Phytochemicals
Nutrient-Gene Interactions

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CHAPTER 8
Saturated Fat Consumption in Ancestral Human Diets: Implications for Contemporary Intakes

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INTRODUCTION

Genetic Discordance

Nutritional requirements for all organisms are ultimately determined by the expression of specific genes within an organism's genome. These genes, in turn, are created and shaped by an ongoing interaction between the genome and its env-

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resentment via evolution acting through natural selection over many generations. Genetic traits may be positively or negatively selected relative to their concordance or discordance with environmental selective pressures. When the environment remains relatively constant over a long period of time, stabilizing selection tends to maintain genetic traits that represent the optimal average for a population. On the other hand, when environmental conditions change over long periods of time, evolutionary discordance arises between a species' genome and its environment, and stabilizing selection is replaced by directional selection, moving the average population genome to a new set point. Initially, when long-term environmental changes occur in a population, individuals bearing the previous average status quo genome experience evolutionary discordance. In the affected genotype, this evolutionary discordance manifests itself phenotypically as disease, increased morbidity and mortality, and reduced reproductive success.

Since the introduction of agriculture and animal husbandry 10,000 years ago, and more recently with the beginning of the Industrial Revolution 200 years ago, crucial changes have occurred in both diet and lifestyle conditions that are vastly different than the prevailing environmental conditions during which the human genome adapted. Numerous Neolithic and Industrial era food introductions have been identified that promote the development of chronic disease in contemporary western populations. In most cases, a dose response exists between these novel foods and the emergence of disease. For instance, occasional seasonal exposure to honey (a refined sugar) results in negligible dental cavities in hunter-gatherers; whereas daily consumption of refined sugar in Western diets almost universally causes a high incidence of cavities and dental decay. In many cases (such as with dental cavities) the proximate physiological and biochemical causes for the diseases are well understood. Despite this knowledge, it is frequently less well appreciated that the ultimate basis for most diet-related diseases results from the evolutionary discordance between our ancient and conservative genome and recently introduced food. By examining pre-agricultural diets and their nutritional characteristics and comparing them to contemporary diets, insight can be gained into complex questions regarding diet and disease in existing populations.

Dietary Saturated Fats

A diet-disease question that has become contentious in recent years is saturated fats and the role they might play in the pathogenesis of coronary heart disease. The traditional view has been that certain saturated fats (12:0, 14:0, and 16:0) downregulate the LDL receptor and thereby increase plasma concentrations of LDL cholesterol, which in turn increases the risk for coronary artery disease (CAD). It is increasingly being recognized that this traditional model of atherosclerosis and CAD is overly simplistic, primarily because CAD is a multifactorial disease involving numerous dietary and genetic factors acting in concert with one another. The dietary glycemic load, the n6/n3 fatty acid balance, chronic inflammation, tran fatty acids, homocysteine, alcohol intake, exercise, smoking, and numerous other dietary and lifestyle factors play key roles in the
pathogenesis of CAD. Nevertheless, the molecular\(^{26}\) and clinical\(^{27}\) basis for the elevation of plasma LDL by saturated fatty acids cannot be ignored, nor can the continuous and graded risk for CAD mortality with increasing LDL and total cholesterol concentrations\(^ {22,23}\) despite suggestions otherwise\(^ {14,15}\).

The relative contribution that dietary saturated fats may make to the overall development and progression of CAD under the backdrop of the typical Western diet and lifestyle is unclear, particularly given that individual genetic differences may modulate the cholesterol-raising effects of saturated fats.\(^ {27}\) However, this lack of precise evidence by no means exonerates dietary saturated fats. Rather, they represent a known risk factor for CAD that should be recognized and considered similar to other known dietary risk factors. In the current U.S.\(^ {25}\) diet, an average of 11% of the daily energy is derived from saturated fat,\(^ {25}\) a figure slightly higher than the 10% or less recommended by the American Heart Association.\(^ {25}\) By examining the amounts of saturated fats in pre-agricultural hominin diets, as an evolutionary baseline can be established regarding the normal range and limits of saturated fats that would have conditioned the human genome.

**SATURATED FATS IN PRE-AGRICULTURAL DIETS**

Figure 8.1 demonstrates that since the evolutionary emergence of hominins, 20 or more species may have existed.\(^ {28}\) Similar to historically studied hunter-gatherers,\(^ {22,24}\) there would have been no single, universal diet consumed by all extinct hominin species. Rather, diets would have varied by geographic locale, climate, and specific ecologic niche. However, a number of lines of evidence indicate that all hominin species and populations were omnivorous; consequently, dietary saturated fats would have always been a component in hominin diets.

**Saturated Fat In Early Pliocene Hominin Diets**

Our closest living primate relative, the chimpanzee (*Pan troglodytes*) is omnivorous and consumes a substantial amount of meat throughout the year obtained from hunting and scavenging.\(^ {26}\) Observational studies of wild chimpanzees demonstrate that during the dry season, meat intake is about 65 g per day for adults.\(^ {26}\) Accordingly, it is likely that the very earliest Pliocene hominins would have been capable of obtaining animal food through hunting and scavenging in a manner similar to chimpanzees. Additionally, fossils of early African hominins including *Australopithecus africus*, and *Australopithecus robustus* maintain carbon isotope signatures characteristic of omnivores.\(^ {32,33}\)

Quantitative estimates of energy intake from animal food sources in these early hominins are unclear, other than that they were likely similar to, or greater than, estimated values (4 to 8.5% total energy) for chimpanzeas.\(^ {36,34}\) Consequently, the amount of dietary saturated in the earliest hominin diets would have been substantially lower than later hominins whose diet became more dependent upon animal food energy sources.
Figure 8.1 The hominin fossil record. Species are indicated with the dates of the earliest and latest fossil record. (Adapted from Wood, B., Nature, 418, 133, 2002.)
Saturated Fat in Pliocene/Paleocene Hominin Diets

Approximately 2.6 million years ago (MYA), the hominin species Sat eventually led to Homo began to include more and more animal food in their diet. A number of lines of evidence support this viewpoint. First, Oldowan lithic technology appears in the fossil record 2.6 MYA, and there is clear cut evidence to show that these tools were used to butcher and disarticulate animal carcasses. Stone tool cut marks on the bones of prey animals and evidence for marrow extraction appear concurrently in the fossil record with the development of Oldowan lithic technology by at least 2.5 MYA. It is not entirely clear which specific early hominin species or species manufactured and used these earliest stone tools, however Australopithecus garhi might have been a likely candidate.

The development of some tools and the increased dietary reliance upon animal foods allowed early African hominins to colonize northern latitudes outside Africa when plant foods would have been seasonally restricted. Early Homo skeletal remains and Oldowan lithic technology appear at the Dmanisi site in the Republic of Georgia (40°N) by 1.75 MYA, and more recently Oldowan tools dating to 1.66 MYA have been discovered at the Majiagou site in North China (40°N). Both of these tool-producing hominins would likely have consumed considerably more animal food than pre-lithic hominins living in more temperate African climates because of reduced availability of plant foods during winter and early spring. Hence, the consumption of saturated fat would have, accordingly, been higher. Once again, qualitative estimates of the saturated fatty content in early Homo species are speculative because of the uncertain plant-animal subsistence ratio. However, there is suggestive isotopic data indicating that the majority of the energy in more northerly living Homo species may have been obtained from animal foods.

Saturated Fat in Late Pleistocene Hominin Diets

Richards et al. have examined stable isotopes (13C and 15N) in two Neanderthal specimens (~23,000 to 29,000 years BP) from Vindija Cave in northern Croatia and contrasted these isotopic signatures to those in fossils of herbivorous and carnivorous mammals from the same ecosystem. The analysis demonstrated that Neanderthals, similar to wolves and arctic foxes, behaved as top-level carnivores, obtaining all of their protein from animal sources. A comparable analysis was made of five Upper Paleolithic Homo sapiens specimens (used to the Upper Paleolithic (~11,700 to 12,380 years BP) from Gough's and Sun Bone Caves in Britain. The data indicated these hunter-gatherers were consuming animal protein on a year-round basis at a higher trophic level than the arctic fox. Although precise quantitative estimates of saturated fat intake are not possible, the saturated fat intake in both Neanderthal and Upper Paleolithic Homo sapiens would have been substantial because of their great dependence upon animal food sources for daily energy.
Saturated Fat in Historically Studied Hunter-Gatherer Diets

Because reasonable estimates exist for the average plant-to-animal subsistence ratio for historically studied hunter-gatherers, it is possible to estimate the amount of saturated fat in their diet. Our analysis (Figure 8.2) of the Ethnographic Atlas data showed that the dominant foods in the majorly historically studied hunter-gatherer diets were derived from animal food sources. Most (73%) of the world’s hunter-gatherers obtained >50% of their subsistence from hunted and fished animal foods, whereas only 14% of worldwide hunter-gatherers obtained >50% of their subsistence from gathered plant foods. For all 229 hunter-gatherer societies, the median subsistence dependence upon animal foods was 56 to 65%. In contrast, the median subsistence dependence upon gathered plant foods was 26 to 35%.

The major limitation of ethnographic data is that the proportion of it is subjective in nature, and the assigned scores for the five basic subsistence economies in the Ethnographic Atlas are not precise but, rather, are approximations. Fortunately, more exact, quantitative dietary studies were carried out on a small percentage of the world’s hunter-gatherer societies. Table 8.1 lists these studies and shows the plant-to-animal subsistence ratios by energy. The average score for animal food subsistence is 65%, while that for plant food subsistence is 35%. When the two polar hunter-gatherer populations, who have no choice but to eat animal food because of the inaccessibility of plant food, are excluded from Table 8.1, the mean score for animal subsistence is 59% and that for plant food subsistence is 41%. These animal-to-plant subsistence values fall within the same respective class intervals (56 to 65% for animal food; 26 to 35% for plant food) as those we estimated from the ethnographic data when the confounding influence of latitude was eliminated. Consequently, there is remarkably close agreement between the quantitative data in Table 8.1 and the data from the ethnographic Atlas.

Figure 8.2 Frequency distribution of subsistence dependence upon total (fished + hunted) animal foods in world wide hunter-gatherer societies (n = 229). (Adapted from Cordain, L. et al., Am. J. Clin. Nutr., 71, 882, 2000.)

Median = (56-65 %)
Mode = (56-65 %)
Table 8.1 Quantitatively Determined Proportions of Plant and Animal Food in Hunter-Gatherer Diets

<table>
<thead>
<tr>
<th>Population</th>
<th>Location</th>
<th>Latitude</th>
<th>% animal food</th>
<th>% plant food</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aboriginals</td>
<td>Australia</td>
<td>12S</td>
<td>77</td>
<td>23</td>
</tr>
<tr>
<td>Ache</td>
<td>Paraguay</td>
<td>25S</td>
<td>38</td>
<td>29</td>
</tr>
<tr>
<td>Anbarra</td>
<td>Australia</td>
<td>12S</td>
<td>75</td>
<td>25</td>
</tr>
<tr>
<td>Eskimo</td>
<td>Greenland</td>
<td>69N</td>
<td>45</td>
<td>4</td>
</tr>
<tr>
<td>Gwi</td>
<td>Africa</td>
<td>22S</td>
<td>25</td>
<td>74</td>
</tr>
<tr>
<td>Hadda</td>
<td>Africa</td>
<td>10</td>
<td>48</td>
<td>52</td>
</tr>
<tr>
<td>Hsei</td>
<td>Venezuela</td>
<td>6N</td>
<td>75</td>
<td>25</td>
</tr>
<tr>
<td>Ikung</td>
<td>Africa</td>
<td>20S</td>
<td>33</td>
<td>67</td>
</tr>
<tr>
<td>Inuk</td>
<td>Africa</td>
<td>20S</td>
<td>68</td>
<td>32</td>
</tr>
<tr>
<td>Nunuk</td>
<td>Columbia</td>
<td>2N</td>
<td>41</td>
<td>59</td>
</tr>
<tr>
<td>Nunamut</td>
<td>Alaska</td>
<td>68N</td>
<td>99</td>
<td>1</td>
</tr>
<tr>
<td>Onge</td>
<td>Andaman Islands</td>
<td>12N</td>
<td>79</td>
<td>21</td>
</tr>
</tbody>
</table>


8.1 and the ethnoparasitographic data that animal food comprised more than half of the energy in historically studied hunter-gatherer diets.

THE ESTIMATION OF DAILY DIETARY SATURATED FATS

Using the same model we developed for estimating the macronutrient content in hunter-gatherer diets, it is possible to estimate the dietary saturated fat content, provided saturated fat values in the plant and animal food databases are known. Similar to our previous model, a range of plant-to-animal subsistence ratios were utilized to estimate the most likely range for dietary saturated fat.

Saturated Fat In Plant Foods

In the current model, fat contributed 24% of the total energy derived from all wild plant food (n = 768), whereas carbohydrate (62% energy) and protein (14%) comprised the balance of plant food energy. The mean fatty acid breakdown for 64 cultivated equivalent category plant foods was 22.4% saturated fatty acids, 28.6% monounsaturated fatty acids, and 49% polyunsaturated fatty acids. Accordingly, in our model, 54% of plant food energy was derived from saturated fat.

Saturated Fat In Animal Foods

The estimation of saturated fat from animal sources is more complex because hunter-gatherers typically ate the entire edible carcass of most vertebrates, thereby necessitating the calculation of the total edible carcass saturated fatty acid content. In mammals and most vertebrates, organ and tissue mass scales closely with body
mass. Consequently, the mass of individual edible organs can be calculated from body mass using allometric equations. The edible carcass mass can then be determined by subtracting the mass of the bones (minus marrow), hide, hooves, antlers, blood, urine, and gastrointestinal content from the total live weight. Edible carcass saturated fatty acid mass can be computed by multiplying individual tissue and organ mass by their respective saturated fatty acid compositions (% mass) and then summing these values. Finally, the edible carcass saturated fatty acid content by energy can be calculated from values by mass using the cubic regression equation developed by Cordain et al. Figure 8.3 shows the cubic relationship between edible body fat percent by mass and edible body saturated fat percent by energy in mammals. Application of this equation along with the saturated fat content of plant and fish foods, as previously described, allows for the estimation of total dietary saturated fat when the relative plant-to-animal subsistence values are known (Table 8.2). In the current model, a range of likely plant-to-animal subsistence values in hunter-gatherer diets have been employed as previously outlined. Note that in the current model, saturated fat content for fish was derived from the mean value (20.1% of total fat energy) from 20 species of fish.

**DISCUSSION**

In Table 8.2 the mean dietary saturated fat as a percentage of total energy is 11.0 ± 3.9 (S.D.). However, it is likely that a number of the projected values are physiologically unrealistic because they encroach upon or exceed the physiological protein ceiling. If those values whose protein intake exceeds 35.1% of total energy are excluded from the analysis, the mean dietary saturated fat as a percentage of total energy is 13.2 ± 2.8. In the typical hunter-gatherer diet, the animal subsistence falls between 55-65% of total energy; consequently, in this group, the mean dietary

![Figure 8.3](image-url)  
**Figure 8.3** Regression of whole edible carcass fat percentage by weight on edible carcass saturated fat % by energy.
### Table 8.2 Dietary Macronutrient (% energy) and Saturated fat (SAT (% Energy) Estimates in Worldwide Hunter-Gatherer Societies (n = 229) with Varying Plant:Animal Subsistence Ratios and with Varying Animal (Hunted + Packed) Body Compositions

<table>
<thead>
<tr>
<th>(Plant:Animal) Subsistence Ratio</th>
<th>% PRO%</th>
<th>% CHO</th>
<th>% FAT</th>
<th>% SAT FAT</th>
</tr>
</thead>
<tbody>
<tr>
<td>35:65 - 20% animal fat</td>
<td>21</td>
<td>22</td>
<td>58</td>
<td>17.6</td>
</tr>
<tr>
<td>35:65 - 15% animal fat</td>
<td>30</td>
<td>22</td>
<td>50</td>
<td>16.3</td>
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<tr>
<td>35:65 - 10% animal fat</td>
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<td>22</td>
<td>43</td>
<td>14.1</td>
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<tr>
<td>35:65 - 5% animal fat</td>
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<td>10.6</td>
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<td>35:65 - 2.5% animal fat</td>
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<td>23</td>
<td>8.1</td>
</tr>
<tr>
<td>45:55 - 20% animal fat</td>
<td>20</td>
<td>28</td>
<td>52</td>
<td>15.8</td>
</tr>
<tr>
<td>45:55 - 15% animal fat</td>
<td>26</td>
<td>28</td>
<td>46</td>
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<td>28</td>
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<td>12.3</td>
</tr>
<tr>
<td>45:55 - 5% animal fat</td>
<td>42</td>
<td>28</td>
<td>30</td>
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<td>28</td>
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<td>50:50 - 2.5% animal fat</td>
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<td>55:45 - 20% animal fat</td>
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<tr>
<td>60:35 - 2.5% animal fat</td>
<td>37</td>
<td>40</td>
<td>23</td>
<td>3.6</td>
</tr>
</tbody>
</table>

* Exceeds low value (27.6% protein energy) for the range of maximal hepatic urea synthesis
* Exceeds mean value (35.1% protein energy) for the range of maximal hepatic urea synthesis
* Exceeds high value (40.9% protein energy) for the range of maximal hepatic urea synthesis

Saturated fat as a percentage of total energy is higher still (15.1 ± 1.9). Even in plant dominated (>50% energy from plant (cocks) hunter-gatherer diets, the mean dietary saturated fat as a percentage of total energy is slightly higher (11.3 ± 2.8) than the recommended healthful values of <10%. The present data suggests that the normal dietary intake of saturated fatty acids that conditioned our species genome likely fell between 10 to 15% of total energy, and that value lower than 10% or higher that 15% would have been the exception rather than the rule. Consequently, population-wide recommendations to lower...
dietary saturated fat below 10% to reduce the risk of CAD have little or no evolutionary foundation in pre-agricultural Homo sapiens. Because no randomized clinica trials of low saturated fat diets of sufficient duration have been carried out, there is a lack of knowledge how low saturated fat intake can be without the risk of potentially deleterious health consequences. Hence, extremely low, or conversely, high, lifelong consumption of dietary saturated fatty acids is likely to be discordant with the human genome.

REFERENCES


