006) although Villa and Roebroeks (2014) propose that the latest appearance was not as late as that. They rely on dates from France, Belgium, and southern Spain, for example, Cueva Anton, Spain, at 37.4 Kya cal BP (calendar years before present) and 36.9 Kya cal BP for Spy, Belgium. Recently, Higham et al. (2014), upon performing an ultrafiltration of samples before 14C radiocarbon analysis from 40 European sites, determined that the Mousterian, as well as the Chatelperronian (CP), which is arguably also associated with the Neandertals, ended 41,030-39,260 BP at 95.4% probability. They were not able to verify the late dates (by 28 Kya) claimed by Finlayson et al. (2006). Other authors (Galvan et al., 2014), using TL and OSL dating methods on samples from El Salt also support an early extinction in the Iberian Peninsula, closer to the Heinrich 5 event which took place 45 Kya while others (Zilhão et al., 2017) support a later, 37 Kya date, in agreement with Villa and Roebroeks.

A determination of the likelihood of the affiliation of Neandertals with the CP is relevant to the dating of their demise, and in this thesis specifically with respect to the inclusion of CP faunal assemblages in the analysis of the dynamics of prey size during the period leading up to and immediately after the extinction of the Neandertal in Southwestern Europe. However, as will be shown, the trend of reduction in the size of the acquired animal was continuous from the Mousterian through the CP to the Aurignacian, so the hypothesis is validated by the faunal record, regardless of the assignment of the CP to Neandertals or AMH.

The CP is part of a group of 'Transitional' European cultures (Hublin, 2015) which are found in multicultural sites, sandwiched between the MP and the UP like the Szeletian, Jerzmanowician, and Bohunician in Eastern Europe (Alex et al., 2017), and the Uluzzian in Southern Europe (Douka et al., 2014). Assigning the CP to Neandertals has been challenged (Bar-Yosef and Bordes, 2010; Mellars, 2010) and so has the source of the knowhow for the seemingly 'modern' characteristics of these cultures, including backed blades, bone tools and ivory body ornaments (Hublin, 2015). I have chosen to assume that the CP is of Neandertal origin, based mainly on the presence of Neandertal fossils in CP layers in Grotte du Renne and Saint Cesaire, and evidence for Mousterian- like lithic technology in CP layers (Soressi, 2011), and the recent Paleoprotenomic evidence, confirming the Neandertal affiliation of the fossil from the CP layers of Grotte du Renne (Welker et al., 2016). The CP is dated to 45-40 Kya (Discamps, 2014; Higham et al., 2014; Hublin, 2015), although as Discamps and Costamagno (2015) point out *"...dating the Middle-to-Upper Paleolithic transition is far from exact science*" and Hublin (2015) states that *"...it is still difficult to provide an accurate picture of the exact process of the replacement of Neandertals by modern humans in western Eurasia*". Hublin (2015)'s conclusions indicate that it is presently impossible to determine whether the 'replacement' was effected by an interaction between the two species.

The earliest occurrence of the Proto-Aurignacian, which is attributed to modern humans and succeeded the CP in sites in Southwestern Europe, is dated to 42 Kya Cal BP from the site of Riparo Mochi in Italy (Hublin, 2015). This evidence points to a period of 2,000 years of possible overlap between the populations bearing these cultures. However there is no evidence for temporospatial overlap between them on a local basis (Hublin, 2015).

Given the relatively extensive faunal record of Southwestern Europe during the end of the Neandertals' occupation and the beginning of the AMH occupation, the analysis of the trends in animal size will concentrate on this region.

2.5.2 Extinction theories

2.5.2.1 *Purely environmental*

The MIS 3, beginning 60 Kya and ending 24 Kya, was a glacial period in which the time frame of 50-30 Kya was characterized by particularly abrupt and severe climate changes (Barron et al., 2003). Since the Neandertals' extinction occurred approximately 40 Kya, environmentally-inclined researchers attribute the extinction to the destructive effect of the MIS 3 climate on them. Bradtmöller et al. (2012) cite rapid climate change as the dominant cause of the Neandertals' extinction through its influence on a set of demographic, economic and cultural aspects. Researchers mostly agree that climate change contributed to the Neandertals' extinction, so the debate concentrates for the most part on whether the encroachment of the AMH accelerated or indeed facilitated the extinction. Prominent among those supporting a critical role for the environmental consequences of climate change is Finlayson (Stringer et al., 2000; Finlayson, 2004; Finlayson and Carrion, 2007), working in Gorham Cave, presumably the last stronghold of Neandertals before their extinction. Finlayson, who maintains that the Neandertals went extinct around 27 Kya, constructed a model based on archaeological site densities in different bioclimatic periods and areas to show that the Neandertal and AMH occupied different ecological niches, and therefore were not in competition with one another. He claims that the Neandertals traditionally occupied the heterogeneous niches that formed along the border between the plains and the Mid-Latitude Belt, which stretched from Portugal to the east for thousands of kilometers. Finlayson and Carrion (2007) argues that these woody niches contained large animals like the straight-tusked elephant (*Elephas antiquus*) and the rhino (*Stephanorhinus hemitoechus*) that could be hunted by ambush in the tree cover. It was this zone that changed dramatically during the 50-30 Kya period causing loss of trees and the appearance of plains mammals, the hunting of which presumably required projectile technology. More importantly, it required anatomical adaptation to movement over long distances that the Neandertal did not possess, but AMH did. Finlayson (2004) shows that the Neandertals retreated to the south where the fauna and vegetation did not change. Finlayson reviews the cultural time-space composition of Europe as it is related to Neandertals and AMH to show that there was no contact between them. When the AMH arrived at the north of the Iberian Peninsula, the Neandertals were not there anymore, and they were already extinct when the AMH arrived at the south end in Gibraltar. The Neandertals' demise in the south came, according to Finlayson, because they were so low in numbers and dispersed that they could not withstand the harsh conditions of MIS 3, after 27 Kya. Recent findings of an admixture of Neandertal genes into the modern human genome in Rumania just before the extinction (Fu et al., 2015) cast doubt on Finlayson's claim of total chronospatial separation between Neandertal and AMH in Europe, It may well be that in Iberia there was a time gap between the extinction of the Neandertal and the settlement of the AMH (Mallol et al., 2012; Jiménez-Espejo et al., 2013). However, in defining a clear difference in ideal niches for Neandertal and AMH, Finlayson emphasizes AMH's larger home range exploitation, social cooperation, communication and hunting technology, all of which are presumably ‘advantages’ of AMH over Neandertal, which can influence competition, if indeed they ever lived in the same ecological region under MIS 3 conditions.

Arguably one of the first researchers to suggest that Neandertals were specialized hunters of very large game who went extinct due to the decline of very large prey was Valerius Geist (Geist, 1978). Analyzing the Neandertal’s skeletal morphology, Geist finds that Neandertals evolved to hunt large animal at close encounter. He states that “*Neanderthal man appears to be the most highly specialized human form to have evolved*.” He explains the reduction in very large prey populations by the collapse of a periglacial ecosystem rich very large prey animals which were replaced by interstadial ecosystem with reduced steppe fauna. Another researcher with similar conclusions is Stewart (Stewart et al., 2004; Stewart, 2005; Stewart, 2007). Stewart sees the Neandertal extinction as an integral part of the faunal change during MIS 3. To him, the Neandertal is a large carnivore that belonged to the extinct southern grouping of the Late Pleistocene Megafauna. Stewart bases his conclusion on the analysis of a database called the Stage Three Mammalian Faunal Database. The database includes “*approximately 470 dated faunas from nearly 300 sites with just under 2000 radiometric dates between them*” (Stewart, 2007) and contains about 120 mammalian taxa. Based on the last date of their appearance, Stewart divided the animals into ‘extant’ and ‘extinct’ groups. In the extant group, three subgroups were created based on the spatial dynamics of their distribution during MIS 3. Within the extinct group, two sub-groups were created; one including animals that went extinct before the Last Glacial Maximum (LGM) and the second includes those animals that went extinct after the commencement of the LGM. The primary finding is that the Neandertal went extinct at the same time as *E. antiquus* and *S. kirchbergensis*, both of which, together with the Neandertal, retreated southwards, as opposed to the extant animals and other extinct animals which retreated eastwards and northwards. Stewart also identified a decrease in the populations of various carnivores as well as a slight decrease in most of the large mammal taxa, which he interprets as a general impoverishment of the environment towards the LGM, which presumably added to the general stress of the Neandertal. While Finlayson excluded the possibility of direct competition between Neandertal and AMH by chronospatial exclusion, Stewart dismisses this claim, based on the extended period (approximately 10,000 years, in his opinion) of sympatry in Europe. He, however, agrees that competition was not a factor in the Neandertal extinction. In his opinion, if competition were to take place, its repercussions would have been felt over a much shorter period.

2.5.3 AMH – Neandertal competition

On the other side of the debate, Mellars (Mellars, 1998; Mellars, 1999; Mellars, 2000; Mellars, 2010; Mellars and French, 2011) attributes the extinction of the Neandertal to competitive exclusion by AMH, who appeared in Europe at the boundary between the MP and the UP. According to Mellars (and see also Burke, 2012; Marean, 2015), it was the inferior adaptive capacity of the Neandertal that brought about his demise. Specifically, Mellars attributes social and cognitive inferiority to Neandertals when compared to AMH. In addition to utilizing more advanced technology, AMH also used a complex form of symbolism and language. Mellars claims that differences in these capabilities could be expected after 500,000 years of separation.

Zilhao and d'Errico (d'Errico et al., 1998; Zilhão and d'Errico, 1999; Zilhão, 2006b; Zilhão et al., 2006; Zilhão et al., 2010) object to Mellars' mental superiority claim on the ground that the CP is a demonstration of the Neandertals' developed mental capacity. The debate centers on whether the CP is an imitation of the Aurignacian or an utterly independent manifestation of modern behavior by the Neandertal. They point to the lack of similarity of the stone tools and bone objects to those of the Aurignacian. However, Zilhão and d'Errico (1999) claim that even if the Neandertal copied the AMH, it does not indicate a mental inferiority in the same manner that present societies, which adopted writing later than others, were not inferior to the modern ones. They explain the Neandertal presence in southern Iberia, in line with Sepulchre et al. (2007), by the fact that the Heinrich 4 (H4) event caused aridity in central Iberia and therefore delayed the advance of the AMH.

A rather extreme, yet not inconceivable, hypothesis by Hortolà and Martínez-Navarro (2013) is based on a synthesis of Stewart, d'Errico, and Mellars. They surmise that the Neandertal was indeed part of the Quaternary Megafauna Extinction, wherein exclusion competition with AMH led, in an ecologically expectable manner, to the hunting of Neandertals by AMH in the same way that other predators would have behaved in a similar situation.

Some researchers (Hockett and Haws, 2005; O'Connell, 2006; Bocherens, 2009; Hoffecker, 2009) concentrated on the difference in diet breadth between the Neandertal and AMH as a possible competitive advantage of the AMH. Hockett and Haws (2005) show that Neandertals concentrated on large- and medium-sized animals, in contrast to the AMH who consumed a more varied range of animals as well as plant food. They claim that more diverse diets result in an adequate supply of nutrients which leads to higher fertility and longevity. Presumably, the animal portion of the diet supplies the energy and the plant portion supply the micronutrients. They claim that the evolution of humans towards a more diverse plant and animal diet is a proof of this concept. I argue later that the evolution of humans was toward specialization and not generalization of the diet and also that animal food can provide sufficient amounts of micronutrients. In the context of the Neandertal extinction, they claim that the higher diversity of the AMH diet led to better demographic performance, which in turn led to the Neandertal being swamped by AMH. Contrary to Hockett and Haws (2005)' assertion there is recent evidence for Neandertals' broader diet including aquatic foods, small fast game as well as plant resources (Villa and Roebroeks, 2014). Widespread consumption of plants by Neandertals was recently documented (El Zaatari et al., 2011; Henry et al., 2011; Henry et al., 2014), though not quantitatively defined. There is also evidence for consumption of fish (Hardy and Moncel, 2011). Cut marked rabbit remains along with cut marked duck and goose bones occur in several MIS 9 to 4 sites in Europe (Churchill, 2014). Fa et al. (2013) also cite the Neandertals' limited ability to catch or consume smaller animals such as rabbits as a reason for their demise. While acknowledging some rabbit exploitation by Neandertals (Blasco and Fernández Peris, 2012), they show, using an extensive faunal record, that there is a marked difference between the prey consumption of Neandertal in the MP and that of AMH in the periods after the MP until the Mesolithic in the Iberian Peninsula and Southwestern France. They show that after the MP, with the local extinction of some megafauna and reduction in the numbers of other large herbivores, rabbits became a major source of calories for the AMH in this area (Fa et al., 2013). Unlike Mellars though, they do not specify the type of ability in which Neandertals were supposedly inferior. In a similar vein, other researchers attributed the limited prey size range of the Neandertals to their inability to use a more sophisticated hunting tool than a thrusting spear, while AMH had already been using throwing spears and bows and arrows when they arrived in Western Europe (Marean, 2005). O'Connell (2006) argues, using ethnographic examples that competition does not have to be active to be effective. He claims that it was too energetically expensive for individual Neandertal males to adopt the AMH technology, although they were capable of doing so. Their best energetic option remained to seek mates within their original group by applying conservative, known technologies, as the present day Hadza HG demonstrate. In the longer term, this would lead to successful encroachment by the more technologically advanced group. The technologically advanced group could also mate with the less advanced group's women, for whom the energetic cost of change would have been lower. O'Connell's hypothesis, however, relies on the existence of a significant technological advantage, similar to the one between HG and pastoralists, as well as territorial overlap between Neandertals and AMH, both of which remain in doubt. Snodgrass and Leonard (2009) have already briefly proposed, as suggested here, that the reason for the large animals' profile in Neandertal sites, was a result of their dependence on the large animals' relatively high fat content. They, however, did not explicitly associate this dependency with their extinction.

Other researchers (Sorensen, 2011), using demographic models, concluded that prey decline and climatic variations alone cannot explain the extinction and suggested an infectious disease as an additional pressure point.

Mellars and French (2011) have proposed that AMH had merely swamped the Neandertals in the transition between the MP and the UP, presenting data that show that after the MP there was a 2-3-fold increase in (1) the number of sites in the Dordogne area, (2) the overall intensity of occupation and (3) the average occupation area in the sites. Mellars and French calculate a possible demographic advantage of 9 to 1 in favor of the AMH. Mellars and French also cite several possible advantages that led to this situation, such as improved technologies in hunting, food storage, and processing, mobility and transportation, as well as increased social integration, expanded exchange, mating and alliance networks between groups, and others.

Harvati mentions, in a review (Harvati, 2010), additional possible factors such as higher birth rates, lower mortality rates, shorter interbirth spacing, and better clothing and shelter in AMH to the causes already mentioned here. She proposes that any intrinsic advantage that AMH may have possessed over the Neandertal acted to provide a *coup de grace* to the Neandertal, who had been already highly stressed due to the severe environmental conditions. Similarly, Kolodny and Feldman (2017) propose that a scenario of migration and selectively neutral species drift predicts the Neanderthals' replacement, and it was the repeated migrations of modern humans from Africa into Eurasia that led to the Neandertal disappearance in Europe.

Extinction hypotheses that rely on classical ecological competition, as well as demographic assimilation, must assume that Neadertals and AMH shared a specific ecological and geographical niche contemporaneously so that they could compete for the same resources for a substantial period. However, despite emerging agreement on the overlap between the groups on a continental scale (Higham et al., 2014) and some interbreeding, "*there is no evidence for prolonged local co-existence of Neandertals and modern humans in any region of Europe*" (Hublin, 2015). A scenario in which Neadertals went extinct in a specific region, followed by AMH settlement in this region cannot be defined as competition in the classical sense, even if the AMH settlement happened shortly after the extinction of Neandertals in the region. Hublin (2017) as well as Roebroeks and Soressi (2016) draw attention to the fact that AMH left Africa some 60 Kya and probably arrived in East Asia and Australia very shortly after, to surmise that AMH was apparently incapable of competing with Neandertals in the Pleistocene environments of the middle latitudes for some 15-20 thousand years. In any event, one cannot rule out a combined scenario in which, as proposed here, the diminution of large animals was the first cause of the demise of the Neandertal, with competition from AMH delivering the *coup de grace* or absorbing a weakened Neandertal population.

Since the Neandertal did go extinct and the AMH survived there is little room for argument over who was better adapted, mentally or physiologically or both, to the environmental conditions that prevailed immediately after the transition between the MP and the UP. The question, however, remains: what was the limitation that prevented the Neandertal from surviving beyond the MP-UP transition? Were they primarily physiological or mental/cultural and to what extent were they a result of AMH presence in the continent?

The hypothesis presented here emphasizes the relatively high energetic costs of the physiological adaptation of Neandertals to the acquisition of large animals (e.g. higher weight due to higher robusticity (Smith, 2013)). Hence, following this hypothesis, the answer may lie in the pace of extinction of the large animals on which Neandertals depended, a pace that presumably didn't allow sufficient time for physiological adaptation to sufficiently reduce the TDEE requirements. The question of whether the Neandertal would have adapted to the acquisition of smaller prey if AMH were not close by at the end of the extinction process shell probably remain forever open.

Since the hypothesis presented here associates the extinction of the Neandertal with the diminution of large animals, an interesting question for future research is how did the AMH survive the megafauna's extinction, which continued throughout the UP in Europe as well as other parts of the world? According to the analysis in Chapter 4, the diet of AMH was also highly carnivorous, so, in theory, AMH should have also been dependent on acquiring relatively fat animals. Other researchers already pointed to differences between AMH and Neandertals that could be interpreted, in the framework of the model presented here, as reducing the relative demand for obligatory fat in the diet. First and foremost, the lower weight of the AMH meant that their TDEE was lower than that of Neandertals (Froehle and Churchill, 2009). According to the bioenergetic model presented here, a lower TDEE results in a lower obligatory dietary fat requirement. Secondly, a body morphology that contributes to the efficiency of locomotion in AMH, compared to Neandertals (Steudel-Numbers and Tilkens, 2004; Been et al., 2012; but see Vidal-Cordasco et al., 2017), also results in a lower TDEE. Thirdly, as Shipman (2015) has suggested, technological developments during the UP, such as the domestication of dogs, could have also contributed to the ability of AMH to hunt smaller animals efficiently. It is interesting to note that dogs, coming from a long line of carnivores, can process protein to energy to the tune of 70% or more of their TDEE in contrast to some 35% for modern humans. This capacity in dogs could be the outlet for the surplus protein, which should result from the hunting of smaller animals, with a higher protein ratio than large animals, as will be shown in Chapter 8. Their domestication for the purpose of saving energy while hunting smaller animals (Mitchell, 2008), could have been a perfect win-win situation for both dogs and AMH. Additionally, as noted in Chapter 4, a gradual increase in plant consumption during the UP, could reduce the obligatory fat requirements.

2.6 METHODOLOGY

Optimal Foraging Theory (OFT) in the framework of Human Behavioral Ecology (Codding and Bird, 2015) provides the theoretical basis for the analysis presented in this work. Behavior is assumed to be dictated by the need to optimize the allocation of a limited energetic budget with the final goal being maximization of reproductive fitness. The obligatory acquisition of calories from fat is introduced as an additional criterion or constraint to the classic OFT goal of maximizing the rate of energy acquisition. The ranking of prey when fat is added as a criterion does not affect the typical ranking by prey size since (as will be shown in Chapter 8) larger animals tend to be relatively fatter than smaller animals. Under OFT, when the availability of highly-ranked items declines in the landscape, the diet is expanded to include lower-ranked items (Broughton et al., 2011). However, one of the implications of the findings by Pontzer (2015), that TDEE, although fluctuating (Bleiberg et al., 1980), is capped at a narrow-evolved range at the species level, is that the option to expand the diet to lower ranking items is only viable if activity-related energetic expenses remain at the evolved range. Otherwise, long-term adverse somatic effects may be encountered, including reproductive viability. Thus, Pontzer findings tie the optimization of the energetic economy that is associated with food acquisition with reproductive success. The regulated evolved range of TDEE means that the net energetic return of the lower-ranked items must be maintained within the previous level. The maintenance of the energetic level can be achieved either as a result of technological and/or biological adaptations. For example, the technological manifestation of dog domestication may represent an attempt to save energy during the tracking and catching of smaller, faster, animals (Mitchell, 2008). Biologically, longer legs in humans enable reduced locomotion costs. Some of these adaptations, as well as presumably spontaneous human actions on the environment, are sometimes assigned to Niche Construction (NC) (Laland et al., 2000), or to Cultural Niche Construction (CNC). Supporters of the CNC claim that changes can also happen without an apparent energetic stress as an underlying cause (Smith, 2015; Zeder, 2015). There is a lively debate regarding which theoretical framework, OFT or CNC, is more suitable for the explanation of human ecological behavior with a concentration on explanations for the transition to agriculture (Gremillion et al., 2014; Zeder, 2015; Stiner and Kuhn, 2016; Piperno et al., 2017). I fail to see, as have Mohlenhoff et al. (2015), why the two theories must be mutually exclusive. The measurement of prey temporal and spatial dynamics, based exclusively on the archaeofaunal record (Chapter 9) merits consideration when applied to OFT. It is conceivable that these assemblages do not fully represent the free-living population of the studied species (Speth, 2013). For example, the fact that the assemblages differ in their preservation potential and are often partially anthropogenic can be a source of misrepresentation of the free-living population.

The possibility that an observed change in abundance patterns is a result of a change in Neandertals' tastes or other agency (social or cultural) considerations cannot be entirely ruled out. However, since there is no doubt that eventual extinction of Neandertals did occur it is reasonable to assume that the room for free agency during the period leading to the extinction must have been limited by the gradually increasing stress. In any event, OFT has been used successfully to explain archaeofaunal phenomena in connection to human behavior and evolution (Lupo, 2007). I, therefore, suggest that OFT provides sufficient theoretical background for the presentation of the hypothesis.

An extinction of Neandertals in Western Europe should have caused a gradual demographic decline and reduction in geographical demographic distribution. To the extent that it could be temporally and spatially compared to the pace of large fauna diminution, it could help in testing the hypothesis. It is, however, difficult to determine whether Neandertals had indeed suffered a demographic contraction starting 50 Kya, in line with the diminution of large animals. A natural baseline low population density of small groups (Bocquet-Appel and Degioanni, 2013; Sánchez-Quinto and Lalueza-Fox, 2015; Mafessoni and Prüfer, 2017), as well as difficulties in the accurate dating of sites, hinders an identification of population dynamics during the period that preceded the arrival of AMH to Western Europe. An example of the difficulties of estimating population trends within the Neandertal pre-extinction period can be found in the work of Mellars and French (2011). Mellars and French (2011) included data from French Mousterian of Acheulian Tradition (MTA) and CP sites in their in their attempt at demographic comparison with AMH's Aurignacian sites. According to their data (fig. 4), the number of Neadertal sites increased from the MTA to the CP, but the occupation area decreased leaving the question regarding the demographic trend within the Neandertal population open (assuming the CP is of Neandertal origin). Dogandžić and McPherron (2013), however, question the use of the MTA alone as a late MP culture, claiming that other cultures such as Discoid-Denticulate may have been contemporaneous with the MTA. If they are taken together, the number of Neandertal sites will have declined in the CP.

Dogandžić and McPherron (2013) indicate that the final MP is rarely dated and when it does, it is so close to the limit of the radiocarbon method that the dating should be taken with caution. In conclusion, better and wider dating of final MP sites may enable a credible analysis of the demography of the last Neandertals in the future.

3 THE PROTEIN CONSTRAINT

The metabolism of protein to energy requires the removal of toxic nitrogen from the body in a process that involves the liver and the kidneys. Cats, which are obligatory carnivores, can safely obtain at least 70% of their energetic consumption from protein (Macdonald et al., 1984; Russell et al., 2000). Humans, however, are constrained in their capacity to process protein to energy, estimated at 35% - 50% of normal caloric consumption (Rudman et al., 1973; Speth and Spielmann, 1983; Speth, 1989; Cordain et al., 2000). This constraint is probably a result of humans' relatively recent evolution as a carnivore.

Excess consumption of lean meat is known to have caused 'rabbit starvation syndrome' among early American explorers and hunters, especially during winters when fat reserves in animals are low. Symptoms of 'rabbit starvation' include nausea and diarrhea followed by death within two to three weeks (Lieb, 1929).

John Speth, a leading researcher of the influence of the protein constraint on human behavior, brings in his book "*Big-Game Hunting: Protein, Fat and Politics*" (Speth, 2010: Chapter 4.3) numerous historical accounts of the deleterious consequences of consuming excessive quantities of protein. A few examples follow (Full references in Speth, 2010):

Marcy (1863:16) reported thus: "We tried the meat of horse, colt, and mules, all of which were in a starved condition, and of course not very tender, juicy, or nutritious. We consumed the enormous amount of from five to six pounds of this meat per man daily, but continued to grow weak and thin, until, at the expiration of twelve days, we were able to perform but little labor, and were continually craving for fat meat".

Jedediah Smiths, who led a group of trappers, reports (Allen 1979:457): "…the party made only 3 miles on the 18th, which taxed their strength to the utmost. The men were almost as weak as the horses, for the poor [spring] venison of this country contained little nourishment".

Another trapper reports (Causes 1898:97): "For about six weeks I lived on nothing but jerked elk meat…. There is little substance in elk meat. I became so weak that I could scarcely get up the river bank with a bucket of water; my knees felt like giving way."

John Ross, an arctic explorer, speaks of the danger of dying from a high protein diet (Ross 1835:135): "It would be very desirable indeed if the men could acquire the taste for Greenland food; since all experience has shown that the large use of oil and fat meat is the true secret of life in these frozen countries and that the natives cannot subsist without it; becoming diseased, and dying under a more meagre diet.”

Signs of oxidative stress with a higher chronic consumption of protein have been noted in rats (Kołodziej et al., 2017). High protein consumption can lead to death when toxic urea levels in the blood exceed the liver and the kidneys' capacity to remove it (Speth, 1989). It is therefore unlikely that long-term testing of the upper dietary protein ceiling in humans will ever be performed. In a comprehensive review of the literature on the subject, Speth remarks that *"The precise nature and value of this limit, however, remain poorly documented and controversial."*

The rate of conversion of amino acid derived ammonia to urea for removal by the kidneys is limited (Bilsborough and Mann, 2006).Rudman et al. (1973) established a maximum rate of urea synthesis which correspond to a daily protein consumption limit of 190 grams (760 calories) for a 50 kg man, which translates into 3.8 g/kg body weight/day. This rate translates into about 35% of a normal daily caloric consumption, but it should be noted that in practice, the protein ceiling should be of an absolute rather than a relative nature. It should also be noted, however, that Rudman et al. tested only six individuals in an acute, 12-hour intravenous infusion of an amino acid mixture, with measurements of blood indicators. No period of adjustment to high protein consumption was attempted, nor was an actual pathological effect of a medium- or even a short-term high protein diet tested.

To this limit one must add the amount of protein that is used by the body for structural and functional purposes estimated at 0.8 gram per kg bodyweight (Bilsborough and Mann, 2006) for a total of 3.8+0.8=4.6 gram per kg body weight.

A prolonged human experiment of high-protein diets with the aim of assessing protein metabolism lasted 50 days (Oddoye and Margen, 1979). The daily protein consumption was below Rodman's limit at 3.0 g/kg/d. The six healthy young adults remained healthy throughout the period. Another experiment tested fourteen healthy resistance-trained men on 3.32 g/kg/d for 2 months at a time, with 4 month lower protein consumption, alternating for a year, with no apparent deleterious effects. Assuming that they require 0.8 gram per kg body weight for structural purposes, the effective deamination requirements in this trial amounted to 3.23-0.8=2.43, well below Rodman’s limit.

The diet of circumpolar populations was almost 100% animal-based before the arrival of external industrialized food supplies (Heinbecker, 1928; Rabinowitch et al., 1936). There are numerous ethnographic reports and personal communications of habitual consumption of high quantities of protein among circumpolar populations, where protein consumption could reach up to 300-320 g/d and 44% - 50% of the normal caloric consumption (Heinbecker, 1928; Rabinowitch et al., 1936; Sinclair, 1953; Rodahl, 1960; Schaefer, 1977; Speth, 1987; Speth, 1989; Snodgrass and Leonard, 2009), which translates into a consumption of about 1.1 kg of lean meat per day. Assuming that they required 0.8 gram per kg body weight for structural purposes, the effective deamination requirements of the circumpolar populations, assuming a weight of 80 kgs, amounted to some to some 3.2 gr/kg bodyweight (320/80-0.8=3.25), well below Rodman's limit.

It should be noted that reports of increased liver size (hepatomegaly) among circumpolar populations at contact can be interpreted as the liver adaptation to increased requirements of urea synthesis ((Ben-Dor et al., 2016) due to a high consumption of protein.

In a series of animal and human trials, Raubenheimer et al. (2015 and references therein) found that animals (including humans) regulate the intake of protein energy more strongly than non-protein energy. It is interesting to note that in the U.S., humans, who have practically unlimited access to the three macronutrients, consume about 16% of the calories as protein (Austin et al., 2011). Simpson et al. (2003 and references therein) state that "*mean protein intake varies the least of the macronutrients across human populations and with time, typically comprising between 11 and 15% of dietary energy.*"

The abovementioned information indicates that present-day humans are capable of consuming around 40% of the energy as protein for long periods, but would prefer to consume lower ratios when fat and/or carbohydrates are available. It may also be that the high level of protein consumption evident in Polar populations may require specific genetic adaptations, so there is potential for ancient DNA studies to determine whether Neandertals had such putative adaptations that accorded them a higher tolerance to protein. Later I will present a hypothesis that the Neandertal 'bell' shaped thorax may represent such an adaptation (Ben-Dor et al., 2016).

4 PRESENTATION OF THE OBLIGATORY DIETARY FAT BIOENERGETIC MODEL (ODFBM)

To identify situations of potential dietary stress, due to the protein ceiling, I developed the Obligatory Dietary Fat Bioenergetic Model. It was first applied to examin the disappearance of *H. erectus* from the Levant, 400 Kya and the appearance of a new hominin (Ben-Dor et al., 2011).

The ODFB model was developed to identify situations of metabolic stress in humans, due to a shortage of dietary fat resources in the environment. It is a bioenergetic model in that it relies on a biological energy budget to explain human behavior and evolution.

4.1 RESEARCH HISTORY - BIOENERGETIC MODELS IN THE STUDY OF HUMAN EVOLUTION AND EXTINCTIONS

Kleiber (1947) determined that the basal metabolic rate (BMR) of mammals can be calculated based on their body weight (BW). BW estimates for Pleistocene humans and estimates of physical activity levels (PAL) as multipliers of BMR enabled researchers to estimate a TDEE and its implications on human evolution and behavior. Early studies concentrated on the association between energetics and early human evolution. Rodman and McHenry (1980) studied the energetic implications of bipedalism, while Martin (1983) concentrated on brain evolution. The investigation intensified in the 1990s (Wheeler, 1991; Steudel, 1996; Leonard and Robertson, 1997). Foley et al. (1991) studied the energetic implications of the larger hominin brain on growth rates, life history, and foraging behavior. Of particular interest to us, they showed that the encephalization quotient among various primates is positively associated with a high-quality (high nutritional density) diet. Aiello and Wheeler (1995) developed the ‘Expensive Tissue Hypothesis,' postulating that the expansion of the human brain was made possible by a compensating decrease in the size of the energetically expensive gut. In agreement with Foley and Lee, they concluded that the result of the increase in brain size was a dependence on an energetically-dense diet. Later studies suggested that the energy savings more likely came from bipedal locomotion (Isler and van Schaik, 2009), increased fat reserves (Navarrete et al., 2011), and reduced muscularity (Leonard et al., 2003). These findings, however, do not challenge Aiello and Wheeler's conclusion that the gut of humans is markedly smaller than that of other primates, and that its smaller size dictates an energetically-dense diet.

Formal reconstruction of energetic budgets on a taxonomic level was initiated by Sorensen and Leonard (2001), who compared the estimated TDEE of Neandertals with present-day foragers to elucidate the Neandertals' foraging efficiency.

Various researchers have developed bioenergetic models to study the effects of stressors like gestation and lactation on hominin survivability (Aiello and Wells, 2002; Hockett, 2012). Others have concentrated on other possible stressors, especially in relation to Neandertals, such as increased mobility, deteriorating climate, and higher body weight (Steegmann Jr. et al., 2002; Froehle and Churchill, 2009; MacDonald et al., 2009; Snodgrass and Leonard, 2009). All of them found that energetic models can aid in explaining the extinction of the Neandertal.

Recently, the concept of fluctuating TDEE levels based on different levels of activity (PAL) was questioned by Pontzer et al. (Pontzer et al., 2012; Pontzer, 2015; Pontzer et al., 2015; Pontzer et al., 2016). Using the doubly-labeled water method, which is the most accurate method for the measurement of TDEE in the field, they found that while the level of activity of individuals in a HG group was higher than of that of their Western counterparts, their TDEE was similar. TDEE remained disassociated from PAL also within the HG population and correlated most strongly with fat-free mass (Pontzer, 2015). Instead of increased TDEE, the increased activity resulted in increased metabolic stress. Pontzer (2015) hypothesizes that the increased demand of the muscular system is compensated by reduced activity of the reproductive system and somatic maintenance. In summary, TDEE seems to be highly regulated, so that chronically increased activity may lead to reduced fitness but not to a higher energetic demand regarding food acquisition. Since the ODFB model is based on fluctuating TDEE under certain conditions, there is a need to address this alternative TDEE concept. The alternative TDEE regulation concept should not hamper the basic validity of the model since the 'increased' TDEE can be regarded as a measure of increased fitness pressure. More energy is directed towards hunting at the expense of somatic, maintenance and reproductive capabilities. Thus, when an 'increase' of TDEE is predicted, from a normal level of 2500 calories to 3000 calories, it means that an additional 500 calories were directed to hunting activity at the expense of other metabolic functions.

The importance of the ceiling on protein consumption in humans in the study of prehistoric human nutrition was first identified by Speth and Spielmann (1983). They, however, did not discuss the protein ceiling in the context of a bioenergetic model. Later, Cordain et al. (2000), with Speth as a co-author, discussed the implications of the protein ceiling on fat consumption and prey choice. No researcher has incorporated the protein ceiling into a formal bioenergetic model. However Snodgrass and Leonard (2009) postulated, in the framework of a bioenergetic investigation, a general high demand for fat, and thus for large animals, among Neandertals.

4.2 DESCRIPTION OF THE OBLIGATORY DIETARY FAT BIOENERGETIC MODEL

4.2.1 The model

The Obligatory Dietary Fat model is used to predict the influence of the relative environmental availability and physiological processing capacity of carbohydrates, protein, and fat on human behavior. It was applied (Ben-Dor et al., 2011) in an attempt to explain the demise of *H. erectus* in the southern Levant ca. 400 Kya as the Acheulian was giving way to the Acheulo-Yabrudian (Barkai and Gopher, 2013). The model is bioenergetic in the sense that it uses the TDEE of the studied humans to predict stress. Unique to this model is the inclusion of expressed separate values for the three macronutrients.

Inputs to the model are TDEE, a physiological ceiling on protein consumption, and an estimated, environmentally based, maximal consumption of carbohydrates (plant foods). The output of the model is the obligatory caloric ratio of animal fat to total calories in animal-sourced food. The ratio is then compared to the caloric percentage of fat in potential prey. If the fat ratio in prey does not meet the dietary obligatory fat ratio for humans, then stress is predicted due the limit on protein consumption. Additional animals have to be acquired, at additional energetic expenditure, from which only the fat portion can be consumed. Alternatively, only fat-bearing parts from captured animals, which on average conform to the calculated ratio, can be utilized with the result of the need to hunt more animals. Since protein and carbohydrates, by definition of the model, are at their limits (see Section 4.2.3), all the additional energetic expense that is spent on the additional hunting will have to come from the metabolism of fat, further increasing the required number of animals and the effective stress.

Alternatively, if we accept that TDEE is highly regulated in humans (Pontzer, 2015), the need to obtain more fat by hunting more animals will not result in increased TDEE but the loss of fitness.

4.2.1.1 *Description of the model*

The fat content of prey animals is a critical component of the model, so a general clarification regarding terms used in its description is required. It is common to refer to animal (or human) fat content regarding weight to weight percentage. A 5% to 10% fat content is not uncommon in such descriptions and gives the impression that fat is a minor component of the animal. However, since animals are acquired as a source of energy, it is appropriate to use a caloric rather than a weight percentage of fat in the model. An animal which has a weight to weight fat percentage of 5% may have a caloric fat percentage of 50%, since most of the animal's weight comprises water, bones and hide, which do not contribute to the caloric value of the animal (Ledger, 1968; Emerson, 1990). Also, a gram of fat contains 2.25 times the amount of calories found in a gram of protein.

In the model, daily food consumption is divided into four categories, expressed in calories:

1. Plant Food Ceiling (PLA)
2. Animal-Sourced Protein Ceiling (PRO)
3. Structural protein requirements (SPR)
4. Animal Fat (FAT)

An environmental ceiling on plant food and a physiological ceiling on animal-sourced protein consumption for energy and separately for structural purposes are estimated. Plant food contains protein that should also be taken into account. Cordain et al. (2000) calculated an average of 14% protein in plant foods, based on a database of plants consumed by Australian aboriginals and smaller databases for worldwide HG. Thus, the plant calories are reduced by 14% to calculate the obligatory fat requirements because only the carbohydrate and fat content of the plant foods reduce the need for animal fat.

Once established, an obligatory animal fat consumption (OAF), in caloric terms, is derived by subtracting the maximum non-protein calories obtainable from plant food and animal protein from the

TDEE. A ratio of OAF calories to total animal calories (OAF/TAC) is determined, which for optimal energy expenditures in hunting activity should correspond to the OAF/TAC of the hunted animals. The following formula describes the model:

OAF = TDEE – 0.86PLA – PRO (Obligatory Animal Fat = Total Energetic Expenditure – 0.86 Plant Food Ceiling (carbohydrates and fat) – Animal sourced Protein Ceiling)

An ideal prey animal is thus one that provides enough fat to satisfy the obligatory animal fat (OAF) consumption. It will have a ratio of calories from fat to total animal-sourced calories (F/T) that is equal to: OAF/ (OAF+(PRO-0.14PLA+SPR) Obligatory Animal Fat / (Obligatory Animal Fat + Protein Ceiling – contribution of plant protein + structural protein requirements). Note that at this stage the structural protein requirements were added to the formula.

For example, let's assume that TDEE is 3000 calories, plants food availability (PLA) is 900 calories, the protein ceiling (PRO) is 1000 calories Then:

OAF = 3000 – 900*0.86 – 1000 = 1226 calories (obligatory fat consumption)

The ideal fat ratio in the acquired animal (F/T) is a crucial step in the application of the model as it determines how limited will be the pool of animals which will be suitable for acquisition. Acquiring animals with a lower fat content than the one calculated here will entail some waste of energy as, because of the protein ceiling, it will be impossible to exploit in full the caloric potential that is stored in their protein. Indeed, as will be shown later, HG sometimes just leave unexploited a hunted animal that is found to be lacking in fat.

The ideal ratio is the obligated fat divided by the total calories in the animal (fat + protein ceiling, minus the protein that is included in the plant food+ structural protein requirements). So, if the calculated obligated animal fat consumption is 1226 calories, and the protein ceiling is 1000 calories, and the protein content in 900 calories from plant food is 126 (900*0.14) and structural protein requiremets are are 80 kgs X 1.2 gr/kg bodyweight so are 96 grams at 4 calories per gram are equal to 384 calories, than the ideal fat to total energy in the acquired animal should be (F/T = OAF/(OAF+PRO – 0.14PLA+SPR)) = 1226/ (1226+1000-126+384) = 49%. This result means that consumption of an animal with a caloric, fat content below 52% will not allow a full exploitation of its caloric value without exceeding the protein metabolic constraint. The next step will be to define which animals meet the minimum fat ratio but first a discussion of the sensitivity of the results to the model parameters is in order.

4.2.2 Sensitivity of the model to various parameters:

4.2.2.1 *TDEE*

It is clear from the model that an increase in TDEE has a substantial effect on the ideal animal fat content, given a fixed caloric ceiling on plant food and animal protein. For example, an increase of 20% in TDEE in the example above will increase the ideal animal fat content (F/T) from 58% to 64.6% (1826/(1826+1000)), which few animals attain. For example, four bisons that were dissected by (Emerson, 1990) were found to contain between 43.4% to 59.6% fat in caloric terms. Smaller animals typically contain less than 25-40% fat (see Table 11). All animals lose significant amounts of fat during dry or snowy seasons. In such a case, TDEE is likely to increase even further with the need to search for fatter animals or a larger quantity of animals with less fat, the protein of which will be partially wasted. Some of the possible causes of an increase in TDEE are:

4.2.2.2 *Free fat mass*

Since TDEE is a function of BMR, and BMR is a function of free fat mass (Pontzer et al., 2015), it is clear from the model that individuals with higher body weight will have higher obligatory fat requirements at a given trophic level. Given identical environmental conditions, Neandertals, whose body weight was substantially higher than that of AMH (McHenry, 2009a), were likely, as will be shown, to have had higher TDEE and thus higher obligatory requirements for fat.

4.2.2.3 *Mobility*

Mobility and cost of mobility is another factor affecting TDEE, so it is clear from this model that increased mobility, or increased energetic costs of a given mobility, will result in a requirement for fatter animals. Alternatively, as discussed, if TDEE is indeed highly regulated (Pontzer, 2015), increased mobility due to a scarcity of fatty animals, will decrease fitness.

4.2.2.4 *Climate*

Another implication of the model is that climate, as it affects plant food availability, both for humans and animals, is a major source of potential stress for hunters. A reduction of 50% in plant food availability for humans during dry or cold periods will increase the optimum fat content of the ideal animal. In the example above, decreasing the available plant calories from 900 to 450 calories will result in an increase of the requirement for minimum fat ratio in animals from 58% to 63%, while the fat content of the animals, especially at the end of the season, is below normal due to the diminishing plant resources which they consume. Presumably, such increased fat requirements can only be met with increased mobility. TDEE is also affected by climate, as cold weather leads to higher BMR and therefore higher TDEE (Snodgrass and Leonard, 2009).

4.2.3 Estimating model parameters

This section will deal with estimations of the parameters of the model as they relate to Neandertals in Europe during their period of extinction, MIS 3. The estimates will relate to the presumed period of maximum stress – European winters during MIS 3. As indicated in the introduction, the MIS 3 was a period of long and cold winters with extended snow cover that minimized the availability of plants for human and animal consumption.

Ideally, a group average TDEE and protein ceiling would have been estimated, as food was most probably shared (as it is in present-day HG societies, especially with regard to large prey (Kelly, 2013:138)). Averaging TDEE would have required an estimate of the demographic composition of a typical group, and then an individual estimate of body weight (BW) for the various components of the group regarding age and sex.

However, both liver size (Müller et al., 2011), which affects the protein ceiling, and TDEE, which affects the F/T requirements, are a function of fat-free mass. This fact means that the result of the model will be close enough if we apply it to a representative individual of the group, such as an adult man, for whom a higher number of fat-free mass estimates (or approximation as BW) exist. Results of studies on present-day humans show that the TDEE/kg BW of adult males and females are very similar (FAO, 2004). Children have a higher TDEE/kg at the same activity level, but they consume in total a smaller portion of the group's calories. The protein ceiling is also a function of body weight, such that the relative relationship between TDEE and the protein ceiling are very similar for males and females. Children's TDEE/kg is higher than that of adults (FAO, 2004: Table 4.5) because children are growing. Since their liver weight (and hence protein-processing capacity) is a function of their body weight, their protein ceiling is lower relative to their caloric requirements, meaning that their F/T is higher than that of adults. The effect of ignoring children then is to underestimate the group F/T ratio. Since in this case, it means erring on the side of caution, I will not correct for the bias and will simply use adult man as a representative of the group for the determination of F/T, the ratio of dietary calories from animal fat to total animal calories.

4.2.3.1 *Estimating the protein ceiling*

I begin by assuming a low protein ceiling for humans of 190 g for 50 kg BW (3.8 g/kg/d), as found by Rudman et al. (1973) and will examine the model's sensitivity to higher limits. To scale this capacity in relation to BW, I use the regression for allometry of liver weight of 0.10 X BW^0.62, as proposed by Müller et al. (2011). Assuming that Neandertals possessed the same protein processing capacity per liver weight, at 77 kg for men (McHenry, 2009a), they could process up to 246 grams of protein into energy per day. These quantities of protein represent 985 calories, at four calories per gram of protein. Circumpolar populations are known for their pre-contact high consumption of protein which can reach 300-320 grams per day (Krogh and Krogh, 1914; Draper, 1977). At the high range of the estimate, assuming a circumpolar population-like level of protein consumption, as Speth (1989) has done (300 grams for an 80 kg man), we arrive at a limit of 292 grams of protein for a 77 kg Neandertal man, or 1,170 calories. In fact, I should have deducted the structural protein requirement of 1.2 grams/kg bodyweight times 77 kgs body weight, so 92 grams or 370 calories, from Speth's 300 grams' reported consumption. This means that the demand on the liver to remove urea in circumpolar populations was only relevant to 200-220 grams or only 2.7 grams/kg body weight, compared to Rodman and McHenry (1980) finding findings of 3.8 grams/kg body weight. Assuming that Neandertals possibly had a larger liver and kidneys as we have hypothesized (Ben-Dor et al., 2016), I chose not to deduct the structural protein requirement and leave the limit at the 292 grams protein, which are 45% higher than the quantity I calculated as protein to energy among circumpolar populations. In conclusion, I estimate a daily range of 985 (low) to 1,170 (high) calories as the protein ceiling for Neandertal males.

4.2.3.2 *Estimating the structural protein requirements*

The RDA for protein, which reflects the structural requirements for protein, was established at 0.8 gram per kg bodyweight (Bilsborough and Mann, 2006). It is unknown, however, if increased physical activity also increase the structural requirements of protein (Simmons et al., 2016). Measurements of protein breakdown, protein synthesis and protein recycling, all of which take place during and post exercise, are at present not reliable enough to support a definite conclusion (Simmons et al., 2016). The current recommendations are to increase the minimum consumption of protein from 0.8 to 1.2 gram per kg bodyweight for male endurance athletes. Therefore, assuming that hunter-gatherers are more active than modern test subjects, although the extra requirement is not proven (Simmons et al., 2016)and the extra DTEE is not proven (Pontzer et al., 2015), I have assumed, for safety sake, an intake of 1.2 grams protein per kg of bodyweight for structural requirements. This adjustment will reduce the fat ratio requirement in the acquired animal by few percentage points. There is no evidence that a further increase in physical activity requires a higher level of structural protein so a dynamic adjustment for higher TDEE was not included in the model.

4.2.3.3 *Estimating the plant ceiling*

The protein ceilling is only relevant in situations where plant food is in limited supply. This can theoretically happen in highly seasonal regions where snow or freezing conditions during winters or dry conditions during summer or winter limit vegetation. It can also depend on the net energetic return of plant food in a specific area as apart fron gathering, detoxification and other preparation of plantss can be time and energy consuming. Extended discussion of relative plant consumption regarding Paleolithic humans in general and Neandertals in particular appear in Chapter 5 and 6. For simplicity’s sake, I discuss below two scenarios. In the first, I estimate the plant ceiling as zero during glacial European winters although it is likely that a small consumption of plant foods did take place. I also consider a consumption of higher plant food proportion in the diet up to 30% plant foods during the MIS winters, which, as discussed before, is highly unlikely based on Ethnographic data for regions with a similar climate.

4.2.3.4 *Estimating TDEE*

BMR of mammals can be estimated based on BW (Kleiber, 1947; FAO, 2004). A customary method of estimating TDEE is first to determine BMR, and then multiply it by a factor representing PAL (FAO, 2004). PAL values are based on measured BMR and TDEE from populations with different activity levels, such as farmers or HG. Estimating TDEE in extinct populations is done by multiplying their estimated BMR by the PAL value for their level of activity. As mentioned, recent empirical research (Pontzer et al., 2012; Pontzer, 2015) calls into question the BMR-PAL model and suggests the TDEE is strongly regulated such that high energy expenditure during extensive activity is compensated by directing less metabolic activity towards body maintenance. High energetic demands, under this research, seem to result in metabolic stress that reduces fitness rather than generating an elevated TDEE. The implication for the model is that instead of denoting increased caloric requirements an increase beyond the TDEE estimates indicate a level of somatic stress rather than actual consumption of extra calories.

Table 1 presents estimates by various researchers of the Neandertals' TDEE, under summer and winter conditions and low and high protein processing capacity. Based on the estimated TDEE I have calculated the minimum F/T of the prey animals.

Table 1. Estimated TDEE of Neandertal males and percent of nutritional fat caloric requirements assuming no carbohydrate consumption

Authors	Mean male body weight (kg)	TDEE° male (A)	PRO - Protein limit (B)		F/T - Relative fat % (A-B)/A	
			Low	High	Low PRO	High PRO
(Steegmann Jr. et al., 2002)	67.3 (ffm)	3360-4480	985	1170	64 - 72	59 - 68
(Churchill, 2006)	77.6	3700-4700	985	1170	67 - 73	62 - 70
(MacDonald et al., 2009)	79.2	4230-5020	985	1170	71 - 75	67 - 71
(Snodgrass and Leonard, 2009)	77.6	4085-6754	985	1170	70 - 81	65 - 78
(Froehle and Churchill, 2009)	75.8	3439 - 4701	985	1170	64 - 73	60 - 70

TDEE – Total daily energetic expenditures in calories. Protein limit – Maximum daily protein consumption in calories. Low estimate and High estimate. Plant consumption assumed to be nil. Structural Protein Requirement assumed to be 77kgs X 1.2 gr/kg bodyweight X 4 calories/gr = 369.6calories. ffm – free-fat body mass

4.2.3.5 *Summary of the results of the obligatory fat estimate*

As can be seen from the results in Table 1, the estimated minimum F/T of the Neandertals' prey during winters is exceptionally high, due to the high estimated TDEE and the presumed near absence of plants.

The model predicts that Neandertal required animals that on average provided 59%-81% of their calories as fat. Although the assumption for near zero contribution of plant-sourced food may look a bit extreme, it may be helpful to note that even an availability of 10% or 20% or even 30% of the calories from plants at the lowest TDEE predicton of 3360 calories would still result, according to the model, in a requirement for animals that contain a relatively high proportion of fat of 56%, 52%, and 48% respectively. As discussed, during MIS 3 winters neither the low TDEE and nor a high or even medium consumption of plant food were likely. As will be discussed in chapter 8, these kind of fat ratios can be found only in large animals.

4.2.4 Application of the model to explain extinctions of human species

By linking obligatory fat requirements to prey animal size, the ODFBM model is used to identify a specific environmental factor that can lead to extinction, namely, a decline in the prevalence of large prey animals. The mechanism that is responsible for the link between a decline in large prey animals and the Neandertal extinction is described as follows:

1. Species operate at an evolutionary determined energy level (Pontzer, 2017).
2. The decline in large prey animal populations forces humans to hunt a larger number of smaller animals. This increased workload, and hence energetic requirements can be substantial, depending on the size difference and relative fat content of the alternative animals. Most importantly, it is made much more substantial when the obligatory requirement for fat is taken into account (Table 11). For example, in terms of weight, one Buffalo is equal to 15 Impala however in terms of caloric fat content it is equal to 34 impalas, nearly doubling the extra workload that results from the decline.
3. A substantial chronic increase in the requirement for energy for activity creates a shortage of energy for reproduction, growth, immune response and other somatic processes (Pontzer, 2017 and references therein), including genetic adaptation (Parsons, 1993).

The risk of extinction is relative to the amount of stress, its duration and the availability of resources to provide energy to underlying change (Parsons, 1993). As will be shown (Chapter 9), the continuous reduction of large prey animal abundance during MIS 3 point to a continuous increase in the amounts of energetic stress throughout the period thus limiting the chances for biological and technological adaptation that will involve sufficient energy savings while acquiring a larger number of smaller animals.

4.2.5 Previous applications of the model

The ODFB model was applied twice in previous papers to explain evolutionary processes. In the first paper (Ben-Dor et al., 2011) we attempted to explain the disappearance of *H. erectus* from the Levant 400 Kya and the appearance of a new hominin lineage that shared dental characteristics with the Skhul/Qafzeh Middle Paleolithic populations and to some extent also with Neandertals (Hershkovitz et al., 2011). A disappearance of elephants from faunal assemblages of the Levant, also 400 Kya, and the development of a new cultural complex, the Acheulo-Yabrudian, were analyzed, using the parameters of the model. The physical and cultural adaptations of the new human species were explained by the need to obtain an adequate level of dietary fat from a population of smaller, faster, animals.

The Paper, Ben-Dor M, Gopher A, Hershkovitz I, and Barkai R. 2011. Man the fat hunter: the demise of Homo erectus and the emergence of a new hominin lineage in the Middle Pleistocene (ca. 400 kyr) Levant. PLoS ONE 6(12):e28689.**”** is attached as **Appendix 4**.

The second application of the model is discussed in Section 5.1 and the paper itself, Ben-Dor, M., Gopher, A. and Barkai, R. (2016), Neandertals' large lower thorax may represent adaptation to high protein diet. *American Journal of Physical Anthropology*, 160: 367–378. doi:10.1002/ajpa.22981 (Ben-Dor et al., 2016). It is attached as **Appendix 5**.

5 THE PLANT-ANIMAL RATIO IN THE PALEOLITHIC HUMAN DIET, A MULTIDISCIPLINARY RECONSTRUCTION

The model that was presented in Chapter 4 requires an estimation of the carbohydrates component in the diet. A high carbohydrates-dominated plant content practically negate the obligatory need for a significant fat content in the diet. This is the situation in many agricultural societies. Thus, in order to determine the relevancy of the ODFBM model to human behavior and evolution during the Paleolithic, patterns in the dietary plant-animal ratio (DPA), if there are any, need to be established.

5.1 INTRODUCTION TO PLANT – ANIMAL RATIO

The relative importance of plant and animal food in the Paleolithic human diet is an old and active research issue (see references for early contributions in Stahl et al., 1984). Its importance stems from the fact that a DPA serves as a basic assumption for hypotheses about human evolution (e.g., Speth, 1989:16; Stiner, 2002; Ungar et al., 2006; Kaplan et al., 2007; Hawkes and Coxworth, 2013; Dominguez-Rodrigo et al., 2014a).

Several attempts have been made to estimate an exact level of dietary consumption of carbohydrates (Plants). Not surprisingly, most, if not all, relied heavily on the ethnographic record. Eaton and Konner (1985) estimated carbohydrate consumption at 40% of the Paleolithic diet (Table 3 therein). Later Konner and Eaton (2010) marginally reduced their estimate to 35-40%. A review of 229 recent HG groups by Cordain et al. (2000) yielded an estimate of 22-40% for carbohydrate consumption as a percentage of energy. Marlowe (2005) used a larger sample of 478 groups of recent HG with the aim of determining patterns of Paleolithic behavior, including diets. He found groups who relied on gathered foods for 90% of their diet and others that relied on hunted and fished foods for 95% of their diet. Mean carbohydrate consumption for the sample was 35% for gathered food. Since carbohydrates form only part of the gathered food calories, the mean of Marlowe's sample would be lower than the estimate given by Konner and Eaton (2010) and somewhat in line with the lower range of Cordain et al.'s estimate. Kuipers et al. (2010) also reached an estimate of 40% carbohydrates in the diet of East African Paleolithic humans, based on review of local resources and the ethnographic record. More recently, Kuipers et al. (2012) published a multidisciplinary reconstruction of the Paleolithic diet and concluded that gathering plants most likely played the major role in food procurement by humans. This conclusion appears immediately after an extended discussion of the ethnographic record of plant-dominant diets' groups, so despite the multidisciplinary nature of the paper, it must have been strongly influenced by the ethnographic record, as was the case with all the previously mentioned research. However, the claimed wide range of DPAs is even more significant for evolutionary research than the average in HG diets. A wide range of DPA s in recent HG diets naturally leads to a conclusion that Paleolithic diets could have been highly varied in their ratios. The scientific validity of using the ethnographic record to reconstructed DPA in the Paleolithic diet is reviewed in Section 5.3.

While chimpanzees and wolves both consume plants and meat, both are not adapted to survive on any DPA. Chimpanzees invariably consume a small portion of meat and wolves invariably consume mostly meat. Different habitats and biological and behavioral evolutionary adaptations make the energetic cost of acquiring plant or animal foods and metabolizing them radically different for different species thus constraining the DPAs in the diet of animals. Similarly, to understand human evolution, it is crucial to determine whether the full range of DPAs that is witnessed in recent HG group is indeed indicative of the Paleolithic evolutionary pattern.

As will be argued in detail later, the relevance of the ethnographic record to the reconstruction of quantitative Paleolithic DPA ratios is questionable, and in fact, may prove to be outright misleading. There is no doubt that humans regularly consumed plants and animals during the Paleolithic. Here, however, we are exclusively interested in searching for a quantitative pattern in the ratio of plant to animal-sourced foods. Most of the zooarchaeological record, or the content of ancient tooth plaque, as merely attesting to a consumption of one type of food or another, provides insufficient information to the question at hand. Further analysis of the archaeological record like that of stable isotopes, genetics, ecological reconstruction and trends in stone tools' uses may be relevant to the reconstruction and will be reviewed

This chapter also presents an additional method for discerning the Paleolithic DPA. Human physiology and genetics reflect long-term adaptations. They are explored for indication of long-term adaptations to specific DPAs.

5.2 METHODOLOGY

The evidence for a historical dietetic pattern will be divided into direct evidence and indirect evidence categories. Direct evidence is defined here as archaeological – skeletal, dental, faunal and botanical records as well as isotope and other geo-archaeological data that is extracted from the archaeological record. Indirect evidence is mainly derived from an interpretation of anatomical, genetic and metabolic phenomena in present humans.

Morphological and physiological adaptation by natural selection to a wider or narrower food niche is the major cause of the observed biological diversity (Darwin, 1859). Morphological, metabolic and genetic characteristics that are the result of the adaptation to the particular food niche are bound to tell us more about the prevailing diet during evolution than direct anecdotal evidence of consumption, be it archeological or ethnographical.

Lindeberg (2009) used physiological evidence in an attempt to infer patterns of the human evolutionary diet from modern human physiology. He reviewed the literature concerning physiological requirements for minerals, vitamins, fat, and protein, and concluded that "*although some meat/fish must be consumed, available evidence suggests that the proportion of meat versus plant food has varied considerably during hominin evolution*." Lindeberg (2009) however did not attempt to support his hypothesis with archaeological data or additional physiological expressions of long-term adaptation.

Shipman and Walker (1989) employed a method combining physiological and behavioral evidence, to predict patterns that humans will have evolved to present if they were to adapt to become significantly predatory, and tested their predictions against the record. They predicted that humans would become much faster in locomotion, more social, develop dental or technological ways of slicing meat, develop longer small intestines and smaller colons, gain free time, have low population densities and shorter gestation, and so become more altricial. They found that all five predictions that could be tested were indeed present in the record to a certain degree and that three of the five were already present in *Homo erectus.*

The method of physiological inquiry adopted by Lindeberg (2009) was limited to nutritional components. Here the scope of the physiological inquiry is expanded to include genetic, metabolic and morphological elements. I reviewed literature for physiological phenomena, in which either the researchers themselves came to the conclusion that their findings represent evidence for a change in dietary patterns during human evolution, or from which a similar conclusion could be drawn. I Also performed a comprehensive review of the archaeological record that relates to the Paleolithic dietary DPA. The archaeological record concerning food consumption is vast, so it should be re-emphasized that I included only data from which inferences could be made regarding DPA.

The question of the DPA dietary ratio can also be conceptualized as stenotopy (specialization) vs. eurytopy (generalization) in *Homo* evolution (Wood and Strait, 2004). It is commonly agreed that *Homo* did not evolve to specialize in plant consumption, so evidence for significant plant consumption can be interpreted as an evolution towards eurytopy, and evidence for a high ratio of animal food as an evolution towards stenotopy. Of particular relevance will be evidence for adaptations that both enabled animal food acquisition and hindered plant food acquisition, following conclusion reached by Wood and Strait (2004) that "*The most compelling evidence for stenotopy consists of specialist features that exclude behaviors other than the preferred one*."

Indirect metabolic evidence will be discussed first and direct evidence later to see whether they agree or disagree with the primary hypothesis. However, before discussing the evidence, it is necessary to deal with what I believe is the source of a critical bias in DPA estimates of Paleolithic antiquity – Ethnography.

5.3 IS ETHNOGRAPHY A RELIABLE SOURCE FOR PREDICTIONS OF PALEOLITHIC PLANT-ANIMAL DIETARY RATIO?

The debate concerning the relevance of the ethnographical record as an analogy to Paleolithic era reconstruction is old and broad (e.g., Wobst, 1978:257; Wilmsen, 1983; Headland et al., 1989; Lee, 1992; Marlowe, 2010). This chapter tries to answer a very narrow question, which is rarely, if ever, discussed in the context of this debate, namely: does the ethnographic record of recent HG groups provides a scientifically sound analog for a Paleolithic DPA dietary ratio?

Stanford Encyclopedia of Philosophy (Bartha, 2016) defines an ‘analogical argument’ as “*an explicit representation of a form of analogical reasoning that cites accepted similarities between two systems to support the conclusion that some further similarity exists*”. The intention of this section is to explore whether accepted similarity exist between the Paleolithic and the recent period to support the conclusion that DPAs, similar to the ones recorded in ethnography, existed in the Paleolithic.

Ethnographic-based reconstruction of the Paleolithic diet is very appealing at first glance since it presumably relies on hard evidence, witnessed directly by observers of groups of hunter-gatherers (HG) who feed on natural resources (Crittenden and Schnorr, 2017). It is not surprising then that the ethnographic record is a popular information source for attempts to estimates Paleolithic diet compositions (Cordain et al., 2000; Marlowe, 2005; Kuipers et al., 2010; Fiorenza et al., 2011; Ströhle and Hahn, 2011; Kuipers et al., 2012; Zaatari and Hublin, 2014). In extreme instances (e.g., Hawkes, 2016) researchers rely on the present diet of a single recent HG group, like the Hadza of Tanzania, to elucidate the diet of early humans, some two million years ago.

Regardless of the specific DPA that these studies provide for individual HG groups, they claim to demonstrate that a wide range of DPAs was prevalent among recent HG groups. All the authors who tried to reconstruct the Paleolithic diet expressly claim, by analogy, that a wide dietary versatility, regarding DPA, could have existed in Paleolithic HG groups. If the notion that recent HG diets represent Paleolithic HG diets is valid than it provides support for the hypothesis that human evolution trended towards eurytopy, a generalization of food sources, as Ungar et al. (2006) and Hockett and Haws (2003) have suggested.

However, the ethnographical record may provide a false feeling of security in the DPA estimates. Methodological dietetic data gathering at the time of contact of ethnographic researchers with HG groups in previous centuries is entirely lacking (e.g., Lee, 1996). Dietary data is challenging to gather. A reliable data collection requires a multi-seasonal follow-up of a statistically significant number of women, men, and children, and entails weighing each dietary item before its consumption and translating the weight of the food item to calories. This level of data gathering was probably never carried out.

Amanda Lee (1996), who performed a comprehensive review of the literature on Australian aboriginal diets, states that little reliable information is available from the areas which were settled rapidly by Europeans starting 1788, and that reports from more remote and desert areas cover only short periods of time. About the Hadza, arguably one of the most systematically researched HG group, Woodburn (1968) admits that systematic calorie based subsistence data has not been gathered in the eight years since the beginning of his research in 1960. In many of the dietary reports in the Ethnographic Atlas (Murdock, 1967) it is not even clear in what terms, volume, weight or calories, the dietary consumption is reported (Cordain et al., 2000). It can, therefore, be assumed with a high degree of certainty that data collection and reporting of anywhere close to an acceptable scientific quality was never done at the time of contact with most HG groups during the 17th to the early 20th centuries. There is no doubt however that the dietary DPA of recently studied HG groups vary from plant to animal dominated diets.

However, even if data gathering of HG dietary history was reliable, two main questions must be answered in order to claim analogy to Paleolithic DPAs. The first question is what was the contribution of recent technological developments to the HG ability to acquire the observed DPA. The second question is whether the environmental conditions in present HG territories or more specifically the prevalence of large mammals, which affect the relative return on the acquisition of animal and plant food, are analogous to those that prevailed during the Paleolithic.

I first review the ecological changes that affected large animals' abundance, worldwide and in Africa.

Since plants have a higher potential of not showing up in the archaeological record, most claims for a highly variable Paleolithic DPAs, or indeed for highly plant-based diets during the Paleolithic, rely on the ethnographic record of HG groups with high plant food consumption (e.g., Hawkes, 2016). I, therefore, concentrate on reviewing the record of two of the most investigated HG groups with observed high DPA dietary ratio, namely the Hadza and the Ju/hoansi. The Ju/hoansi reside in the Kalahari, and the Hadza reside near the southern edge of the Serengeti, within 100 km from Olduvai Gorge, a fact which presumably adds credence to relations of analogy between the Hadza and Paleolithic humans (Marlowe, 2010:18; Hawkes, 2016).

Also, I shortly review the evidence for DPA among Australian Aboriginals. Australia is unique in that early-contact HG still used lithic based technology, had no contact with agricultural societies and no usage of iron, although, in contrast to most of the Paleolithic era, some groups used dogs for hunting starting some 5,000 years ago (Savolainen et al., 2004).

5.3.1 Changes in the abundance of large animals – implications for HG economy

Ranking of a prey animal by size, where larger animals top the list, is one of the most robust conclusions about food ranking in studies of recent HG groups (see review in Broughton et al., 2011). Post-encounter return rates rise substantially with animal size. According to Kelly (2013:Table 3-4.) the porcupine, a small animal that is often hunted by the Hadza, returns 2,152 Kcal per hour while middle size animals, such as caribou and white tail deer, return 6,050-31,450 Kcal/hr, or 3 to 14.5 times that of a porcupine. There are no data regarding the return rate of large and very large animals. However, the highest return is listed for black bear at 37,352-61,434 kcal/hr, i.e. up to 28 times that of a procupine. Barries and tubers return in thrange of 267 to 4018 calories per hour. Apart from the sheer return advantage, large prey animals may also be critical to humans' survival as a source of dependable fat. Humans are limited in the amount of protein they can metabolize to energy to about 35% of calories (Speth and Spielmann, 1983; Ben-Dor et al., 2016); they depend on a substantial supply of either carbohydrates (from plants) or fat or a combination of both. Larger animals pack more fat per bodyweight (Pitts and Bullard, 1967; Ben-Dor et al., 2011) and maybe more importantly, maintain more fat during periods of vegetation shortage (Lindstedt and Boyce, 1985).

The relative abundance of large animals is therefor an important factor with significant impact on the relative return of hunting vs. gathering.

A marked decline in the abundance of large size prey animals worldwide and in the territories of the reviewed groups, may be the most significant development that prevents an analogy of DPA of recent HG groups with Paleolithic DPA. Part of that decline is a local phenomenon that happened relatively recently due to the expansion of herding, agriculture and the extensive hunting of elephants and rhinos for foreign consumption. However, a significant part of this decrease occurred in the Late Pleistocene and was a worldwide phenomenon, known as LQE (The Late Quaternary Megafauna Extinction). About 90 genera of animals weighing >44 kg became extinct beginning some 50 Kya (Koch and Barnosky, 2006). The rate of extinction by body size follows a common pattern in which the largest size genera became more completely extinct. In all the continents, apart from Africa and the Indian sub-continent, all genera exceeding 1000 kg became completely extinct, and those in the 1000-320 kg became 50-100% extinct. In Africa, Some 25% of the African megafauna (>45 kg) became extinct during the late Quaternary (Faith, 2014). Some 50% of the over 3000 kg group became extinct and so did 30% of the genera in the next two size groups (>1000 kgs and >320 kgs) (Koch and Barnosky, 2006:Figure 1). The extinction, however, did not end at the Pleistocene-Holocen boundary and in fact continues worldwide with a current wave of extinctions that presumably started around 1500 CE (Dirzo et al., 2014), again disproportionally affecting larger animals.

The late quaternary extinction may not tell the full story of large animal extinction in Africa during the Paleolithic. Recently, Bibi et al. (2017) compared the faunal communities of Olduvai Middle Bed II at 1.7-1.4 million years ago (Mya) to faunal communiteis in the present day Serengeti near the Hadza territory. They concluded that "*The sheer diversity of species, including many large-bodied species, at Neogene and Pleistocene African sites like Olduvai is perplexing and makes extant African faunas look depauperate in comparison*". Indeed, they present a hypothesis, supported by the loss of carnivore diversity in the early Pleistocene, that human predation may have been the cause of the loss of large herbivores during the Pleistocene (see also Werdelin and Lewis, 2013).

Megaherbivores maintain vegetation openness, control fire frequency, and play a major role in seed dispersal (Johnson, 2009; Rule et al., 2012; Bakker et al., 2016; Hoag and Svenning, 2017). Their decline induces major alterations in landscape structure and ecosystem function including the degradation of savannas, thus decreasing the faunal carrying capacity of the environment and increasing vegetation carrying capacity to a significant extent. In Kruger Park the exclusion of herbivores for a period of 6 years in some areas caused a reduction of 38%-80% in bare ground (Asner et al., 2009). In the context of the African HG groups' environments, elephants have a particularly strong effect on vegetation and their exclusion may result in some 42% more trees (Kimuyu et al., 2014). Smaller herbivores often prefer grassland due to lower risk of ambush by predators (Bakker et al., 2016). This may also be true for humans and may have limited hunting activity, mainly to waterholes. Increased tree cover and vegetation could also have made locating prey more energy consuming while reducing the energy devoted to plant foraging and wood collection for cooking (Henry, 2017) that is essential for most of plant-foods' preparation (Stahl et al., 1984). Similar expansion of forest ecology took place worldwide during the early and mid-Holocene as a result of the megafauna extinction (Doughty, 2013), presumably with similar consequences to many HG groups worldwide.

5.3.2 The Hadza

Herders lived near the Hadza for many centuries. The Hadza do not make or use stone tools, a fact that is rarely mentioned, let alone dealt with, in the literature when Paleolithic a dietary pattern is deduced from their record. They have most probably relied on traded iron from neighboring farmers for at least 500 years since Bantu-speaking farmers arrived in the area (Marlowe, 2010:18). At the time of contact with European researchers, many of them were speaking their neighbors' language as a second language (Marlowe, 2010:16). Although in 1912 they are described as not having dogs, evidence from 1931-38 mentions that they keep dogs (Marlowe, 2002:Table 1)

5.3.2.1 *Ecological history*

Considerable ecological changes must have impacted the Hadza territory for many years before European contact due to the encroachment of the Bantu speaking herders some 500 years ago. 200-300 years ago Nilotic-speaking cattle herders, arriving from Sudan, gradually took over the best foraging spots (Marlowe, 2010:17,18). Herding may have an ecological effect over a larger area than the herding area itself through, for example, migration interruption and transmission of infectious disease (Fynn et al., 2016; Lankester and Davis, 2016). Marlowe (2010:17) cites a personal communication from Woodburn that indicate a significant increase in herders' presence during the 50's. To quote one example that Marlowe provides: "*The underground spring in Mangola that flows into Lake Eyasi and creates a large marsh with fertile soil has attracted people from various tribes who are now farming onions there*". Despite this, the Hadza still have camps around the spring and even continue to hunt game in the forest that surrounds the water. From exclusive exploitation of over 2500 km² at the time of the late 19th-century European encounter, they retained only 800-1000 km² by the beginning of the 1980s. By that time a further encroachment by Datonga herders took place with striking environmental effects, both on humans and particularly on wild ungulates, which were kept away from water holes. The Datonga's practice of digging large wells caused channel erosion during subsequent wet seasons, further decreasing the prevalence of natural water holes, which previously supported fauna during the dry season (O'Connell, 2006). Elephants were hunted for their tusks by foreign hunters for more than 100 years in this region until they became rare (Marlowe, 2010:19,30). Marlowe (2010:35,36) states that the availability of prey animals and specifically large animals in the Hadza territory diminished and suggested that historically they probably ate more meat. One of the most significant consequences of the diminishing prey, and especially diminishing larger prey, was that the three largest animals that were hunted in the past by the Hadza; rhinos, hippos, and elephants, are no longer hunted today (Marlowe, 2010:58). The significance of large animals to hunting yield is demonstrated by the fact that although the number of large and small animals hunted by the Hadza was approximately equal (Marlowe, 2010: figure 8.7), the contribution of large animals to the total weight of hunted meat was close to 90%. As will be discussed later in this work, a ranking of a prey animal by size, where larger animals top the list, is one of the most robust conclusions about food ranking in studies of recent HG groups (e.g., Broughton et al., 2011). In a wider perspective, megaherbivores maintain vegetation openness, control fire frequency, and play a major role in seed dispersal. Their decline induces major alterations in landscape structure and ecosystem function including the degradation of savannas, thus decreasing the faunal carrying capacity of the environment (Johnson, 2009; Rule et al., 2012; Bakker et al., 2016; Hoag and Svenning, 2017). Consequently, a diminishing larger prey must have had a profound effect on the environmental landscape of the Hadza and consequently on the energetic net returns of hunting versus foraging.

Women tend to specialize in activities that expose children to fewer hazards than other activities (Hurtado et al., 1992). Consequently, another effect that the diminishing large prey could have had on the Hadza is a decrease in the risk of predation while gathering due to the consequent diminishing population of large carnivores.

5.3.2.2 *Technology*

Researchers recognize that there are substantial technological differences between recent HG and Paleolithic groups (Marlowe, 2010:Table 4.2). Among the artifacts that Marlowe lists that did not exist in the Paleolithic, and that could conceivably affect the Hadza ability to obtain and consume a high quantity of plant foods one can count 1. Rubber tire soles, 2. Bow and arrows, 3. Iron arrows, 4. Metal knife, 5. Metal axe, 6. Metal chisel, 7. Metal hammer, 8. Metal needles, 9. Metal cooking pot.

The degree of contribution of each of these artifacts to an improved ability to obtain and process energy from plants, honey and animals are difficult to quantify. However, it may not be negligible. For example, the fact that Rubber tire soles are used may mean that they provide a significant advantage to the Hadza, presumably in improved walking speed over a rough terrain. In turn, more efficient exploitation of territories may improve the Hadza efficiency, regarding time and energy, in the acquisition of prey and plant foods.

Technology can help in coping with a scarcity of large animals by allowing an easier hunting of smaller animals. The Hadza hunted only with bows and arrows (Woodburn, 1968:51). In ethnographic settings, bows and arrows are used to hunt smaller, fleeting prey (Churchill, 1993). Bows and arrows became available relatively late in human prehistory, with the earliest claimed evidence of arrow points some 64 Kya in Africa and more widespread evidence during the UP (Backwell et al., 2008). The Upper Paleolithic and Epipaleolithic in the Levant, when presumably (based on projectile points morphology and size) bows and arrows were used, are associated with evidence of a reduction in the average size of hunted fauna and increased consumption of plant foods (Bar-Yosef, 2014:260,263). To this relatively late Paleolithic technology, the Hadza added the iron arrowhead. One can only speculate as to the advantages that access to iron tips accorded the Hadza regarding efficiency in hunting small animals and energetics. Several researchers have dealt with the substantial mobility considerations and energetic costs that were associated with a lithic economy (e.g., Jeske, 1992; Wood and Wood, 2006; Wilson, 2007; Browne and Wilson, 2011; Kuhn, 2014). It is logical to assume that doing away with the need to maintain a lithic economy allowed the Hadza to divert a significant amount of energy and time to other activities, possibly including food gathering and hunting of smaller prey with lower return rates. Apart from food acquisition, metal tools could also allow more efficient cooking and other forms of food processing (Lee, 1979:277).

One example of such food could be honey. Honey forms about 8% of the present Hadza diet (Marlow Table 5.3). Most of the honey is obtained from a bee species that live on the top of baobab trees that can reach 30 meters (9 stories) in height. In preparation for honey acquisition, the Hadza men cut pegs with the axe and set a fire. They then climb the tree while carrying the pegs, a torch, and a metal ax. With the help of the metal ax, which they also use to insert the pegs, they climb the tree. It is doubtful that honey acquisition could take place as efficiently with a stone axe that may need to be replaced or re-sharpened half way up.

A study of the prevalence of cavities among the Hadza supports the notion that honey was probably not consumed in the Paleolithic in high quantities. Comparing Hadza HG men with Hadza men who were engaged mainly in agriculture, Crittenden et al. (2017) found a significantly higher prevalence of cavities among the HG group. Both groups had a high prevalence of caries. They attribute the difference to the consumption of large amounts of honey by the Hadza HG men group. It is noteworthy that caries are very rare among Paleolithic human fossils. Humphrey et al. (2014) claim that the first evidence of extensive caries during the Paleolithic is found in the Grotte des Pigeons in Morocco and is dated between 15 Kya and 13.7 Kya. There, the researchers associate the high prevalence of dental caries (51%) with increased reliance on wild plants. Crittenden et al. (2017) review the ethnographic literature and find that contrary to the Hadza, the Aka, Mbuti, and Efe, men in the bush had better overall health than women. They attribute the difference either to age difference between the women and men study groups or to the fact that women in these groups may consume more plants (i.e., carbohydrates) in their diet than men. They conclude that part of the high prevalence of cavities in the Hadza HG group stems from consumption of honey

When applying Ethnography to Early Paleolithic circumstances, account must also be taken of the massive use that the Hadza make of fire. Fire arguably was not available to humans on a habitual basis before 400-300 Kya (Roebroeks and Villa, 2011; Shahack-Gross et al., 2014; Shimelmitz et al., 2014; Gowlett, 2016; but see Wrangham, 2016). The Hadza use fire for cooking, warming, roasting and honey gathering, using ten different type of fires (Mallol et al., 2007). Some plant food requires cooking for consumption, and extra energy is extractable from meat and plant food by cooking (e.g.,Wrangham and Carmody, 2010). It is quite apparent then that without the habitual use of fire, food exploitation of the Hadza would have been different.

5.3.3 The San Ju/’hoansi (!Kung)

The San and more specifically the Ju/hoansi are one of the most thoroughly researched HG groups in Africa (Lee and Guenther, 1993). They were at the center of the debate, known, among other names, as ‘The Great Kalahari Debate.' The debate discusses to what extent recent HG can be considered, for anthropological research, as a true example of traditional, autonomous HG. The ‘traditionalists’ side, epitomized by Lee (e.g., Lee, 1992), claimed with regard to the Ju/hoansi, that although they were “living under changed circumstances” (Lee and Guenther, 1993), they were sufficiently isolated from their pastoralist neighbors, to represent a pristine indigenous culture that is adapted to these changes. Because of their isolation, they could be studied anthropologically as a unit that fairly represents historical HG groups. The other side of the debate, epitomized by Wilmsen (e.g., Wilmsen, 1983; Mitchell, 2017), claimed that the Ju/hoansi have been so entangled with other, more modern, groups that they cannot represent traditional HG. In the eyes of the Wilmsen, they are also seen as an underclass in the framework of a much larger system of commodity capitalism.

Lee (1979) documented a high plant diet for the Ju/hoansi. Not much discussion was devoted to the effect of the ‘changed circumstances,' as Lee define them, on the composition of the Ju/hoansi’s diet. I will limit the discussion here, geographically to the northern part of the Kalahari where the Ju/hoansi lived, and only to parameters that could affect their DPA.

5.3.3.1 *Ecological history*

Lee’s research took place in the Dobe area at the northwest Kalahari Desert. In 1963, when Lee began his research, the area consisted of ten waterholes spreading over an area of about 8000 square kilometers. A fence, marking the border between Botswana and Namibia, was erected in 1965, cutting off about one-third of the area to Ju/hoansi foraging (Lee, 2012) and certainly also affected the movement of animals.

As of 1964, 340 Bantu people with several thousand heads of livestock were sharing nine out of the ten waterholes of the Dobe area with 460 Ju/hoansi. Some 28% of the Ju/hoansi worked for herders. There was a significant movement of people between the waterholes. Each year about 35% of the Ju/hoansi population spent time with other groups and 13% switched permanent groups (Lee, 1979:42,51,60). Lee claims that until the 1920's the Dobe area was occupied exclusively by Ju/hoansi. It is not clear however when this exclusivity began as there is archaeological evidence that compound HG-Pastoralists economies prevailed in the area already early in the first millennium AD (Denbow and Wilmsen, 1986; Robbins et al., 2005).

There is little doubt that herding diminishes hunting and gathering opportunities in the same area (Thomas et al., 2000). The introduction of cattle herding to the Dobe area must have had a pronounced effect on the area ecology. Lee (1979) quotes a 70-year-old, /Xai/Xai, Ju/hoansi man: "*When I was young the elephants, buffalo, and rhino were thick at /Xai/Xai. Before I was born white hunters would visit /Xai/Xai and shoot the elephants with guns*". Another witness describes the /Xai/Xai area as a place where he went hunting elephants, and in which hippopotamuses and waterfowl abounded. Today the area is a "*dustbowl*" in the words of Lee. On the effect of the arrival of pastoral herders to another San area, Malherbe (1983:36) writes: "*After a while the San noticed that livestock scared the game away, damaged the veldkos (plant food) and made the water dirty. Their own food supply decreased…*". The evidence may amount to a complete replacement of a fauna-rich ecosystem by a fauna-depleted ecosystem.

Major ecological changes may have occurred even before the introduction of herding in 1920 to the area (Lee, 2012:155). The Dobe area apparently was not at the center of the ivory trade that flourished during the second half of the 19th century in Africa. Nonetheless, reports of mass killing of elephants in the area by white hunters do exist (Lee and Guenther, 1993). Ju/hoansi hunted elephants in pre-colonial times for subsistence, while Lee's reports on present hunting techniques mention mainly smaller animals, the largest being a kudu (Lee, 2012:53,257).

5.3.3.2 *Technology*

The three most important hunting techniques that Lee (2012:53) describes use tools and technologies that were not available during the Paleolithic or a large part of it. All three help in the hunting of smaller animals. Bow and arrows with metal tips were used to hunt medium size animals like kudu and wildebeest. Dogs were used throughout the Kalahari to hunt smaller animals like Warthogs, steenbok, duikers, and hares but never big game except for gemsbok (Mitchell, 2008). Most hunters in Dobe owned dogs and hunting with dogs was the second most common means by which they obtained meat. Lee (1979) cites a Dobe hunter as saying that "*if you do not have dogs, you do not even bother to hunt warthogs*." Much of the hunting of the Ju/hoansi is done underground, pursuing borrowing animals to their lairs. Some of these animals are dug with the aid of a long pole with an iron hook at the end. Iron tips and hooks were not available during the Paleolithic and dogs, and bow and arrow were available only relatively late in the Paleolithic.

Also, Ju/hoansi have, at least since the 1920's, had access to iron knives and cooking pots, which are used in butchering, plant food processing, and cooking. In earlier periods they had access to clay pots (Lee, 2012:155,257). It is worth mentioning here that most of the Ju/hoansi plant food (mongongo for example) requires heavy processing before consumption, including cooking roasting and milling, in which metal tools provide an advantage over the stone tools of the Paleolithic, especially in the cooking (Lee, 1979:198). According to Hawkes and O'Connel (1981)'s calculations, for mongongo, a major food item for the Ju/hoansi, the caloric return per forager hour drop from 1900 kcal to 670 kcal when processing is taken into account. Presumably, the return would have dropped further if stone tools, instead of iron tools were used in the processing. Just for comparison, the return per hour on large prey is in the tens of thousands of calories (Stiner and Kuhn, 2009).

Stone mortars and hammerstones are also used in the preparation of about a third of the mongongo quantity (Lee, 1973). Grinding tools appear in Africa in the Middle Stone Age (MSA), much earlier than elsewhere. However they are mostly associated with the grinding of pigments (McBrearty and Brooks, 2000). Grinding and harvesting tools first appear in the Levant in the early Epipaleolithic at Ohalo some 23 Kya but become widespread only during the Natufian, 15.5-11.6 Kya (Groman-Yaroslavski et al., 2016). The earliest archaeological record of grinding stones in the Ju/hoansi area is dated to 12 Kya (Robbins and Campbell, 1990). The absence of an earlier record is explained by Robbins and Campbell as either a result of the small sample or a climatic change to a wetter climate which is not suitable for mongongo growth. In any event, it seems that the archaeological record in the area and other areas do not support comparable exploitation of mongongo nuts during the Paleolithic.

5.3.4 Australian aboriginals

Australia is, in theory, a more appealing ethnographic source for an analogy with Paleolithic diets. Local HG had never met pastoralists and farmers before contact with Europeans. They, almost uniquely among HG worldwide, were still practicing stone tool economy at the time of contact. However, in comparing the Australia record with a Paleolithic record, it should be noted that Australia has been devoid of megafauna during most of its human occupation. According to Rule et al. (2012), megafauna extinction in Australia has caused "*a replacement of mixed Rainforest by sclerophyll vegetation through a combination of direct effects on vegetation of relaxed herbivore pressure and increased fire in the landscape*." They note that this change may be indicative of the magnitude of that may have followed megafaunal extinction elsewhere in the world. Megafauna's extinction took place in most of the world during the late Pleistocene and early Holocene (Koch and Barnosky, 2006; Faith, 2014; Sandom et al., 2014). As previously discussed, megafauna's extinction may influence the DPA dietary ratio in the direction of the reduced animal component in the diet due to the reduction in the availability of highest ranking food items in the environment.

The Ethnographic Atlas (Murdock, 1967) which serves as a source for data in some of the recent HG diet reconstruction attempts (Cordain et al., 2000; Marlowe, 2005) list four of nine Australian aboriginal groups as having a higher plant component than an animal component in the diet. However, Amanda Lee (1996), who performed a comprehensive review of the literature on Australian aboriginal diets, states that little reliable information is available from the fertile temperate seaboard areas, which were settled rapidly by Europeans starting 1788, and that reports from more remote and desert areas cover only short periods of time. The limited quantitative data she could find was from studies of groups that reverted to traditionally-oriented lifestyles for experimental purposes for a small number of days. Amanda Lee (1996) concluded that, contrary to previous assessments, aboriginal diets were meat-oriented with vegetable foods providing an important supplement rather than an alternative to animal foods.

5.3.5 Section conclusion

The purpose of this chapter was to review the scientific validity of inferring dietary DPAs during the Paleolithic by analogy with ethnographic HG data. Worldwide and African ecological changes that affected the megafauna and flora of the two environments that are presumed to analogical were reviewed. The ethnographic record of two of the most extensively studied recent HG groups that obtain most of the calories from plants was reviewed. Major discrepancies were found in the ecological and technological aspects of the purported analogy of recent conditions with the Paleolithic circumstances. The review leads to the conclusion that key determinants of the DPA dietary ratio, namely ecology, and technology, fail to show the analogy between the “known” and inferred period. The accurate dietetic record for time of contact of HG populations with non-HG populations, as well as more recently with Europeans, is lacking. A partial devastation of the historical and prehistoric environment and the diminishing populations of very large prey animals appear concomitantly with relatively recent Paleolithic and post-Paleolithic technological innovations like bows and arrows, dogs and iron tips that appear to contribute to the efficiency of the acquisition of smaller animals. At the same time, relatively recent technological innovations like tire sandals, metal axes, and metal cooking pots may contribute to the efficiency of the acquisition and preparation of plant food. These changes put into question the usage of the ethnographic record as a scientifically valid source of information for the estimation of a dietary DPA in Paleolithic diets. In Australia, which due to its isolation, may serve as a more robust model for Paleolithic conditions, typically, no detailed reports of early contact diets exist. A review of the literature concludes that, contrary to some of the information in the Ethnographic Atlas, diets were meat dominated.

A more general conclusion that can be drawn from this chapter to other parts of the world is that megafauna’s extinction, which took place during the late Pleistocene and the Holocene at most of the world, may have created a profound deviation from the Paleolithic environments of most of the HG groups worldwide and consequently in the net return on hunting activity. Since at least some of the technological innovations that were mentioned here were also available to many recent HG groups worldwide, it may be concluded that, both from an ecological and a technological perspective, there is good reason to doubt the applicability of recently measured dietary DPAs in HG groups to the prediction of Paleolithic DPAs.

Methods which I consider to be more useful and valid for that purpose will be described henceforth.

5.4 PLANTS AS A DIETARY SOURCE OF ENERGY

Before listing results of physiological indirect evidence, it is necessary to define the major Paleolithic source of energy from plants, as its metabolism is most relevant to our inquiry.

Most plants store most of their energy as carbohydrates, although some seeds contain significant quantities of fat and even protein (Stahl et al., 1984). The carbohydrates appear in three distinct chemical forms that are metabolized in the body to energy in three different ways. Simple sugars are shuttled to the cells for direct exploitation, while starches, which are complex sugars, first need to be degraded into simple sugars by a specific enzyme (amylase). The third form, fibers, which are too complex to be degraded by human enzymes, are fermented in the large intestine by bacteria. Short-chain saturated fatty acids, which are the by-product of this fermentation, are shuttled through the intestinal wall to the blood and the cells to be used for energy. It can be safely said that primates, australopithecines, Paleolithic humans, and post-Paleolithic humans all consumed plants. However, the relative amount of energy that they received from the various carbohydrate types must have been significantly different. As shown in the example in Table 2, chimpanzees obtain most of their energy from fiber and simple sugars, but not from starch. The early hominin diet is unknown but probably relied to a large extent on the fermentation of fiber, in addition to seeds, nuts and possibly starch from tubers, most of which are also quite fibrous. Post-Paleolithic humans who relied on a plant-based diet obtained a large part of their diet from seeds (mainly starch), nuts, and less so from tubers (starch), fiber, and simple sugars (Kuhn and Stiner, 2001). Consequently, when a claim for a high proportion of plant-sourced food throughout human evolution is made (e.g., Bar-Yosef, 2014), its validation will require a consideration of which of the three types of carbohydrates was presumably consumed in large quantities? Was it fiber, simple sugars or starch? It is quite clear that the human mastication apparatus and gut were not suitable to process large quantities of fiber (Aiello and Wheeler, 1995; Wrangham et al., 1999; Milton, 2003; Ungar, 2004). It is also clear that simple sugars, which are found in nature mainly in fruits and honey (Stahl et al., 1984), could not be counted on as a dependable, year-round, significant source of calories, once hominins got off the trees (Milton, 2003). Despite periods of superabundance, frugivores do compete for most of the year for fruits (Fleming, 1979). In the savanna food for frugivores is scarce and widely distributed, and this is the case especially for ripe fruit which contains more carbohydrates in the form of sugars than in the form of fiber (Pruetz, 2006). As shown in Table 2, even with the competitive advantage of being on the trees, simple sugars still supply only approximately a third of the calories in the chimpanzee's diet, so they rely on a significant capacity to process and metabolize fiber to energy. This paucity of sugars in the environment leaves starch as the only candidate for a potentially sizable amount of carbohydrate/plant-sourced calories during human evolution. The starch that is available year-round is rare and found mostly hidden underground, stored in roots and tubers, and in sedges (Hardy, 2010; Dominy, 2012). Seeds and legumes also contain starch and other macronutrients, but they are more seasonal, vary widely in yield between seasons (Abbo et al., 2008), and require intensive processing, for which there is no evidence before the LUP (Kuhn and Stiner, 2001; Bar-Yosef, 2014). This must be the reason that researchers proposed roots and tubers, otherwise named underground storage organs (USO), as a major plant food item for Paleolithic humans (Peters et al., 1984; Piperno and Holst, 1998; Wrangham et al., 1999; Hardy, 2010; Henry et al., 2014; De Vynck et al., 2016). However, because plant evidence is poorly preserved, most of the evidence indicates potential rather than actual consumption. Wrangham et al. (1999) originally developed the cooking hypothesis to explain how humans, with a smaller gut and mastication apparatus, could process enough USO starch to provide sufficient energy for a growing brain. Hardy (2010) postulated that there are enough USOs year-round to supply plenty of energy to humans. Hardy et al. (2016) and Henry et al. (2014) located starch residues in teeth plaque, which proved that humans ate USOs or sedges. However, finding starch in teeth plaque, like finding animal bones in archaeological sites, is not sufficient to determine the proportion of starch consumption.

In summary, evidence for and against the significant year-round plant-sourced carbohydrates consumption and its relative contribution to the diet during the Paleolithic should focus on starch consumption.

5.5 INDIRECT METABOLIC EVIDENCE FOR DEPENDENCY ON TYPES OF FOOD IN HUMANS.

This section reviews morphologic, metabolic, and genetic phenomena in humans that can point to adaptations to carnivory and starch consumption. Starch, as explained in the previous section, is what we should look for when we look for signs of adaptation to high plant consumption during the Paleolithic. In some instances, the timing of the adaptation is not known, and in many cases, some interpretation is required to assign a phenomenon to one of the two sides of the DPA. For this reason, it is important to look at the totality of the indirect metabolic evidence and direct evidence from the various scientific fields that are reviewed in this work. A summary is presented in Table 5.

5.5.1 Energy

The basic metabolic constraint in any animal is energetic. The body is limited in the amount of energy it can produce, and there is a strong association between body mass (BM) and basal metabolic rate (BMR) (Kleiber, 1947; Hudson et al., 2013). Recently, Pontzer (2015) found that in humans, even TDEE is highly regulated within a narrow range, meaning that a high energetic expense, in mobility, for example, is compensated by lower energetic expense for body maintenance functions. Pontzer et al. (2016) also found that humans have higher TDEE than expected from their body mass, reaching an additional 400 calories per day, when compared with chimpanzee of the same body size. It seems then that humans were under strong selective pressure to supply adequate and consistent energy to their bodies and especially to their brains. The need for consistency is evidenced by the higher fat reserves in humans (Pontzer et al., 2016). This adaptation will be discussed in more details in Section 5.5.7. In this context, it seems highly useful to ask which food source, plant or animal, was more reliable, more energy-efficient to acquire, to prepare, to consume and digest. In general, animal-sourced calories are more efficiently acquired, and thus carnivores spend less time feeding than herbivores of the same size (Shipman and Walker, 1989). Stiner and Kuhn (2009) reviewed published data on the energetic yield of acquiring various food sources by humans. Acquiring and consuming large animals, at 63,398 kJ/hr, was found to be 6 to 33 times more time-efficient than acquiring and consuming roots and tubers, at 10,412-1882 kJ/hr, and 10 to 18 times more-efficient than acquiring and consuming seeds and nuts, at 6508-3520 kJ/hr. Given the discussion in Section 5.3 with regard to ethnography as a source of estimates of DPA dietary ratios during the Paleolithic, it should be noted that since Stiner and Kuhn (2009) relied on post megafauna extinction ethnographic data, it is highly likely that their sources for energetic yield on the acquisition of large animals did not include megafauna and possibly included data from areas with reduces populations of other large animals. It also must have included plant energetic yields estimates that relied to some extent on processing with metal tools. Both factors will tend to lower the energetic return on large animals while increasing the return on plant food compared to Paleolithic conditions. Moreover, the seasonal fluctuations in the availability of many plant species should also hamper long-term reliance on plants for a significant portion of the diet. In contrast, animals are always available though their fat content may fluctuate. Statements regarding the unexpected, fluctuating nature of animal hunting return (Hawkes et al., 1991) rely, as is often the case, on ethnographic anecdotes from areas of groups like the Hadza. As was shown in Section 5.3, the Hadza were hunting in an area with radically changed ecology compared to the Paleolithic, with reduced populations of megafauna and other large animals.

5.5.2 Vitamins

Findings that diverse diets increase overall health patterns by lowering infant mortality rates and increasing average life expectancy were used by Hockett and Haws (2003) as a basis for a hypothesis that the basic tenant of the ancestral human diet was its diversity. Presumably, the wide range of vitamins and minerals that are associated with diverse diets is advantageous. A further hypothesis (Hockett and Haws, 2005) that stemmed from these findings was that the more diverse diet of AMH in Europe during the MP-UP transition provided them with better health and thus a survival advantage over Neandertals that could have been the reason for the demise of the Neandertal.

The relevancy of the initial findings, cited at Hockett and Haws (2003) to the Paleolithic is questionable. These findings relate to modern societies living on an agricultural, mostly plant-based, diet. Diversification may, in this case, actually show benefit due to the increase of the animal portion of the diet. Kenyan schoolchildren on a high plant diet who received meat supplementation improved growth, cognitive and behavioral outcomes (Neumann et al., 2007).

Hockett and Haws (2003) list in Table 1 the content of key vitamins in 100 grams of plants compared to various animal foods (Vitamin C, Thiamin, Riboflavin, Niacin, B-6, B-12, A, Folate, D, E). Comparison of the vitamin density (per 100 calories) between terrestrial mammals and plants shows that in eight of the ten chosen vitamins, terrestrial mammals' food is denser, and in most cases several times denser, than in plants. This result is not surprising if we consider that we are also terrestrial mammals, containing basically the same chemicals and requiring mostly the same vitamins.

Plant food is denser in vitamin E and C, however it is well known that Polar societies did not suffer from scurvy despite a lack of significant plant component in their diet (Thomas, 1927; Draper, 1977; Fediuk, 2000). Western individuals who spent several years among polar populations also did not show signs of vitamin shortage (Stefansson, 1960:171). A controlled follow up of two of these individuals on an exclusive meat diet for a year, while in the U.S., didn't reveal any clinical signs (McClellan and Du Bois, 1930). Levine (1941) found, based on his own measurements and those of others, that freshly killed muscle meat of reindeer and seal contain 2-3 milligrams vitamin C per 100 grams. According to his calculations, based on the amount of meat they consume, Eskimo and northern Indians would have no problem in attaining sufficient vitamin C quantities. According to the glucose-ascorbate antagonism (GAA) hypothesis (Hamel et al., 1986), given the structural similarity between glucose and vitamin C, the two molecules compete for the same transport system to enter cells (Wilson, 2005). Thus, higher requirements for vitamin C in the western population may be the result of the higher consumption of carbohydrates and the consequent higher blood glucose level. Two clinical studies comparing diabetic patients to non-diabetics did show, as predicted by the GAA hypothesis that diabetic patients with higher blood glucose levels have decreased levels of plasma ascorbic acid (Cunningham et al., 1991; Fadupin et al., 2007).

It therefor seems that the evidence does not support Hockett and Haws (2005) hypothesis that "*diverse diets in the form of energy-rich animal foods and micronutrient-rich plant foods may also help explain the early success of hominids*." It is very likely that Paleolithic diets were higher in plants than polar diets. However, the significantly higher nutrient density of animal food, compared to plant food, and the evidence for the healthy life of humans on a very low plant diet lead to the conclusion that energetic considerations and not micronutrient considerations dictated food acquisition behavior during the Paleolithic.

5.5.3 Stomach acidity

The Proper acidity of the stomach is an essential requirement for the initial digestion of any food. With regard to meat, high acidity is needed to neutralize external pathogens, denature proteins, and activate enzymes that enable digestion of proteins into amino acids. Beasley et al. (2015) compared stomach acidity across trophic groups. They found the lowest acidity (high pH) in herbivores, and an increasing trend towards higher acidity in omnivores and carnivores, peaking in scavengers. Humans, although usually considered omnivores, had the highest acidity among the 43 reviewed mammals at a pH of 1.5, identical to ferrets which are carnivores, and to possums, which are facultative scavengers. The average pH in omnivorous primates in the sample (N=4) was 3.2 and the average in mammalian carnivores (N=7) was 4. The acidity of the stomach is created by the secretion of acid solution into the lumen of the stomach. The process involves the action of an enzyme, gastric H_/K_-ATPase. With the aid of the hormone gastrin, the maximum volume of acid secretion occurs after a meal, reducing the pH in humans to 1 (Gennari and Weise, 2008). This pattern proves that maintaining acidity is an energy costing process so the adaptation to high acidity in human must have been a subject to natural selection and not drift (Gennari and Weise, 2008). Beasley et al. (2015) speculate that carrion feeding with its high load of pathogens was more important in human evolution than is currently considered. Another possible explanation, however, is that humans, as opposed to other carnivores, transport and guard their prey in a central place and are therefore able to consume it over a number of days, during which the density of pathogens in the meat increases. A common African prey animal such as the buffalo contains about 500,000 calories (Ben-Dor et al., 2011), so its acquisition could sustain a typical group of HG for about seven days (30 people at 2,500 calories per person). Moreover, fermentation and deliberate putrefaction of meat, fish, and fat is a common practice among northern populations who rely on hunting for a large portion of their diet (Speth, 2017). Neandertals show a seasonally intermittent use of fire to the extent that some researchers even hypnotized that they were unable to start fires (Dibble et al., 2017). It may, therefore, be that the ability to consume highly petrified food was a common requisite during the Paleolithic. To summarize it could be hypothesised that the high stomach acidity enabled reliance on the acquisition of large animals.

5.5.4 Adipocyte morphology

Another indication for a strong tendency towards carnivory in human evolution comes from the morphology of adipocytes (fat cells). Ruminants and carnivores, which absorb very little glucose directly from the gut, have four times the number of adipocytes per adipose unit weight than non-ruminants, which feed on carbohydrates. Humans have about three times the number of adipocytes (25 - $60\,x\,10^9$) predicted for carnivores ($8.08\,x\,10$^9) and eight times those of non-ruminant, carbohydrate-feeding mammals (Pond and Mattacks, 1985). Nomadic East African humans have 6-12% body fat compared to approximately 5% for other animals (Pontzer et al., 2015). To normalize the data to typical mammals' body fat we need to divide the number of actual adipocytes by 1-3 (6% to 12% divided by 5%). Taking the higher product, 3, humans fall squarely within the carnivores' pattern of adipocyte morphology. Pond and Mattacks (1985) sum up their finding as follows: "*These figures suggest that the energy metabolism of humans is adapted to a diet in which lipids and proteins rather than carbohydrates, make a major contribution to the energy supply*".

5.5.5 AMY1 gene

As previously discussed, plant consumption during the Paleolithic should manifest itself in increased consumption of starch rather than of simple sugars and fiber. Therefore the level and timing of adaptation to the consumption of starch can provide a strong indication with regard to the consumption of plants during the Paleolithic. Amylase is used in the degradation of starch to glucose, the form in which it is metabolized to energy by the cells. A significant evolution of amylase-producing genes in *Homo* species was discerned by Vining and Nunn (2016) although the temporal dynamics of this evolution could not be determined. The number of copies of the human gene AMY1, which produces salivary amylase, is one such evolutionary adaptation. The copy number of the AMY1 gene corresponds to the quantity of amylase in the saliva (Perry et al., 2007; Alberti et al., 2015; Perry et al., 2015). Carnivores have little salivary amylase, and the AMY1 genes are contracted, whereas omnivores have relatively large quantities of salivary amylase (Boehlke et al., 2015; Kim et al., 2016). Thus, the placement of humans on the continuum between obligate carnivores and plant-dominant omnivores during *Homo* evolution could potentially benefit from the study of the AMY1 gene in humans.

Individuals from human populations that consume high-starch diets have, on average, more copies of the gene than those that consume little starch (Perry et al., 2007), although the distribution around both averages is widespread, ranging from 2 to 16 copies. Neandertal and Denisovan samples have been found to have only two copies (Perry et al., 2015) though only few samples were tested. Perry et al. conclude from these findings that the common ancestor of Neandertals and *H. sapiens*, some 500-600 Kya, also had only two copies. Their conclusion is supported by Inchley et al. (2016), who added that the appearance of multi-copy AMY1 genes in *H. sapiens* probably took place quite early after the split from the Neandertals. Chimpanzees also have two copies (Perry et al., 2007), which is commensurate with a diet composed mainly of fruits (simple sugars and fiber) and low in starch.

A low AMY1 gene copy number was found to be associated in modern humans with obesity, insulin resistance, and risk of diabetes (Mandel and Breslin, 2012; Falchi et al., 2014; Choi et al., 2015; Mejía-Benítez et al., 2015). It should be noted that in a large study Usher et al. (2015) didn't find any association between AMY1 copy number and obesity. Also, a mechanism for the proposed beneficial effect of increased salivary amylase in high starch consuming populations has yet to be described. Thus, we can only carefully speculate that a low copy number in pre-*sapiens* may indicates a low-starch diet in early *Homo* species. The wide copy number distribution around the mean in high-starch-consuming populations investigated by Perry et al. (2007), suggests that even in those groups the adaptation to a high-starch diet is not yet complete (fixed) so is most likely quite recent, if indeed natural selection is at work. An analysis of a 7,000-year-old Mesolithic human from La Brana-Arintero, Spain (Olalde et al., 2014) found a relatively low number of 5 AMY1 copies, which is equal to the median copy number in present populations that consume a low-starch diet. An analysis of three additional humans from present-day Germany from that same period determined a low copy number for two humans (5, 6) but a high copy number for one (13), indicating that by that time high starch consumption may have existed in some HG groups (Lazaridis et al., 2014) or that the nature of the association of AMY1 copy number with high starch consumption is yet to be elucidated. In this connection, it is worthwhile noting that dogs start to show an increase in copy number of a gene (AMY2B) that is responsible for pancreatic amylase. The researchers interpreted the change as an adaptation to a starchy diet. At that same period (7000 BP) in Southwestern Europe (Ollivier et al., 2016) and other parts of the world, commensurate with the development of farming communities, and not with their domestication, which took place earlier (Arendt et al., 2016). Since humans were responsible for feeding the dogs, it may mean that meat was easier for humans who owned dogs to obtain than starch until that period. The physiological ceiling on the consumption of protein in humans is a probable reason that until the beginning of agriculture lean meat, which contains mainly protein and less fat, was in surplus and could be fed to the dogs, while starch and fat were scarcer.

It is quite probable that early hominids consumed tubers, roots, and sedges that included starch (Conklin-Brittain et al., 2002; Ungar and Sponheimer, 2011; Dominy, 2012; Cerling et al., 2013). However, unlike humans, Australopithecine probably retained their predecessor's large colon (Aiello and Wheeler, 1995), and had a well-developed mastication apparatus that enabled them to utilize the significant quantities of fiber (Conklin-Brittain et al., 2002) in undomesticated tubers (Schnorr et al., 2015), in addition to starch. If we accept the notion that AMY1 copy number is an indication for adaptation to high starch diet, the evidence of low AMY1 copy numbers in pre-*sapiens* humans weakens the support for the need for cooking in order to consume starch from USO's in early human evolution, as proposed by Wrangham et al. (1999).

It should be noted, however, that as expected from our primate ancestry, humans were genetically adapted to the consumption of carbohydrates, particularly in the form of sugar, not starch, and there are genetic indications that they became more so during the Upper Paleolithic and the Mesolithic (Pontremoli et al., 2015: Figure 5). It should also be noted that the body readily produces sugar (glucose) from proteins, so genetic adaptation to sugar metabolism does not necessarily mean a higher carbohydrate component in the food and may reflect increased consumption of protein. An indication of low AMY1 copy numbers during part of human evolution does not preclude the possibility of a significant consumption of sugars in the form of honey and fruits during the Paleolithic. However, as discussed, undomesticated fruits contain much more fiber than sugars, and honey acquisition in present-day HG is mostly associated with the use of fire (smoke), which was most probably not available to early humans, and the use of iron axes when climbing very tall trees and opening the honeycomb (Marlowe, 2010:116). Also, both fruit and honey are seasonal in their availability, In summary, examination of the AMY1 gene history may support a limited consumption of starch, and therefore of plants, in the diet of pre-*H. sapiens* humans and Neandertals. If we accept a tight association of AMY1 copy number and starch consumption, there is an indication, that *H. sapiens* consumed more starch than Neandertals quite early after the split 500-600 Kya (Perry et al., 2015). At this stage, however, it cannot be determined how much more starch *H. sapiens* consumed.

5.5.6 Fat metabolism

The lipase enzyme plays a dominant role in the storage and metabolism of fats. Comparing the pace of genetic changes between humans and other primates, (Vining and Nunn, 2016) found that lipase production underwent substantial evolution in humans, based on one of their models, while in the other it was found to be almost significant at a $p = 0.06$.

In this connection, it is interesting to note that Weyer and Pääbo (2016) found some indication that both the regulation and activity of the pancreatic lipase have changed in modern humans when compared to Neandertals and Denisovans. Since Neandertals probably consumed a diet higher in meat and fat than that of modern humans, it may indicate that modern humans were becoming adapted to a lower consumption of fat. However, these changes are found in present-day humans and there is no indication of how early in *H. sapiens*' evolution they took place. These changes could be a result of a shift to a diet higher in plants in the period leading to the adoption of agriculture, in which a marked increase in genetic changes is evident (Hawks et al., 2007). It should also be noted that storage of higher fat reserves is a derived trait in humans, regardless of the source of nutrition (Pontzer, 2015), so a change in the capacity to metabolize fat may not necessarily point to a change in dietary source. In addition, high-fat diets are not exceptional in human ancestors, past and present, who relied on the fermentation of fiber to short-chain fatty acids (SCFA) for a good portion of their diets (see Table 2 for chimpanzees). Although SCFA metabolism is not identical to medium- and long-chain fatty acids, they do share some processes like beta-oxidation (Wang et al., 2014)

Another aspect of fat metabolism that has received much publicity is the theory that the enlargement of the early human brain was made possible by the acquisition of aquatic foods. Presumably, these foods were the only source that could supply the high amount of docosahexaenoic acid (an omega-3 fat, DHA) found in the expanding human brain (e.g., Crawford, 2010; Cunnane and Crawford, 2014; Kyriacou et al., 2016). In contrast, Cordain et al. (2002) argued that terrestrial animals' organs contained sufficient amounts of DHA for a growing brain. Furthermore, Speth (2010:135) showed that humans have the capacity to biosynthesize enough DHA de novo from precursors. This last argument is supported by the present existence of billions of people, including some in HG groups, who haven't seen or eaten an aquatic sourced food in their lives, yet they and their children were able to grow a brain that is much larger than early humans' brains. Since a large part of this population does not consume a high proportion of animal food, an increased need for DHA for a large brain cannot even be used to support a diet based on terrestrial animals in early humans. In as far as Neandertals are concerned, stable isotope analysis shows that at least some of them did not consume aquatic dietary resources (Richards and Trinkaus, 2009), although their brain was at least as large as that of modern humans. Even some late Paleolithic, Epigravettian human groups did not consume aquatic dietary resources, despite living on an island (Mannino et al., 2012).

Mathias et al. (2012) have identified a genetic change that took place among African humans about 85 Kya in a genes family known as FADS that shows an increase in the efficiency of converting plant source omega-3 fatty acids to DHA. The change may signify an increase in the plant component of the diet at that time in Africa. In Europe however, a similar change took place only with the arrival of the Neolithic (Ye et al., 2017), suggesting that a plant-based diet was not common beforehand. In fact, Ye et al. found that in Europe, the positive genetic selection was in the opposite direction in HG in the period leading to the Neolithic which may signify increased reliance on aquatic foods. The sample of pre-Neolithic HG also included Neandertal aDNA, but no specific reference to its result is made.

5.5.7 Higher fat reserves

Some Researchers argue against a probable massive reliance on animal acquisition during the Paleolithic due to its erratic nature (Hawkes, 2016). Some have interpreted food sharing in HG societies as a behavioral adaptation to the erratic nature of animal acquisition (e.g., Hill and Hurtado, 1989; Gurven and Hill, 2006; Grove, 2010). In this context, higher fat reserves in humans can be interpreted as physiological adaptation to reliance on animal acquisition. Comparison between captive chimpanzees, bonobos, and Western human population found body fat reserves of humans to be two times (males) to four times (females) higher (Pontzer et al., 2016:Table 1). Typical HG fat reserves allow many weeks of complete fasting. For example, Pontzer et al. (2015:Table 1) measured Hadza males' and females' TDEE and fat reserves. Assuming nine calories per gram of fat, one arrives at six weeks reserve for women and three weeks reserve for men. Most researchers see the higher fat reserves in humans as necessary because of the high energetic demands in general and the brain's energetic demands in particular (Leonard et al., 2007; Cunnane and Crawford, 2014; Pontzer, 2017). However, the high fat reserve can just as easily be attributed to a high reliance on unpredictable, animal-based dietary resources by bridging unsuccessful hunts with fasting on higher fat reserves. Short periods of fasting or low caloric feeding seem, in fact, to be advantageous to human health, leading to increased autophagy, a vital cellular process which is responsible for the recycling of defective proteins and organelles in the cell (Masiero et al., 2009; Alirezaei et al., 2010; Jeong et al., 2016).

5.5.8 APOE gene

APOE is a protein that circulates in the plasma and is present in the central nervous system, helping to regulate cholesterol and lipid metabolism, as well as aiding cellular reparative processes. The APOE 4 allele, which is prevalent today on average in 15% of the population, is considered the early human allele and is associated with an increased risk for Alzheimer, stroke and cardiovascular diseases (Finch, 2012). It is different from the chimpanzee APOE gene. At 226 Kya (range 180-580 Kya) (Finch, 2012) a new allele evolved - APOE 3, which although not identical to the chimpanzees APOE, is expected to resemble it in function more than APOE 4 (Finch and Stanford, 2004). Finch (2012) argues that the APOE allele confers a reduced risk of these diseases because it represents an adaptation to a higher meat diet in the *H. sapiens* who became better at hunting. Raichlen and Alexander (2014) argue, however, that as extended longevity began as early as 1.8 Mya when APOE 4 was the prevalent allele, it was the increased physical activity that enabled a mitigation of the deleterious effects of the APOE 4 allele, regardless of the diet. The distribution of the frequency of the APOE 4 allele in human populations around the world follows a U-shaped latitudinal gradient, with the highest frequencies (up to approximately 40–50% of the population) in equatorial and high latitudes (Eisenberg et al., 2010). If we accept that these two regions had different historical diets, one high in meat and one arguably lower in meat (Cordain et al., 2000), the association between APOE alleles and diet as claimed by (Finch and Stanford, 2004) seems to be weak. A U shaped latitudinal gradient is also not expected if we assume that high meat diet was prevalent across all latitudes. Moreover, It has been shown recently (Trumble et al., 2016) that under a heavy pathogen burden, as expected with a consumption of a single large animal over days, the APOE 4 allele preserves cognitive functions, further supporting its probable usefulness even in conditions of high-fat diets.

5.5.9 Insulin resistance

Another hypothesis that claims a genetic predisposition in humans to a carnivorous, low-carbohydrate diet is known as ‘the Carnivore Connection.' It postulates that humans, like carnivores, tend to have low sensitivity to insulin (Brand-Miller et al., 2011) although not as low as that of carnivores (Schermerhorn, 2013). Brand-Miller et al. (2011) speculate that insulin resistance allows humans on a low-carbohydrate diet to conserve blood glucose, and to feed an energy-hungry brain. The genetic manifestation of insulin resistance is complex and difficult to pinpoint to a limited number of genes (Moltke et al., 2014), however recently Ségurel et al. (2013) were able to ascertain a significantly higher level of insulin resistance in a Central Asian population (Kirghiz) of historical herders, compared to a population of historical farmers (Tajiks), despite both groups being presently on a similar diet. Their findings indicate that there is a genetic predisposition to a high level of insulin resistance among groups that consumed mainly animal-sourced foods. Additionally, a significant difference in the prevalence of insulin resistance is found, between groups who had long-term exposure to agriculture and those that hadn’t, like Australian aborigines, who have higher insulin resistance. If indeed higher insulin resistance is ancestral, the fact that it endured in the past suggests that a high consumption of carbohydrates (starch, sugar) was not prevalent.

5.5.10 Taste

The sense of taste informs the organism about the quality of the ingested food, possible toxins, and its desirability. As such it is an attractive candidate to elucidate dietary changes during human evolutions. However, review of the literature provides only a few hints about the Paleolithic dietary DPA.

Loss of taste receptor function is considered to be directly related to feeding specialization (Jiang et al., 2012). Relying on genetic data, Wang et al. (2004) report a loss of function in humans for some of the TAS2Rs group of genes that enables the recognition of a bitter taste. Since bitter taste is typical of toxins in plants, Wang et al. (2004) speculate that the loss of function of these genes is a result of the reduction in consumption of plants during human evolution as well as the introduction of cooking. Wang et al. (2004) date the change to 0.75 Mya with a large margin of error of 0.1-2.5 Mya. Fujikura (2015) also found a loss of function of genes for bitter and sour taste but with extreme polymorphism among and within present human groups. Since a similar loss of function was not found in the Neandertal and Denisovan samples, Fujikura concludes that it must have happened after the speciation of AMH. He raises the possibility that cooking with its effect of neutralizing toxins could have been a cause for the loss of function of these taste genes. Wooding et al. (2006) Found that the genes that encode one of the receptors for a bitter taste are different in chimpanzee and humans. They conclude that although both share taste sensitivity to bitter taste this sensitivity has arisen twice. It can, therefore, be that this receptor was once lost during the evolution of humans and then regained. If this evolutionary path is accepted, it is commensurate with a decline in the importance of plant food with the evolution from the common ancestor of chimpanzee and humans and then an increase in the importance of plant food sometime during human evolution.

Fujikura (2015) points out that unlike in some carnivores, genes for sweet taste have not undergone a loss of function in humans. This genetic evidence then points to a possible preservation of fruits and honey as components of the human diet throughout human evolution.

Indicatively, Fujikura summarizes by saying that "the relationships among taste perception, polymorphism, and dietary choices still remain unclear".

Another recent finding is the existence of a unique taste for fat (Tucker et al., 2014; Running et al., 2015) which is not unique to humans (Degrace-Passilly and Besnard, 2012). The chronology of the evolution of fat taste in humans is not known so not much can be said at present regarding the significance of this discovery to the reconstruction of the dietary DPA.

5.5.11 Neu5Gc

Recently, a group of researchers (Samraj et al., 2015) used a derived genetic trait that developed in humans 2-3 Mya to claim that humans are poorly-adjusted to the consumption of red meat. They asserted that a compound found in red meat, *N*-glycolylneuraminic acid (Neu5Gc), can cause cancer and chronic inflammation. Humans, unique among primates, ceased to synthesize Neu5Gc 2-3 Mya. So far, however, two untypically large and long clinical trials (Prentice et al., 2006; Lanza et al., 2007) showed that reduced meat consumption was not associated with reduced risk for cancer. It is interesting to note that humans share the genetic background for non-synthesis of Neu5Gc with two groups of carnivores (Pinnipedia and Musteloidia) (Ng et al., 2014), one of which consumes almost exclusively fish. Fish contains three times more Neu5Gc than meat (Samraj et al., 2015:Table S3). Also noteworthy is the non-prevalence of cancer in meat-consuming HG groups, many of whom live to the old ages of 60-70 (Gurven and Kaplan, 2007; Marlowe, 2010:140)

5.5.12 Gut morphology

Gut morphology in itself cannot predict diet within lineages. Ancestral patterns, especially regarding gut components, tend to dominate gut morphology (Milton, 1987). However, within lineages, differences in gut proportion and scale can be informative about diets. The most outstanding differences in gut morphology in humans, in relation to chimpanzees, are its smaller size, longer small intestines, and smaller colon. Overall, the gut of humans is 60% of the size of the gut predicted for chimpanzees of the same size (Aiello and Wheeler, 1995). This reduced volume is attributed to the consumption of a higher-quality (energy-dense) diet. Most indicatively, this 40% size difference is a product of a smaller colon in humans, that is 77% shorter, and a small intestine that is 62% longer than that predicted for Chimpanzees of the same size[1] (Calculated from Milton, 1987:Table 3.2; Aiello and Wheeler, 1995). Hladik and Pasquet (2002) objected to the data presented by Aiello and Wheeler (1995) and Milton (1987), arguing that area rather than weight should be used when comparing relative gut organ sizes.

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[1] Average colon length for *H. sapiens* is 20% of gut size, times 60% of the gut size of chimp, divided by 52% of gut size in chimp = 0.23 which means 1-0.23 = 0.77, i.e.77% shorter from same size chimp. Similarly Average small intestine for *H. Sapiens* is 62% of gut and chimp is 23% of gut so 0.62X0.6/0.23=1.75 i.e. 75% longer.

However, recent measurements, using light and electron microscopy (Helander and Fändriks, 2014), found that the mucosal area of the colon in humans is much smaller than previously reported, meaning that the gut morphological changes could have been even more significant than reported by (Milton, 1987). Measurements by the same method of chimpanzee's and *H. sapiens*' various gut components is required to reach a definitive conclusion.

Aiello and Wheeler (1995) attribute the reduced gut size already to H. ergaster, based on his trunk reconstruction by Ruff and Walker (1993). More recently, however, Holliday (2012) has claimed, based on multi-species analysis of Bi-Iliac breadth in relation to Acetabular height, that a relatively narrow bi-iliac breadth is autapomorphic of *H. sapiens*. However, the reduced mastication system that is evident already in *H. erectus* provide support for a reduced gut as both are part of one digestion system (Lucas et al., 2009)

To assess the dietary significance of these changes in gut morphology, we need to determine the chimpanzees' diet. Table 2 presents an estimate of an average yearly diet of chimpanzees based on Table 1 in (Wrangham et al., 1998). The percentages of the three macronutrients in the diet are estimated in calories.

Table 2. Chimpanzee diet - Percentage calories by food component

	Lipids	**Proteins**	**Sugars**	**Fiber***
Conversion factor (cal/g)	9	4	4	1.5
Percentage of dry weight (Conclin-Brittain et al. 1998)	2.5	9.5	14.9	57.5
Normalization for calories	0.225	0.38	0.596	0.8625
Percentage of calories	11%	18%	29%	42%

* Fiber = 100% minus lipids, proteins sugars and ash (ash @15.6% of dry weight). Conversion factor for fiber is based on (Popovich et al., 1997)

Similarly, Popovich et al. (1997) found that gorillas obtain about 60% of their calories from the fermentation of fiber by bacteria to short-chain fatty acids. It can also be seen from Table 2, that contrary to common perception, chimpanzees, also obtain more calories from fiber fermentation than from sugars. In fact, they obtain more than half of their calories from fats. Assuming a similar reliance on fiber fermentation as a source of energy in the diet of our tree-dwelling common ancestor, such a substantial change in the dimensions of the colon and the small intestine points to two significant changes in the diet during human evolution: 1. The colon is where plant fiber is turned into energy, so a 77% reduction in its size means a significant reduction in reliance on fiber as a food source. 2. The elongated small intestine is where sugars, proteins, and fats are absorbed. Glucose is absorbed at a rate of 60 to 100 grams per hour (g/h), fat at 14 g/h and proteins at 5-8 g/h (Bilsborough and Mann, 2006). Since proteins and fats are absorbed in the small intestine at a much slower rate than glucose (See also Johansson, 1974; Caspary, 1992), an increase in protein and fat consumption should have provided higher selective pressure to an increase in the length of the small intestine. In support of this hypothesis, a long small intestine relative to other parts of the *gut* is a dominant morphological pattern in the guts of carnivores (Shipman and Walker, 1989 and references therein). There is no argument that meat consumption increased in *Homo* compared to his predecessors, so an increased need to absorb protein (amino acids) and fat is more likely to have been the driver behind the small intestine extension. The question of how old this adaptation is can be answered, at least partially, by examining the pre-gut preparatory apparatus, namely the mandibular-dental complex that must be coordinated to work in tandem with the gut in order not to overload it with fiber (Lucas et al., 2009). A marked reduction in the chewing apparatus, and a genetic change that reduced the jaw muscle bite force appear already 2-1.5 Mya (Lucas et al., 2006), pointing to a similar development in the gut of *H. erectus* and consequently in his diet. The reduced ability to process fiber also means a reduction in the ability to efficiently exploit starch and sugars, specifically from tubers and fruits, because the digestible carbohydrates they contain are associated with significant quantities of fiber (Vincent, 1985; Schnorr et al., 2015), most of which will now go to waste.

5.5.13 Reduced mastication and the cooking hypothesis

Teeth, in line with the rest of the masticatory system, should closely reflect the physical form of the diet, as the masticatory action is repeated thousands of times each day, and is thus subject to continuous pressure to adjust to efficiently process the diet (Lucas et al., 2009).

One of the main derived features of *Homo* is the reduction in the relative size of all the components of the masticatory apparatus (Aiello and Wheeler, 1995). That reduction has been associated with a substantial decrease in feeding time (approx. 5% of daily activity in humans compared to 48% of daily activity in chimpanzee) starting, as argued, with *H. erectus* 1.9 Mya (Organ et al., 2011).

The masticatory system size together with feeding time reductions have been attributed by researchers to the increased proportion of meat in the diet (e.g., Aiello and Wheeler, 1995; Zink and Lieberman, 2016), high proportion of fat in the diet (Ben-Dor et al., 2011) or to the introduction of cooking, early in *Homo* evolution (Wrangham et al., 1999; Wrangham and Conklin-Brittain, 2003; Wrangham and Carmody, 2010; Wrangham, 2016; Wrangham, 2017). While it is agreed that the reduction in the size of the masticatory apparatus and in feeding time reflects a diet that became more energy-dense in relation to volume, its meat-plant ratio cannot be deduced if one accepts the cooking hypothesis, which proposes to bring fibrous, starchy plant tubers into the energy-dense food category already 1.8 Mya, when the relatively small toothed *H. erectus* appeared (McHenry, 2009b).

In their initial presentation of the hypothesis, Wrangham et al. (1999) claimed that wild meat is a low-fat food, which may have low nutritional quality during lean periods, based on research by Speth and Spielmann (1983) and Speth (1989). After excluding several plant food alternatives as too seasonal or too fibrous, Wrangham et al. focused on underground storage organs (USOs) (Wrangham et al., 1999). They state, in agreement with Stahl et al. (1984), that the starch of uncooked USOs (potatoes in their example) is resistant to amylase, the human enzyme that turns starch into usable energy. They proposed that the cooking of USO must have been practiced by *Homo erectus* 1.8 Mya, if he were to consume enough energy to feed a growing brain, with a reduced masticatory apparatus. In a series of experiments on snakes and rats (Boback et al., 2007; Carmody et al., 2011) Wrangham et al. showed that the energy benefits of cooking include a reduced cost of digestion and a reduced investment in immune defenses when meat is eaten (Carmody and Wrangham, 2009; Carmody et al., 2016). Schnorr et al. (2015) found that starch gelatinization by roasting, which is more relevant than cooking to early Paleolithic conditions, does not improve digestion in USO's consumed by the Hadza but that it makes them easier to peel and chew.

The first question that was debated, and is still debated today, regarding the cooking hypothesis, is whether the archaeological record supports the habitual use of fire by humans at this early period of 1.8 Mya. The record for a fire at that early period is scant and cannot be safely assigned to human activity (Gowlett, 2016; but see Wrangham, 2017). Later, at 1-0.5 Mya, a few individual cases can be assigned to human activity (Gowlett, 2016). The cooking hypothesis predicts daily, habitual use and control of fire. This pattern is not evident in any site before 400 Kya (Gowlett, 2016), but is evident in several locations after that date (Roebroeks and Villa, 2011; Shahack-Gross et al., 2014; Shimelmitz et al., 2014; Gowlett, 2016). In summary, the status of the present archaeological evidence for fire control and use does not seem to support cooking by *Homo erectus* 1.8 Mya, clearly not in a habitual manner, while it does support a habitual use of fire much later than predicted by Wrangham et al., some 0.4 Mya.

Neandertals used fire, and there is even evidence that they were cooking plants (Henry et al., 2011; Hardy et al., 2012). While at some sites fire was used continuously over long periods of time (Cabanes et al., 2010), recent attention has been drawn to the fact that some Neandertal's cave sites, where archaeological signs of fire usually are better preserved, do not show signs of fire usage during long periods of time despite extensive evidence for ongoing occupation (Dibble et al., 2017; Henry, 2017). Dibble et al. (2017) proposed that Neandertals may not have been capable of starting up fires in colder periods and were depended on natural fires, available in wormer periods. Henry (2017) proposed to consider the cost-benefit ratio of collecting wood in different circumstances as a decision rational for setting up fires. In either case, it seems that Neandertal could survive for extended period on raw foods.

The assumption of Wrangham et al. (1999) that the physical softness of cooked food enabled the masticatory apparatus reduction in *H. erectus* was contested recently by Zink and Lieberman (2016), who proved experimentally that merely cutting lean meat and USOs with stone tools into smaller pieces can reduce the masticatory effort sufficiently to allow the observed reduction of the masticatory apparatus in *H. erectus*. They state that their findings negate the presumed need for cooking by *H. erectus*.

Zink and Lieberman (2016) did not take into account the significant contribution of fat consumption to the lessening of the masticatory effort of *H. erectus*. In an earlier paper (Ben-Dor et al., 2011) we showed that African prey, especially large ones, contain plenty of fat, thus eliminating the problem of presumably-low meat consumption, that was supposed to be solved by Wrangham et al. (1999) cooking hypothesis. Thus, it is more likely that fat, which adds zero chewing effort while providing as many calories as meat in a typical large African prey animal (see Chapter 8), was a significant factor in reducing the load on the masticatory apparatus of *H. erectus.*

A critical assumption that Wrangham et al. use in the various papers that were cited above is that humans could not survive on a raw, uncooked, diet. The assumption is supported by the presumed fact that people on a raw diet suffer from low BMI and women suffer amenorrhea. This assertion, which is defined as "*key evidence*" (Wrangham, 2017) is based on a single study in a German population (Koebnick et al., 1999) whose data was obtained by gathering replies to a mail questionnaire. No physiological examinations or personal interviews were carried out. Participants were asked about their BMI and their health status. Self-reporting food questionnaires are notoriously biased (Briefel et al., 1997; Heerstrass et al., 1998; Subar et al., 2003; Archer et al., 2013). The authors describe the diet as mainly vegetarian where "*staple foods like meat, dairy products, cereals and cereal products are avoided*" and where "*fruits and vegetables make up a high percentage of the food consumed*." In a puzzling contradiction to the above description, they do include a large group in the study which is defined as 'meat eaters'. One possible explanation for this contradiction is that any respondent who reported consumption of any meat quantity at any frequency was included in the meat eaters' group. In any event, it does not appear as if the "meat eaters" group consumed meat and fat in amounts that are close to those of Paleolithic humans. Also, no mention of intake of supplemental vitamin 12 or iron is made. Shortage of Iron and vitamin B12 is rampant among vegan and vegetarian populations (Alexander et al., 1994; Haddad et al., 1999) of which this group seems to be an extreme example. The diet also recommended fasting periods of between several days and several weeks. About half of the 572 participants fasted at least once a year. The most apparent shortcoming of the study, however, is that "*about 55% of the participants changed to raw food diet because of their disease*". The most important disorders were a disease of the gut, allergies, asthma, and rheumatism. To sum up, it seems that the study population is highly morbid at the base and not even representative of the present western population, let alone early Paleolithic populations like those of *H. erectus*. Furthermore, their raw diet of western foods could have been depleted of bioavailable vitamins that are found in abundance in animal fat, meat, and organs (see Section 5.5.2), including ones that are found exclusively in animal meat and fat like vitamins A, D, and B12. In other words, it seems that the Koebnick et al. (1999) study does not provide sufficient evidence for a detrimental effect of a diet high in raw meat on humans.

Early in the 20th century several northern polar populations still ate most of their food raw (Davies and Hanson, 1965; Trowell and Burkitt, 1981). Meat that has become rotten was eaten raw (Heinbecker, 1928:462). In fact, consumption of raw animal organs, as well as stomach content is considered to be an adequate source of vitamin C for northern polar populations that relied almost exclusively on animal food (Fediuk, 2000; Fediuk et al., 2002).

It is interesting to note that the Hadza HG, who consume tubers, don't cook them but merely burn them to allow peeling. Also, the tubers are highly resistant to digestion because of their high fiber content, resulting in low glucose accessibility (Schoeninger et al., 2001; Schnorr et al., 2015). USOs, in fact, serve the Hadza only as a fall back food at times when other, more nutritious food like meat, honey, berries, and baobab, are not available (Marlowe, 2010:108). This phenomenon is apparently common in recent HG groups, where dependence on plant foods entails typically a focus on seeds and nuts (Kuhn and Stiner, 2001), as is expected from their relatively higher ranking, taking into account their lower fiber content and toxin levels (Stahl et al., 1984).

Another argument that is raised by Wrangham (2017) is that *H. erectus* will have had to chew for eight hours a day if he was to consume raw food. Wrangham base that conclusion on a paper that describe feeding times among primates which are feeding mostly on high fiber diet (Fonseca-Azevedo and Herculano-Houzel, 2012). However, if feeding times of meat by carnivores are considered, then the feeding time is no longer an issue. For example, wolves can consume over 1 kg of raw meat per minute (Wilmers and Stahler, 2002). Inuit who consumed meat exclusively, were able to consume four kgs meat per day on a regular basis, most of it in a single meal, and ingestion of daily quantities of 15 kgs of meat per person has also been observed (Krogh and Krogh, 1914; Sinclair, 1953). Fat, which is hypothesized here to have provided up to some 50% of the calories, is the densest food and requires little mastication in relation to its caloric content.

In summary, the availability of stone cutting tools and a considerable quantity of fatty meat seems to provide an acceptable explanation for the reduced mastication already in *H. erectus* while the cooking hypothesis is still dependet on weakly supported assumptions, for example, that meat and fat based raw food diet would have been deleterious to *H. erectus* and that fire was habitually used 1.8 Mya.

5.5.14 Age at weaning

Life history is a very indicative measure of speciation, and humans have a substantially different life history to that of primates (Robson and Wood, 2008).

One of the life history variables, in which humans differ significantly from all primates, is the age at weaning. While the age at weaning of primates such as orangutans, gorillas, and chimpanzees ranges between 4.5 and 7.7 years, humans' age at weaning in HG societies is much shorter, at 2.5-2.8 years, despite a longer period of infant dependency (Kennedy, 2005; Robson and Wood, 2008:Table 2). Kennedy (2005) explains this shorter nursing period by the inability of the mother to sustain long periods of high nutritional demands of a growing infant's brain, and by the availability of more nutritious adult foods, in the form of meat and fat. More recently, Psouni et al. (2012) found that an early age at weaning is strongly associated with the level of carnivory. They state that their findings: "*highlight the emergence of carnivory as a process fundamentally determining human evolution*."

5.5.15 Longevity

Another life history variable, in which humans differ markedly from great apes, is longevity.

While the modal age at death (MAAD) in chimpanzees is 15 years, the MAAD in present-day HG groups is the late 60s to early 70s (Gurven and Kaplan, 2007:Table 4). There is no argument that longevity extension began with early *Homo*, although the pace of change is disputed. Caspari and Lee (2004) argue for an accelerated extension in *H. sapiens* while others, such as Hawkes and Coxworth

(2013) argue for an early extension. Two hypotheses attempt to explain the adaptation for life extension in humans, and it appears that at the base of their difference from each other lies a different perception regarding plant-food ratios in the human diet during evolution. Hawkes and Coxworth (2013) support the ‘grandmother hypothesis,' in which longevity of grandmothers enabled the collection of sufficient plant food to feed babies in need of extended care, due to their slower development in comparison with primates. Hawkes and Coxworth (2013) rely on the Hadza dietary patterns, in which women’s gathering provides a large portion of the calories, to demonstrate the marked effect of releasing the grandmothers’ daughters to gather. At the other gender end, Kaplan et al. (2000), (see also Kaplan et al., 2007) rely on a diet dominated by animal-sourced foods of other HG groups such as the Ache. They propose that experience in hunting, which fully develops only at around 40 years of age, is crucial to the group’s survival. It allows the acquisition of surplus calories needed to feed the less productive, younger members of the group. The importance of experience in hunting caused the extension of longevity in humans. The problematic assumption that the Hadza, with their metal culture and diminished large prey, can serve as a model for dietary patterns during evolution is discussed extensively in Section 5.3. It is interesting to note, however, that even in the Hadza, peak productivity in food acquisition is reached after age 40 in both sexes (Marlowe, 2010:Figure 5.11). In summary, it can be concluded from the extended longevity of humans that a need for efficient calorie acquisition to maintain both self and an extended period of dependency of siblings, was a dominant driving force in human evolution. It can thus be assumed that the caloric density of the obtained food, in relation to acquisition time and energy spending, was an essential criterion in the decision about which type of food to pursue. In this respect, the significant advantage in time-calorie efficiency of animal- over plant-sourced foods (Stiner and Kuhn, 2009) supports the hypothesis of Kaplan et al. (2000), although the two hypotheses are not necessarily mutually exclusive.

5.5.16 Recent adaptation to USO consumption

The necessity for various recent adaptations, presumably as a response to the evident increased consumption of plants in the Epipaleolithic and Neolithic (to be discussed) can also teach us about the diet in prior periods, when presumably these adaptations were not needed for optimal fitness. One example that was already discussed is the relatively recent enrichment of copies of the AMY1 gene. Another genetic indication of a recent adaptation to a high-starch diet may be seen in the study by Hancock et al. (2010:Table 4), which showed that populations that presently depend on roots and tubers are enriched in SNPs that are associated with starch and sucrose metabolism and folic acid synthesis. These adaptations presumably compensate for these foods' poor folic acid content. Another SNP in these populations may be involved in the detoxification of plant glycosides, such as those contained in roots and tubers (Graaf et al., 2001). This specific recent adaptation to a high consumption of roots and tubers is of particular significance, as root and tuber are considered by researchers supporting a high-plant-food diet as ideal candidates for significant plant-food consumption (Wrangham et al., 1999; Hardy, 2010; Dominy, 2012; Henry et al., 2014; Hardy et al., 2016).

5.5.17 Microbiome

In recent years, the existence and importance of the symbiotic relationships between the microbiome and the human body have gained significant recognition. The gut microbiome, which is said to contain as many cells as the whole human body, has been found to influence human metabolism in many parts of the body, including a strong influence on the brain and autoimmune system (Schnorr et al., 2016). The gut microbiome relies mainly on plant fiber as food. Its significant role in human metabolism supports claims of the importance of fiber in the diet (Warinner et al., 2015). Fiber content is naturally high in wild plants and was also available as prey stomach content, even to populations that subsisted exclusively on hunting (Buck and Stringer, 2014). Fiber metabolism does not induce amylase, so evidence for a recent adaptation to starch does not preclude the significant consumption of fiber during evolution. There is still no indication as to an optimum level of fiber consumption, and it is known that northern humans happily survived on a limited consumption of fiber. It is not known how much energy humans can extract from fiber, as increased dietary fiber results in a decrease in the digestibility of other components that are associated with the fiber in the food (Stahl et al., 1984). A rough calculation, assuming chimpanzees obtain 42% of their daily energy from fiber (Table 2) and a 77% reduction in the colon size in humans, will result in an estimate of a quarter of that amount so roughly 10% of the daily energy for humans.

5.5.18 Postcranial morphology

Several derived morphologic phenotypes of humans have been interpreted as adaptations to carnivory. Probably the best known is the adaptation to endurance running, presumably to enable 'persistence hunting' (Bramble and Lieberman, 2004). Bramble and Lieberman list 28 derived features of the human skeleton with a cursorial function to show that humans are adapted to endurance running that exceeds the capabilities of cursorial carnivores. They conclude that these adaptations were caused by the need to hunt animals by a method known as persistence hunting that is still rarely practiced today, whereby animals, which are less adapted than humans to extended, continuous, and fast movement, are followed and chased to exhaustion and then speared at close range. According to Bramble and Lieberman, most of these adaptations were in place in *H. erectus*. Recently, Vining and Nunn (2016) found genetic adaptations that may have contributed to long distance running. Pickering and Bunn (2007) raised doubt as to the prevalence of the persistence hunting method as early as the Acheulian and the cognitive ability of *H. erectus* to practice the necessary animal tracking. Lieberman et al. (2007) replied that even animals track and *H. erectus* with more encephalization than animals, must have also been able to track. They also claimed that taking into account the lack of stone points, it is difficult to see how else *H. erectus* could hunt. They also reject the relevance of Bunn and Pickering's assertion, that modern HG uses the persistence hunting method only rarely, demonstrating that modern HG has technological means at their disposal that were not available to *H. erectus*, and so cannot serve as a relevant example. Bunn and Pickering (2010) later used ungulate mortality data from FLK Zinji to further test and reject Bramble and Lieberman's hypothesis and suggested that the record supports an ambush hunting practice (Bunn and Gurtov, 2014). In summary, Bramble and Lieberman have identified a wide-reaching adaptation to running early in human evolution, which has not been explained so far other than as an adaptation to carnivory in humans, although some doubts exist as to the widespread application of this adaptation to hunting.

Another adaptation that researchers associate with hunting in early stages of human evolution is an adaptation of the shoulder to the throwing action (Roach et al., 2013; Kuhn, 2015; Roach and Richmond, 2015). Roach et al. (2013) show that a combined configuration of adaptations, some of which are specific to the shoulder and arm and some, like long legs and wide shoulders that were selected for other functions, all contributed to improving the ability to efficiently throw already in *H. erectus* (Roach and Richmond, 2015). Young et al. (2015) and Feuerriegel et al. (2016) argue that adaptation of the shoulder to throwing came at the expense of a reduced ability to use arboreal niches, meeting the criteria proposed by Wood and Strait (2004) for compelling morphological evidence for stenotopy (specialization).

5.6 DIRECT EVIDENCE

This chapter will review evidence that relies on the archeological and paleontological records. The archaeological record has been used extensively in the study of Paleolithic diets but the paleontological record less so. I review the published literature and try to interpret the record as it relates to the dietary DPA.

5.6.1 Lithics

Although lithic research is one of the cornerstones of prehistoric studies, a surprisingly little indication as to DPA can be learned from it. There is widespread evidence of cut marks of stone tools on animal bones, attesting to various butchering activities, starting with early humans and continuing throughout the Paleolithic (Potts and Shipman, 1981; Marean and Assefa, 1999; Stiner and Munro, 2002; Domínguez-Rodrigo and Yravedra, 2009; Sahnouni et al., 2013; Garriga et al., 2017; Merritt, 2017; Rodríguez-Hidalgo et al., 2017). Similarly, there is evidence on the tools themselves for their use in meat processing in the form of use wear, protein residues, and fat residues (Lemorini et al., 2006; Barkai et al., 2010; Stiner et al., 2011; Lemorini et al., 2015; Solodenko et al., 2015; Nowell et al., 2016; Zupancich et al., 2016). Recently, however, usage of stone tools for the processing of plants in the early Paleolithic was also detected (Lemorini et al., 2014; Arroyo and de la Torre, 2016; Yravedra et al., 2017). This imbalance of evidence frequency cannot however be used to support a higher prevalence of animal food in the diet since plant consumption may not require intensive tool processing. However, an appearance of new tools and an increase in the relative abundance of plant processing tools in successive cultures may provide some indication of a trend of increasing relative importance of plant food in the diet of these cultures. Kuhn and Stiner (2001) note an increase in the frequency of stone tools that can be attributed to plant food processing towards the end of the Pleistocene. A similar intensity of grinding tool use is also found in recent HG plant-dependent groups (Kuhn and Stiner, 2001). Other direct evidence for increased plant consumption during the Upper Paleolithic (Bar-Yosef, 2014) corroborates the relation between the frequency of plant-processing tools and consumption. Also, increased sedentism during the second half of the Upper Paleolithic is also interpreted as evidence for increased consumption of plant food (Soffer, 1989; Bar-Yosef, 2002). In Europe there seems to be a similar trend where grinding stones first appear sporadically in the Early Upper Paleolithic/Aurignacian, but it is from later cultures, such as the Gravettian and the Magdalenian that these tools become more frequent (Kuhn and Stiner, 2001; Stiner, 2002; Aranguren et al., 2007; Revedin et al., 2010). In a multi-dimensional analysis of the Eurasian archaeological record, Stiner (2002) found a significant decline in humans' trophic level by the Late UP.

Grinding tools appear in Africa in the Middle Stone Age (MSA), much earlier than elsewhere. However they are mostly associated with the grinding of pigments (McBrearty and Brooks, 2000),. The transition between the MSA and Later Stone Age (LSA) is claimed to be less revolutionary in Africa than in Europe and the Levant (McBrearty and Brooks, 2000). The time of the transition from MSA to LSA is debated (Villa et al., 2012), and in any event, is less conspicuous than in Europe and the Levant (Bar-Yosef, 2002). The MSA/LSA transition was gradual and spanned an extended period between some 56 and 38 Kya in East and South Africa according to some (Ambrose, 1998; Villa et al., 2012; Eren et al., 2013), or 22 Kya according to others (references in Villa et al., 2012). An increase in plant-processing tools is less conspicuous than in Europe and the Levant (Clark, 1997; Bar-Yosef, 2002; Barton et al., 2016) and includes, in addition to grinding stones that are known from the MSA, bored stones that may have served as digging stick weights (Villa et al., 2012). In fact, hunting and cutting tools dominate the tool innovation list of the LSA (Clark, 1997; Villa et al., 2012). In summary, there is little lithic evidence of increased plant food consumption in Africa, at least during the early parts of the LSA. It may be that plant consumption was always higher in Africa or that it was always low and remained low. In China, an increase in evidence for plant food consumption seems to follow the same timeframe of the European – Levantine UP (Liu and Chen, 2012:46-57; Guan et al., 2014). It is important to note that during this period of increased plant consumption, hunting continued to be practiced with increased technological complexity and, presumably, time investment.

In summary, evidence of increased presence of new stone tools that are specifically designed for the preparation of plant food may testify to a gradual increase in plant consumption during the UP. Accepting this interpretation must lead to a conclusion that less plant food was consumed in earlier periods. This conclusion must be qualified, however, since the new tools may be a result of a substitution in the type of plant food, like grains for example, rather than an evidence for increased plant food consumption.

5.6.2 Isotopes and trace elements

Nitrogen δ^{15}N Isotope measurement in protein residues (mainly collagen) in human fossils is the most extensively used method for determining the animal-plant ratio in Paleolithic diets (see Makarewicz and Sealy, 2015 for a recent review). As dietary protein makes its way up the trophic food chain, the isotope δ^{15}N gets ‘enriched’ in body proteins. Nitrogen isotope ratios (δ^{15}N values) of human bone collagen are between 3 to 5‰ higher than in dietary protein (Richards and Trinkaus, 2009). This ‘‘trophic level effect’’ is widely used in archaeology and modern ecology as a mean of determining the trophic position of organisms in food webs.

However, several theoretical concerns (reviewed in Hedges and Reynard, 2007; and Makarewicz and Sealy, 2015) prevent incontestable certainty in the results:

- The isotopic level in plants is variable, depending on plant species and climate. This problem is solved, where it can be solved, by comparing δ^{15}N levels of humans to δ^{15}N levels of herbivores from the same location and period. However, at prehistoric levels of dating resolution, this is difficult to ascertain. Comparisons to local carnivores are also helpful, but usually the sample sizes are small.
- Local herbivores’ protein diet is thus assumed to be representative of a human plant diet, which is not necessarily the case.

- Interspecific differences in herbivores living in the same environment can be significant, so comparative sampling of herbivores, which is typically limited, may be too small and not representative of the presumed herbivorous second trophic level.
- It is unknown whether mixed diets of plant- and animal-sourced proteins are represented in linear relations of the $\delta^{15}N$ residues in humans.
- There could be inter-individual variations of $\delta^{15}N$ enrichment in humans, as well as in other animals. Periods of growth and starvation are two examples of possible causes of such variations.

Having these possible sources of bias in mind, I review the results of $\delta^{15}N$ studies from the UP and later pertaining to AMHs.

Table 3. $\delta^{15}N$ studies

Period (Kya BP)	**Region**	**# Individuals**	**# Sites**	**Diet**	**Reference**
31.5-29.5	Moravia	2	1	**Carnivore**	(Bocherens et al., 2015)
40-23	Europe	10	9	**Carnivore**	(Richards and Trinkaus, 2009)
UP	Med. Eur.	15	4	**Carnivore**	(Mannino et al., 2012)
14-10	Europe	31	11	**Carnivore**	(Richards et al., 2015)
Mesolithic	Germany	3	1	**Carnivore**	(Bollongino et al., 2013)
Mesolithic	Med. Eur.	27	10	**Carnivore**	(Mannino et al., 2012)
Mesolithic	Doggerland	56	-	**Marine**	(van der Plicht et al., 2016)
10	Germany	1	1	**Carnivore**	(Drucker et al., 2016)

Period (Kya BP)	**Region**	**# Individuals**	**# Sites**	**Diet**	**Reference**
10-9	Spain	15	3	**Carnivore**	(Salazar-García et al., 2014)
8-5	Japan	4	1	**Mixed**	(Naito et al., 2013)
Neolithic HG	Germany	10	1	**Carnivore**	(Bollongino et al., 2013)
AD	USA	65	1	**Variable**	(Beasley et al., 2013)

The results for Europe in Table 3 show an exclusively carnivorous diet (including fish) for HG throughout the Upper Paleolithic, including the Mesolithic and even Neolithic HG (Bollongino et al., 2013). It is worth noting that while a carnivorous diet is expected in Northern Europe, samples from more southern parts of Europe, such as Sicily, still show carnivorous diets through the Mesolithic. In the Mesolithic there is a trend to add freshwater fish to the diet in some places (Richards et al., 2015). It should be noted that in many of the cited studies, the comparative environmental sampling was small, so a bias such as the one identified by Bocherens et al. (2014) of periodically high $\delta^{15}N$ levels for the early Aurignacian, may skew results towards a highly carnivorous diet for that particular period. In any event, the dominance of the European record in these studies is a limitation that should be considered. Only one paper could be found (García-González et al., 2015) that reconstructed a mixed diet for a Lower Magdalenian El Miron individual. Although an ordinarily carnivorous $\delta^{15}N$ value of 10.2 ‰ was measured, the determination of the mixed diet was mainly based on dental microwear analysis, as no comparative values for local carnivorous or herbivorous $\delta^{15}N$ were available.

Some researchers (O'Connell et al., 2012) claim that humans show higher $\delta^{15}N$ values than their diet entails. The weakness of the argument lies with modern foods and the modern diet composition that was used in the experiments. It is known, for example, that manuring adds $\delta^{15}N$ to domesticated plants (Fraser et al., 2011). Also in Neolithic sites, where increased plant consumption is evident, $\delta^{15}N$ isotope analyses were able to discern subtle differences in meat consumption among individuals (Pearson et al., 2013; Pearson et al., 2015), as well as a higher plant consumption at many sites after the Mesolithic (Beasley et al., 2013). Recently, examining single amino acids instead of the whole collagen, Naito et al. (2016) show a higher plant content in the diet of Neandertals from Spy cave than was previously reported. They found the diet to contain 20% plants, in comparison to no plants in the previous analysis. It remains to be seen if this is a common finding of the new method as O'Connell and Collins (2017) express doubts as to accuracy of Neito et al.'s measurements (but see relpy Naito et al., 2017). However, even the new method still identified a carnivorous diet, in this case of Neandertals.

In summary, with the caveats that have been listed in this chapter in mind, the $\delta^{15}N$ record listed in Table 3, seems to be commensurate with a carnivorous diet for *H. sapiens* during the Upper Paleolithic, at least in Europe.

The trace elements strontium and barium, in relation to calcium, have also been used, alongside isotopes, to gauge the relative importance of plant vs. animal foods in the diet of early humans. It was found that the ratio of strontium/calcium diminishes, while barium/calcium increases with the increase in trophic level. The advantage of trace elements over isotopes is that they are measured in longer-lasting bone and tooth tissue. However, a concern regarding diagenesis has practically halted their use (Ungar and Sponheimer, 2013).

Recently, however, Balter et al. (2012) reported that they overcame the problem of diagenesis by using laser ablation of tooth enamel. They tested permanent molars from *Australopithecus africanus*, *Paranthropus robustus*, and early *Homo* from Sterkfontein, Swartkrans, and Kromadraai in South Africa. They found that: "*Compared to fauna…early Homo and P. robustus are indistinguishable from carnivores and browsers respectively*". The method that Balter et al. used has not been widely adopted as yet.

5.6.3 Dental caries and gingivitis

Caries is readily observable in fossilized dental human remains. The presence of caries in wild chimpanzee to the tune of 30.6% in older animals supports the notion that natural sources of carbohydrates can produce caries (Lanfranco and Eggers, 2012).

Single cases of caries are known from as early as 1.8 Mya (Lordkipanidze et al., 2013). Dental caries is present but still rare among early modern humans in Europe and the Near East during the UP (Lanfranco and Eggers, 2012). A high prevalence of carries, a sign of intensive consumption of carbohydrates, first appears 13.7-15.0 Kya (Humphrey et al., 2014), together with evidence for exploitation of starchy foods. Phylogenetic analysis of the dental caries-associated pathogen *Streptococcus mutans* indicates that it underwent a rapid population expansion within the last 10,000 years, strongly implicating the adoption and intensification of agriculture in this process (Cornejo et al., 2013). In support, Adler et al. (2013) found that the prevalence of gingivitis and caries in humans increased markedly after the agricultural revolution.

It should also be noted that caries is extremely rare among Neandertals. Six cases have been reported among approximately 1250 known Neandertal teeth (Lanfranco and Eggers, 2012).

5.6.4 Dental wear and plaque

Wear on teeth, both short-term microscopic and long-term macroscopic has been used to infer DPAs (dietary plant-animal ratio) in diets of Paleolithic humans.

Microwear studies were used to infer diets of Australopithecines and early humans, as well as more recent humans. However, a lack of measurement standards led to errors, and a lack of comparison to known diets prevented an accumulation of conclusive evidence from the many studies (Ungar and Sponheimer, 2013). Employing newer standards and technology, Ungar et al. (2012) compared the microwear of *H. habilis*, *P. boisi*, and *H. erectus*. They concluded that the microwear data provided no evidence for mastication of extremely tough or hard foods in early *Homo* species. Pontzer et al. (2011) found that the diet of the Dmanisi *H. erectus* was similar in microwear terms to that discovered by Ungar et al. (2012). Unfortunately, a lack of comparison to groups with a known DPA dietary ratio precludes a consideration of their results in this work.

A bolder attempt at estimating the DPA dietary ratio based on tooth microwear analysis was made by Zaatari and Hublin (2014). They compared several European Upper Paleolithic groups to groups of recent HG, whose diet and microwear patterns were presumably known, and ranged from an exclusive animal- to mostly plant-sourced diet. They found that the earlier groups of Aurignacians (40-36 Kya) and Gravettians (26-20 Kya) "*clustered to the mostly meat-eating groups…regardless of their geographic location or paleoecological conditions*." The later Upper Paleolithic group of the Magdalenians (17-12 Kya) showed a definite shift to a higher ratio of DPA sources in their diet. The results of this study significantly contradict the results of two previous studies (Lalueza et al., 1996; Pérez-Pérez et al., 2003), in which Upper Paleolithic European specimens tended to cluster together outside the carnivorous range, and defined as '''mixed diet'. No specific indications were given in the paper as to the relative DPA composition of their mixed diets. Both earlier studies also investigated earlier humans and Neandertals and found variability within the diets of both species.

While the results of Zaatari and Hublin (2014) agree with the isotopic data described earlier, the obvious weakness of the microwear method is the short period of several days that it samples. These days may or may not be representative of the long-term diet, especially as, by definition, these are the last days of the subjects in which there were higher chances of not consuming their typical diet (the 'Last Supper' phenomenon). Another major weakness of the microwear method, which makes the identification of plant consumption difficult, is that sand, dust, and grit leave substantial dental wear marks that are mostly indistinguishable from those of plants (Pérez-Pérez et al., 2003; Lucas et al., 2013). Pérez-Pérez et al. (2003) speculate that different stone tool modes may have a significantly different effect, possibly through the presence of grit, on the observed microwear pattern.

A longer-term dietary trend can be obtained from an analysis of dental macrowear. Fiorenza et al. (2011) measured occlusal fingerprints, derived from optical 3D topometry, with the aim of comparing UP *H. sapiens* with Neadertals in different ecoregions. They found that both species had a mixed diet in the evergreen Mediterranean habitat and a more meat-restricted diet in upper latitude steppe-coniferous forest environments.

Table 4. Dental microwear and macrowear studies

Period	***Homo***	**Plant-Animal***	**Reference**
Acheulian	*H. erectus*	Unknown	(Ungar et al., 2012)

Period	***Homo***	**Plant-Animal***	**Reference**
MP (Europe)	Neandertal	Carnivore	(Lalueza et al., 1996)
MP (Europe)	Neandertal	Carnivore	(Fiorenza et al., 2011)
MP (Open habitat)	Neandertal	Carnivore	(El Zaatari et al., 2016)
MP (Wooded habit.)	Neandertal	Mixed?	(El Zaatari et al., 2016)
MP (Mediterranean)	Neandertal	Mixed?	(Fiorenza et al., 2011)
UP (Europe)	*H. sapiens*	Mixed?	(Lalueza et al., 1996)
UP (Aurign./Grav.)	*H. sapiens*	Carnivore	(Zaatari and Hublin, 2014)
UP (Europe)	*H. sapiens*	Carnivore	(Fiorenza et al., 2011)
UP (Mediterranean)	*H. sapiens*	Mixed?	(Fiorenza et al., 2011)
UP (Magdalenians)	*H. sapiens*	Mixed?	(Zaatari and Hublin, 2014)

*‘Mixed’ findings may, in fact, indicate a carnivorous diet – see the body of the text.

One shortcoming is common to both the microwear and macrowear methods is that they both rely on recent HG groups as comparison groups. As demonstrated in Section 5.3, information on the relative DPA composition of recent HG diets can be highly inaccurate. For example, Fiorenza et al. (2011) rely on the Khoe-San and the Australian aborigines as groups indicative of a ‘mixed diet.' The difficulty to accept the reconstruction of the San’s Paleolithic diet as ‘plant based’ was described in Section 5.3.2. About Australian aborigines, Fiorenza et al. (2011) cite Brand-Miller and Holt (1998) as evidence for a ‘mixed-diet’ for that comparison group. However, Brand-Miller and Holt (1998) define their diet in the cited paper as being ‘animal-dominated’. It is probable that the difference in diets between ecological regions did exist, as found by Fiorenza et al. (2011). However, it is more likely, based on the Australian aborigines’ data, that the examined diets could be described more accurately as being ‘animal-dominated’.

Similarly, another research group, (El Zaatari et al., 2011; Zaatari and Hublin, 2014; Estalrrich et al., 2017), used the San (without reference to a specific San group) as a comparison group that supposedly represents a plant-dominated diet. They refer to reports on the diet of the Kalahari-based San, but actually use teeth from the ‘montane forest’ South African San site of Oakhurst Shelter. The reference paper, supposedly providing support for a substantial amount of plant food in the South African San group diet (Sealy et al., 2006), point to a diet abundant in shellfish. The $\delta^{15}N$ for the population (13‰) is normally indicative of a high trophic position, and most of the faunal remains in the site were of shellfish. The author does use the word ‘mixed,' but in the sense of mixed aquatic and terrestrial sourced foods, and there is no mention of a plant-dominated diet as has been interpreted by El Zaatari et al. (2011). Another group that they (El Zaatari et al., 2011) use for comparison, supposedly representing a ‘mixed diet’ is the Chumash of California. However, the paper to which they refer (Erlandson et al., 2009) discusses subtleties of a diet based on aquatic food in this Santa Cruz island, and never mentions plant-sourced food. The problematic aspect of using the ethnographic record for comparison in this type of analysis is emphasized by Pérez-Pérez et al. (2003), who concluded that Australian aborigines and Bushmen (San) show a less-abrasive microwear pattern than UP humans, indicative of a higher meat content in the recent HG diet. They state that buccal microwear patterns in recent HG groups were not in accordance with their stated diet.

Ancient dental plaque has recently gained attention as a source for dietary information, as it enables identification of plant particles that have accumulated in plaque (Henry and Piperno, 2008; Henry et al., 2011; Hardy et al., 2012; Henry et al., 2014; Hardy et al., 2016; Hardy et al., 2017). All studies, including of the earliest-studied population of Sima del Elefante 1.2 Mya (Hardy et al., 2017) and the 400 Kya Qesem Cave, Israel (Hardy et al., 2016), were able to identify plant remains in tooth plaque. Unfortunately, this source of dietary information is not more suitable than the vast archaeozoological record in determining the DPA of the diet.

Fiorenza et al. (2015) justify significant consumption of plant food, based on the wide variety of species that were identified in the plaque. However, a wide variety of species does not necessarily correspond to their significant portion in the diet. For example, Hill et al. (1984) reported that the vegetal component in the diet of the Ache HG of Paraguay is characterized by a low variance in absolute numbers of calories, but by a high variance in species composition (some 34 in this case). Likewise, in the Hadza, birds make up 84.4% of the exploited plant and animal species but contribute only a negligible number of calories to the diet (Marlowe, 2010: Table 5.2).

5.6.5 Paleontology and zoology

Due to the uneven preservation of plant and animal residues in archaeological sites, it is practically impossible to say much about the dietary DPA of groups whose archaeological site assemblage is studied. However, the vast archaeozoological and archaeobotanical record may contribute to the identification of significant trends in dietary DPA, especially when combined with the lithic record.

The early human record in archaeological sites starting some 2.6 Mya shows a gradual increase in the presence of bones and stone tools, and especially bones that bear marks that were inflicted by these tools, (Domínguez-Rodrigo and Pickering, 2017). This change may mark the entrance of the *Homo* genus into the omnivore, carnivore, and scavenger guilds (Werdelin and Lewis, 2013 and references therein).

Mostly, the debate regarding the early humans' archaeozoological record centers on their definition as hunters or scavengers (e.g., Blumenschine, 1995; Bunn and Gurtov, 2014). For our purpose, active predation presumably represents a higher degree of investment in animal food acquisition in comparison to scavenging. Higher investment in its acquisition may indicate that animal food formed a higher percentage of the diet. It may also be assumed that the introduction of hunting brought in additional animal food to the one that was brought at earlier stages of human evolution by scavenging. It may be worthwhile mentioning that a third form of acquisition, gathering of invertebrates and aquatic animals, is also considered by some researchers to have contributed significantly already early in human evolution (McGrew, 2014; O'Malley and McGrew, 2014; Tattersall, 2014). Much like plants, the dearth of evidence prevents the determination of the level of invertebrates' contribution to the dietary DPA.

Early researchers, who identified the acquisition of large animals by early humans, did not hesitate to determine that they were hunting or at least were gaining primary access to the animals (Bartholomew and Birdsell, 1953; Dart, 1953; Isaac, 1983). However, during the 80's, scavenging as the primary mode of obtaining animal food by early humans gained support to the extent that Blumenschine (1986) claimed that a consensus has emerged, quoting Binford (1983) opinion on the relative share of meat in the diet so: "*far from appearing as a mighty hunter of beasts [early hominids] seem to have been the most marginal of scavengers*". Blumenschine claimed that "*most analysts of the earliest archaeological* *faunas now, too, assign probable or even important role for scavenging in the acquisition of animal foods*.” In general, Blumenschine (1986) based the new recognition of the importance of scavenging on the fact that carnivores and recent H-G practice mixed scavenging-hunting strategies and on research (e.g., Binford, 1985) that showed that “*Plio-Pleistocene hominids may not have been as “human” as previously supposed*.”

However, the consensus, if there ever was one, didn’t last for long and the debate continued over the central question of the relative importance of scavenging versus hunting. The debate was, and sill is, a cause of a major expansion of techniques and interpretation of taphonomic markers of primary access and exploitation of acquired animals like cut and teeth marks on bones, biases in body parts acquisition and mortality age profiles (Blumenschine and Selvaggio, 1988; Blumenschine and Madrigal, 1993; Bunn and Ezzo, 1993; Blumenschine, 1995; Domínguez-Rodrigo, 2002; Bunn and Pickering, 2010; Pante et al., 2012; Bunn and Gurtov, 2014; Dominguez-Rodrigo et al., 2014a; Dominguez-Rodrigo et al., 2014b; Pante et al., 2015).

Recently, in direct reply to the extent of ‘human’ capabilities in early humans, Pickering and Domínguez-Rodrigo (2010) and Domínguez-Rodrigo and Pickering (2017) reviewed the literature regarding the association of predation (capturing) and carnivory (consumption) with the early stages of the human evolution. They point out that active predation and carnivory are apparent in our closest relatives, the chimpanzee and the bonobo, and so may have been prevalent in our lineage many million years before the appearance of humans. They notice that in chimpanzees hunting is more expensive and multifaceted at the most seasonal sites. Chimpanzee populations who reside in acutely seasonal savanna woodlands hunt a wider range of prey. Chimpanzees at the extremely arid site of Fongoli use specially modified sticks and tree brunch to hunt (Pruetz and Bertolani, 2007). In line with that evidence, it is worthwhile adding here that baboons also actively hunt, and that they are more active during the dry season (Hausfater, 1976).

It is difficult to quantify the present degree of academic support for predation or scavenging as the dominant method of animal food acquisition by early humans. It can be said, however, that there is considerable evidence in support of the hypothesis that active predation became “*full blown and* *instantaneous with the invention of stone tool technology*” (Pickering, 2010), marking the increased importance of animal food in the human diet early in human evolution.

Another lively debate (see Monjeau et al., 2015 for a review) which has a bearing on the DPA is whether humans’ introduction into certain environments caused the extinction of large herbivores and/or a diminution in the carnivore guild due to competition from humans.

A case for late Pliocene – early Pleistocene influence of humans on the carnivore guild in East Africa, was presented by Lewis and Werdelin (2007) and further developed later (Werdelin and Lewis, 2013). According to their analysis, which is based on functional richness and evenness in Pliocene-early Pleistocene assemblages, hominins of the Plio-Pleistocene competed successfully, first with omnivores and later with large-bodied carnivores. Hominins are shown to be responsible in the Pleistocene for the increased extinction rates among carnivorans. According to their analysis, the omnivore space became significantly reduced in the 2-1.5 Mya time slice, due to a process that started in an earlier period. However, beginning 1.5 Mya, hyper-carnivores were significantly affected, mainly through the extinction of saber-tooth predators and hyenas. During the whole period, there was no unusual pattern in the under-21 kg, hypo-carnivore group. Werdelin and Lewis (2013) admit that it is also possible to build an equally-valid scenario around a climatic cause for the earlier reduction in the omnivore space. However, they maintain that with regard to the later reduction of the hyper-carnivore space, a case for a direct role for climate is more difficult to sustain. Recent evidence for the habitual hunting of large animals by *H. erectus* at FLK Zinj and Upper Bed II, Olduvai Gorge, Tanzania, (Bunn and Pickering, 2010; Bunn and Gurtov, 2014; Dominguez-Rodrigo et al., 2014a) lends support to the analysis of Werdelin and Lewis (2013) (but see Blumenschine, 1995).

A similar situation, of a decrease in carnivore richness, despite an increase in the numbers of large herbivores, was interpreted by Palombo and Mussi (2006) as ideal conditions for the introduction of humans into Italy and other parts of the Southwestern Mediterranean, 0.65 Mya. Palombo (2010) assumes that humans were classic omnivores, and so does not discuss the possibility of competition from humans as a contribution to the decrease in carnivore richness. She does, however, see the degree of presence of large predators as a main factor affecting the chance for a successful human dispersal in the Mediterranean area during the early Pleistocene. She also points to changes in prey fauna richness as the driver behind humans' early migrations out of Africa. Similarly to the classic explanation of the emergence of humans in Africa, Palombo (2014) sees the dispersal of humans to Southern Europe 1.5 Mya as a result of opening up of the environment which led to change and expansion of the prey spectrum. In a similar vein, Muttoni et al. (2010) developed the 'migration with the herd' hypothesis of the human colonization of Italy, France and possibly Spain around 0.9 Mya, when migrating large herbivores, and particularly elephants, entered Europe through the Danube-Po Gateway (Muttoni et al., 2014; Muttoni et al., 2015). They identified an opening of the landscape to a savannah-like area in the Danube and Po valleys, which led to migrations of large herbivores and of humans, who were already known to consume these or similar herbivores, such as the African straight-tusked elephant and the Asian steppe mammoth. Rodríguez et al. (2012) also identified a potential megafauna predator niche for humans at the end of the Villafranchian (1 Mya) with decline in competition inside the predator guild and increase in human activity. They, however, conclude, based on TD6-2 in Atapuerca, that humans preferred prey size in the 90-360 kgs. They admit, though, that evidence of humans prey preference at the end of the early Pleistocene is scarce and that large mammals' remains are usually not transported to the home base.

Mortality profiles have been used by zooarchaeologists to investigate relationships between hominids and prey species (Discamps and Costamagno, 2015). Stiner (1990) (and see also (Stiner, 2002; Stiner et al., 2011; Stiner, 2012) identified a specific niche, 'prime adults', for humans, beginning 400-250 Kya (Stiner, 2002; Stiner et al., 2011; but see Blasco et al., 2014; Bunn and Gurtov, 2014 regarding early occurance). Other carnivores' prey patterns can be divided into two strategies. The first one is to choose weak animals. This strategy generates a U-shaped, young and old animal mortuary profile. The second strategy is to target animals randomly. This strategy generates a profile typical of the population structure. No other carnivore, except for humans, generates a prime adult inverted U profile (Stiner, 1990). Stiner (2002) speculates that this pattern may be sustainable only for an omnivore. However, the fact that humans practiced what seems to be the most energetically costly and risky hunting strategy, by sidestepping young and old prey, demands an explanation. Stiner explains the 'prime adult' niche as a product of an inter-specific carnivore guild competition. However, it is unlikely that age itself was the hunters' selection criteria. It seems much more likely that a caloric or nutritional benefit, which could be visually identified by the hunters, was at play. In an earlier paper (Ben-Dor et al., 2011), we developed the argument that it was the higher fat content of the 'prime adult' prey that was the attractive characteristic, and by choosing fat animals, a 'prime adult' archaeozoological pattern was created (see Section 7.3.3). In any event, occupying an energetically expensive, precarious and specialized niche in the carnivore space suggests that man evolved to be a most proficient member of the carnivore guild.

An additional possible indication of the degree of carnivory which researchers attribute to humans is embedded in one of the most contentious debates in paleontology - the extent of human contribution to the Late Quaternary megafaunal extinction (see Monjeau et al., 2015 for a recent review of the controversy space). Beginning 50 Kya and ending about 10 Kya, all the megafauna of Australia, America, and Europe went extinct (Barnosky et al., 2004; Koch and Barnosky, 2006). In America and Australia, the extinction was clearly associated, temporally, with the introduction of humans into the ecosystem. This association by itself does not necessarily mean that humans predation was the cause of the extinction. Supporters of an anthropogenic cause actively publish new data and interpretations to that effect (Zimov et al., 2012; eg. Sandom et al., 2014; Bartlett et al., 2015; Faurby and Svenning, 2015; Bakker et al., 2016; Johnson et al., 2016; Saltré et al., 2016), as do their opponents (Grayson and Meltzer, 2015; Meltzer, 2015). There is little argument, though, that on islands humans were indeed responsible for the extinction of large animals (Anderson, 2002; Duncan et al., 2002; Burney et al., 2003; Stuart, 2015; Cooke et al., 2017). In summary, it seems, as Koch and Barnosky (2006) have suggested, that hunting was indeed an important factor in the extinction but "*that the timing and geography of extinction might have been different and the worldwide magnitude less, had not climatic change coincided with human impact in many places*." Recntly, a much more protracted process of megafauna extintion in Africa has been suggested (Bibi et al., 2017). Comparison of between the mammal communities of Olduvai Middle Bed II, dated to 1.7 to 1.4 Mya, and present day Sarangati mammal comnuities led the researchers to hypothesize that humans's predation may have been responsible for the sharp decline of >300 kg. herbivore species during the Pleistocene.

As discussed earlier, competition between humans and carnivores is evident throughout the Paleolithic (Rosell et al., 2012; Stiner, 2012) implying a carnivorous trophic level for humans. However, even a higher trophic level for humans can be implied by identification of targeted hunting and exploitation of large carnivores. Evidence for such exploitation exists for the middle Pleistocene and the MP (Blasco et al., 2010 and references therin), as well as for the Upper Paleolithic of Europe (Tagliacozzo et al., 2013), when humans' exploitation of wolf, fox, and brown bear at Grotta di Fumane during the Uluzzian is described. A case of systematic exploitation of carnivores during the UP by humans is described by Camarós et al. (2016) at several sites in the Swabian Jura (Germany). Cut mark analysis provides evidence of hunting of large carnivores, (lions, cave bears and hyenas) for the use of hides and the consumption of meat. In a similar vein, the domestication of the wolf during the UP may also be considered as carnivore exploitation (Ovodov et al., 2011; Germonpré et al., 2012; Camarós et al., 2016; Germonpré et al., 2017).

5.6.6 Behavioral adaptations to carnivory

Similarly to morphology, metabolism, genetics, and life history, the behavioral ecology of humans should also reflect carnivorous tendencies, if they exist. Quite a few researchers (cited in Arcadi, 2006) have dealt with the behavioral similarity between humans and carnivores and compared this to the similarity between humans and primates. Among the earliest, Schaller and Lowther (1969) compared the behavior of recent HG to social carnivores in Africa, and concluded that the selective forces shaping human society were different from those of primates and more similar to those of carnivores, especially concerning co-operative hunting, food sharing and a division of labor.

Arcadi (2006) went a step further and proposed that humans are similar to one specific carnivore, namely, wolves. Firstly, they are adapted for endurance locomotion. Secondly, they have a diverse diet, and thirdly, they are socially flexible. Variability in prey size selection is extreme in wolves, ranging between 1 and 1000 kg, while humans' prey size range is also extreme at 1 to 6000 kg. As in humans, they are poorly morphologically adapted to catch large prey alone. Carnivore species tend to be more geographically dispersed, reflecting the fact that consuming animal tissue requires less adaptation to specific species. In contrast, plant eater species are more localized because plants boast a myriad of physical and chemical defenses that require specific adaptations (Vrba, 1980). Most indicatively, both humans and wolves display an exptionally wide geographic distribution, unlike primates, which are quite limited in their distribution. In fact, humans and wolves are the most and second most, widely spread species respectively. Both species can thrive in diverse habitats, from desert to arctic. Interestingly, as in present-day humans, the wide geographical spread of wolves comes with minimal genetic differentiation, despite noticeable morphological variation. To the question at hand, the conclusion that the analogy between humans and wolves provides is that it is more likely that carnivory, and specifically the ability to hunt a wide range of animals with respect to size and habitats, were the key facilitators of human dispersal. This conclusion stands in contrast to other hypotheses that attribute the successful human introduction into various environments to a general omnivorous dietary 'flexibility' (Teaford et al., 2002; Ungar et al., 2006 for early humans). Indeed, it seems that a significant plant component in the diet may, in fact, be a hindrance to wide dispersal.

5.6.7 Stenotopy vs. eurytopy

Instead of looking to determine a specific DPA, it may be more meaningful to ascertain whether *Homo* evolved towards becoming a 'specialist' (stenotopy) or a 'generalist' (eurytopy). This subject was previously researched, particularly with regard to early *Homo*, and the success of his survival in contrast to *Paranthropus* (Wood and Strait, 2004). It was generally agreed that the versatility of early *Homo* was a critical component of his success in adapting to changing ecological conditions (Wood and Strait, 2004; Ungar et al., 2006). Wood and Strait (2004) list ten criteria besides diet breadth for evaluating the degree of specialization, such as dispersal patterns and population density, to name but two. However, it is doubtful that many of the non-dietary criteria are relevant to the study of *Homo*. Wood and Strait (2004) caution that wide geographical spread, and high ecological tolerances of the preferred resources, even if they are narrow, may falsely present patterns of a generalist. *Homo* seems to have been precisely such a special case. *Homo* acquired animals, ranging in size from turtles to elephants, across a wide range of habitats. Stenotopy then is, in fact, a relative term. It is also relative to the diet breadth of ancestral species, so the identification of a direction of change is significant. Apparently, for a species whose ancestors were mostly plant eaters, the addition of significant quantities of meat to the *Homo* diet, clearly evident in *H. erectus*, is a move in the direction of eurytopy (flexible, general diet). However, as Wood and Strait (2004) point out, if adaptation to include new food sources precludes the ability to consume another source, then it becomes compelling evidence for specialization. The reduction of plant fiber as a source of energy, as evident by the diminution of the colon and masticatory system (Section 5.5.12) is an excellent example of evidence for specialization rather than versatility. This substantial reduction in the ability to turn plant fiber into energy, in comparison to primates and early hominins, is a most significant specialization event.

Adaptations that preclude climbing can also be considered to indicate specialization away from plant food. These adaptations may have begun in early hominins but continued in *Homo* (Wood and Strait, 2004). The described shoulder adaptation to throwing at the expense of climbing is another example of adaptation to hunting that reduced the economy of plant (and possibly honey) consumption.

In other metabolic phenotypes, the tradeoff between the presumed increased ability to consume animal tissue, and the reduced ability to consume starch, if any, is not so apparent. Among them are the high stomach acidy and adipocyte morphology that indicates an adaptation to a high level of carnivory, but does not immediately demonstrate anti-plant adaptations. It should be noted however that maintaining high acidity in the gut is an energy-costly feature.

Rather than reviewing the direct evidence in the same manner, the results are summarized in Table 5.

Table 5. Paleolithic dietary reconstruction - summary of the results.

Name	**Carnivory**	**Plant**	**Stenotopy**	***Homo***
Indirect evidence				
Energy (brain growth)	Positive	Neutral	+	*H.e.*
Stomach acidity	Positive	Negative?	+ (?)	?
AMY 1 gene	Positive	Neutral	+	*H.e.*
APOE gene	Negative?	Neutral	- (?)	*H.e.*
Insulin resistance	Positive	Negative	+	*?*
Neu5Gc	Negative?	Positive?	- (?)	*?*
Gut morphology	Positive	Negative	+	*H.e.*

Name	Carnivory	Plant	Stenotopy	*Homo*
Mastication	Positive	Negative	+	*H.e.*
Age at weaning	Positive	Neutral	+ (?)	*?*
Longevity	Positive	Neutral	+ (?)	*H.e.?*
Late Adaptations to USOs	Neutral	Negative	+	*?*
Body morphology	Positive	Negative	+	*H.e.*
Direct evidence				
Lithics (<UP)	Positive	Neutral	+	*H.e.*
Isotopes (<LUP)	Positive	Neutral	+	*?*
Dental pathology	Neutral	Negative	+	*H.e.*
Dental wear	Positive?	Neutral	+ (?)	*?*
Paleontology	Positive	Neutral	+	*H.e.*
Behavioral adaptations	Positive	Negative	+	*H.e.*

H.e. – H. erectus

Adaptability through enhanced cognitive ability with its influence on culture, learning and niche construction are considered as a hallmark of the human species (e.g., Laland and Brown, 2006; Boyd et al., 2011). However, at least as far as diet is concerned, as Table 5 and the discussion of the various items show, the evidence for specialization towards carnivory is sustantial. Many items here provide support for the conclusion that a significant level of carnivory was already in place in *H. erectus*. It doesn't mean that plants could not have been a regular component of the diet. It just means that acquiring and consuming animal food was the primary attractor of adaptations and behavior of the *Homo* species, at least until the UP.

5.7 IMPLICATIONS FOR THE ODFBM MODEL

The conclusion that humans specialized in carnivory means that fluctuations of the ecological availability and functional richness of prey animals should have been a key factor in both evolutionary and cultural changes in humans. More specifically to this study, a high level of carnivory in humans, throughout evolution, means that the constraint on protein consumption was often reached, with the result that an obligatory need for significant amounts of animal fat was a constant feature in the lives of humans throughout their evolution.

6 THE NEANDERTAL DIET

As was shown in the previous chapter, carnivory, and therefore meat and fat, were central features of the *Homo* diet since the early days of its evolution and during the Paleolithic. Neandertals are considered to have been the most carnivorous of all *Homo* species. Until recently many researchers agreed that, in Europe, the Neandertal diet had a narrow breadth, and focused on larger prey (Hockett and Haws, 2005; Gaudzinski, 2006; O'Connell, 2006; Bocherens, 2009; Richards and Trinkaus, 2009; Salazar-Garcia et al., 2013; Smith, 2013; Churchill, 2014; Villa and Roebroeks, 2014; Wissing et al., 2015). A higher dietary plant content was postulated in more southern regions of the Neandertal's presence such as the Levant (Madella et al., 2002; Lev et al., 2005). We are particularly interested in MIS 3 which was a cold period leading to the Glacial Maximum. Cold regions like tundra and taiga go through long periods of minimal vegetation, so it is reasonable to assume that Neandertals were also exposed to long periods of minimal vegetation in MIS 3 Europe.

There have been several recent attempts at multidisciplinary reconstruction of the Neandertal diet (Hockett and Haws, 2005; Gaudzinski-Windheuser and Niven, 2009; Salazar-Garcia et al., 2013; Fiorenza et al., 2015). The Neandertal archaeological faunal record in Europe is dominated by large and medium-sized herbivores, including proboscideans and rhinoceroses (Hockett and Haws, 2005; Gaudzinski, 2006; Stiner, 2013; Panera et al., 2014).

Stable isotope research (e.g., Bocherens et al., 2005; Bocherens and Drucker, 2006; Bocherens, 2009; Richards and Trinkaus, 2009; Bocherens, 2011; Wissing et al., 2015; Naito et al., 2016) unilaterally supports a carnivorous profile for the Neandertal diet in Western Europe (but see discussion and some reservations in Fiorenza et al., 2015). Small animals and birds were also consumed (e.g., Blasco and Fernández Peris, 2012).

In recent years, evidence for consumption of plants and cooking has emerged, based on plant residues in Neandertal dental plaque, taken from fossils in Europe and Asia (Hardy et al., 2012; Salazar-Garcia et al., 2013; Henry et al., 2014; Weyrich et al., 2017). A general trend of increased reliance on plant food in a north to south axis was suggested (El Zaatari et al., 2011) but see discussion in Section 5.6.4 which questions the validity of this study.

A single study of 5 sediment samples of Neandertal coprolites from El Salt (Spain) some 50 Kya found that "*Neandertals predominantly consumed meat…but also had a significant plant intake*" (Sistiaga et al., 2014).

In discussing the Neandertal diet, it is important to note that the evolution and life of Neandertals took place mostly in Europe (Arsuaga et al., 2014) from MIS 8 to MIS 3, through extended glacial cycles (VanAndel and Tzedakis, 1996). The most extreme conditions that Neandertals had to cope with were undoubtedly extended winters during the long glacial periods. It meant dealing with low temperatures, extended snow cover (Barron et al., 2003 for OIS 3 glacial period), and even permafrost or seasonal soil freezing, that reached Southwestern France at times (Bertran et al., 2014).

Indeed, ethnographic evidence points to zero plant food foraging in tundra winters, and in fact, even summer plant food consumption is mostly limited to berries and sometimes roots (Krogh and Krogh, 1914; Heinbecker, 1928; Rabinowitch et al., 1936; Lee and Daly, 1999:51; 56; 61; 137; 143; 152; 156; 161; 167). Pleistocene European tundra may have been more productive than present-day tundra (Huntley and Allen, 2003). The reliance of many circumpolar populations on aquatic mammals, their use of guns and the absence of very large prey preclude detailed analogy between them and Neandertals. However, even in lower latitude regions, such as the northern plains of Canada, winters were too cold and snowy for HG to rely on meaningful quantities of plant-based resources (Malainey et al., 2001).

It is also worthwhile mentioning here that the area covering middle and southern Europe, northern Asia and Alaska during the Neandertal's period is called the Mammoth Steppe given the dominance of the faunal assemblage by mammoths as well other large animals (Guthrie, 1982). Contrary to present tundra environments, the Mammoth Steppe is estimated to have been very productive, even as productive as the present African savanna (Guthrie, 1982; Guthrie, 2001; Zimov et al., 2012), providing ample opportunities to Neandertals to acquire large animals like mammoths.

Large animals, and specifically megaherbivores, may have formed an even higher proportion of the Neandertal prey than is apparent from the present faunal record. Morin et al. (2016) argue that megaherbivores are under-represented in Neandertal's faunal assemblages in central places due to the high cost of their bones' transportation. Isotope-based analysis of Neandertals' trophic level led some researchers to conclude that they consumed large quantities of proboscideans, compared to other carnivores (Bocherens et al., 2001; Bocherens et al., 2005; Wissing et al., 2015) but others (e.g., Morin et al., 2016) have offered different interpretation of the same results. Recently, Naito et al. (2016) concluded, based on isotopic analysis of amino acids rather than proteins, that the Neandertal of Spy did not consume relatively high amounts of mammoth meat but O'Connell and Collins (2017) doubt the accuracy of Naito et al.'s measurements.

I therefore conclude, on the basis of the previous analysis that found carnivory to be the dominant pattern of Paleolithic human nutrition and in agreement with Salazar-Garcia et al. (2013), that although there are strong indications that the Neandertal diet included plant-sourced foods at certain times, and in specific areas, it is highly likely that Neandertals became adapted, during glacial periods, to live for a significant number of months, at least during winters, on a diet that included mostly meat and fat.

6.1 NEANDERTALS' LARGE LOWER THORAX MAY REPRESENT ADAPTATION TO A HIGH PROTEIN DIET

One of the presumed outcomes of a highly carnivorous diet, in Neandertals with high energetic requirements, would have been an obligatory high consumption of fat. We (Ben-Dor et al., 2016) published a paper that presented a hypothesis that the Neandertals' 'bell-shaped' thorax, and possibly also wide pelvis, represent, at least in part, adaptations to a high-protein diet. Extending their capacity to process protein into energy would have enabled the consumption of the large quantities of meat in the large animals they acquired, by elevating the protein ceiling.

It is accepted that Neandertals had a relatively voluminous thorax (Franciscus and Churchill, 2002; Sawyer and Maley, 2005; Voisin, 2005; Weinstein, 2008; Gomez-Olivencia et al., 2009; Garcia-Martinez, 2013; Garcia-Martinez et al., 2014). Recently, a previous assertion of a 'bell-shaped' thorax with a larger inferior section (Franciscus and Churchill, 2002; Sawyer and Maley, 2005) was supported by a reassessment of the Kebara 2 thorax (Garcia-Martinez et al., 2014).

Most researchers (Franciscus and Churchill, 2002; Churchill, 2006; Weinstein, 2008) have attributed the evolution of a large thorax to the need to cope with increasing energetic demands. Other researchers have interpreted a reduced area of the trunk, in relation to the Neandertal's mass, as adaptation to cold weather (Ruff, 1994; Weinstein, 2008) although this interpretation cannot apply to a wider lower chest.

Another explanation for the elongated form of the Neandertal's pelvis was proposed by Rosenberg et al. (1988). She suggests that the longer pelvis allows the birth of the larger Neandertal's babies, compared to modern humans.

We hypothesize that the Neandertals' lower thorax had evolved to accommodate a relatively large liver, which evolved to metabolize relatively large quantities of protein into energy, in conditions where:

- Carbohydrates were in short supply due to cold or dry weather.
- Relatively large quantities of protein were readily available, following the hunting of large game, and the exploitation of their fat.

Since increased metabolism of protein to energy also requires increased kidney activity (Hammond and Janes, 1998), we hypothesize that the wider pelvic space of the Neandertal also allowed for the housing of larger kidneys and bladder.

The paper, Ben-Dor, M., Gopher, A. and Barkai, R. (2016), Neandertals' large lower thorax may represent adaptation to high protein diet. *American Journal of Physical Anthropology*, 160: 367–378. doi:10.1002/ajpa.22981 (Ben-Dor et al., 2016) is attached as **Appendix 5.**

7 DIETARY FAT IN PALEOLITHIC HUMAN SUBSISTENCE

In the previous chapters, it was shown that the Paleolithic diet in general, and the Neandertal diet in particular, were high in animal content. Thus I argue that their diet must have been relatively high in fat. Due to the protein constraint, protein by itself could never comprise the majority of the diet. It is therefore only natural to investigate whether fat content was indeed an essential consideration in humans' prey acquisition during the Paleolithic. Also, the prey choice implications of the dependency on fat for Paleolithic humans in general, and Neandertals in particular will be investigated.

7.1 FAT AS THE PRIMARY TARGET IN HUMANS' ANIMAL ACQUISITION

The criticality of the protein ceiling to human diet, and its solution through a significant consumption of fat can be learned by studying humans' attitudes towards fat in general, and of prey choice in particular. The presumed association of animal fat consumption with heart disease, and the inclusion of recommendations to limit animal fat consumption in many public dietary guidelines may have been responsible for the wanting recognition of the importance of animal fat in Paleolithic nutrition, and hence in human behavior and decision making. Recent research (Chowdhury et al., 2014; Lamarche and Couture, 2014; Harcombe et al., 2015) rejects the prevailing dogma and hasn't identified any health concerns related to significant consumption of animal fat, although the debate continues (Hooper et al., 2015).

7.2 HG AND TRADITIONAL ATTITUDES TOWARDS FAT

Despite the reservations regarding the suitability of the ethnographic record for the prediction of DPA during the Paleolithic (Section 5.3), I believe that discerning qualitative rather than quantitative conclusions from the record is less prone to inaccuracies.

Numerous examples of a preference for fat among HG groups are listed by Jochim (2013:81). Among them are Northern groups such as the Copper Eskimo, Nunamiut, Kutchin, Cree, and Ojibwe, but also groups in Tropical and Subtropical regions such as the !kung, Pitjantjara, Wanindijaugwa, Valley Bisa, Miskito and Kalapalo.

Analyzing archaeozoological bison remains in the site of Garnsey, southeastern New Mexico, Speth (2010:xiii) writes: *"In other words, fat, not protein, seemed to play a very prominent role in the hunters' decisions about what animals (male vs. female) to kill and which body parts to discard or take away".*

In his seminal book on hunter-gatherers, Kelly (2013) writes: *"...although ethnographic accounts abound with references to the importance of meat they equally convey the importance of fat…."* He adds: *"It, therefore, may be fat rather than protein that drives the desire for meat in many foraging societies*."

Similarly, Brink (2008:234) notes that *"...fat, not meat, was the essential food of survival to hunting and gathering cultures*."

About the James Bay Cree, Rockwell (1993) writes: "*The Cree considered fat the most important part of any animal. One reason they valued bears above other animals was because of their body fat and because the fat rendered down into a high quality grease*". O'Dea et al. (1991) state that Australian aborigines hunted animals at those times of the year when their fat deposits were the largest, or in other words, following the '*fat cycle.'* The essentiality of fat is best demonstrated in Tindale's account of the decision criteria of Pitjantjara of Australia (Tindale, 1972). He writes: "*When killing the animal, they immediately feel the body for evidence of the presence of caul fat. If the animal is njuka, fatless, it is usually left unless they are themselves starving*". Coote and Shelton (1992) report a similar attitude among the Yolngu of Arnhem, Australia, saying that "*Animals without fat may indeed be rejected as food*." Similarly Haynes and Klimowicz (2015) report that elephant body parts that were low in fat were left by the Ituri forest people at the hunting site.

Interestingly, despite the negative sentiment by health authorities towards animal (saturated) fat, in the U.S. the degree of fatty marbling of the meat is the primary quality grading criterion in which the higher the fat content the higher the quality (http://meat.tamu.edu/beefgrading/).

Reviewing the literature (Ben-Dor, 2015), I found 200 cases of symbolic expressions that use animal fat as a symbol, in the context of ceremony, mythology, and language, among geographically-diverse, traditional societies. An analysis of these cases shows an overwhelming association of animal fat with positive meanings. Among other meanings, fat was used to denote fertility, richness, desirability, sacredness and even life itself.

The paper, Ben-Dor, Miki (2015) "Use of Animal Fat as a Symbol of Health in Traditional societies Suggests Humans may be Well Adapted to its Consumption," Journal of Evolution and Health: Vol. 1: Iss. 1, Article 10. (Ben-Dor, 2015) is attached as **Appendix 6.**

7.3 FAT IN PREY ANIMALS

Fat content varies significantly between species, between animals in the same species, and between seasons in the same animal (Owen-Smith, 2002; Jochim, 2013:39). Fat is the primary energy reserve in animals (Lindstedt and Boyce, 1985). It is acquired during a season of relative plenty to buffer periods of shortage. There are energetic and predation-risk costs associated with the carrying of fat reserves, so they usually would be built up late in the growing season, and amount to no more than is stochastically needed during seasons of shortage (Owen-Smith, 2002).

7.3.1 Fat-containing body parts as choice criteria

As will be discussed separately, two patterns of prey choice - preference for large game and ‘prime adults’ - can be explained as stemming from the concentration on fat as the primary prey choice criterion. Another diagnostic pattern is the decision regarding the transportation of body parts.

A significant body of literature deals with the distribution of animal body parts in archaeological sites with a view to understanding hunters’ decisions about the transportation of sepcific parts to a central place (e.g., Speth, 1983; Blumenschine, 1986; O'Connell et al., 1988; Grayson, 1989; Bunn and Ezzo, 1993; Lupo, 2001; Domínguez-Rodrigo, 2002; Codding et al., 2010; Edwards and Steele, 2011). Binford (1978) developed some 21 different indices designed to explain prey body parts transport decisions. One of the most useful among them was found to be a marrow index. Binford’s marrow index took into account the presumed quality of the marrow in different animal body parts in addition to the quantity, however, Jones and Metcalfe (1988) found that a simpler index that takes into account only the volume of the marrow cavity in the bone better explain the Inuit assemblage that Binford were using. Later, Morin (2007) emphasized the importance of oleic acid (a monounsaturated fat) and published the Unsaturated Marrow Index. Using bison as a model, Emerson (1990) developed a fat index which takes into account the fat that is contained in the meat of the various body part. Morin (2012) found the fat index to best fit prey body part choice in Saint-Cesaire by both Neandertals and modern humans. Further analysis by Morin and Ready (2013) of 167 European Paleolithic and Mesolithic faunal assemblages from the LP to the UP found that the best correlations of the faunal remains were with the Unsaturated Marrow Index, and not the meat itself. This evidence ties in with the abundant evidence of a systematic exploitation of the fatty marrow in animals of all sizes, from elephants to rabbits, in many sites worldwide, throughout the Paleolithic (e.g., Binford, 1985; Blumenschine and Madrigal, 1993; Bar-Oz and Munro, 2007; Garvey, 2010; Pickering and Domínguez-Rodrigo, 2010; Stiner, 2013; Boschian and Gerometta, 2014; Starkovich, 2014; Martínez-Polanco et al., 2016). Agam and Barkai (2016) postulate that high fat content is among the major reasons for the preferential transport of proboscideans' heads to central places. In summary, the content of fat, in the form of marrow and possibly intramuscular fat, seems to have been major decision criteria in the transport of prey animal body parts.

7.3.2 Exploitation of bone fat (grease)

A convincing evidence for the criticality of fat to HG is the exploitation of bone fat or grease as it is sometimes called. Bone fat is difficult to extract. Brink (2008:195) describes an experiment on bone fat extraction, where the bones had to be broken into small pieces at great effort and inconvenience. The extraction of fat from bones demanded lengthy boiling, which, in the absence of cooking vessels, is done by using heated stones of specific quality in hide-lined pits filled with water. These stones break after some time, and new suitable stones have to be brought from further and further afield (Brink, 2008:202). All this effort is invested in extracting what is a mere 6% or so of the total fat in the animal or some 3% of the total calories (Emerson, 1990: Table 7.1), sometimes because it is the only fat that is left in the animal (Outram, 2001). This low yield, in relation to the extraction effort, led some researchers (Lupo and Schmitt, 1997; Outram, 2003; Outram, 2004) to suggest that the exploitation of bone fat, as opposed to the marrow, is a sign of dietary fat stress, when carbohydrates are in short supply. It is interesting to note then that bone fat was also extracted in temperate environments in late Paleolithic periods (Bar-Oz and Munro, 2007), and by recent HG (Outram, 2001 and references therein), which may signal that carbohydrates, as a replacement to fat, can be scarce also in temperate environments. The earliest evidence for bone fat extraction comes from two French Mousterian Neandertal sites, Noistier Cave and Roc de Marsal, dated to late MIS 4 and MIS 3 (Costamagno, 2013; Castel et al., 2016). Later sites with evidence of bone fat extraction are found in the UP of Europe (Mateos, 2005; Manne et al., 2006; Fladerer et al., 2014; Manne, 2014), the Levant (Munro and Bar-Oz, 2005; Bar-Oz and Munro, 2007), and the New World (Saint-Germain, 2005; Karr et al., 2015 and references therein).

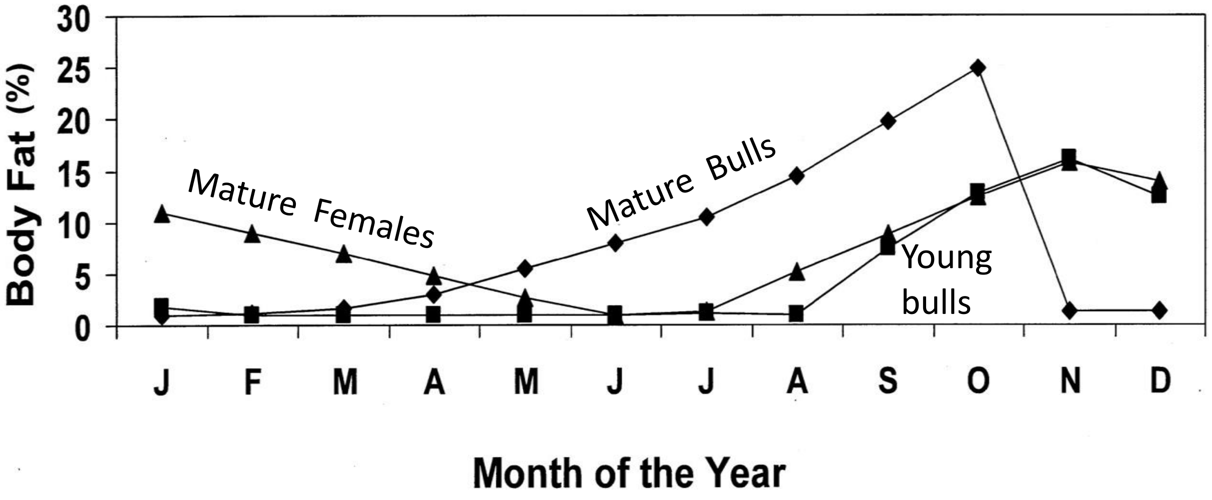
7.3.3 Fat and hunting of 'Prime Adults'

As discussed earlier, a trend towards hunting 'Prime Adult' animals is evident beginning 400-250 Kya (Stiner et al., 2011; Domínguez-Rodrigo et al., 2015), and perhaps 800 Kya (Saladié et al., 2011), or even 1.8 Mya (Bunn and Pickering, 2010). This phenomenon is also very apparent in Neandertals' archaeofauna throughout their wide-ranging habitat (Pike-Tay et al., 1999; Gaudzinski and Roebroeks, 2000; Valensi and Psathi, 2004; Adler, 2006; Burke, 2006; Speth and Clark, 2006; Gaudzinski-Windheuser and Roebroeks, 2011; Niven et al., 2012; Speth, 2012; Stiner, 2013; Yravedra et al., 2015; Castel et al., 2016; Morin et al., 2016). A notable exception may have been Mammoth and other Elephantidae where younger animals seem to have been preferred (Fladerer, 2003; Svoboda et al., 2005; Chazan and Horwitz, 2006; Blasco and Fernández Peris, 2012), possibly due to higher quality fat in specific organs (Guil-Guerrero et al., 2014; Reshef and Barkai, 2015) and ease of transport.

It is highly unlikely that hunters chose animals because of their age, as age by itself is unlikely to provide any benefit in return for the loss of encounter frequency, and for the additional difficulty and risk of tracking and subduing a relatively experienced and fit sector of the population. Rendu (2010) speculates that males were hunted after the rut when they are at their weakest. However the pattern of hunting weak animals is typical of cursorial carnivores and not humans (Stiner et al., 2011). Two conceivable criteria for a potential benefit from hunting prime adults are size and fat. Gaudzinski-Windheuser and Niven (2009) argue that prime adults would provide the best yield in terms of nutrition (meat, marrow, organs) and other resources such as skins, tendons, and antlers. If the size of hide, organs, antlers and such were the criterion, we would expect to find almost exclusively adult and older males. However, we find mostly either female adults or male adults, depending on the hunting season (see references above). Speth (1983) noticed that bison males were hunted and processed preferentially to females and calves in the spring at the Garnsey site, based on their fat content, in line with historical and ethnographic observations. It seems then, that fat content is the most logical criterion that arises due to the changing annual distribution of fat content among the different age and gender groups, in the 'prime adult' age profile.

Fat reserves change, depending on season and life history stage. Immature animals invest resources in growth at the expense of fat reserves (Owen-Smith, 2002:160). Consequently, during most of the year, prime adult animals will have a higher fat content than immature animals. Reindeer (caribou in N. America) was the Neandertal's species that most frequently exhibited the 'prime adult' hunting pattern (Gaudzinski-Windheuser and Niven, 2009).

Figure 1. Monthly fat distribution in caribou: comparison among young bulls, mature bulls, and mature females throughout the year



After Cordain et al. (2005: Figure 5, based on Spiess 1979 as cited in Cordain 2005)

As can be seen from Figure 1, hunting only mature females from November to April, and mature males from May to October will maximize the fat content of the acquired animals. So, throughout the year, mature animals provide the highest fat content as a percentage of calories. It is also important to notice that from November to April, the winter period, when the fat acquisition is most crucial, due to the minimal availability of plant food, acquiring mature females of caribou is the optimum fat acquisition strategy.

Based on Figure 1 and the cubic regression of body fat ratio in Cordain et al. (2000: Figure 3), J. Stanton (http://tinyurl.com/juafse7) calculated that targeting mature bulls and females, alternately, will result in an average caloric fat content of 56%, compared to 36% if animals are chosen randomly. However, the potential for premium fat content based on animal selection is even greater when concentrating on fatter animals within the age/gender group. Brink (2008:40) quotes Josiah Gregg in 1830: "*In the chase, the experienced hunter singles out fattest buffalo as his victim*". Identifying fat animals is apparently one of the most important skills that experienced hunters bring to the hunt. Buffalo Bird Woman lists the signs of a fat animal (Brink, 2008:42): *"…the fat ones have a patch of black hair over the eyes…and the new-grown hair is very black… Also, there is a black stripe on the highest point of the spine over the shoulders, and there is a little black hair around the horns*". It is thus quite safe to assume that the ability to single out fatter animals may have resulted in an even higher fat content in the prey than the 56% achieved by just hunting random 'prime adults' of the correct gender.

8 FAT AS A FUNCTION OF ANIMAL SIZE

The Neandertal is known to have been a hunter of large animals (Nougier, 1954; Marean and Kim, 1998; Patou-Mathis, 2000; Hockett and Haws, 2005; Stiner, 2006; Discamps et al., 2011; Gaudzinski-Windheuser and Roebroeks, 2011; Niven et al., 2012; Morin et al., 2016). Researchers attribute his solid frame to the need to withstand close encounters with large animals (Geist, 1978; Smith, 2013; Churchill, 2014). There is some basis to conclude that Neandertals may have specialized in hunting megafauna such as elephants and rhinos (Geist, 1978; Wissing et al., 2015; Morin et al., 2016).

8.1 RANKING OF ANIMALS BY SIZE

Optimal foraging models from evolutionary ecology serve as a basis for a large body of literature concerning the association between prey body size and its preference order (ranking) (see dicussion and references in Broughton et al., 2011). The majority of the experimental and ethnographical studies (Ugan, 2005: Table 1; Stiner and Kuhn, 2009: Table 11.1; Broughton et al., 2011: Table 1) did find a correlation between post-encounter return rates and body size. Two studies out of ten in the Broughton 2011 sample, where the correlation was not found, were carried out with a narrow body-size range and small maximum size (22-28 kg compared to 261-498 kg in other studies). The return rates did account for missed hunting attempts. However no concern was directed to the fat content of the hunted animals in the testing of these models. Broughton et al. (2011) found that the width of the range of weights of exploited prey was positively associated with the strength of the correlation between size and rank. This finding indicates that correlations in pre-megafaunal extinction Paleolithic size ranges (say 22-6500 kg (*Elaphus antiquus*)) could have been much stronger than in the 22 - 498 kg range in their study. As will be shown later in this chapter, the difference in fat content between large and small animals is approximately 65% higher than the difference in caloric return, so if fat was indeed the principal criterion of HG hunting decisions, the ranking, based on animal size, is much more pronounced than previously thought.

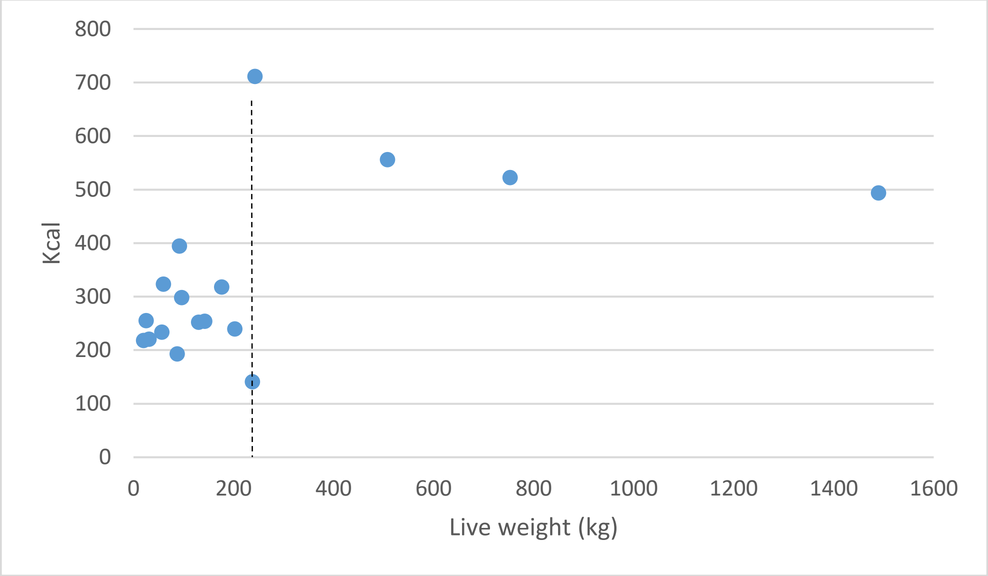
Pitts and Bullard (1967) were the first to measure total fat stores as a function of body size in a variety of mammals from North and South America. They found that larger animals contain relatively larger amounts of fat. Calder (1984) reexamined their data in eutherian terrestrial mammals only and found the same pattern on a subsample of terrestrial animals. Cordain et al. (2000) already mention increased body fat as a reason for the attraction of HG to large game. Speth (2010:125); (see also Speth et al., 2013) objects to Cordain et al.'s hypothesis and presents a hypothesis associating large game hunting with male signaling. Speth was skeptical as to the applicability of the study by Pitts and Bullard (1967) to the explanation of "*human predilection for big game hunting*." Speth (2010:126) cites geographical, sexual, and seasonal heterogeneity as well as a sample biased towards small animals and small sample size as reasons for skepticism. Speth (2010:127) calls for a study that will be more geographically limited, look only at wild animals, truly span the size of small to large terrestrial animals, and measure peak and low seasonal fat content. As it turns out, a study (Ledger, 1968) that answers all but one of Speth's requirements, did exist. Speth has even cited data from this study, although somewhat partially (Speth, 2010: Table 4.2), to support a (probably correct) claim for low body fat content among African prey animals, compared to North American animals in the spring. In 1968 Ledger (1968) published data about the body composition of 257 wild African prey animals of both genders, from 16 different species, ranging in size from hippopotamus at 1489.8 kg to Thomson's gazelle at 16.9 kg. Ledger (1968) did not include data for marrow fat, cancellous fat, and intramuscular fat, or fat from the brain, heart, liver, and tongue, so the absolute fat percentage calculation for each animal requires some adjustments. However, taking into account only the 'carcass fat' and 'offal fat' in Ledger (1968: Appendix II,III) shows a clear trend of increasing fat content with increasing live weight, such that the average fat weight per kg body weight (table 6) of the five largest animals in the dataset is more than double than the average of the five smallest animals.

Table 6. Total fat per kg live weight in African wild animals (based on Ledger 1968: Appendix I, II, III). Average for males (M) and females (F) unless otherwise indicated

Animal	**Live weight kg**	**Carcass fat kg**	**Offal fat kg**	**Total fat kg/kg live weight**
Hippopotamus (M+F))	1383.0	51.55	16.2	0.04

Animal	**Live weight kg**	**Carcass fat kg**	**Offal fat kg**	**Total fat kg/kg live weight**
Buffalo (M)	753.0	21.3	9	0.05
Eland (M)	508.0	12.7	9.2	0.04
Wildebeest (M+F)	217.5	8.35	3.9	0.04
Oryx (M+F)	168.5	4.85	1.65	0.06
Topi (M+F)	117.5	1.35	0.8	0.04
Kob (M+F)	79.4	1.5	0.75	0.02
Lesser kudu (M)	92.0	1.9	0.9	0.03
Warthog (M+F)	88.0	0.8	0.45	0.03
Grant's gazelle (M+F)	50.7	1.1	0.55	0.01
Impala (M+F)	49.4	0.55	0.4	0.03
Gerenuk (M)	31.0	0.4	0.1	0.02
Thomson's gazelle (North) (M+F))	21.9	0.25	0.2	0.02
Thomson's gazelle (South) (M+F)	18.6	0.25	0.15	0.02

Figure 2. Fat calories per kg live weight as a function of live weight (Average for males and females) based on Table 6 and 9 Kcal per gram of fat.



As can be seen from Figure 2, there is a steep decrease in fat calories per 1 kg of live weight as live weight decreases below 200 kg, maybe due to an increased reliance on escape as an anti-predation strategy, where the increased starvation risk due to lower fat content is offset by a decreased predation risk.

Although African wild animals are less fatty than Northern animals, as Speth (2010:80) convincingly argues, Ledger's data show that their actual fat content is not negligible. Speth (2010:80) claims that their fat content is meager, and brings ample anecdotal evidence to support his claim. However, interestingly, he singles out (Speth, 2010:59-70) four animals as unusually fat – hippopotamus, eland, giraffe, and zebra. It so happens that these four animals are among the largest in Africa. A fifth animal that is mentioned as relatively fat in one of Speth's anecdotes (Drummond 1875:281 in Speth, 2010:70), is the rhinoceros, the second largest animal in Africa. So, in the end, even the anecdotes that Speth provides support the conclusions of the analysis of Ledger (1968), that larger animals are fattier than smaller animals.

A comparison of percentage fat weight by animal weight (w/w) between the data published by Ledger (1968) and the predictions of Pitts and Bullard (1967) (based on their formula of 1.5 X Fat-Free Weight^0.2), is problematic, as they measured fat content using different methods. However, Ledger's data and Pitts and Bullard's predictions show a very similar trend, when comparing the relative average fat content of the group of large animals in Ledger dataset, weighing at least 100 kg, with the average for smaller animals. Both Ledger's data and the predicted fat content based on Pitts and Bullard's formula result in a surprisingly similar higher average fat content for the larger animals' group (an average of +44% higher fat content according to Pitts and Bullard's formula compared with +46% according to the Ledger dataset).

Conditions of extended cold as well as snowy climatic periods, as found in Europe during the MP, tend to benefit large herbivores (Lindstedt and Boyce, 1985; Churchill, 2014: Chapter 4.4). Three factors may cause large animals to contain more fat, in relative terms, than smaller animals.

- The risk of carrying the fat is smaller for them, since their behavior is less affected by predation risk than that of smaller animals (Cooper and Stankowich, 2010; Hopcraft et al., 2012),
- Energetically, since their ratio of BMR to size is lower than that of smaller animals (Clauss et al., 2003) they lose less fat than smaller animals during dry seasons.
- Unlike smaller animals, they can extract energy from the lower-quality forage during the dry season (Owen-Smith, 2002:86; Clauss et al., 2003). Lindstedt and Boyce (1985) have shown that large animals have longer fasting endurance, which explains their relative abundance in highly seasonal territories.

It is the availability of fat during seasons of reduced availability of plants, for both animals and humans, which would have made large animals so critical to the fat-dependent Neandertal. During periods of extremely low plant food availability, such as extended European winters in MIS 3 with extended snow cover periods, smaller animals contain very little fat, and plants (carbohydrates) are in short supply. Most of the energy, beyond the energy that protein can supply, has to come from fat. So how does the obligatory need for fat compares with its availability in animals? For this reason, it is essential to estimate the total content of fat in animals, and not just to establish variation according to size.

8.2 ADJUSTMENTS TO LEDGER 1968

Several adjustments to the dataset published by Ledger (1968) must be made since he did not measure the fat content of marrow, internal organs, cancellous fat, and most importantly, intramuscular fat

(Ledger, 1963; Ledger, 1968). There is little systematic data for these fat components in prey animals. The most detailed data can be found in Emerson (1990), who for a Ph.D. thesis dissected and measured extracted fat and protein from four bisons from a North American reserve and reported the measurements in unmatched detail. The data required further processing to arrive at the ratios presented here, and are based on Tables 6.12 and 7.1 in Emerson (1990). It should be noted that data from Northern animals are used here to adjust data from African animals. However, since in the end, we are interested in animals that were acquired in Europe, the fact that we are basing it on large Northern animals may be an advantage. Also, the raw bison numbers can also be used to gauge the typical fat content of large Northern animals.

It should be noted that the relative fat content should be stated and analyzed in caloric terms, and not as weight percentages, as is so common. There are two reasons for doing this: 1. There are 2.25 times more calories in a gram of fat than in a gram of protein, and since animal acquisition is calorie-driven, and not weight-driven, these units should form the basis for the analysis. 2. The fat content of animals reported as weight percentage from the total weight of the animal is usually in the low single digit, which gives the impression that there is little fat in the animal. Since most of the animal weight is composed of water, bone, and hide, this low percentage figure is misleading, in relation to the relative importance of fat as a caloric source. For example, in the following table of bison content (Table 7), the average fat content by live weight is 4.7%, but the caloric percentage of fat from total calories is 51.3%.

Table 7. Percentage of fat from total fat in body parts of four bison and total caloric percentage of fat (calculations based on data from Tables 6.12 and 7.1 in Emmerson (1990)

Body parts	**Fall yearling male**	**Spring adult male**	**Spring adult female**	**Fall adult female**	**Average relative fat**
Subcutaneous	6%	9%	19%	12%	12%
Intermuscular	45%	31%	28%	36%	35%
Body cavity	15%	10%	10%	9%	11%
Intramuscular	**13%**	**32%**	**28%**	**26%**	**25%**

Body parts	**Fall yearling male**	**Spring adult male**	**Spring adult female**	**Fall adult female**	**Average relative fat**
Marrow	**8%**	**6%**	**4%**	**3%**	**5%**
Bone grease	**6%**	**5%**	**7%**	**5%**	**6%**
Combined organs	**8%**	**7%**	**4%**	**8%**	**7%**
TOTAL FAT (kg)	10.0	22.1	28.8	28.7	
Live weight (kg)	288	640	481	496	
Fat to live weight	3.5%	3.4%	6.0%	5.8%	4.7%
Fat cal. to total cal.	43.4%	44.9%	59.6%	57.1%	51.3%

As can be seen from Table 7, the fat from the parts that were not measured by Ledger (1968) (intermuscular, marrow, bone grease, organ fat) form some 42% of the total fat of the bison. Intramuscular fat, at an average of 25% (13%-32%) of the fat, is by far the most substantial component that was not included in Ledger (1968). A study of six white-tailed deer from a reserve in Michigan (McCullough and Ullrey, 1983: Table 4) yielded an average of 19% (11%-26%) of the fat from intramuscular fat. There is no direct reference in Ledger (1968) to that omission, except to say that "*lean meat includes intramuscular fat*", but elsewhere Ledger (1963) indicates, when discussing the tenderness of African game meat, that it is known that very little fat is present in its muscular tissue. The adjustments to Ledger (1968) have to depend on the questions asked. Here we would like to answer two questions about fat content in animals of various sizes: 1. Do large African animals indeed contain little fat as argued by Speth in (Speth, 1989) and (Speth, 2010)? 2. What was the fat content of Northern animals during MIS 4-3 in Europe?

In answer to the first question regarding early African Paleolithic prey, I accept, for argument's sake, that because African animals have so little intramuscular fat an adjustment is superfluous. Since archaeological evidence for marrow exploitation in Africa throughout the Paleolithic abounds (Bunn and Ezzo, 1993), adjustment for marrow is in order. Table 7 shows an average marrow content of 5% (3%-8%) of the total fat. If we deduct the 25% intramuscular fat from the bison sample, to compare to

Ledger’s data, the relative content rises to 6.6%. In white-tailed deer, McCullough and Ullrey (1983: Table 4) found an average of 2.3% for marrow so that an adjustment that deduct the 18% intramuscular fat in their table brings the average up to 3%. It should be noted that the other body parts of Northern animals that we use here for adjustment are fatter than African animals, so naturally, the marrow portion, which tends to remain constant under normal conditions (McCullough and Ullrey, 1983), will come out smaller in percentage terms in northern animals. I have chosen to adjust for marrow at 4.8%, being the average between the bison and the white-tailed deer, when intramuscular fat is excluded from the total. In a similar vein, I have arrived at 6.4% for bone fat and 9.9% for inseparable fat in internal organs. It could be argued that fat in internal organs should be treated like intramuscular fat, however since fat is functional in these organs (e.g. brain, tongue), it is highly likely that African animals do have a substantial amount of fat in these organs. Again, in the name of caution, I reduced the adjustment of fat in internal organs by half to 5%, in the ‘African’ adjustment. Also, since bone fat extraction for the early African Paleolithic is in great doubt, no adjustment is made in the ‘African’ adjustment.

Another adjustment that must be made to the data published by Ledger (1968) is the deduction of the moisture content of the measured fat tissue since Ledger measured raw fat tissue that includes water. I used 5% water content in fat tissue, following data from Kuhnlein et al. (2002: Table 2), regarding moisture content in the raw fat of caribou and moose. Following these adjustments, Table 8 and 9 provide fat percentages by calories and weight of male and female species in Ledger’s database, adjusted for the fat content that was not measured by Ledger. African and European adjustments are made to account for the presumed lower intermuscular fat content in African animals.

Table 8. Fat content in African male animals based on Ledger (1968: Appendix I,II,III), adjusted to simulate results of fat extraction by chemical methods.

Animal (n)	**Weight kg**	**Unadjusted Ledger fat E%**	**Adjusted 'African' fat E%**	**Adjusted 'European' fat E%**	**Unadjusted Ledger fat w/w %**	**Adjusted 'African' fat w/w %**	**Adjusted 'European' fat w/w %**
Hippopotamus (4)	1489	56%	57%	67%	4%	4%	6%
Buffalo (8)	753	54%	55%	65%	4%	4%	6%
Eland (5)	508.1	50%	51%	61%	5%	5%	7%
Wildebeest (K) (10)	243.3	58%	59%	69%	6%	6%	9%
Waterbuck (10)	237.7	20%	20%	28%	1%	1%	2%
Wildebeest (S) (10)	203	34%	35%	45%	2%	2%	3%
Oryx (10)	176.4	36%	38%	48%	3%	3%	4%
Kongoni (hartebeest) (5)	142.5	31%	32%	43%	2%	2%	3%
Topi (10)	130.8	32%	33%	43%	2%	2%	3%
Kob (10)	96.7	34%	35%	46%	2%	2%	4%
Lesser kudu (10)	92.1	40%	41%	51%	3%	3%	5%
Warthog (10)	87.8	26%	27%	36%	2%	2%	2%
Grant's gazelle (6)	60.1	36%	37%	47%	3%	3%	4%
Impala (10)	56.7	29%	30%	39%	2%	2%	3%

Animal **(n)**	**Weight kg**	**Unadjusted Ledger fat E%**	**Adjusted 'African' fat E%**	**Adjusted 'European' fat E%**	**Unadjusted Ledger fat w/w %**	**Adjusted 'African' fat w/w %**	**Adjusted 'European' fat w/w %**
Gerenuk (10)	31.2	26%	27%	36%	2%	2%	3%
Thomson's gazelle (N) (10)	25.3	32%	33%	43%	2%	2%	3%
Thomson's gazelle (S) (10)	20.3	30%	31%	41%	2%	2%	3%

'African' animals – adjusting for marrow fat +4.8%, organ fat +5%, moisture -5%

'European' animals – adjusting for marrow fat +4.8%, organ fat +9.9%, intermuscular fat +21.5%, bone grease +6.4%, moisture -5%

Protein – Ledger (1968: Table I)

E% – calories from fat as a percentage of total calories.

(K), (S), (N), (S) – Different regions

Table 9. Fat content in African female animals based on Ledger (1968: Appendix I,II,III), adjusted to simulate results of fat extraction by chemical methods

Animal **(n)**	**Weight kg**	**Unadjusted Ladger fat E%**	**Adjusted 'African' fat E%**	**Adjusted 'European' fat E%**	**Unadjusted Ledger fat w/w %**	**Adjusted 'African' fat w/w %**	**Adjusted 'European' fat w/w %**
Hippopotamus (4)	1277.2	67%	68%	77%	4%	6%	10%
Wildebeest (K) (10)	192	62%	64%	73%	6%	6%	9%
Waterbuck (10)	181	45%	46%	57%	1%	4%	6%

Animal (n)	**Weight kg**	**Unadjusted Ledger fat E%**	**Adjusted 'African' fat E%**	**Adjusted 'European' fat E%**	**Unadjusted Ledger fat w/w %**	**Adjusted 'African' fat w/w %**	**Adjusted 'European' fat w/w %**
Wildebeest (S) (10)	160.3	55%	56%	66%	2%	5%	8%
Oryx (10)	161.5	55%	56%	66%	3%	6%	9%
Kongoni (hartebeest) (5)	126.2	49%	50%	61%	2%	4%	6%
Topi (10)	103.9	29%	30%	39%	2%	2%	3%
Kob (10)	62.1	45%	46%	56%	2%	4%	6%
Warthog (10)	60.2	28%	29%	39%	2%	2%	3%
Grant's gazelle (5)	41.3	50%	51%	62%	3%	5%	7%
Impala (10)	42	29%	30%	39%	2%	2%	3%
Thomson's gazelle (N) (10)	18.4	34%	35%	45%	2%	2%	3%
Thomson's gazelle (S) (10)	16.9	47%	49%	59%	2%	4%	7%

'African' animals – marrow fat +4.8%, organ fat +5%, moisture -5%

'European' animals – marrow fat +4.8%, organ fat +9.9%, intermuscular fat +21.5%, bone grease +6.4%, moisture -5%

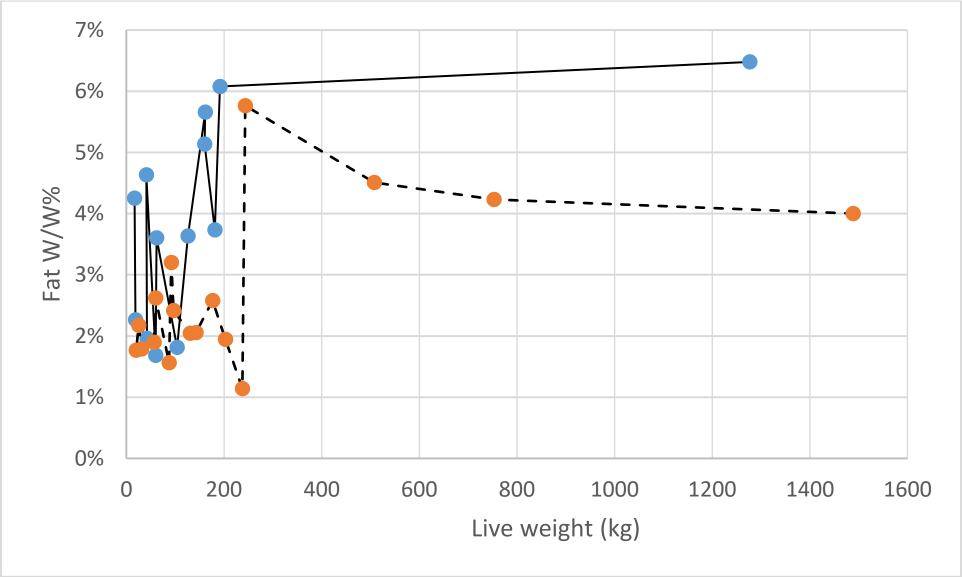
Protein – Ledger (1968: Table I) for males, adjusted to females according to live weight ratio.

E% – calories from fat as a percentage of total calories.

(K), (S), (N), (S) – Different regions

As a side issue, a chart superimposing male and female fat w/w ratio shows that in Africa, females, in general, seem to contain, on average, higher fat than males.

Figure 3. Males vs. females w/w fat content in African game (based on Ledger (1968) without adjustments) as a function of body weight.



Males – Dotted line, Females – Full line

Two conclusions stand out from this analysis:

1. African game animals have a significant amount of fat. In females, five out of the 13 species studied by Ledger have an average unadjusted caloric fat percentage of between 50%-67% and an additional four female species have above 40%. This fat can be easily accessed with the use of a knife (separable fat) and does not include marrow, intramuscular fat, or bone fat.
2. The weight to weight ratio (w/w), in which fat is usually reported, is grossly misleading about the relative contribution of fat from an animal. For example, a female hippopotamus, whose (unadjusted) weight to weight fat ratio is 4%, contributes 67% of her calories as fat. Even in smaller animals such as Kob and Gazelle a 4% w/w still corresponds to a caloric contribution of 45%-47%.

To ascertain that the validity of adjusting the data published by Ledger (1968) to 'European' fat content, I have collected information regarding the fat content of Northern wild animals, and compared it to similar-size animals in Table 8 and Table 9.

Table 10. w/w% or E% fat content of wild Non-African animals compared to the European adjustment of Ledger (1968) for similar-size animals.

Animal (n)	**Live weight[1]**	**Fat content w/w% or E%**	**'European' estimate**	**Reference**
Reindeer (23)	58.5-79.5	12.7%-25.5% w/w	3%-7%	(Pond et al., 1993)
Adult bison (3)	496-640	3.4%-6% w/w	6%-9%	(Emerson, 1990)
Giant deer	388	19.1% w/w	7%	(Morin, 2012: Table 3.5)
Mule deer	? (68-92)	3.1%-16.9% w/w	3%-6%	(Anderson et al., 1972)
Grizzly bear	? (130-160)	68% E%	57%-73%	(Foote, 1965)
Alaskan caribou (reindeer)	? (90-110)	55% E%	39%-61%	(Foote, 1965)
Wombat (15)	14-28	49% E% 2.6% - 19.3% w/w	41%-59%	(Woolnough et al., 1997)

[1] ? – Data not provided. Estimated based on similar animals in Ledger (1968).

As can be seen from Table 10, the fat percentage varies substantially between and within species in the Non-African sample. This variability is due to a fluctuation in fat content as a function of species, size, gender, season and age. In general, it seems that the estimated 'European' values are in line with the cited data. In the case of the three adult bison in Emerson (1990), the estimate seems to be higher than what she found. It should be noted, however, that two of Emerson's animals were culled in the summer and the female, which was culled in the fall, when fat is at its peak, had a fat content of 6% w/w, in line with the European estimate. In another case, the reindeer of Pond et al. (1993), the fat content is 3-4 times greater than in the European estimate. This reindeer sample is from an Arctic island (Svalbard), where access to feed during winters is extremely limited, compared to other Northern areas, due to the freezing of the snow, so that fat accumulation is apparently higher in preparation for winter.

Another reason for Paleolithic humans to prefer large game could be simply that by single kill of a larger animal they could acquire as much fat as in numerous kills of smaller animals. Since, as was shown in Figure 3, percentage fat content rises with body size, assuming that fat content is the hunting criterion, and then Table 11 illustrates this point. It states the fat content of an animal in terms of the fat content of another animal. So, in terms of fat, hunting one eland is equal to hunting 24 impalas, whereas the eland weighs only ten times more than the Impala (Table 6.). It emphasizes the point that accepted ranking of prey animals by weight or a total number of calories grossly underestimate the relative attractiveness of large animals if one accepts that fat content is the major criterion.

Table 11. Average fat content ratio of large animals in terms of small animals' fat content, compared to the weight ratio (in parentheses)

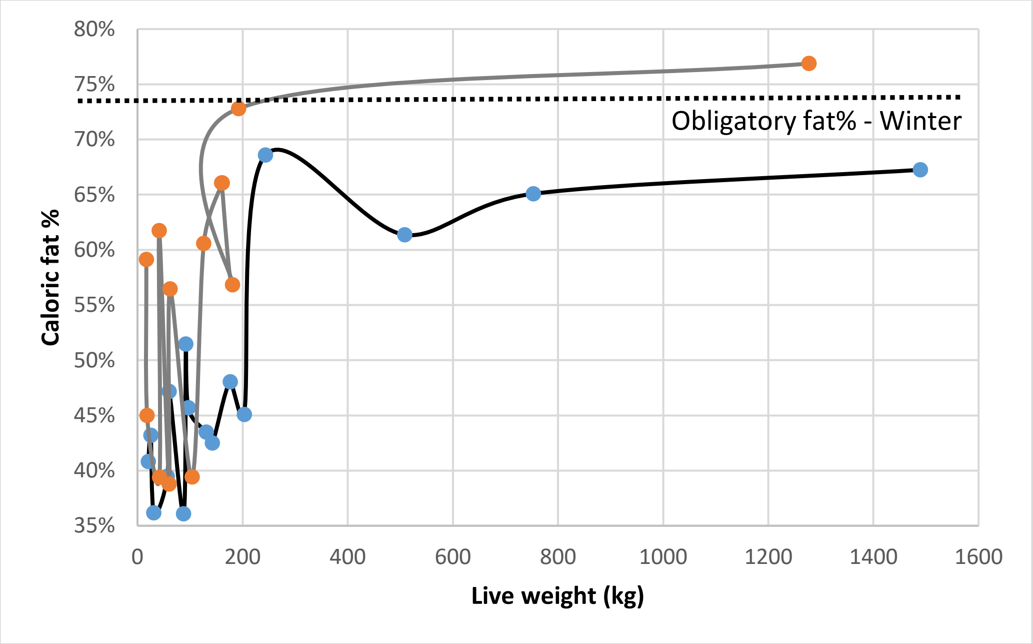
Animal (weight, kgs)	**Hippopotamus (1383)**	**Buffalo (753)**	**Eland (508)**
Oryx (169)	10 (8)	5 (4)	3 (3)
Kob (79)	31 (17)	14 (10)	10 (6)
Impala (49)	75 (28)	34 (15)	24 (10)
Thomson's gazelle (22)	147 (62)	66 (34)	47 (23)

8.3 COMPLETING THE MODEL APPLICATION – WHICH ANIMALS SATISFY THE NEANDERTAL'S OBLIGATORY FAT REQUIREMENTS?

Regarding energetic efficiency, groups which could acquire animals having a fat content that is higher or equal in caloric percentage to the obligatory fat caloric ratio would be able to exploit all the protein calories in the acquired animal.

The following chart compares the fat caloric percentage of ‘European’ adjusted males and females to the obligatory fat content that was calculated in Table 1. I took the obligatory fat value that was calculated based on the most conservative estimate of Steegmann Jr. et al. (2002) as an estimated winter of 75% obligatory fat requirement.

Figure 4. Obligatory fat vs. fat in prey animals. Grey – females; black – males; dashed – obligatory dietary fat (Table 1).



The chart is based on Ledger’s data, obtained in Africa, with unknown seasonal distribution, adjusted to ‘European’ conditions. Ledger (1968) states that “*only healthy, normal looking, animals were shot*.” The chart shows that out of the 16 male animal species and 13 female animal species, only the 1,200 kg female hippopotamus (grey line) would have satisfied the Neandertals’ obligatory fat requirements during winter, even before adjustment for loss of fat during winter. The animals’ fat content during winter is invariably lower than at the end of summer/fall. Hence, none of the animals satisfy the obligatory fat ratio, and most of them are far below, especially the smaller species. This chart also demonstrates how dependent Neandertals were on large animals, that lose less fat during winters (Lindstedt and Boyce, 1985), to minimize the gap between their fat requirements and the fat in their prey.

So, what could a Neandertal do during winters in the face of such a considerable fat shortage? Several options were explored here: 1. Adapt morphologically and metabolically to consume more protein. 2. Concentrate on large animals 3. Hunt prime adults. 4. Preferentially exploit fat-bearing parts.

8.4 SUMMARY OF CHAPTERS 6-8

Given the protein constraint, the logical conclusion for a diet that is highly dependent on animal sources, as laid out in Chapter 6, is that Neandertals were highly dependent on fat to meet their high energetic demands. The obligatory energy from animal fat was calculated to be very high at 75%-80% during glacial winters (Table1). Two patterns in Neandertals' faunal assemblages were discussed in the context of fat acquisition – the dominance of both 'prime adults' and large animals. The best available database of fat content in prey animals of various sizes (Ledger, 1968) was analyzed, and a previous assertion that larger animals contain significantly higher ratios of fat to protein was verified. An adjustment of the African database to European conditions was carried out. Matching the obligatory fat requirements from the model with the fat content in the animals showed that during winters it was challenging for Neandertals to obtain enough fat, even from the largest animals. In other words, it is apparent that Neandertals were highly dependent on acquiring large animals, more so during the harsh glacial winters that developed during MIS 3. That dependency on large game, in the face of a decreased availability of large game during MIS 3 is a potential source of stress, which could have led to the extinction of the Neandertal. To identify a potential reduction in the availability of large prey and megafauna, it, therefore, becomes necessary to study the dynamics of the availability of large prey animals during MIS 3, the period during which the Neandertal disappeared.

9 CHANGES IN PREY SIZE IN SOUTHWESTERN EUROPE DURING MIS 3

After describing the dependency of Neandertals on large prey for the supply of fat, specifically during MIS 3 winters, I analyze the trends in prey size during MIS 3, to determine whether large prey populations decreased to the extent that made it energetically stressful for Neandertals to obtain sufficient fat.

The analysis of relative prey abundance in an archaeological site assumes that the changes in the relative abundance of prey in the archaeological sites reflected a similar change in the abundance in the environment. This assumption is commensurate with the hypothesis that larger prey was preferable over smaller prey so that a reduction of its abundance in archaeological sites does not reflect other changes like a change in technology, taste or social and political motivations. Also, it should be noted that many of the sites also contain non-anthropogenic accumulations of bones.

It is agreed that worldwide megafaunal (>44 kg) extinction began about 50 Kya (Barnosky et al., 2004) so that by 10 Kya, 97 out of 150 genera of megafauna were extinct. In Europe, the relative pace of extinction during that period is not very well known.

Several researchers have dealt with the dynamics of prey animal distributions in Europe during MIS 3: Stewart (2007) analyzed the Stage Three Mammalian Faunal database, regarding presence and absence of species from defined areas of Europe, using data from dated archaeological and non-archaeological sites. Stewart lists an inventory of 42 mammals. From that list, most of the animals that went extinct did so around the late Pleistocene - early Holocene. Of the four animals that went extinct before the LGM, as did the Neandertal, three – *Elephas antiquus, Stephanorhinus kirchbergensis* (a rhino), and possibly *S. hemitoechus* (a rhino) – belong to the largest group, which also includes the cold-adapted *Mammuthus primigenius* (wooly mammoth) and *Coelodonda antiquitatis* (wooly rhino), which survived until a later stage. It is interesting to note that, according to Stewart's data, both *Elephas antiquus* and *Homo neanderthalensis* retreated in the same direction – southwest. About mammoths, Stewart writes: "*Certainly we have evidence for a reduction in carrying capacity through OIS 3, in the form of … a decrease of mammoth numbers on non-archaeological sites towards the LGM*".

Also, Stewart identified a reduction in the population density of some larger carnivores towards the LGM, such as hyenas, which by their being at the top of the food chain, point to a reduction in the carrying capacity of the environment for large prey animals. To summarize, Stewart provides evidence that the extinction, which began 50 Kya, began with the largest species. Only the two species that were more adapted to cold weather survived.

The differences in prey and hunting practices between Neandertals and modern humans have been researched intensively (Grayson and Delpech, 2002; Costamagno et al., 2006; Discamps et al., 2011; Yravedra et al., 2015). However, animal size as a primary criterion in choosing prey has arguably never been researched.

Fa et al. (2013) did investigate shifts in prey size and compared the faunal record of Neandertals and AMH. They established a decline in large prey. They deduced that AMH adjusted to a decline in prey size by hunting significant quantities of very small prey, such as rabbits. Fa et al. (2013) hypothesized that Neandertals were less capable of hunting small prey, but did not explain this shortcoming.

As mentioned in Section 2.5.2.1, Stewart (2007) concluded that the Neandertals became stressed and went extinct due to the extinction of some of their largest prey animals. However, according to his database, other large animals like wooly mammoth and wooly rhino became extinct only much later. In fact, he shows that the wooly mammoth population increased between 37 and 28 Kya and only then started to decline. Therefore, to better identify environmental stress that stems from large prey decline we need to consider the net result, possibly regarding average prey size, of the dynamics of population changes of the various species.

9.1 THE DATABASES

I used three databases, as well as data from 13 individual sites (5 Spanish caves, 8 French sites of which 7 are caves), which allow a comparison of animal size within the MP, and between the MP and the Aurignacian. There is some overlap between the data in the three databases, but since I do not compare between them, that overlap is immaterial.

1. **Discamps et al. (2011)** – Appendix 2 – A database of 148 Mousterian and Aurignacian assemblages dated between 115 and 30 Kya from 39 sites in France, detailed for the presence and absence of species, by Chrono-cultural units, without regard to their relative frequency at the site.

2. **Álvarez-Lao and Méndez (2016)** – Appendix 1 – NISP by taxon (ungulates only) of 89 dated MIS 3 assemblages, from 61 sites in Western Europe. Since the dating record is of different levels of certainty, I added a general culture (MP, Aurignacian, Gravettian) to each assemblage, to also enable a more temporally-dependable comparison. In the database, the designation 'MP' was added to assemblages with Neandertals' designated cultures, including Chatelperronian (CP). AU (Aurignacian) was added to AMH designated, early cultures and Gravettian (Gr) to all post-Aurignacian cultures.

3. **Grayson and Delpech (2006)** – Data in the paper – NISP by taxon for 219 assemblages from the Mousterian, Chatelperronian, and Aurignacian in France. The database contains 169 Mousterian, 9 Chatelperronian and 41 Aurignacian assemblages.

4. **Individual sites** – Appendix 2 – Data from 13 multi-layer sites, with NISP and MNI (Minimum Number of Individuals) record from MIS 3 were analyzed individually for each site. The sites were selected based on the existence of multi-layers with sufficient NISP (above 50) during the end of the MP and the beginning of the UP in Spain and France.

Prey animals' body size – Appendix 3 – Prey body weight is based largely on a database created by Faurby and Svenning (2015). Where estimates of body weight of European taxa during MIS 3 existed, I used those (Magniez and Boulbes, 2014).

9.2 METHODS

Four methods of comparisons were used:

NISP frequency analysis - The relative frequency of the NISP of each species was compared between the periods.

Standardized Adjusted Residual -This statistical method was applied by Grayson and Delpech (2006). In our case, this method provides ratios of the difference between NISP ratios of specific species in the compared periods and the standard deviation of the ratio in later periods. I sorted the results of (Grayson and Delpech, 2006) by animal size.

NISP-based Mean Body Mass (NMBM) –The use of relative abundance index is common in the analysis of trends in species abundance (Cannon, 2000; Codding et al., 2010; Lyman, 2018). The index is the simple division of the NISP or MNI for the studied species divided by the total NISP or MNI for the assemblage. Here, the research question is not the abundance of a single species but the net effect regarding energy and fat of a change in the relative abundance of a group of animals from different species. A common relative abundance index cannot provide us with a quantitative estimate of the combined effect of changes in species prevalence and distribution. For that, we need to account for the relative body weight (and better still the caloric content and fat content) of the animals whose relative frequency changed. A NISP-based Mean Body Mass (NMBM) sensu Fa et al. (2013) was calculated for each assemblage, such that every species/assemblage data point of relative NISP frequency of a species was multiplied by the body weight of the species, in order to arrive at a mean that represents the mean of the weight of the animals in the assemblage. With regard to animal body weight, this method was used by Fa et al. (2013). Thus, for example, if an assemblage were composed of 40% NISP of a 750 kg *Megaloceros giganteus,* and 60% of the total NISP of a 180 kg *C. elaphus,* the NMBM would be (750*0.4+180*0.6) = 408. Using NMBM, a regional analysis of temporal trends in body size was calculated, based on the dates provided in the database of Álvarez-Lao and Méndez (2016). Using NMBM allows for a finer analysis of trends in animals size acquisition. If the bias in the relative accumulation of NISP with regard to body size is null, the relative NISP per species represents the relative number of animals. In this case, NMBM is the true mean weight of the acquired animals in the assemblage. However, the validity of the index for comparative purposes is a function not of the bias itself, but of the consistency of the bias in NISP accumulation with regard to size in the studied assemblages. If the bias of accumulation by size is consistent, then the comparison is valid.

Individual sites - The comparison of layers from the same site allows for a clean temporal comparison of prey availability, leaving geographical and landscape variables fixed through the temporal range.

Several Spanish and French sites with reliable, multilayer data that span the MP and the Aurignacian were analyzed for a trend in animal size, on an individual basis, using NMBM. The debate about the relative validity of MNI and NISP figures for the determination of relative species abundance is old (Watson, 1979). For example, Grayson (2014) in his seminal book on quantitative Zooarchaeology leans slightly towards NISP as a better measure of relative abundance. More relevant to our situation, he states that in a case where data exist for multiple sites in a certain region if results of relative abundance are coherent with results from other sites than whatever measure is used becomes more valid. Grayson and Delpech (2006) Database, which is used here is NISP based and was used by Grayson and Delpech to determine the relative abundance of reindeer. Reviewing the history of MNI and NISP employment for the estimation of relative abundance Lyman (2018) concludes that NISP "*with respect to quantifying taxonomic abundance, works quite we*ll" and is preferable to MNI. Morin (2004), also argued that NISP is a preferable measure of the relative frequency of species with increasing distance of the site from the kill site. In any event, when MNI data were available, a version of the index, MNI-based Mean Body Mass (MMBM), using relative MNI of the species from the total MNI for the assemblage, multiplied by the prey animals' body weight, was also presented. In our case the debate is somewhat theoretical since the practice depends on the availability of NISP and MNI data. As will be shown, here using either MNI or NISP provided similar results.

9.3 DISCAMPS (2011) DATABASE

9.3.1 NISP frequency analysis

Discamps built a database of species frequency by a relative number of sites, in which species appear, regardless of the actual frequency in the assemblage itself. Only clearly anthropogenic assemblages were included. The uniqueness of this database lies in assigning assemblages to cultural entities within the Mousterian and the Aurignacian and dating the cultural entities. The dating allows for a comparison of the very late Neandertal presence to the very early AMH presence. I chose to compare the mean of Neandertal cultures of Discoid Denticulate Mousterian, and the Chatelperronian, together composing 21 sites, to the AMH cultures of the Proto Aurignacian and Early Aurignacian, together composing 29 sites. This choice allowed a comparison of Neandertal cultures, which according to Discamps et al. (2011), began between 48-46 Kya and ended 40-39 Kya, and AMH cultures that began 39 Kya and ended 31-29 Kya (see Discamps et al. (2011:Table 5) for the dating, using ‘Subsequent select’ rounded to the nearest thousand). By a different Bayesian assumption, these cultures extended from 53-47 Kya to 37-33 Kya for Neandertals, and from 45-41 Kya to 31-29 Kya for AMH (Discamps et al. (2011: Table 5).

To test differences in frequencies of animal types between the chosen cultures, Z tests for comparing two proportions were conducted. The results are presented below (Table 12):

Table 12. Percentage of assemblages with species for the Disc+CP (late Neandertal) and P.Au+Au A (early AMH) cultures. (Disc+CP N=21, P.Au+Au A N=29)

	Animal size	**Disc+CP**	**P. Au+Au A**	**Z value**	**P-value**
Capreolus	22	14	10	0.33	0.37
Rupricapra	26	43	24	-1.58*	0.05
Dama dama	56	0	0	-	-
Capra sp.	85	33	34	0.99	0.16
Sus scrofa	101	24	34	2.22**	0.01
Rangifer tarandus	130	95	100	1.84*	0.03
Cervus elaphus	180	91	55	-1.94*	0.03
Equus hydruntinus	227	57	21	-3.42**	0.00

	Animal size	**Disc+CP**	**P. Au+Au A**	**Z value**	**P-value**
Equus caballos	450	100	90	-0.60	0.27
Megaloceros giganteus	750	14	24	2.22**	0.01
Bovinae	900	100	90	-0.60	0.27
Rhinocerotidae	2692	38	21	-1.63*	0.05
Proboscidea	5500	24	21	0.18	0.42

**p<.05, **p<.01,* Disc – Discoid denticulate Mousterian, CP – Chatelperronian, P. Au – Proto Aurignacian, Au A - Aurignacian

As shown in Table 12, significant **decline** in animal proportions between the late Neandertal cultures (Disc+CP) and the early AMH cultures (P. Au+Au A) were found in the following species: *Rupricapra*, *Cervus elaphus*, *Equus hydruntinus*, *M. giganteus*, and Rhinocerotidae. Specifically, significant declines were identified among large animals only in Rhinocerotidae and *E. hydruntinus*. However, it should be noted that five of the seven largest species show a decline in appearance in the early Aurignacian, compared to the late MP and the CP.

9.4 ALVAREZ-LAO (2016) DATABASE

9.4.1 NISP frequency analysis

The database of Álvarez-Lao and Méndez (2016) contains assemblages from present-day Spain, France, Belgium, Germany, and the U.K. to test differences in the frequencies of NISPs between the MP and the Aurignacian, Z tests comparing two proportions were conducted. The first proportion is the average frequency of NISPs of each species in the MP, accounting only for sites that contained the species, and the second is the same for the Aurignacian. Results are shown below (Table 13).

Table 13. Average percentage in assemblages with species for the MP (Middle Paleolithic) and AUR (Aurignacian) cultures

	Animal Size (kg)	**MP**	**AUR**	**Z value**	**P value**
Capreolus capreolus	22	1	3	0.69	0.25
Rupricapra rupicapra/pyrenaica	26	9	4	-1.12	0.13
Saiga tatarica	29	0	0	-	-
Dama dama	56	1	0	-1.11	0.13
Capra ibex/pyrenaica	85	29	14	-2.06*	0.02
Rangifer tarandus	86	21	39	2.98**	0.00
Sus scrofa	101	1	2	0.54	0.29
Cervus elaphus	180	32	30	0.14	0.44
Equus hydruntinus	227	2	1	-0.10	0.46
Equus caballus	250	20	13	-0.84	0.20
Bovinae spp.	500	14	12	-0.13	0.45
Megaloceros giganteus	700	4	1	-1.37	0.45
Coelodonta antiquitatis	2692	6	5	-0.09	0.46
Stephanorhinus hemitoechus	2943	2	1	-1.01	0.16
Mammuthus primigenius	5500	14	17	0.80	0.21

**p<.05, **p<.01*, MP – Middle Paleolithic, AUR – Aurignacian

As shown in Table 13, significant declines in animal proportions between the MP and the Aurignacian were found only for *Capra ibex/pyrenaica*. On the other hand, a significant rise in animal proportions between cultures was found for *Rangifer tarandus*.

Here again, as in the analysis of the database of Discamps et al. (2011), although the individual changes in species frequencies were not significant, the chart shows that seven out of the eight largest species (excluding Mammoth) declined in relative frequency between the MP and the Aurignacian.

9.4.2 NISP-based Mean Body Mass (NMBM)

The assemblages in Álvarez-Lao and Méndez (2016), together with two MP assemblages from Tournal cave (Magniez and Boulbes, 2014), were divided into regions and sorted by age. Due to the questionable reliability of the dates, and the topographic and circumstantial differences between the layers in the various sites, I decided to add a 'moving average' for each assemblage, where each data point in the moving average represents an average of four consecutive data points.

9.4.2.1 *Animal size trends within the late MP*

I tried to discern the dynamics of prey size within the MIS 3 MP, immediately before the extinction of the Neandertal. The following figures (Figures 5 – 8) describe the MP (including CP) assemblages of the database in each of the regions. Due to the small number of sites in the analysis, no statistical testing was attempted. All four charts show a decline in prey size at the end of the MP compared to the beginning of the MIS 3. The peak of the decline seems to have been during 43-37 Kya, depending on the region. Three of the regions show a slight increase in prey size between 40 and 37 Kya. In any event, in none of the regions does the late increase restore the mean size to the initial mean size in the early MIS 3. It is interesting to note that the most dramatic decline takes place in Central Western Europe, where the means are some ten times higher than in other regions, due to a significant record of *M. primigenius* remains at the beginning of the period, that disappear towards the end of the MP (NMBM of 5141 declining to a mean of 626 for the latest 4 assemblages). *M. primigenius* with a weight of 5500 kg is an exception when it comes to mean size of animals in an assemblage, since it is equivalent to some 6 – 20 times the body weight of the other animals in the assemblage. This difference is greater in terms of calories, and greater still in terms of fat, so a decline in proboscidean availability had the potential to be a 'game changer' in the Neandertal economy. It is interesting to note that later, in the Gravettian, there is evidence for a strong association of AMH in Northern Europe with *M. primigenius* (Svoboda et al., 2005). This resurgence of the mammoth as a source of meat is commensurate with the finding of a resurgence of the mammoth population during the Gravettian throughout Northern Europe (Markova et al., 2013).

Figure 5. NMBM as a function of site age: Cantabria - MIS 3 MP

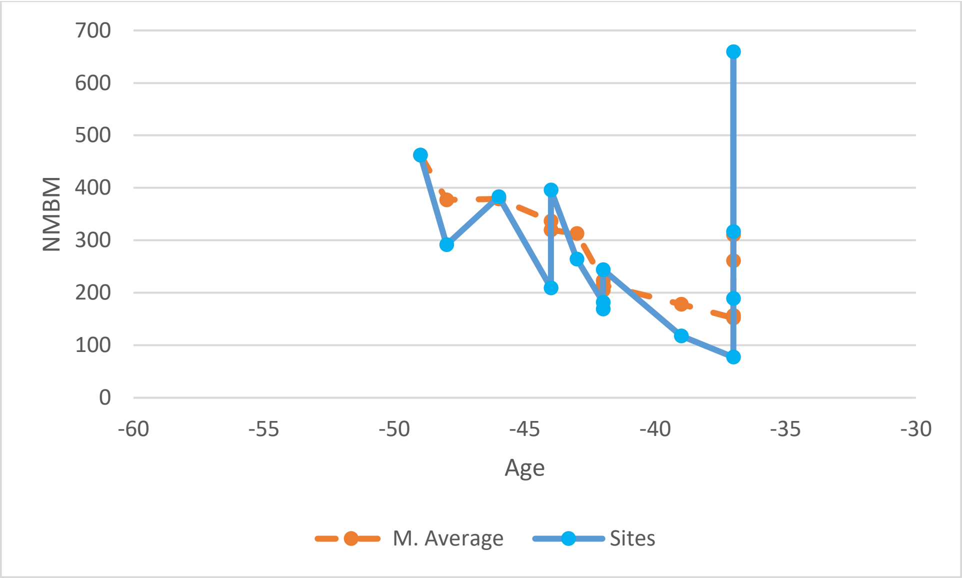


Figure 6. NMBM as a function of site age: Other Iberian sites - MIS 3 MP

Figure 7. NMBM as a function of site age: South France - MIS 3 MP

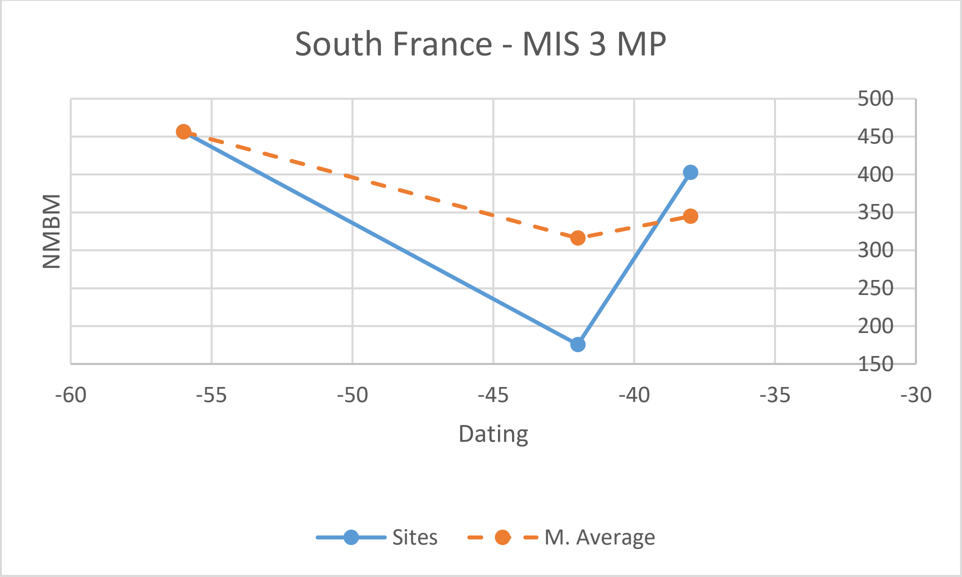


Figure 8. NMBM as a function of site age: Central Western Europe - MIS 3 MP

9.4.2.2 *Comparison between the MP and the Aurignacian*

Another relevant analysis is a longer-term prey size trend, during the entire MIS 3. The above figures (Figures 5 – 8) show the four-site moving average of the NMBM of assemblages, as a function of site age. In all the regions, the trend towards a reduction in mean prey size continues throughout MIS 3. However, in Cantabria (Figure 5) and Southern France (Figure 7), there seems to have been a temporary rebound in mean animal size during a part of the Aurignacian, which is not evident in other Iberian regions and Central West Europe (Figures 6 and 8). In these regions, the trend towards a reduction in prey size is continuous.

To determine a correlation between site age and mean mass of animals, a Pearson correlation, and a linear trend line were calculated.

As seen in Figure 9, in Cantabrian sites, a low and non-significant correlation was found between assemblage age and mean animal mass. However, there was a marked decline in mean prey size toward the end of the MP that lasted until the early stages of the AU around 40-37 Kya. A temporary increase in mean prey size around 35 Kya is apparent, followed by a decline at the end of the AU. There is a clear decline in prey size, with strong and significant correlations ($P < .001$), throughout MIS 3 in the other three regions (Figures 10 – 12).

Figure 9. Mean animal mass as a function of site age: Cantabrian sites MIS 3

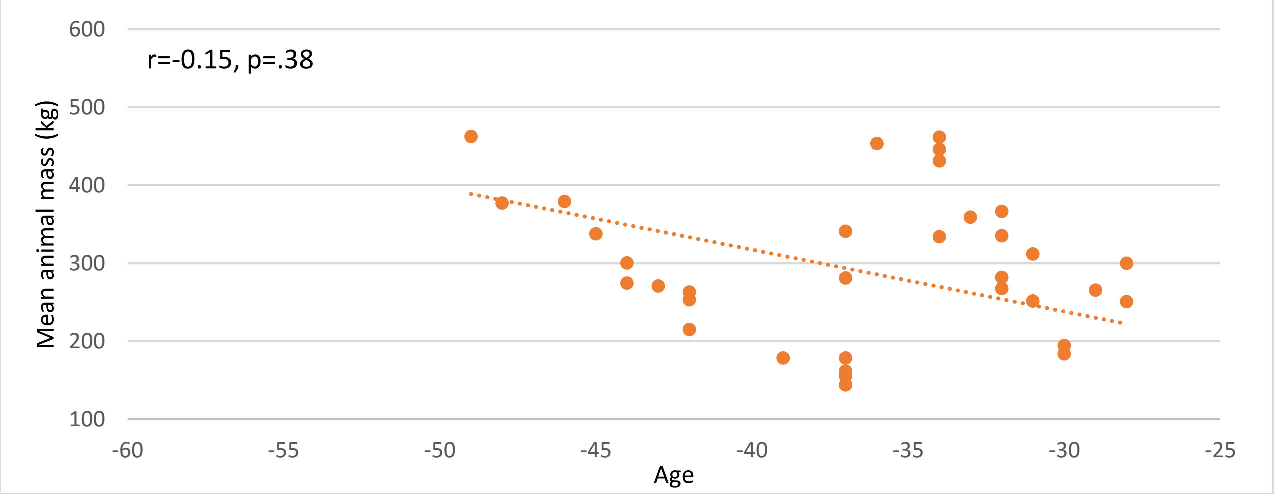


Figure 10. Mean animal mass as a function of site age: Other Iberian

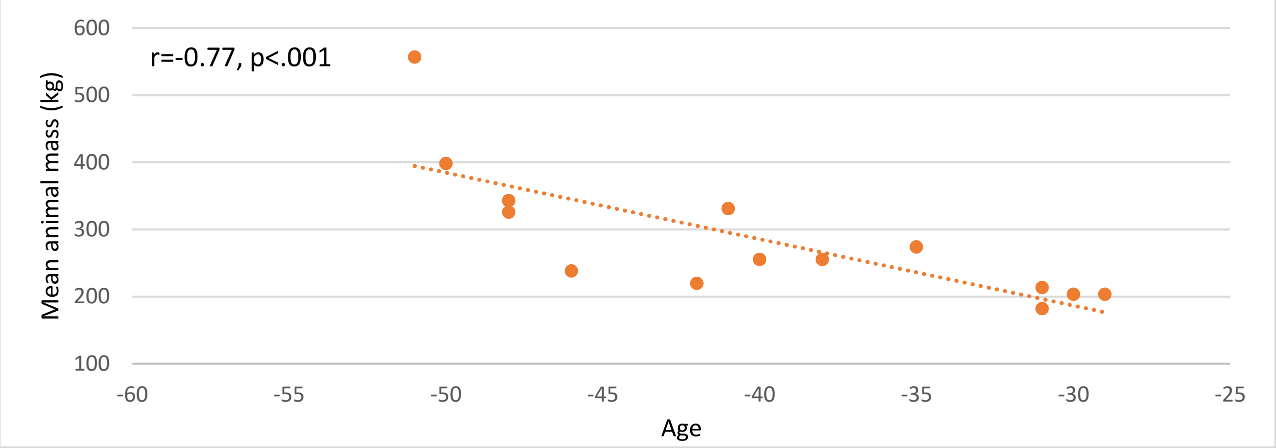


Figure 11. Mean animal mass as a function of site age: South French sites

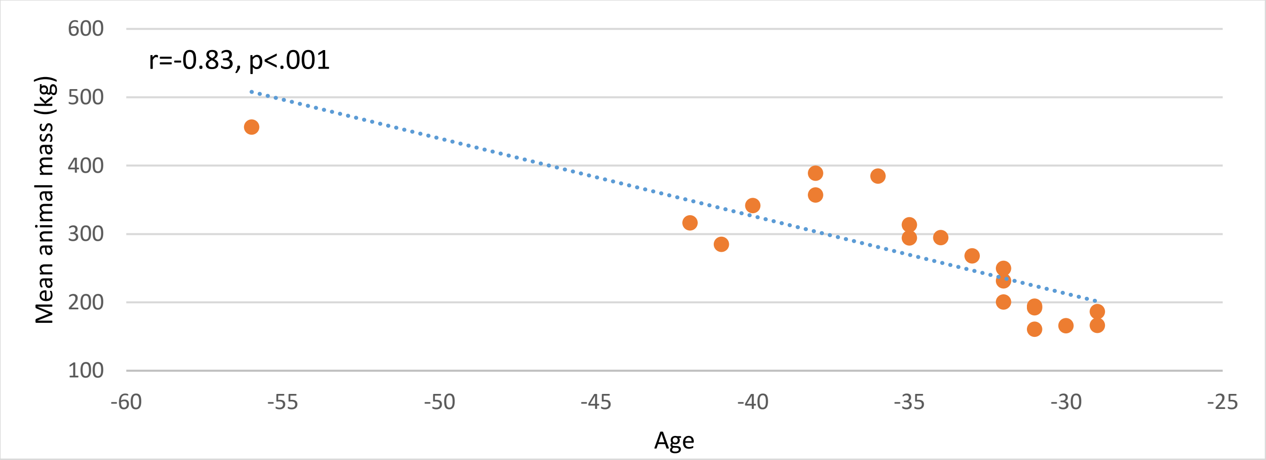
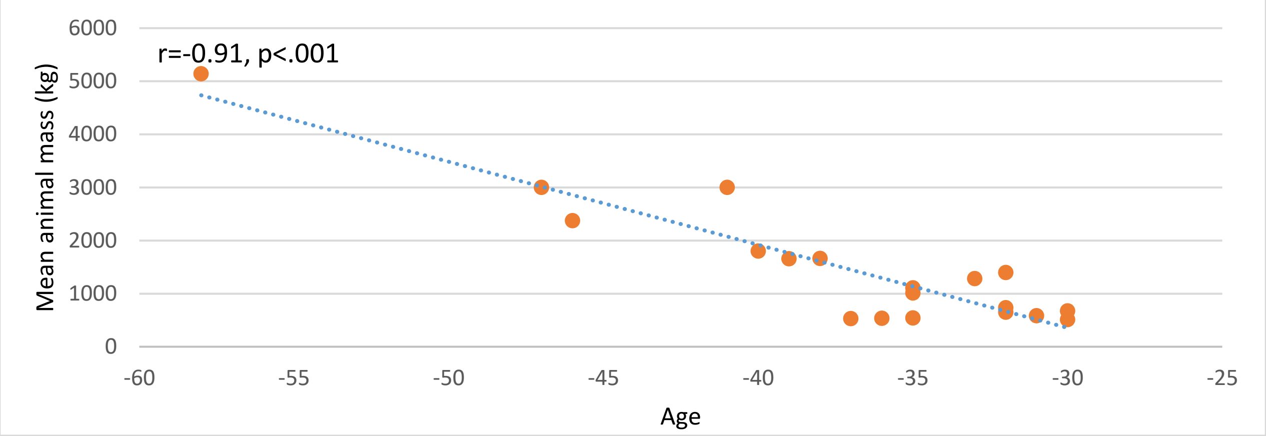


Figure 12. Mean animal mass as a function of site age: Central Western Europe



9.5 GRAYSON (2006)

Grayson and Delpech (2006) used a different statistic, the Standardized Adjusted Residual (SAR), to deal with changes in species' relative frequencies. They aimed to compare the taxonomic abundances between the Mousterian, Chatelperronian and Aurignacian assemblages. They, however, did not deal with animal size as a parameter. I sorted their results (their Table 6) by the body weight of the various species.

Table 14. Standardized adjusted residual by animal size between periods

Taxon	Au-CP	Au-Mo	CP-Mo
Elephantidae	-19.58*	-15.03*	8.67*
Rhinocerotidae	-10.54*	-12.8*	-0.28
Bison or Bos	-33.73*	-53.61*	-1.64
Megceros giganteus	1.84	-6.81*	-4.08*
Equus sp.	6.38*	-23.9*	-18.04*
Cervus sp.	-1.66	-47.93*	-22.15*
Rengifer tarandus	22.86*	108.46*	35.65*
Sus scrofa	-0.98*	-3.24	-0.74
Dama asp.		-2.43	-1.12

Taxon	**Au-CP**	**Au-Mo**	**CP-Mo**
Capra sp.	1.47	-27.96*	-13.71*
Rupicapra rupicapra	-2.2*	3.44	4.61*
Capreolus capreolus	6.92*	-8.45*	1.85

*- Statistically significant, Au – Aurigniacian, CP – Chatelperronian, Mo - Mousterian

A reduction in the relative abundance of animals larger than Rangifer tarandus is marked by a grey cell in Table 14. A statistically significant reduction in the SAR of the six largest animals in the sample is evident between the Mousterian and the Aurignacian. Increasing the resolution, the decline is already evident between the Mousterian and the CP, where it seems that an increase in the frequency of Elephantidae compensated somewhat for a decrease in the other five largest animals. The main difference between the CP and the Aurignacian is a marked decline in the three largest families, Bovidae, and the megaherbivores of the Rhinocerotidae and Elephantidae families. In summary, analyzing the database of Grayson and Delpech (2006) shows that there was a staged decline in the prevalence of the largest Neandertal prey in France, first between the Mousterian and the CP, and then between the CP and the Aurignacian, such that all of the six largest species that were acquired during the Mousterian, declined significantly in prevalence by the Aurignacian.

9.6 INDIVIDUAL SITES

A comparison of assemblages from layers within a specific site provides a tighter control of geographic and topographic variables. Several researchers of faunal temporal trends (e.g., Janetski, 1997; Cannon, 2000) have emphasized that whenever substantial spatial variability exists within a region, which is likely to be often, the preferred means of analysis should be to consider changes occurring at individual points on the landscape, insofar as the archaeological record allows.

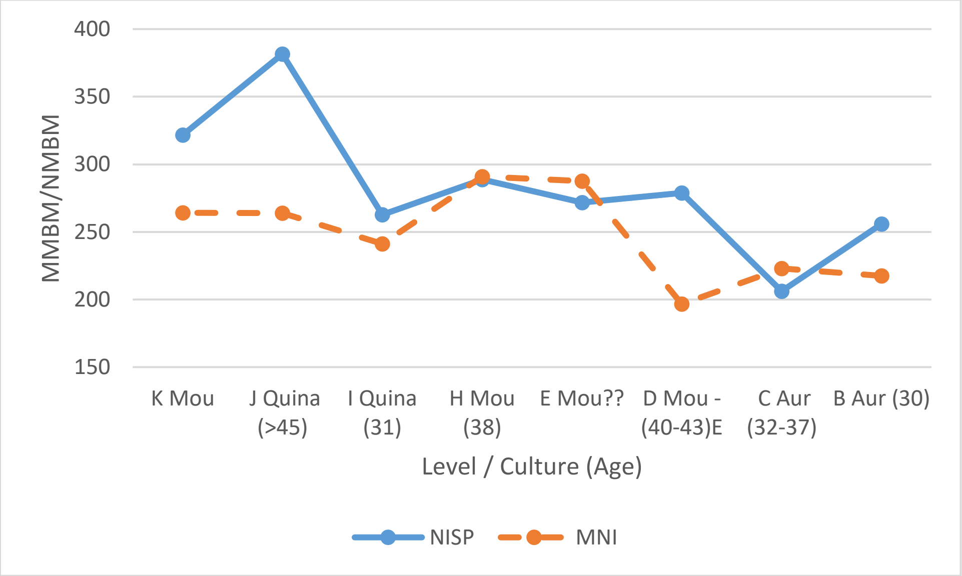
All multi-layer sites with a sufficient number of NISPs were analyzed using NMBM and MMBM, where MNI data were available. In general, the trend that appeared in the previous types of analysis remained, regardless of whether NISP or MNI was used to determine the relative frequency of species in the assemblage.

In all the charts: Mou – Mousterian, CP – Chatelperronian, P. Au – Proto Aurignacian, E. Au – Early Aurignacian, Au or Auri – Aurignacian, Gr – Gravettian, Magd – Magdalenian, Solu - Soluterian

9.6.1 Covalejos – Cantabria (Yravedra et al., 2016)

The assemblage contains faunal collections from the 1997 – 2002 excavation campaigns, directed by R. Montes and J. Santiago. Several assemblages with a small number of NISP (F, G, L, M, O) were not included in the analysis. Layers B and C are defined as Early Aurignacian and D, H, I, J and K as Mousterian. The 'Unidentified large-intermediate' in their Table 2 was taken as the mean weight of *Bos-Bison*, *Equus*, and *Cervus*, the most prevalent species in the category. 'Small indent' was taken as a simple average of the weight of the small identified species in the category. Both NISP and MNI show a trend of decreasing mean body mass towards the end of the MP (Layer D), compared to previous layers, while the transition between the MP and the UP (Layer D to layer C) shows a slight increase in mean body weight in the MNI dataset, and a marked decrease in the NISP dataset (Figure 16).

Figure 13. Prey size trends in NISP and MNI as a function of excavation level: Covalejos

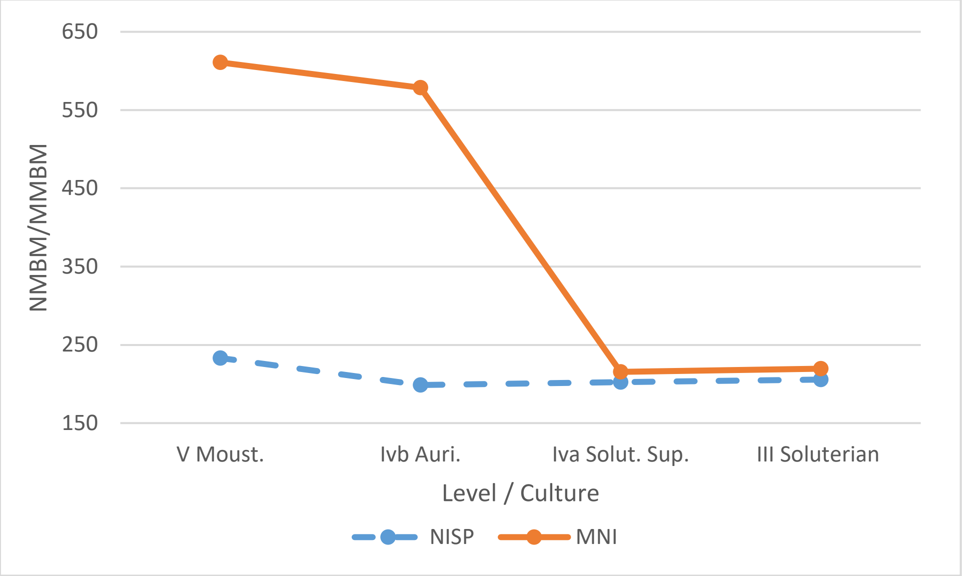


Culture abbreviations: Mou – Mousterian, Aur - Aurignacian

9.6.2 Ruso – Cantabria, Spain (Yravedra, 2010)

Ruso is a small cave in Cantabria. In terms of MNI, there is a small decline in the mean animal size between the Mousterian, and the Aurignacian and a significant decline after the Aurignacian, due to the absence of mammoths in the post-Aurignacian periods (Figure 17). In terms of NISP, there is no apparent change in mean size, because the MNI of mammoths was determined from one NISP out of some 200 (Figure 17). The presence of mammoths in the Aurignacian, as per MNI, is doubtful, however, since there is no NISP attribution to it in the NISP table (their Table 1).

Figure 14. Prey size trends in NISP and MNI as a function of excavation level: Ruso

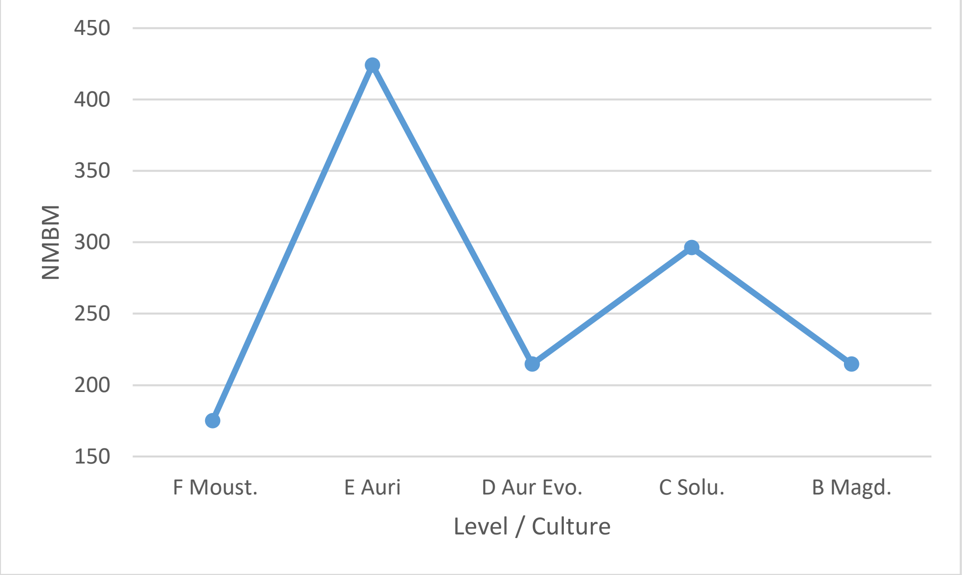


Culture abbreviations: Moust – Mousterian, Auri – Aurignacian, Solut - Soluterian

9.6.3 Hornos de la Pena – Cantabria, Spain (Yravedrad et al., 2010)

Contrary to most other sites, this site demonstrates a trend of increasing mean prey size between the Mousterian and the Aurignacian (Figure 18). A higher NMBM than in the Mousterian is evident even in the Soluterian and the Magdalenian. The increase in NMBM in the Aurignacian stems from the presence of two NISPs of *M. primigenius*

Figure 15. Prey size trend in NISP as a function of excavation level: Hornos de la Pena

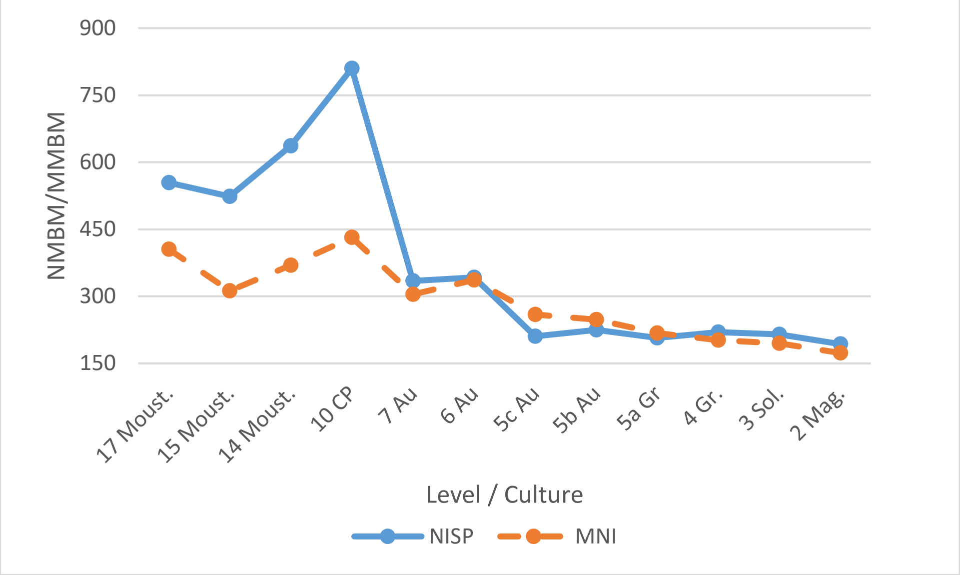


Culture abbreviations: Moust – Mousterian, Auri – Aurignacian, Solu – Soluterian, Magd – Magdalenian

9.6.4 Morin – Cantabria, Spain (Yravedra, 2010)

Several assemblages (8, 9, 13, 16) were not taken into account due to very low NISP numbers. The cultural assignment of the assemblages is based on Pike-Tay et al. (1999). There is an increase in prey size during the Mousterian and CP, but a clear trend of a decrease in prey size in the Aurignacian, in terms of both NISP and MNI (Figure 19). The CP layer (10) shows the highest NMBM in the sequence, but unfortunately, it is based on a very low count of NISP of 29. 25 of the 29 NISP in the CP layer were of *Bison*. A similar *Bison*-dependent record from the CP is found in a nearby El Pendo cave.

Figure 16. Prey size trends in NISP and MNI as a function of excavation level: Morin

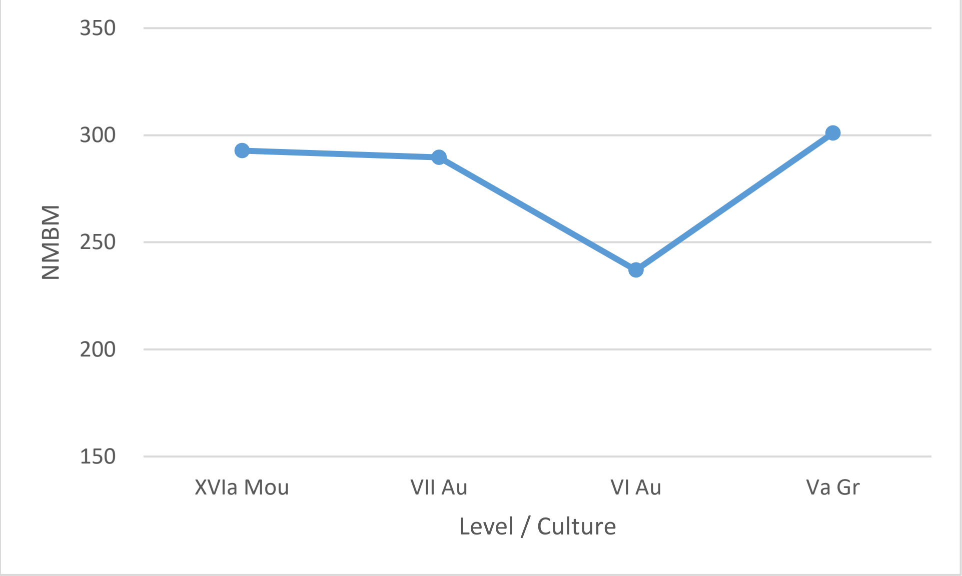


Culture abbreviations: Moust – Mousterian, CP – Chatelperronian, Au – Aurignacian, Gr – Gravettian, Sol – Soluterian, Magd - Magdalenian

9.6.5 El Pando - Cantabria (Pike-Tay et al., 1999)

Only assemblages with more than 100 NISP were included. Other assemblages, including a CP (VIII) layer with 20 NISP, and an Aurignacian layer (VIIIb) with 51 NISP, were excluded, also given the reverse order of AU – CP to the common CP – AU order in all other sites. The transition from the Mousterian to the Aurignacian is practically uneventful in terms of prey size, although a later Aurignacian layer shows a significant decline in mean prey size (Figure 20).

Figure 17. Prey size trend in NISP as a function of excavation level: El Pondo

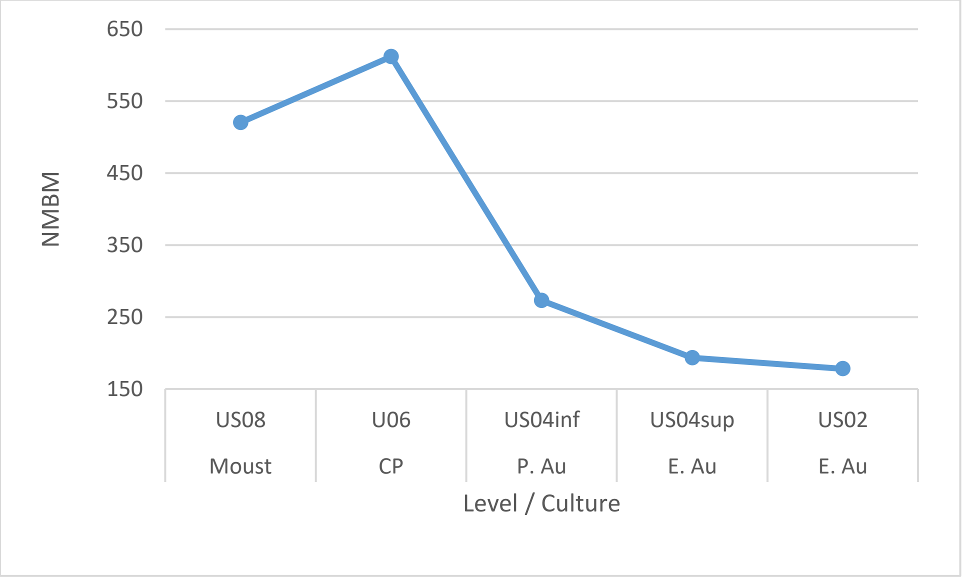


Culture abbreviations: Mou – Mousterian, Au – Aurignacian, Gr – Gravettian

9.6.6 Le Cottes – Southern France (Welker et al., 2015 Supplementary Table 3)

The existence of CP and Proto-Aurignacian layers at the site, assuming that they represent Neandertal and AMH occupations respectively, allows for a fine temporal comparison of the mean weight of prey animals between the two species, at the time of the Neandertal extinction. A marked reduction in mean prey weight is evident between the CP and the first Aurignacian layer (Figure 21). This reduction is attributed to an increasingly cooler environment. The increase in mean weight between the Mousterian and the CP is due to the presence of five NISPs of Elephantidae.

Figure 18. Prey size trend in NISP as a function of excavation level: Le Cottes

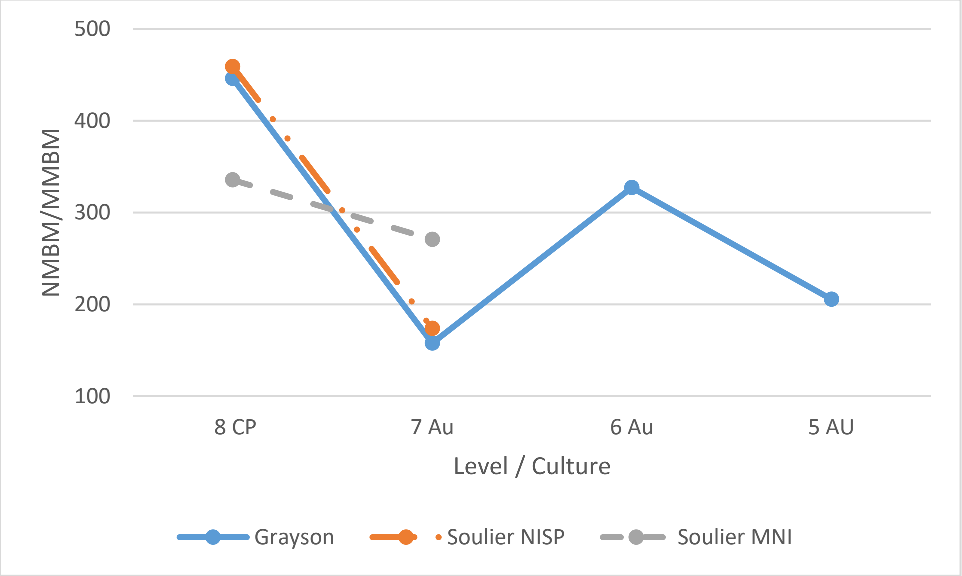


Culture abbreviations: Moust – Mousterian, CP – Chatelperronian, P. Au – Proto Aurignacian, E. Au – Early Aurignacian

9.6.7 Roc de Comb – Southern France (Grayson and Delpech, 2008)

Grayson and Delpech did not include the Mousterian layer of Roc de Comb due to an inadequate stratigraphic analysis of the layer. There is a very significant reduction in mean prey size between the adjacent CP and Aurignacian layers which is, similarly to Le Cottes, the result of a shift in the dominant species from *Bos/Bison* to reindeer (Figure 22). The presence of mammoths in the later Aurignacian layers (6 and 5) causes an increase, after the initial Aurignacian decline, but NMBM does not return to the layers of the CP. I have also included the revised numbers of Soulier and Mallye (2012) that also contain MNI data. The results are not noticeably different. The NISP data are identical, and the MNI shows a more moderate decline between layer 8 (CP) and 7 (AU) (Figure 22).

Figure 19. Prey size trends in NISP and MNI as a function of excavation level: Roc de Comb

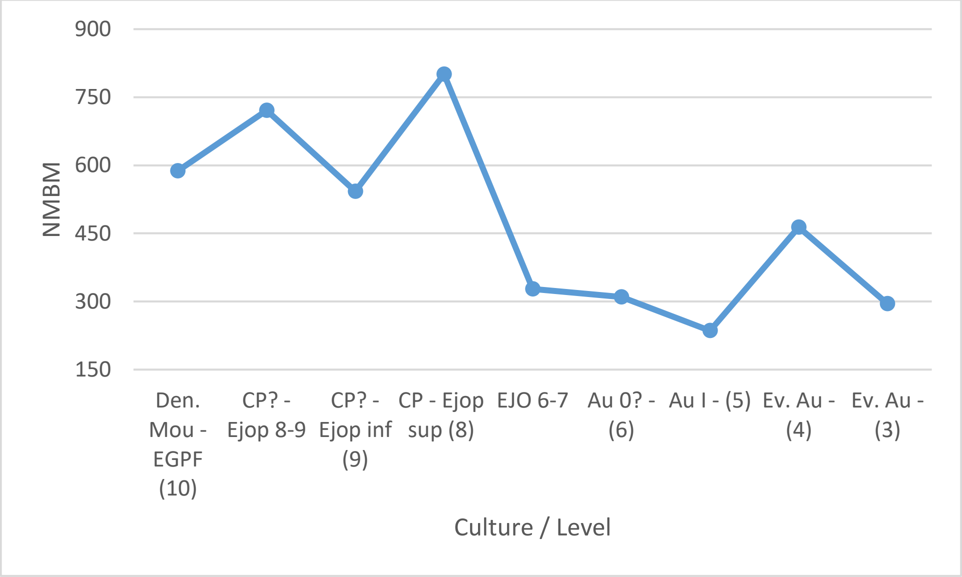


Culture abbreviations: CP – Chatelperronian, Au - Aurignacian

9.6.8 Saint-Cesaire (La Roche- a-Pierrot) – Southern France (Morin, 2006)

Saint-Cesaire is one of a few sites that have consecutive Late Mousterian, CP and Aurignacian layers. The site was excavated by Leveque during 12 consecutive seasons, ending in 1987. Morin (2006) performed a re-fit of a small part of the NISPs. There is an increase in NMBM between the Denticulate Mousterian layer EGPF (10) and the CP layer EJOP superior, which is a result of the higher NISP count for mammoths (Figure 23). As in other sites in this region, there is a marked decline between the Mousterian and Chatelperronian layers on the one hand and Aurignacian layers on the other. The reason for this decline is, as in the previous sites described here from Southern France, a shift to a dominance of reindeer in the Aurignacian, compared to a dominance of bison during the Mousterian and CP.

Figure 20. Prey size trends in NISP as a function of excavation level: Saint-Cesaire

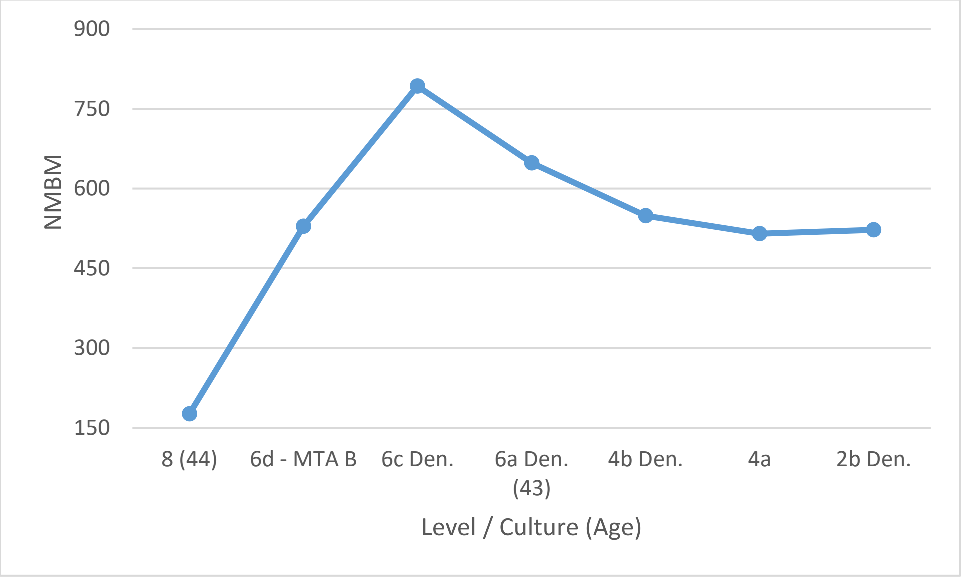


Culture abbreviations: Mou – Mousterian, CP – Chatelperronian, Au - Aurignacian

9.6.9 La Quina Locus C – South Western France (Rendu and Armand, 2009)

La Quina Locus C is assigned culturally to the MTA and Denticulate Mousterian and is dated to 44 -43 Kya. It is analyzed here in order to discern inter-MP trends. It is defined as a ‘jump site,' where a local cliff was used to mass kill one type of animal. The kill season is estimated to have been late summer/autumn (Rendu, 2007). In North America, mass kill sites are also assigned to this season and are associated with intensive fat extraction, in preparation for winter (Brink, 2008). In this season fat is at a maximum level (Figure 1 for Caribou). A similar site, Morean, which is not analyzed here, since 99% of its assemblage is composed of bison, has also been identified as a mass kill site from the same period, and with the same seasonal pattern. The difference in NMBM between the various layers at La Quina is due to changing ratios of reindeer to bison in the assemblages (Figure 24). Layer 8 is almost exclusively composed of reindeer, and Layer 6c of bison. A declining trend in the ratio of bison to reindeer in later layers may be indicative of its population decline. Results from other sites support a conclusion of bison population decline at La Quina.

Figure 21. Prey size trend in NISP as a function of excavation level: La Quina locus C

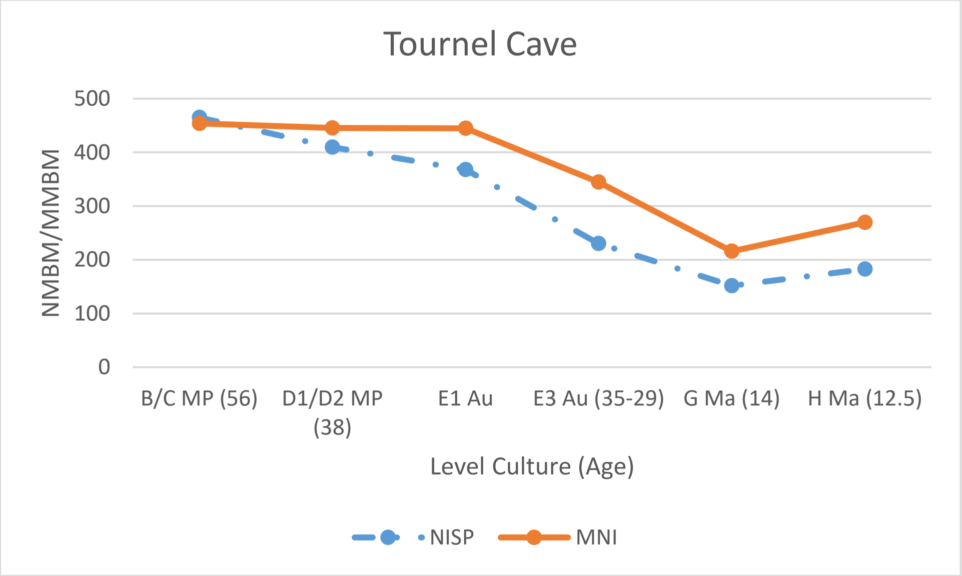


Culture abbreviations: Den. – Denticulate Mousterian

9.6.10 Tournel Cave - Southern France (Magniez and Boulbes, 2014)

The MP layers are dated to 56- 36 Kya and correspond to the Denticulate Mousterian. An apparent decline in mean prey size between the MP and the later periods is evident, based both on NISP and MNI data (Figure 25). A decline during the MP is only evident based on NISP.

Figure 22. Prey size trends in NISP and MNI as a function of excavation level: Tournel



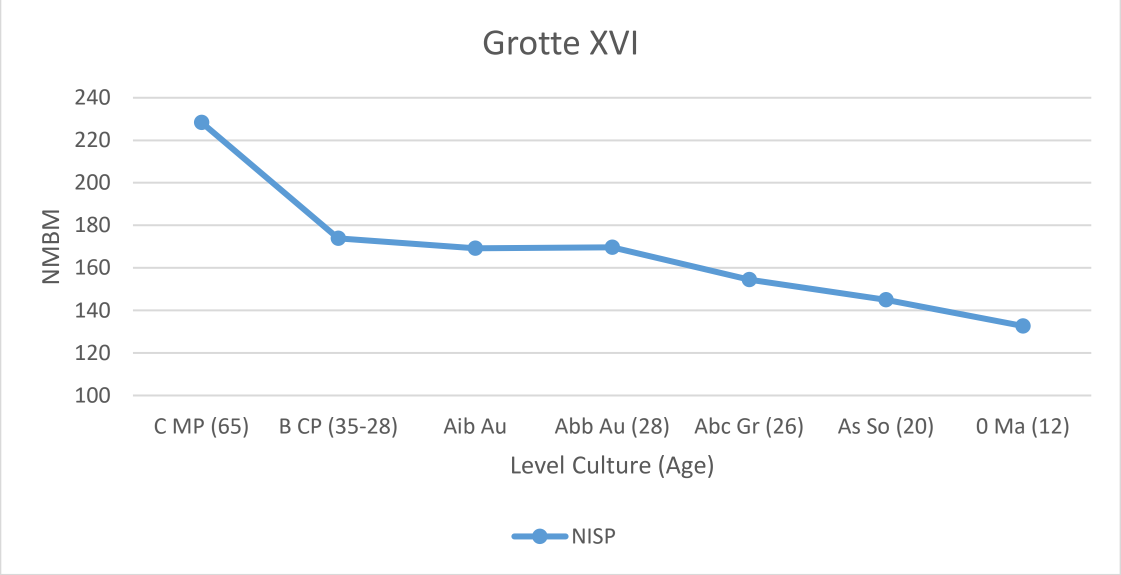
Culture abbreviations: MP – Middle Paleolithic, Au – Aurignacian, Ma – Magdalenian Grotte XVI,

Southern France (Grayson and Delpech, 2003)

Grayson and Delpech define Grotte XVI as: “the first site from southwestern France to have provided substantial ungulate assemblages from securely stratified, carefully excavated Mousterian, Chatelperronian, and early Aurignacian contexts.”

A marked decline in mean prey size is evident between the MP layer (C) and the CP layer (B). This declining trend stabilizes in the Aurignacian and then continues up to the Magdalenian (Figure 26). Grayson and Delpech attribute the change in the relative composition of the fauna at Grotte XVI to climate forcing.

Figure 23. Prey size trend in NISP as a function of excavation level: Grotte XVI

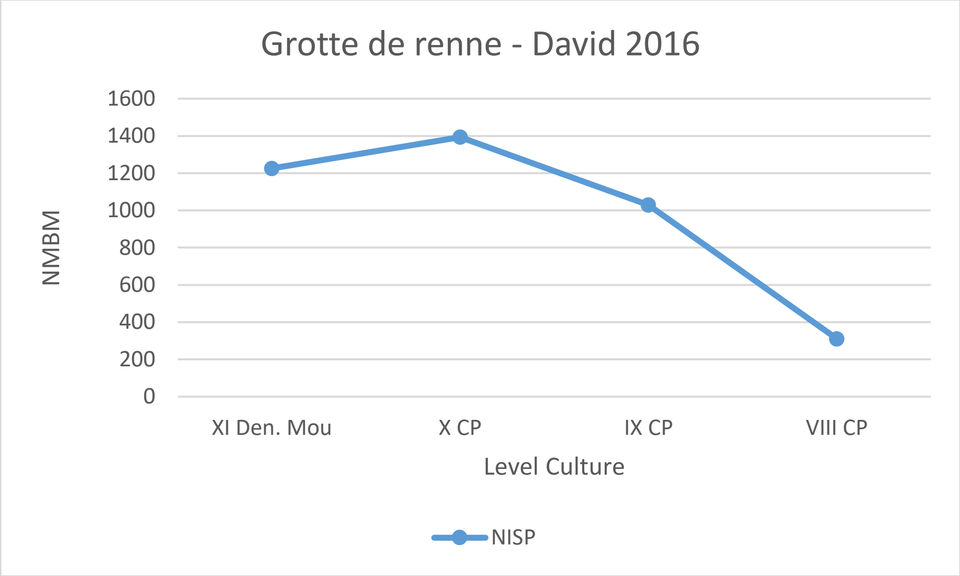


Culture abbreviations: MP – Middle Paleolithic, CP – Chatelperronian, Au – Aurignacian, Gr – Gravettian, So – Soluterian, Ma – Magdalenian

9.6.11 Grotte de Renne – Central France (David et al., 2001; David et al., 2006)

The number of NISP is relatively small, in the 8 – 83 range, except for layer VIII, which has 1,150. Layer X is an amalgamation of layers Xc, Xb2, Xb1, and Xa, due to the low NISP number for each assemblage. A decline in NMBM from the Mousterian to the CP is evident, although initially there is a slight rise (Figure 27).

Figure 24. Prey size trend in NISP as a function of excavation level: Grotte de Renne

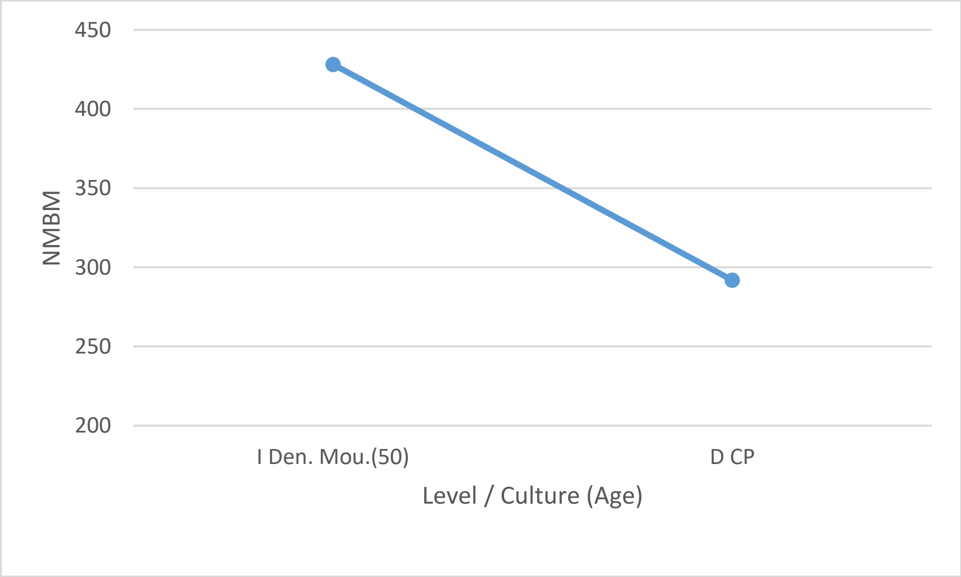


Culture abbreviations: Den. Mou – Denticulate Mousterian, CP – Chatelperronian

9.6.12 Grotte du Bison - Central France (David et al., 2006; Enloe, 2012)

Grotte du Bison is adjacent to Grotte du Renne, with a respectable number of NISPs for the two layers. The same trend of declining NMBM between the Denticulate Mousterian and the CP layers is evident in both sites (Figures 27, 28).

Figure 25. Prey size trend in NISP as a function of excavation level: Grotte du Bison



Culture abbreviations: Den. Mou. – Denticulate Mousterian, CP – Chatelperronian

9.6.13 Summary – Individual sites

In summary, using the NMBM index, individual sites with dependable and sizeable NISP, and sometimes MNI records were analyzed separately to allow a tighter temporal comparison, which would not be influenced by different geographical variables. The following table (Table 14) summarizes the results within the MP and CP, presumably Neandertal layers (Within MP+CP), Between Neandertal layers and Aurignacian layers (MP+CP/AU) and between the last MP and the first Aurignacian layers, excluding CP layers (MP/AU). Differences were calculated using change in proportion by z tests.

Table 15. Summary of individual sites' prey trend analysis

Site	**Within MP+CP (NISP**	**Within MP+CP (MNI)**	**(MP+CP)/AU (NISP)**	**(MP+CP)/AU (MNI)**	**MP/AU (NISP)**	**MP/AU (MNI)**
Covalejos	↓ ***	↓***	↓	↑**	↓**	↑**
Ruso	-	-	↓***	↓***	↓	-
Hornos de la Pena	-	-	↑*	-	↑	-
Morin (1)	↑***	↑	↓***	↓***	↓*	↓***
El Pondo	-	-	↔	-	↔	-
Le Cottes (1)	↑	-	↓	-	↓***	↓**
Roc de Comb (1)	-	-	↓***	↓***	-	-
Saint-Cesaire (1)	↑***	-	↓***	-	↓**	-
La Quina	↔	-	-	-	-	-
Tournel	↓***	↔	↓***	↔	↓***	↔

Site	**Within MP+CP (NISP**	**Within MP+CP (MNI)**	**(MP+CP)/AU (NISP)**	**(MP+CP)/AU (MNI)**	**MP/AU (NISP)**	**MP/AU (MNI)**
Grotte XVI(1)	↓***	-	↓***	-	↓***	-
Grotte du Renne (1)	↓***	-	-	-	-	-
Grotte du Bison	↓***	-	-	-	-	-
Decline/Rise	5/3	1/1	8/1	3/1	7/1	2/1
Total ***	5/2	1/0	6/1	3/1	6/0	2/1

↓ - Decline in mean body mass, ↑ - Increase in mean body mass, ↔ - Stable body mass

**p<.05, **p<.01, ***p<.001* MP – Middle Paleolithic, CP – Chatelperronian, AU - Aurignacian

Table 14 shows a statistically significant decline in the size of prey animal at most sites, in the transition from the MP and the CP to the Aurignacian ((MP+CP)/AU column in the table), both in the NISP and MNI records. In NISP, Decline is noted in eight out of nine sites and in six out of seven sites if only statistically significant results are considered. The record within the MP is similar but less pronounced, with a decline in mean body size, based on NISP, at five sites out of seven with statistically significant record.

Given the disagreement about the association of the CP with Neandertals, a summary of the comparison between Mousterian and Aurignacian layers, ‘skipping’ the CP, could also be indicative (MP/AU column in the table). This analysis does not change the conclusion of a marked reduction in prey size between the late MP and the early UP, with seven out of nine sites showing a decline in mean body mass, one stable and one site showing an increase.

9.7 CHAPTER SUMMARY

The hypothesis presented in this study relates an increase in energetic stress in the Neandertal to a decline in the availability of large prey animals. Therefore, depicting the dynamics of large prey availability during MIS 3, especially in the period leading to, and immediately after, the extinction of the Neandertal, is critical to the testing of the hypothesis.

An early extinction of some of the Elephantidae and rhino species, the largest animals in MIS 3 Europe, and not of smaller animals, as documented by Stewart (2007), may indicate that larger animals were more vulnerable to the conditions that developed during MIS 3 in Europe. It was, however, important to find out whether large animals that were not extinct, nonetheless experienced population declines during the first half of MIS 3, when Neandertals became extinct. To the extent that the resolution of the data allowed, it was also important to determine whether a decline could be identified just before the Neandertal extinction.

Using three databases for Western Europe, the relative frequency of large animals, in culturally-assigned layers, was analyzed in four different ways, for the absolute and relative presence in the sites/layers. In all forms of analysis, most of the largest animals (seven out of eight) were found to decline in relative presence, in the layers between the late MP and the early UP. It can be thus deduced that the decline in the frequency of large species in the Aurignacian, compared to the MP, is evident, both in the geographic distribution (absolute appearance in assemblages) and in the relative frequency in the assemblages.

This state of affairs explains why researchers who looked for a difference in hunting preferences and behavior between Neandertals and AMH, such as Yravedra et al. (2016) and Grayson and Delpech (2006), did not find any. It seems that Neandertals and AMH hunted the same species, but the relative composition of the hunted species, in terms of size, seems to have been significantly different.

To allow for fine-scale analysis, an index (NMBM) that represents the mean weight of animals in the assemblage, based on the relative NISP or MNI count in the assemblage, was used. Analyzing the (NISP) database of Álvarez-Lao and Méndez (2016) for assemblages that can be attributed to the MIS 3 MP showed a decline in the mean size of the animals in the MP layers, in all four regions of Western Europe. A similar analysis that included all of the MIS 3 layers (MP, CP, Aurignacian, and post-

Aurignacian) in this database showed that the decline continued during MIS 3 and beyond the MP, with a notable temporary increase during part of the Aurignacian in Cantabria and South France.

All in all, there seems to be a strong support for a trend of declining mean animal mass within the MIS 3 MP, when the results from the 36 MP layers in the database of Álvarez-Lao and Méndez (2016) are considered together with the NISP and MNI data from 13 individual sites. A statistically significant decline, within the MP and the CP, is also evident in France according to Grayson and Delpech (2006). It seems that an increase in the availability of mammoths during the CP partially compensated for a decrease in the availability of other large animals. The trend becomes even more apparent when the late MP and the early Aurignacian are compared, based on all methods of analysis of all the databases that were used here.

10 DISCUSSION AND CONCLUSIONS

As was shown in Chapters 5 and 6, most of the Neandertals' diet was composed of meat and fat. The zooarchaeological record shows that the meat and fat were acquired by the acquisition of large and very large terrestrial animals. The derived robust morphology of Neandertals is interpreted as adaptation to hunting of large prey in close proximity.

The hypothesis that the Neandertals' extinction was caused by a reduction in the abundance of very large animals has been described in this study in the following steps:

1. There was a ceiling on the capacity of the Neandertals' body to metabolize protein into energy. This ceiling dictated an obligatory acquisition of significant amounts of carbohydrates and/or fats (Chapters 3 and 4).
2. Carbohydrates (from plants) could not have been a major component of the Neandertals' diet, especially during MIS 3 winters (Section 2.2, and Chapters 5 and 6).
3. Therefore, according to the ODFBM model a significant continuous supply of dietary fat was essential for their survival (Section 4.2.2).
4. Only very large animals contained a sufficient portion of fat to supply the Neandertals' needs and allow full exploitation of the contained protein (Chapters 7 and 8).
5. As a consequent of the essentiality of fat for their survival, Neandertals were depended on a stable abundance of large prey animals (Section 8.3).
6. A trend of decline in abundance of very large animals is seen in archaeological sites in Western Europe beginning some 50 Kya and continuing for thousands of years before the arrival of AMH to Western Europe (present-day France and Spain) (Chapter 9).
7. This decline must have caused Neandertals to devote more energy to the acquisition of a larger number of smaller animals, of which not all the protein could be used due to the lower content of fat. The increased energetic expense for the acquisition of many more small animals must have resulted in reduced somatic repair and fecundity (Section 4.1 (Pontzer, 2017)) leading to their demise.

Underlying the claim of this hypothesis of somatic stress that led to extinction is an assumption that humans act to optimize the return on their energetic expenses. This assumption is a fundamental tenet of the Optimal Foraging Theory (Section 2.6). It has recently received substantial support by the findings of Pontzer et al. (2015), that TDEE is highly regulated. If so, at times of an increase of activity, the resulted increase in energetic expense is balanced by a decrease in the energy that is devoted to other somatic functions. Fertility would have been one of the most crucial functions to be affected. Of course, reduced fertility plays an important role in extinctions, but other somatic consequences such as reduced growth and diminished autoimmunity can also contribute to the threat of continuity across generations (Section 4.2.3).

The hypothesis presented here introduces a different ranking element for prey animals – fat content (Chapter 8). At first glance, this change in emphasis from calories to fat content is not so dramatic, since large animals are considered to be highly ranked (Stiner and Kuhn, 2009), and, as shown in Chapter 7, large animals also have a higher relative fat content. However, the decline in fat content with animal size is much more acute than the decline in calories (Table 11). This means that the ranking of large animals is much higher when the obligatory fat requirement is considered than in the commonly-discussed goal of maximum caloric acquisition.

The cause of the energetic stress to have inflicted Neandertals during MIS 3, is the limited ability of humans to metabolize protein into energy (Chapter 3). As Speth and Spielmann (1983) have suggested, it seems that the protein metabolism constraint was a fundamental problem that the human race had to solve to move up the omnivorous spectrum towards a higher trophic level, by relying on acquiring meat and fat for a significant share of his subsistence.

Thus, the protein constraint is presented at the beginning of the thesis. It should be emphasized that the protein constraint is absolute and not relative, such that an increase in energetic requirements beyond the normal TDEE must be met exclusively by non-protein dietary sources. The presented model deals with the nutritional and behavioral implications of this basic constraint. One possible solution for the protein constraint is to stay at a relatively low trophic level by gathering plants. The other possible solution is to complete a significant proportion of the nutritional requirements, which cannot be met by protein, by consuming animal fat.

The model is designed to discern situations of energetic stress, caused by a shortage of fat. When humans are forced to adopt a high trophic niche, the protein constraint (Chapter 3) is in effect. The implications of the need to obtain large quantities of fat become interesting when we realize that protein and fat come in one package – an animal. A conclusion of OFT under conditions of obligatory requirement for fat is that the optimal prey animal would have to have a minimum fat to protein ratio, so that a full exploitation of the protein content of the animal can take place in order to maximize the net energetic return.

The calculation of this minimal fat – protein ratio (the obligatory fat ratio) is the first step in the model. The second step is to compare the obligatory fat ratio with the fat ratio in animals that were available in the environment, with the aim of identifying potential environmental stress for humans when their prevalence dwindles. Assuming a high trophic position for MIS 3 Neandertals, and relatively high daily energetic requirements, especially during MIS 3 winters, the model predicts a very high level of obligatory fat consumption, at 65-85% of the acquired calories (Chapter 4).

Was the Neandertal's trophic position during MIS 3 high so as to dictate a high obligatory requirement for fat? This question was dealt with in some detail in Chapters 5 and 6, beginning with an attempt to reconstruct general trends in the *Homo* diet, and concluding with a reconstruction of the Neandertal diet.

Past attempts to determine the trophic levels of humans were largely deduced from the archaeological and ethnographical record, as well as from investigations and interpretations of genotypic and phenotypic phenomena in present-day and Paleolithic humans. In Chapter 4 I tried to widen the scope of the inquiry by including data from additional scientific disciplines, as well as by reviewing past findings. Particular attention was given to genetic and physiological data, which presumably are embedded by evolution in the form of genes, morphology, and metabolism in our body as a record of past dietary trends. With the advance of genetics and ancient DNA acquisition methods more relevant data is expected to be added to the data presented here and help in further testing of the hypothesis.

One scientific discipline that is widely used to discern Paleolithic human diets, ethnography, was found to be problematic when it comes to the prediction of a Paleolithic Dietary Plant–Animal ratios (DPAs) (Section 5.3). A valid analogical inference requires that the underlying parameters in the two sides of the analogy will be as identical to one another as possible. In our case, if one proffers to infer the DPA in the diet from one (recent) period to another (much earlier) period, the underlying technological and environmental conditions should at least resemble each other. Ignoring the difference in capabilities of the various human species for most of the Paleolithic, two discrepancies between the ethnographic and archaeological records were found to be most significant. The first is a substantial technological difference between the compared periods. Recent HG utilize many tools and technologies that were not available through all or most of the Paleolithic such as metal axes, metal arrowheads, metal containers, and dogs. Also, some of them rely on food and labor exchange with herders and farmers. The second difference is in the ecology during the two periods. Recent HG environments were found to be depleted of megafauna compared to the Paleolithic, with constantly shrinking borders which have been encroached for hundreds of years by herders and farmers, with substantial ecological ramifications on fauna and vegetation.

I argued (Section 5.3) that the dominance of ethnography in Paleolithic dietary reconstruction has led to two conclusions that cannot be supported by the ethnographic record as analyzed here. The first is that the Paleolithic diet was highly flexible in terms of DPAs. The second is that the Paleolithic diet had been, at times, very high in plant content. To be sure, the analysis in Section 5.3 is not intended prove the opposite. It just suggests that specifically with respect to the quantitative prediction of dietary plant-animal ratios during the Paleolithic, the accuracy and analogic power of ethnographic record are in doubt.

The multidisciplinary analysis of dietary adaptations in humans (Sections 5.5 and 5.6) conclude that carnivory was the default state of humans during the Paleolithic, with an increase in plant consumption beginning only during the UP. This, of course, doesn't mean that humans did not consume plants, or indeed that plants were not an ordinary component of the diet. It simply means that acquiring animal food seems to have been the major attractor of physiological, behavioral and cultural adaptations, at least until the UP. In the context of this study, the most critical result of the conclusion that humans were mostly carnivores, is that the protein ceiling was in effect and thus obligatory fat consumption was the norm rather than the exception.

Having concluded that carnivory was the default state of humans during the Paleolithic, the Neandertal diet was estimated (Chapter 6)

It is agreed by most, but not all, researchers that Neandertals focused on larger prey than did *H. sapiens*. The analysis performed in this study (Chapter 6) shows that this pattern is indeed evident in Western Europe during MIS 3. As shown in Section 4.2.2 two factors contributed to a higher energetic demand in the Neandertal – heavier built and extremely cold weather (Sections 2.2. and 2.3). The extreme weather also contributed, especially during winters, to the low availability of plant food, thereby forcing Neandertals to rely on high animal fat consumption to fulfill the high caloric demand that protein could not provide. The conclusion of the high trophic level of the Neandertal diet was additionally supported by interpreting his 'bell' shaped thorax as an adaptation to a high-protein diet, by allowing room for large liver and kidneys that are necessary to process large quantities of protein to energy (Section 6.1).

The obligatory need for fat must have found expression in Neandertals' behavior. Evidence from the archaeological record for an obligatory requirement for high fat consumption was presented in Chapter 7. Specifically, preference for the acquisition of large and 'prime adult' prey animals at the cost of narrowing the choice, the transportation of fatty animal parts and the exploitation of bone marrow and bone grease were interpreted as stemming from the need to obtain fat. Assuming that the ethnographic record is better suited to discern innate qualitative preferences than exact quantitative DPAs, it was reviewed and found to contain evidence for a preference for the acquisition of fatter animals to the extent of leaving hunted lean animals unexploited. Also, a review of the use of animal fat as a symbol in traditional and HG groups shows an overwhelming association of animal fat with positive meanings. Among other meanings, fat was used to denote fertility, richness, desirability, sacredness and even life itself.

The preference for large animals can also serve to support an obligatory need for fat. The association between animal size and relative fat content was first elucidated by Pitts and Bullard (1967). It was later contested by Speth (1989); (Speth, 2010), about African ungulates. The only dataset of fat content in prey animals of different sizes (Ledger, 1968) was extensively analyzed here to elucidate whether there is indeed an association between animal size and fat content. The analysis shows that there is a strong association between size and fat content in African prey animals. Two distinct groups emerge from the analysis, one of the animals over 250 kg, with a high fat content, and one of the animals below 250 kg, with a significantly lower relative fat content. It was also shown that the standard tendency to discuss animal fat content in terms of weight to weight percentage could be misleading as animals with weight to weight fat content of 5% may actually have over 50% fat in terms of calories.

Having established the Neandertals' dependency on large animals for the supply of a large quantity of obligatory dietary animal fat, Chapter 9 deals with the dynamics of prey animal distributions during MIS 3.

Three databases and 13 individual multilayer sites were analyzed for the dynamics of the relative prevalence of large animals within both the MP and the CP, and between the MP and the CP, as representing the Neandertals, and the Aurignacian as representing AMH. Each database brings a unique geographical and temporal resolution to the analysis. Discamps et al. (2011) cover France during MIS 3. It allows a fine-scale, secure and temporal comparison of the presence of species in assemblages in Neandertal and AMH's associated cultures. The database's shortcoming is that it only indicates absence or presence of species and not the relative frequency of species in the assemblages. The database in Álvarez-Lao and Méndez (2016) covers all of Western and West-Central Europe during MIS 3 and contains the assemblages' absolute age. To overcome inaccuracies in estimating assemblage age, I added cultural assignments to the assemblages. The database in Grayson and Delpech (2006) covers France during the MP, CP, and Aurignacian. In contrast to Discamps et al. (2011), it includes data on the relative frequency of animals in the assemblages.

Most of the results of the analysis confirm a clear, and in many cases statistically significant, diminution of large animals when comparing Neandertal-generated assemblages with those generated by AMH. Most importantly, there is support, in the databases of Álvarez-Lao and Méndez (2016) and Grayson and Delpech (2006), as well as in the individual sites examined, for a diminution of large animals in Neandertal sites between 50 Kya and 40 Kya. The identification of a significant environmental stress before the arrival of AMH in Western Europe is crucial to the debate regarding the responsibility of AMH to the extinction of Neandertals. The findings here, together with the proposed fat dependency, suggests that the Neandertal was under constant and possibly increasing stress during MIS 3, well before the arrival of AMH.

The conclusion of this work suggests that the Neandertal should have been already demographically stressed by the time the AMH arrived in Europe, several thousand years after the diminution of large animals began. It is, however, as stated in the Methodology section, difficult, based on the present resolution and accuracy of the dating of the various sites and layers, to reliably determine whether Neandertals had indeed suffered a demographic contraction, in line with the diminution of large animals, starting 50 Kya. A natural initial low population density also hinders an identification of population decline during the period that preceded the arrival of AMH to Western Europe. A high-resolution study of Neandertal demographics during the 50-40 kya period in the area, if and when data becomes available, could help in testing the proposed hypothesis.

In conclusion, the results of the obligatory dietary fat estimates, the reconstruction of the Neandertal diet, the prey size - fat content association, and the analysis of large prey abundance during the periods preceding and following the Neandertal extinction all support the hypothesis.

It cannot be ruled out, that the presence of AMH helped delivering the *coup de grace* in what was a long extinction process either by accelerating the large animals' rate of diminution during the later stage of the Neandertals' extinction or by demographically absorbing their remnant population. This question could be a subject for future research, but in any event, it seems that the megafaunal extinction process began in earnest some five to seven thousand years before the arrival of AMH in Western Europe and thus most of the extinction pressure was not related to the presence of AMH.

Additionally, since every retreat of Neandertals from a given area could also be considered a form of local extinction, it would be interesting to see whether the present model can explain retreats from other areas, such as the Levant, the Caucasus, and Eastern Europe where megafaunal extinctions have occurred and where harsh winters or prolonged droughts may have concomitantly prevailed.

Finally, this study is the third application of the Obligatory Dietary Fat Bioenergetic Model in the explanation of human evolutionary events, such as extinctions and adaptations (Ben-Dor et al., 2011; Ben-Dor et al., 2016). Kelly (2013:74) states in his seminal book on recent and present-day hunter-gatherers: "*…it therefore may be fat rather than protein that drives the desire for meat in many foraging societies*". This statement indicates that the protein constraint may have been still effective in recent HG societies, so that until quite recently obligatory fat consumption still formed part of the solution for this constraint in humans. Given the protein constraint in humans, the model has the potential to explain more recent cultural adaptations, which were possibly aimed at coping with the protein constraint, such as the domestication of dogs to maintain energetic efficiency while hunting smaller animals, and indeed at least a partially explain the transition to agriculture with the need to replace fat with carbohydrates.

11 APPENDICES

Appendix 1 – (Álvarez-Lao and Méndez, 2016) with cultural designation for each layer

The database is available as an excel file via the following link:

https://drive.google.com/file/d/0B_9-lhl4tLP8eVluN2VuLV9jRW8/view?usp=sharing

Appendix 2 – NISP in Individual Southwestern European MIS 3 sites and Discamps et al. (2011)

The database is available as an excel file via the following link:

https://drive.google.com/file/d/0B_9-lhl4tLP8UFpfc19pYmpyR00/view?usp=sharing

Appendix 3 - Animal sizes (Faurby and Svenning, 2015) and (Magniez and Boulbes, 2014)

Animal sizes - Based on Svenning (2016) plus Magniez 2014				
			kg	
		Bison priscus	900	Magniez 2014
Bison	bonasus	Bison_bonasus	500	
Bos	primigenius	Bos_primigenius	900	
Capra	caucasica	Capra_caucasica	55	
Capra	caucasica	Capra_caucasica	55	
Capra	ibex	Capra_ibex	85	
Capra	pyrenaica	Capra_pyrenaica	50	
Capreolus	capreolus	Capreolus_capreolus	23	
Cervus	elaphus	Cervus_elaphus	180	
Coelodonta	antiquitatis	Coelodonta_antiquitatis	2693	
Dama	dama	Dama_dama	56	
Dicerorhinus	sumatrensis	Dicerorhinus_sumatrensis	1267	
Elephas	antiquus	Elephas_antiquus	6500	
		Equus	450	Magniez 2014
Equus	ferus	Equus_ferus	250	
Equus	hydruntinus	Equus_hydruntinus	227	
Mammuthus	primigenius	Mammuthus_primigenius	5500	
		Megaloceros_giganteus	750	Magniez 2014
Megaloceros	giganteus	Megaloceros_giganteus	700	
		ovibus moschantus	300	
Pelea	capreolus	Pelea_capreolus	20	
		Rangifer_tarandus	130	
Rangifer	tarandus	Rangifer_tarandus	86	
Rupicapra	rupicapra	Rupicapra_rupicapra	26	
Saiga	tatarica	Saiga_tatarica	29	
Stephanorhinus	hemitoechus	Stephanorhinus_hemitoec	2943	
Stephanorhinus	kirchbergensis	Stephanorhinus_kirchberg	3631	
Sus	scrofa	Sus_scrofa	101	
Ursus	arctos	Ursus_arctos	181	

Appendix 4

The Paper, Ben-Dor M, Gopher A, Hershkovitz I, and Barkai R. 2011. Man the fat hunter: the demise of Homo erectus and the emergence of a new hominin lineage in the Middle Pleistocene (ca. 400 kyr) Levant. PLoS ONE 6(12):e28689." Is available in the following link https://drive.google.com/file/d/0B_9-lhl4tLP8dDRDVFNZYkttb1E/view?usp=sharing

Appendix 5

The paper Ben-Dor, M., Gopher, A. and Barkai, R. (2016), Neandertals' large lower thorax may represent adaptation to high protein diet. *American Journal of Physical Anthropology*, 160: 367–378. doi:10.1002/ajpa.22981 is available in the following link

https://drive.google.com/file/d/0B_9-lhl4tLP8eFB4YzQydzZDSjA/view?usp=sharing

Appendix 6

The paper, Ben-Dor, Miki (2015) "Use of Animal Fat as a Symbol of Health in Traditional societies Suggests Humans may be Well Adapted to its Consumption," Journal of Evolution and Health: Vol. 1: Iss. 1, Article 10.

https://drive.google.com/file/d/0B_9-lhl4tLP8b0tOcjI2cDI1NW8/view?usp=sharing

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אוניברסיטת תל אביב
הפקולטה למדעי-הרוח ע"ש לסטר וסאלי אנטין
בית הספר למדעי היהדות וארכיאולוגיה ע"ש חיים רוזנברג
החוג לארכיאולוגיה ותרבויות המזרח הקדום ע"ש יעקב מ. אלקוב

הקשר הסיבתי בין היכחדות החיות הגדולות והיכחדות הניאנדרטל במערב אירופה – יישום המודל הביואנרגטי של הצריכה התזונתית החיונית של שומן

חיבור לשם קבלת תואר דוקטור לפילוסופיה
מאת: מיכאל (מיקי) בן דור

מנחים: פרופ' רן ברקן ופרופ' אבי גופר

הוגש לסינט האוניברסיטה
ספטמבר 2018

תקציר

מקובל היום שהניאנדרטל התפתח בהדרגתיות במשך לפחות 400,000 שנה באירופה. הניאנדרטל נעלם ממיצא המאובנים במערב אירופה (צרפת, ספרד) לפני כ- 40,000 שנה. האדם המודרני (א"מ) התחיל להתנחל בחלקים מאירופה לפני כ45-43,000 שנה, כמה אלפי שנים לפני היעלמותו של הניאנדרטל.

הסיבה להיכחדות הניאנדרטל במערב אירופה, ובמיוחד השאלה האם הא"מ שיחק תפקיד פעיל בהיכחדות זו, היא אחת השנויות ביותר במחלוקת במחקר הפרהיסטורי (Villa and Roebroeks, 2014), ו"נשאר אניגמה, אפילו לאחר יותר ממאה וחמישים שנים של מחקר" (Bradtmöller et al., 2012). אכן, Smith (2013) מזהה את הויכוח כ"אחד מהארוכים והשנויים ביותר במחלוקת במדע".

התזה הזו מכוונת להציג ולבדוק היפותיזה שהיכחדות החיות הגדולות שבמערב אירופה החלה לפני כ- 50,000 שנה, שיחקה תפקיד משמעותי בהיכחדות הניאנדרטל.

הפחתה טבעית בזמינות מזון צמחי במשך החורפים הארוכים של תקופת ה MIS מספר 3 במערב אירופה מביאה למסקנה שהניאנדרטל הסתמך במידה רבה על מזון מן החי, במיוחד במשך החורף. מגבלה פיזיולוגית על צריכת החלבון שלהם, יחד עם זמינות מוגבלת של מזון צמחי הייתה צריכה להביא לתלות בהשגה וצריכה של כמות נכבדת של שומן מן החי. צריכה הכרחית זו הייתה יכולה להיות מסופקת על ידי צייד של חיות גדולות אשר מכילות, באופן יחסי, כמות גבוהה יותר של קלוריות משומן מאשר חיות קטנות יותר, במיוחד בחורף. כאשר החיות הגדולות החלו להיעלם התפתח לחץ אנרגטי כרוני אשר יכל לגרום להיכחדות הניאנדרטל.

הזיהוי של מחסור בשומן כלחץ סביבתי שיכול היה להשפיע באופן משמעותי על שרידות הניאנדרטל מסתמך על תובנות שהושגו מ'המודל הביואנרגטי של שומן תזונתי הכרחי, (ODFBM). מודלים ביואנרגטיים שימשו החל משנות ה-80 להסבר תופעות אבולוציוניות, כולל היכחדות הניאנדרטל. מודל ה- ODFBM מיוחד בכך שהוא משתמש בשלושת אבות המזון כפרמטרים במודל. המודל מסתמך על העובדה הידועה שבני אדם מוגבלים יותר מטורפים ביכולת ניצול החלבון התזונתי להפקת אנרגיה זמינה לגוף. המודל לוקח בחשבון את הדרישות האנרגטיות של האדם נשוא המחקר ואת המגבלה הפיזיולוגית על צריכת חלבון כדי להגיע ליחס הכרחי של קלוריות מאבות המזון האחרים. בהנחה שמזון צמחי היה נדיר בחורפים של תקופת MIS 3, המודל קובע שהצריכה ההכרחית של שומן של הניאנדרטל בתקופות אלה הייתה של 75% עד 85% מהקלוריות. הצעד האחרון במודל משווה את הצריכה ההכרחית של שומן לתכולה היחסית של שומן בחיות הזמינות לצייד כפי שהן מיוצגות בממצא הארכיאולוגי של האזורים הרלוונטים. חיות גדולות מכילות יותר שומן באופן יחסי לסך הקלוריות שלהן. אני טוען שהניאנדרטל היה תלוי בקלוריות שהשיג מחיות גדולות עם התמקדות בשומן כספק גדול של קלוריות. אפשר לכן להסיק שהירידה בזמינות החיות הגדולות, לנוכח דרישה הכרחית גבוהה של שומן, גרמה ללחץ אנרגטי בגלל הצורך להשיג את אותה הכמות של שומן ממספר רב יותר, מעבר ליחס של משקל גופן, של חיות קטנות יותר.

גוף התזה מוקדש לאימות ההנחות שעמדו בבסיס חישובי המודל.

שיחזור התזונה של הניאנדרטל מתחיל בניתוח של מאפיינים כלליים של התזונה האנושית במשך התקופה הפליאוליתית. בהתאם לדרשות המודל, המחקר מתרכז בשאלה האם ניתן למצוא דפוס של צריכה תזונתית יחסית

מהצומח לעומת מן החי או בקיצור 'יחס החי:צומח' כזה שגרם לאדם להגיע למגבלת החלבון והכתיב צריכה הכרחית של שומן.

רוב הניסיונות להעריך את יחס הצומח:חי בתזונה הפליאוליתית הסתמכו במידה רבה על הממצא האתנוגרפי. הממצא האתנוגרפי של שתיים מקבוצות הציידים – לקטים הנחקרות ביותר, ההדזה והסאן, נסקר במגמה לבדוק את תאימותו כמקור לאנלוגיה עם התקופה הפליאוליתית. הסקירה מצאה שיחס החי:צומח בקבוצות בנות ימינו הושפע במידה רבה מהירידה בזמינות החיות הגדולות ששינתה לחלוטין את היחס סיכון-סיכוי של פעולת הצייד. כן נמצא שצייד החיות הקטנות יותר נעשה יותר יעיל בעזרת כלים ממתכת שלא היו זמינים כמובן בתקופה הפליאוליתית. החיסכון בזמן שהושג בעזרת כלים אלה איפשר הקדשת זמן למעקב אחר חיות קטנות שהתמורה הקלורית שלהן לשעת פעילות קטנה יותר. מבחינה אקולוגית השטח שבו פעילות קבוצות אלו עבר שינויים דרמטיים בחמישים אלף השנים האחרונות. התהליך העולמי של היכחדות החיות הגדולות לא פסח על אפריקה והוא נמשך למעשה עד היום. כתוצאה מכך ההדזה לדוגמה לא צדים יותר פילים, קרנפים והיפופוטמים כפי שנהגו בעבר.

הממצא הארכיאולוגי יכול להיחשב כמקור חלקי מאוד לניבוי היחס חי:צמחי בתזונה הפליאוליתית מפני שהשרידות של צמחים קטנה לאין ערוך מזו של חיות שעצמותיהן מתאבנות ואפשר למצוא את שרידיהן אפילו לאחר מיליוני שנה. לעומת זאת הגוף האנושי מכיל מידע גנטי ופיזיולוגי שיכול להצביע על התאמה אבולוציונית לדפוס כזה או אחר של תזונה. סקירה של התאמות אבולוציוניות כאלה בתוספת מידע פליאונטולוגי וסוגים אחרים של מידע ארכיאולוגי כולם תומכים במסקנה שהאדם הותאם לדרגה גבוהה של טורפות במשך רוב תקופת התפתחותו. סימנים של צריכה מוגברת של תזונה מהצומח מופיעים בהומו ספיינס למרות שהתזונה כנראה נשארה קרניבורית ברובה עד לתוך עומק התקופה של הפליאולית העליון. לקראת המעבר בחקלאות יש סימנים לעליה נוספת בצריכת מזון צמחי.

תיאור כזה של התזונה במשך האבולוציה האנושית מגבה את המסקנה הדי מקובלת שהתזונה של הניאנדרטל הייתה מאוד קרניבורית. שיחזור ספציפי של התזונה של הניאנדרטל מאשר שהם היו 'טורף על' למרות שצמחים היוו חלק מהתזונה באופן רגיל ומילאו כנראה תפקיד יותר גדול באזורים יותר דרומיים.

בגלל מגבלת החלבון תזונה עתירת מזון מן החי משמעותה תלות בכמות נכבדה של שומן. הממצא התנוגרפי והארכיאולוגי נסקרו כדי לאתר תלות כזו. הממצא האתנוגרפי מראה על שימת דגש רב על השגת שומן כקריטריון מרכזי בבחירת חיות לצייד עד לכך שחיות שניצודו ונמצא שאין להם כמות סבירה של שומן ננטשות ללא ניצול. מספר דפוסים בממצא הארכיאולוגי זוהו כנובעים מהצורך להשיג שומן. התמקדות בחיות בוגרות, העדפה של הובלת חלקי חיה עתירי שומן לאתר המרכזי, ניצול מוח עצם ושומן מהעצמות והעדפה לציד חיות גדולות כולם זוהו כדפוסים כאלה אצל גם אצל הניאנדרטל וגם אצל האדם המודרני.

ניתוח פרטני של בסיס נתונים של 273 חיות שניצודו באפריקה מצא קשר ישיר הדוק בין גודל החיה ובין אחוז השומן שבה.

לבסוף, שלושה בסיסי נתונים ארכיזאולוגיים המכסים את מערב אירופה במשך תקופת MIS 3 נותחו יחד עם נתונים מ- 13 אתרים רב-שכבתיים כדי לזהות מגמות בניצול חיות גדולות החל מחמישים אלף שנה לפני זמננו. הניתוח אישר שהייתה ירידה משמעותית בציד חיות גדולות בין 50 ל-40 אלף שנה לפני זמננו, התקופה שבה התרחשה היכחדות הניאנדרטל. מגמה זו המשיכה גם לאחר היכחדותו.

לסיכום, יישום של המודל הביואנרגטי של צריכה הכרחית של שומן למקרה של היכחדות הניאנדרטל מצביע על כך שהיכחדותו הייתה תוצאה של לחץ אנרגטי שהתפתח במערב אירופה ושהחל לפני כ-50 אלף שנה לפני זמננו בגלל ירידה בזמינות החיות הגדולות.

אין אפשרות לקבוע שלאדם המודרני שהגיע לאירופה בסופה של התקופה לא הייתה תרומה נוספת להיכחדות הניאנדרטל אך ברור מיישום המודל שתרומתו להכחדה, אם הייתה, לא הייתה התרומה העיקרית.