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ORIGINAL COMMUNICATION

The paradoxical nature of hunter-gatherer diets: meat-based, yet non-atherogenic

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Objective: Field studies of twentieth century hunter-gathers (HG) showed them to be generally free of the signs and symptoms of cardiovascular disease (CVD). Consequently, the characterization of HG diets may have important implications in designing therapeutic diets that reduce the risk for CVD in Westernized societies. Based upon limited ethnographic data ($n=58$ HG societies) and a single quantitative dietary study, it has been commonly inferred that gathered plant foods provided the dominant energy source in HG diets.
Method and Results: In this review we have analyzed the 13 known quantitative dietary studies of HG and demonstrate that animal food actually provided the dominant (65%) energy source, while gathered plant foods comprised the remainder (35%). This data is consistent with a more recent, comprehensive review of the entire ethnographic data ($n=229$ HG societies) that showed the mean subsistence dependence upon gathered plant foods was 32%, whereas it was 68% for animal foods. Other evidence, including isotopic analyses of Paleolithic hominid collagen tissue, reductions in hominid gut size, low activity levels of certain enzymes, and optimal foraging data all point toward a long history of meat-based diets in our species. Because increasing meat consumption in Western diets is frequently associated with increased risk for CVD mortality, it is seemingly paradoxical that HG societies, who consume the majority of their energy from animal food, have been shown to be relatively free of the signs and symptoms of CVD.
Conclusion: The high reliance upon animal-based foods would not have necessarily elicited unfavorable blood lipid profiles because of the hypolipidemic effects of high dietary protein (19–35% energy) and the relatively low level of dietary carbohydrate (22–40% energy). Although fat intake (28–58% energy) would have been similar to or higher than that found in Western diets, it is likely that important qualitative differences in fat intake, including relatively high levels of MUFA and PUFA and a lower ω-6/ω-3 fatty acid ratio, would have served to inhibit the development of CVD. Other dietary characteristics including high intakes of antioxidants, fiber, vitamins and phytochemicals along with a low salt intake may have operated synergistically with lifestyle characteristics (more exercise, less stress and no smoking) to further deter the development of CVD.

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Introduction

In the past decade there has been increasing awareness in the medical and nutritional communities that insight can be gained into potentially therapeutic and healthful diets by examining the nutritional patterns of less Westernized cultures. Field studies carried out in the early and mid-twentieth century of the few remaining hunter-gatherer societies showed them to be generally free of the signs and symptoms of cardiovascular disease (CVD), and other so-called diseases of civilization (Eaton *et al*, 1988a). Although the nutritional patterns of contemporary hunter-gatherers probably would not have been identical to hominids living during the Paleolithic period, these diets represent a likely surrogate of the range and quantity of wild/minimally processed foods that would have embodied humanity's original or native diet. Consequently, the characterization and description of hunter-gatherer diets may have important implications in

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designing therapeutic diets that reduce the risk for CVD in modern, Western cultures.

Ethnographic and anthropological studies of hunter-gatherers carried out in the nineteenth and twentieth centuries clearly revealed that no single, uniform diet would have typified the nutritional patterns of all pre-agricultural human populations. However, based upon a single quantitative dietary study of hunter-gatherers in Africa (Lee, 1968) and a compilation of limited ethnographic studies of hunter-gatherers (Lee, 1968), many anthropologists and others inferred that, with few exceptions, a near-universal pattern of subsistence prevailed in which gathered plant foods would have formed the majority (> 50%) of food energy consumed (Beckerman, 2000; Dahlberg, 1981; Eaton & Konner, 1985; Lee, 1968; Milton, 2000; Nestle, 1999; Zihlman, 1981). More recent, comprehensive ethnographic compilations of hunter-gatherer diets (Cordain *et al*, 2000a), as well as quantitative dietary analyses in multiple foraging populations (Kaplan *et al*, 2000; Leonard *et al*, 1994), have been unable to confirm the inferences of these earlier studies, and in fact have demonstrated that animal foods actually comprised the majority of energy in the typical hunter-gatherer diet.

In Western diets, increasing meat consumption (particularly red and processed meat) has been frequently shown in epidemiologic studies to be positively correlated with CVD mortality (Hu *et al*, 1999, 2000; Menotti *et al*, 1999). Additionally, meats contribute the highest percentage (27%) of total fat for all food groups to the US diet as well as the highest percentage (28%) of saturated fat (Popkin *et al*, 2001). Hence, a high meat diet regardless of its fat quantity and type is generally perceived to be unhealthy and to promote cardiovascular and other chronic diseases (Barnard *et al*, 1995). In this paper, we provide further evidence substantiating the dominant role of animal foods in hunter-gatherer diets and show how these nutritional patterns do not necessarily promote atherosclerosis and CVD.

Historical and ethnographic perspectives on Pre-agricultural diets

Early theories on the natural or native human diet viewed Paleolithic hominids as adept hunters of big game whose diets were primarily carnivorous in nature (Ardrey, 1961; Dart, 1957; Washburn & Lancaster, 1968). However by the late 1960s and early 1970s, this 'Man the Hunter' explanation was soundly contested by Richard Lee and others because of certain evidence that suggested most contemporary hunter-gatherer populations consumed more gathered

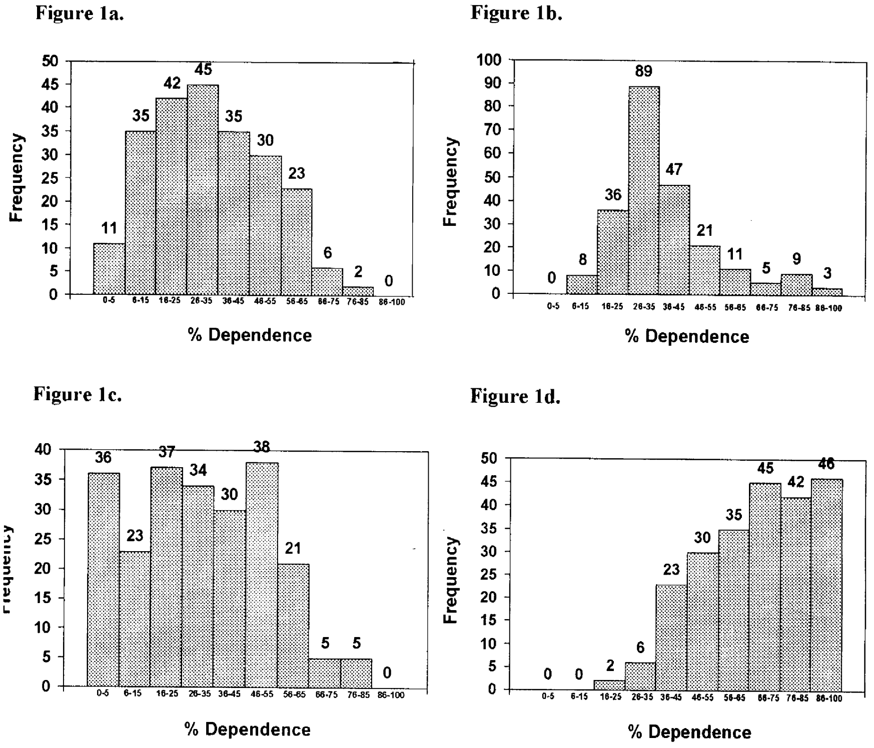
Figure 1a. **Figure 1b.** **Figure 1c.** **Figure 1d.**

Figure 1 Frequency distributions of subsistence dependence of: (a) gathered plant foods (median = 26–35%, mode = 26–35%); (b) hunted animal foods (median = 26–35%, mode = 26–35%); (c) fished animal foods (median = 26–35%, mode = 46–55%); and (d) fished + hunted animal foods (median = 66–75%, mode = 86–100%) in worldwide hunter-gatherer societies ($n = 229$).

plant food than hunted animal food (Lee, 1968). Lee's studies of the African !Kung people demonstrated that gathered plant foods comprised 67% of their average daily sustenance while hunted animal foods encompassed the remaining 33% (Lee, 1968). Lee (1968) further compiled data from 58 hunter-gatherer societies listed in the *Ethnographic Atlas* (Murdock, 1967) and showed that the mean, median and mode for hunted animal food, 'all converge on a figure of 35% for hunter gatherers at all latitudes'.

Lee's (1968) analysis was widely misinterpreted over the next 32 y to mean that gathered plant foods typically provided the major food energy (65%) in worldwide hunter-gatherer diets, while hunted animal foods made up the balance (35%; Beckerman, 2000; Dahlberg, 1981; Eaton & Konner, 1985; Milton, 2000; Nestle, 1999; Zihlman, 1981). As we have previously pointed out (Cordain *et al*, 2000a, b), this general perception is incorrect because fished animal foods must be summed with hunted animal foods in the analysis of the ethnographic data to more correctly evaluate dietary plant to animal subsistence ratios (ie the percentage of energy contributed by plants *vs* animal foods). Our analysis (Figure 1) of the *Ethnographic Atlas* data (Gray, 1999) showed that the dominant foods in the majority of 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 66–75%. In contrast, the median subsistence dependence upon gathered plant foods was 26–35%. Further, we re-analyzed Lee's original subsample ($n=58$) of the *Ethnographic Atlas* and obtained results almost identical to those of our study of the entire 229 hunter-gatherer societies (Cordain *et al*, 2000b). The subsistence dependence upon hunted and fished animal foods was 66–75% (median value), whereas the median value for gathered plant foods was 26–35%.

Quantitative studies of hunter-gatherer diets

The major limitation of ethnographic data is that the preponderance of it is subjective in nature, and Murdock's assigned scores for the five basic subsistence economies in the *Ethnographic Atlas* are not precise, but rather are approximations (Hayden, 1981; Keeley, 1992). Fortunately, more exact, quantitative dietary studies were carried out on a small percentage of the world's hunter-gatherer societies. Table 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%. These values are similar to our analysis of the entire ($n=229$) sample of hunter-gatherer societies listed in the *Ethnographic Atlas* in which the mean score for animal food subsistence was 68% and that for plant food was 32%. When the two polar hunter-gatherer populations, who have no choice but to eat animal food because of the inaccessibility of plant foods, are excluded from Table 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 (56–65% for animal food; 36–45% for plant food) as those we estimated from the ethnographic data when the confounding influence of latitude was eliminated (Cordain *et al*, 2000a). Consequently, there is remarkably close agreement between the quantitative data in Table 1 and the ethnographic data.

Isotopic, anatomic and physiologic evidence for meat eating

Recent isotopic evidence from the skeletons of Neanderthals (Richards *et al*, 2000) and Paleolithic humans (Richards & Hedges 2000) suggests that the dominance of animal foods in the human diet was not simply a recent phenomenon limited to contemporary hunter-gatherers, but rather has a long history in the human lineage. These studies provide objective data showing that the diets of hominids living in Europe during the Paleolithic were indistinguishable from

Table 1 Quantitatively determined proportions of plant and animal food in hunter-gatherer diets. Adapted from Kaplan *et al* (2000)

Population	*Location*	*Latitude*	*Animal food (%)*	*Plant food (%)*	*Reference*
Aborigines (Arhem Land)	Australia	12S	77	23	McArthur (1960)
Ache	Paraguay	25S	78	22	Hill *et al* (1984)
Anbarra	Australia	12S	75	25	Meehan (1982)
Efe	Africa	2N	44	56	Dietz *et al* (1982)
Eskimo	Greenland	69N	96	4	Sinclair (1953); Krogh & Krogh (1913)
Gwi	Africa	23S	26	74	Silberbauer (1981); Tanaka (1980)
Hadza	Africa	3S	48	52	Blurton Jones *et al* (1997); Hawkes *et al* (1989)
Hiwi	Venezuela	6N	75	25	Hurtado & Hill (1986); Hurtado & Hill (1990)
!Kung	Africa	20S	33	67	Lee (1968)
!Kung	Africa	20S	68	32	Yellen (1977)
Nukak	Columbia	2N	41	59	Politis G (1996)
Nunamiut	Alaska	68N	99	1	Binford (1978)
Onge	Andaman Islands	12N	79	21	Rao *et al* (1989); Bose (1964)

top trophic level carnivores such as arctic foxes and wolves. Indeed, hominids may have experienced a number of genetic adaptations to animal-based diets early on in our genus's evolution analogous to those of obligate carnivores such as felines. Carnivorous diets reduce evolutionary selective pressures that act to maintain certain anatomical and physiological characteristics needed to process and metabolize high amounts of plant foods. In this regard, hominids, like felines, have experienced a reduction in gut size and metabolic activity along with a concurrent expansion of brain size and metabolic activity as they included more and more energy-dense animal food into their diets (Aiello & Wheeler, 1995; Cordain *et al*, 2001; Leonard & Robertson, 1994). Further, similar to obligate carnivores (Pawlosky *et al*, 1994), humans maintain an inefficient ability to chain elongate and desaturate 18 carbon fatty acids to their product 20 and 22 carbon fatty acids (Emken *et al*, 1992). Since 20 and 22 carbon fatty acids are essential cellular lipids, then evolutionary reductions in desaturase and elongase activity indicate that preformed dietary 20 and 22 carbon fatty acids (found only in animal foods) were increasingly incorporated *in lieu* of their endogenously synthesized counterparts derived from 18 carbon plant fatty acids. Finally, our species has a limited ability to synthesize taurine from precursor amino acids (Chesney *et al*, 1998; Sturman *et al*, 1975), and vegetarian diets in humans result in lowered plasma and urinary concentrations of taurine (Laidlaw *et al*, 1988). Like felines (Knopf *et al*, 1978; MacDonald *et al*, 1984), the need to endogenously synthesize taurine may have been evolutionarily reduced in humans because exogenous dietary sources of preformed taurine (found only in animal food), had relaxed the selective pressure formerly requiring the need to synthesize this semi-conditional amino acid.

Hunter-gatherer foraging strategies

Our analyses of both the ethnographic data (Cordain *et al*, 2000a) and the quantitative dietary data (Table 1) show that, even when plant food sources would have been available year round at lower latitudes, animal foods would have been the preferred energy source for the majority of worldwide hunter-gatherers. Only when it was ecologically difficult to procure animal food sources, and/or when energy-rich and easily obtainable plant foods such as the mongongo nut (in the case of the !Kung people studied by Lee, 1968) were available, did plant foods prevail in hunter-gatherer diets. Accordingly, the tissues of wild animals would have almost always represented the staple food for the world's contemporary hunter-gatherers.

Foraging humans are similar to other animals in natural settings in that they attempt to maximize the energy capture to energy expenditure ratio while hunting, fishing or collecting food (Hawkes *et al*, 1982; Kaplan & Hill, 1992; Winterhalder, 1981). Table 2 shows the energy return rates upon encounter for a variety of plant and animal foods that are known components of hunter-gatherer diets. The data in Table 2 are not all encompassing, however they do demonstrate that animal foods yield the highest energy return rates, and that larger animals generally produce greater energy return rates than smaller animals. Although the potential food mass would be similar between a single deer weighing 44.8 kg and 1600 mice weighing 28 g each, foraging humans would have to expend significantly more energy capturing the 1600 mice than a single deer. Hence, the killing of larger animals increases the energy capture/energy expenditure ratio because it reduces energy expenditure, but it also increases the total energy captured on a per weight basis because larger animal species generally contain more body fat than smaller species (Figure 2).

Table 2 Energy return rates upon encounter from foraged foods. Data adapted from (Hawkes *et al*, 1982; Lee, 1979; O'Connell & Hawkes, 1984; Simms, 1987)

Food	*Food type*	*Return rate (kcal/h)*
Collared peccary	Animal	65 000
Antelope, deer, bighorn sheep	Animal	16 000–32 000
Jack rabbits	Animal	13 500–15 400
Cottontail rabbits, gophers	Animal	9000–10 800
Paca	Animal	7000
Coati	Animal	7000
Squirrel (large)	Animal	5400–6300
Roots	Plant	1200–6300
Fruits	Plant	900–6000
Armadillo	Animal	5900
Snake	Animal	5900
Bird	Animal	4800
Seeds	Plant	500–4300
Lizard (large)	Animal	4200
Squirrel (small)	Animal	2800–3600
Honey	Plant	3300
Ducks	Animal	2000–2700
Insect larvae	Animal	1500–2400
Fish	Animal	2100
Palm heart	Plant	1500
Acorns	Plant	1500
Pine nuts	Plant	800–1400+
Mongongo nuts	Plant	1300
Grass seeds	Plant	100–1300

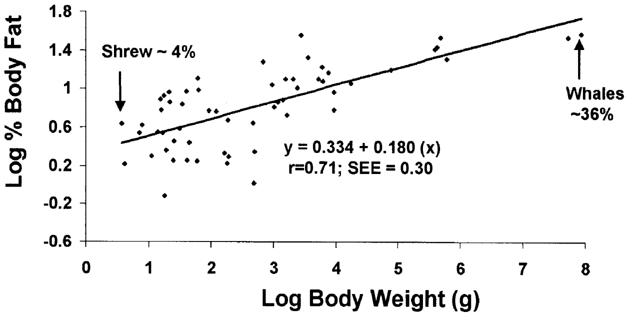

Figure 2 Regression of log body fat percentage to log body weight (g) in 49 mammalian species. Adapted from Pitts and Bullard (1968).

Due to the relative constancy of the protein content of an animal's fat-free body (Pace & Rathbun, 1945; Pitts & Bullard, 1968), the energy density of an edible carcass is almost entirely dependent upon varying amounts of body fat. In a likewise manner, varying amounts of body fat also exclusively determine the relative protein to fat energy ratio in an edible carcass (Cordain *et al*, 2000a). Because smaller animal species have less body fat than larger species, their carcasses contain relatively more protein as a percentage of their available food energy (Figure 3). The nature of this relationship is virtually identical among all vertebrates (Cordain *et al*, 2000a) and is exemplified by the cubic polynomial equation in Figure 4. Hunter-gatherers tended to shun very small animals or fat-depleted animals because of their excessive protein content (Noli & Avery, 1988; Speth & Spielmann, 1983; Speth, 1989), and numerous historical and ethnographic accounts have documented the adverse health effects that have occurred when people were forced to rely solely upon the fat depleted lean meat of wild animals (Speth & Spielmann, 1983). Excessive lean protein consumption without adequate fat or carbohydrate causes a condition referred to as 'rabbit starvation' by early American explorers that results in nausea, diarrhea and eventual death (Speth & Spielmann, 1983). Clinically, this syndrome probably results from the finite ability of the liver to up-regulate the rate-limiting enzymes of urea synthesis, thereby culminating in hyperammonemia and hyperaminoacidemia (Rudman *et al*, 1973). For a foraging human, the avoidance of the physiologic effects of excessive dietary protein was an important factor in shaping their subsistence strategies (Noli & Avery, 1988; Speth & Spielmann, 1983; Speth, 1989). Lean meat therefore could not be eaten in unlimited quantities, but rather had to be accompanied by sufficient fat or by carbohydrate from plant food sources.

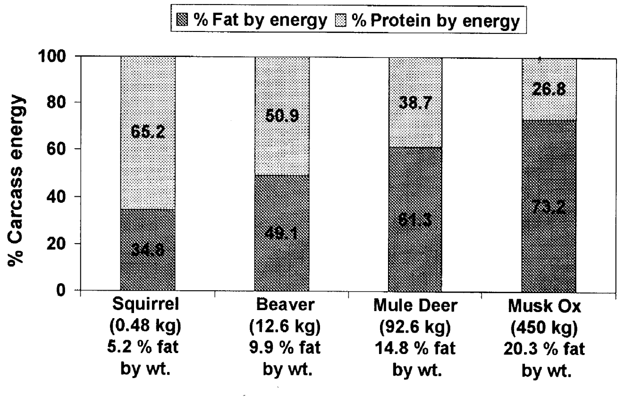

Figure 3 Protein to fat ratios by energy with increasing body fat by weight in four mammalian species: squirrel (*Citellus undulates*), beaver (*Castor canadensis*), mule deer (*Odocoileus hemionus*) and musk ox (*Ovibos moschatus*).

Diet and cardiovascular disease in hunter-gatherers

Dietary fat

Our previous analysis (Cordain *et al*, 2000a) showed that the dietary fat intake of 97% ($n=221$) of the world's hunter-gatherer societies would have exceeded recommended guidelines ($\leq 30\%$ fat). For the majority (53% $n=122$) of the world's foraging cultures the dietary fat intake would lie between 36 and 43% of total energy (Cordain *et al*, 2000a), values not dissimilar from current Western intakes (McDowell *et al*, 1994). Despite this dietary characteristic, the available evidence suggests that hunter-gatherers were generally free of the signs and symptoms of CVD.

Over the past 64 y, anthropological research has consistently demonstrated relatively low serum cholesterol and triacylglycerol levels among indigenous populations that derive the majority of their diet from animal products (Bang & Dyerberg, 1980; Biss *et al*, 1971; Corcoran & Rabinowitch, 1937; Day *et al*, 1976; Eaton *et al*, 1988a; Leonard *et al*, 1994; Scott *et al*, 1958; Shaper *et al*, 1961; Wilber & Levine, 1950). Further, a low incidence of coronary heart disease among the Inuit and other indigenous populations of the circumpolar regions has been recognized for at least 30 y from autopsy studies (Arthaud, 1970; Gottman, 1960; Lederman *et al*, 1962), analyses of death certificates (Bjerregaard & Dyerberg, 1988; Middaugh, 1990; Young *et al*, 1993) and clinical data (Bang & Dyerberg 1980; Kromann & Green, 1950). However with acculturation, the diets of these peoples are becoming increasingly Westernized (Draper 1977; Nobmann *et al*, 1992), and the incidence of CVD and its symptoms may now equal or exceed that found in Western populations (Young *et al*, 1995). Because in Western diets higher animal food consumption is frequently associated with increased mortality from CVD and other cardiovascular maladies (Barnard *et al*, 1995), it is somewhat paradoxical that in partially and recently acculturated hunter-gatherers, who consume the majority of their energy from animal-based food, there is a substantially lower mortality rate from CVD than in Western societies (Arthaud, 1970; Bang & Dyerberg, 1980; Bjerregaard & Dyerberg, 1988; Gottman 1960; Kroman & Green, 1980; Lederman *et al*, 1962; Middaugh, 1990; Young *et al*, 1993).

The low incidence of hyperlipidemia and CVD among populations subsisting largely on animal foods is likely to be attributable to a variety of factors. There is now substantial evidence to indicate that the absolute amount of dietary fat is less important in lowering blood lipid levels and reducing the risk for CVD than is the relative concentrations of specific dietary fatty acids (Connor & Connor, 1997; Gardner & Kraemer, 1995; Oliver, 1997; Nelson *et al*, 1995). Low (22% energy) and high (39% energy) fat diets which had identical polyunsaturated/saturated, ω-3/ω-6 and monounsaturated/total fat fatty acid ratios produced no significant differences in total or LDL cholesterol following a 50 day trial (Nelson *et al*, 1995). Hypercholesterolemic fatty acids include 12:0, 14:0, 16:0 and *trans*-9 18:1 (Grundy, 1997), whereas monounsaturated (MUFA; Gardner & Kraemer, 1995; Yu *et al*, 1995) and polyunsaturated (PUFA, Grundy, 1997) fatty acids are hypocholesterolemic, and 18:0 is neutral (Yu *et al*, 1995). Omega 3 PUFA have wide-ranging cardiovascular protective capacities including lowering of plasma VLDL cholesterol and triacylglycerol (TG) concentrations (Connor & Connor, 1997). Consequently, it is entirely possible to consume relatively high-fat diets that do not necessarily produce a plasma lipid profile that promotes CVD (Garg *et al*, 1988; Nelson *et al*, 1995) given sufficient MUFA, PUFA (Gardner & Kraemer, 1995; Mensink & Katan, 1992) and an appropriate ω-6/ω-3 PUFA ratio (Connor & Connor, 1997) relative to the hypercholesterolemic fatty acids.

In their classic study of Greenland Eskimos who had a near absence of CVD, Bang and Dyerberg (1980) contrasted the dietary and blood lipid profiles of the Eskimos to Danes (Table 3). Despite a much greater animal food intake than the Danes, the Eskimos maintained a more healthful blood lipid profile (lower LDL, VLDL and total cholesterol concentrations, lower TG concentrations and higher HDL concentrations). Although Bang and Dyerberg (1980) largely attributed the relative freedom from CVD of these people to the increased dietary intake of ω-3 PUFA, Table 3 indicates that other factors may be involved as well. The reduced total and LDL cholesterol levels in the Eskimos are likely to be accounted for by the higher dietary MUFA and PUFA and lower saturated fat intake. Reductions in plasma VLDL and TG of the Eskimos certainly could have resulted from an increased ω-3 PUFA intake, but also may in part be due to a relatively lower intake of carbohydrates. Isocaloric replacement of fat with carbohydrate often results in relative increases in plasma VLDL and TG concentrations with concomitant lowering of plasma HDL concentrations (Grundy, 1986; Jeppesen *et al*, 1997). Therefore, the relatively higher plasma HDL concentrations in the Eskimos may have resulted from a reduced carbohydrate intake or higher ω-3 PUFA intake, since total fat intakes were similar to the Danes. It should also be noted that the protein intake of the Eskimos was more than twice as high as the Danes, and this pattern (elevated protein at the expense of carbohydrate) is characteristic of worldwide hunter-gatherers (Cordain *et al*, 2000a). Although rarely considered in terms of dietary management of hyperlipidemia, protein when isocalorically replaced for carbohydrate has been shown to improve blood lipid profiles by reducing LDL, VLDL and total cholesterol and TG while simultaneously increasing HDL cholesterol (Wolfe & Giovannetti, 1991; Wolfe & Giovannetti, 1992; Wolfe & Piche, 1999). From the Bang and Dyerberg (1980) observation, it can be demonstrated that high animal food diets do not necessarily promote dyslipidemia, particularly when the protein content of the diet is relatively high, the carbohydrate content relatively low and when the fatty acid composition is appropriately balanced (Table 3).

Table 3 Dietary and blood lipid characteristics of Greenland Eskimos, adapted from Bang and Dyerberg (1980)

Variable	*Eskimos*	*Danes*
Dietary intake		
Protein (percentage energy)	26.0	11.0
Fat (percentage energy)	37.0	42.0
Carbohydrate (percentage energy)	37.0	47.0
Saturated fat (percentage total fat)	22.8	52.7
Monounsaturated fat (percentage total fat)	57.3	34.6
Polyunsaturated fat (percentage total fat)	19.2	12.7
n-6 PUFA (g)	5.4	10.0
n-3 PUFA (g)	13.7	2.8
Blood lipid values		
Total cholesterol (mmol/l)	5.33 ± 0.78	6.24 ± 1.00
Triglycerides (mmol/l)	0.61 ± 0.44	1.32 ± 0.53

Dietary protein

Our previous data (Cordain *et al*, 2000a) indicates that the projected range (19 – 35% energy) of dietary protein for worldwide hunter-gatherers would considerably exceed the average values (15.5% energy) found in Western diets (McDowell *et al*, 1994). Although high levels of protein in Western diets are known to cause hypercalciuria (Lutz, 1984) and can increase the rate of progression in renal dysfunction (Anonymous, 1996), there is an increasing body of evidence that suggests high protein diets may improve blood lipid profiles (O'Dea, 1984; O'Dea *et al*, 1989; Wolfe & Giovannetti, 1991, 1992; Wolfe & Piche, 1999) and thereby lessen the risk for CVD. Further, high protein diets have been shown to improve metabolic control in type 2 diabetes patients (O'Dea, 1984; O'Dea *et al*, 1989). Wolfe and colleagues have shown that the isocaloric substitution of protein (23% energy) for carbohydrate in moderately hypercholesterolemic subjects resulted in significant decreases in total, LDL and VLDL cholesterol, and TG while HDL cholesterol increased (Wolf & Giovannetti, 1991). Similar blood lipid changes have been observed in type 2 diabetic patients in conjunction with improvements in glucose and insulin metabolism (O'Dea, 1984; O'Dea *et al*, 1989).

In her study of Australian Aborigines temporarily reverting to a hunter-gatherer lifestyle, O'Dea showed that animal foods contributed 64% of the total energy producing an overall macro-nutrient distribution of 54% protein, 33% carbohydrate and 13% fat energy (Naughton *et al*, 1986). Following a 7 week period living as hunter-gatherers in their traditional country in north-western Australia, these 10 diabetic, overweight Aborigines experienced either a great improvement or complete normalization of all of the major metabolic abnormalities of type 2 diabetes (O'Dea, 1984). Because the energy intake was low (1200 kcal) during the treatment period, the estimated daily protein intake (154.3 g/day) would have fallen well within the limits established by the mean maximal hepatic urea synthesis rates (Cordain *et al*, 2000a; Rudman *et al*, 1973). It is possible that the improvement in type 2 diabetic symptoms could in part be attributed to reduced caloric intake, however studies in which energy levels were controlled still yielded similar results (O'Dea *et al*, 1989; Wolfe & Giovannetti, 1991).

Because the calciuretic effect of increases in protein intake with controlled levels of calcium and phosphorous is well established (Linkswiler *et al*, 1981; Lutz, 1984), high-protein diets may have the potential to increase the risk of osteoporosis and bone demineralization, however this effect cannot always be demonstrated in epidemiological surveys (Munger *et al*, 1999). Although hunter-gatherer diets would have been devoid of dairy products and quite high in animal protein, the fossil record indicates pre-agricultural humans generally maintained greater cortical bone cross-sectional areas than modern humans and hence greater bone robusticity and resistance to fractures (Bridges, 1995; Ruff *et al*, 1993). This greater bone robusticity has been attributed to the greater activity patterns of pre-agricultural humans, which in turn would have increased bone loading (Bridges, 1995). It is also quite likely that the high fruit and vegetable consumption in hunter-gatherer diets (Cordain *et al*, 2000a) would have buffered the high acid, and hence calciuretic load brought about by a high protein diet. Previous studies have demonstrated that ingestion of an alkalinizing agent prevented the calciuria which normally accompanies high protein diets (Lutz, 1984) and that when base is administered at a dose sufficient to neutralize endogenous acid production, calcium balance is improved, bone resorption is reduced, and bone formation is increased (Sebastian *et al*, 1994). In Western diets meats, cheeses and cereal grains yield high potential renal acid loads (Remer & Manz, 1995) and hence may promote osteoporosis by producing a net metabolic acidosis (Barzel, 1995). In contrast, fruit and vegetables yield a net alkaline renal load (Remer & Manz, 1995), and high fruit and vegetable diets have been shown to improve urinary calcium excretion rates (Appel *et al*, 1997). Consequently, in hunter-gatherer populations consuming high protein diets, a concomitant consumption of high levels of fruit and vegetables may have countered the calciuretic effects of a high-protein diet.

Dietary carbohydrate

Our previous study demonstrated that the carbohydrate content of worldwide hunter-gatherer diets would have ranged from 22 to 40% of total energy, given an assumed macro-nutrient distribution in plant food of 62% carbohydrate, 24% fat and 14% protein (Cordain *et al*, 2000a). The values within this range (22–40%) are considerably lower than average values (49% energy) in Western diets (McDowell *et al*, 1994), or recommended (55–60% or more of total energy) healthful values (Krauss *et al*, 1996). Although current advice to reduce risk of CVD is, in general, to replace saturated fats with carbohydrate (Krauss *et al*, 1996), there is mounting evidence to indicated that low-fat, high-carbohydrate diets may elicit undesirable blood lipid changes, including reductions in HDL cholesterol and apolipoprotein A-1, while concurrently elevating TG, VLDL cholesterol and small dense LDL cholesterol (Denke & Breslow, 1988; Dreon *et al*, 1995; Jeppesen *et al*, 1997; Mensink & Katan, 1992). Because of these untoward blood lipid changes, substitution of MUFA for saturated fats has been suggested as a more effective strategy than substitution of carbohydrate for saturated fats in order to lower total and LDL serum cholesterol concentrations without adversely influencing HDL, VLDL, TG and apoprotein A-1 (Grundy, 1986; Mensink & Katan, 1987; Wahrburg *et al*, 1992). While we did not specifically analyze the projected MUFA intake in hunter-gatherer populations, our data demonstrate that elevated dietary protein at the expense of carbohydrate would be the macro-nutrient pattern that is most characteristic of hunter-gatherer diets when contrasted to Western diets (Cordain *et al*, 2000a).

Hunter-gatherer diets would not only have contained less total carbohydrate than that typically found in Western diets, but there are important qualitative differences in the types of carbohydrates which may have important health implications. Western diets are characterized by carbohydrate foods with relatively high glycemic indices (eg potatoes, bread, cereal products) whereas the wild plant foods which would have been consumed by hunter-gatherers generally maintain a high fiber content, are slowly digested and produce low glycemic and insulin responses (Thorburn *et al*, 1987a, b). Observational studies suggest that foods with a high glycemic load and low fiber content increase the risk of type 2 diabetes (Salmeron *et al*, 1997a, b) and CVD (Liu *et al*, 2000; 2001).

Other environmental factors

In addition to the macro-nutrient characteristics of hunter-gatherer diets that have the potential to positively influence the development and progression of CVD, it is quite likely that relatively high intakes of antioxidants (Eaton & Konner, 1985, Eaton *et al*, 1988b) and phytochemicals (Eaton & Eaton, 2000) as well as more intense exercise/work patterns (Cordain *et al*, 1998) provided pre-agricultural people further protection from CVD. Nutritional studies of hunter-gatherers have shown them to maintain high plasma concentrations of folate and vitamin B_{12} (Metz *et al*, 1971). Adequate intake of these two vitamins along with vitamin B_6 reduces plasma homocysteine concentrations, an independent risk factor for CVD (Gerhard & Duell, 1999; Mann *et al*, 1999). Hunter-gatherers rarely if ever added salt to their foods, and studies of salt-free Yanomamo Indians have shown these indigenous people to maintain low blood pressures that do not increase with aging (Oliver *et al*, 1975). Finally, except for certain American Indian societies (starting about 5000 y ago), regular smoking of tobacco was unknown in hunter-gatherers (Eaton *et al*, 1988b). Any or all of these dietary and environmental elements probably would have operated together with the macronutrient characteristics of hunter-gather diets to reduce signs and symptoms of CVD that are commonplace in Western societies.

Conclusions

The high reliance upon animal-based foods would not have necessarily elicited unfavorable blood lipid profiles because of the hypolipidemic effects of high dietary protein (19–35% energy) and the relatively low level of dietary carbohydrate (22–40% energy). Although fat intake (28–58% energy) would have been similar to or higher than that found in Western diets, it is likely that important qualitative differences in fat intake, including relatively high levels of MUFA and PUFA and a lower ω-6/ω-3 fatty acid ratio, would have served to inhibit the development of CVD. Other dietary characteristics including high intakes of antioxidants, fiber, vitamins and phytochemicals along with a low salt intake may have operated synergistically with lifestyle characteristics (more exercise, less stress and no smoking) to further deter the development of CVD.

Although high-carbohydrate, low-fat diets are almost universally recommended for the treatment of hyperlipidemia and prevention of CVD, these diets often adversely influence certain components of the blood lipid profile, including HDL, VLDL cholesterol, TG, small dense LDL cholesterol and apoprotein A-1. One of the present strategies for overcoming these untoward effects of low-fat, high-carbohydrate diets is to replace carbohydrate with MUFA, while keeping saturated fat levels low. An alternative strategy, which has recently been clinically demonstrated and which positively influences HDL, VLDL cholesterol and TG, is the replacement of carbohydrate with protein. This dietary approach to reducing dyslipidemia and preventing CVD is consistent with the dietary macro-nutrient patterns found in the native diet of virtually all hunter-gatherer societies—societies which are relatively free of CVD and its symptoms.

References

Aiello LC & Wheeler P (1995): The expensive tissue hypothesis. *Curr. Anthropol.* **36**, 199–222.

Anonymous (1996): Effects of dietary protein restriction on the progression of moderate renal disease in the Modification of Diet in Renal Disease Study. *J. Am. Soc. Nephrol.* **12**, 2616–2626.

Appel LJ, Moore TJ, Obarzanek E, Vollmer WM *et al* (1997): A clinical trial of the effects of dietary patterns on blood pressure. *New Engl. J. Med.* **336**, 1117–1124.

Ardrey R (1961): *African Genesis*. New York: Dell.

Arthaud JB (1970): Causes of death in 339 Alaskan Eskimos as determined by autopsy. *Arch. Pathol.* **90**, 433–438.

Bang HO & Dyerberg J (1980): Lipid metabolism and ischemic heart disease in Greenland Eskimos. *Adv. Nutr. Res.* **3**, 1–22.

Barnard ND, Nicholson A & Howard JL (1995): The medical costs attributable to meat consumption. *Prev. Med.* **24**, 646–655.

Barzel US (1995): The skeleton as an ion exchange system: implications for the role of acid-base imbalance in the genesis of osteoporosis. *J. Bone Mineral Res.* **10**, 1431–1436.

Beckerman S (2000): Game. In *The Cambridge World History of Food*, ed. KF Kiple & KC Ornelas, pp 524–528. Cambridge: Cambridge University Press.

Binford LR (1978): Food processing and consumption. In *Nunamiut Ethnoarchaeology*, ed. LR Binford, pp 135–167. New York: Academic Press.

Biss K, Ho KJ, Mikkelson B, Lewis LA & Taylor CB (1971): Some unique biological characteristics of the Masai of east Africa. *New Engl. J. Med.* **284**, 694–699.

Bjerregaard P & Dyerberg J (1988): Mortality from ischemic heart disease and cerebrovascular disease in Greenland. *Int. J. Epidemiol.* **17**, 514–519.

Blurton Jones NG, Hawkes K & O'Connell J (1997): Why do Hadza children forage? In *Uniting Psychology and Biology: Integrative Perspectives on Human Development*, ed. NL Segal, GE Weisfeld & CC Weisfield, pp 297–331. New York: American Psychological Association.

Bose S (1964): Economy of the Onge of Little Andaman. *Man India* **44**, 298–310.

Bridges PS (1995): Skeletal biology and behavior in ancient humans. *Evol. Anthropol.* **4**, 112–120.

Chesney RW, Helms RA, Christensen M, Budreau AM, Han X & Sturman JA (1998): The role of taurine in infant nutrition. *Adv. Exp. Med. Biol.* **442**, 463–476.

Connor SL & Connor WE (1997): Are fish oils beneficial in the prevention and treatment of coronary artery disease? *Am. J. Clin. Nutr.* **66**, 1020S–1031S.

Corcoran AC & Rabinowitch IM (1937): A study of the blood lipoids and blood protein in Canadian eastern arctic Eskimos. *Biochemistry* **31**, 343–348.

Cordain L, Gotshall RW, Eaton SB & Eaton SB (1998): Physical activity, energy expenditure and fitness: an evolutionary perspective. *Int. J. Sports Med.* **19**, 328–335.

Cordain L, Brand Miller J, Eaton SB, Mann N, Holt SHA & Speth JD (2000a): Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets. *Am. J. Clin. Nutr.* **71**, 682–692.

Cordain L, Brand Miller J, Eaton SB & Mann N (2000b): Macronutrient estimations in hunter-gatherer diets. *Am. J. Clin. Nutr.* **72**, 1589–1590.

Cordain L, Watkins BA & Mann NJ (2001): Fatty acid composition and energy density of foods available to African hominids: evolutionary implications for human brain development. *Wld Rev. Nutr. Diet.* **90**, 144–161.

Dahlberg F (1981): Introduction. In *Woman the Gatherer*, ed. F Dahlberg, pp 1–33. New Haven: CT Yale University Press.

Dart RA (1957): The osteodontokeratic culture of *Australopithecus prometheus*. *Memo. Transvaal Museum* **10**, 1–105.

Day J, Carruthers M, Bailey A & Robinson D (1976): Anthropometric, physiological and biochemical differences between urban and rural Maasai. *Atherosclerosis* **23**, 357–361.

Denke MA & Breslow JL (1988): Effects of a low fat diet with water and without intermittent saturated fat and cholesterol ingestion on plasma lipid, lipoprotein, and apolipoprotein levels in normal volunteers. *J. Lipid Res.* **29**, 963–969.

Dietz WH, Marino B, Peacock NR & Bailey PH (1982): Nutritional status of Efe pygmies and Lese horticulturalists. *Am. J. Phys. Anthropol.* **78**, 509–518.

Draper HH (1977): The aboriginal Eskimo diet in modern perspective. *Am. Anthropol.* **79**, 309–316.

Dreon DM, Fernstrom HA, Miller B & Krauss RM (1995): Apolipoprotein E isoform phenotype and LDL subclass response to a reduced-fat diet. *Arterioscler. Thromb. Vasc. Biol.* **15**, 105–111.

Eaton SB & Eaton SB (2000): Paleolithic vs modern diets—selected pathophysiological implications. *Eur. J. Nutr.* **39**, 67–70.

Eaton SB & Konner M (1985): Paleolithic nutrition. A consideration of its nature and current implications. *New Engl. J. Med.* **312**, 283–289.

Eaton SB, Konner M & Shostak M (1988a): Stone agers in the fast lane: chronic degenerative diseases in evolutionary perspective. *Am. J. Med.* **84**, 739–749.

Eaton SB, Shostak M & Konner M (1988b): *The Paleolithic Prescription*. New York: Harper & Row.

Emken RA, Adlof RO, Rohwedder WK & Gulley RM (1992): Comparison of linolenic and linoleic acid metabolism in man: influence of dietary linoleic acid. In *Essential Fatty Acids and Eicosanoids: Invited Papers from the Third International Conference*, ed. A Sinclair & R Gibson, pp 23–25. Champaign IL: AOCS Press.

Gardner CD & Kraemer HC (1995): Monounsaturated versus polyunsaturated dietary fat and serum lipids. A meta analysis. *Arterioscler. Thromb. Vasc. Biol.* **15**, 1917–1927.

Garg A, Bonanome A, Grundy SM, Zhang Z-J & Unger RH (1988): Comparison of a high-carbohydrate diet with a high-monounsaturated fat diet in patients with non-insulin dependent diabetes mellitus. *New Engl. J. Med.* **319**, 829–834.

Gerhard GT & Duell PB (1999): Homocysteine and atherosclerosis. *Curr. Opin. Lipidol.* **10**, 417–428.

Gottman AW (1960): A report of one hundred and three autopsies in Alaskan natives. *Arch. Pathol.* **70**, 117–124.

Gray JP (1999): A corrected ethnographic atlas. *World Cultures J.* **10**, 24–85.

Grundy SM (1986): Comparison of monounsaturated fatty acids and carbohydrates for lowering plasma cholesterol. *New Engl. J. Med.* **314**, 745–748.

Grundy SM (1997): What is the desirable ratio of saturated, polyunsaturated, and monounsaturated fatty acids in the diet. *Am. J. Clin. Nutr.* **66**, 988S–990S.

Hawkes K, Hill K & O'Connell JF (1982): Why hunters gather: optimal foraging and the Ache of eastern Paraguay. *Am. Ethnol.* **9**, 379–398.

Hawkes K, O'Connell JF & Blurton Jones N (1989): Hardworking Hadza grandmothers. In *Comparative Socio-ecology of Humans and Other Mammals*, ed. V Standen & RA Foley, pp 341–366. London: Basil Blackwell.

Hayden B (1981): Subsistence and ecological adaptations of modern hunter/gatherers. In *Omnivorous Primates*, ed. RSO Harding & G Teleki, pp 344–421. New York: Columbia University Press.

Hill K, Hawkes K, Hurtado M & Kaplan H (1984): Seasonal variance in the diet of Ache hunter-gatherers in Eastern Paraguay. *Hum. Ecol.* **12**, 101–135.

Hu FB, Stampfer MJ, Manson JE, Ascherio A, Colditz GA, Speizer FE, Hennekens CH & Willett WC (1999): Dietary saturated fats and their food sources in relation to the risk of coronary heart disease in women. *Am. J. Clin. Nutr.* **70**, 1001–1008.

Hu FB, Rimm EB, Stampfer MJ, Ascherio A, Spiegelman D & Willett WC (2000): Prospective study of major dietary patterns and risk of coronary heart disease in men. *Am. J. Clin. Nutr.* **72**, 912–921.

Hurtado AM & Hill K (1986): Early dry season subsistence ecology of the Cuiva (Hiwi) foragers of Venezuela. *Hum. Ecol.* **15**, 163–187.

Hurtado AM & Hill K (1990): Seasonality in a foraging society: variation in diet, work effort, fertility, and the sexual division of labor among the Hiwi of Venezuela. *J. Anthropol. Res.* **46**, 293–345.

Jeppesen J, Schaaf P, Jones C, Zhou M-Y, Ida Chen Y-D & Reaven GM (1997): Effects of low-fat, high carbohydrate diets on risk factors for ischemic heart disease in postmenopausal women. *Am. J. Clin. Nutr.* **65**, 1027–1033.

Kaplan H & Hill K (1992): Human subsistence behavior. In *Evolution, Ecology and Human Behavior*, ed., EA Smith & B Winterhalder, pp 167–202. Chicago, IL: Aldine.

Kaplan H, Hill K, Lancaster J & Hurtado AM (2000): A theory of human life history evolution: diet, intelligence, and longevity. *Evol. Anthropol.* **9**, 156–185.

Keeley LH (1992): The use of plant foods among hunter-gatherers: a cross-cultural survey. In *Prehistoire de l'Agriculture. Nouvelles Approches Experimentales et Ethnographiques (The Prehistory of Agriculture. New experimental and Ethnographic Approaches)*, CRA Monograph no. 6, ed. PC Anderson, pp 29–38. Paris: National Center for Scientific Research.

Knopf K, Sturman JA, Armstrong M & Hayes KC (1978): Taurine: an essential nutrient for the cat. *J. Nutr.* **108**, 773–778.

Krauss RM, Deckelbaum RJ, Ernst N & Fisher E *et al* (1996): Dietary guidelines for healthy American adults. A statement for health professionals from the nutrition committee, American heart association. *Circulation* **94**, 1795–1800.

Krogh A & Krogh M (1913): A study of the diet and metabolism of Eskimos undertaken in 1908 on an expedition to Greenland. *Medd. Gronland* **51**, 1–52.

Kromann N & Green A (1980): Epidemiological studies in the Upernavik district, Greenland. Incidence of some chronic diseases 1950–1974. *Acta Med. Scand.* **208**, 401–406.

Laidlaw SA, Shultz TD, Cecchino JT & Kopple JD (1988): Plasma and urine taurine levels in vegans. *Am. J. Clin. Nutr.* **47**, 660–663.

Lee RB (1968): What hunters do for a living, or how to make out on scarce resources. In *Man the Hunter*, ed. RB Lee & I DeVore, pp 30–48. Chicago, IL: Aldine.

Lee RB (1979): *The !Kung San: Men, Women, and Work in a Foraging Society*. Cambridge: Cambridge University Press.

Lederman JM, Wallace AC & Hildes JA (1962): Arteriosclerosis and neoplasms in Canadian Eskimos. In *Biological Aspects of Aging: Proceedings of the Fifth International Congress on Gerontology*, pp 201–207. New York: Columbia University Press.

Leonard WR & Robertson ML (1994): Evolutionary perspectives on human nutrition: the influence of brain and body size on diet and metabolism. *Am. J. Hum. Biol.* **6**, 77–88.

Leonard WR, Crawford MH, Comuzzie AG & Sukernik RI (1994): Correlates of low serum lipid levels among the Evenki herders of Siberia. *Am. J. Hum. Biol.* **6**, 329–338.

Linkswiler HM, Zemel MB, Hegsted M & Schuette S (1981): Protein-induced hypercalciuria. *Fed. Proc.* **40**, 2429–2433.

Liu S, Willett WC, Stampfer MJ, Hu FB, Franz M, Sampson L, Hennekens CH & Manson JE (2000): A prospective study of dietary glycemic load, carbohydrate intake, and risk of coronary heart disease in US women. *Am. J. Clin. Nutr.* **71**, 1455–1461.

Liu S, Manson JE, Stampfer MJ, Holmes MD, Hu FB, Hankinson SE & Willett WC (2001): Dietary glycemic load assessed by food-frequency questionnaire in relation to plasma high-density lipoprotein cholesterol and fasting plasma triacylglycerols in postmenopausal women. *Am. J. Clin. Nutr.* **73**, 560–566.

Lutz J (1984): Calcium balance and acid-base status of women as affected by increased protein intake and by sodium bicarbonate ingestion. *Am. J. Clin. Nutr.* **39**, 281–288.

Mann NJ, Li D, Sinclair AJ, Dudman NP, Guo XW, Elsworth GR, Wilson AK & Kelly FD (1999): The effect of diet on plasma homocysteine concentrations in healthy male subjects. *Eur. J. Clin. Nutr.* **53**, 895–899.

MacDonald ML, Rogers QR & Morris JG (1984): Nutrition of the domestic cat, a mammalian carnivore. *A. Rev. Nutr.* **4**, 521–562.

McArthur M (1960): Food consumption and dietary levels of groups of aborigines living on naturally occurring foods. In *Records of the American-Australian Scientific Expedition to Arnhem Land*, ed. CP Mountford, pp 90–135. Melbourne: Melbourne University Press.

McDowell MA, Briefel RR, Alaimo K, Bischof AM *et al.* (1994): Energy and macro-nutrient intakes of persons ages 2 months and over in the United States: third national health and nutrition examination survey, phase 1, 1988–1991. Advance data from vital and health statistics, no. 225. Hyattsville, MD: National Center for Health Statistics.

Meehan B (1982): *Shell Bed to Shell Midden*. Canberra: Australian Institute of Aboriginal Studies.

Menotti A, Kromhout D, Blackburn H, Fidanza F, Buzina R & Nissinen A (1999): Food intake patterns and 25-year mortality from coronary heart disease: cross-cultural correlations in the Seven Countries Study. The Seven Countries Research Study Research Group. *Eur. J. Epidemiol.* **15**, 507–515.

Mensink RP & Katan MB (1987): Effect of monounsaturated fatty acids versus complex carbohydrates on high density lipoproteins in healthy men and women. *Lancet* **i**, 122–125.

Mensink RP & Katan MB (1992): Effect of dietary fatty acids on serum lipids and lipoproteins: a meta-analysis of 27 trials. *Arterioscler. Thromb.* **12**, 911–919.

Metz J, Hart D & Harpending HC (1971): Iron, folate, and vitamin B12 nutrition in a hunter-gatherer people: a study of the Kung Bushmen. *Am. J. Clin. Nutr.* **24**, 229 – 242.

Middaugh JP (1990): Cardiovascular deaths among Alaskan natives, 1980 – 86. *Am. J. Public Health* **80**, 282 – 285.

Milton K (2000): Hunter-gatherer diets — a different perspective. *Am. J. Clin. Nutr.* **71**, 665 – 667.

Munger RG, Cerhan JR & Chiu BC-H (1999): Prospective study of dietary protein intake and risk of hip fracture in postmenopausal women. *Am. J. Clin. Nutr.* **69**, 147 – 152.

Murdock GP (1967): Ethnographic atlas: a summary. *Ethnology* **6**, 109 – 236.

Naughton JM, O'Dea K & Sinclair AJ (1986): Animal foods in traditional Australian Aboriginal diets: polyunsaturated and low in fat. *Lipids* **21**, 684 – 690.

Nelson GJ, Schmidt PC & Kelley DS (1995): Low-fat diets do not lower plasma cholesterol levels in healthy men compared to high-fat diets with similar fatty acid composition at constant caloric intake. *Lipids* **30**, 969 – 976.

Nestle M (1999): Animal v. plant foods in human diets and health: is the historical record unequivocal? *Proc. Nutr. Soc.* **58**, 211 – 218.

Nobmann ED, Byers T, Lanier AP, Hankin JH & Jackson MY (1992): The diet of Alaska native adults: 1987 – 88. *Am. J. Clin. Nutr.* **55**, 1024 – 1032.

Noli D & Avery G (1988): Protein poisoning and coastal subsistence. *J. Archaeolog. Sci.* **15**, 395 – 401.

O'Connell JF & Hawkes K (1984): Food choices and foraging sites among the Alyawara. *J. Anthropol. Res.* **40**, 504 – 535.

O'Dea K (1984): Marked improvement in carbohydrate and lipid metabolism in diabetic Australian Aborigines after temporary reversion to traditional lifestyle. *Diabetes* **33**, 596 – 603.

O'Dea K, Traianedes K, Ireland P, Niall M, Sadler J, Hopper J & DeLuise M (1989): The effects of diet differing in fat, carbohydrate, and fiber on carbohydrate and lipid metabolism in type II diabetes. *J. Am. Diet. Assoc.* **89**, 1076 – 1086.

Oliver MF (1997): It is more important to increase the intake of unsaturated fats than to decrease the intake of saturated fats: evidence from clinical trials relating to ischemic heart disease. *Am. J. Clin. Nutr.* **66**, 980S – 986S.

Oliver WJ, Cohen EL & Neel JV (1975): Blood pressure, sodium intake, and sodium related hormones in the Yanomamo Indians, a 'no-salt' culture. *Circulation* **52**, 146 – 151.

Pace N & Rathbun (1945): Studies on body composition. III. The body water and chemically combined nitrogen content in relation to fat content. *J. Biol. Chem.* **158**, 685 – 692.

Pawlosky R, Barnes A & Salem N (1994): Essential fatty acid metabolism in the feline: relationship between liver and brain production of long-chain polyunsaturated fatty acids. *J. Lipid Res.* **35**, 2032 – 2040.

Pitts GC & Bullard TR (1968): Some interspecific aspects of body composition in mammals. In *Body Composition in Animals and Man*, Publication 1598, pp 45 – 70. Washington, DC: National Academy of Sciences.

Politis G (1996): *Nukak*. Columbia: Instituto Amazonico de Investigaciones Cientificas-SINCHI.

Popkin BM, Siega-Riz AM, Haines PS & Jahns L (2001): Where's the fat? Trends in U.S. diets 1965 – 1996. *Prev. Med.* **32**, 1 – 10.

Rao DH, Brahman GV & Rao ND (1989): Health and nutritional status of the Onge of Little Andaman Island. *J. Ind. Anthrop. Soc.* **24**, 69 – 78.

Remer T & Manz F (1995): Potential renal acid load of foods and its influence on urine pH. *J. Am. Diet. Assoc.* **95**, 791 – 797.

Richards MP, Pettitt PB, Trinkaus E, Smith FH, Paunovic M & Karavanic I (2000): Neanderthal diet at Vindija and Neanderthal predation: the evidence from stable isotopes. *Proc. Natl. Acad. Sci.* **97**, 7663 – 7666.

Richards MP & Hedges RM (2000): Focus: Gough's Cave and Sun Hole Cave human stable isotope values indicate a high animal protein diet in the British Upper Palaeolithic. *J. Archaeol. Sci.* **27**, 1 – 3.

Robbins CT, Moen AN & Reid JT (1974): Body composition of white-tailed deer. *J. Anim. Sci.* **38**, 871 – 876.

Ruff C, Trinklaus E, Walker A & Larsen CS (1993): Postcranial robusticity in *Homo*. I: Temporal trends and mechanical interpretation. *Am. J. Phys. Anthropol.* **91**, 21 – 53.

Rudman D, DiFulco TJ, Galambos JT, Smith RB, Salam AA & Warren WD (1973): Maximal rates of excretions and synthesis of urea in normal and cirrhotic subjects. *J. Clin. Invest.* **52**, 2241 – 2249.

Salmeron J, Ascherio A, Rimm EB, Colditz GA *et al* (1997a): Dietary fiber, glycemic load, and risk of NIDDM in men. *Diabetes Care* **20**, 545 – 550.

Salmeron J, Manson JE, Stampfer MJ, Colditz GA, Wing AL & Willett WC (1997b). Dietary fiber, glycemic load, and risk of non-insulin-dependent diabetes mellitus in women. *J.A.M.A.* **277**, 472 – 477.

Scott EM, Griffith IV, Hoskins DD & Whaley RD (1958): Serum cholesterol levels and blood pressure of Alaskan Eskimo men. *Lancet* **ii**, 667 – 668.

Sebastian A, Harris ST, Ottaway JH, Todd KM & Morris RC (1994): Improved mineral balance and skeletal metabolism in postmenopausal women treated with potassium bicarbonate. *New Engl. J. Med.* **33**, 1776 – 1781.

Shaper AG, Jones M & Kyobe J (1961): Plasma lipids in an African tribe living on a diet of milk and meat. *Lancet* **ii**, 1324 – 1327.

Silberbauer G (1981): *Hunter and Habitat in the Central Kalahari Desert*. Cambridge: Cambridge University Press.

Simms SR (1987): *Behavioral Ecology and Hunter-Gatherer Foraging. An Example from the Great Basin*. BAR International Series 381, p 47. Oxford: BAR.

Sinclair HM (1953): The diet of Canadian Indians and Eskimos. *Proc. Nutr. Soc.* **12**, 69 – 82.

Speth JD (1989): Early hominid hunting and scavenging: the role of meat as an energy source. *J. Hum. Evol.* **18**, 329 – 343.

Speth JD & Spielmann KA (1983): Energy source, protein metabolism, and hunter-gatherer subsistence strategies. *J. Anthropol. Archaeol.* **2**, 1 – 31.

Sturman JA, Hepner GW, Hofmann AF & Thomas PJ (1975): Metabolism of [35S] taurine in man. *J. Nutr.* **105**, 1206 – 1214.

Tanaka J (1980): *The San, Hunter-gatherers of the Kalahari: a Study in Ecological Anthropology*. Tokyo: Tokyo University Press.

Thorburn AW, Brand JC, O'Dea K, Spargo RM & Truswell AS (1987a): Plasma glucose and insulin responses to starchy foods in Australian aborigines: a population now at high risk of diabetes. *Am. J. Clin. Nutr.* **46**, 282 – 285.

Thorburn AW, Brand JC & Truswell AS (1987b): Slowly digested and absorbed carbohydrate in traditional bushfoods: a protective factor against diabetes? *Am. J. Clin. Nutr.* **45**, 98 – 106.

Wahrburg U, Martin H, Sandkamp M, Schulte H & Assmann G (1992): Comparative effects of a recommended lipid lowering diet vs. a diet rich in monounsaturated fatty acids on serum lipid profiles in healthy young adults. *Am. J. Clin. Nutr.* **56**, 678 – 683.

Washburn SL & Lancaster CS (1968): The evolution of hunting. In *Man the Hunter*, ed. RB Lee & I DeVore, pp 293 – 303. Chicago, IL: Aldine.

Wilber CG & Levine VE (1950): Fat metabolism in Alaskan Eskimos. *Exp. Med Surg.* **8**, 422 – 425.

Winterhalder BP (1981): Optimal foraging strategies and hunter-gatherer research in anthropology: theories and models. In *Hunter-gatherer Foraging Strategies*, ed. BP Winterhalder & EA Smith, pp 13 – 35. Chicago, IL: University of Chicago.

Wolfe BM & Giovannetti PM (1991): Short term effects of substituting protein for carbohydrate in the diets of moderately hypercholesterolemic human subjects. *Metabolism*, **40**, 338 – 343.

Wolfe BM & Giovannetti PM (1992): High protein diet complements resin therapy of familial hypercholesterolemia. *Clin. Invest. Med.* **15**, 349 – 359.

Wolfe BM & Piche LA (1999): Replacement of carbohydrate by protein in a conventional-fat diet reduces cholesterol and triglyceride concentrations in healthy normolipidemic subjects. *Clin. Invest. Med.* **22**, 140 – 148.

Yellen J (1977): *Archaeological Approaches to the Present: Models for Reconstructing the Past*. New York: Academic Press.

Young TK, Moffatt MEK & O'Neil JD (1993). Cardiovascular diseases in an artic population: an epidemiological perspective. *Am. J. Public Health* **83**, 881 – 887.

Young TK, Nikitin YP, Shubnikov EV, Astakhova TI, Moffat ME & O'Neil JD (1995): Plasma lipids in two indigenous arctic populations with low risk for cardiovascular disease. *Am. J. Hum. Biol.* **7**, 223 – 236.

Yu S, Deer J, Etherton T & Kris-Etherton P (1995): Plasma cholesterol-predictive equations demonstrated that stearic acid is neutral and monounsaturated fatty acids are hypocholesterolemic. *Am. J. Clin. Nutr.* **61**, 1129 – 1139.

Zihlman AL (1981): Women as shapers of the human adaptation. In *Woman the Gatherer*, ed. F Dahlberg, pp 75 – 120. New Haven, CT: Yale University Press.