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# Nature and Variability of Human Food Consumption [and Discussion]

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# Nature and variability of human food consumption

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**SUMMARY**

The early human diet was characteristically extremely varied, and a wide range of plant species and plant organs were consumed. Foods of animal origin included those taken opportunistically, such as invertebrates, amphibians, reptiles, small mammals, birds and their eggs, and the scavenging and hunting of larger mammals. Each of these types of food have characteristic nutritional compositions. Comparison of these compositional features shows that an adequate diet could be obtained in many different ways. The selection of food providing fat had substantial advantages in reducing the amount of plant foods to be gathered, in the satiety provided and in supplying essential micronutrients. Obtaining adequate water and energy would probably be the main physiological drives. Many plant foods contain natural toxicants, and would only have been suitable as major items in the diet once cooking had been developed, and the preference for sweet tastes would have protected humans from eating bitter, toxic plants.

## 1. INTRODUCTION

The human diet is characteristically extremely varied, and the ability to select a dietary mixture from a wide range of edible plants and animals, coupled with great ingenuity in making intrinsically unpromising materials into nutritious, if not necessarily palatable foods, can be seen as an important factor in the development of human societies (Le Gros Clark 1967). The capacity to identify and to make edible, natural materials in the most hostile of environments has enabled the human species to expand its range. The acceptance of variety was also a key factor in surviving in times of extreme food shortages that were common before the development of the continuity of food supply, which characterizes the present position in developed industrial societies.

In discussing the 'natural' diet of humans I think that this characteristic of extreme fluctuations in the amounts and types of foods available for consumption is an important one, and that the control of appetite and the choice of foods evolved under conditions of alternating abundance and scarcity, circumstances which are still the norm in many developing countries today.

In this paper I shall use 'natural' for diets composed of plant foods that have not been cultivated in any developed agricultural system and foods derived from undomesticated animals (Southgate 1988). It would be incorrect to think of these foods as unprocessed because, as I will show, the development of the human diet has been characterized by the use of processing technologies, albeit of a simple nature by modern standards, but of great dietary significance when they were introduced.

I shall first discuss the range and compositional features of the various major types of food that were available to early human societies. In this I will draw on the many studies that have been made on surviving populations of hunter–gatherers. In doing this I recognize that these societies have undoubtedly developed themselves, and that they have had extensive contacts with agricultural and pastoral societies. It would be naïve to assume that these contacts have not affected their food patterns, and it would be equally naïve to believe that their societies and environment have been stable (Schrire 1984). It is important to recognize that the residual populations of hunter–gatherers have to a great extent been driven, by the development of agriculture and the consequential reduction in their hunting ranges, into less productive environments. Second, I shall discuss briefly the factors influencing the choice of the foods. I shall then discuss how the composition of the various foods, when considered against the nutritional needs of humans, imposes constraints on dietary selection.

This analysis raises some hypotheses regarding the evolution of the determinants of food choice.

## 2. THE FOODS AVAILABLE: THEIR COMPOSITION AND OTHER ATTRIBUTES

It is reasonable to assume that the types of foods eaten by modern higher primates provide a starting point for considering the foods eaten by early human populations, although one must also recognize that primate societies have also developed and their eating patterns may have developed alongside other changes (Jolly 1985). These, taken with the range of foods eaten by present-day hunter–gatherers, provide the basis for this analysis.

### (*a*) *Plant foods*

A wide range of plant foods is consumed including most parts of the plant, such as fruits, seeds, leaves, roots and tubers. Studies of many present hunter–gatherers show that the numbers of plant species

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Table 1. *Compositional features of plant foods/grams per 100 g edible matter*

| | fruits | nuts | seeds | seed legumes | leafy vegetables | roots and tubers |
|---|---|---|---|---|---|---|
| water | 61.0–89.1 | 4.5–51.7 | 12–15 | 74.6–80.3 | 84.3–94.7 | 62.3–94.6 |
| protein | 0.3–1.1 | 2.0–24.3 | 8.4–13.6 | 5.7–6.9 | 0.2–3.9 | 0.1–4.9 |
| fat | trace–4.4 | 2.7–64.0 | 1.5–5.4 | 1.0–15 | 0.2–1.4 | 0.1–0.4 |
| sugar | 4.4–34.8 | 3.2–7.0 | traces | 1.8–3.2 | 1.5–4.9 | 0.5–9.5 |
| starch | trace–3.0 | 1.8–29.6 | 72.9–73.9 | 5.4–8.1 | 0.1–0.8 | 11.8–31.4 |
| dietary fibre (plant cell wall) | 2.0–14.8 | 5.7–14.3 | 4.0–12.0 | 4.5–4.7 | 1.2–4.0 | 1.1–9.5 |
| energy/kJ | 90–646 | 720–2545 | 1356–1574 | 247–348 | 65–177 | 297–525 |
| energy/kcal | 22–155 | 170–639 | 324–376 | 59–83 | 24–43 | 71–138 |
| micronutrients | vitamin C<br>carotenoids<br>K, Mg | B-vitamins<br>vitamin E<br>K, Mg, P, Fe | B-vitamins<br>vitamin E<br>K, Mg, P, Fe | B-vitamins<br>vitamin C<br>K, Mg, P, Fe | vitamin C, folates<br>carotenoids<br>Ca, Fe | vitamin E<br>carotenoids<br>Fe, K, Ca |
| toxic constituents | cyanogenetic glycosides in seeds | — | — | haemoagglutonins, anti, tryptic, lectins | glucosinolates | glycoalkaloids |

Sources: Paul & Southgate (1978); Brand *et al.* (1983); Brand *et al.* (1985); Kuhnlein, (1989; 1990); Woodburn & Southgate (unpublished data).

collected is high: Gonzalez (1972), in studies of North American Indians, found that more than 400 species were collected, and of these 130 were consumed as foods. The remainder were collected for their herbal properties in relation to medicinal or ritual use. The nutritional compositions of the different plant organs are distinctive and need to be considered separately.

(*i*) *Fruits.* Some of the key compositional features of a range of fruits are given in table 1. Characteristically fruits have a high water content, and contain low levels of protein and fat; the protein, moreover, is often concentrated within the seeds, which are usually lignified and therefore resistant to both digestion in the small intestine and bacterial degradation in the large intestine, and is therefore unavailable to the body. The major nutrients provided by fruits are carbohydrates; fruits characteristically contain fructose, glucose and sucrose, but usually little or no starch when mature. The other carbohydrates present are derived from the plant cell walls, and these are usually parenchymatous, relatively undifferentiated structures (Selvendran 1984). As such they are rich in soluble polysaccharides (pectic substances) and are readily degraded by the microflora of the large intestine (Cummings *et al.* 1979). Fruits, therefore, contribute metabolizable energy as carbohydrate from the sugars, and small amounts of energy as free fatty acids from the cell wall materials degraded in the large bowel. They are also important sources of essential micronutrients, especially vitamin C and carotenoids (provitamin A).

Fruits, as foodstuffs, are available for a limited time, and when ripe, and most acceptable, are sometimes difficult to collect and transport. Many fruits, therefore, are best consumed at the time and place they are picked, whereas others lend themselves to being gathered in the strict sense. When ripe they have a short period of acceptability before senescence intervenes.

(*ii*) *Nuts and seeds.* Nuts and seeds, especially the former, are important in the diet of primates and present hunter–gatherers (Brand *et al.* 1985). Their compositional features are given in table 1. These foods are characterized by having thickened, usually lignified, outer seed coats. Many seeds have less rigid testae that contain high levels of polyphenolic materials such as tannins. These protect the seed from desiccation and, more importantly, from fungal and insect damage: they also protect the seed from bacterial degradation in the rumen and large bowel of animals consuming them. Compositionally seeds are rich in protein in the embryo, and contain a store of either lipids or polysaccharides (which may include starch) which serves as an energy source for the germinating plant. The plant cell wall material of seeds includes thin-walled structures in the endosperm or cotyledons and thicker lignified outer coats. Seeds form the most energy- and protein-rich plant foods.

Seeds have much lower water content than all other plant foods, and are therefore stable and easily gathered, transported and stored.

The most important seeds consumed in the present human diet are those of the cereals. It is possible that grains of wild cereals were part of the diet of early humans but it is reasonable to assume (Eaton & Konner 1985) that cereals only began to be significant in the human diet within the last 9000 years with the development of agriculture.

The seeds of the Leguminosea form a distinct group compositionally; they may be eaten as mature seeds, sharing many of the characteristics of other seeds: that is, being rich in protein and either lipids or polysaccharides with a high nutrient density. They may also be consumed immature with the seed pod when the nutrient densities are correspondingly lower. However, many legumes contain toxic plant metabolites, haemoglutenins, saponins and lectins, and some of them are very toxic indeed (Liener 1969; Silverstone 1985). The wider use of these very nutritious foods would only have become possible when foods began to be cooked in water, so that they would only have become significant in the human diet relatively late (Stahl 1984). To use the nuts and seeds as foodstuffs, the outer shells or coats must be broken and this would have marked the first type of food processing. Without this treatment the nutrients would not become available. Additionally the seed husks that are rich in polyphenolic materials impart a bitter taste to the broken seed, so some type of winnowing would be required. Mature cereal grains from wild cereals are virtually indigestible unless the grain is cracked or soaked in water, and maximum nutritional value requires reduction of particle size by grinding; the value of cereals would therefore be limited until simple querns were developed.

(*iii*) *Leaves and stems*. These are widely consumed, especially the emerging buds, by many primates, and leafy plants are widely consumed by humans. Table 1 summarizes the main compositional features of these structures. The protein contents are higher than fruits, and they contain lower amounts of sugars. Some leaves contain small amounts of starch but the plant cell walls are the major polysaccharides present; these are similar to those found in fruits. Leaves, however, are often characterized by having cutinized epidermal layers which restrict the degradation of the polysaccharides by the intestinal flora. The effective extraction of the soluble contents of the leaves and stems also requires extensive mechanical disruption of the cellular structures (Pirie 1973) which would not be achievable with human dentition. The maximal nutritional use of leaves as a source of protein requires either the assistance of a microflora such as that present in the rumen of ruminant animals or the stomachs of the leaf-eating monkeys. The range of micronutrients present include vitamin C, folates and carotenoids, as well as iron and calcium.

Young leaves lend themselves to consumption at the time of gathering. Both leaves and stems are bulky material to transport and are not very stable when stored.

Many plants produce secondary metabolites that have bitter or astringent properties, and many produce toxic alkaloidal and other compounds such as haemoglutenins. Others produce intestinal enzyme inhibitors and compounds, such as lectins, which bind to the mucosal surfaces and inhibit digestion, especially of proteins (Leiner 1969). These natural toxicants would, firstly, make many plants unattractive as foods from a sensory point of view and, secondly, often produce profound intestinal discomfort when eaten. Present day hunter–gatherers recognize these unattractive and toxic foods and may collect them for use as herbal medicines or as sources of poisons for use in hunting or fishing. Until fire was discovered and foods were heated, a process which inactivates or destroys many of these components, the use of many leaves would have been limited (Stahl 1984).

(*iv*) *Roots and tubers*. These are important in the diet of many present hunter–gatherers. The composition of roots and tubers is given in table 1. Many tubers and some roots contain significant amounts of starch. Roots tend to contain more sugar than starch, and the major sugar is often sucrose. The plant cell walls are undifferentiated and rich in soluble polysaccharides. Vitamin levels are lower than in the aerial parts of plants. Some roots such as cassava (manioc) contain toxic secondary metabolites and require soaking in water before they are safe to consume. As foodstuffs roots, and especially tubers, can be time-consuming to collect but they are often protected from desiccation and fungal damage by external suberinized layers, and so can be stored for long periods.

(*v*) *Fungi*. Some fungi are highly valued as foods by present hunter–gatherers; many, however, are extremely toxic, and societies that consume fungi have learned to avoid the more toxic varieties or to restrict their use to medicinal or ritual purposes.

### (*b*) *Foods of animal origin*

By analogy with the behaviour of non-human primates it is probable that foods of animal origin were widely consumed. The activities involved in collecting plant foods would lead to the opportunist taking of a wide range of animals; insects and their grubs, for example, are eaten by many communities. Honey is a highly prized food in many hunter–gatherer societies. It provides the sweetest food that is available to hunter–gatherers; it is a seasonal crop and the harvests are associated with festivals. The yields from a nest range from 1 to 30 kg, and the honey frequently contains dead bees and grubs (E. V. Crane, personal communication).

Eggs and fledgling birds would also be found during the collection of plant foods, as would reptiles such as lizards, although the consumption of snakes appears less likely. Communities close to water would also find a wide range of molluscs and Crustacea which could be harvested readily. The shell middens associated with many human sites show that molluscs were extensively consumed (Schrire 1984). These animal foods could be obtained without the need for weapons or tools, and may have been eaten very early in human evolution. One can also speculate that the young of many small animals, for example rodents, would be found during searching for tubers, and these can be skinned using the hands alone, as can young birds.

Large animals would have required the development of organized hunting, initially using trapping methods with pits or by driving animals towards cliffs or ravines. Tools for skinning these animals and for butchering carcasses into suitable joints for transport would have been a pre-requisite for these foods being available. The development of weapons for killing at a distance would have made hunting less hazardous and more effective. Chimpanzees exhibit effective organized hunting skills involving driving animals towards flanking and stopping members of the troop, and it is reasonable to assume that similar skills were developed early in human evolution.

Communities near water developed analogous skills in catching fish and other aquatic animals. In considering the composition of these foods it is convenient to consider them in four major categories: invertebrates; amphibians, reptiles, eggs and birds; fish; and mammals.

(*i*) *Invertebrates*. These include insects, both mature and as grubs, Crustacea and molluscs (table 2). These

Table 2. *Composition of invertebrates/grams per 100 g*

| | insects | | | |
|---|---|---|---|---|
| | grubs | mature | molluscs[a] | Crustacea[a] |
| water | 36.6–66.6 | 35.2–62.2 | 75.8–84.6 | 76.8–82.0 |
| protein | 8.7–18.6 | 20.5–26.8 | 8.4–18.7 | 14.6–18.1 |
| fat | 13.2–37.5 | 3.8–38.8 | 0.2–2.2 | 0.5–2.0 |
| carbohydrates[b] | 6.9–16.0 | 1.4–5.5 | traces | traces |
| energy/kJ | 833–1760 | 715–1912 | 289–410 | 285–418 |
| energy/kcal | 199–420 | 170–457 | 69–98 | 69–100 |
| micronutrients | B-vitamins K, Mg, Ca, Fe, Zn | B-vitamins Fe, Zn | B-vitamins ($B_{12}$) vitamin E Fe, Zn | B-vitamins Ca, Mg, P, Fe, Zn |

[a] Edible matter only.
[b] These are principally chitins from exoskeleton.
Source: Cherikoff *et al.* (1985); Wu Leung (1968); Paul & Southgate (1978).

Table 3. *Composition of amphibians, birds and eggs/grams per 100 g edible matter*

| | frog[a] | lizard[a] | snake[a] | turtle[a] | young birds | eggs[b] |
|---|---|---|---|---|---|---|
| water | 83.6 | 58.8–73.2 | 75.0 | 71.7–80.9 | 66.2–68.2 | 70.4–79.8 |
| protein | 15.3 | 24.6–31.6 | 14.4 | 17.5–25.4 | 20.2–23.7 | 10.7–13.9 |
| fat | 0.3 | 1.2–11.3 | 3.3 | 0.2–1.5 | 8.5–9.6 | 7.0–14.2 |
| carbohydrate | trace | trace | trace | traces | traces | traces |
| energy kJ | 285 | 472–906 | 393 | 343–469 | 742–749 | 485–787 |
| energy kcal | 68 | 113–217 | 94 | 82–112 | 175–179 | 116–188 |
| micronutrients | B-vitamins P, Fe, Zn | B-vitamins P, Fe, Zn | B-vitamins P, Fe, Zn | B-vitamins P, Fe, Zn | B-vitamins ($B_{12}$) Fe, Zn | B-vitamins retinol Ca, Fe, Zn |

[a] These animals have fat depots as isolated organs which contain 40–60% fat.
[b] Reptile eggs are similar in composition.
Source: Cherikoff *et al.* (1985); Wu Leung (1968).

Table 4. *Composition of some mammalian sources/g per 100 g edible meat*

| | rabbit | squirrel | pig[a] | horse | buffalo | heart | kidney | liver |
|---|---|---|---|---|---|---|---|---|
| water | 74.3 | 72.2 | — | 70.0 | 76.5 | 73.6–79.2 | 78.8–79.8 | 67.3–72.9 |
| protein | 16.9 | 26.3 | 10–14.0 | 19.0 | 17.7 | 15.2–17.1 | 15.7–17.1 | 19.1–21.3 |
| fat | 7.9[b] | 0.4[b] | 35.0–55.0 | 10.0[b] | 4.9[b] | 2.6–9.3 | 2.6–2.7 | 6.3–10.3 |
| carbohydrate | — | trace | trace | glycogen | — | — | — | glycogen in fresh |
| energy kJ | 594 | 460 | 1550–2240 | 713 | 502 | 363–629 | 363–380 | 567–683 |
| energy kcal | 142 | 110 | 371–535 | 170 | 120 | 86–150 | 86–150 | 153–179 |
| micronutrients | B vitamins $B_{12}$ retinol Ca, Fe, Zn | B vitamins $B_{12}$ retinol Ca, Fe, Zn | B vitamins $B_{12}$ retinol Ca, Fe, Zn | B vitamins $B_{12}$ retinol Ca, Fe, Zn | B vitamins $B_{12}$ retinol Ca, Fe, Zn | B vitamins $B_{12}$ retinol Ca, Fe, Zn | B vitamins $B_{12}$ retinol Ca, Fe, Zn | B vitamins $B_{12}$ retinol Ca, Fe, Zn |

[a] Whole carcass.
[b] Fat associated with muscle. Fat deposits would also be present.

foods are characteristically rich sources of protein, although they have a high moisture content; some insect grubs are rich sources of fat but in the other invertebrates fat contents are low. They are relatively small animals, and the insects were probably eaten when taken; the other invertebrates would be reasonably easy to collect.

(*ii*) *Amphibians, reptiles, eggs and birds* (see table 3). The smaller amphibians and reptiles share many of the compositional characteristics of the invertebrates: high water content, with modest protein and low fat levels. Eggs, however, are relatively rich sources of both protein and fats. Eggs of all species are good sources of micronutrients, especially the fat-soluble vitamin A (retinol). Young birds, especially just before they start to fly, have substantial fat stores, and many present-day communities with access to large nesting colonies harvest the young birds and render them to produce fats (Chambers & Southgate 1969).

(*iii*) *Mammals*. The carcass of an animal provides a wide range of types of food. In bulk terms the musculature is the major part, providing meat and some fat. Most wild animals have a lower total carcass fat than domesticated species, and the fats tend to be less saturated even in the ruminant animals (Crawford 1968; Talbot 1964). There is less 'marbling' of fats within the muscles, fat storage being subcutaneous, mesenteric and perirenal. Organs, especially liver, kidney and heart, are rich sources of protein and many micronutrients. Bones, in addition to providing material for tools and ornaments, contain in their marrow a rich source of protein, fat and iron. Typical values are given in table 4.

(*iv*) *Fish*. The fishes forming part of the diet of early man would have been primarily freshwater or estuarine species, and may have included both fatty and non-fatty white fish. Fish are characteristically rich sources of protein, and the fatty fish, such as salmonoids returning to fresh waters to spawn, are rich in fats and the fat-soluble vitamins.

Before concluding this section it is important to recognize one major animal food that would have been part of the natural diet of virtually all humans, that is breast milk. The milk of all species is highly characteristic, and human milk is no exception. It has a low protein content, and fat provides around 50% of the total energy. All milks contain the sugar lactose, and it is almost certain that this sugar would only have been present in the diet of early humans during the suckling period, which may have been in excess of two years.

## 3. THE DETERMINANTS OF FOOD CHOICE

It is important to consider briefly some of the factors that would have acted as the major determinants of food choice from the range of foods in the natural environment.

### (*a*) *Availability*

This would have been a very important factor; even in the tropical and sub-tropical regions many foods are only available for consumption at certain times during the year. The gathering of sufficient amounts of plant foods involves travelling over considerable distances, and so the size of the range and its productivity determine food availability. The pattern of consumption of plant and animal foods in some existing hunter–gatherers is very closely determined (Coles–Rutishauser 1986) and seasonal variations in the types and amounts of foods consumed must have been a common feature of life.

### (*b*) *Sensory preferences*

The primary senses have a major role in the selection of foods, and the use of visual appearance is a key factor in identifying fruits at the desired stage of maturity and selecting the youngest and most tender shoots. The learned associations between appearances and unpleasant tastes or after-effects of eating plant foods or insects and other animals are very important. Thus the preference for sweet tastes, which appears to be instinctive (Steiner 1987), and the avoidance of bitter tastes would protect against the consumption of plant foods containing toxic alkaloids, or other bitter plant constituents. Sensory factors would therefore be very important in avoiding potentially dangerous foods. Learned associations between the unpleasant effects of consuming toxic or microbiologically contaminated foods would have been important for human survival (Garcia *et al.* 1974).

### (*c*) *Satiety*

This is the power of foods to assuage hunger or the desire to eat. Although the mechanisms involved are unclear, there are strong physiological arguments for evoking a cascade of effects: a short term one that induces the response to stop feeding, a satiating effect and satiety, a long term one that prolongs the interval between periods of consuming food. The latter is strongly influenced by the fat content of a meal, and thus a learned association of fatty foods in delaying the need to seek more foods is possible (Rogers & Blundell 1990).

### (*d*) *Social transmission*

Many of the learned associations between the consumption of certain foods are transferred by social interactions, especially during childhood when an infant's early exploration of the environment by oral means leads to training in which materials are acceptable as foods. In hunter–gatherer societies the children are exposed to the norms of that society very early in life.

Many of these societal norms develop into a complex set of food taboos and religious food laws which serve to protect the society from food-borne disease (Fieldhouse 1986). The food taboos may also restrict the exploitation of an available food resource, and introduce conservative food behaviours that may be detrimental, for example the avoidance of fish in some communities, and the prohibition of women eating eggs in others.

Food choice is an integration of psychosocial and biological influences (Rogers & Blundell 1990) and factors discussed up to now have not included the physiological determinants of food choice; early human societies had to select a diet which satisfied nutritional requirements.

## 4. SELECTION OF DIETARY MIXTURES TO MEET NUTRITIONAL REQUIREMENTS

In this section I shall discuss how the foods available to early human societies could be combined to meet their nutritional requirements. It is clear that suitably nutritious combinations were achieved but there has been substantial debate about the type of diet eaten during early human evolution (Eaton & Konner 1985). Others have argued for the benefits of the natural diet in relation to the effects of present-day 'unnatural' diets on the incidence of chronic disease (National Research Council 1989*a*). The argument revolves around the thesis that humans evolved under the influence of this natural diet and are therefore adapted to it.

Before we consider how the available foods could be combined to meet nutritional requirements it is

Table 5. *Estimates of energy requirements*

| | | | | |
|---|---|---|---|---|
| male | body mass 65 kg; height 1.72 m estimated basal metabolic rate (BMR) 284 kJ or 68 kcal $h^{-1}$. | | | |
| activity | | time h | kJ | kcal |
| sleeping at 1 × BMR | | 8 | 2272 | 544 |
| hunting at 3.6 × BMR[a] | | 8 | 8179 | 1954 |
| sitting resting 1.4 × BMR | | 4 | 1590 | 381 |
| sitting working 2.1 × BMR[b] | | 4 | 2386 | 571 |
| | total for 24 h: | | 14427 | 3454 |
| female | body mass 50 kg; height 1.60 m estimated BMR 220 kJ or 53 kcal $h^{-1}$. | | | |
| activity | | time h | kJ | kcal |
| sleeping at 1 × BMR | | 8 | 1760 | 424 |
| gathering food and water[c] at 3.4 × BMR[c] | | 6 | 4488 | 1081 |
| preparing food 2.7 × BMR | | 2 | 1188 | 286 |
| other activities 2.0 × BMR | | 8 | 3520 | 848 |
| | total for 24 h | | 10956 | 2639 |

[a] Hunting pig.
[b] Carving weapons.
[c] Walking at normal pace.

important to establish estimates of physiological requirements. These are different from current dietary recommendations, for example the Recommended Dietary Allowances (RDA) issued by the National Research Council of the U.S.A. (National Research Council 1989*b*) and other official bodies, which include safety factors to meet the needs of the majority of the population.

The primary nutritional requirement for any human population is to satisfy energy needs as the proper utilization of other nutrients is dependent on adequate energy metabolism.

It is important to note that the primary physiological requirement, that of an adequate and regular supply of water, must also be met. Many present hunter–gatherers live in habitats where water is scarce and where the primary drive for survival is the securing of water. One imagines that before agricultural development the choice of habitat was less restricted, and settlement near water fulfilled this requirement and contributed to the food supply incidentally.

### (*a*) *Energy requirements*

The estimation of energy requirements demands assumptions about body size and physical activity. By using the equations suggested by the Food and Agriculture Organisation, World Health Organisations and the United Nations University (1985) for estimating resting metabolic rates and the expenditures on hunting and gathering activities for males and females respectively, it is possible to arrive at reasonable estimates for use in constructing models for diet selection (see table 5).

These provide a basis for estimating the amounts of

Table 6. *Approximate weight of foods required to meet energy requirements*[a] *and protein supplied by that mass*

| food | typical energy density/MJ $kg^{-1}$ | mass to satisfy energy requirement/kg | typical protein content/g per kg | protein supplied/g |
|---|---|---|---|---|
| plant foods | — | — | — | — |
| fruits | 3.68 | 3.4 | 7 | 24 |
| nuts | 16.33 | 0.77 | 132 | 101 |
| seeds | 14.65 | 0.85 | 110 | 94 |
| seed legumes | 2.97 | 4.21 | 63 | 265 |
| leaves | 1.21 | 10.3 | 21 | 217 |
| roots and tubers | 4.11 | 3.0 | 25 | 76 |
| animal foods | | | | |
| invertebrates | | | | |
| insect grubs | 12.9 | 0.97 | 137 | 132 |
| insects | 13.1 | 0.95 | 237 | 226 |
| molluscs | 3.49 | 3.6 | 136 | 487 |
| crustacea | 3.52 | 3.6 | 164 | 582 |
| vertebrates | — | — | — | — |
| frog | 2.85 | 4.4 | 153 | 671 |
| lizard | 6.89 | 1.8 | 275 | 499 |
| snake | 3.13 | 4.0 | 144 | 575 |
| turtle | 4.06 | 3.1 | 214 | 217 |
| young birds | 7.40 | 1.69 | 219 | 370 |
| eggs | 6.36 | 1.97 | 123 | 241 |
| fish | | | | |
| fatty fish | 7.16 | 1.75 | 177 | 309 |
| white fish | 4.12 | 3.03 | 176 | 534 |
| mammals | | | | |
| rabbit | 5.94 | 2.10 | 169 | 355 |
| squirrel | 4.60 | 2.71 | 263 | 715 |
| pig | 18.95 | 0.66 | 120 | 79 |
| horse | 7.13 | 1.75 | 190 | 333 |
| buffalo | 5.02 | 2.49 | 177 | 441 |

[a] This has been taken as 12.5 MJ per day per adult.

the different foods that would be required (see table 6). The calculations make no allowance for the amount of actual live weights of animals that would need to be caught.

A diet of leafy plant foods would require the greatest mass of food, and the amount of plant material (over 10 kg) is such that the bulk would be excessive both to gather and to consume. The advantages of nuts and seeds in terms of amounts to be collected are clear. The protein provided by the fruits is inadequate, and that by roots and tubers only marginally adequate.

The most effective food selection in terms of amounts therefore requires a proportion of animal foods, especially those that contain fat (Hayden 1981). These have several advantages; firstly, in the amounts required; secondly, as sources of substantial amounts of protein of high biological value, free from natural toxicants; thirdly, as sources of essential inorganic nutrients; fourthly, as sources of the B-vitamins, especially B12 and, very importantly, as a source of vitamin A and the other fat-soluble vitamins. Although the carotenoids can act as provitamin A these require an adequate fat intake for absorption.

### (*b*) *Protein and other nutrients*

All the available foods, with the exception of fruits, would supply adequate protein and, provided energy needs were being met, protein supply would not be limiting. Effective food strategies in selecting a mixture of plant and animal foods would ensure that the biological quality of the protein would be satisfactory (FAO, WHO, UNU 1985).

All the foods that contain fat would provide essential fatty acids at levels above requirements, and the meats and fish would provide long-chain polyunsaturated fatty acids of the $n$-3 series (Paul & Southgate 1978).

The supply of inorganic nutrients from the plant foods alone would be marginally adequate, and the animal foods are important as sources of iron and zinc in biologically available forms. In the absence of dairy foods, calcium intakes would be low by western standards but biological adaptations to low calcium intakes are well documented, and exposure to sunlight would maintain high vitamin D status and maximize the efficiency of calcium utilization.

The supply of water-soluble vitamins, especially vitamin C and folates, from diets with a large amount of fresh plant foods would be more than adequate. The supply of fat-soluble vitamin A depends on animal sources, as does vitamin B12, and these provide circumstantial evidence for the role of animal foods in the early human diet. The animal foods available opportunistically are important potential sources of fat and micronutrients, and the importance of insects is very evident.

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### *Discussion*

K. Hawkes (*Department of Anthropology, University of Utah, Salt Lake City, U.S.A.*). In the list of determinants of diet choice Professor Southgate did not include acquisition costs, something apart from availability. Some potential foods may be quite abundant in the environment of human foragers, and may even have quite high nutrient per unit mass values, yet be very costly to process. One view of the 'mesolithic transition' that happened in many places about 8000–18000 years ago emphasizes the incorporation of previously unexploited 'high cost' resources – like grass and tree seeds – into the diet as more profitable alternatives became increasingly scarce. These processing costs seem to play an important role in diet choice among contemporary human foragers; would Professor Southgate not expect this to be quite general?

D. A. T. Southgate. Yes, I was alluding to this in relation to the productivity of the food ranging area; clearly some foods would require considerable effort to collect. However, I suspect that sensory or satiety factors would still be more dominant in choice; satiety value is closely linked to energy density so that these factors are linked.

O. T. Oftedal (*Smithsonian Institution, Washington D.C., U.S.A.*). As, in most cases, animals cannot directly sense nutrients and must base their food preferences on sensory perceptions, and as animals in different environments must be faced with divergent sensory characteristics of foods, does Professor Southgate not think that evolutionary pressures may have moulded the perceptual abilities and preferences of different species in different ways? Is there evidence of differences in sensory abilities and preferences among different species?

D. A. T. Southgate. Quite clearly this is so, but I do not think that the basis of the differences in sensory preferences is understood. They may relate to differences in the metabolic processing of food constituents.

O. T. Oftedal. Professor Southgate mentioned that vitamin $B_{12}$ must come from animal foods and yet clearly some primates eat little if any animal foods in the wild. Does he think microbial contamination or microbial activity on plant products could supply adequate vitamin $B_{12}$?

D. A. T. Southgate. It is possible that some humans obtain vitamin $B_{12}$ from microbial contamination of foods or the environment, but I suspect that the small amounts of animal foods consumed by primates when foraging on leaves and fruits could also provide a source of vitamin $B_{12}$. Many reports of vitamin $B_{12}$ in plants have resulted from contamination or analytical artifacts.

I. Crowe (*23 Lockhart Close, Dunstable, Bedfordshire, U.K.*). I believe that one of the factors affecting the choice of foods is visual information – to locate, identify, and to determine suitability – learnt by example, with colour vision being a prime factor: a characteristic of primate vision shared by the birds who originally exploited the same food resources, i.e. fruit.

D. A. T. Southgate. I agree: detection of fruits or leaves at the desired maturity would depend greatly on colour discrimination.





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