What Are the "Costs and Benefits" of Meat-Eating in Human Evolution? The Challenging Contribution of Behavioral Ecology to Archeology

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Despite the omnivorous diet of most human populations, meat foraging gradually increased during the Paleolithic, in parallel with the development of hunting capacities. There is evidence of regular meat consumption by extinct hominins from 2 Ma onward, with the first occurrence prior to 3 Ma in Eastern Africa. The number of sites with cut-marked animal remains and stone tools increased after 2 Ma. In addition, toolkits became increasingly complex, and various, facilitating carcass defleshing and marrow recovery, the removal of quarters of meat to avoid carnivore competition, and allowing the emergence of cooperative (i.e., social) hunting of large herbivores. How can we assess the energy costs and benefits of meat and fat acquisition and consumption for hunter-gatherers in the past, and is it possible to accurately evaluate them? Answering this question would provide a better understanding of extinct hominin land use, food resource management, foraging strategies, and cognitive abilities related to meat and fat acquisition, processing, and consumption. According to the Optimal Foraging Theory (OFT), resources may be chosen primarily on the basis of their efficiency rank in term of calories. But, could other factors, and not only calorific return, prevail in the choice of prey, such as the acquisition of non-food products, like pelts, bone tools or ornaments, or symbolic or traditional uses? Our main goal here is to question the direct application of behavioral ecology data to archeology. For this purpose, we focus on the issue of animal meat and fat consumption in human evolution. We propose a short review of available data from energetics and ethnographic records, and provide examples of several various-sized extant animals, such as elephants, reindeer, or lagomorphs, which were some of the most common preys of Paleolithic hominins.

Keywords: Pleistocene, energetics, extinct hominins, behavioral ecology, meat and fat consumption

INTRODUCTION

Energetics (e.g., food accessibility and availability, energy intake and balance...) comprise critical information for enhancing our understanding of human evolution (Aiello and Wheeler, 1995; Leonard and Robertson, 1997; Aiello and Wells, 2002; Snodgrass et al., 2009; Isler and Van Schaik, 2014; Burini and Leonard, 2018). A shift to a more energetical-rich food, such as meat, contributes

to meeting elevated daily energy requirements (Pontzer, 2017; Pontzer and Wood, 2021). Meat consumption behavior and hunting are also observed in non-human primates. For example, bonobos focus primarily on small herbivores. Chimpanzees occasionally hunt monkeys using tools (Pruetz et al., 2015), but process carcasses without any use of tools. Meat represents less than 0.01–0.19 kg/day in their diet and only small proportions of their feeding time (Watts, 2020). During human evolution, meat consumption seems to increase and to become less sporadic than in extant non-human primates. As a famous primatologist, Washburn, expressed: "The taste for meat is one of the main characteristics distinguishing man from the apes, and this habit changes the whole way of life. It is therefore important to date the beginning of hunting in order to interpret the origin of human behavior" (Washburn, in Brain, 1981).

The purpose of this short literature review is to present the main steps of meat-eating in human evolution, and to discuss its cost and benefits in terms of biological and sociological aspects. In order to do so, we present different approaches for addressing the energetics of past hominins, crossing extant and archeological data. Finally, we discuss the relevance of paleoanthropological and archeological data in the context of meat consumption and assess the interests and limitations of applying behavioral ecology to archeology.

MEAT-EATING IN HUMAN EVOLUTION: ARCHEOLOGICAL EVIDENCE

The first occurrences of meat consumption by early hominins are recorded in Africa around 3.4 Ma at Dikika, Ethiopia (McPherron et al., 2010; Thompson et al., 2015), although the identification of the butchery marks is still questioned (Domínguez-Rodrigo et al., 2010, 2011; McPherron et al., 2011). Pliocene stone tools discovered at Lomekwi 3, Kenya, 3.3 Ma, support the hypothesis of stone tool making by Pliocene hominins more than 3 Ma ago, 500,000 years before the emergence of the *Homo* genus (Harmand et al., 2015). In addition, dental and cranial morphology, gut size or endurance running point to increased meat and fat consumption among Late Pliocene and Early Pleistocene African hominins (Aiello and Wheeler, 1995; Teaford and Ungar, 2000; Teaford et al., 2002; Bramble and Lieberman, 2004; Ungar, 2004; Daegling and Grine, 2007; Ben-Dor et al., 2021), as do stable isotopes analyses (Balter et al., 2012; Martin et al., 2020). We observe an increased number of sites with cut-marked animal remains and stone tools after 2 Ma, in eastern Africa (Bunn, 1981; Potts and Shipman, 1981; De Heinzelin et al., 1999). For example, the Oldowan site of Kanjera (2 Ma), South Kenya, yielded numerous bone elements processed by hominins, comprising small as well as medium-sized bovids, highlighting meat consumption and also the first evidence of hunting small animals (Ferraro et al., 2013). In parallel to this early consumption of small animal tissues, some evidence shows the input of aquatic and plant-based resources. Meat from terrestrial mammals was not the only, nor the main source of protein. For example, in the Koobi Fora Formation, Kenya, some crocodile, fish and turtle remains bearing cut marks highlight the exploitation of water habitats by early *Homo*

erectus (i.e., *H. ergaster*) (Braun et al., 2010; Archer et al., 2014). Besides, dental wear patterns and isotope ratios indicate wide diversity in the diet of Late Pliocene and Early Pleistocene hominins, including plants and hard foods such as nuts, seeds and underground storage organs (Ungar and Sponheimer, 2011; Balter et al., 2012; Grine et al., 2012). Animal fats were also an important source of calories for past hunter-gatherers, and large herbivores in particular provide omega-3 fatty acids (Guil-Guerrero et al., 2014, 2015).

Toolkits may also have been essential to hominins for butchering carcasses, with cutting edges for processing soft tissue as well as percussion tools to extract marrow. With the onset of the Acheulean and the emergence of *H. erectus* sensu lato populations in Africa, between 1.9 and 1.7 Ma (Lepre et al., 2011; Hammond et al., 2021), we observe a dietary change with greater evidence of carnivorous and predatory behavior in faunal assemblages (Shipman and Walker, 1989; Echassoux, 2012; Pante, 2013; Domínguez-Rodrigo et al., 2014; Diez-Martín et al., 2015; Arriaza et al., 2017; Yravedra et al., 2020). However, although meat consumption occurred quite early in human evolution, common meat consumption, complex forms of cooperative hunting, entire butchery sequences and stone and carcass transport, which require advanced cognitive skills such as planning and more decision-making, seem to have developed later, after 1 Ma, throughout the African continent and the Levant in conjunction with early Middle Pleistocene environmental changes (Clark et al., 2006; Rabinovich et al., 2008; Forrest et al., 2018; Altamura et al., 2019; Daujeard et al., 2020).

Later, in Western Europe, the large quantities of herbivore remains found in Middle Paleolithic sites (c. 400–40 ka) (Gaudzinski and Roebroeks, 2000; Costamagno et al., 2006; Daujeard et al., 2012; Niven et al., 2012; Rendu et al., 2012), stable isotope ratios (Bocherens et al., 2005; Wißing et al., 2016; Jaouen et al., 2019) and tooth wear data (Estalrrich et al., 2017), highlight the high intake of animal proteins in the Neanderthal diet. Neanderthals could rely for up to 80% on animal protein and 20% on plant proteins (Naito et al., 2016), making them the most emblematic carnivorous and competitive big game hunters among extinct hominins (Karavanić et al., 2000). Despite this mostly carnivorous diet, more recently, dental calculus residues show that many Neanderthal groups consumed plants for food, medicinal or gustatory purposes (mushrooms, pine nuts, leguminous plants, etc.) over a widespread area ranging from the Mediterranean Basin to Central Europe (Henry et al., 2011; Hardy et al., 2012; Krief et al., 2015; Weyrich et al., 2017; Power et al., 2018). Moreover, in their recent article, Hardy et al. (2022) emphasize the importance of plants in nutrition for all hominin species, including Neanderthals, through indirect evidence, such as physiological requirements.

For Pleistocene Anatomically Modern Humans (AMH), interpretations also point toward a high quantity of meat in their diet, predominantly from large game (Prat et al., 2011; Drucker et al., 2017; Ben-Dor et al., 2021). Although small game was consumed since the Early Paleolithic (Fernández-Jalvo et al., 1999; Braun et al., 2010) and the Middle Paleolithic (Hardy and Moncel, 2011; Cochard et al., 2012; Hardy et al., 2013; Blasco et al., 2016; Morin et al., 2019; Pelletier et al., 2019; Guillaud et al., 2021), we note an increase in small prey and fish at the

end of the Upper Paleolithic in Europe and the Levant (Stiner et al., 2000; Costamagno and Laroulandie, 2004; Rufà et al., 2018). Concerning carbohydrates intake in the AMH diet, alongside the more numerous direct evidence, recent studies on the oral microbiome highlighted a high degree of similarity between modern humans and Neanderthals, with the specific acquisition of starch digestion (Fellows Yates et al., 2021).

Finally, whether prey species were passively or actively scavenged, trapped or hunted, the intensification of animal meat and fat in the diet of extinct hominins exposes them to competition with various other predators and scavengers, increasing interactions: direct attacks, passive confrontations, dispersals, commensalism, etc., and mutual contributions: providers of carrion, models for hunting strategies, etc. (Marean, 1989; Shipman and Walker, 1989; Turner, 1992; Rodríguez et al., 2012). Whatever the types of strategies used and the amount consumed, the consumption of meat and fat may have had significant consequences on human evolution in terms of biology, societies and also in terms of energetic costs and benefits.

CONTRIBUTION OF ECOLOGICAL MODELS AND EXTANT DATA TO THE STUDY OF PAST HOMININ DIETS

Ecological Models

In order to address subsistence practices and the energetics of past hominins, a multi-proxy approach is necessary, taking into account various factors: hominin capacities (biological, social and cultural features), paleoenvironmental constraints (biomass, prey availability, seasons, topography, other competitors, etc.), archeological and geochemical data (faunal remains, isotopes, etc.) and actualistic data and ecological models, used for example in human behavioral ecology (HBE) (Smith, 1992). HBE is a neo-Darwinian approach in which changes in behavior may result from natural selection (adaptation to the environment), rather than from cultural motivations. HBE emerged in the mid-1970s with the application of optimal foraging models to hunter-gatherer decisions relating to resource selection and land use (Winterhalder and Smith, 2000; Codding and Bird, 2015).

In the 1980s, a theory developed by ecologists, called The Optimal Foraging Theory (OFT) (Stephens and Krebs, 1986; Pyke and Stephens, 2019), was applied to anthropology and archeology to specifically explain dietary patterns in hunter-gatherer societies (Smith, 1979; Winterhalder, 1981; Smith et al., 1983). OFT provides predictions and valuable models for grasping the relations between the environment and foragers in the past. What should be eaten? Where should food be sought and how large a group is needed to catch and exploit the food? According to the OFT, resources may be chosen primarily on the basis of their efficiency rank in term of calories. The most current of these foraging models is diet breadth, also called prey-choice model (PCM) or optimal diet (Winterhalder and Smith, 2000; Bird and O'Connell, 2006). According to this model, high-ranked resources are pursued whenever encountered, and lower-ranked resources are included in the diet depending on encounter rates with higher ranked resources. Thus, prey choice

takes into account various parameters such as the main goal, which corresponds to the maximization of foraging efficiency, currency, which is usually a measure of energy costs and benefits; constraints, which are all the limiting factors, such as the time spent foraging, processing or digesting capacities; and the alternative options for making a decision, which incorporate the possible set of food resources, daily needs and other ways of spending time (childcare for example).

According to these models, energy is one of the main parameters influencing subsistence strategies in past hunter-gatherer societies, it is important to calculate the return rate of the animal. The Energy Cost-benefit or Post-Encounter Return Rate (PERR) or Efficiency rank is defined as the ratio of the Energetic benefit of the animal (expressed in kcal) to the Energetic cost related to searching and handling time (expressed in person-hours). Handling time corresponds to the time spent pursuing and dispatching prey, carcass processing and transport and consumption (chewing and digesting time). The latter depend on several parameters, such as the type of prey (size, weight, age, aggressiveness, encounter rate, etc.), consumed body parts, season, topography, distance, group size, other competitors, etc.

Extant Data on Animal Nutrients and Human Biology

The energy intake and nutrients supplied by terrestrial animals correspond to meat, fat, yellow, and red marrow, brain, tongue, viscera, etc. Meat and marrow nutrients provide proteins (amino acids), fats (saturated and unsaturated fat), vitamins (A, B1, B2, B3, B6, B12, and C) and minerals (Iron, Calcium, Zinc). Fat is the most energy-dense macronutrient (Ben-Dor et al., 2021). For example, lean beef meat provides between 100 and 200 kcal/100 g, but beef fat contains about twice as many calories (900 kcal/100 g) as protein or carbohydrates (400 kcal/100 g). Indeed, although meat-eating is of high calorific value, it induces high energy expenditure for the elimination of nitrogenous waste products. As a result, a diet rich in lean meat requires very high daily food rations to cover body energy requirements. In addition, excessive protein consumption leads to liver and kidney disorders. Excessive animal protein intake may lead to protein toxicity which can be dangerous for pregnant women and new-borns (Fiorenza et al., 2015). These deficiencies and health risks can be overcome by increasing the fat intake in the diet. Fat has a high energy value, and enables gluconeogenesis, a metabolic process occurring primarily in the liver and kidneys that produces carbohydrates from protein and fat (Speth and Spielmann, 1983; Speth, 2010). These advantages therefore go a long way to explaining why Paleolithic human groups sought to harvest fat wherever it was available, including fat contained in the marrow and cancellous tissue of very large and large mammals long bones (Costamagno and Rigaud, 2013; Smith et al., 2015; Ben-Dor et al., 2016; Blasco et al., 2019a; Boschian et al., 2019; Morin, 2020; Dodat et al., 2021). The preparation of broths based on fat contained in bone tissue observed among the Nunamiut by Binford (1978) suggests that such processes may have existed in Paleolithic societies (Speth, 2015). Moreover, in order to avoid excessive meat protein, in addition to animal fat, other alternative

food resources, such as plants, might have been incorporated in the diet (Henry et al., 2011, 2014; Fiorenza et al., 2015).

Since the 1970s, the plethora of ethnographic studies of hunter-gatherer societies have provided abundant data on human biology and diet, and fostered the development of ethnoarchaeological research through the 1980s and 1990s (Binford, 1978; Keene, 1985; O'Connell et al., 1988a, 1990; O'Connell and Marshall, 1989; Bartram, 1993; Bunn, 1993, 1994; Kelly, 1995; Bartram and Marean, 1999). We know for example that we have a daily energy expenditure of 2,000–3,000 kCal per day, which is related more to body size, age, and sex than to cultural differences (Pontzer et al., 2012). Relative to other great apes, hunter-gatherers spend more daily energy for food-finding, but with a greatest return rate, making possible the sharing with others, and thus the possibility for some to carry out tasks other than foraging (Kraft et al., 2021). The similarity in daily energy expenditure among hunter-gatherers and sedentary Westerners suggests that the effect of marked lifestyle differences is minor and that differences between populations result primarily in energy intake, rather than expenditure. In the same way, variation in the diet is mainly related to temperatures and primary production, for example, hunting territories are generally larger in northern latitudes (Kelly, 1995). Regarding the proportion of meat, animal fats or plants in the human diet, we have to be careful with the data from present-day hunter-gatherers. Environmental conditions, technical, and physiological adaptations must prevent us from making direct analogies with Pleistocene hominins, and even more so with the earliest ones (Ben-Dor and Barkai, 2020; Ben-Dor et al., 2021).

Eating Raw or Cooked Meat: What Is the Energetic Impact?

The control of fire and its use for cooking marks another critical shift in the diet. Indeed, despite the apparent importance of meat in human evolution, some studies (Carmody and Wrangham, 2009) showed that a raw food diet provides insufficient energy for the maintenance of body weight, suggesting that food processing and cooking are very important. Indeed, when starch or proteins are cooked, they are more tender, more digest, mastication is facilitated (reduction of chewing time), the cost of digestion is reduced and energy extraction per unit mass increases (Wrangham et al., 1999; Carmody and Wrangham, 2009; Carmody et al., 2011; Hardy et al., 2015). Furthermore, cooking kills food pathogens. However, iron and certain vitamins, such as for example vitamins B12 and C (which primates are unable to synthesize), decrease with high temperatures and cooking time. Cooking can be quite costly in terms of energetic expenditure in terms of fuel collection, the time needed to make and maintain fire, and requires some cognitive skills, such as for example for fuel collection (choice of wood, bones, stones etc.), and fireplace location (Henry et al., 2018; Magargal, 2022). Cooking or fire use was initially very occasional, and could have occurred with *H. erectus* in Africa c. 1.8 Ma ago. This hypothesis is based on indirect evidence of hot springs (Sistiaga et al., 2020), thermally altered lithics and bone fragments at 1.5 Ma in Kenya (Hlubik et al., 2017), microstratigraphic evidence at 1 Ma in South Africa (Berna et al., 2012), and the decrease in the size of

the digestive system (see below "Expensive Tissue Hypothesis"). Therefore, this indirect evidence predates the first evidence of the control of fire in the Near East at 790 ka (Alperson et al., 2004; Alperson-Afil, 2008) and the oldest evidence of the habitual use of fire attested around 300–400 ka in Europe, Africa and the Levant, which suggests that this behavior is relatively recent (Roebroeks and Villa, 2011; Shahack-Gross et al., 2014; Barkai et al., 2017; Richter et al., 2017; MacDonald et al., 2021).

Aiello and Wheeler (1995) put forward the "Expensive Tissue Hypothesis" to explain how primates can have relatively large brains without a high basal metabolic rate. For those authors, the increased energetic demands of a larger brain are compensated by the reduction in the mass-specific metabolic rates of other tissues, such as the gastro-intestinal tract. Their analyses in human and non-human primates infer coevolution between brain and gut sizes, which is dependent on energy intake and could be determined by dietary quality. They consider that hominins, especially after 2 Ma (e.g., early *H. erectus* sensu lato), had small guts, and would have required the use of fire and cooking to efficiently process difficult-to digest food, such as meat. However, some authors consider that this trade-off scenario seems to be insufficient (Navarrete et al., 2011; Isler and van Schaik, 2012), and they stress that brain size is not correlated with other energetic expensive organs or with digestive tract mass, and that encephalization and fat storage in primates are strategies to buffer against caloric shortfalls. Furthermore, Cornélio et al. (2016), revisiting correlations between brain size and cooking, showed that large primate encephalization occurred long before the control of fire and that hominins were likely to obtain enough calories from raw meat to afford brain size increase. Indeed, processing methods such as pounding (Zink et al., 2014; Zink and Lieberman, 2016), or eating rotten or putrefied meat, also result in an important increase in energy compared to unprocessed raw diets (meat or tubers). In addition, such methods preserve vitamins, favor pre-digestion and do not require fuel (Speth, 2017). Likewise, other studies propose that the increased need for more energetical-rich nutrients due to reduced gut size might also have been compensated by animal fat (Ben-Dor et al., 2011), or even by semi-digested chyme, i.e., gastrophagy (Buck et al., 2016).

Meat-Eating and the Origin of Social Cooperation and Food Sharing

Meat involves a relatively high level of cooperation. Compared to plants, meat is difficult to obtain, and very demanding in both time and energy. This becomes particularly critical when the subsistence strategy focuses on big game, where cooperation is often needed to acquire resources and fend off predators. In such cases, distribution needs to be efficient within the group and all the participants have to receive a payoff (Alvard, 2011). Food sharing, and in particular meat sharing, is thought to be central to the evolution of hominin behavior and to hunter-gatherer economics where food transfer practices vary greatly, depending on resource availability in the environment, or/and social organization (Hawkes et al., 1991; Winterhalder, 1997; Lee and Daly, 1999; Enloe, 2003). Food sharing reduces the risk of caloric shortfall, especially when it concerns large animals,

which are high-risk food as they are difficult to obtain but also high-reward food. Hunting is considered to be one of the most difficult foraging activities. Direct encounters with big game and successful capture require substantial skills and knowledge sharing which develop at least 10 years after attaining adult body size (Gurven et al., 2006). In most hunter-gatherer populations, the meat of big animals is widely shared with the opportunity to get it back later. The cost of sharing with the whole group is quite low, as the total amount of meat cannot be eaten at one time by the hunter's family. On the contrary, the benefits of the reciprocity are quite high, as sharing avoids meat spoilage, long-term food storage and reduces the risk of nutrients shortfalls, especially for large prey such as elephants (Hawkes et al., 1991; Enloe, 2003; Gurven and Jaeggi, 2015; Barkai, 2019). Hadza populations consider carcasses of large sized animals as public goods. There are few nutritional advantages to being an efficient hunter, and the benefits to the generous sharers might only be their hunter reputation (Kaplan et al., 1985; Stibbard-Hawkes et al., 2020).

Hominins could have used different acquisition modes over time to obtain meat from small or large animals: trapping, passive or confrontational scavenging, ambush or pursuit hunting using short or long distance weapons, hand capture of small-sized prey, etc., which favored the development of social cooperation and food sharing (Domínguez-Rodrigo, 2002; Stiner et al., 2009; Gaudzinski-Windheuser et al., 2018; Conard et al., 2020). Primary distribution occurred at the kill site, as the carcass was partitioned for transport. Secondary distribution, which is redistribution to family, took place at the campsite or the consumption area. These two stages can be observed in the archeological record thanks to the spatial distribution and butchering patterns of the carcasses. However, the origins of food sharing and its definition and purpose are still debated in evolutionary anthropology and Paleolithic archeology (Isaac, 1978; Kaplan et al., 1985; Blurton Jones, 1987; Hawkes, 1991; Winterhalder, 1996, 2001). It is reasonable to expect that Pleistocene hominins lived in social groups, but food-sharing patterns must have differed a lot through time and depended on the size of game (Stiner et al., 2009). Willems and Van Schaik (Willems and van Schaik, 2017) suggest that at the time of the emergence of the *Homo* genus, the social organization of *H. ergaster* revolved around reduced fission-fusion dynamics and very large multi-male groups, which could have helped to defend the group against predators. Through time, when hominins moved toward higher latitudes (further north), increasingly complex multilevel fission-fusion social systems could have helped hominins to adjust foraging patterns, constrained by large group size, low population densities and increased foraging demands (Grove et al., 2012). Furthermore, the most common anthropological scenario also suggests a link between the transition toward eating a high-quality diet, such as meat, for example, and cooperation among hominins (including care of the young, protection from predators, group hunting, and food storage) (O'Connell et al., 1988b, 2002; Hawkes et al., 2001; Bramble and Lieberman, 2004; Pontzer, 2012). Intergenerational cooperation brings increased energetic benefits, with the coevolution of increases in the duration

of lactation, gestation, longevity, neonate and adult body mass and daily energy expenditure, but a decrease in sexual dimorphism (Smith et al., 2012). Indeed, according to Smith et al. (2012) evidence from carnivores indicates that both the pace of reproduction and the emergence of cooperative defense against predators can respond in a flexible fashion to variations in the availability and acquisition of energy-rich foods. Thus, for those authors, it is possible that similar flexibility influenced shifts in reproductive investment and reproduction rates among hominins.

Another adaptive reason why Late Pliocene and Early Pleistocene hominins had to amplify forms of cooperation regarding immature individuals is related to human life history, with juveniles remaining dependent for a longer time on mothers than other species. In the course of human evolution, this was made possible through the support of group members other than the mother, i.e., "food transfer between alloparents and offspring: cooperative breeders" (e.g., Burkart et al., 2009; Hrdy, 2009; Strassmann and Kurapati, 2010; Kramer et al., 2015). Cooperative breeding, which affects parental care (shorter birth intervals, juvenile dependence), is presumed to appear in the Lower Pleistocene with early *H. erectus* (O'Connell et al., 1999; Hrdy, 2009; van Schaik and Burkart, 2010). Indeed, Aiello and Key (2002), suggest that *H. erectus* females were able to cope with increased energetic costs per offspring (daily energy requirements during gestation and lactation) by shortening interbirth intervals and cooperating with others in feeding dependent children. Moreover, Wrangham and Conklin-Brittain (2003) have also suggested that cooking, which makes raw food soft enough for young individuals to chew, may have facilitated shorter inter-birth intervals.

To conclude, animal acquisition and consumption represent an undeniable advantage in terms of time and energy benefits, by providing considerable quantities of proteins, fat and other nutrients. However, it may also sometimes constitute a high-cost food source, and if considering only meat, it can be even unhealthy in excessive amounts. Hunter-gatherers should not exceed a maximum quantity of protein intake (plant and animal) per day, and so they must also obtain a large part of non-protein food in their environment (fat and carbohydrates) (Speth, 1989). As a matter of fact, big-game hunting is not always advantageous for feeding a human group. The risk of failing, the time to pursuit, the type and size of the prey, their physiological condition throughout the year, sometimes with a scarcity of fat, and many other parameters, all challenge the prominence of hunting large mammals in the early human diet (Speth, 2010).

THE CASE OF THREE TYPES OF PREY SIZE: AT THE CROSSROADS BETWEEN EXTANT AND ARCHEOLOGICAL DATA

We can hypothesize on the prey acquisition and carcass transport strategies developed by past hunter-gatherer societies using extant and energetic data. These strategies depend on

several parameters in terms of energy costs and benefits: (1) the number of hunters; (2) the type of prey (size, weight, age, aggressiveness, encounter rate, etc.); (3) the nutritive value of chosen carcass elements; (4) the season; (5) the topography and the distance from the kill site to the camp; (6) the distribution within the group and repayment; and (7) the presence of other competitors; etc. Concerning the latter parameter, early experimental and actualistic research in African national parks yield a better idea of carcass availability in the environment, the degree of competition and resource partitioning strategies for the different predators and scavengers (Brain, 1981; Blumenschine, 1986; Brantingham, 1998; Domínguez-Rodrigo, 1999). Besides, as far as the weight of the animal is concerned, we know that for the Hadza in Tanzania, 80% of the anatomical elements of skeleton are abandoned at the kill site for large or very large adult animals, compared to only 30% for those of medium size, in relation with the cost/benefit rate of each carcass portion (O'Connell et al., 1990; Lupo, 2001). The age of the animal and season of death may also be relevant in the transport strategies. Adult marrow is richer than that of juveniles, and in the same way, marrow represents the last fat resource during the winter, which explains the interest for bones such as metapodials, which are poor in meat but rich in yellow marrow (Speth and Spielmann, 1983; Speth, 1987). Here, we will take the example of three animals of different sizes (elephants, reindeer, and lagomorphs) exploited by past and extant hunter-gatherers, and examine their specificities in term of energy and capture difficulty.

An adult elephant provides a huge amount of meat; almost two tons. Despite its weight, this colossal animal is not always sought by past and present hunter-gatherers. According to Lupo and Schmitt, whose data come from ethnographic and historic sources (Lupo and Schmitt, 2016): "Applications of the Prey Choice Model to ethnographic populations show that prey size does not always predict profitability." First of all, hunting failure has to be considered, considering many variables, including the prey itself. According to the authors, the bigger the prey, the more likely hunters are to miss it. Larger-sized preys are less abundant in the landscape, and hunters spend more time tracking them. The success rate for elephants is only 20% for Bisa hunters in Zambia, which drastically reduces the PERR. Secondly, the time spent pursuing the animal can be up to 38 h for an elephant. Lupo and Schmitt highlight the strong and positive correlation between the size of the prey and pursuit time. Lastly, large game requires extensive processing and transport efforts involving many individuals, with 86 h of butchering time for an elephant.

In comparison, for the Paleolithic, the role of megafauna in the hominin diet is often questioned. The association of megafauna with archeological sites is sometimes problematic and the full range of possibilities should be discussed. One of the critical factors for many of the megafauna sites is that some may be the results of scavenging or bone collecting for fuel, tools and building materials (Gaudzinski et al., 2005; Domínguez-Rodrigo et al., 2014; Lupo and Schmitt, 2016). Besides, zooarchaeological evidence of megafauna exploitation

in Early and Middle Paleolithic assemblages is scarce, which rather supports the opportunistic role of megafauna during these ancient periods (Demay et al., 2012, 2016a,b; Smith, 2015). Nevertheless, the role of proboscideans in human evolution should not be minimized. In this regard it is important to notice that butchery and fracturing marks are particularly difficult to observe on pachyderm bones, as it was previously pointed out (Crader, 1983; Haynes and Krasinski, 2021). In the same way, a large quantity of food from Proboscideans in the Paleolithic has been highlighted by high ratios of nitrogen in humans (Wißing et al., 2016; Drucker et al., 2017). Yet, these data should be treated with caution as other parameters can induce high nitrogen levels, such as a diet based on aquatic resources, breastfeeding, putrefied meat or episodes of caloric shortfalls (Speth, 2017). Although evidence for elephant hunting is mostly provided for the Upper Paleolithic times (Svoboda et al., 2005; Agam and Barkai, 2018; Demay et al., 2021), for earlier periods there is the case of the Pleistocene elephant single-carcass sites, such as the Acheulean sites of Nadung'a 4, Kenya (Delagnes et al., 2006), or that of Barranc de la Boella, Spain (Mosquera et al., 2015). There are also the example of the Middle Pleistocene sites in the Latium in Italy with many Elephant remains (Anzidei et al., 2012; Boschian and Saccà, 2015). They have given rise to various hypotheses. Are they related to specific human behavior, to an exceptional preservation context or to a higher number of pachyderms in the environment?

Concerning reindeer, the two most famous ethnographic examples of reindeer husbandry and hunting in Northern latitudes are the Nunamiut (Alaska) and the Evenki (Russia), among others (Winterhalder, 1983; Costamagno and David, 2009). The Nunamiut are large bands of a hundred individuals. They are 80% dependent on reindeer hunts and can kill more than 200 reindeer for a year through the mass killing of migratory tundra gregarious reindeers (Binford, 1978, 1981). Evenki are small family groups of 5–10 individuals. Among the Evenki, Abe observed the kills of four woodland reindeer for 21 reindeer hunts for a year, which represents a very low success rate (19%) compared to those of the Nunamiut (43%) (Abe, 2005). Tracking a reindeer on foot can last more than 11 h, including kill site butchery. The PERR of a reindeer is thus 80,000 kcal/11 h, and lower once the success rate is considered.

To illustrate the exploitation of reindeer by past societies, we will take the example of a Middle Paleolithic site from south-eastern France. The Abri du Maras yielded Neanderthal occupations dated to around 50–40 ka for layer 4.1 (Moncel et al., 2021). Like many other archeological records with monospecific assemblages from the Middle Paleolithic of Western Europe, a great number of reindeers were present in the layer (88% of the NISP, representing 16 individuals), which also includes horse, bison, giant deer, red deer, ibex, and lagomorphs. Zooarchaeological analyses evidence a catastrophic age profile and autumnal kills, highlighting mass reindeer predation during migration events (Daujeard et al., 2019). At this camp site, we have *in situ* evidence of the reindeer exploitation of all the edible resources (marrow, meat, bone grease, etc.). The

scarcity of the spongious part of the skeleton, axial parts (heads, vertebrae, and ribs), as well as girdles (pelvis and scapula), long bone epiphyses and short articular bones (carpals, tarsals, and phalanges), underlines either their abandon at the kill site and/or specific processing methods at the camp for grease bone extraction and/or for fuel. Only a few portions of the skeleton are represented in relation to their utility index (expressed in meat, grease, and marrow quantity). Anyway, although the choice of some portions is correlated to the Food Utility Index, bone grease as well as non-food products (like animal pelts) may also have mattered in the choice of past hunter-gatherers.

We have taken here the example of this faunal assemblage to illustrate Prey Choice Model and Carcass transport strategies. For that purpose, we assessed the energy intake from the faunal spectrum, and classified species according to their weight in meat. The total amount obtained is 3.5 tons of available meat if we count the whole carcasses of slaughtered animals, representing 4 M kcal, which can feed about 20 hunter-gatherers for two and a half months. In terms of Optimal Foraging Theory, some assumptions can be made:

- The selective diet would highlight a rich environment with a short encounter time;
- Reindeer probably had the highest encounter rate, with great autumnal migration events along the Rhone Valley;
- They were also safer and more easily transportable than Bison, while 16 reindeer are equal to two bison in term of meat weight;
- The few processed lagomorphs were probably the result of opportunistic encounters.

Finally, although this type of modeling opens up assumptions in terms of subsistence strategies, little can be said in the end as many occupations have certainly succeeded and mixed in this assemblage, as it was taken here as a whole.

Concerning lagomorphs, the encounter rate is much higher than for elephants (80% success) but they are much less productive. Indeed, the rabbit is small, only provides around 2.5 kg of meat and is in addition very poor in lipids, which can lead to protein toxicity called "rabbit starvation" (Cochard, 2004; Rufa Bonache, 2017). For lagomorphs, similarly, exploitation is scarce during the Early and Middle Paleolithic, with only a few archeological examples (Fernández-Jalvo et al., 1999; Blasco and Fernández Peris, 2012; Cochard et al., 2012; Hardy et al., 2013; Morin et al., 2019).

In spite of the low energy efficiency of lagomorphs when they are not slaughtered *en masse*, like other small preys, at the end of the Upper Paleolithic and during the Mesolithic, small prey hunting intensified. This could be explained by various hypotheses: cultural changes; environmental pressure with too many lagomorphs in a valuable territory; decrease of mobility and longer human occupations; or demographic pressure, which would have led to the broad-spectrum revolution. The demographic pulses of the UP and Epi-Paleolithic would have then forced the human diet to exploit fast-growing preys (Stiner et al., 2000).

DISCUSSION AND CONCLUSION: THE LIMITS OF APPLYING BEHAVIORAL ECOLOGY TO ARCHEOLOGY

Above, we saw how relevant energetic and ethnographic studies can be to human evolution. Here, we would like to address some of the more problematic points related to these approaches.

The Problem of the Scarcity of Archeological Evidence and Time Scales

To start with, it should be noted that data from extinct populations only yield isolated points in the paleoanthropological and archeological record. In addition, the range of error for the chronological framework could be around 50,000–100,000 years for Late Pliocene and Early Pleistocene periods, due to the dating methods used, and it is thus difficult to precisely link two different subsistence proxies. In addition, information on the diet consumed and the quality of the diet cannot be strictly compared between hominins and extant human and non-human primates. For hominins, dental microwear analyses provide data on the diet consumed a few days before the death of the individual. Isotopic analyses based on dental remains give some information of the diet consumed in early life. Furthermore, as data are cumulative, we only have an overall picture of the diet and it is impossible to gauge the diet consumed on a daily basis. Moreover, it is difficult to discern the ratio of meat in the diet of past hominins, and especially for the Late Pliocene and Early Pleistocene periods, although some new isotopic analyses using barium, calcium or zinc isotopes seem quite relevant for this purpose (Balter et al., 2012; Jaouen et al., 2016; Martin et al., 2020; Dodat et al., 2021).

Most of the time, Paleolithic sites are composed of palimpsests of multiple human occupations, often mixed with natural and carnivore deposits. Such mixed accumulations really challenge the reconstruction of ecological models, based on the balance between hominins' daily energetic needs, and the energetic intake provided by animals accumulated over very long time periods. Moreover, we have seen that little is known of the past hominin diet, especially during the Early Paleolithic. The diet of Late Pliocene and Early Pleistocene hominins was probably more diverse and less carnivorous than thought. Indeed, evidence of butchery is scarce and mostly based on a very small number of remains with some questionable cut marks (Domínguez-Rodrigo et al., 2010; McPherron et al., 2010, 2021; Sahle et al., 2017; Toth, 2017; Domínguez-Rodrigo and Baquedano, 2018).

The Problem of Applying Anatomical and Energetic Data From Extant Primates to Ancient Hominins

A higher-quality diet (and for example meat consumption) is often linked to an increase in brain size and a decrease in posterior tooth size (Aiello and Wheeler, 1995; Aiello and Wells, 2002; Snodgrass et al., 2009; Ungar, 2012). Improvements in dietary quality probably played an important role in brain expansion during the course of human evolution, but cannot alone explain why hominin brains grew (Leonard et al., 2011). Therefore, it is important to note that the measurement of the

whole brain could be a poor proxy. Indeed, some more specific brain regions are more precisely related to feeding ecology, in particular to dietary quality, than the whole brain (DeCasien and Higham, 2019; Louail et al., 2019).

The reduction in molar size in *H. erectus*, Neanderthals and modern humans can be explained by a shorter chewing time owing to non-thermal food processing or cooking methods rather than by the rate of craniodental and body size evolution (Organ et al., 2011). This assumption is based on molar size (M2) and body mass. Firstly, we must be cautious about estimating body mass. Indeed, its inference in hominins takes into account the length of lower limb bones based on data from non-human primates. However, it is very difficult to associate isolated lower limb bones with skulls (from which species are determined), especially when different species are in the same spatio-chronological setting, as for example in the Turkana Basin during the Early Pleistocene (*Paranthropus boisei*, *H. ergaster*, *H. habilis*, and *H. rudolfensis*). Furthermore, the scenario is often only based on a few individuals, and does not consider the range variation of past populations. Secondly, the use of M2 size alone does not consider molar proportion variation across the dental arch, hominin species with a small overall dental size, and disproportionally highlights M2s and M3s. Furthermore, it has been shown that brain enlargement and dental reduction were decoupled and evolved at different rates (Gómez-Robles et al., 2017).

Moreover, the morphology of the masticatory system, in particular dentition, does not represent the diet, but reflects what individuals were able to eat rather than what they ate. This is Liem's paradox (Liem, 1980), of which *Paranthropus* is a good illustration, with its apparent ambiguity between anatomy and diet.

With regard to energetics, some researchers have proposed models to investigate hominin energy requirements, based on activity patterns, body mass and life history data from extant primates, with inferences based on hominin body mass. However, as mentioned in the previous paragraph, extreme caution should be taken with this proxy. For example, it has been estimated that the daily energy expenditure (DEE) of a *H. erectus* female was 2,086 kilocalories per day, 2,269 during gestation and 2,487 during lactation (Aiello and Key, 2002), and that she had to chew raw meat for 5.7–6.2 h/day to satisfy her energetic needs (Wrangham and Conklin-Brittain, 2003). However, according to Simmen et al. (2021) DEE increased with the augmentation of the resting metabolic rate, but life-history variables (maximum lifespan, gestation and lactation duration, interbirth interval, litter mass, age of first reproduction) would not be correlated with DEE after controlling for body mass and phylogeny. In the same way, Pontzer et al. (2012) stressed that the DEE seems to be more related to body size, age and sex than to cultural differences. The similarity of the DEE in hunter-gatherers and sedentary Westerners suggests that even our strong differences in lifestyle only produce a minor effect, and differences between populations result mainly from energy intake rather than expenditure (Pontzer et al., 2012). It should also be noted that the total DEE is measured outside a laboratory using the doubly labeled water method on extant primates in

free-living conditions (Pontzer, 2017; Simmen et al., 2021), which of course, cannot be applied to extinct hominins. Therefore, most estimations of daily energy cost should be used with caution.

The Silent Part of Culture and Symbolism

While human behavioral ecology models are useful to predict which resource is edible and suitable or not in the diet, when a potential resource is not consumed, it may be a question of tradition, for example, totems or taboos, or of non-foraging activities, such as childcare or reproduction. Indeed, we have to keep in mind that other goals, and not only calorific return may prevail in diet choices, such as the acquisition of fat, vitamins, minerals or non-food products like pelts, bone tools or ornaments. For example, to date, a dozen European Middle Paleolithic sites have yielded evidence of the use of large raptor phalanges as personal ornaments or for symbolic purposes by Neanderthals (Morin and Laroulandie, 2012; Laroulandie et al., 2016; Rodríguez-Hidalgo et al., 2019). Others showed evidence of intentional feather removal, proffering another type of explanation for the Neanderthal exploitation of raptors (Peresani et al., 2011). Thus, we may ask what really governed forager's subsistence strategies in the past. Was it acquisition circumstances and the energetic return rate, as assumed by ecological approaches, or cultural and symbolic representations of animals, which is very difficult to assess for past societies. In reality, both probably played their part (Blasco et al., 2019b; Barkai, 2020). The role of culture and symbolism in food choices should of course not be overlooked. Far from being restricted to so-called "complex" societies, the eminently cultural nature of food is indeed a feature common to all human societies (Lévi-Strauss, 1964). Thus, choosing the appropriate food does indeed depend to a large extent on the available techniques and resources, but also on cultural and symbolic parameters. For example, in the case of the elephant, considerations other than the energetic return rate can motivate big game hunting, such as maintaining social position (Lupo and Schmitt, 2016). The development of ethnoarchaeological approaches through the 1970s and 1980s provided insights into these socio-cultural, but also technological aspects (Leroi-Gourhan and Brézillon, 1972; Yellen, 1977; Binford, 1978, 1980; Gallay, 1980). But this type of approach calls for caution. Indeed, when using current data from ethnology, we have to overcome the inherent biases of ethnoarchaeology, i.e., a too strict and direct analogism and the determinism that this may imply (Lévi-Strauss, 1952; Cleuziou, 1984).

In any case, for the Paleolithic, the social and symbolic dimension of food is unfortunately particularly difficult to approach (see Costamagno and Daujeard, 2021). Nevertheless, some recent studies show that the marks left by marrow extraction can highlight the existence of traditional butchery practices specific to certain Middle and Late Paleolithic groups of hunter-gatherers (Blasco et al., 2013; Masset et al., 2016; Vettese et al., 2017). It has been also been suggested for example that the intense disarticulation and fragmentation of phalanges and short bones in the European Middle Magdalenian, may reflect ritualized butchery practices, in connection with the relationships maintained between Paleolithic people and their

game (Birouste, 2020). These works extend slightly beyond the strictly economic character to which the diet of our Paleolithic ancestors is generally reduced in zooarcheological studies.

Finally, we must be aware that in applying HBE to Archeology, it is necessary to contextualize data according to palimpsest biases, using geoarchaeology, refitting, seasonal data, spatial analyses, etc., in order to obtain the best time resolution. We also have to keep in mind that a whole section is missing from our understanding of animal acquisition choices among past societies, i.e., cultural and symbolic representations, which explain a large part of the relationships we have with nature, if not all (Descola, 2005).

AUTHOR CONTRIBUTIONS

CD and SP wrote the body of the manuscript. Both authors contributed to the article and approved the submitted version.

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