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## **Dietary Intake of Long-Chain Polyunsaturated Fatty Acids during the Paleolithic**

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### **Introduction**

The more biologically significant polyunsaturated fatty acids (PUFA) include two with 18-carbon chains, linoleic acid (LA; C18:2 $\omega$ 6) and  $\alpha$ -linolenic acid (LNA; C18:3 $\omega$ 3), which are considered essential fatty acids (EFA). The longer chain members of this biochemical class have been termed long-chain PUFA (LCP) or, alternatively, highly unsaturated fatty acids. Dietary recommendations for LA and LNA are usually about 2 and 0.5%, respectively, of total energy intake but, to the authors' knowledge, formal recommendations for LCP (1.5 g/week) are limited to a single publication [1]. It has been suggested that the current intake ratio of  $\omega$ 6 and  $\omega$ 3 PUFA is undesirable and that a pattern more in line with that which developed during the Pleistocene would be more appropriate [2]. There was no one universal regimen during this epoch. However, despite the variability of ancestral diets, certain features were widespread across our genus' past experience. These dietary traits, taken together, may be considered the diet of evolutionary adaptedness (DEA), a statistical composite which integrates nutritional practices from many time periods and geographical settings [3]. The DEA influenced evolutionary selection of the height, body proportions, sexual dimorphism, brain size, resting metabolic rate, and day range which characterize anatomically modern humans [4, 5]. The  $\omega$ 6: $\omega$ 3 PUFA intake ratio during this crucial evolutionary phase

Table 1. Animal foods

Organ/tissue	% Total weight	% Total edible	% Fat
Skeletal muscle	45.0	90.2	2.3
Brain	0.5	1.0	9.0
Liver	1.9	3.8	3.3
Bone marrow	1.5	3.0	50.0
Separable fat	1.0	2.0	80.0

has been estimated at from 4:1 to 1:1; however, the bases for such estimates have been specified imprecisely, if at all. This paper presents a further estimate for Paleolithic PUFA nutrition.

## Method

We have collected from the literature nutrient analyses of wild plant and animal foods which have been utilized by recent hunter-gatherers and which were presumably available to preagricultural humans as well [6–26]. Almost none of these foods (255 plants, 85 animals) has had all relevant nutrients analyzed; for some only one or two data points are available. In certain cases different investigators have presented varying data for the same species; for these we have simply averaged the available figures – weighted for the number of observations. This exercise provides mean energy values for wild plant foods and for game of: 112 and 129 kcal/100 g, respectively.

Given these mean energy values, a simple model allows calculation of average daily intake:

$$A(C^aX) + B(C^vX) = \text{daily energy intake,}$$

where A and B are the mean energy content (kcal/g) of animal and vegetable foods, respectively;  $C^a$  and  $C^v$  are the proportions of animal and vegetable foods, respectively, and X is the total number of grams required to provide daily energy. We have taken 12.5 MJ (3,000 kcal)/day as energy intake [27] and a 35:65 animal:plant subsistence ratio [28] although any number of alternative parameters can be considered [29]. The model estimates gross amounts of food consumed: 890 g meat and 1,653 g vegetable food per day (5.75 lbs!).

For plant foods current data are sufficient to determine only overall average values for individual PUFA. However, for animal foods the calculations can be more sophisticated. This requires estimates of the edible portion as a fraction of total body weight, the proportional contribution of each organ or tissue to the edible portion, the proportion of fat in each organ or tissue, correction for the proportions of triglyceride and phospholipid in total fat (to give total fatty acid), and the content of individual PUFA as a proportion of total fatty acid in the organ or tissue. For game animals, about 50% of total body weight is edible [30] and we have estimated the proportions of total edible and the proportion of fat in each organ or tissue as shown in table 1. The database providing information on individual PUFA as a proportion of total fatty acid within specific organs or tissues is shown in table 2. For

Table 2. Database

	Species	Observations
Plants	20	?
Skeletal muscle	50	289
Brain	28	80
Liver	42	136
Bone marrow	3	24
Separable fat	12	40

each organ or tissue the calculations required are: organ or tissue as % total edible  $\times$  % total fatty acid in organ or tissue  $\times$  individual PUFA as % total fatty acid in organ or tissue. This operation generates the amounts of each individual PUFA per 100 g animal food and these values, with those for plant material, allow the model to estimate the individual PUFA intake which might be expected from any given subsistence pattern and daily energy requirement.

## Results

Values for individual PUFA, as percent total fatty acid, for game and wild plant foods, as derived from existing literature reports, are presented in table 3. Using these data, the model retrojects the DEA intake pattern shown in table 4. The diet would have provided C18 PUFA at nearly 21.5 g/day, with about 73% coming from plant sources. LA intake is estimated at 8.84 g/day, with LNA about 12.61 g/day for an overall  $\omega 6:\omega 3$  ratio of about 0.70 in the C18 category. For the longer chain PUFA (LCP or highly unsaturated fatty acids, C20 and above), animal sources would have provided about 94% of intake. Altogether about 3.01 g of LCP would have been consumed each day with an  $\omega 6:\omega 3$  ratio of about 1.79 for the category as a whole. Arachidonic acid (AA, C20:4,  $\omega 6$ ) would have been the dominant individual LCP at 1.81 g/day with docosapentaenoic acid (C22:5,  $\omega 3$ ) in second place at 0.42 g/day. Eicosapentaenoic acid (EPA, C20:5,  $\omega 3$ ) consumption is estimated at 0.39 g/day and docosahexaenoic acid (DHA, C22:6,  $\omega 3$ ), 0.27 g/day. AA: $\omega 3$  LCP would have approximated 1.68. The overall  $\omega 6:\omega 3$  intake pattern for total daily PUFA consumption would have been about 0.79.

## Discussion

### *Weaknesses*

The existing model has numerous weaknesses which fall into two general categories. The first is a need for more PUFA data. Information on wild plant

Table 3. Individual PUFA as % total fatty acids

	n	18:2 ω6	18:3 ω3	20:4 ω6	20:5 ω3	22:4 ω6	22:5 ω3	22:6 ω3
Game meat								
Skeletal muscle	50	16.49	2.97	8.31	1.19	0.44	1.99	0.77
Brain	28	0.35	0.04	4.40	0.17	2.16	0.25	8.05
Liver	42	10.19	1.61	10.45	1.45	0.37	3.42	3.98
Bone marrow	3	7.08	0.86	0.16	0.08	0.07	0.06	0.07
Separable fat	12	7.85	3.73	0.37	0.00	0.03	0.00	0.07
Plants	20	12.33	32.82	0.64	0.60	0.32	0.15	0.26

foods is limited to just 20 species, nearly all from Spain [9]<sup>1</sup>. A much greater number of uncultivated fruits and vegetables, especially varieties native to East Africa – currently considered the likeliest location for human evolution prior to about 100,000 years ago – need to be analyzed for PUFA content. More data on whole brain, not just gray matter, are necessary. Ancestral humans ate all the brain tissue, gray and white, they could obtain. Data on PUFA content of adipose tissue and, especially, bone marrow are scarce. More wild game values in these categories will improve the model's predictive accuracy. Similarly, PUFA data for other organs, e.g. tongue, heart, etc., consumed by hunter-gatherers will be helpful.

The second general category involves anthropological issues. Information on the relative contributions of individual organs and tissues, by weight, that foragers are able to obtain from the edible portions of average carcasses is meager. There are some data on butchering practices and taste preferences, but more would be desirable. The existing model is unable to weight plant food usage by category (e.g. fruits, seeds/pods, leaves/shoots, stems/stalks, underground storage organs, etc.) because too few PUFA analyses of wild plants have been made. An analysis of plant variety usage for African foragers is available [31] and when more vegetal PUFA analyses are published the contribution of plant foods to

<sup>1</sup> Guil et al. [9] evaluated the lipid content of the following wild plant foods: *Amaranthus viridis* (amaranth); *Beta maritima* (wild beet); *Cakile maritima* (sea rocket); *Cardaria draba* (hoary cress); *Chenopodium album* (goosefoot); *Chenopodium murale* (goosefoot); *Chenopodium opulifolium* (goosefoot); *Crithmum maritimum* (rock samphire); *Malva sylvestris* (common mallow); *Parietaria diffusa* (pellitory-of-the-wall); *Pichris echioides* (ox-tongue); *Plantago major* (plantain); *Portulaca oleracea* (purslane); *Rumex crispus* (curly dock); *Salicornia europaea* (glasswort); *Sisymbrium irio* (hedge mustard); *Sonchus oleraceus* (sow thistle); *Sonchus tenerrimus* (sow thistle-of-the-wall); *Stellaria media* (chickweed), and *Verbena officinalis* (vervain).

Table 4. Late Paleolithic sources of PUFA (g/day)

PUFA	Plant foods	Animal foods	Total intake
LA, 18:2, $\omega$ 6	4.28	4.56	8.84
LNA, 18:3, $\omega$ 3	11.40	1.21	12.61
AA, 20:4, $\omega$ 6	0.06	1.75	1.81
EPA, 20:5, $\omega$ 3	0.14	0.25	0.39
DTA, 22:4, $\omega$ 6	0.00	0.12	0.12
DPA, 22:5, $\omega$ 3	0.00	0.42	0.42
DHA, 22:6, $\omega$ 3	0.00	0.27	0.27

average daily PUFA intake can be assessed with greater sophistication. Hunter-gatherers often consume invertebrates, eggs, fungi, gums, and other foods of this sort, but their fractional importance to overall dietary intake has not been established. Further understanding in this area, together with relevant PUFA proximate analyses will also add to the model's validity.

#### *Effects of Varying Assumptions*

Any reconstruction of Paleolithic nutrition must be speculative and analysis of PUFA intake is no exception. The assumptions upon which we base 'average' intake figures are widely, but by no means universally accepted. Changes in these assumptions affect the model to varying degrees.

#### Subsistence Ratio

Prevailing wisdom is that anatomically modern humans evolved in Africa, with emigration from that continent beginning about 100,000 years ago, so low latitude foraging patterns (e.g. from 20 to 40% animal foods) assume special significance. Higher latitude patterns (e.g. 50% or more animal foods) appear to have become important for anatomically modern humans only 'recently' (i.e. 50–30,000 to 10,000 years ago), but prevailed in important areas such as the Siberian mammoth steppe where ancestors of today's Mongoloids were probably located from 30,000 to 10,000 years ago. In the Epipaleolithic, period of broad-spectrum foraging which occupied the few millenia just before emergence of agriculture, animal foods are estimated to have provided only 10–20% of subsistence [32]. In general, high animal food subsistence patterns yield substantially higher  $\omega$ 6: $\omega$ 3 ratios and slightly higher AA: $\omega$ 3 LCP ratios.

Animal: Plant	20:80	95:5
Overall $\omega$ 6: $\omega$ 3	0.59	2.65
AA: $\omega$ 3 LCP	1.53	1.87

### Preferential Butchering

When animal foods are plentiful, and especially when plant foods are concurrently scarce, hunters tend to emphasize use of high-fat adipose tissue, organ meats, brain, and marrow and to harvest less low-fat, high-protein muscle tissue. Taste preferences presumably explain these choices to some extent, but there is probably an upper limit (of perhaps 50% total energy intake) for protein in the human diet, at least on a long-term basis [33], which taste preferences may ultimately reflect. If the 'take' of marrow, brain, liver and adipose tissue be increased (2 x = selective butchering; 4 x = hyper-butchering) and the resulting weight subtracted from the amount of muscle consumed, a 35:65 subsistence pattern would change as follows:

	Standard	Selective butchering	Hyper-butchering
Overall $\omega 6:\omega 3$	0.79	0.84	0.92
AA: $\omega 3$ LCP	1.68	1.57	1.37

### Plant Fat

The importance of fat as percentage of total edible plant food depends greatly on the proportion of high-fat seeds and nuts included in the diet. For the California Miwoks who ate great quantities of acorns and the !Kung San Bushmen of Botswana, whose reliance on mongongo nuts is well known, vegetable fat was a major component of energy intake. Prior to the epipaleolithic, optimal foraging considerations limited consumption of small cereal grains to periods of severe dietary scarcity. Weighting a multicontinental series of 255 wild plant species by the utilization pattern of African hunter-gatherers suggests that fat made up about 2.1% of the energy provided by vegetables, but groups like the Miwoks and San would have had substantially higher vegetable fat intakes.

Varying the percentage of energy from vegetable fat would have altered overall  $\omega 6:\omega 3$  and AA: $\omega 3$  LCP ratios reciprocally:

	1% Fat	2% Fat	5% Fat
Overall $\omega 6:\omega 3$	1.11	0.79	0.57
AA: $\omega 3$ LCP	1.79	1.68	1.49

### Plant LCP

The existence of LCP in plants is disputed, some investigators contending that apparent plant LCP actually represent technical artifacts. If plants contrib-

uted no LCP at all to preagricultural diets, then overall  $\omega 6:\omega 3$  ratios would change little and AA: $\omega 3$  LCP ratios would increase slightly.

	No plant LCP	Small amount plant LCP <sup>a</sup>
Overall $\omega 6:\omega 3$	0.79	0.79
AA: $\omega 3$ LCP	1.68	1.87

<sup>a</sup> As per table 3.

### Assumptions Overview

This analysis reveals that widely differing preagricultural human dietary regimens would have had surprisingly little impact on PUFA nutrition (table 5). On the other hand current Western PUFA intake is outside the range retrojected for the Paleolithic in all cases. This dramatic difference probably reflects introduction of cereal grains (a major source of LA). These now provide a substantial fraction of dietary energy in most Western nations and as animal feed they affect the PUFA partition in commercial meat as well. For Paleolithic humans, as for other free-living primates, cereals were ordinarily a negligible dietary factor and the  $\omega 6:\omega 3$  ratio of commercial meat is far higher than that of wild game.

### Brain Size

While DHA and AA can be biosynthesized from LNA and LA, respectively, the reaction rate, for DHA at least, appears too slow to provide a sufficient supply during early human brain development: intake of preformed LCP from the diet seems essential [34]. Three LCP: AA, DHA and docosatetraenoic acid (DTA; C22:4;  $\omega 6$ ) constitute over 94% of all LCP in human gray matter (and in mammalian gray matter generally) [16]. If the subsistence pattern of our most recent hominoid ancestors, who probably lived about five million years ago, was comprised of 95% plant foods and 5% from small game, i.e. like that observed for current chimpanzees [35] (the mammalian species to whom humans are most closely related), the model retrojects combined AA, DTA and DHA intake of 0.16 g/1,000 kcal. If during subsequent hominid-human evolution the subsistence pattern gradually changed to that observed in recent foragers (65% plants, 35% game) combined AA, DTA and DHA intake would have increased to about 0.9 g/1,000 kcal, a 5.7-fold increase.

Over the same time period the cranial capacity of our ancestral line grew from about 400 to 1,517 cm<sup>3</sup> for Cro-Magnons living 30,000 years ago [4, 5]. This change represents a 3.79-fold increase, so the retrojected 5.7-fold increase

Table 5. The effects of varying assumptions (g/day)

Description	Sub- sistence Ratio <sup>1</sup>	LA 18:2	LNA 18:3	AA 20:4	EPA 20:5	DTA 22:4	DPA 22:5	DHA 22:6	AA:ω3 LCP	ω6:ω3 ratio
<i>Ardipithecus ramidus</i> <sup>2</sup>	5:95	7.22	17.59	0.35	0.25	0.02	0.06	0.04	1	0.42
No plant LCP	5:95	7.22	17.59	0.26	0.04	0.02	0.06	0.04	1.86	0.42
Plants 1% fat, 80 kcal/100 g	5:95	5.19	11.59	0.41	0.19	0.02	0.08	0.06	1.24	0.47
Plants 5% fat, 167 kcal/100 g	5:95	11.1	28.45	0.32	0.37	0.01	0.04	0.03	0.73	0.4
Gatherer-hunters	20:80	8.05	15.04	1.1	0.32	0.07	0.24	0.16	1.53	0.59
No plant LCP	20:80	8.05	15.04	1.03	0.14	0.07	0.24	0.16	1.91	0.59
Plant 1% fat, 80 kcal/100 g	20:80	6.72	9.68	1.36	0.29	0.09	0.31	0.2	1.7	0.78
Plants 5% fat, 167 kcal/100 g	20:80	11.21	25.22	0.86	0.41	0.05	0.18	0.11	1.23	0.47
Selective butchers (2 ×)	20:80	8.74	15.4	1.13	0.32	0.08	0.25	0.22	1.43	0.61
Hyper-butchers (4 ×)	20:80	10.12	16.1	1.19	0.33	0.12	0.26	0.36	1.25	0.67
DEA	35:65	8.84	12.61	1.81	0.39	0.12	0.42	0.27	1.68	0.79
No plant LCP	35:65	8.84	12.61	1.76	0.25	0.12	0.42	0.27	1.87	0.79
Plants 1% fat, 80 kcal/100 g	35:65	8.01	8.06	2.16	0.38	0.14	0.5	0.33	1.79	1.11
Plants 5% fat, 167 kcal/100 g	35:65	11.32	21.75	1.45	0.44	0.09	0.32	0.21	1.49	0.57
Selective butchers (2 ×)	35:65	10.02	13.21	1.87	0.39	0.14	0.42	0.38	1.57	0.84
Hyper-butchers (4 ×)	35:65	12.38	14.42	1.98	0.4	0.2	0.44	0.61	1.37	0.92
Hunter-gatherers	60:40	10.08	8.77	2.94	0.49	0.19	0.69	0.45	1.8	1.27
No plant LCP	60:40	10.08	8.77	2.91	0.41	0.19	0.69	0.45	1.88	1.28
Plants 1% fat, 80 kcal/100 g	60:40	9.78	5.84	3.26	0.5	0.22	0.77	0.5	1.84	1.74
Plants 5% fat, 167 kcal/100 g	60:40	11.32	21.75	1.45	0.44	0.09	0.32	0.21	1.49	0.57
Selective butchers (2 ×)	60:40	12.04	9.77	3.03	0.5	0.24	0.7	0.63	1.66	1.32
Hyper-butchers (4 ×)	60:40	15.95	11.78	3.21	0.51	0.33	0.73	1.01	1.43	1.39
High-latitude peoples	95:5	11.69	3.83	4.39	0.63	0.29	1.04	0.68	1.87	2.65
No plant LCP	95:5	11.69	3.83	4.39	0.62	0.29	1.04	0.68	1.88	2.65
Plants 1% fat, 80 kcal/100 g	95:5	11.68	3.45	4.45	0.63	0.3	1.05	0.68	1.89	2.83
Plants 5% fat, 167 kcal/100 g	95:5	11.86	4.84	4.31	0.63	0.29	1.02	0.66	1.87	2.3
Selective butchers (2 ×)	95:5	14.64	5.34	4.53	0.64	0.36	1.06	0.96	1.7	2.44
Hyper-butchers (4 ×)	95:5	20.55	8.37	4.8	0.66	0.49	1.1	1.52	1.46	2.22
Minimum		5.19	3.45	0.26	0.04	0.01	0.04	0.03	0.73	0.04
Maximum		20.55	25.22	4.8	0.66	0.49	1.1	1.52	1.91	2.83
Current Western pattern	35:65	22.5	1.2	0.6	0.05	n.a.	0.05	0.08	3.33	16.74

<sup>1</sup> Animals: Plant.

<sup>2</sup> Earliest known hominid genus-existed >4 million years ago.

in AA, DTA and DHA availability would have provided more than adequate raw material for brain-building structural purposes. It is not necessary to hypothesize that humans evolved at the land-water interface with special access to marine resources [36]; improvements in terrestrial hunting and scavenging would have been entirely sufficient.



Brain size has declined since the Paleolithic: the current average, 1,350 cm<sup>3</sup>, is about 11% less than estimates for early anatomically modern humans living before the development of agriculture [5]. This decrease has occurred very rapidly compared with the several million year period during which the human brain enlarged. Current DHA intake is estimated at 80 mg/day [37] and AA intake probably ranges from 100–1,000 mg/day [38]. Late Paleolithic intake for these nutrients is retrojected at 270 and 1,810 mg/day, respectively, so current DHA and AA consumption are both much below Paleolithic levels. Assuming the discrepancy for DTA is similar (we are unaware of estimates for current DTA intake), it is tempting to conjecture that decreases in the availability of brain structural substrate may be related to the decline in brain size which has occurred during recent millennia.

#### *Cardiovascular Disease*

Paleolithic diets provided 2–3 times the meat consumed in current affluent nations and, hence, much more AA, the metabolic precursor of proaggregatory eicosanoids such as thromboxane (TxA<sub>2</sub>) [39]. Although EPA and DHA, which counter the effects of AA, were also important constituents of preagricultural subsistence, equations designed to evaluate the diet-related tendency for thrombotic disorders mediated by  $\omega$ 6 eicosanoids suggest that the Paleolithic LCP intake pattern might have promoted a high prevalence of coronary atherosclerosis, stroke and other disorders related to hemostatic factors [40]. Such equations predict disease prevalence accurately for contemporary populations; however, the diet (and lipid intake in particular) for humans living before agriculture was so different<sup>2</sup> that mathematical models based on current conditions may not be applicable to ancestral circumstances.

Studies of high-meat diets suggest this may be the case. Replication of the traditional Australian Aboriginal subsistence pattern – no cereal grains, little total fat, and considerable lean kangaroo meat – increased plasma LCP in all categories, including AA, EPA and DHA. Urinary metabolites of TxA<sub>2</sub> and prostacyclin (PGI<sub>2</sub>) both increased, but only that of PGI<sub>2</sub> was statistically significant and the TxA<sub>2</sub>/PGI<sub>2</sub> metabolite ratio was not significantly altered [40]. These findings complement those of an earlier study in which a similar dietary regimen produced a 44% increase in bleeding time and a decreased cold pressor response, the latter possibly reflecting increased arterial prostacyclin production [41]. The overall import is that high levels of dietary  $\omega$ 3 LCP may modulate the thrombotic potential of increased AA intake to the extent that a net antithrombotic effect is achieved [40, 41]. The high dietary intake of LNA by Paleolithic humans may have augmented this process [42, 43].

<sup>2</sup> Lower total fat, higher P:S ratio, roughly equal  $\omega$ 6: $\omega$ 3 intake, and greater overall LCP content. Furthermore serum cholesterol levels averaged 3.2 mmol/l (125 mg/dl).

## Conclusion

Evolutionary considerations are not (yet) a basis upon which to make nutritional recommendations, but insights derived from this perspective may nevertheless provide valuable adjunctive understanding about human dietary needs and about the relation of diet to fetal and childhood development, adult health, and chronic illnesses. Conventional nutrition research sometimes produces conflicting, inconsistent findings that are hard to interpret or reconcile [44]. An understanding of human ancestral experience during evolution can shed light on issues of this nature, providing a fundamental benchmark against which the results of more traditional research can be assessed. Furthermore, evolutionary awareness can generate logical yet novel hypotheses which can be rigorously tested by conventional techniques.

In the case of EFA, current intake clearly differs from that of our ancestors: preagricultural humans generally consumed  $\omega 6$  and  $\omega 3$  PUFA in roughly equal amounts. This pattern fueled the emergence and development of our genus; evolutionary considerations commend its restoration.

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