


# How carnivorous are we? The implication for protein consumption

Miki Ben-Dor

Follow this and additional works at: <https://jevohealth.com/journal>

 Part of the [Archaeological Anthropology Commons](#), and the [Biological and Physical Anthropology Commons](#)

---

---

# How carnivorous are we? The implication for protein consumption

## **Keywords**

Protein, Paleo Diet, Ethnography, Evolution

---

# How carnivorous are we? The implication for protein consumption

## Introduction

The Paleo Diet evolutionary mismatch principle suggests that the closer we stay to the diet that we evolved to consume the better chances we have to stay healthy.

There is little doubt that meat was a significant component of the Paleolithic diet and that it was acquired largely by hunting [1] and thus Paleolithic humans can be defined as carnivores.

The definition of carnivory, however, is vague as a dietary pattern. There are 'carnivores' belonging to the Carnivora family that doesn't eat meat (Panda bears). There are 'obligate carnivores' that rely on very high protein consumption (cats). There are hypercarnivores that by definition consume more than 70% of the calories from animal sources and there are even 'epic carnivores' at the very top of the food chain (lions).

The purpose of the present investigation is not to assign humans to any of these categories but to find out whether during our evolution we became adapted to consume large quantities of meat on account of a previous adaptation to consume large quantities of plants. If so, we can assume that a relatively large quantity of meat will be safer than consuming a relatively large quantity of plant foods. Another question that comes up is to what level of protein consumption we became adapted. Since in diet, every item that we consume replaces an item that we could consume, if we are adapted to consume animal sourced protein, we can consider it to be a safer food than other foods, like domesticated plants,

In this context, the question of the evolutionary level of protein consumption during the Paleolithic has never received adequate attention. Since there is relatively little protein in plants, the answer is derived from the relative amount of animal food in the human diet. If animal food consumption were relatively high during the Paleolithic, then relative protein consumption would have also been high.

Quite a few authors tried to estimate the caloric Plant:Animal ratio (DPA) in the humans' Paleolithic diet [2-8]. A wide variation of DPA's was predicted with averages ranging between 66% plants and 33% animal [4] to 35% plants and 65% animal [2]. Alas, because in the archaeological record plants preserve poorly or not at all, all of the estimates relied to a great extent on the ethnographic record of diets of recent hunter-gatherers' (HG) groups with a tacit or expressed claim for the analogy between the periods. However, I claim that the HG's ethnographic record

should not be used to predict Paleolithic diets, or indeed even variability in the diet, as the ecologies of the two periods are so different as to deny any scientific validity to such prediction. Here I outline a short review of the relevant ecological conditions in support of my claim. A full paper is in preparation.

## **Recent hunter-gatherers ethnography is a misleading source of Paleolithic diet reconstruction**

In discussing the use of ethnographic sourced analogies in archaeology, Ascher (9) summarized his contemporaries, Clack, Willey, and Childes' opinions thus: "...*the cannon is: seek analogies in cultures which manipulates similar environments in similar ways.*" In other words, the degree of similarity between the ecological and technological conditions of the known and unknown periods is the key criteria in judging the validity of ethnographic sourced analogies.

A review of the recent ecological conditions reveals that especially in one crucial aspect, availability and size of faunal and floral resources, there is a drastic and unbridgeable gap between the Paleolithic and the recent modern HG period.

In a recent paper, Smith et al. [10] calculated the mean body weight of non-volant (not flying) terrestrial mammals during the last 2.5 million years. A drastic decline in terrestrial mammals took place from approximately 500 kgs at the beginning of the Pleistocene 2.5 million years ago to about 10 kgs today.

In the same vein, Bibi et al. [11] compared the faunal assemblages of Olduvai Middle Bed II at 1.7-1.4 million years ago (Mya) to faunal communities in the present day Serengeti. 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 reduced carnivore richness in the Early Pleistocene [12], that human predation may have been the cause of the loss of large herbivores during the Pleistocene.

A significant part of the reduction occurred in the Late Pleistocene and is a global phenomenon. During the Late Quaternary Megafauna Extinction, about 90 genera of animals weighing >44 kg became extinct beginning some 50 Kya [13]. The rate of extinction by body size follows a typical 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 category became 50-100% extinct. In Africa, Some 25% of what was left in the Late Quaternary's megafauna (>45 kg) became extinct [14].

In Africa, however, even the few large animals that remained were hardly available for hunting by HG groups that form the basis for many analogies with the Paleolithic, the Hadza, and the San. Elephants were hunted by Europeans with guns in the Hadza and San's territories for over a hundred years. There is evidence for a drastic decline in the availability of animals as a result of herders and farmers encroachment abound [15, 16]. The result is that the Hadza no longer hunt the three largest animals in Africa, elephants, rhinos, and hippos.

Moreover, the disappearance of large animals, and especially elephants, caused a substantial increase in the availability of plant food sources. Elephants are known to be a formidable predator of baobab trees [17]. Baobab is the single largest contributor of calories to the Hadza as well as a home for their most popular species of honey bees. A similar phenomenon occurs in the San (!Kung) territory where the mongongo tree, their staple food source, was subject to partial destruction and growth retardation when elephants were present in its vicinity [18:312].

In summary, the differences in the relative availability of plants and animals and especially big animals, between the Paleolithic and modern HG's period are so critical that they prevent any inference from the recent HG DPA to Paleolithic DPA, including any conclusion regarding the degree of DPA variability during the Paleolithic.

So, if ethnography and archaeology are poor sources for DPA estimates, are there other fields of knowledge we can explore? As it turns out, physiology can be a trove of information for evolutionary DPA, as adaptations to one DPA or another are stored in our body in the forms of genetics, morphology, metabolism, and sensitivity to pathogens.

## **Reconstruction of the Paleolithic diet based on human physiology**

*A more detailed reconstruction which was performed as a part of my Ph.D. thesis and is in preparation for publication. What follows is a short review of some of the physiological adaptations or lack thereof that provide evidence for the nature of our past diet.*

The first three adaptations are unique in that the authors themselves point out (maybe to their surprise) that according to their finds, we have various physiological processes that align with that of carnivores.

### **Weaning like a carnivore**

Life history, the age at which animal reach certain stages in life like gestation, weaning, mating, and death, is strongly defined in a species. Psouni et al. [19] found that adult brain mass, limb biometrics, and dietary profile can explain 89.2% of the total variance in time to weaning. Comparing 67 species, they found humans to be in the carnivores' group while chimpanzees and other primates with the non-carnivore's group. They conclude: *"Our findings highlight the emergence of carnivory as a process fundamentally determining human evolution."*

### **Many smaller fat cells like all carnivores**

Pond and Mattacks (20) compared the structure of fat cells in various types of animals. Carnivores were found to have a higher number of smaller fat cells and omnivores a smaller number of larger fat cells. Humans were found to be at the top of the carnivorous pattern. Pond and Mattacks conclude: *"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."*

### **Stomach acidity of a unique carnivore**

Beasley, Koltz (21) emphasize the role of stomach acidity in protection against pathogens. They found that carnivores' stomachs at a pH of 2.2 are more acidic than omnivores' stomachs at a pH of 2.9 but less acidic than obligate scavengers at pH of 1.3. According to Beasley, Koltz (21) Humans had a high level of acidity of 1.5 that lies between that of obligate and facultative scavengers. Producing acidity, and retaining the stomach walls to contain that acidity, is energetically expensive, so would presumably only evolve if the level of pathogens in the human diet was high. The authors surmise that humans were more of a scavenger than we thought. However, there is a more likely conclusion if we take into account that humans were a particular kind of carnivore. Unlike other carnivores, they consumed the meat over several days either in a central place (home base) [22] or, for very large animals, where it was acquired [23]. Big animals, like elephants and bison, and even smaller animals like zebra, provide enough calories to last a 25-member HG group for days and weeks [24]. During this time the pathogen load is bound to build up to a higher level than even a regular scavenger encounters under normal circumstances and hence the presumed need for high acidity.

### **Reduced energy extraction capacity from plants**

Most plant eaters extract a large part of their energy from the fermentation of fiber by gut bacteria [25]. In primates, the fermentation takes place in the large intestine. For example, a gorilla extracts some 60% of its energy from fiber [26]. The fruits that chimps are consuming are also very fibrous [27]. Their large intestines form

52% of the volume of the gut, similar to the 53% in the gorilla [28], indicating that, like a gorilla, they also drive a similarly high portion of their energy from fiber. An adaptation that prevents humans from efficient exploitation of fiber to energy may point to a shift in the dietary emphasis away from plants towards specialization in animal's sourced food [See 29 considering criteria for specialization]. Our gut is 40% smaller [30], and one can therefore calculate that our large intestine, where fiber is processed to energy, is 77% smaller by volume than that of a chimpanzee our size [28]. The size and our small intestine, where -macronutrients are absorbed is 62% larger than that of a chimpanzee our size. Since the Chimpanzee was able to absorb a large amount of sugar with a shorter small intestine, The 66% extension could represent an adaptation to consuming more fat and protein in humans. Since the mastication system prepare the food for the gut a reduced mastication system already 1.7 million years ago (Mya) in *H. erectus* suggests that the gut size of *H. erectus* was already reduced [31]. We can thus propose that *H. erectus* speciated in non-plant food items. The omnivorous pigs are sometimes mentioned as a good model for human nutrition [32], however, the volume of their large intestine is higher than the volume of their small intestine [32] the reserve ratio in humans[28], pointing to the adaptation of pigs to highly fibrous food.

The changed gut composition meets the criteria for specialization proposed by Wood and Strait (29). They propose that adaptation towards specialization is marked by a change that enables the acquisition of one resource while interrupting in the acquisition of another resource. In our case, the gut morphology adaptations both improved animal food exploitation and at the same time hindered the full exploitation of fibrous plant foods.

### **Endurance running**

Bramble and Lieberman [33] list 22 specific adaptations to endurance running and claim they represent an adaptation to 'persistence hunting'. There is some disagreement as to the significance of the 'persistence hunting' technique [34], but as it represents an adaptation to better mobility, it may also indicate adaptation to operating in a larger home-range. Carnivores with a large proportion of flesh in their diets such as Canids and Felids have particularly large home-ranges whereas omnivorous carnivores like Ursidae have a narrower home-range [35].

### **Adaptation to a spear throwing**

Roach et al. [36] claim that the structure of our shoulder represents an adaptation to carnivory. They describe how our shoulder is perfectly adapted to throwing, which must be useful, in their opinion, mainly in hunting and protection from predators. They show that in contrast, the chimpanzee's shoulder is adapted to climbing trees.

This evidence may serve as another evidence for specialization in carnivory, like the smaller gut, the improved ability to obtain animal food comes at the account of reduced ability to obtain plant-sourced food, fruits in this case.

### **High-fat reserves**

Humans have much higher fat reserves than chimps, our closest relatives [37]. Carrying a high amount of fat cost energy and reduce the speed of chasing or fleeing [38]. Most carnivores and fleeing herbivores do not pack much fat as, unlike humans, they rely on speed for predation or evasion. Recent HG were found to have enough fat reserves to fast for three weeks for men and six weeks for women [39]. This ability may represent an adaptation that is unique to carnivory of large animals by a predator who does not rely on speed. The large fat reserves may have allowed human to bridge longer periods between less frequent hunts of larger animals due to their relatively lower abundance.

### **The AMY1 gene - Incomplete adaptation to metabolize starch?**

Humans have a varying number of AMY1 gene copies (2-12 copies [40] ) which synthesize salivary amylase whereas chimpanzees have only two copies. The higher copy number may represent different degrees of adaptation to consuming starch [40] although the results of actual health markers associations with the number of copies are equivocal [41-47]. Herbivores and carnivores do not seem to have salivary amylase (although the data are limited) whereas omnivores usually produce high quantities of the enzyme [48]. This variance in the number of copies in humans in itself can be (but doesn't have to be) a testimony that the adaptation is relatively recent and have not been fixed yet. However, until better grasp is obtained on the timing of the change in copy number, little can be said about its significance to the question of DPA in humans.

### **Recent genetic adaptation to tuber consumption**

Tubers, which are available year-round and are as energy dense as wild fruits, are mentioned as a good candidate for Paleolithic plant-based diet [49]. Populations that presently depend on tubers are enriched in genes that are associated with starch metabolism, folic acid synthesis, and glycosides neutralization, but other populations are not [50]. These adaptations presumably compensate for these tubers' poor folic acid and relatively high content of glycosides. The very limited geographic distribution of these genes [50] may mean that their presence in humans is quite recent so that tubers did not form an important part of the human Paleolithic diet.



### **The earliest evidence for caries - 15,000 years ago**

High consumption of starch and sugars is associated with the development of oral caries cavities [51]. Frequencies of carious lesions in archaeological populations range from 2.2–48.1% of teeth for agricultural populations, but only 0–14.3% for hunter-gatherers [52]. A high prevalence of caries first appeared some 15.0 Kya in a site in Morocco, together with evidence for exploitation of starchy foods [53]. This recent phenomenon may mean that high carbohydrates (plants) consumption is a relatively recent end-of-Pleistocene phenomenon. It should be pointed out that in some more recent traditional societies high starch consumption was not associated with a high prevalence of caries [54].

### **Paleolithic dietary reconstruction based on human Physiology – conclusion**

Although physiology is only one of the sources for Paleolithic dietary reconstruction, looking into the information that is stored in our body provide an interesting and sometimes new evidence that we underwent substantial adaptation towards carnivory and that it started quite early in our evolution as the genus Homo. It also supports the notion that we remain adapted to carnivory despite over 10,000 years of agricultural subsistence. Consequently, it seems, in reply to the question at the heart of this paper, that we are adapted to consume high quantities of protein. How high? The answer lies in reconstructing our behavior during prehistory regarding fat [24, 55].

### **What was the protein consumption level during human evolution?**

The question of the desirable level of dietary protein consumption comes up in the literature and among professional and lay people who are interested in nutrition. This section tries to answer that question by discerning the Paleolithic level of consumption, assuming that it is a safe level, following the evolutionary mismatch theory of chronic disease [56].

Protein processing for energy in humans is estimated to be physiologically limited to 35-45% of the daily calories [57, 58]. If humans were at the protein limit during the Paleolithic era, the remaining 55-65% of the calories should have come either from fat or carbohydrates, namely plants.

There is ample ethnographic evidence for human dependence on and preference for animal fat as a food source. Kelly [59] writes in his authoritative book on HG: “...*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*”.

Lee [16] writes about the !Kung of the Kalahari: “*Fat animals are keenly desired, and all !Kung express a constant craving for animal fat*”. The essentiality of fat is best demonstrated in Tindale’s account of the Pitjandjara of Australia [60]. 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 [61] report a similar behavior among the Yolngu of Arnhem, Australia, saying that “*Animals without fat may indeed be rejected as food*”.

The importance of fat is also evident in its use as a symbol of fertility, sacredness, wealth, health and even life itself in recent traditional societies' rituals, linguistics and mythology [55]

The archaeological record similarly shows that many of humans’ particular acquisition and food exploitation behaviors can be interpreted as stemming from the need to obtain fat. Behaviors like the hunting of fatter animal or processing of fat from body parts at greater energetic expenditure than would have otherwise been needed indicate a concentration on fat as the primary criterion in prey selection and butchering. The preference of hunting larger animals and prime adult animals within prey species [24, 62, 63], the preference to bring fatty parts to a central place and the extraction of bone grease [64], at great energetic costs, all point to a strategy of fat maximization. This energetically expensive set of behaviors also supports the conclusion that plants could not provide a sufficient contribution to complement the protein at the limit of its consumption. This energetically expensive behavior is difficult to explain unless we assume that humans were at the limit of their protein consumption.

Therefore, the implication for protein consumption from this reconstruction is that throughout our evolution as humans we obtained a high portion of our calories from protein. Although no clear official statement of the upper limit on the consumption of protein has ever been published, there are reports of consumption of over 40% of the daily calories, or about 4 grams per kg body weight per day (g/kg/d) by circumpolar groups [65]. Rudman, Difulco (66) found the limit on urea removal to be 3.8 g/kg/d of protein to which the demand of structural protein at a minimum of 0.8 grams per kg per day should be added [57] to a total of 4.6 g/kg/d. The present level of protein intake in the U.S. is some 15.7% [67] of the daily calories. Based on consumption of 2000 calories for a 60 kgs person the current consumption is 314 calories whereas the Paleolithic level of consumption, according to this analysis was in the vicinity of 800 calories (40% of 2000) and possibly even higher at 1100 calories (4.6 g/kg/d X 60 kgs X 4 cal/g).

## **Conclusion**

As mentioned, this paper is just a part of a wider review, in preparation, of scientific evidence for the human evolutionary diet. Although we are undoubtedly omnivores, the biologic evidence that was presented here claims to show that we evolved, quite early in our evolution as the genus *Homo*, to become highly carnivorous and that we continue to retain a biologic adaptation to carnivory. This high level of carnivory means that during a large part of our evolution our diet was high in protein besides being high in fat. If we look at the Paleo nutrition template as a safety templet, this paper concludes that it seems to be safe to consume a high portion of the diet from animal protein, possibly to the tune of 30-40% of the daily calories. Since every calorie of protein that we do not consume is a calorie that will be consumed from another food source, the Paleo template guides us to consider the relative safety of alternatives to protein when deciding on the actual level of protein consumption. Not many alternatives foods can claim to have nearly two million years of safe consumption.

References:

1. Domínguez-Rodrigo M, Pickering TR. The meat of the matter: an evolutionary perspective on human carnivory. *Azania: Archaeological Research in Africa*. 2017;52(1):4-32.
2. Cordain L, Miller JB, Eaton SB, Mann N, Holt SHA, Speth JD. Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets 1 , 2. *The American Journal of Clinical Nutrition*. 2000;71(3):682-92.
3. Marlowe FW. Hunter-gatherers and human evolution. *Evolutionary Anthropology: Issues, News, and Reviews*. 2005;14(2):54-67.
4. Lee RB. What hunters do for a living, or, how to make out on scarce resources. *Man the Hunter*. Chicago: Aldine Publishing Company; 1968.
5. Eaton SB, Konner M. Paleolithic nutrition - a consideration of its nature and current implications. *New Engl J Med*. 1985;312(5):283-9. doi: 10.1056/nejm198501313120505. PubMed PMID: WOS:A1985AAQ2000005.
6. Ströhle A, Hahn A. Diets of modern hunter-gatherers vary substantially in their carbohydrate content depending on ecoenvironments: results from an ethnographic analysis. *Nutr Res*. 2011;31(6):429-35.
7. Konner M, Eaton SB. Paleolithic nutrition twenty-five years later. *Nutr Clin Pract*. 2010;25(6):594-602.
8. Kuipers RS, Joordens JC, Muskiet FA. A multidisciplinary reconstruction of Palaeolithic nutrition that holds promise for the prevention and treatment of diseases of civilisation. *Nutr Res Rev*. 2012;25(01):96-129.
9. Ascher R. Analogy in archaeological interpretation. *Southwestern journal of Anthropology*. 1961;17(4):317-25.
10. Smith FA, Smith REE, Lyons SK, Payne JL. Body size downgrading of mammals over the late Quaternary. *Science*. 2018;360(6386):310-3.
11. Bibi F, Pante M, Souron A, Stewart K, Varela S, Werdelin L, et al. Paleoecology of the Serengeti during the Oldowan-Acheulean transition at Olduvai Gorge, Tanzania: The mammal and fish evidence. *J Hum Evol*. 2017.
12. Werdelin L, Lewis ME. Temporal change in functional richness and evenness in the eastern African Plio-Pleistocene carnivoran guild. *PLoS ONE*. 2013;8(3):e57944.
13. Koch PL, Barnosky AD. Late Quaternary Extinctions : State of the Debate. *Annu Rev Ecol, Evol Syst*. 2006;37:215-52. doi: 10.1146/annurev.ecolsys.34.011802.132415.
14. Faith JT. Late Pleistocene and Holocene mammal extinctions on continental Africa. *Earth-Sci Rev*. 2014;128:105-21.

15. Marlowe F. *The Hadza: Hunter-gatherers of Tanzania*: University of California Press; 2010. 325 p.
16. Lee RB. *The Kung San: men, women, and work in a foraging society*. Cambridge: Cambridge University Press; 1979. 526 p.
17. Barnes R. The decline of the baobab tree in Ruaha National Park, Tanzania. *Afr J Ecol*. 1980;18(4):243-52.
18. Lee RB. Mongongo: the ethnography of a major wild food resource. *Ecol Food Nutr*. 1973;2(4):307-21.
19. Psouni E, Janke A, Garwicz M. Impact of carnivory on human development and evolution revealed by a new unifying model of weaning in mammals. *PLoS ONE*. 2012;7(4):e32452.
20. Pond CM, Mattacks CA. Body mass and natural diet as determinants of the number and volume of adipocytes in eutherian mammals. *J Morphol*. 1985;185(2):183-93.
21. Beasley DE, Koltz AM, Lambert JE, Fierer N, Dunn RR. The evolution of stomach acidity and its relevance to the human microbiome. *PLoS ONE*. 2015;10(7):e0134116.
22. Isaac GL. The Harvey Lecture series, 1977-1978. Food sharing and human evolution: archaeological evidence from the Plio-Pleistocene of east Africa. *J Anthropol Res*. 1978;34(3):311-25.
23. Yravedra J, Rubio-Jara S, Panera J, Martos JA. Hominins and Proboscideans in the Lower and Middle Palaeolithic in the central Iberian Peninsula. *Quat Int*. 2017.
24. Ben-Dor M, Gopher A, Hershkovitz I, Barkai R. 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*. 2011;6(12):e28689. doi: 10.1371/journal.pone.0028689.
25. McNeil N. The contribution of the large intestine to energy supplies in man. *The American journal of clinical nutrition*. 1984;39(2):338-42.
26. Popovich DG, Jenkins DJ, Kendall CW, Dierenfeld ES, Carroll RW, Tariq N, et al. The western lowland gorilla diet has implications for the health of humans and other hominoids. *The Journal of nutrition*. 1997;127(10):2000-5.
27. Wrangham RW, Conklin-Brittain NL, Hunt KD. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *Int J Primatol*. 1998;19(6):949-70.
28. Milton K. Primate diets and gut morphology: implications for hominid evolution. In: Harris M, Ross E, editors. *Food and evolution: toward a theory of human food habits*. Philadelphia: Temple University Press; 1987. p. 93-115.
29. Wood B, Strait D. Patterns of resource use in early *Homo* and *Paranthropus*. *J Hum Evol*. 2004;46(2):119-62.

30. Aiello LC, Wheeler P. The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *CurrAnthr.* 1995;36(2):199-221.
31. Lucas PW, Sui Z, Ang KY, Tan HTW, King SH, Sadler B, et al. Meals versus snacks and the human dentition and diet during the Paleolithic. *The Evolution of Hominin Diets*: Springer; 2009. p. 31-41.
32. Miller E, Ullrey D. The pig as a model for human nutrition. *Annu Rev Nutr.* 1987;7(1):361-82.
33. Bramble DM, Lieberman DE. Endurance running and the evolution of Homo. *Nature.* 2004;432(7015):345-52.
34. Pickering TR, Bunn HT. The endurance running hypothesis and hunting and scavenging in savanna-woodlands. *J Hum Evol.* 2007;53(4):434-8.
35. Gittleman JL, Harvey PH. Carnivore home-range size, metabolic needs and ecology. *Behav Ecol Sociobiol.* 1982;10(1):57-63.
36. Roach NT, Venkadesan M, Rainbow MJ, Lieberman DE. Elastic energy storage in the shoulder and the evolution of high-speed throwing in Homo. *Nature.* 2013;498(7455):483-6.
37. Zihlman AL, Bolter DR. Body composition in *Pan paniscus* compared with *Homo sapiens* has implications for changes during human evolution. *Proceedings of the National Academy of Sciences.* 2015:201505071.
38. Pond CM. Morphological aspects and the ecological and mechanical consequences of fat deposition in wild vertebrates. *Annu Rev Ecol Syst.* 1978;9(1):519-70.
39. Pontzer H, Raichlen DA, Wood BM, Emery Thompson M, Racette SB, Mabulla AZ, et al. Energy expenditure and activity among Hadza hunter-gatherers. *Amer J Hum Biol.* 2015;27(5):628-37.
40. Perry G, Dominy N, Claw K, Lee A. Diet and the evolution of human amylase gene copy number variation. *Nature.* 2007;39(10):1256.
41. Falchi M, Moustafa JSE-S, Takousis P, Pesce F, Bonnefond A, Andersson-Assarsson JC, et al. Low copy number of the salivary amylase gene predisposes to obesity. *Nat Genet.* 2014;46(5):492-7.
42. Des Gachons CP, Breslin PA. Salivary amylase: digestion and metabolic syndrome. *Curr Diab Rep.* 2016;16(10):102.
43. Fernández CI, Wiley AS. Rethinking the starch digestion hypothesis for AMY1 copy number variation in humans. *Amer J Phys Anthropol.* 2017;163(4):645-57.
44. Atkinson FS, Hancock D, Petocz P, Brand-Miller JC. The physiologic and phenotypic significance of variation in human amylase gene copy number. *The American journal of clinical nutrition.* 2018;108(4):737-48.

45. Yong RY, Mustaffa SAB, Wasan PS, Sheng L, Marshall CR, Scherer SW, et al. Complex copy number variation of AMY1 does not associate with obesity in two East Asian cohorts. *Hum Mutat.* 2016;37(7):669-78.
46. Alberti G, Parada J, Cataldo LR, Vega J, Aguilera CM, Alvarez-Mercado AI, et al. Glycemic Response after Starch Consumption in Relation to Salivary Amylase Activity and Copy-number Variation of AMY1 Gene. *Journal of Food and Nutrition Research.* 2015;3(8):558-63.
47. Choi YJ, Nam YS, Yun J, Park J, Cho B, Son HY, et al. Association between salivary amylase (AMY1) gene copy numbers and insulin resistance in asymptomatic Korean men. *Diabet Med.* 2015;32(12):1588-95.
48. Boehlke C, Zierau O, Hannig C. Salivary amylase—The enzyme of unspecialized euryphagous animals. *Arch Oral Biol.* 2015;60(8):1162-76.
49. Wrangham RW, Jones JH, Laden G, Pilbeam D, Conklin-Brittain NL, Brace CL, et al. The raw and the stolen. *CurrAnthr.* 1999;40:567-94.
50. Hancock AM, Witonsky DB, Ehler E, Alkorta-Aranburu G, Beall C, Gebremedhin A, et al. Human adaptations to diet, subsistence, and ecoregion are due to subtle shifts in allele frequency. *Proceedings of the National Academy of Sciences.* 2010;107(Supplement 2):8924-30.
51. Law V, Seow W, Townsend G. Factors influencing oral colonization of mutans streptococci in young children. *Aust Dent J.* 2007;52(2):93-100.
52. Lanfranco LP, Eggers S. The usefulness of caries frequency, depth, and location in determining cariogenicity and past subsistence: a test on early and later agriculturalists from the Peruvian coast. *Amer J Phys Anthropol.* 2010;143(1):75-91.
53. Humphrey LT, De Groote I, Morales J, Barton N, Collcutt S, Ramsey CB, et al. Earliest evidence for caries and exploitation of starchy plant foods in Pleistocene hunter-gatherers from Morocco. *Proceedings of the National Academy of Sciences.* 2014;111(3):954-9.
54. Price WA, Nguyen T. Nutrition and physical degeneration: a comparison of primitive and modern diets and their effects: *EnCognitive.com*; 2016.
55. Ben-Dor M. 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.* 2015;1(1):10.
56. Eaton SB. The ancestral human diet: what was it and should it be a paradigm for contemporary nutrition? *Proc Nutr Soc.* 2006;65(1):1-6.
57. Bilsborough S, Mann N. A review of issues of dietary protein intake in humans. *Int J Sport Nutr Exerc Metab.* 2006;16(2):129-52.
58. Speth JD. Early hominid hunting and scavenging - the role of meat as an energy-source. *J Hum Evol.* 1989;18:329-43. doi: 10.1016/0047-2484(89)90035-3.

59. Kelly RL. *The lifeways of hunter-gatherers: The foraging spectrum*. Cambridge: Cambridge University Press; 2013.
60. Tindale NB. The Pitjandjara. In: Bicchieri MG, editor. *Hunters and gatherers today*. New York: Holt, Rinehart and Winston; 1972. p. 217-68.
61. Coote J, Shelton A. *Anthropology, Art, and Aesthetics*: Clarendon Press; 1992.
62. Speth JD. Big-Game Hunting: Protein, Fat, or Politics? *The Paleoanthropology and Archaeology of Big-Game Hunting*: Springer; 2010. p. 149-61.
63. Stiner MC, Gopher A, Barkai R. Hearth-side socioeconomics, hunting and paleoecology during the late Lower Paleolithic at Qesem Cave, Israel. *J Hum Evol*. 2011;60:213-33. doi: 10.1016/j.jhevol.2010.10.006. PubMed PMID: 21146194.
64. Outram AK. Identifying dietary stress in marginal environments: bone fats, optimal foraging theory and the seasonal round. In: Miondini M, Munoz S, Wickler S, editors. *Colonisation, migration and marginal areas: A zooarchaeological approach*: Oxford Books; 2004. p. 74-85.
65. Ben-Dor M, Gopher A, Barkai R. Neandertals' large lower thorax may represent adaptation to high protein diet. *Amer J Phys Anthropol*. 2016;160(3):367-78. doi: 10.1002/ajpa.22981.
66. Rudman D, Difulco TJ, Galambos JT, Smith RB, Salam AA, Warren WD. Maximal rates of excretion and synthesis of urea in normal and cirrhotic subjects. *J Clin Invest*. 1973;52:2241-9. doi: 10.1172/jci107410.
67. Raubenheimer D, Machovsky-Capuska GE, Gosby AK, Simpson S. Nutritional ecology of obesity: from humans to companion animals. *Br J Nutr*. 2015;113(S1):S26-S39.