Eur J Nutr 39 : 71–79 (2000)
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SPECIAL ISSUE

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Dietary lean red meat and human evolution

Received: 24 February 2000
Accepted: 20 March 2000

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Summary Scientific evidence is accumulating that meat itself is not a risk factor for Western lifestyle diseases such as cardiovascular disease, but rather the risk stems from the excessive fat and particularly saturated fat associated with the meat of modern domesticated animals. In our own studies, we have shown evidence that diets high in lean red meat can actually lower plasma cholesterol, contribute significantly to tissue omega–3 fatty acid and provide a good source of iron, zinc and vitamin B_{12}. A study of human and pre-human diet history shows that for a period of at least 2 million years the human ancestral line had been consuming increasing quantities of meat. During that time, evolutionary selection was in action, adapting our genetic make up and hence our physiological features to a diet high in lean meat. This meat was wild game meat, low in total and saturated fat and relatively rich in polyunsaturated fatty acids (PUFA). The evidence presented in this review looks at various lines of study which indicate the reliance on meat intake as a major energy source by pre-agricultural humans. The distinct fields briefly reviewed include: fossil isotope studies, human gut morphology, human encephalisation and energy requirements, optimal foraging theory, insulin resistance and studies on hunter-gatherer societies. In conclusion, lean meat is a healthy and beneficial component of any well-balanced diet as long as it is fat trimmed and consumed as part of a varied diet.

Key words: Encephalisation – dietary fat – hunter-gatherer – meat – protein

Introduction

In promoting reductions in dietary fat intakes, many health professionals have encouraged people to reduce their use of red meat, even though red meat is an excellent dietary source of iron and zinc, as well as being the main source of vitamin B_{12} in the diet *[1]*. The health message to reduce red meat intake seems to have been taken up largely by women and yet the Australian National Dietary Survey found that 30 % of women had mean daily iron intakes of less than 70 % of the Reference Dietary Intake (RDI) *[2]*. In Australia, the fat content of red meat at the point of sale ranges from 5–19 g/100 g fresh weight for beef and 17–26 g/100 g for lamb *[3]*. The fat content of lean (fat-trimmed) beef and lamb, however, can be less than 5 percent *[4]*.

Our meat research program was originally stimulated by observations that, when urbanised, diabetic Australian Aborigines reverted temporarily to their traditional hunter-gatherer diet, there were improvements, not only in the metabolic abnormalities of diabetes *[5]*, but also in several risk factors for cardiovascular disease: reduction in hyperlipidaemia and blood pressure, and prolongation in the bleeding time (an indication of reduced thrombotic risk).

These beneficial changes occurred despite the diet containing substantial quantities of meat from wild game animals *[6, 7]*. The diet was low in fat (13 % energy) despite being rich in red meat, as meats from wild animals are extremely lean, of the order of 1–2 % fat *[8]*, much of which is structural lipid and, therefore, rich in polyunsaturated fatty acids (PUFA) *[9]*.

Subsequently, our research group carried out a number of dietary studies involving consumption of domesticated red meats and were able to show a reduction in serum cholesterol concentrations on a low fat meat *[10]*, a PUFA oil-rich meat diet *[11]* and an olive oil-rich meat diet involving hyperlipidaemic subjects *[12]*. A cross-sectional study of healthy males *[13]* investigated a range of blood factors linked with health status and correlated these factors with habitual dietary practice, including meat consumption. Vegetarians, especially vegans, had a significantly increased platelet aggregation compared with meat-eaters and a significantly higher mean platelet volume, associated with much lower levels of the long-chain n-3 PUFA, eicosopentaenoic acid (EPA) and docosohexaenoic acid (DHA) in their tissues. As EPA and DHA occur in animal foods only (particularly fish and red meat), this was not a surprise finding. The meat component of the diet was also contributing some other valuable micro-nutrient factors to the diet (Table 1). For instance, meat-eaters had a significantly higher iron, retinol, zinc and vitamin B_{12} intake than vegetarian groups, combined with higher plasma levels of iron and vitamin B_{12} and lower homocysteine levels. *[14]*. These findings, indicating various beneficial aspects of lean meat consumption, led us to question the assumption that meat in the diet was responsible for a range of metabolic problems. The obvious question that required answering in light of these findings and the observation of Australian Aborigine food habits was: what constitutes an "appropriate" diet for humans? As with all animal species, the answer lies in our evolutionary past.

Boyd Eaton of Emory University (Atlanta) has spent over 12 years reconstructing prehistoric diets from anthropological evidence and observations of surviving HG societies. In his book "The Stone-Age Health Programme" *[15]*, he states that "We are the heirs of inherited characteristics accrued over millions of years, the vast majority of our biochemistry and physiology are tuned to life conditions that existed prior to the advent of agriculture some 10,000 years ago. Genetically, our bodies are virtually the same as they were at the end of paleolithic some 20,000 years ago. The appearance of agriculture and domestication of animals some 10,000 years ago and the Industrial Revolution some 200 years ago introduced new dietary pressures for which no adaptation has been possible in such a short time span. Thus, an inevitable discordance exists between our dietary intake and that which our genes are suited to". This discordance hypothesis postulated by Eaton and supported by a wide range of nutritionists explains many of the chronic "diseases of civilisation" *[16]*.

Table 1 Comparison of dietary intake and plasma level of selected micro nutrients in the four dietary groups studied

	Dietary Group			
	High Meat[1]	Moderate Meat	Ovolacto Vegetarian	Vegan
Intake (mg/day)				
Zinc	25.0 ± 5.3^a	14.6 ± 3.0^b	12.3 ± 3.1^c	13.4 ± 4.0^c
Calcium	24.4 ± 5.3^a	16.8 ± 3.9^b	20.5 ± 5.6^b	25.7 ± 9.5^a
Retinol	1577 ± 558^a	1201 ± 360^b	1229 ± 459^b	977 ± 362^c
Iron	1640 ± 2210^a	761 ± 776^b	438 ± 216^c	218 ± 144^d
Plasma Status				
Retinol (mg/L)	0.90 ± 0.16^a	0.89 ± 0.20^a	0.81 ± 0.17^b	0.77 ± 0.14^b
Vitamin B_{12} (pg/mL)	544 ± 228^a	449 ± 134^b	285 ± 132^c	188 ± 89^d
Ferritin (mg/L)	153 ± 117^a	111 ± 86^b	48 ± 29^c	50 ± 29^c
Haemoglobin (g/L)	151 ± 6^a	149 ± 8^a	142 ± 9^b	143 ± 7^b
Homocysteine (mmd/L)	11.0 ± 2.5^a	11.6 ± 2.7^a	15.8 ± 9.3^b	19.2 ± 10.7^b

[1] Mean ± SD, All figures on the same row with differing superscripts are significantly different ($P < 0.05$)

In this article, a number of metabolic, physiological and anthropological issues are briefly reviewed which give an indication of our diet of "evolutionary adaptiveness" and the central role of meat in that diet.

Hunter-gatherers as a model

Apart from information reconstructed from archaeological evidence, the best model available to ascertain some idea of paleolithic food procurement and consumption patterns is the study of modern day hunter-gatherer (HG) societies or the study of records left by anthropologists regarding these groups in the early part of the twentieth century. However, the hunter-gatherer mode of life is now almost extinct, without a comprehensive nutritional study ever being conducted. Nevertheless, indirect calculations have been made from Murdock's Ethnographic Atlas *[17]*, including Lee's compilation of data for 58 hunter-gatherer societies *[18]*. These data indicated a mean plant:animal (PA) food subsistence ratio of 65:35. However, a more recent analysis of 229 HG societies in the updated Ethnographic Atlas *[19]* by Cordain et al. has shown that the majority of HG societies obtained > 56–65 % of their subsistence from animal foods *[20]*. No HG society was above 86 % dependence on plant foods whereas 3.8 % (n = 11) were above 86 % dependence on animal foods. The only significant latitude effect was a decreasing plant food intake and an increasing fish food intake above 40° north or south. Using P:A subsistence ratios from 35:65 through to 65:35 and allowing for a ceiling on protein intake, the predicted macronutrient intake ranges were carbohydrate 22–40 %, protein 19–35 % and fat 28–47 % *[20].*

One of the most studied groups with extensive data available are the Australian Aborigines, reviewed extensively by O'Dea *[21–23].* These HGs were omnivores, with relative proportions of plant and animal foods influenced by season and geographic location. In general, women provided the "subsistence" diet, gathering plant foods, wild honey, eggs, small mammals, reptiles, fish, shellfish, crustaceans, grubs and insects. The men provided the "feast" aspect of the diet through hunting large mammals. There was usually one large meal a day in the late afternoon when the group all returned to their camp to cook the game procured *[22].* Consumption of up to 2–3 kg meat was not uncommon *[23].* Consumption of "snacks" (grubs, insects, wild honey, wild fruits and nuts) would occur throughout the day, with hunters often removing the liver from a "kill", and eating it on the spot, often raw *[22].* In studies with settled Aborigines reverting to a traditional diet, the foods consumed and their macronutrient contributions at an inland location were recorded. The average total energy intake of individuals was 5040 kJ/person/day, of which animal foods contributed 64 % of energy (kangaroo, fish, reptiles, small mammals). The dietary composition in terms of total energy was 54 % protein, 13 % fat and 33 % carbohydrate *[5],* figures amazingly close to those subsequently predicted by Cordain et al *[20].*

Fossil isotope ratios

The C13/C12 isotope ratio in fossil remains is indicative of diet, and is a particularly good marker of the intake of broad leaf plant material versus grasses. Basically, trees, bushes and shrubs use the C3 photosynthetic pathway, which discriminates against the heavier carbon isotope C13 during fixation of CO_2, compared with the grasses, which use the C4 or Hatch-Slack photosynthetic pathway *[24, 25].* Evidence from studies on a 3 million year old hominid (Australopithecus africanus) remains from South Africa show that early hominids ate large quantities of the C13 enriched foods *[26].* As hominids in general have shown no capacity for digestion of grasses or teeth microwear patterns indicative of grass mastication *[27, 28],* it can be speculated that these hominids were consuming grazing animals existing on the C4 grasses. This shift to open grassland foraging/scavenging would have increased survival chances given the worldwide expansion of the biomass of C4 grasses approximately 6 million years ago, which is believed to have been linked to a decrease in atmospheric CO_2 concentrations *[29].* This expansion of C4 grasses was accompanied by a worldwide faunal change *[30]* including the spread of large grazing mammals. The determination of the ratio of the two atomically similar elements, strontium and calcium in fossil bones or enamel has also been used as an indicator of dietary intake *[31].* The determination of the ratio of the two atomically similar elements, strontium and calcium, in fossil bones or enamel has also been used as an indicator af dietary intake *[31].* There is a discrimination against uptake of strontium in favour of calcium by terrestrial vertebrates (ionic transfer across biological membranes). Thus as we examine animals further up the food chain the uptake of calcium increases at the expense of strontium; hence the bone Sr/Ca ratio in present day mammals show an inverse correlation with trophic level, with pure carnivores showing the lowest ratio. This pattern is paralleled in fossil remains of paleolithic fauna, with early hominids showing a Sr/Ca ratio midway between contemporary carnivore and herbivore species *[32].* These results alone would indicate that early hominids (1.8 million years ago) consumed a considerable proportion of meat in their diet *[33].*

Optimal foraging

An indirect method of gauging food consumption patterns is to consider the energy requirements of our hominid ancestors and the energy content of the available foods in conjunction with energy expenditure involved in procurement and processing of these foods *[34].* It was often assumed by earlier researchers that plant resources were the dominant element in the diets of hunter-gatherers, particularly those in the mid to low latitudes, on the basis that plant resources are more dependable than animal foods and more efficiently exploited *[18].* Thus, meat would provide the bulk of hunter-gatherer diets only where plant foods are unavailable, such as in the case of the Eskimos. Others have argued that this misconception results from the observed high plant intake amongst some modern day hunter-gatherers, but that this plant food predominance came about because of the depletion of the population of large mammals through over-hunting and climatic change during the late Paleolithic period combined with marginalisation of hunter-gatherer societies in modern times to poorly resourced areas. Hence, some modern hunters take plants in spite of the fact that they are associated with higher energy costs than meat, simply because meat is scarce.

Essentially, the subsistence patterns of hunter-gatherers, early hominids and our paleolithic ancestors can be explained in terms of cost/benefit analysis. The major survival determinant for hunter-gatherers was daily energy procurement (less energy expenditure). Various models have been developed to explain this phenomenon, loosely described as the "Theory of Optimal Foraging" *[35].* The wild fruits, vegetables, foliage and tuberous roots available to hunter-gatherers and early hominids are generally of low energy density *[36].* The high energy/time spent in collection and preparation of such plant foods is not well rewarded in terms of energy gain and hence these foods are not feasible as a primary energy source in most cultures, as indicated by the optimal foraging theory. This area is well reviewed in the case of the Ache of Eastern Paraguay *[37]*. This particular group of hunter-gatherers is noted for their high meat intake despite abundant plant food availability. Cost/benefit analysis of energy content of plant and animal foods versus energy expenditure in procurement and preparation revealed larger mammals as giving the best return. Only seasonal fruit and honey were ranked moderately highly amongst the non-meat dietary factors. In general, rarer high fat, carbohydrate or protein plant items available to hunter-gatherers, are often limited in terms of area and seasonality. However, these plants are a valuable source of fibre and micronutrients *[38]*.

Animal foods and dietary fat

In comparison with domesticated animals, wild game animals have a consistently lower fat content *[39]*. Domesticated animals have fat deposits under the skin, within the abdomen, between and within muscles, whereas wild game animals have small discrete depots of fat, primarily around the gonads, kidney and intestines and only during times of the year when feed is plentiful. The muscle meat is lean and does not "marble" *[22]*. Thus, a high proportion of the little fat present is structural fat, making up the membranes of muscle cells and being relatively rich in monounsaturated (MUFA) and PUFA of both the n-6 and n-3 family. Game muscle meat has fat levels generally below 2.6 % wet weight *[40]*, with PUFA levels greater than 30 % of total fatty acids and often up to 50 %, with the n-3 PUFA alpha-linolenic acid (18:3n-3) and EPA, (20:5n-3) making up 8–9 % of the total fatty acids and an n–6:n–3 ratio of the order of 3:1 *[39]*. Fat, and hence energy intake, was maximised by consumption of brain and organ fat (rich in PUFA) and bone marrow (rich in MUFA). Fat, therefore, was possibly a much higher percentage of total energy than we now consider to be healthy. The absolute level of fat, however, may not have been excessive as the total energy intake was likely to be low, as shown in O'Dea's studies on Australian Aborigines *[5]*. This is a far different scenario from the current Western diet where the n-6 PUFA from seed oils dominates and produces an n-6:n-3 intake ratio of the order of 12:1 *[8]*. Furthermore, the meat consumed, and particularly the liver, was an excellent source of iron, zinc, vitamin C, folic acid and vitamin B_{12} *[21]*.

The fat content of the diet is often cited as the predominant cause of Western lifestyle diseases with the hypercholesterolaemic saturated fatty acids, palmitic (16:0), myristic (14:0) and lauric (12:0), being singled out for greatest concern *[41]*. These particular fatty acids have been associated with meat fat and hence have led to the perception that animal meat is a direct causative agent in cardiovascular disease. The type of fats consumed by humans, therefore, has undergone substantial change since the progression from our natural hunter-gatherer state to agriculturalists up to modern Western society, a topic reviewed extensively elsewhere *[8, 42, 43]*.

Animal size – fat content

Virtually all of the fat contained in an animal carcass is/was consumed by Hunter-gatherers *[8]*. The mean value of carcass fat content within a species is determined by body size, specifically free fat mass (FFM) *[44]* and follows the equation:

$$\%\ \textbf{body fat} = \mathbf{1.5 \times FFM^{0.2}}$$

The larger the animal the greater the dietary fat available, both on a relative and absolute basis *[20]*. As mammalian tissue is almost totally devoid of carbohydrate and the protein content of the FFM is relatively constant, the energy density of the edible carcass is almost entirely dependent upon varying levels of fat *[20]*. An animal with 10 % total body fat would contain 51 % of its energy as fat and 49 % as protein. However, if the lean muscle tissue only was consumed (2–3 % fat) *[45]*, then approx. 80 % of the energy would be protein and 20 % fat, a situation which could lead to protein toxicity.

In terms of hunter-gatherer societies studied, where the median dependence on animal foods was between 56–65 %, then consumption of animals with 10 % body fat or greater would be required to maintain protein intakes below protein toxicity levels *[20]*. Although increasing plant food intake would be the simplest solution to the dietary protein ceiling predicament, it was not the path taken by hunter-gatherers, even when plant food resources were readily available. Once again, the answer lies in the optimal foraging theory, where animal based foods yield a higher energy capture/expenditure ratio than plant foods *[37]*. The preferred solution to this dilemma was either to increase dietary fat from animal foods, particularly by selective consumption of fatty portions of the carcass *[46, 47]* and/or the selection of larger prey species where possible *[20]*. It is not surprising, following this line of logic, that megafauna became extinct in various regions following the arrival of paleolithic man.

Gut morphology

Another line of investigation, which is useful in ascertaining the dietary preferences and suitability of a species to certain food types, is to study the structural features of the gastrointestinal tract. Both pure herbivores (folivores and frugivores) and pure carnivores (such as felids) have physiological and metabolic adaptations suited to their diet *[48, 49]*. Humans fit neither category, but are truly omnivores, falling between the largely frugivorous make-up of such anthropoid relatives as the chimpanzee and the adaptations of the true carnivores such as felids *[50]*.

In general, primates have relatively unspecialised gut structure, and in the case of most anthropoids have relied on high quality plant foods that are not extensively fibrous or lignified and supplemented them with some animal food *[48]*. A sacculated stomach and well-developed caecum and colon are associated with plant-based diets. The lower the plant quality (or higher the fibre content) the more pronounced is this development. The ruminant animals (foregut folivores) show the greatest volume in the stomach. Non-ruminant herbivores (mid-gut folivores), such as the horse, have greatest development in the caecum and colon.

Carnivores tend to have a well-developed acid-stomach and small intestine. Humans have evolved a simple acid stomach with their greatest gut volume concentrated in the small intestine and with a correspondingly reduced colon. The size of the human gut relative to body size is small in comparison with other anthropoids *[48]*. Approximate relative proportions of gut volume for humans and some other primates are shown in Table 2.

The evolutionary adaptations of mammalian gut structure to match diet has been reviewed *[50]*. Using a multidimensional plot of indices for surface areas of stomach, small intestine and caecum and colon, mammalian species were shown to fit four broad categories: (i) faunivores, simple but enlarged acid stomach and small intestine, short colon and vestigial or absent caecum (e.g. felids), (ii) foregut fermenting folivores with a large complex sacculated stomach for bacterial fermentation of cellulosic material (e.g. cattle), (iii) midgut fermenting folivores with an enlarged caecum and colon for bacterial fermentation of cellulosic materials (e.g. horse), and (iv) frugivores, gut size and proportions intermediate between faunivores and folivores, but with a larger colon than faunivores (e.g. chimpanzee). Using this approach the human gut, with its simple stomach, relatively elongated small intestine and reduced caecum and colon, does not fit any one group but lies between the frugivore and faunivore groups, suggestive of reliance on a high quality diet in which meat is a predominant component.

Table 2 Relative gut volume proportions for some primate species (percentage of total volume)

Species	Stomach	Small Intestine	Caecum	Colon
Gorilla	25	14	7	53
Orangutan	17	28	3	54
Chimpanzee	20	23	5	52
Gibbon	24	29	2	45
Human	17	67	na	17

Adapted from *[48]*

The brain-gut trade off

Primates in general, and humans in particular, have larger brain sizes than would be expected for their body size, a phenomenon described as "encephalisation" and reviewed in detail elsewhere *[51, 52]*. The most commonly used equation for prediction of brain size for placental mammals is the Martin equation *[53]*.

$$\mathbf{Log_{10}\,E = 0.76\,log_{10}\,P + 1.77}$$

Where E = brain mass (mg) and P is body mass (g). The ratio of expected: observed brain size (encephalization quotient) in humans is 4.6 while other primates average 1.9 *[52]*. In humans, this dramatic increase in brain size has occurred predominantly in the last 2–3 million years. Since the time of *A. aferensis* some 4.5 million years ago, brain size has increased threefold. What the driving force was for this dramatic increase can only be speculated, although many sound hypotheses based on socio-ecological factors have been put forward.

Irrespective of the driving force for encephalisation, two critical requirements had to be met: (i) the brain's chemical requirement for long chain PUFA, particularly arachidonic acid (20:4n-6) and docosahexaenoic acid (DHA, 22:6n-3) *[54, 55]* and (ii) the increased metabolic requirements of a larger brain *[56, 57]*.

The fatty acids mentioned are the major structurally significant and biochemically active components of the brain grey matter of all mammalian species *[58]*. The availability of these particular fatty acids may have provided a selective pressure acting to increase brain size, by simply supplying adequate dietary substrate to allow formation of brain tissue *[54, 59]*.

The metabolic cost of the human brain per kilogram is approximately nine times higher than the human body as a whole *[52]*. To sustain such a metabolically expensive large brain, there are two possible evolutionary adaptations that could be employed: (i) elevate the basal metabolic rate (BMR); or (ii) compensate for higher brain energy with lower mass-specific metabolic rates of other tissues. The BMR of eutherian mammals is accurately predicted by the Kleiber equation, based on body mass *[60]:*

$$\mathbf{BMR\ (W) = 3.39 \times mass^{0.75}\ (kg)}$$

Humans fit this predictive value well, indicating no increase in basal metabolism sufficient to account for the additional metabolic expenditure of the enlarged brain *[52]*. However, there is an evident reduction in the size of another metabolically active organ, that is the gastro-intestinal tract. Numerous studies have predicted organ masses in humans and other primates *[61]*. In general, the total mass of the metabolically active organs is close to that predicted. When examining individual organs, the brain mass surplus (and energy requirement), however, is closely balanced by

Table 3 Observed and expected organ mass and metabolic increments

Tissue	Mass[a] (kg)			Metabolic
	Observed	Expected	Difference	Increment (W)
Brain	1.30	0.45	+0.85	+ 9.5
Heart	0.30	0.32	–0.02	– 0.6
Kidney	0.30	0.24	+0.06	+ 1.4
Liver	1.40	1.56	–0.16	–11.5
Gastro-intestinal tract	1.10	1.88	–0.78	

Adapted from *[52]*. [a] Based on a 65 kg human.

the reduction in size (and energy requirement) of the gastrointestinal tract (Table 3).

This finding is not surprising. Considering the function of other metabolically expensive tissues, the gut is the only organ which can vary in size sufficiently to offset the metabolic cost of the larger brain. Although gut size is related to overall body size it can vary in size and proportion as a result of diet *[53]*. Diets high in bulky food of low digestibility require relatively enlarged gut size with voluminous fermenting chambers (rumen and caecum). Diets consisting of higher levels of high quality foods are associated with relatively smaller guts with simple stomachs, reduced colon size, but proportionately long small intestine *[62]* as seen in carnivores (Table 2). This pattern is seen clearly in primates where higher food quality relates to smaller gut size and larger brain size, with humans being the extreme case *[52]*.

For hominids, as a large-bodied species with increasing brain size during the past 3.5 million years *[63]*, the problem would have been to provide adequate levels of high-quality food to permit the necessary reduction in gut size. With the relatively poor macronutrient density of wild plant foods, particularly in the open woodland areas, the obvious solution was to include increasingly large amounts of animal-derived food in the diet *[64]*. The increasing consumption of meat rich in fats (particularly unsaturated forms) could also be responsible for the threefold increase in human brain size in the last 4.5 million years, both from the perspective of energy supply *[57]* and brain substrate availability *[55]*.

In summary, humans consume a diet much higher in quality than is expected for our size and metabolic needs. This energy-rich diet appears to reflect an adaptation to the high metabolic cost of our large brain. Evidence from the hominid fossil record implies that major changes in diet and relative brain size occurred with the emergence of the genus *Homo [65]*.

The transition to agriculture

The dietary changes involved with the transition from hunting and gathering to agriculture have been extensively reviewed *[66–68]*. This transition began in the Near East and Mediterranean region approximately 12,000 years ago with the growing of wild cereal crops and domestication of small mammals as a response to population increase and/or scarcity of large mammalian wild game. The transition, however, was associated with physiological stresses owing to undernutrition and infectious disease *[69]*. The transition to cultivation and domestication was not immediate, but rather lasted for around 5,000 years. The archaeological evidence indicates a gradual shift from consumption of root plants, wild pulses, various nuts and fruit and of hoofed mammals (gazelle, antelope and deer) during the late paleolithic to domesticated sheep, goats, cattle and pigs *[66]* and cultivated wheat and barley *[70]* during the Neolithic. Not only did the type of meat consumed alter dramatically but also the quantity was reduced enormously *[66]*. As mentioned previously, the fat content and type also changed considerably from wild game meat. This, combined with the greater reliance on grains, resulted in a profound shift to a diet containing greater levels of saturated fats and n-6 PUFA with a decrease in n-3 PUFA intake *[8]*. This transition also corresponded with a fundamental reversal of the high protein, low carbohydrate diet of the previous hunter-gatherer societies.

Insulin resistance and dietary preference

Eperimental evidence shows that, in the short term, high protein, low carbohydrate diets produces insulin resistance in the liver and peripheral tissue *[71]*. A high protein diet based on increasing meat consumption during the evolution of the hominid line (particularly the past 2 million years) would favour the selection of insulin resistance (IR), which results in increased hepatic gluconeogenesis and decreased peripheral glucose uptake *[72]*. The survival advantage of IR in our ancestral line was that the little available glucose from carbohydrate consumption was preserved for brain function and fetal/placental/mammary tissue in reproduction *[73]*.

Populations with the longest exposure to agriculture (high carbohydrate diets) have the lowest levels of IR. The selection pressure for IR has been relaxed for a longer time period in agricultural societies compared with recently acculturated hunter-gatherer societies which show increased levels of IR and NIDDM *[74]* when consuming "modern" diets rich in carbohydrates, much of which is of high glycaemic index (GI). Brand-Miller and Colagiuri *[73]* make four extremely salient points in their definitive paper in this area: (i) during the last two million years of evolution, humans were primarily carnivorous, i.e., flesh-eating hunters consuming a low-carbohydrate, high-protein diet;

(ii) a low-carbohydrate, high protein diet requires profound insulin resistance to maintain glucose homeostasis, particularly during reproduction; (iii) genetic differences in insulin resistance and predisposition to NIDDM can be explained by differences in exposure to carbohydrate during the past 10,000 years; (iv) changes in the quality of carbohydrate can explain the recent epidemic of NIDDM in susceptible populations *[73]*.

Protein limitations

Despite the suggested reliance of paleolithic humans on large game animals and the recorded dependence of more recent hunter-gatherer societies on large game, this in no way suggests humans are carnivores. The consumption of high levels of protein from lean game meat, particularly during the winter months when animals themselves are experiencing nutritional stress and may be severely fat depleted, leads to metabolic abnormalities in humans *[75]*. Hunter-gatherers would leave lean cuts of meat from hunted game despite food scarcity *[76]*. Although in some societies, at times, protein intake provided in the order of 80 % of total energy *[5]*, this is not common for prolonged periods of time. These groups tended to maximise fat intake from lean animals by selective butchering, consuming the brain, liver, kidneys and any other fat source in conjunction with the lean muscle meat *[5]*.

A number of accounts of early explorers in the American and Canadian wilderness record their experiences eating lean game meat with little fat or carbohydrate intake. These travellers experienced what was known as "rabbit starvation", a condition in which individuals ate successively bigger meals of lean meat while simultaneously experiencing the symptoms of starvation, stomach distension, restlessness and diarrhoea with death occurring after 2–3 weeks, if a source of fat or carbohydrate was not obtained *[77]*. Thus, a diet composed largely of lean meat (mainly protein energy) even in quantities that would appear to satisfy energy requirements can result in serious nutritional problems *[75]*. The principle problems peculiar to protein metabolism which affect the overall dietary intakes are (i) the high "specific dynamic action" (SDA) of protein ingestion and (ii) the toxic effect of over consumption. More so than carbohydrate or fat, protein raises the metabolism or heat production (diet-induced thermogenesis) resulting from food ingestion. An almost completely protein diet would have an SDA in the order of 30 %, indicating that 30 kJ of every 100 kJ intake is needed to compensate for increased metabolism *[75]*. It has been estimated that a diet composed almost entirely of lean meat requires 9 %–18 % more energy to satisfy metabolic and physiological functions relative to a more balanced diet *[78]*. However, such intake levels result in toxic nitrogen build-up in the body owing to the finite ability of the liver to upregulate enzymes necessary for urea synthesis. The maximum rate of urea synthesis (MRUS) in normal adults is reached at approximately 65 mg N/h/kg body weight. Protein intake above this results in hyperammonemia and hyperaminoacidemia *[79]* which manifest as the previously mentioned rabbit starvation. If we assume protein is approximately 16 % N/g, the maximal protein intake for an 80 kg adult is 250 g/day. On a typical "Western diet" of 3000 Calories (12,600 kJ) per day, this would allow a maximum protein energy contribution in the order of 35 %. On a low energy diet such as the 5040 kJ/day diet, recorded amongst Australian Aborigines *[5]*, this would translate to approximately 84 % energy from protein, a figure close to that observed by O'Dea during certain parts of the travels of these nomadic hunter-gatherers. It is estimated, however, that typical paleolithic diets would have been well above this energy intake level *[16]*.

Both fat and carbohydrate have a protein sparing effect. For HG societies existing on a low P:A subsistence, particularly during the winter months, fatter animals need to be consumed to maintain protein intakes within the physiological limits imposed by MRUS. Any HG society with a greater than 55 % subsistence on animal foods *[20]* would need to consume animals with > 10 % body fat. If we consider consumption of lean wild game meat at 2–5 % fat by weight, then 80 % of the available energy is protein and 20 % fat. For any extended period this would be impossible for humans to survive on as a sole dietary intake, as the MRUS is exceeded. A limited number of choices faced our paleolithic ancestors as for modern day HG societies: (i) hunt large animals (higher fat content) (ii) increase plant consumption (if available) (iii) selectively butcher game animals to obtain maximum fat and (iv) combine all three strategies.

Summary

It is proposed that *lean* meat does not contribute to vascular disease via increased serum cholesterol or elevated blood clot formation. Hence, if the meat supply to the consumer can be minimal in saturated fat content, no detrimental effects will be observed and substantial dietary advantages (protein, iron, zinc and vitamin B_{12} intakes) will be maintained. This conclusion is strongly supported by direct and indirect evidence that lean game meat and PUFA- and MUFA-rich organ meat and bone marrow made up a substantial part of the diet of hominids for a period of time stretching back well beyond and including the paleolithic. Thus meat is a significant part of our diet of evolutionary adaptiveness and advice to eliminate meat from the diet has no basis in evolutionary perspective or health implications, if low in saturated fat content.

European Journal of Nutrition, Vol. 39, Number 2 (2000)
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