Interdisciplinary Contributions to Archaeology

John D. Speth

# The Paleoanthropology and Archaeology of Big-Game Hunting

## Protein, Fat, or Politics?

Springer

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# INTERDISCIPLINARY CONTRIBUTIONS TO ARCHAEOLOGY

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John D. Speth
Museum of Anthropology
University of Michigan
4013 Museums Building
Ann Arbor, MI, 48109-1079
USA
jdspeth@umich.edu

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*To my family—Lisa, Larrea, and Robin—for their patience, good-natured teasing, and obvious amusement as they queried me about what bizarre topic I happened to be dabbling in that day—Why do elephants have such big brains? Why does chimpanzee breast milk have so little protein? Why are human babies born with more body fat than baby seals? Judging by their ear-to-ear grins, I know my kids are convinced that archaeology must be the weirdest field on the planet….*

*to the Garnseys, Elmer (Skip) and Jane, the Slash/G Cattle Company, and a lot of yellow paint, where all of this began so long ago….*

*to Kate Spielmann, whose insights into Pueblo hunting and protein needs were critical catalysts in the development of these ideas….*

*to Glynn Isaac, who invited me to East Africa "to see for myself"….*

*to Aram Yengoyan, who once quipped: "Speth thinks culture is nothing but verbalized fat."* Well, maybe….

*and to my parents, Fred and Lottie, who let me follow my dreams, even if it meant never truly climbing out of the sand box….*

# Foreword

For more than a century, conventional anthropological wisdom has assigned big-game hunting a central role in human evolution. As the story generally goes, men's adoption of this practice gave access to a rich, readily available, yet previously untapped source of subsistence. This, in turn, favored the emergence of nuclear families as units of common economic and reproductive interest, spreading the responsibility for the provisioning of offspring beyond mothers, reducing the demands of the food quest, and enabling women to bear and raise more children. It further selected for a pattern of delayed maturity that allowed more time for learning, ultimately leading to the development of peculiarly human cognitive and behavioral capabilities. In short, it was meat that made us human – or so the "Man the Hunter" model still widely encountered in college textbooks and popular media would lead one to believe.

Over the last four decades, this basic idea has been deployed in diverse, often mutually conflicting evolutionary scenarios, some envisioning the presence of nuclear families headed by big-game-hunting, offspring-provisioning fathers among the earliest representatives of genus *Homo* more than two million years ago, others suggesting that this same pattern emerged much later, coincident with and largely responsible for the spread of "anatomically modern" *Homo sapiens* beyond Africa beginning only about 50,000 years ago. Depending on the specific archaeological data cited, each of these scenarios and others as well can be made to sound equally plausible, in most cases due to the persistent appeal of the underlying premise – meat is and always has been good and good for you – and because the bones of large animals figure so prominently in so much of the archaeological record.

In the important book at hand, anthropological archaeologist John Speth gives us two reasons to be skeptical of this received wisdom. First, drawing on a steadily increasing body of quantitatively sophisticated ethnographic work among traditionally oriented hunter–gatherers, Speth shows that big-game hunting is often less than the best approach to the problem of feeding one's family. Even in environments where large animals are abundant, the short term, day-to-day risk of failing to take one can frequently be quite high. Even when a hunter succeeds, the chances are good that most of the meat so acquired will go to others, outside his own family, with no guarantee of timely, commensurate reciprocity when those "others" themselves do well at the game. Take away the weapons – bows and arrows, atlatls and javelins – that allow traditional hunters to succeed as often as they do but that have been available for less than a quarter of the time genus *Homo* has existed and the prospects for securing a reliable nutrient stream based on big-game hunting become even less promising. As Speth points out, this same ethnographic research further shows that hunters truly concerned with feeding their wives and children would generally do better by targeting a broader range of prey, including small game and plant foods that are often more reliably acquired and always more easily defended from the claims of non-family members. The fact that traditionally oriented hunters so often focus on big game to the near-complete exclusion of these alternative food sources strongly suggests the pursuit of some other goal.

Speth's second point, one that he himself has developed extensively over the last three decades, is that meat isn't always and everywhere good and good for you. His survey of the historical and recent nutritional literatures on the perils of heavy reliance on animal protein clearly indicates the existence of surprisingly strict limits on human ability to subsist on a heavy meat diet. The "obvious" archaeological evidence of past pursuit and consumption of large animal prey does not necessarily mean that big game were a major component, let alone the mainstay of early human diets. It almost certainly wasn't the resource that fed the increase in brain size, drove the changes in cognitive and behavioral capabilities, or encouraged the development of patterns in social organization that distinguish us so markedly from our nearest living great ape relatives and our common primate ancestors.

Like many good pieces of science, Speth's book not only challenges long-standing paradigms on the basis of emerging knowledge but also identifies new and important problems for future research. If offspring provisioning often *isn't* the main goal of big-game hunting among modern foragers and *wasn't* in many cases in the past as well, how do we account for its prominence either as a modern practice or as reflected in the archaeological record? If meat consumption didn't provoke the evolution of our distinctive morphologies, capabilities, and patterns of behavior, what did? Speth's informative, highly readable work throws these questions into sharp relief and encourages the next generation of anthropological archaeologists to pursue them aggressively.

University of Utah,
Salt Lake City, Utah

James F. O'Connell
February, 2010

# Preface

Regardless of what particular academic track you may have followed as a college undergraduate, whether it was paleoanthropology, archaeology, biology, geosciences, or even premed, at some point you probably learned about the earlier stages of human evolution and the pivotal role played by big-game hunting (preceded perhaps by a "stage" of big-game scavenging) in transforming a bipedal ape-like ancestor into what we are today. Over the years, more and more evidence for our ancestral interest in hunting and meat-eating has accumulated and by now few would question the importance of hunting in our heritage. Hand-in-hand with Paleolithic ("Stone Age") flaked stone tools, we find dense concentrations of broken-up animal bones, often the remains of more than one species that some ancient hominin (roughly synonymous with hominid) had transported to a single locality. And many of the bones bear unmistakable traces of human butchery in the form of cutmarks made by stone tools when the carcasses were dismembered and defleshed, as well as impact fractures produced when hominins broke open the limb bones to retrieve their content of fatty marrow and, in more recent sites, even occasional charred bones, the tell-tale evidence that early humans had begun cooking their food.

Few, however, seriously question what big-game hunting was really all about. That part of the puzzle has always seemed pretty self-evident – hunting provided a critical part of our ancestor's diet and, through the gradual evolution of our behavioral and technological wherewithal, our ancestors became ever more effective and efficient at putting meat on the family table. In a way, the "big-game hunting" issue bears certain resemblances to issues surrounding the concept of evolution. When undergraduates ask me "is evolution a fact," I have to respond to their question in two parts: "yes, evolution *as a description of events* is a fact – we can make it happen in the lab, as is routinely done in genetic experiments with fruit flies; we can see it in our environment, as so clearly demonstrated by the growing resistance of many bacteria to antibiotics; and we can see its results in the fossil record." But I then have to hasten to add that "evolution *as explanation* is not fact but theory, a good one and a powerful one, but theory nonetheless." We know it happens, few scientists would question that, but we are still far from agreement about precisely how it works. That debate will keep us busy for many years to come.

The issues surrounding big-game hunting in our evolutionary history are somewhat analogous: "yes, we can see direct evidence of our ancestor's interest in big game and, through a variety of techniques, we can even be fairly confident that the animals were hunted." By now I think we can safely take that as fact, although there is continuing debate and disagreement about precisely when and how humans gained sufficient technological know-how to take the really big and dangerous animals. Some would argue that humans were capable of killing animals much larger than themselves right from the first appearance of our genus, perhaps as early as 2.0 or even 2.5 million years ago, while others maintain that humans did not become competent and committed big-game hunters until the latter part of the Middle Pleistocene ("ice age"), perhaps as recently as 300,000 or 400,000 years ago. However, in either case, as I hope this book will illustrate, the explanation of "why" humans hunted (or scavenged) big game is not as self-evident as most textbook treatments of the topic would lead us to believe. The standard offering, of course, one that is often presented as though it were an irrefutable fact, is that humans hunted to put food on the table and that big-game hunting in particular offered the optimal way of acquiring a high-quality food (meat) in large packages at "least cost." This line of thinking seems almost trivially obvious and it has guided our thinking for well over a century. But what we generally take as fact should better be taken as explanation and hence theory, one that is in need of much closer scrutiny. Big-game hunting may have emerged and developed, not as a means of bringing home food to the family, but as a form of costly signaling, a way for males to demonstrate their worth, skill, reliability, and suitability as mates and alliance partners. In other words, the meat the hunters brought home may have been ear-marked first and foremost not for wife and kids but for other members of the social group, members who often were not even related to the individuals who procured the meat. There are other possible explanations, of course, such as showing off or signaling generosity (Gurven et al. 2000), or perhaps even sexual conflict (Arnqvist and Rowe 2005), that might better account for why men devote inordinate amounts of time and effort in the pursuit of big animals. Whichever, if any, of these more socially- or politically based explanations ultimately wins out, they share in common a focus on social, demographic, and political forces in the explanatory chain, not family provisioning and nutrition. In fact, the costs in time, energy, and risks associated with big-game hunting may sometimes outweigh the nutritional benefits of what is acquired through the pursuit of big game.

I should point out immediately that the goal of this book is not to argue that hunting in our evolutionary past was unimportant as a way of providing food. Instead, the issue that I am zeroing in on is why our ancestors spent so much time and effort pursuing really big and often quite dangerous prey when they could acquire adequate, and often comparable, amounts of protein and calories *on a day-to-day basis* by pursuing small game, or even insects, not to mention a variety of nutrient- and energy-rich seeds, nuts, and other plant foods, at far less cost in time and energy, and at greatly reduced risk of failure or bodily harm. In many cases the detailed quantitative data now becoming available for some of our best studied hunters and gatherers – for example, the San (also called

"Bushmen"; see Bank 1998; Biesele and Royal/O/oo 1997:10; Lee 2006) and Hadza in sub-Saharan Africa – are showing that if providing the family with food were the principal goal of male hunting activities they would do better by focusing their efforts on resources other than big game. In fact, to generate a steady, predictable input of food to the family larder, they might do best by doing more or less what the women do.

I have no illusions that the arguments I present in this book will instantly sway my readers to the view that big-game hunting evolved more for social and political reasons than for nutritional ones. In all honesty, I am still having trouble convincing myself. The traditional view seems so simple and compelling. Meat from large animals has always held a position of prominence in Euro-American culture. So it is no surprise that those same values have been extended to our explanations of how we as a species evolved. I still remember the catchy TV commercials from the late 1980s when actor James Garner touted the value of beef as "*real food for real people.*" That simple ad captured the essence of what underlies the big-game hunting perspective even today. What we then called "real" food would in today's more academic parlance be referred to as "high-quality" food. Bolstered by the theoretical elegance of diet breadth models and empirically by a lot of archaeological and taphonomic data, and despite some important but only marginally successful attempts to redirect our attention to the food-getting activities of women (e.g., Slocum 1975), big-game hunting is still seen by most today as the core of what hunter–gatherer foraging is all about.

My own path to the arguments presented in this book has been anything but direct. I have been interested in hunter–gatherer subsistence strategies ever since the late 1960s when I was a graduate student in anthropology and archaeology, but in those days I saw no reason to question the nutritional primacy of big-game hunting. While Richard Lee's famous Bushman studies of the 1960s emphasized the importance of plant foods and women's foraging activities in the subsistence practices of foragers outside of the arctic, to this day I am still struck by the irony of the fact that the most famous publication to emerge from those studies was entitled *Man the Hunter* (Lee and DeVore 1968), not *Woman the Gatherer* as one might have expected given the revelations of Lee's research. *Woman the Gatherer* (Dahlberg 1981; see also Chap. 7 in Martin and Voorhies 1975:178–211), a reaction to the androcentric big-game hunting bias of the *Man the Hunter* era, did not appear for another decade. As Fedigan (1986:62) puts it: "*Man the Hunter*, a model drawn from primate, ethnographic, and archaeological evidence, became the dominant theory of the 1960–1980 period."

> *Man the Hunter* [Lee and DeVore, 1968] never addressed the question of why women also evolved. Because of its failure to take the female sex into account in human evolutionary models, the book created a backlash against sexism that was centuries overdue in the study of humanity. Whole schools of anthropological thought coalesced, partly in reaction to the blatant failure of Washburn and Lancaster [1968] even to consider women in the evolutionary process. Female biological anthropologists in turn have taken *Man the Hunter* apart, analyzed its approach, and asked what role females played in human origins.
>
> Stanford (2002:108)

Despite the lip service paid to the importance of plant foods in hunter–gatherer diet during the 1960s and 1970s, undergraduates in virtually every introductory anthropology course offered at universities across the USA and Canada were weaned on the images from John Marshall's classic film, *The Hunters* (shot in 1952–1953, and released in 1957). In this fascinating glimpse into the lives of traditional African hunters and gatherers, students were treated to over an hour of footage documenting the uncanny skill of Bushman hunters and trackers as they relentlessly pursued a wounded but very mobile and uncooperative giraffe across the vast expanses of the Kalahari Desert (the film is actually a composite of several different giraffe hunts pieced together to create what appears to be a documentary of a single 5-day-long hunt; see Barnard 2007:57; Henley 2003:47–48). If plant foods played any significant role in the lives of the Bushmen, it was certainly not evident in this film.

My interest in big-game hunting continued following my graduate studies, and one of my first serious excavations as a young PhD was a late prehistoric (fifteenth century AD) bison kill – the Garnsey site – in southeastern New Mexico (Speth 1983). At the time I was digging the site, it never occurred to me that social forces, not just food, might have played an important role in the kill events that I was uncovering. The first inkling that all was not what it seemed came during the analysis of the masses of bones that I recovered from the site. These studies revealed that the hunters had done things that didn't make sense to me in terms of the conventional wisdom of the day. First, the hunters killed the bison in the spring and focused on bulls instead of cows, in striking contrast to the predominant pattern that had been documented over and over again in Northern Plains bison kills, where most events took place in the fall or winter and where the focus was clearly on cows, not bulls (e.g., Frison 1978).

My analysis of the Garnsey material showed that even those cows that had been killed were treated differently than the bulls: if a part was to be discarded, the chances were that the abandoned part was from a female, not a male. I began to ask myself why? If the hunters had gone through all the trouble of killing a cow, why would they throw parts of it away while keeping the equivalent parts from bulls? Perhaps it was simply a matter of bulk. Bison are very dimorphic animals (i.e., the males are much bigger than the females); hence, body parts from males were bigger and had more meat and marrow than the analogous parts from cows. But upon closer scrutiny it turned out that size wasn't the only factor. As I probed the data further, and at the same time began to explore the wildlife literature and the voluminous reports of early North American explorers, military officers, and fur-trappers, it became evident that the Garnsey hunters had preferentially targeted males over females because males in the spring generally were in better condition (i.e., they had more body fat) than females, most of which were either pregnant or nursing and as a consequence in much poorer shape.

The hunters were also selecting specific female body parts that were most likely to have significant reserves of fat in them at the time of the kill (spring). Body fat in wild ungulates (hoofed animals) that are nutritionally stressed is mobilized in an ordered sequence. The first to go is the fat under the skin, the so-called "back-fat" or subcutaneous deposits. If the stress persists, the fat around the kidneys and other internal organs is the next to be mobilized. If conditions remain stressful or deteriorate further, the next fat deposits to go are in the marrow cavities of the limb bones, often starting close to the body (proximally) and then gradually progressing toward the feet (distally). The Garnsey hunters seemed well aware of this depletion sequence because the bones they discarded in greatest numbers were not only from cows but the bones that were least likely to retain significant reserves of fat in the spring. In other words, fat, not protein, seemed to play a very prominent role in the hunters' decisions about what animals (male vs. female) to kill and which body parts to discard or take away.

These observations gave rise to the first small crack in my perception of why foragers hunted, a perception that was squarely though implicitly founded upon the assumption that men hunted big game because it was the most efficient way to acquire protein in large quantities. The Garnsey work showed that, at least in the spring, fat may have been more important to the hunters than protein. Excess protein would not simply be converted to calories or "love handles" as I had assumed; instead, protein intake above a certain threshold might lead to loss of body weight, something that is unlikely to be beneficial to most hunter-gatherers, and ultimately might be detrimental to their health. At first, of course, this realization did not seriously compromise the structural integrity of the big-game-hunting-equals-food-provisioning perspective that had been so deeply ingrained in my psyche since my graduate student days. The crack in the edifice remained relatively small. The Garnsey insights simply meant that protein might not always be the high-quality food that most paleoanthropologists at the time (1980s) assumed it to be.

So when I began thinking about this book several years ago I envisioned the arguments as a detailed exploration of the circumstances under which hunters might be more interested in the fat provided by big animals than by the lean muscle tissue. And a lot of the arguments my readers will find here are just that – evidence drawn from a wide range of medical, nutritional, and health science literature documenting the drawbacks, costs, and negative consequences that can arise from sustained high-protein intakes. But as I continued to pursue these issues and arguments, one nagging problem kept surfacing: *if large intakes of protein can be costly and risky to acquire, and above a certain threshold even deleterious to health, then why do hunters devote so much time and effort to killing big animals that yield protein in quantities that they and their families can't possibly consume safely?*

Over the past two decades or so, paleoanthropologists have increasingly come to accept the idea that meat, because of its high-protein content, may be an inefficient way to provide calories and at times even deleterious to health. Instead, many paleoanthropologists now suggest that hunters went after big animals, not just for meat, but especially for their fat content, particularly the fat in their brains and marrow. But this begs the question of why African foragers like the San and Hadza spend so much time and effort pursuing big animals when most of these animals remain lean throughout the year (e.g., Ledger 1968; Ntiamoa-Baidu 1997:65; Smith 1970; see also Burchell 1822:187; Burton 1860:281; Burton et al. 1873:27; Dane 1921:75; McKiernan 1954:99; Shostak 1981:76)? Does it make sense to go after them when the tissue that may be most vital to the hunter – the fat – is only a small fraction of the total yield? If fat is so critical, why not go after oil-rich nuts and seeds or grubs and other fatty insects? Why spend 5 days chasing a recalcitrant giraffe across a waterless landscape, like in John Marshall's movie *The Hunters*, when other resources could provide the same nutrients far more quickly and at considerably less cost and risk?

These thoughts led me to reexamine the wonderful body of detailed, quantitative subsistence data that has been generated by behavioral ecologists over the past decade or so for modern hunter–gatherers in Africa, the New World tropics, and elsewhere. This literature is a real eye-opener. Although we have known for years that foragers share big animals more widely than small game or plant foods, these recent studies have shown that much of the sharing of big animals is with non-kin, and not uncommonly with a distinct bias in favor of unrelated adult men. In other words, the hunters aren't necessarily provisioning their spouse or kids, as all of us had assumed, but other members of the group who may not be closely related to them.

Also, only certain hunters become really accomplished at what they do, creating an asymmetry in these sharing relationships that may persist for years, if not an entire lifetime. This observation challenges the traditional idea that meat-sharing served over the long run to even out the day-to-day variability in individual hunting success ("pooling risk" in the parlance of behavioral ecologists). Moreover, our quintessential hunters, the San and Hadza, fail to acquire prey far more often than they succeed, and when they manage to wound an animal they spend hours, even days, tracking it, often failing to find it or get to it before carnivores have devoured the carcass. And finally, a number of hunter-gatherer studies have shown that men would do better in terms of overall *day-to-day* returns if they did what women did rather than engaging in costly and unpredictable hunts of large game. These and other arguments, spelled out at some length in the pages to follow, raise serious doubts about big-game hunting as primarily a food-getting enterprise. While hunting of large animals certainly produces edible returns, the motivating factor underlying the evolution of big-game hunting more likely lay in the sociopolitical realm, not in putting food on the family table.

I feel compelled to comment briefly here on how this book actually came into being, since the process was totally unlike anything I'd done before and has changed forever the way I do scholarly research. For better or for worse, this book is entirely a child of the Internet – lock, stock, and barrel. When I began to put the ideas that form the core of this book to (digital) "paper," I happened to be on Hebrew University's Givat Ram campus in Jerusalem coding mountains of Middle Paleolithic (Neanderthal-period) animal bones. Each afternoon, when the aches in my back told me I had been sitting hunched over a microscope long enough, I retired to a little bed-and-breakfast a few hundred meters from the lab, stretched out on the bed, propped my laptop up with a pillow, connected to Hebrew U's WiFi network, and commenced downloading literally hundreds of articles – god knows how many different scientific and technical journals – via a link to the University of Michigan's main library system (I literally never set foot in a library during the entire process of writing this book). When Michigan didn't have the online version of a particular periodical, which was true for the early issues of a number of them, and for some of the more obscure applied food- and animal-science literature, I would purchase online versions directly from the publishers (at up to $30 a pop, this ultimately turned into quite an expensive venture). When that wasn't possible either, I approached the authors directly via email, and sometimes had a pdf of the article on my (computer) "desktop" within 5 min, and a "long" wait might mean 12 h, or, god forbid, 24 h. I could accomplish in an hour or two from my bed thousands of miles away from my real office what would have taken me months in the "good old days," combing the stacks of the more than 20 divisional libraries on Michigan's main campus, thumbing through journals, hauling teetering piles of massive bound tomes to the nearest copy machine (which was invariably already in use, out of order, or out of paper), quietly cursing when an issue was checked out, misshelved, or missing, and sometimes driving all the way to East Lansing, Michigan, 60 miles away, in a blinding snow storm with a stack of dog-eared 3 × 5 cards to use Michigan State University's library. As a last resort, I would try to get the item through interlibrary loan, which often took weeks.

In the process of Web surfing from the quiet comfort of my guest room, I discovered lots of unfamiliar but interesting journals, and even entire disciplines that I never knew existed. As virtual articles accumulated on my virtual desktop, I entered them into a bibliographic database which by now contains more than 17,000 entries, each reference accompanied by a string of searchable keywords and detailed notes on the content with appropriate page numbers. So when it came to actually writing a section of the book, a quick keyword search brought up all of the relevant references and from there it was an easy matter to compose the text. When I encountered an obvious gap in my argument – for example, some piece of missing data or a case study that would provide an example of a particular phenomenon – I went back on the Web. When I encountered an unfamiliar technical term, or when I needed to know the full name of an early African explorer or the dates of his expedition, a few seconds searching the Web and I had the information.

A wonderful benefit of this procedure is the fact that I not only ended up with thousands of keyword-searchable references in my bibliographic database, but I have most of the articles as well (as pdf files), and yet the computer still weighs the same miniscule 5 lbs that it did when I bought it. Wherever I go now – be it my lab, an airport waiting lounge, motel room, train, or in front of a tent on a rockhounding trip – the "library" is right there with me. So when I'm stranded somewhere waiting for an overdue flight, instead of going into mental "veggie" mode to wile away the hours, I can pull out the computer and get some work done (accompanied by an endless variety of music if I feel so inclined). I've taken real paper, the kind made from trees, almost totally out of the loop. In fact, most of my journals, many "board feet" worth, recently went to a needy university library in Ho Chi Minh City, Vietnam. Other journals are lined up, ready to go, as soon as they become available online. Even my clumsy banks of four-drawer filing cabinets are rapidly being purged of their contents and disappearing. The world's forests are breathing a collective sigh of relief…

There is another real value of the Internet age. Virtually every book in the libraries of a number of major research universities in the USA – and we're talking about millions of volumes – has been scanned, or will be scanned by *Google*™ in the not-too-distant future, and most of these are now searchable at some level (i.e., *snippet*, *limited preview*, *full view*). Likewise, many research museums and other scholarly institutions are systematically digitizing their own publications and making them available to the public, often for free. Each year more and more of these become available online. Many of the older books digitized by *Google*™ and other organizations, particularly those written in the eighteenth and nineteenth century, are now in the public domain and can be downloaded in their entirety and, with a little OCR magic from *Adobe Acrobat® Pro*, can be converted to a form that is keyword-searchable. For example, many years ago I read an early twentieth-century monograph published by New York's American Museum of Natural History that contained an interesting description of Plains Indians eating the fetus of a bison. The circumstances under which people eat such immature individuals is of interest in the present context because fetuses and newborns of most ungulate species have very little body fat and, for that reason, are often ignored. So I wanted to find that particular quote in order to see if the author happened to mention the time of year when the behavior had been observed. I discovered that in the interim the monograph had become available in digital form. So I downloaded the entire document, a process that took all of about 2 min, and searched for the word "fetus," which took at most another couple of seconds. No result. On a hunch, I changed the spelling from "fetus" to "foetus" and, bingo, there it was. Only a few years ago finding that quote might have taken hours, if you include the time it took to drive into the university, find a place to park (utterly hopeless after 9:30 AM), walk from there to the library, thumb through the card catalog to get the call number (which often meant trying to figure out how the item in question had been indexed, a nightmare with monographs), check a map of the library to figure out what floor it was on, find the book in the stacks or rummage the reshelving carts in hope of finding it, photocopy the relevant pages, and then return home again, perhaps to find that you had forgotten to jot down a critical part of the citation.

There is another truly invaluable benefit of the digital age to the scholarly enterprise. How often over the years I have heard one of my colleagues bemoan the fact that none of the present generation of graduate students ever reads anything that is more than 10 years old (I'm sure that same accusation was leveled at me years ago, and justifiably so) – "if it isn't new, it probably doesn't have anything worth reading in it, so why bother" (in archaeology the notable exceptions to this are site reports; these are timeless because you can only dig a site once). But with so much of the early literature now almost instantly at one's finger tips online, in a matter of minutes you can keyword-search hundreds, maybe thousands, of tattered, leather-bound treasures that have been locked away for decades in the dusty bowels of "rare book rooms." While some number of these decaying tomes have been reprinted, so they aren't truly inaccessible, until now the only way you could search them was to sit down in a cramped library carrel hidden away somewhere in the stacks, and painstakingly thumb through them cover to cover. Now, in a matter of seconds you can plow through them and download the ones that look interesting.

A few examples will illustrate just how wonderful and revolutionary this new information technology is. Just searching on the word "pemmican," a topic I will return to later, instantly brings up hundreds of nineteenth-century accounts that mention the word in some context, and among these are many gems – extremely informative descriptions of precisely how to make pemmican, the proper mix of dried meat and fat, which cuts of meat and which types of fat are most useful, and the difficulties an explorer or trapper or fur trader might experience if the pemmican didn't have the right mix of ingredients. While these nineteenth-century accounts obviously don't couch their discussion in terms of amino acids, rate-limiting enzymes, or urea synthesis and excretion, they nonetheless make it patently clear that the traveler who for whatever reason had to rely on lean meat without an adequate supply of fat or some alternative source of carbohydrates was in for tough times. In the process I discovered *charqui*, a South-American variant of jerky and probably the word from which "jerky" was derived, bringing up hundreds of additional references, and that led me to *Kavurmeh* or *Kavurma*, a Near Eastern cousin of pemmican, and again many new references and insights. Even as this book went to press I was still finding more interesting threads to follow in what has become an almost limitless digital universe.

Here's another interesting example of the kinds of insights that await discovery in this newly emerging digital world. As first pointed out to me by Michael C. Wilson of the Department of Geology at Douglas College (New Westminster, BC), and amply confirmed by a search of *Google*™ *Books*, these early accounts hint at the possibility that elk fat, at least under certain circumstances, is less palatable than fat from other North American cervids, and that explorers like Lewis and Clark had more difficulty preserving its meat:

> The hair is usually of a sandy red; and they are frequently called by the English who visit the interior parts of the country, red deer. Their flesh is tolerable eating; but the fat is as hard as tallow, and if eaten as hot as possible, will yet chill in so short a time, that it clogs the teeth, and sticks to the roof of the mouth, in such a manner as to render it very disagreeable.
>
> Hearne (1971[1795]:360)

> The fat of the elk partakes of the nature of tallow, and is much less fusible than that of other animals, so that unless eaten very hot it consolidates and adheres to the mouth.
>
> Keating (1825:16)

> The external fat is so hard as to make special precautions necessary to prepare this venison for the table in order to appreciate its full excellence. It must be served hot and kept hot, or else if there be much fat in it one will find a thin scale of the fat coating the roof of the mouth, which to most persons is very disagreeable…
>
> Caton (1877:407)

> The Elk or what the Canadians call Biche rut &c &c about the same time as the others – they make a curious whistlening [sic] noise when uneasy about or looking after their mate – they are reckoned the handsomest of all wood animals, & they become by far the fattest, but the least that their fat or Grease is exposed to the air it congeals in a moment & becomes exceeding [sic] hard….
>
> Nelson (2002:159)

> They resolved, therefore, to remain 1 day where they had killed [the elk], so that the skin might be dried and receive a partial dressing. Moreover, they intended to "jerk" some of the meat – although elk-venison is not considered very palatable where other meat can be had. It is without juice, and resembles dry short-grained beef more than venison. For this reason it is looked upon by both Indians and white hunters as inferior to buffalo, moose, caribou, or even the common deer. One peculiarity of the flesh of this animal is, that the fat becomes hard the moment it is taken off the fire. It freezes upon the lips like suet, and clings around the teeth of a person eating it, which is not the case with that of other species of deer.
>
> Reid (1889:148)

> Another peculiarity is that this is the most difficult of all to preserve. The difficulty of curing Elk meat, is first mentioned by Lewis and Clarke, at their winter camp near the month of the Columbia River, about Christmas in 1805. They say. "Our Elk meat is spoiling in consequence of the warmth of the Weather – though we have kept a constant smoke under it." Again, "The whole stock of meat being now completely spoiled our pounded fish became again our chief dependence."
>
> Caton (1877:407)

> There was also a want of meat, for the buffaloe were not to be found, and though the elk are very abundant, yet their fat and flesh is more difficult to dry in the sun, and is also much more easily spoiled than the meat or fat of either the deer or buffaloe.
>
> Lewis and Clarke (1815:345–346)

Interestingly, these early reports receive support from a relatively recent forensic study, also kindly furnished by Mike Wilson, which shows that the fatty acid composition of elk meat is clearly distinguishable from that seen in other North American cervids (McClymont et al. 1977). Incidentally, I have found no mention of a comparable problem with the meat or fat of red deer, a close cousin of the American Elk. Perhaps the distinctive properties of the fat in elk meat may help account for the seeming underrepresentation of elk bones in archaeological sites in many parts of western North America, despite the abundance of these animals encountered by eighteenth- and nineteenth-century travelers.

Could there be similar differences in the properties of the fat among the many species of African antelopes that might influence a hunter's decisions about which to exploit and which to avoid when circumstances permit? A comment by Frederick Selous, a nineteenth-century explorer and hunter in southern Africa, suggests that the answer is "yes," and the antelope in question – the wildebeest – is one of the more common denizens of the African grasslands (see also Earl of Suffolk and Berkshire 1911:319; Oliver 1993:217–218):

> In the evening, being rather short of meat, I shot a tsessebe antelope, in very fine condition. Though the meat of these antelopes is tolerably good, the fat, like that of the wildebeest, turns hard, unless very hot, and sticks to the palate in a most disagreeable manner.
>
> Selous (1907:220)

I was also amazed at some of the surprisingly informed taphonomic insights that I found buried in these ancient digitized tomes, insights that I naively thought we owed entirely to twentieth- and twenty-first century paleontologists and zooarchaeologists. Taphonomy had its formal beginnings in paleontology in the 1940s largely through the pioneering work of Russian-born Ivan Efremov (1940). Then, over the next three to four decades, taphonomy found its way into mainstream archaeology, introduced by scholars such as C. K. (Bob) Brain (1967, 1969), Kay Behrensmeyer (1975), and Lewis Binford (1981), and by the mid- to late-1980s had assumed a central position within the discipline. Anticipating issues that I will discuss more fully a little later in the book, taphonomy is the study of what happens to the bones of animals from the time they die until their bones become part of the fossil or archaeological record. Much current taphonomic work looks at what modern bone-crunching and bone-schlepping predators like hyenas do to bones. To my astonishment the Rev. William Buckland did precisely that almost 200 years ago in his famous *Reliquiae Diluvianae* (1824). I had certainly heard of the book – it gets mentioned frequently in discussions of the development of ideas about the antiquity of humans and their association with the remains of extinct animals. But I had never read it – in part because it was too old to bother with, in part because the Latin title was so off-putting – and I certainly had no idea that Buckland thought about taphonomy, let alone in such a sophisticated way:

> Since this paper was first published, I have had an opportunity of seeing a Cape hyaena at Oxford, in the travelling collection of Mr. Wombwell, the keeper of which confirmed in every particular the evidence given to Dr. Wollaston by the keeper at Exeter 'Change. I was enabled also to observe the animal's mode of proceeding in the destruction of bones: the shin bone of an ox being presented to this hyaena, he began to bite off with his molar teeth large fragments from its upper extremity, and swallowed them whole as fast as they were broken off. On his reaching the medullary cavity, the bone split into angular fragments, many of which he caught up greedily and swallowed entire: he went on cracking it till he had extracted all the marrow, licking out the lowest portion of it with his tongue: this done, he left untouched the lower condyle, which contains no marrow, and is very hard. The state and form of this residuary fragment are precisely like those of similar bones at Kirkdale; the marks of teeth on it are very few, as the bone usually gave off a splinter before the large conical teeth had forced a hole through it; these few, however, entirely resemble the impressions we find on the bones at Kirkdale; the small splinters also in form and size, and manner of fracture, are not distinguishable from the fossil ones. I preserve all the fragments and the gnawed portions of this bone for the sake of comparison by the side of those I have from the antediluvian den in Yorkshire: there is absolutely no difference between them, except in point of age. The animal left untouched the solid bones of the tarsus and carpus, and such parts of the cylindrical bones as we find untouched at Kirkdale, and devoured only the parts analogous to those which are there deficient.
>
> Buckland (1824:38)

In 1863 the renowned geologist, Charles Lyell, while commenting on the archaeological remains recovered by Édouard Lartet from a cave near Aurignac in southwestern France, makes another astute taphonomic observation concerning the probable role of hyenas in the formation of ancient faunal assemblages:

> The bones of the herbivora were the most numerous, and all those on the outside of the grotto which had contained marrow were invariably split open, as if for its extraction, many of them being also burnt. The spongy parts, moreover, were wanting, having been eaten off and gnawed after they were broken, the work, according to M. Lartet, of hyenas, the bones and coprolites of which were plentifully mixed with the cinders, and dispersed through the overlying soil… These beasts of prey are supposed to have prowled about the spot and fed on such relics of the funeral feasts as remained after the retreat of the human visitors, or

> during the intervals between successive funeral ceremonies which accompanied the interment of the corpses within the sepulchre.
>
> Lyell (1863:185–186)

Another example of the marvelous things one can stumble into when keyword searching the "virtual" editions of books that have been quietly guarding their secrets for years or, in this case, for millennia. Years ago, in the 1970s, when I first began working on faunal remains, I wondered why immature animals were so strikingly underrepresented in many archaeological assemblages. Following upon the pioneering work of people like Bob Brain (1967, 1969) and Kay Behrensmeyer (1975), the 1970s was also the decade when the field of taphonomy began making its grand entry into mainstream zooarchaeology and it offered a very simple and compelling answer – the unfused elements of young animals were fragile and easily destroyed by ravaging carnivores, trampling, and other natural processes like weathering and chemical dissolution (e.g., Lyman 1994). But I noticed in several of the assemblages I was analyzing that the limb bones of the youngest animals not only displayed very few signs of carnivore damage, many were also intact, or nearly so, while those from fully adult animals had almost invariably been broken open for marrow. In my search for an explanation, I began perusing the contemporary wildlife literature and came upon what seemed to be a consistent difference between the bones of adult animals and immature ones – the marrow of very young animals often contains much less fat than the marrow of adults. In my naïve exuberance, fostered no doubt by the thrill of "discovery" after sitting cross-legged for days on end on the floor of the science library thumbing through unfamiliar journals, I thought I had stumbled on to something that was genuinely new; my recent Web surfing revealed that Aristotle had already made that same observation quite explicitly in his "Historia Animalium" in 350 BC!

> Concerning marrow, for this is one of the fluids which exist in some animals. All the natural fluids of the body are contained in vessels, as the blood in the veins, and the marrow in the bones, and others in membranes, skin, and cavities. The marrow is always full of blood in young animals; but when they grow older, in the adipose it becomes adipose, in fat animals fatty.
>
> Aristotle (1897:69)

Here is one final example of the marvels that one can discover searching the Web: I was surprised to find that Frederich Engels anticipated by more than three-quarters of a century one of Richard Lee's more important insights about the role of plant vs. animal foods in the foraging strategies of hunting and gathering societies like the San. In Lee's (1968:41) words: "…the Bushmen of the Dobe area eat as much vegetable food as they need, and as much meat as they can." Frederich Engels, writing in 1884, doesn't sound all that different:

> Exclusively hunting peoples, such as figure in books, that is, peoples subsisting *solely* by hunting, have never existed, for the fruits of the chase are much too precarious to make that possible. (Engels, 1972:40) [Ausschliessliche Jägervölker, wie sie in den Büchern figurieren, d.h. solche, die nur von der Jagd leben, hat es nie gegeben; dazu ist der Ertrag der Jagd viel zu ungewiss.] (Engels, 1884:30)

The two most obvious downsides of this wholesale shift from paper to digital bits and bytes, aside from a serious case of eye-strain and a cabinet full of DVDs devoted to backing up the many gigabytes of pdf files now in my computer, is reflected by the length of my bibliography – what one reviewer referred to as "Speth's missionary zeal" – and the number of direct quotes in the text. First, a comment about the number of references. When all of this literature is so readily available at one's finger tips, there is no excuse not to use it. Why should others have to reinvent the wheel? One obligation of any piece of research is to situate the work within the broader context of existing knowledge, and the references are an essential part of that.

The citations are also a way of giving credit where credit is due. All too often people cite only the work of a very limited circle of familiar authors – the "old boy" network – giving the (false) impression that they are the only ones who have worked on a problem or, worse yet, that they are the only ones whose ideas are interesting or worthwhile enough to cite. There's an unbelievable wealth of interesting and creative thinking out there and the Web allows one to find it easily and get one's hands on it at lightning speed, regardless of where it originates.

The other downside – the number of quotes in the text – is undoubtedly in part a reflection of my laziness and the fact that one can now "cut and paste" text so easily in this computer age that it becomes a quick way of piecing together an argument. However, using a fair number of quotes is not all bad either. It's a way of letting the author who came up with an idea express it in his or her own words, which in all probability will be clearer, more succinct, and in the long run more compelling than my not so elegant attempts to paraphrase it.

Unfortunately, there is one area where the Internet still seems woefully antiquated, almost helpless – online translation. While OCR has made incredible strides in digitizing text, the gobbledygook that I usually got back when I attempted to translate some portion of a text, even when the text of concern was written in an academically mainstream language like French, German, Spanish, Italian, or Russian, was (putting it politely) pathetic. Using the Web I was able to access publications in an amazing number of different languages, but my linguistic skills are often not up to the task, and the online translators available on the Web, as well as through software that I (unfortunately) invested a considerable amount of money in, produced results that, at best, were less convincing than my attempts with a dictionary, and, at worst, amounted to pure (and sometimes hilarious) gibberish. That has led to a clear bias in what I have been able to read and use effectively – a reasonable amount of French, a smattering of Spanish, Italian, and German, and not much else. For that I apologize. I hope that in the not-too-distant future computer translators improve to the point where language is no longer a major barrier.

I write a book of this nature with considerable trepidation. I am an archaeologist by training, not a nutritionist or a behavioral ecologist. So I am pulling together arguments from diverse fields that have their own complex methodologies, assumptions, histories, and conventional wisdom. I can only hope that in doing so the insights that emerge here outweigh the many blunders I undoubtedly make along the way. Of course, nutritionists and behavioral ecologists interested in the evolution of human diet face much the same dilemma in the opposite direction. While nutritionists are fluent in the concepts, methods, assumptions, and data of biochemistry, nutrition, and health sciences, and behavioral ecologists are experts in evolutionary theory and behavioral modeling, these specialists are confronted by a body of archaeological, taphonomic, and fossil data, and associated theoretical baggage, that is not only voluminous but complex, not uncommonly contradictory, and often quite contentious. Wading unwittingly into paleoanthropology and archaeology can be akin to wandering into a mine field without a detailed map of exactly where, and where not, to step…

As I waded through many hundreds of papers on countless different issues related to human origins and evolution, hunter–gatherer subsistence practices, and human health, diet, and nutrition, what became increasingly clear to me was the pressing need for more direct interaction and exchange between scholars in paleoanthropology, archaeology, primatology, behavioral ecology, human nutrition, and genetics. Each of these fields has become too vast and too complex for any single individual to correctly and productively integrate the data and insights from such a broad and multifaceted landscape of scholarly knowledge. But without such interchange and integration our understanding of our origins, our evolution, and our present condition will remain woefully incomplete. Of course, there have been such attempts at integration in the past, a number of them, but not enough and not recently enough. My hope is that this book will encourage scholars from the many different disciplines that share a common interest in human evolution to find new ways, and more permanent ways, to cross the disciplinary boundaries that presently divide us. There is so much we can yet learn from each other…

# Acknowledgments

My interest in nutrition, and particularly in protein, began over two decades ago when my results from studying a late prehistoric bison kill in New Mexico (Garnsey Site) converged on ideas that Kate Spielmann was developing through her work on maize farmers at a more or less contemporary farming community located not far from the kill (Pecos Pueblo). We both realized that during times of resource stress not all macronutrients were created equal, and high-protein intakes seemed to stand out as particularly problematic. This led to a joint publication on the strategies that hunter–gatherers might use to avoid recurrent periods of excessive protein intake (Speth and Spielmann 1983), sparking an interest that has been with me ever since. At more or less the same time, when the ink on my PhD diploma had yet to fully dry, Glynn Isaac invited me to participate in a Gordon Conference on diet in human evolution, a fantastic experience both professionally and personally, that further sparked my interest in nutritional issues. Despite detours over the intervening years, I maintained an interest in the role that protein and meat-eating played in hominin origins and evolution. As these ideas gradually developed, I benefited enormously from the assistance, guidance, insightful comments, and suggestions offered by a great many people. And while not everyone will agree with where I've taken these arguments, and many have probably forgotten that they had anything to do with them, their help is nonetheless most gratefully acknowledged. I particularly want to thank Leslie Aiello, Susan Antón, George Armelagos, Françoise Audouze, Graham Avery, Ofer Bar-Yosef, Anna Belfer-Cohen, Robert J. Blumenschine, Barrett Brenton, W. F. Buchanan, Henry T. Bunn, Graham Burdge, George Cahill, Loren Cordain, Tamar Dayan, Richard Ford, Roberto Frisancho, Stanley Garn, Naama Goren-Inbar, Alfred Harper, Kim Hill, Robert Hitchcock, Liora Horwitz, Erella Hovers, Glynn Isaac, Greg Johnson, Richard Klein, Steve Kuhn, Harriet Kuhnlein, Alan Mann, Paul Martin, Bill McGrew, Lauren Milligan, Katharine Milton, Preston Miracle, John Mitani, Eugene Morin, Dieter Noli, Jim O'Connell, John Olsen, Sue O'Shea, John Parkington, Rivka Rabinovich, Richard Redding, David Rush, Michael Schiffer, Jeanne Sept, Pat Shipman, Kate Spielmann, Craig Stanford, Eitan Tchernov, Francis Thackeray, Erik Trinkaus, Robert Whallon, Polly Wiessner, Ed Wilmsen, Bruce Winterhalder, Milford Wolpoff, Richard Wrangham, Henry Wright, and Lisa Young. I owe a special debt of gratitude to Loren Cordain, who generously read the manuscript at two different stages in its metamorphosis and

provided me with advice, critique, and innumerable helpful leads and suggestions. He also provided me with the encouragement I needed to tread into nutritional terrain where I am truly a novice. While Loren is in no way responsible for the final product, whatever its shortcomings he gave me the courage to take the plunge. For that I am eternally grateful. I would also like to thank Kristen Hawkes and Mary Stiner, both of whom spent a lot of time with an earlier draft of this undertaking. Their comments were spot on, and helped me to clarify a number of the arguments, address key issues that I had omitted or side-stepped, and improve the overall organization and flow of the manuscript. And of course the successful completion and publication of the book would not have been possible without the help of the "Interdisciplinary Contributions to Archaeology" series editor, Jelmer Eerkens, and the archaeology editors at Springer in New York, Teresa Krauss and Katherine Chabalko. A number of individuals and institutions provided valuable assistance in getting access to a wide range of images, many though not all of which are included in this volume. Among these were Jim O'Connell, who made available several wonderful photos of the Hadza. Similarly, Marylène Patou-Mathis allowed me to reproduce a superb 1985 photo of a San man and his bow. An earlier (1955) image of a San archer was made available with the help of Cynthia Close and Frank Aveni from The Marshall Family Collection courtesy of Documentary Educational Resources (DER). Bob Hitchcock generously offered me access to a number of his color slides on various facets of San life in the Kalahari. I am also delighted to be able to include Jay Matternes's beautiful painting of early hominins butchering a zebra. Thanks also to Elizabeth Sandler of the American Association for the Advancement of Science, Rights and Permissions, for her efforts assisting me in obtaining the go-ahead to reproduce a cover from a 1983 issue of *Science*. While it ultimately proved too expensive and too complex to obtain the necessary artist's permission, Elizabeth's efforts are gratefully acknowledged. Melissa Levine and Greg Grossmeier, copyright specialists in the University of Michigan Library, were both very helpful in suggesting ways to navigate through the almost impenetrable bureaucratic fog surrounding the embassies of Botswana and Tanzania in what proved to be a futile attempt to determine whether permissions were needed to reproduce images of stamps and coins from these countries in a scholarly work on human evolution and, if so, how one might go about obtaining such permissions. After a good faith effort of sending emails to the embassies and to the respective governmental postal agencies and central banks in both countries, all of which went unanswered, and phone calls to the embassies in the USA and direct personal visits to the embassies (high commissioners) in London, I came to the conclusion that no one had a clue how this might be done and no one was willing to help me find out. Since similar images are already widely available online, including via *Wikipedia* and various royalty-free stock image distributors, and since they are distributed widely in published catalogs, albums, and guides for coin and stamp collectors and dealers, I gave up trying to obtain written permissions and used the images that I arranged to be photographed from specimens in my possession. These photos were taken by Kay Clahassey of the University of Michigan's Museum of Anthropology, for which I am very appreciative. In addition, I extend my gratitude to Fiona Bradley and the Royal Botanic (Kew) Gardens, Aase Solvej Hansen, Helen Moss, Emmy De Caluwé, and Spencer Woodard for images of some of the key plants that were, and continue to be, important to African hunters and gatherers. Thanks are also due to Rob Toms, Bernie Olbrich of afripics.com, Jet de Boer of FotoNatura.com, and Lee Dalton and Kris Hook of Photoshot.com for help in getting images of mopane worms. I also wish to acknowledge the various photos that were made available through the large online image libraries of Dreamstime.com and istockphoto.com. And last but not least, over the many years that these ideas have been gestating, support for various facets of the work have come from a number of different sources, including the Museum of Anthropology and the Horace H. Rackham School of Graduate Studies, both of the University of Michigan, as well as from NSF and the Leakey Foundation.

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# Chapter 1
# Introduction

> *The reconstruction of hominid evolutionary history is a scientific problem of exceptional difficulty. Direct observation is impossible; fossil and archaeological evidence are scarce. It is also a pivotal problem, not only because of the scope and crucial character of the issues it addresses about modern human nature, but also because of the challenge it presents to evolutionary biologists. Humans are so singular a species, with such zoologically unprecedented capacities, that it is a major biological mystery how evolutionary processes could have produced us out of our primate ancestors.*
>
> Tooby and DeVore (1987:183)

Since its inception, paleoanthropology has been closely wedded to the idea that big-game hunting by our hominin ancestors arose, first and foremost, as a means for acquiring energy and vital nutrients, especially protein, and that a significant part of the human story can be seen as a record of our ever-increasing prowess and sophistication at taking large prey. The assumption that big-game hunting was primarily motivated by nutritional needs has rarely been questioned, though this is perhaps not too surprising. After all, few things in human evolution have seemed so intuitively obvious – meat is a nutrient-rich food, full of protein with the ideal array of essential amino acids, all in the right proportions; and big animals provide meat in large convenient packages, making them, hands down, the preferred target for foragers who have the organizational and technical means to kill them. Add in a "dash" of prestige for good measure, and you have the classic model of *Man the Hunter*. But what seems so obvious and compelling at face value may be less so when looked at more closely. Thus, the central goal of this book is to explore and ultimately challenge the view that *big-game* hunting by our hominin ancestors was primarily a nutrition-getting enterprise. Instead, I develop the argument that, for our African forebears, *big-game* hunting was first and foremost about social, reproductive, and political goals, prestige among them, and that the nutritional component was actually the "dash" that got added in.

I deliberately underscore the words "big game" here because this book is not a blanket dismissal of all animal foods as sources of nutriment. There is no question that animals, including insects and other invertebrates, provide a valuable source of protein, as well as fat, various micronutrients (e.g., vitamin $B_{12}$), and of course

J.D. Speth, *The Paleoanthropology and Archaeology of Big-Game Hunting*,
Interdisciplinary Contributions to Archaeology, DOI 10.1007/978-1-4419-6733-6_1,

calories. Rather, my focus in this book is explicitly on the big ones – the large, often fleet-footed, sometimes dangerous prey like the many species of African antelope, warthogs, buffalo, hippos, John Marshall's famous giraffe in the film *The Hunters*, and other such animals that foragers for the most part do not passively trap or snare, net, pluck, scoop up, poke with a stick, dig out of burrows, or, like tortoises, merely pick up from the ground.

I approach the "big-game-hunting-as-food-getting" issue from a number of different, though overlapping and interrelated angles. I begin with a look at the history of the West's "love affair" with protein, particularly animal protein, a relationship that began in Africa in the 1930s with the first formal recognition of *kwashiorkor*, an extreme form of protein malnutrition, and grew to a fever pitch in the 1950s and 1960s as more and more nutritionists and health professionals came to see protein as the root cause of malnutrition and hunger worldwide. In the 1970s, perspectives began to change as the health professions took a broader look at the causes of world hunger and concluded that the real culprit was not protein deficiency but inadequate overall calorie intake, combined with shortages of various micronutrients and the negative health consequences that often accompany poverty and squalid living conditions.

Not surprisingly, paleoanthropology got caught up in this same trend. While paleoanthropologists have always recognized that early hominins were omnivores, not carnivores, there has nonetheless been the widespread assumption that meat obtained by hunting large game played a central role in our evolutionary history, and that the nutrient that made meat so valuable and attractive was protein [for a recent and refreshingly different perspective, see Alemseged and Bobe (2009); these authors see meat, initially at least, primarily as a fallback food for early *Homo* during hard times]. It was not until the 1980s and 1990s that advocates of the "hunting hypothesis" began to recognize the nutritional shortcomings of the lean meat that one typically gets from African game, and since then many paleoanthropologists have begun to place greater emphasis on the fat that our ancestors could have gleaned from the marrow and brain of their large-bodied prey.

I then take a close look at some of the negative sides of protein. Most important of these is the limit to the amount of protein that one can safely consume on a daily basis. Though often misleadingly depicted in the literature as a percentage of total calories, the limit appears to be finite and, taking into account a certain degree of adaptation, relatively inflexible. What this means is that a forager can safely use only a portion of the protein provided by a large carcass and the rest must either be given away or wasted. However, a look at the protein- and fat-rich plant foods, insects, reptiles, small mammals, and other such resources that are available to modern hunter-gatherers at more or less the same time of year that they devote the lion's share of their efforts to pursuing big game suggests that they could probably fulfill their daily protein and fat needs faster and far more reliably with little or no recourse to big-game hunting.

I then explore in more depth the assumption that foragers can circumvent the nutritional problems of lean meat consumption by focusing more on the marrow and brain gleaned from their kills. Although this view is now fairly widely accepted, a review of the Bushman and Hadza literature suggests that, by comparison to other available resources, African ungulates are an expensive, unreliable, and probably inadequate source of fat to warrant the time and effort required to make a successful kill. *Their hunting activity appears to reflect the demands or expectations of their traditional gendered division of labor, not their nutritional needs.*

I also look at a number of other limitations of high-protein intakes. Among these are the potential impact that such intakes have during pregnancy on the health of the fetus and final birth outcome, the considerable inefficiency of using protein as a source of calories, the increased water needs that may accompany a diet high in protein, and the controversial effect that protein ingestion has on calcium metabolism.

Understandably, the high degree of encephalization in humans has attracted a great deal of attention in paleoanthropology, since it is one of the most striking contrasts between us and our nearest primate relatives. For many years it was common to see arguments in paleoanthropology that linked our unique degree of brain enlargement to meat-eating, with the sometimes explicit, more often implicit, assumption that the growth of our large brains requires high intakes of protein. I review a wide range of studies to show that our brain needs a lot of energy and a fatty acid known as docosahexaenoic acid (DHA), but not much protein. A look at the amount of protein in the milks of a wide range of different mammals makes this patently clear – humans have the lowest-protein milk in the mammalian world.

An interesting argument has emerged over the last decade or so that has shifted the focus in scenarios of human evolution from meat and protein to foods high in DHA. These arguments tend to follow two different trajectories, one maintaining that the best sources of DHA are aquatic foods, such as fish and molluscs, a position for which there is scant archaeological support, and the other suggesting instead that early hominins targeted the DHA-rich brains of large game, supplementing their diet with marrow fat (which supplied energy but little or no DHA). The latter position keeps the focus on big game and is therefore an important part of this discussion.

The literature on DHA is vast and daunting. The reason it has become so important nowadays is that humans are thought to be very inefficient at biosynthesizing their own DHA and instead have to acquire preformed DHA through their diet. In the modern Western world, where most people do not consume a great deal of fish or other DHA-rich foods, pregnant and nursing mothers may not get enough DHA to meet the needs of their developing fetus or nursing infant. I explore the DHA issue at some length and join a growing but still minority view that pregnant women (and presumably early hominin women as well) are actually capable of biosynthesizing more DHA than is often believed. In other words, the DHA argument, interesting as it is, may ultimately prove to be unnecessary in discussions of encephalization in our hominin ancestors.

In closing, I combine various nutritional insights with subsistence data drawn from a number of well-documented modern hunter-gatherers that together provide at least a reasonable basis for arguing that big-game hunting evolved largely in the social and political arena, not as an essential way of putting food on the table.

# Chapter 2
# How Do We Reconstruct Hunting Patterns in the Past?

> *Everything preceding* [Christianity], *everything from the earliest heathen period hangs before us as if in a thick fog, in an unmeasurable period of time. We know it is older than Christendom, but if by a few years or a few hundred years – even maybe a thousand years – older, is sheer guesswork and at best only likely hypotheses….*
>
> Nyerup (1806:1), translated by Rowley-Conwy (2007:35)

> *Archaeologists recover material remains of past human behavior. And, like geologists, archaeologists must look to the contemporary world for hypotheses that account for the formation and deposition of these material remains. This is an important point: Observation of the contemporary world provides the information necessary to infer past human behavior and natural processes from observations on archaeological objects.*
>
> Kelly and Thomas (2009:179)

> *Most analysts agree that a shift in diet was crucial to the evolution of early Homo. The problem lies in identifying the resources involved and showing how their exploitation led to the indicated changes in morphology, life history, and ecology.*
>
> O'Connell et al. (2002:834)

Since this book is about big-game hunting – and, as will become apparent shortly, scavenging as well – in the distant past, some of my non-paleoanthropologist readers may wonder how, in the absence of written records, we find out what people hunted, and how they went about it, thousands, hundreds of thousands, or even millions of years ago. Hence, before launching into a discussion of *why* ancient humans hunted big game, it may be useful to take a brief detour here to talk about the principal techniques, approaches, and assumptions that paleoanthropologists use and make to arrive at such reconstructions.

A comprehensive discussion of this topic is obviously far beyond the scope of this book. My purpose here is twofold: to provide enough background so that the reader can better appreciate how we go about studying ancient food habits, particularly those related to hunting; and, in the process, to point out some of the more obvious and troublesome pitfalls that paleoanthropologists encounter in making these sorts of reconstructions. Should the reader want more information detailing how we get at various aspects of diet, subsistence, and food processing in the past, including the much more difficult plant food component, there are many excellent sources that

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delve into these topics. The sampling of references offered here merely provides a place to start for those who wish to explore these issues in greater depth (e.g., Ambrose and Katzenberg 2001; Gilbert and Mielke 1985; Harris and Hillman 1989; Larsen 1999; Lee-Thorp and Sponheimer 2006; Lyman 1994, 2008; Pearsall 1989; Piperno 2006; Rapp and Hill 2006; Sobolik 2003; Sponheimer et al. 2005; Sponheimer and Lee-Thorp 2007; Stiner 2002; Ungar 2007; Ungar and Teaford 2002).

## 2.1 Uniformitarianism in Paleoanthropology and Archaeology

Perhaps the most obvious starting point for generating inferences about past foodways is by looking at the present, an approach growing out of the pioneering geological work of Hutton (1795) and Lyell (1830–1833), and now generally referred to in the scientific community as *uniformitarianism* (see Shea 1982, for an interesting discussion of the concept, as well as its widespread use, and misuse, in science). Simply put, when working within a uniformitarian framework we assume that specific *events* in the past, such as the formation of the Alps, are unique and will never happen again in precisely the same way, but the *processes* that gave rise to those events, in this example plate tectonics, still operate today and are therefore knowable and observable. That's how paleontologists go about deciding, for example, if dinosaurs were warm- or cold-blooded. They obviously can't just walk up to a dinosaur and take its temperature (except perhaps in Steven Spielberg's classic 1993 film, *Jurassic Park*). So paleontologists look at the kinds of differences that exist today between warm-blooded and cold-blooded animals in such things as skeletal morphology, the structure of their circulatory systems, their social organization and foraging behavior, their distribution and population sizes by latitude, and so forth, and then use these observations to generate hypotheses about what we should expect to find in the fossil record that would be indicative of body temperature.

In a like manner, since most of human existence has been without agriculture (a conclusion drawn from well over a century of archaeological research), we turn to "modern" hunters and gatherers (peoples with little or no dependence on agriculture) as a source of insight into how peoples without agriculture might have lived in the past. We try (not always successfully) to avoid merely projecting the present into the past, but instead use the present to identify what variables are relevant to the problem we are investigating and how they are causally linked or interrelated to each other. This in turn allows us to generate hypotheses that we can then test with archaeological data.

This is anything but a straight-forward undertaking, however. As already noted, in order to learn something about the past, we must avoid simply turning the past into a mirror image of the present:

> There has long been a dynamic tension in the interpretation of past events between the scientific goal of creating a "window" through which we can observe the past, and the powerful compulsion to create a "mirror" in which we simply reflect images of ourselves (both our realities and our aspirations) onto the past.
>
> David Black, personal communication to Melanie G. Wiber, cited in Wiber (1997:45)

"Modern" hunter–gatherers are *not* fossils of former lifeways miraculously preserved on the margins of humanity. They are present-day peoples living in the present-day world, engaged in a wide range of interactions with non-hunter–gatherer peoples, and using technologies that incorporate many tools and techniques that were invented comparatively recently in the evolutionary scheme of things (e.g., atlatl, bow and arrow, pottery, grinding stones, mortars and pestles, cordage, nets, fish hooks, decoys, domestic dogs), not to mention many things that are outright modern (e.g., metals, plastics, glass, firearms, snowmobiles, portable radios, and even cell phones).

Likewise, since the chimpanzee is our closest living primate (ape) relative – a conclusion based on skeletal morphology, genetics, and numerous other lines of evidence – we use observations of modern chimpanzee behavior to develop hypotheses about what our common ancestor might have been like, and the ways in which humans deviated from chimps over the course of our (and their) evolution (Lewin and Foley 2004). But, as with hunter–gatherers, we cannot simply assume that modern chimps are relics of the past, unchanged over the past five or six million years. They too have their own evolutionary history, and modern chimps may be quite different from the common ancestor that gave rise to both us and them.

Incidentally, there are actually two different species of chimpanzees (the Common chimpanzee, *Pan troglodytes*, and the Pygmy chimpanzee or Bonobo, *Pan paniscus*). The Common chimp is the one most often mentioned in studies of human evolution, in part because these apes show a great deal of interest in meat and do a fair amount of hunting (Stanford 2001b). Our perception of human evolution might take on a rather different cast if we focused instead on Bonobos, who happen to show very little interest in hunting (e.g., Boesch et al. 2002).

So "modern" hunters and gatherers figure very prominently in our ideas about what humans were doing (and eating) in the past when they didn't have the benefits of agriculture and neighborhood supermarkets. But using "modern" hunter–gatherer data to infer behavior in the past is fraught with pitfalls, as the following discussion will illustrate. Before proceeding, however, I need to digress a moment to explain why I've been putting the word "modern" in quotation marks, because it has a very specific meaning in this context that might not be obvious to those who aren't familiar with the jargon of anthropology. Since most hunter–gatherers until quite recently had no writing systems, our understanding of their organization and behavior is heavily dependent on written descriptions provided by explorers, military personnel, missionaries, colonial officials, naturalists, ethnologists, and behavioral ecologists, among others. Needless-to-say, not all of these descriptions were recorded at the same time. The earliest speculations about hunters and gatherers go back at least to the Greeks (Zvelebil 2002). Others were made by European explorers in the fifteenth and sixteenth century, while others were made in the eighteenth and nineteenth century as colonial powers began to make inroads into Australia, Tasmania, tropical Africa, the arctic, and western North America (Barnard 2002; Pluciennik 2002). And, of course, many detailed studies of foraging peoples date to the twentieth century when the field of anthropology (particularly ethnology or sociocultural anthropology) began to materialize into a formal discipline. Productive research on hunter–gatherers continues unabated today as well, despite the inroads of the "world system," because there are a lot of questions about foraging societies that remain unanswered and the opportunity to do research of this sort is rapidly disappearing.

In studies of prehistoric hunting and gathering peoples, we tend to draw heavily from this corpus of written observation, for the most part ignoring when a particular observation was actually made. Thus, writing in the *present tense*, which is a common practice in anthropology, we might say that "the Kalahari San move frequently, aggregating near water holes in the dry season and dispersing into smaller social units in the rainy season." While such a statement seems eminently reasonable, it ignores (or at least is not explicit about) whether these observations derive, for example, from Passarge's (1907) description of the Kalahari Bushmen in the late nineteenth century; Schultze's (1907) or Lebzelter's (1934) observations in the early twentieth century; Thomas' (1959) extensive studies at Nyae Nyae in the 1950s; Silberbauer's (1981) long stay among G/wi San in the Central Kalahari between 1958 and 1966; the subsequent Central Kalahari work of Japanese anthropologists, beginning with Jiro Tanaka's 16 months among the G/wi between 1966 and 1968 (Sugawara 2004; Tanaka 1980); Heinz's (1966) various studies among the !Kõ San in the 1960s; Lee's (1979) classic work with the !Kung or Ju/'hoansi in the 1960s; Hitchcock's (1982), Wilmsen's (1989) and Wiessner's (1977) work in the 1970s and 1980s, or, for that matter, whether the reconstructions are based on the memories of elderly informants who at the time of writing were already living year-round in settled villages, herding domestic sheep and goats, and hunting with rifles from donkeys (e.g., Biesele et al. 1989; Kent 1996; see Hitchcock et al. 2009 for a detailed summary of Kalahari San studies since the 1950s; see also Willett 2003 for a useful guide to available literature on the San). This "time-blending" is what ethnologists call the "ethnographic present," a common gloss in standard anthropological parlance that can mask a lot of very important variability and culture change (e.g., the introduction of firearms and domestic plants and animals, significant dietary change, fundamental alterations in village and community organization, drastic declines in population, involvement in regional conflicts, and incorporation into regional and global market economies).

Despite the many problems in comparability that may arise from differences in when various observations were made or written down, as well as differences in the skill, thoroughness, background, reliability, and agenda of the observers, one can't overemphasize the fundamental importance of the "ethnographic present" in any work that relates to foragers in the past. As archaeologists and paleoanthropologists, we simply cannot escape it. "Archaeologists are now arguably the largest 'consumers' (and producers) of research on hunting and gathering peoples, even though the opportunities for basic ethnographic research are shrinking rapidly" (Lee and Daly 1999:11). For example, we talk a lot about mobility in the past – that is, the frequency with which foragers moved their camps, the composition of the group that made such moves, and the distance and time of year of these moves (e.g., Kelly 1995). But in actuality there is no "mobility" in the archaeological record, just flint or chert flakes and broken animal bones that archaeologists recover from a site – a bunch of items (garbage, if you like) that were inadvertently lost, abandoned, or deliberately discarded. The flakes and bones obviously don't wander around the landscape; they just sit there weathering, decaying, or getting shifted around by trampling, burrowing animals, flowing water, and archaeologists. Mobility is a concept derived from the living, not from the artifacts. Our observations of the living allow us to define what mobility is, draw inferences about how and why mobility happens, and make predictions about the material correlates that we, as archaeologists, might expect to find in the prehistoric record that would help us test our ideas about forager movements over a landscape. With no expectations from the living, there is no way to know whether what we see in the past is the same or something quite different. To borrow a very shopworn statement: "the data don't speak for themselves."

Similarly, there is no band-level social organization, no division of labor, and no food sharing in the bones and stones that archaeologists dig up. Again, these are ethnological constructs, still quite contentious ones in fact, that are based on our knowledge of how men and women in living hunter–gatherer groups organize themselves, divvy up their day-to-day activities, and distribute food or other resources to each other and to their offspring (e.g., Binford 2006; Brightman 1996; Gurven et al. 2004; Winterhalder 1997). Without our knowledge of the present, and our ongoing attempts to understand how living societies are organized and operate, we would be hard put to derive these and other such concepts inductively from the static material record of the past.

In fact, there isn't even any "hunting" in the archaeological record. Again, what we recover as archaeologists are broken animal bones and stones. We have to infer that humans were somehow involved in acquiring the bones (presumably with something edible still on them or in them) and transporting them to some desirable spot on the landscape, that the stones have any functional connection to the bones, and that what the hominins did was "hunting," a complex pattern of behavior that we really only know about through our observations of the modern world.

So knowledge of the living is absolutely essential to the success of our archaeological endeavors. It is through our studies of living systems that we decide which variables are interesting and relevant and how these variables interrelate with one another. These observations, in turn, form the basis of models that we use as *frames of reference* against which to compare and evaluate the archaeological data (e.g., Binford 1981:21–30, 2001).

So how do we actually go about using information drawn from present-day hunter–gatherers to learn something about foragers in the past? As an example, let us consider the size of hunter–gatherer bands. Anthropologists have known for decades that many hunter–gatherers live (note my use of the ethnographic present here) in small, highly mobile "local groups" or "microbands" numbering between roughly 25 and 50 people, and that about 15–20 of these microbands share sufficient similarities in language and other features to constitute a larger social unit which we call a "band" or "macroband." Interestingly, these bands typically include about 500 individuals, sometimes more, but rarely do their numbers drop below 500 (Birdsell 1953, 1958; Wobst 1974). Because this value shows up over and over again in the living world of hunter–gatherers, and across a wide range of habitats from deserts and rainforests to the arctic, it has come to be known as the "magic number 500" (there are other intriguing "magic numbers" in the hunter–gatherer literature as well: as already noted, for example, microbands typically contain between 25 and 50 people – "magic number 25" – and macrobands typically occupy territories that make contact with no more than six surrounding territories – the "magic number 6").

Might bands in the past also have had population sizes at or above 500 members, but rarely below? In the "old days," anthropologists and archaeologists were content to simply project this value into the archaeological record, rationalizing that such a figure was plausible given its near ubiquity in the modern world of hunters and gatherers. But scientifically this sort of "plausibility" argument or *empirical generalization* is not very satisfying, since it offers no real explanation of the phenomenon. As a consequence, how do we know when we're wrong? By using it, we simply turn the past into a mirror image of the present, denying us the possibility of identifying demographic patterns in prehistory that were *not* like what we see today. Is there any reason to believe, for example, that australopithecines some two to three million years ago were organized in bands with populations at or above 500 individuals? Few paleoanthropologists would seriously entertain such an idea. But what about Neanderthals or early anatomically modern humans? Were they organized into macrobands or something quite different? What we need is a model that specifies the conditions under which foraging groups would be expected to have memberships numbering around 500, and the conditions that might favor smaller or larger social groups. We can then evaluate or test predictions drawn from our explanatory framework against the patterning in the archaeological record – and in the ethnographic realm as well, so long as we use cases that were not included in the original formulation of the model.

Many years ago Wobst (1974) did just that in a pioneering study of the magic number 500. Using a computer, he simulated the demography of a hypothetical macroband, starting out with an initial population comprised of male and female adults and children of various ages, and a minimal set of mating and incest rules (e.g., you can't mate with your parents, siblings, or children, you can have only one mate at a time, and so forth). As part of the study he modified these and other parameters to see how such changes affected the outcome. Using various probabilities to determine the values of critical demographic parameters, the simulation examined each individual to see what their sex was, whether they were of mating age, whether they were in fact already mated, whether the mating produced a viable birth, and what the sex of the offspring was. He then aged each individual in the population by 1 year and put everyone through a mortality loop to determine who lived and who died.

If an individual was of mating age but was not already mated, the simulation had the individual search through the population in an ordered manner to find an eligible mate. The program kept track of how many people an individual had to search in order to find a mate. As the simulation continued through hundreds of iterations, it became apparent that, with minimal restraints on whom one could select as a mate, as the total population dropped below about 175 individuals, which Wobst called the "minimum equilibrium size" or MES – the probability of an individual being able to find a suitable mate and produce viable offspring of both sexes that survived to reproductive age – declined, and the band headed toward extinction. Not surprisingly, when Wobst made the model parameters more realistic by adding additional rules about whom one could or could not mate with (e.g., mating with a cross-cousin but not with a parallel cousin), and whether one could mate in the same year with more than one individual (e.g., polygyny), the minimum equilibrium size increased, moving closer to the magic number 500. In subsequent papers, Wobst (1976, 1977, 1993) explored some of the demographic, social, and stylistic consequences of altering the shape and size of the mating network, as well as the degree of band endogamy and exogamy (matings within and between bands) (see also Hill 1978; Owen 1965). Changes in these parameters altered the minimum equilibrium size of the macroband, and the degree to which individuals might, or might not, seek mates beyond the boundaries of their own network. Studies such as these, whether conducted by archaeologists, ethnologists, behavioral ecologists, or others, provide critical frames of reference (Binford 2001) that allow us to explain patterns of behavior in the present and generate testable hypotheses by which to evaluate our ideas about the past.

Like any other science, archaeology, and paleoanthropology constantly face the daunting problem of *equifinality*, finding patterning in the archaeological record that appears to match one's expectations but that may in fact be the result of some very different causal chain, perhaps one that nobody has yet thought of (Lyman 2004; Munro and Bar-Oz 2004). Thus, we are on securest ground when we can falsify our hypotheses rather than "confirm" them, although again like any science we often deceive ourselves into thinking we have "proven" something, when in fact what we really have done is fail to falsify it.

Going all the way back to the time of Darwin (1871), and before, observations of living foragers have guided us in our search for how we evolved into what we are today. Most hunter–gatherers of the ethnographic present (i.e., "modern" hunter–gatherers) assign a great deal of value to hunting, especially the hunting of big game and, when they can, they do a lot of it. And common chimps, though they too hunt, do so less frequently and generally pursue smaller animals. Thus, for well over a century these observations of the living, of both humans and apes, have kept our focus squarely on big-game hunting as one of the key factors that increasingly differentiated us from our cousins in the primate world. At face value this seems like a no-brainer – all we need to do is track the increasing importance of big-game animals in the archaeological record and we will know when, where, and perhaps even how our forebears transformed themselves from an ape-like ancestor into what we are today.

## 2.2 Anthropological Bias in the Study of Hunter–Gatherers

Unfortunately, the real world is complex. Just how important *is* (or was) big-game hunting among "modern" hunter–gatherers? This is not as simple a question as it might at first seem. The early explorers and missionaries, and many of the pioneering ethnologists of the nineteenth century, were men – European men to boot. They came to the foragers laden with their own Western cultural baggage about the importance of hunting and the value of meat, and simply assumed that hunter–gatherers around the globe would share the same view (Hart and Sussman 2008:228). So hunting is what these early observers expected, hunting is what they saw, and hunting is what they described.

> The picture that was painted of the social role of women in much early ethnographic and ethnological work on hunter-gatherers was of a dependent, lesser, and even passive social category. Ethnographers, mainly men, studied social phenomena of greater interest to men and talked mainly to male informants. The emphasis on hunting, weapons, and warfare ignored the contributions of women to subsistence and to social dynamics. Theoretical models viewed men as actors and women as objects of sexual exchange.
>
> Fedigan (1986:46)

This bias was compounded by the fact that most of these male Europeans had access only to male foragers, who often shared similar views about the "importance" of hunting and meat:

> Although vegetable foods form the bulk of their diet, the Hadza attach very little value to them. They think of themselves and describe themselves as hunters. From informants' assertions, one would gather that little but meat is eaten.
>
> Woodburn (1968:52)

Many European visitors were simply not interested in learning about what women did and thought, a sentiment still unabashedly expressed in the mid-1960s in Elman Service's *The Hunters*, one of the most widely read introductions to the lifeways of hunting and gathering societies. As Service (1966:1) put it: "The Hunters" was suggested as the title for this book simply because it sounds more interesting than "Woman's Work," "The Gleaners," or "The Foragers." Moreover, European visitors were often actively kept away from the women by the forager men themselves. In essence, Europeans came already knowing that hunting was the core activity in hunter–gatherer economies, and forager males often echoed a similar view. So hunting, especially big-game hunting, assumed an unshakeable position of prominence in the anthropological literature on hunter–gatherers right from the start (see, for example, the theoretical and historical discussion in Service 1962, 1971). Despite occasional attempts to unseat it by focusing more explicitly on the activities and contributions of women and switching the order of the terms in the label from "hunter–gatherers" to "gatherer–hunters" (e.g., Bird-David 1990; Dahlberg 1981; Slocum 1975), hunting remains central to our perception of foraging economies even today (e.g., Stanford 2001b).

Bias was obviously not unique to eighteenth or nineteenth century observers. There are widespread biases among contemporary anthropologists that also have a bearing on our understanding of the role of hunting in both contemporary and prehistoric hunter–gatherers. For example, one hears over and over again that the foragers of today occupy *marginal* environments (one of course immediately thinks of barren deserts and frozen, wind-swept tundras). The implication is that the habitats occupied by present-day foragers are resource poor, and hunter–gatherers are there because at some time in their past they were pushed out of better areas by more powerful intruders, usually societies whose economies were based on agriculture. Had the foragers been left unmolested, their resource base – *including hunted resources* – would have been much more productive and reliable.

Anthropologists unfortunately seldom ask “marginal with respect to what?” When one peers beneath the surface, the statement really seems to be saying something like “marginal with respect to the habitats that we, as modern farmers, would consider optimal.” Needless-to-say, the way one uses an environment is very much dependent on one’s group size, organization, and especially technology. Many of the habitats we consider “non-marginal” qualify as such primarily because we have vast, complex, energy-guzzling, agricultural technologies that allow us to exploit them. They might look much less promising to mobile foragers with small populations and limited technologies.

“Marginality” is a very slippery concept, and I know of only one study that has seriously investigated whether this anthropological truism has any demonstrable basis in reality (Porter and Marlowe 2007). These authors came to the provocative, and rather counterintuitive conclusion that the habitats occupied by modern hunter–gatherers are, on average, *not* significantly more “marginal” than those occupied by farmers:

> It is frequently suggested that human foragers occupy ‘marginal’ habitats that are poor for human subsistence because the more productive habitats they used to occupy have been taken over by more powerful agriculturalists. This would make ethnographically described foragers a biased sample of the foragers who existed before agriculture and thus poor analogs of earlier foragers. Here, we test that assertion using global remote sensing data to estimate habitat productivity for a representative sample of societies worldwide, as well as a warm-climate subsample more relevant for earlier periods of human evolution. Our results show that foraging societies worldwide do not inhabit significantly more marginal habitats than agriculturalists. In addition, when the warm-climate subsample is used, foragers occupy habitats that are slightly, though not significantly, more productive than agriculturalists. Our results call into question the marginal habitat criticism so often made about foragers in the ethnographic record.
>
> Porter and Marlowe (2007:59)

The arctic provides a clear example of just how problematic the concept of “marginality” can be when used uncritically in studies of hunters and gatherers. For farmers, the arctic was and remains one of the most “marginal” habitats on the globe. I doubt anyone would contest this. And I suspect many would agree to the assertion that the arctic was also at least somewhat “marginal” for hunter–gatherers who lacked the complex technology needed to exploit marine mammals. However, once that technology became available (Oswalt 1973, 1976), arctic habitats, coastal ones in particular, gave rise to hunter–gatherer systems with semi-sedentary villages, marked social inequality, heritable statuses, and other classic hallmarks of complexity (e.g., Fitzhugh 2003; Fitzhugh and Habu 2002).

If modern hunter–gatherers do in fact occupy habitats that in some real sense are significantly more marginal than those inhabited by subsistence farmers, we might expect the foragers to be confronted by greater levels of food insecurity – the classic “boom-bust” pattern so often thought to have characterized human existence before the advent of agriculture. This expectation, which lies at the heart of the classic "thrifty genotype" hypothesis (Neel 1962, 1982, 1999), also appears not to be met (Benyshek and Watson 2006; see also Dirks 1993), casting further doubt on the idea that modern hunters and gatherers have been "squeezed" into the least habitable corners of the globe.

> The results of this study suggest that the overall food securities of recent foragers and preindustrial agriculturalists are very similar to one another. Thus, while our results do not dispute the likely ubiquity of food shortages and periodic famine, presently and in the past…, they imply that foragers may be no more likely to suffer from these shortages than agriculturalists. While our findings should be interpreted with caution, given the uneven quality of ethnographic data and the potential pitfalls of the strict application of ethnographic analogies, our results are suggestive. As such, they offer no support for the thrifty genotype proposition that past foraging populations likely had access to less food, and experienced particularly severe and frequent "feast or famine" cycles of nutrition, thereby providing a selective advantage to thrifty genotypes.
>
> Benyshek and Watson (2006:124–125)

There are many other sources of potential bias that permeate the anthropological study of hunters and gatherers. For example, anthropologists are perpetually concerned about the "objectivity" of their ethnographic observations. So, when Richard Lee in his classic fieldwork among the Kalahari San in the 1960s found peoples who were egalitarian and with a remarkable degree of gender equality, seemingly peaceful, non-territorial, sharing, and living more or less in harmony with their environment and resources, was he describing the "objective reality" of Bushman life, or did his findings somehow subconsciously reflect his search for a "better place" in contradistinction to the tumultuous political climate of his own "world" at the time he conducted the research – the heady days of the ecology movement, civil rights protests, women's rights movement, and Vietnam War protests (see Myers 1988:262–263)? Not an easy question to answer, but an important one to think about….

> In the preface to *Man the Hunter*, DeVore and I wrote, "We cannot avoid the suspicion that many of [the contributors] were led to live and work among the hunters because of a feeling that the human condition was likely to be more clearly drawn here than among other kinds of societies" (Lee and DeVore 1968:ix). I now believe this is wrong. The human condition is about poverty, injustice, exploitation, war, suffering. To seek the human condition one must go…to the barrios, shantytowns, and palatial mansions of Rio, Lima, and Mexico City, where massive inequalities of wealth and power have produced fabulous abundance for some and misery for most. When anthropologists look at hunter-gatherers they are seeking something else: a vision of human life and human possibilities without the pomp and glory, but also without the misery and inequity of state and class society.
>
> Lee (1992:43)

Over the past few decades, an increasing number of ethnographic studies have looked into the cultural, political, and other preconceptions and biases that anthropologists invariably, though inadvertently, bring to their work, an introspective concern that the field often dubs "reflexive anthropology." One can see just how important a reflexive approach can be by looking at how the profession's views of the San, our quintessential foragers, have morphed and changed within just a few short generations of field work, beginning with the almost "utopian" image that characterized the *Man the Hunter* era of the late 1960s and 1970s.

> Briefly stated, the !Kung have…been called upon to remind us of Shangri-La. While they were spared the attribution of free love that came rather easily to the minds of observers in the South Seas, they have received considerable attention for other alleged characteristics that also drew attention to Samoa. These included a relative absence of violence, including both interpersonal and intergroup violence; a corresponding absence of physical punishment for children; a low level of competition in all realms of life; and a relative material abundance. In addition to these features that the !Kung and Samoan utopias seemed to have in common, the !Kung were described as having exceptional political and economic equality, particularly in relations between men and women.
>
> Konner and Shostak (1986:71)

Each major research team that worked with the San saw them in a somewhat different light, and saw fit to emphasize different aspects and characteristics of the foraging way of life. These differences of perspective are nicely described by Melvin Konner and Marjorie Shostak as they attempt to situate their own work within the changing landscape of Kalahari research:

> Members of the Marshall expeditions of the 1950s tended to emphasize the absence of violence and competition, while being more realistic about the questions of abundance and equality. Members of the Lee-DeVore expedition of the 1960s and 1970s tended to be more insistent about abundance and equality while being more forthcoming about the presence of violence. We ourselves, for at least the first year of our field work, were quite convinced that !Kung culture was superior in all these ways to many others.
>
> Konner and Shostak (1986:71)

But with each generation of research, more and more cracks and "imperfections" began to appear in the initial utopian picture of San life. Once seen as peaceful, newer data revealed them to have a remarkably high level of homicide, in fact a level that approached that seen in the USA (Lee 1979); once seen as the paragon of egalitarianism, more recent evidence uncovered a greater than unexpected degree of gender inequality (Konner and Shostak 1986; see also Becker 2003); once pictured as the "original affluent society" (Sahlins 1968), subsequent demographic and nutritional work showed the San to be "chronically undernourished" and with higher adult mortality than anticipated (Draper and Howell 2006; Howell 1986).

> Our own difficulties with this characterization – a characterization that, we emphasize, we initially shared – arose in the course of life history interview research conducted by one of us (Marjorie Shostak) in 1969-1971 and 1975. !Kung individuals, particularly women in middle and late life, were encouraged to talk freely about their past lives. These retrospective interviews produced a picture of !Kung life at variance with our own beliefs and with many published accounts. Deprivation of material things, including food, was a general recollection, and the typical emotional tone in relation to it was one of frustration and anger. Episodes of violence, including homicide, were reported with a disturbing frequency. Often these violent acts centered on occurrences of adultery, and the details revealed a double standard of morality concerning extramarital sex. Coercion of women by men in relation to sexual acts, including what seemed to be clear instances of rape, was also reported. Finally, a number of !Kung individuals recalled having been physically punished in childhood, including some severe beatings – for example, in response to breaking ostrich eggshell water containers.
>
> Konner and Shostak (1986:72)

It is clear that ethnographic field work among the San, as among any other human group, is a complex and difficult undertaking, far more so than a controlled science experiment in the lab. The social, political, and intellectual background and agendas of the field worker become important dimensions in the endeavor, because they influence what questions the anthropologist will ask and what data he or she will consider relevant or important.

These problems are compounded by many other factors, including the difficulty, in the absence of written historical records, of interpreting what one observes during a comparatively short stint of field work (usually lasting only a year or two, not uncommonly followed up a decade or so later by at least one additional stint in the field).

> Ethnographers contribute a steady stream of support for the parochial model of hunter-gatherers because of time and space constraints on their fieldwork. If human populations behave in certain ways to avoid, or minimize, exposure to major stresses, hazards, and catastrophes…, the shorter the observation period the less likely it is that ethnographers will observe the major driving variables behind the behaviors they observe. Major stresses are usually not observed because, under normal circumstances, normal behavior circumvents the most stressful situations. This makes it easy to attribute what is observed to what is within the ethnographic field of vision: small group dynamics, small units of space, and temporal and spatial variability of low amplitude. In this way, the ethnographic literature perpetuates a worm's-eye view of reality….
>
> Wobst (1978:304)

There are often major language problems as well, not to mention the relatively small number of informants that an ethnologist can effectively work with on a close one-to-one basis during the course of a single 1- or 2-year field stay. And, of course, one has to consider the personality traits, agendas, knowledge, and experience of the informants themselves.

> Unable to observe simultaneous spatial variability in behavior, ethnographers are forced to reconstruct it with the help of informants. But informants are not much better off than ethnographers. Their knowledge of human behavior is also acquired by observation and hearsay. Both modes structure their knowledge in ways that distort reality, even with the best of intentions. This is because the information field of individuals is bounded and patterned.
>
> Wobst (1978:305)

In addition, anthropologists are constantly struggling to differentiate between what their informants believe someone in their culture should do in a given situation vs. what that person in fact actually does. Moreover, while it is important to determine norms of behavior (i.e., what most people do in a given situation), it is also important to know just how variable a particular behavior is, and what factors cause or constrain that variability. Unfortunately, the nature and degree of variability may be very difficult to assess reliably because of the limited spatial scope of most field projects.

> Salvage-ethnographers studied the rapidly acculturating or disappearing hunter-gatherers to generate a maximum of contrastive information, that is, to document all those behaviors that still differentiated hunter-gatherers from the encroaching agriculturalists. It is not surprising that salvage ethnographers, in their vast majority, focused on locally distinct behavior, rather than on those (intra- and interregional) processes that the studied populations shared with others in culture contact situations – processes, moreover, that

> continually eroded the behaviors that remained locally distinct. In other words, the rationale of salvage ethnography left little room to worry about regional and interregional process.
>
> Wobst (1978:304)

This is not the time or place to review all of the many problems, constraints, and biases that affect the outcome of ethnographic field work. Suffice it to say that the process of explanation in anthropology, like in any other social science, is fraught with difficulty and uncertainty, and there are plenty of opportunities for all sorts of bias to creep into the picture.

Though of a different nature from the other sources of bias I have already discussed, there is another widespread form of bias that pervades the study of hunter–gatherers, at least when viewed from the perspective of anthropology in North America. This bias concerns the position of prominence that studies published in English play in many of our conceptions and understandings of the hunting and gathering way of life. *Mea culpa.* A glance at the "References" section at the end of this book shows all too clearly that my own work suffers from this same bias. In the USA this problem is exacerbated by the very limited, often dismal, exposure most of us get as kids to literature, be it fiction or scientific, that is written in another language. So in 1968 when Lee and DeVore's tremendously and deservedly influential *Man the Hunter* symposium was published, it immediately became the gold standard of hunter–gatherer studies, in North America and elsewhere, and we began to see the world "through Bushman eyes." And because the Kalahari San, particularly the !Kung or Ju/'hoansi, were featured so prominently in *Man the Hunter*, generation after generation of undergraduate students in the USA and Canada came away from their beginning anthropology courses with the impression that Bushmen were the quintessential hunters and gatherers, that most other "noncomplex" foragers were pretty much the same as the Bushmen (a myth that persisted more or less unchallenged for some two decades; see, for example, Blurton Jones 2002; Blurton Jones et al. 1992; Hill and Hurtado 1989), and, at the risk of some slight exaggeration, that Richard Lee and the Harvard Kalahari Project had more or less "discovered" them.

This is no fault of either Lee or the Kalahari Project, and in fact is clear testimony to the quality of the research, the symposium, and the resulting publication. But the ascendancy of the !Kung in our thinking about hunter–gatherers is also a reflection of the fact that Lee's studies, particularly his early ones, were written in English and drew mostly on English sources, while the rather sizable German literature on the Bushmen from the late nineteenth and early twentieth century remained in obscurity, as did the quite vast literature on other foragers in central Africa, Tierra del Fuego, Amazonia, mainland Southeast Asia, Indonesia, and elsewhere that were written in French, German, Dutch, Portuguese, Russian, Japanese, and other languages (see Schweitzer 2004, and other essays in Barnard 2004).

This "language bias" can lead to more than just lopsided bibliographies; it can often lead to theoretical arguments that are hashed out in ignorance of important evidence that is buried in these largely unread ethnographies. This was clear, for example, in debates, sometimes quite heated ones, that took place in the 1970s about whether the San and other similar foraging groups were territorial. Leaving aside the issue of whether it made sense to dichotomize "territoriality" into just two mutually exclusive states, the debate might have unfolded differently if the protagonists had been aware of the late nineteenth-century German accounts of the Bushmen. My hope is that as computer-based translation improves beyond its current dismal state this bias will disappear, but at present it still plays an important, though unmeasurable, role in shaping our views about foragers.

There is another bias in our understandings of hunter–gatherers that the noninitiated should be aware of. As in any other field, our theoretical underpinnings have undergone steady transformations over the years, and these changes affect the questions we ask and the kinds of data we collect. Aram Yengoyan (2004) has written eloquently on this topic in relation to hunter–gatherers, and his ideas are worth commenting on here. In the nineteenth century and extending into the earlier part of the tweniteth century, anthropological (i.e., ethnological) interest was squarely focused on "cultures," describing and examining the tremendous diversity of cultural practices and beliefs that characterized and distinguished the many hunting and gathering peoples of the world.

Beginning in the mid-portion of the twentieth century, most notably with the work of Steward (1938) in the Great Basin and somewhat later with the stage-based synthesis published by Service (1962, revised in 1971), the focus gradually shifted from cultures to societies, with the distinctive features and idiosyncrasies of different cultures being increasingly relegated to the margins. Service and others were looking for cross-cultural regularities that characterized hunter–gatherer bands rather than examining each culture as a unique entity. While as a scientific endeavor this shift was important and productive, a major part of what makes us distinctively human was pushed aside as overly particularistic and ultimately uninteresting – epiphenomena rather than core features of the peoples upon whom anthropology traditionally focused.

In the last few decades, behavioral ecology has moved into a very prominent position within the realm of hunter–gatherer studies, and this marks another shift away from anthropology's earlier focus on culture. One of the real "pluses" of hunter–gatherer studies from the perspective of behavioral ecology is its emphasis on explicit hypothesis testing and quantification, and the reader will quickly find that I have made heavy use of the data and insights generated by this approach.

However, there is a flip-side as well. Despite years of research by behavioral ecologists among foraging groups like the Hadza, Ache, and many others, most of the publications that have resulted from this work are virtually devoid of traditional ethnographic substance. Reading these studies, it is almost impossible to gain a picture of what their cultures were really like. Topics like kinship, religious beliefs and practices, marriage systems, and many others that were once mainstream in the anthropological enterprise have all but disappeared. To most behavioral ecologists, culture is little more than an epiphenomenon, with no real role in explanation. As Yengoyan (2004:59) puts it, behavioral ecology has "…created a new discourse in which evolutionary and economic models have reduced human actors to disemboweled humans who no longer have cultural anchors."

> …while some [behavioral ecologists] acknowledge the impact of outside forces…on the people they study, others focus narrowly on quantitative models of foraging behaviors as if these existed in isolation. In addition to criticizing their science, critics of this school have argued that by treating foragers primarily as raw material for model building, the behavioral ecologists fail to acknowledge foragers' humanity and agency….
>
> Lee and Daly (1999:11)

One might counter that broad topics like religious beliefs and kinship are largely or entirely irrelevant for most questions that behavioral ecologists are trying to address, so it is not surprising that many of these traditional domains of anthropology don't enter into their studies. Nonetheless, topics like diet and food choices are very much of interest to behavioral ecologists, but they are arguably also very much influenced by a peoples' culture, that is by systems of belief that define which foods are "edible" and which are not, which foods are taboo, which can be eaten together and which must be kept separate, how foods should be prepared, when they should be consumed, and by whom. Reading studies on Hadza foraging by behavioral ecologists I have obtained a wealth of valuable information on energy, nutrient content, time allocation, and return rates, but I would never have guessed just how strongly gender politics entered into the diet equation – namely, that through a practice called *epeme*, initiated Hadza males control access to the most valued cuts of meat from large game:

> *Epeme* is the name given [by the Hadza] to certain fatty portions of large game. This meat is sacred, supposedly reserved for the eponymous spirit being, but in fact eaten by initiated men at special *epeme* feasts. The men consume the meat secretly; attendance at the *epeme* feast is a male privilege from which women are excluded on pain of rape or death….
>
> Power and Watts (1997:550)

Male privilege with regard to fatty meat is further enhanced by the fact that most *epeme* rituals take place during the dry season, when Hadza aggregate into larger social groups, coinciding with the time of year when men do most of their big-game hunting (Power and Watts 1997:550). Clearly, a comprehensive understanding of Hadza diet must consider not just the nuts and bolts of foraging efficiency and nutrition, nor just the culturally defined beliefs and practices that come into play when food is involved, but the interplay between the two that ultimately determines how those foods get selected, distributed, and utilized.

## 2.3 Nutritional Bias in the Study of Hunter–Gatherers

Specialists in the nutrition and health science fields bring some of their own biases and *a priori* assumptions to the study of hunter–gatherer diets. Many nutritionists believe that traditional foragers consumed a diet that was healthier than the diets found throughout much of the Western world today (e.g., Eaton et al. 1988; Simopoulos 1999). Implicit in these studies is the perception that there is (or was) a "Paleolithic diet" that characterized human foodways prior to the Neolithic and the advent of farming.

While it is likely true that hunter–gatherer diets worldwide may have shared certain broad commonalities, what is noteworthy is how strikingly varied they were, not how similar. Hunter–gatherers successfully colonized virtually every corner of the globe, from arctic tundras to equatorial rainforests, from humid coasts to interior deserts, from lowlands to extremes of altitude. Not surprisingly, over such a vast range of habitats forager diets are incredibly varied and eclectic – some almost totally carnivorous, others bordering on vegetarian, and just about every possible permutation and combination in between.

Perhaps more important in this regard is the fact that over the course of human evolution the technology and techniques available to foragers to procure different types of foods and process them for consumption changed frequently and often dramatically (e.g., Klein 1999). Wrangham (2009:127), in fact, suggests that the continual growth in the size of the human brain over the long course of the Pleistocene serves as a proxy for the ever-increasing effectiveness of our ancestors' culinary know-how: "Advances in food preparation may…have contributed to the extraordinary continuing rise in brain size through two million years of human evolution – a trajectory of increasing brain size that has been faster and longer-lasting than known for any other species."

Archaeologists often refer to these broad technological changes under the overarching rubric of "intensification" – in essence, squeezing more calories and nutrients out of the same foods; and adding new foods to the diet that were previously inedible, or of only limited food value, or which required considerably more time and effort to harvest or prepare. Intensification has been transforming forager foodways since the first appearance of the genus *Homo*. It began in earnest in East Africa some 2.6 million years ago (mya) with the development of the first stone tool technologies, the so-called Oldowan, making possible a wide range of cutting, slicing, and chopping activities that would have been much more difficult, if not impossible, to do without these technical aids (Semaw 2000).

Perhaps the most significant addition to the repertoire of human culinary technology, appearing (at least according to some) by at least 1.0–1.5 mya, if not earlier, was the control of fire (Wrangham and Conklin-Brittain 2003; Wrangham 2009; Carmody and Wrangham 2009). With fire many plant foods, which might otherwise have been toxic or indigestible, could become regular contributors to the foragers' larder (see Ames 1983, and especially note the provocative "eat-die" cover inspired by Ames' article that graced that issue of *Science*; see also Dominy et al. 2008; Johns 1990; Nabhan 2004).

> He [mankind] has discovered the art of making fire, by which hard and stringy roots can be rendered digestible, and poisonous roots or herbs innocuous. This discovery of fire, probably the greatest ever made by man, excepting language, dates from before the dawn of history.
>
> Darwin (1890a:48–49)

Then, beginning perhaps a mere 20,000 or so years ago, toward the end of the Pleistocene, and in many different parts of the inhabited world – both glacial and non-glacial – came a real inflection point in the rate of food-related intensification, with the addition in rapid succession of many new food types and many new practices and technologies for processing these foods, such as baking, grinding, pounding, steaming, parching, leaching, fermenting, and technologies that permitted boiling and stewing, first using skin, basketry, or gut bags that could be heated indirectly with hot rocks, and then using ceramic containers that could be placed directly over the fire (e.g., Benison 1999; Holt and Formicola 2008; Jones 2009:177–178; Manne et al. 2005; Nakazawa et al. 2009; Stahl 1989; Thoms 2009; Wandsnider 1997; Wollstonecroft et al. 2008). The impact of these comparatively recent innovations in food-processing technologies is indirectly reflected in the dramatic changes that have occurred over the Late Pleistocene and Holocene in tooth size and craniofacial structure (e.g., Brace et al. 1987; Lieberman et al. 2004). While these skeletal alterations very likely stem in large part from reduction of the biomechanical stresses and strains associated with mastication, they almost certainly are also linked to major changes in the nutritional properties and digestibility of our foods (e.g., Lucas 2006; Lucas et al. 2009; Wrangham 2009; Carmody and Wrangham 2009).

There are many other important technologies, each of which added significantly to the array of foods humans could exploit and the way they were processed for consumption. Unfortunately, for most of these we have little or no direct archaeological evidence that would help us pin down the timing of their introduction. Among these – and this is by no means an exhaustive list – are digging sticks, snares, traps, starch presses, leaching baskets, geophagy, or clay-eating (e.g., Johns and Duquette 1991; Rowland 2002), nets, decoys, weirs, fish hooks, atlatls, boomerangs, bolas stones, seed-beaters, and many other hunting and gathering technologies. Each of these altered what foods could be procured and in what quantity, as well as their toxicity, digestibility, and nutritional properties.

Some of these technological innovations are often thought to have appeared during the "Neolithic" – that is, sometime after about 10,000 years ago, and therefore to be developments that came hand-in-hand with the origins of agriculture. One of the most important of these innovations is pottery, because it provides an effective way of improving the digestibility of starchy plant foods, particularly seeds (including cereal grains, the staples of the modern world), but also underground storage organs like tubers, rhizomes, corms, and bulbs. Boiling in pots also detoxifies many otherwise inedible plant foods, and it offers an efficient way of extracting fat from the cancellous (spongy) portions of animals bones, providing an invaluable source of calories that would otherwise have been costly for foragers to extract in any significant quantity.

The idea that pottery is part and parcel of the agricultural revolution is one of those classic misconceptions that is so deeply entrenched in popular thinking that, no matter how much data accumulates to the contrary, it is still not sufficient to unseat the myth. It is true that farmers generally have pottery, but it is *not* true that hunters and gatherers generally do not.

> Once regarded as a sort of ethnographic oddity, it is now increasingly apparent that nonsedentary, nonagricultural peoples make frequent use of pottery. In an ethnographic sample of 862 societies, 103 (nearly 12%) were pottery-making, nonsedentary societies….
>
> Rice (1999:28)

Whether or not foragers do have pottery depends a lot on what one selects as one's "ethnographic present." Pottery was a fairly common part of the technological repertoire of foragers worldwide until Europeans introduced metal pots and pans, at which point many groups abandoned the use of clay containers. For example, if one relies on the descriptions of the San from the twentieth century, as most of us do, the ethnographies are virtually silent on the topic of pottery. But if one looks at the Later Stone Age archaeology of southern Africa, or the written accounts left by the first Dutch and English explorers to set foot in South Africa, it becomes evident that pottery was a fairly widespread component of Bushman culinary technology (Bollong et al. 1997; Mazel 1992; Rudner 1979).

The earliest pottery thus far known appears in Late Pleistocene hunter–gatherer sites in eastern Russia, Japan, and China, with dates as early as ~13,000 radiocarbon years ago or up to 18,000 calibrated years ago (Boaretto et al. 2009; Keally et al. 2004; Kuzmin 2006; Zhang 2002). Ceramics also appear quite early in Africa, dating between 9,000 and 9,500 years ago in the central Sudan, as well as in northeast Niger and Libya (Garcea 2006; Haaland 1992). "In most of North Africa… the production of pottery and groundstone is independent of the origins of food domestication. It occurred about 3,000 years earlier, dating from around 9,000 years BP and 6,000 BP, respectively" (Garcea 2006:201).

Turning to the New World, in South America pottery has been reported in hunter–gatherer contexts more than 7,000 years ago in Brazilian Amazonia (Roosevelt et al. 1991), although this date is not universally accepted (see, for example, Williams 1997). However, by 5,000–6,000 years ago, ceramics are widely reported from a number of different hunter–gatherer sites in Ecuador, Colombia, and elsewhere in South America (e.g., Damp and Vargas 1995; Hoopes 1994; Pratt 1999). Ceramic vessels, as well as grinding technology, increased in importance during the last 1,500 years among Patagonian (Argentina) hunter–gatherers, while rates of dental attrition declined, pointing toward significant changes in the way these foragers prepared their foods (Bernal et al. 2007). In Mesoamerica pottery shows up in pre-agricultural contexts somewhat later than in South America, with dates falling between about 3,500 and 4,000 years ago (e.g., Clark and Gosser 1995). Moving to North America, pottery becomes an integral part of Eskimo (Inuit) technology by at least 2,500 years ago (Harry et al. 2009; see also Oswalt 1955; McCartney 1970; Stimmell and Stromberg 1986), and even earlier in coastal southeastern North America, where it appears during the Late Archaic sometime prior to 4,000 years ago (Sassaman 1993; Thompson et al. 2008).

Pottery was also part of the inventory of many of our classic ethnographically documented hunter–gatherers. While it is often uncertain whether the pottery was made by the foragers themselves or obtained through trade with neighboring farmers or pastoralists, what matters here is the fact that the foragers were cooking food in pots, not how and where they got them. Thus, pottery was used by Pygmy groups in the Ituri Forest for at least the last 1,000 years (Mercader et al. 2000) and, as already noted, Bushman groups in Southern Africa were apparently cooking in ceramic vessels for at least the past 1,300 years (Bollong et al. 1997) and perhaps in excess of 2,000 years (Mazel 1992). Pottery use, and probably manufacture, is also well documented in the American Great Basin among the Paiute and Shoshone, beginning as much as 1,000 years ago (e.g., Baldwin 1950; Eerkens 2003; Eerkens et al. 1999, 2002); and ceramics were in widespread use among hunter–gatherers in many other parts of North America as well, as discussed in a classic paper on the distribution of cooking pots published more than half a century ago by Linton (1944).

Thus, many Old and New World hunter–gatherers have used pottery for centuries, some for millennia, to cook and detoxify starchy plant foods, and render the fat from animal bones. Together with grinding technologies, which are also found in many pre-agricultural contexts, as in Australia and Israel where grinding stones date back more than 20,000 years (Denham et al. 2009; Fullagar and Field 1997; Morwood and Trezise 1989; Piperno et al. 2004), in East and southern Africa where they certainly date back to the Middle Stone Age, some 200,000–300,000 years ago, and possibly even into the Late Acheulian (McBrearty and Brooks 2000:511, 531), in Europe where they may appear as early as 25,000 years ago and become prominent at the end of the Pleistocene in the Mesolithic (e.g., Aranguren et al. 2007; Clark 2000; Zvelebil 2008), and in many parts of the New World (e.g., Adams 1999; Dillehay et al. 2003; Jackson 2004; Rhode et al. 2006), it is clear that a number of so-called Neolithic processing technologies have been part of the day-to-day culinary practices of foragers for a very long time.

The archaeological record amply demonstrates that forager diets have not been static. Quite the contrary, human food choices, as well as their food-getting and food-processing technologies, have been evolving, broadening, and intensifying for at least the past three million years (e.g., Sponheimer and Dufour 2009), most likely broadly tracking growth in human populations, with the pace of change accelerating dramatically in many parts of the Old and New World during the last 20,000 years or so. Often referred to by archaeologists as the "broadening food spectrum" or "broad spectrum revolution" (Binford 1968; Flannery 1969; Stiner 2001), intensification of forager foodways impacted hunter–gatherers in nearly every corner of the globe (*and, incidentally, did not invariably culminate in plant and animal domestication and agriculture*). These cultural changes would have had a tremendous impact on what foragers could and could not eat. As Solomon Katz (1990:237) put it:

> What humans eat is largely dictated by cultural traditions, but the degree to which a diet satisfies basic nutritional needs largely depends on human biology. This obvious interface between biology and culture has encouraged the development of [an]…approach or "paradigm" that analyzes and interprets biological and cultural adaptability as continuously interacting phenomena throughout human evolution.

One can also envision an increase in ethnic and ideological differentiation, not just technological advance, as populations grew in size and/or density toward the close of the Pleistocene. Such differentiation would have augmented substantially the diversity of belief systems that guided and constrained human foodways.

> The human omnivore uses his freedom of choice in a most peculiar way. One of his specific features is that he is amazingly particular – even finicky – about his food. Man feeds not

> only on proteins, fats, carbohydrates, but also on symbols, myths, fantasies. The selection of his foods is made not only according to physiological requirements, perceptual and cognitive mechanisms, but also on the basis of cultural and social representations which result in additional constraints on what can and cannot be eaten, what is liked and what is disliked. As Levi-Strauss puts it, things must be "not only good to eat, but also good to think."
>
> Fischler (1980:937)

At what point in this complex and constantly morphing landscape of food-getting and food-processing technologies and belief systems do we decide that we are dealing with "*the* Paleolithic diet?" The choice is clearly arbitrary and masks complexity and variability that may be of considerable importance in understanding our nutritional heritage (Ströhle et al. 2009).

There is an additional problem with the search for a "Paleolithic diet." Most nutritionists draw their insights from the "ethnographic present," using this information as a frame of reference or model for inferring what human *nutrition* was like in the past. As already pointed out, this is precisely what archaeologists do in studying the human *cultural* past – we start with "modern" foragers to figure out what variables and relationships are relevant and from this we build a model *that we then test against the archaeological record*. It is this last step that nutritionists seeking the "Paleolithic diet" generally omit – which means they are creating a "past" that for all practical purposes is an untested projection of an homogenized view of what in fact is a very diverse "present." In other words, these nutritionists are not actually discovering what hunter–gatherer diets were like in the past; how variable they were; how they differed from the diets of today's foragers; or how these diets changed over time in response to the dramatic climate upheavals of the Ice Age, fluctuations in the size and distribution of human populations, and evolving food-processing technologies. In the end, many of the health-related recommendations made by "Paleolithic" nutritionists are likely beneficial (see, for example, Cordain 2002; Crawford and Marsh 1995; Eaton et al. 1988; Simopoulos 1999), but at this point they derive from analogies that to a large extent remain untested, and a series of somewhat tenuous assumptions about the homogeneous and static nature of forager diets in the past.

The "Paleolithic diet" approach is sometimes further justified on the assumption that so little time has elapsed since the onset of the Neolithic (~10,000 years ago in some parts of the world, later in many other parts) that our genetic makeup surely must be more or less the same as that of our hunter–gatherer forebears (e.g., di Costanzo 2000; O'Keefe and Cordain 2004; Simopoulos 1999). In other words, our bodies are still attuned to a forager diet and lifeway (whatever that may actually have been), even though we are now living in a totally different world.

> A central tenet of evolutionary or Darwinian medicine is that many chronic diseases and degenerative conditions evident in modern Western populations have arisen because of a mismatch between Stone Age genes and recently adopted lifestyles. In a nutshell, genes or traits that may have been selectively advantageous or neutral in the past are argued to be potentially deleterious within the context of industrialisation and modernisation. Some suggest that this mismatch can be extended even further back in time, to the widespread adoption of agriculture. It is believed that chronic and degenerative conditions persist at such high levels in many populations because the rate at which selection operates is not sufficient to respond to the current pace of cultural and environmental change. In other

> words, it is thought by many advocates of evolutionary medicine that our environments are evolving faster than we are.
>
> Elton (2008:9–10)

The idea that our biological evolution has all but stopped has received support over the years from many eminent biologists, including Stephen Jay Gould – "There's been no biological change in humans in 40,000 or 50,000 years. Everything we call culture and civilization we've built with the same body and brain" (Gould 2000:19, cited in Cochran and Harpending 2009:1 – and Ernst Mayr 1963, also cited in Cochran and Harpending 2009:1) – "Something must have happened to weaken the selective pressure drastically. We cannot escape the conclusion that man's evolution towards manness suddenly came to a halt…."

Although at face value this assumption seems plausible and reasonable, an explosion of recent genetic work suggests otherwise (Akey et al. 2004; Balaresque et al. 2007; Barreiro et al. 2008; Cochran and Harpending 2009; Hawks et al. 2007; International HapMap Consortium 2007; Luca et al. 2008; Magalon et al. 2008; Mekel-Bobrov et al. 2005; Nielsen et al. 2007; Patin et al. 2006; Patin and Quintana-Murci 2008; Perry et al. 2007; Pickrell et al. 2009; Sabeti et al. 2007; Scheinfeldt et al. 2009; Smith 2007; Stock 2008; Tishkoff et al. 2001, 2007; Voight et al. 2006; Williamson et al. 2007). It seems that natural selection continued to alter the human genome throughout the Late Pleistocene and Holocene as human populations grew, diversified, and adapted to radically new environments, diseases, and diets, and this process continues unabated today. In fact, human evolution did not come to a standstill with the onset of the Neolithic, if anything the process has accelerated dramatically. If so, it would appear that our genetic makeup is not a relic of our hunter–gatherer past, somehow frozen since the onset of the Neolithic, but a dynamic system that is constantly in flux in response to our ever-changing physical, demographic, pathogenic, and socioeconomic environment.

> It is sometimes claimed that the pace of human evolution should have slowed as cultural adaptation supplanted genetic adaptation. The high empirical number of recent adaptive variants would seem sufficient to refute this claim. It is important to note that the peak ages of new selected variants in our data do not reflect the highest intensity of selection, but merely our ability to detect selection. Because of the recent acceleration, many more new adaptive mutations should exist than have yet been ascertained, occurring at a faster and faster rate during historic times. Adaptive alleles with frequencies <22% should then greatly outnumber those at higher frequencies. To the extent that new adaptive alleles continued to reflect demographic growth, the Neolithic and later periods would have experienced a rate of adaptive evolution >100 times higher than characterized most of human evolution. Cultural changes have reduced mortality rates, but variance in reproduction has continued to fuel genetic change. In our view, the rapid cultural evolution during the Late Pleistocene created vastly more opportunities for further genetic change, not fewer, as new avenues emerged for communication, social interactions, and creativity.
>
> Hawks et al. (2007:20756–20757)

Cochran and Harpending (2009) argue that as the pace of cultural evolution has accelerated so too has the pace of biological evolution, responding and adapting to the environment that we ourselves are creating and rapidly altering.

> Human evolution didn't stop when anatomically modern humans appeared, or when they expanded out of Africa. It never stopped – and why should it? Evolutionary stasis requires a static environment, whereas behavioral modernity is all about innovation and change. Stability is exactly what we have not had. This should be obvious, but instead the human sciences have labored under the strange idea that evolution stopped 40,000 years ago.
>
> Cochran and Harpending (2009:226)

As a final thought concerning our foods and our genes, Gary Nabhan, in a provocative book entitled *Why Some Like It Hot: Food, Genes, and Cultural Diversity* (Nabhan 2004), points out that on a global scale human cuisine makes use of tens of thousands of plant species that contain an unbelievably varied and complex cocktail of secondary compounds. And while only a small fraction of these have been carefully studied by biochemists, quite a few of those that have been examined are known to be mutagenic (see, for example, Schmitt and Stopper (2001) and Stopper et al. (2005) for an interesting example concerning phytoestrogens or Hesse (2002), and Wiedenfeld et al. (2008) for other examples involving the vast array of alkaloids). If we also acknowledge that human diets have expanded and diversified over the past 2.5 million years, as our ancestors gradually spread throughout the Old and then the New World, and over this same period of time came to rely on an increasingly diverse and complex set of tools and techniques for processing what we deemed edible, it is hard to escape the conclusion that our bodies and our genes have been exposed to an ever-broadening array of potentially carcinogenic and mutagenic substances. Hence, just in terms of the plant food component of human diet, the Paleolithic was hardly a period of stability in which genes and foods came to a steady-state of the sort envisioned by many advocates of the "Paleolithic diet."

> Let us try to fathom how pervasive the influence of the chemicals in plant foods might be – and why numerous secondary compounds, not just macronutrients – have influenced the shapes of human diets and genetic variation through time. Some phytochemists have hazarded the guess that 40,000 to 50,000 secondary compounds have already been described from the 270,000 named plant species, and yet, not even a fraction of the 30,000 edible plant species have been subjects of substantive laboratory analyses. The chemists therefore concede that they have barely scratched the surface in characterizing the structure of these compounds, let alone in understanding their ecological function, their role in nutrition, or their mutagenic capacity (that is, their ability to induce genetic changes).
>
> Nabhan (2004:58)

## 2.4 The Nature of the Archaeological Record

Now, let us shift gears and turn to a consideration of the nature of the archaeological record itself, looking at some of the problems it poses for us in our attempts to understand the role of big-game hunting in human evolution, and at some of the more widely used approaches that we can employ to help us peer into the distant past. If hunter–gatherers today focus a great deal of their time and effort pursuing large animals, as both ethnohistory and ethnography would suggest, and chimpanzees do so less, then archaeology should be able to tell us when and how big-game hunting evolved to its position of prominence among humans. Simple? One would think so. After all, bones, especially big ones, ought to preserve well, certainly much better than the perishable remains of plant foods. Thus, archaeological sites with the bones of big animals should be fairly easy to find. And the stone tools used to hunt and butcher these big animals will almost certainly preserve. So reconstructing the story of human hunting should be a fairly straight-forward and unambiguous undertaking, but….

Unfortunately, once again the complexities of the real world have proven to be very difficult to untangle. Let us consider just a few of the more significant issues and problems (see Haynes 2002). These examples should be sufficient to alert the reader to the potential pitfalls that paleoanthropologists and archaeologists face in their attempts to reconstruct the role of big-game hunting in the human past. First, precisely because the big bones of big animals are more likely than remains of small animals or plants to survive the vicissitudes of time and the scavenging and bone-crunching proclivities of hyenas, big game is likely to be *overrepresented* in our samples of the archaeological record. Moreover, humans and hyenas often competed for the same prey and transported their remains to the same caves for shelter (albeit at slightly different points in time, but close enough to often be beyond the resolution of current archaeological methods; see Stiner 1994). Thus, deciding which bones relate to human activities as opposed to the scavenging behavior of hyenas is actually a very thorny problem, and underlies the explosion of *taphonomic* studies over the last two to three decades that are designed to try to sort out the contributions of man and carnivore to the archaeological record (Lyman 1994, 2008).

There are other problems as well. For example, in the open savannas of East Africa, shade and water would have been valued resources, and both humans and hyenas were undoubtedly attracted to them (Binford 1981). This could easily bring animal bones and stone tools together in space and time, giving the illusion of a functional connection between the two when such a connection did not in fact exist. Running water can produce similar sorts of spurious associations and palimpsests. Artifacts and bones originally deposited at different times in two discrete superposed stratigraphic levels can become mixed together in a single horizon as the enclosing sediments are blown away by the wind. Burrowing animals can also produce spurious associations of bones and tools. Teasing apart the effects of these different agents of transport is at the heart of a lot of current taphonomic research.

Even when one can demonstrate that stone tools were used to butcher animal carcasses, as indicated for example by the presence of unambiguous cutmarks directly on the bones (Binford 1981), we still can't be sure whether the hominins killed the animal or scavenged the carcass after it had been abandoned by predators. If hominins were able to drive big predators like lions and hyenas off the carcass before all of the meat had been devoured (what we call "active," "power," or "confrontational" scavenging), there would have been a fair amount of edible tissue available to the foragers (Blumenschine 1995). On the other hand, if the hominins were unable to gain early access to the carcass ("passive" scavenging), what would remain might be very limited, amounting to little more than marrow in the limb bones and perhaps the fatty tissues of the brain. The actual amount of tissue remaining on a carcass would have been affected by many other factors as well, including the size of the animal, its physical condition at the time it died, the number of carnivores competing with each other for the same resource, and the local environment in which the carcass was found (e.g., open grassland vs. dense undergrowth). In open habitats carnivores can devote more time and effort to consuming a carcass while still monitoring the activities of dangerous competitors, whereas in closed habitats they are more vulnerable to attack while eating at the kill and, as a result, may spend less time there (Blumenschine 1986).

It is actually much harder to determine if hominins killed a large animal than one might at first think. A definitive answer hinges on knowing when hominins developed thrusting or throwing spears. One might immediately respond: "that's easy, as soon as we find 'spear points' in the archaeological record." That may be a no-brainer in the latter part of the Pleistocene and Holocene, when we find sharp, finely flaked triangular flint tools with unambiguous haft elements, such as basal notching or projecting basal stems that clearly served to attach the tool to a shaft. But even evidence for hafting is not sufficient to establish the presence of spears. There is ample evidence in the ethnohistoric and ethnographic literature that foragers hafted "points" to short handles for use as knives. How do we distinguish a "knife" from a "spear point?" One approach used nowadays is to look for impact damage on the tips of these tools, damage that would indicate thrusting or throwing rather than slicing, scraping, or whittling (Lombard et al. 2004; Villa et al. 2009; Villa and Lenoir 2006, 2009). Using insights from fracture mechanics, it is even possible in very fine-grained materials like obsidian to determine the type of weapon that was being used when the tip damage was produced (Hutchings 1997, 1999). Unfortunately, tip damage of this sort, as well as organic residues indicative of hafting, only become clearly evident in the Middle Stone Age or Middle Paleolithic, after about 300,000 years ago, and no one to my knowledge has yet tried the Hutchings approach on Paleolithic artifacts of any age. Were there no weapons suitable for killing large animals prior to this? This is the most common position taken by paleoanthropologists (e.g., Hart and Sussman 2008; Stiner 2002; but see Domínguez-Rodrigo et al. 2007; Bunn 2007a, b; Villa and Lenoir 2009). Given the evidence, or lack thereof, it certainly is the safest position, but is it correct?

What about much earlier archaeological sites with remains of big animals, such as the famous 1.8-million-year-old site of FLK-*Zinjanthropus* (FLK-*Zinj*) in Olduvai Gorge, Tanzania (Figs. 2.1 and 2.2), or the slightly younger FxJj50 site in Koobi Fora, Kenya (Isaac 1997; Leakey 1971)? Because of the absence of unambiguous stone projectile points at these sites, many archaeologists see them as evidence that over much of the human career meat and fat from larger animals were acquired by scavenging abandoned predator kills, not by hunting. To other archaeologists, many of these same localities are thought to be little more than palimpsests of materials brought together by different agents, with hominins contributing the stone tools and perhaps the bones of smaller

**Fig. 2.1** Olduvai Gorge, Tanzania. ©iStockphoto.com; filename "iStock_000009774511XLarge.jpg"

**Fig. 2.2** 1.3-Shilling stamp issued by Tanzania in 1965 to commemorate the discovery of the famous *Zinjanthropus* skull (now called *Australopithecus boisei* or *Paranthropus boisei*), found in Olduvai Gorge in 1959 by Mary and Louis Leakey at the FLK-*Zinj* archaeological site. The original stamp is in the author's possession. The photograph was taken by Katherine Clahassey, Museum of Anthropology, University of Michigan, Ann Arbor, Michigan

animals, and hyenas (particularly the spotted hyena, *Crocuta*) contributing the larger remains at times when the sites were not being used by humans.

Our ideas about the antiquity of hunting weapons received a jolt in the 1990s, when an archaeologist – Hartmut Thieme – discovered 400,000-year-old wooden spears at the site of Schoeningen (Schöningen) in Germany (Thieme 1997; Thieme et al. 1993; Voormolen 2008). The morphology of these spears provides quite compelling evidence that Middle Pleistocene hominins nearly half a million years ago already possessed effective *projectile* weaponry suitable for killing big animals at a distance (Rieder 2000, 2003; Steguweit 1999). This is nicely demonstrated by the morphology and balance of the spears themselves and by a series of throwing experiments reported by Steguweit (1999) and described and nicely illustrated by Rieder (2003), the results of which stand in stark contrast to the prevailing English-language view, as reflected for example by Shea (2006), that these spears were suitable primarily as close-quarters thrusting weapons (see also Schmitt et al. 2003; Churchill and Rhodes 2009). The "close-quarters" argument was thought, in particular, to be reflected by the unusual pattern of injuries seen in Neanderthals (Berger and Trinkaus 1995), but newer research by Virginia Hutton Estabrook (2009) seriously challenges this piece of the argument as well.

> …I found no evidence that Neandertals experienced trauma more frequently or with a different distribution throughout the body beyond what is commonly experienced by modern humans in the context of hunter-gatherers, nomads, semi-sedentary foragers and medieval small landowners. Therefore, the assertion that trauma played a more influential role in the lifeways of Neandertals than any of these other groups is not supported by the data. These results imply Neandertals possessed a higher degree of cultural and/or physical adaptation to mitigate their environmental stresses than previously suggested by some of the research into their trauma.
>
> Hutton Estabrook (2009:346)

The Schoeningen spears offered up another surprise, one that paleoanthropologists have not really taken to heart – *they were not designed to carry stone tips*. The Schoeningen finds underscore the possibility that stone tips may not be essential to the successful functioning of thrusting or throwing spears (see the discussion in Moncel et al. (2009) and Waguespack et al. (2009)). For example, spears, atlatl darts, and arrows recovered from dry caves and rockshelters in western North America frequently lack stone tips and clearly were not designed to have them (Ellis 1997). Instead, their wooden ends were tapered to a point (which was sometimes fire-hardened), or the end was socketed to receive a sharpened wood foreshaft.

Ethnographic observations and experimental studies using replicated weapons reinforce the picture provided by the data from the dry caves and rockshelters (Cheshier and Kelly 2006; Dockall 1997; Ellis 1997; Fischer 1989; Odell and Cowan 1986). For example, Nicole Waguespack et al. (2009), in a global survey of 59 ethnographically documented subsistence hunters, found that nearly 65% of the groups they examined used wooden-tipped projectiles in addition to ones armed with stone or metal, and that many of these hunting peoples employed organic-tipped projectiles for both small and large game.

In addition to the ethnographic overview, these authors conducted a series of controlled archery experiments using a remotely triggered 60-lb bow and a series of arrows of comparable dimensions and weight, some of which were stone-tipped, others having only sharpened wooden ends. While the former penetrated farther into gel targets than those tipped with wood, the differences, though statistically significant, were relatively small (both attained depths greater than 20 cm) and therefore may have been of little consequence to hunters in real-life situations. In concluding, the authors raise the interesting possibility that the incentive to invest time and labor in the manufacture and maintenance of arrows tipped with stone may lay more in the realm of costly signaling than in the more mundane sphere of "lethal efficiency" (Waguespack et al. 2009:797).

There is another dimension that needs to be considered – chipped-stone projectile points can be quite fragile. Notched specimens carried as spares may break easily in transport, even before they are hafted and used. Those of my readers who had to cut glass tubing in a high school or college chemistry lab may remember having to first make a shallow groove or notch across the tubing with a small triangular file and then bending it. The tube would snap cleanly at the groove. The notch in an arrowhead or spear point creates a similar point of weakness. So hunters often carried un-notched spares or "preforms," finishing the point and adding the notches on an as-needed basis. But there are data to suggest that darts and spears armed with stone tips, not just arrows, were also susceptible to breakage, often losing the sharp tip, fracturing along the blade or at the haft, or shattering on the first or second attempt to kill a large animal, leaving the hunter in the unenviable position of having to face an angry adversary while armed with a very blunt-tipped weapon (Churchill 1993; Cheshier and Kelly 2006; Ellis 1997; Odell and Cowan 1986). Thus, prior to the widespread use of metal points, hunters might first have used a wooden-tipped spear to disable the prey and only once it no longer presented a serious threat would they then have switched to a stone-tipped spear to deliver the *coup de grâce*.

These observations put archaeologists in somewhat of a pickle. If large game were hunted with wooden-tipped spears, as the 400,000-year-old Schoeningen examples clearly suggest, how are we going to see this in the more remote reaches of the archaeological record? Schoeningen was a marvelous discovery, but totally fortuitous and not the kind of discovery we can count on for sites dating to a million or more years ago. We have to find alternative ways of seeing hunting in the archaeological record that are not as dependent on the vagaries of preservation and discovery.

This dilemma is far from resolved, but there are two interesting faunal approaches that are being used nowadays as a way of tracking big-game hunting in its formative stages. One such approach relies on "utility indices," measures of the nutritional value of the different carcass parts that were available to the hunter (Binford 1978); the other relies on the age structure of the animals that were being exploited (Stiner 1990, 1994). In fact, the two approaches are best used together.

Utility indices were first introduced by Lewis Binford, an archaeologist who did ethnoarchaeological fieldwork among Nunamiut Eskimos (Inuit) in northern Alaska as a way of gaining insight into the hunting, butchering, and transport decisions made by foragers who relied heavily on reindeer or caribou (Binford 1978). Ultimately, Binford's goal was to use these insights to better understand the foraging behavior of Neanderthals in Late Pleistocene Europe. Using Nunamiut butchering practices as a guide, Binford determined the amount of meat, marrow, and grease (the term commonly used by archaeologists for the fat or triglycerides in the spongy cancellous tissue of the joints) in each major anatomical unit (e.g., proximal femur, distal femur, proximal metatarsal, first phalanx, etc.) of a caribou and sheep carcass, and then expressed these amounts as percentages of the highest values observed. He then combined the individual meat, marrow, and grease values into a single composite index which he called the "General Utility Index" or GUI. As a final step, he adjusted the GUI values of certain elements, particularly small ones such as the knee-cap (patella) and the wrist and ankle bones (carpals and tarsals), because these are often transported away from a kill as "riders" attached to other bones, even though they have little or no inherent food value. The resulting index is known as the "Modified General Utility Index" or MGUI.

The MGUI provides a valuable frame of reference against which to compare archaeological data. If forager decisions about what to transport or abandon at a kill were based solely on the food value of each part, one would be able to predict which elements would be taken away (and in what approximate proportions), and which would be left behind. Deviations from expected would then provide useful insights into factors other than food value that may have influenced the hunters' transport decisions. For example, if the people were hungry, or if the number of people available to help transport meat back to camp was large, or if the distance from kill to camp was relatively short, the hunters might keep higher-than-expected proportions of low- to intermediate-utility parts. The archaeologist can then turn to other data to help discriminate among these different possibilities. For example, if the hunters were transporting many of the low-utility first and second phalanges (toe bones of the front and hind limbs) back to camp and cracking them open to extract their content of marrow, the hunger scenario would be the most likely. There are several reasons that justify such a conclusion: (1) the phalanges contain relatively little marrow, though what they do contain is tasty, (2) despite the limited amount of marrow, the fat in these bones is likely to persist even in an animal suffering from fairly severe nutritional stress, (3) these bones are bulky to transport and are therefore often jettisoned at the kill, and (4) in order to get at the marrow, the hunters have to invest a fair amount of time and effort to remove the tough skin, ligaments, and tendons that tightly encase the phalanges. Stefansson (1921:233) clearly recognized the low utility of the phalanges ("while delicious, the marrow of the small bones near the hoof is seldom eaten because it is bothersome to get at and there is so little of it"), anticipating Binford's (1978:148–149) comments concerning the handling of phalanges by the Nunamiut Eskimos more than half a century later ("if food is in short supply, or if marrow bones from the legs are not available at the meal, consumers may break the phalanges for marrow").

According to Binford (1978), the way hunters handled the mandible or lower jaw can be looked at in much the same way as the phalanges:

> In my experience, the number of broken mandibles is a fair measure of the food security of the group in question. If many are broken, then little animal food is regularly available and the people are utilizing morsels of very limited utility.
>
> Binford (1978:150)

The mandible of a large animal such as an eland or buffalo is heavy and bulky, and one can easily remove the highly prized, fatty tongue without having to remove and transport the entire jaw. But there is a small amount of marrow in the base of the mandible directly beneath the cheek teeth (molars and premolars). Carnivores often get at this marrow by biting the mandible near the angle at the back of the jaw. This splits off the base of the jaw, allowing the animal to lick out the exposed marrow. Hunters can accomplish the same thing by placing the skinned and defleshed mandible on a stone anvil and striking the bone near the angle. This breaks off the lower border of the jaw, exposing the marrow. Thus, schlepping large numbers of mandibles back to a campsite to process them for marrow is another likely indication of hunger (Binford 1978:149–150).

Since Binford's original introduction of the utility concept in the late 1970s, archaeologists have used the indices in a wide variety of different contexts and time periods, and there have been a number of attempts to refine and simplify the indices, and to develop separate indices for a wide range of other animal taxa – big and small; marine and terrestrial; mammal and avian (e.g., Diab 1998; Emerson 1993; Friesen 2001; Giardina 2006; Jones and Metcalfe 1988; Lyman et al. 1992; Madrigal 2004; Outram and Rowley-Conwy 1998; Rowley-Conwy, et al. 2002; Savelle and Friesen 1996). An analogous approach is even being used in the study of plant foods (see Barlow and Metcalfe 1996).

The application of utility indices to the hunting–scavenging debate is fairly straightforward. If foragers kill a large animal, they may not be able to transport everything back to a central location or camp. Instead, they will have to make decisions about what to take and what to discard. Since the foragers are the ones who make the kill, they have access to the entire carcass and hence to the highest-utility parts. In their transport decisions, therefore, one would expect the hunters to take elevated proportions of the nutritionally most valuable parts and abandon those that are low in utility.

On the other hand, if the foragers are passive scavengers, gaining access to the carcass only after other predators have finished with it, then the parts available to them for transport back to camp would be biased toward elements of intermediate-to low-utility – the parts that were either of little interest to the predators (such as the feet), or the parts that the predators were unable to open (for example, the brain enclosed within the thick, heavy skull of large animals).

The utility approach allows us to distinguish passive from confrontational scavenging fairly readily, but it doesn't really tell us whether the hominins killed the prey or simply possessed the wherewithal to drive predators off the carcass before they were able to devour the best parts. One could argue, of course, and some have, that if hunters had the capability of driving off ferocious predators like lions, they might well have had the ability to kill the prey in the first place. Unfortunately, in the absence of unambiguous stone projectile points, or the wooden spears themselves, we still lack a direct means of demonstrating this. So archaeologists have turned to another indirect way of seeing whether early hominins were hunters or scavengers of large animals. This approach makes use of the age structure of the prey.

Non-human predators often pick off animals that are in weakened condition because of illness, malnourishment, or injury (e.g., Schaller 1972). Many of these animals are old adults. Immature animals are often targets as well, either because they are less wary than more experienced adults or simply because they can't flee as quickly as the more mature individuals. Thus, scavenged assemblages are likely to display a bias toward very young and especially very old individuals, whose more robust bones stand a better chance than the immature ones of entering the fossil record. In contrast, later Pleistocene and Holocene human hunters typically took larger numbers of prime-adult animals, yielding assemblages that more closely resemble the age structure of a living population (Stiner 1990, 1994, 2002:20).

How does one determine the age of the prey? One way is to make thin-sections of the roots of the teeth in order to examine the structure of the cementum which surrounds the root and anchors the tooth within the jaw (Lieberman 1994). Cementum forms incremental or annular growth rings that under a microscope resemble tree rings, each pair of dark and light bands representing a year of growth. While cementum analysis is widely used by wildlife biologists, the technique unfortunately has a number of problems and drawbacks that limit its utility in archaeology. Bands can be missing, damaged, or altered by the process of fossilization (*diagenesis*), obscuring the annular structure and sometimes producing false bands (Stutz 2002). In warm tropical latitudes, where seasonality may not be very pronounced, annual banding may again be irregular and sometimes missing altogether. And, most importantly, cementum analysis is destructive and archaeologists are understandably reluctant to sacrifice precious fossils when the outcome is far from certain.

More commonly, archaeologists estimate the age at death of animals by studying the extent to which the molars and premolars are erupted (e.g., tooth "buds," fully formed but unerupted, just erupting above the alveolus or gum line, and fully erupted and in wear) and the degree of wear on the chewing (occlusal) surface of the teeth. As the animal ages, the enamel wears away and by carefully tabulating which cusps are worn, and how much, one can assign teeth to discrete "wear stages" which correspond roughly to the age of the animal at the time it died (Grant 1982; Klein and Cruz-Uribe 1984; Payne 1987). This qualitative approach is sometimes combined with actual measurements of the height of the enamel remaining on the tooth crown ("crown height"). Wear stages and crown-height measurements, of course, are not without their drawbacks – the rate of wear varies with a host of factors including the abrasiveness of the diet, the health of the animal, variability in the timing of tooth eruption, and so forth. But this approach does have two distinct advantages over cementum analysis: it is relatively quick and easy to do, and it is non-destructive.

Once the ages of the animals in an archaeological faunal assemblage have been determined, either via cementum analysis or by tabulating eruption and wear patterns, it is common practice nowadays to group them into three broad age categories – juvenile, prime adult, and old adult – and then display the results, expressed as percentages, in a triangular graph (Stiner 1990). Often the range of ages of prey taken by ambush and cursorial predators (e.g., leopards and cheetahs, respectively) are shown on the same graph. Not surprisingly, the prey hunted by modern humans during the Late Pleistocene and Holocene generally fall within the same area of the graph as the animals killed by ambush predators, although the age structure of the human kills is often shifted toward the prime adults (Fig. 2.3).

This approach has been successfully applied to many European and Near Eastern faunal assemblages from sites occupied by Neanderthals, showing beyond a reasonable doubt that these archaic humans, who lived between about 300,000 and roughly 40,000 years ago, were effective hunters of the prime-age adults of large and often very dangerous prey such as bison, aurochs, wild boar, and others

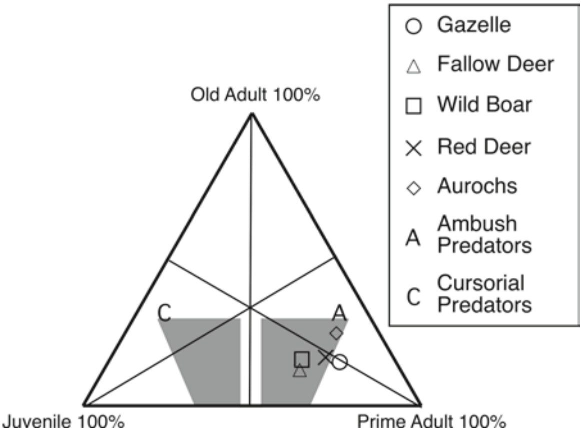

**Fig. 2.3** Triangular diagram showing the age structure (based on tooth crown heights) of the principal large prey in the Middle Paleolithic (Neanderthal) levels of Kebara Cave (Israel). Note that all of the animals, including the large and dangerous aurochs, fall within the zone typical of ambush predators (*gray* zone "A") and display a distinct bias toward prime adults. Adapted from Speth and Clark (2006:7, Fig. 5)

(e.g., Gaudzinski 2000; Gaudzinski and Roebroeks 2000; Speth and Clark 2006; Speth and Tchernov 2001; Steele 2003; Stiner 1990).

Unfortunately, this technique has not yet been applied systematically to significantly earlier archaeological faunal assemblages, and hence there is still considerable disagreement about the antiquity of big-game hunting (for an excellent summary of the data and the debate, see Stiner 2002). Nevertheless, a preliminary study by Henry Bunn (2007a, b) of the age structure of the larger mammals from Olduvai's FLK-*Zinj* shows that prime adults are well represented among the prey at this 1.8-million-year-old site, a pattern that one would most expect if early hominins already by the beginning of the Pleistocene were capable of hunting larger prey (see also Domínguez-Rodrigo et al. 2007; Stiner 2002:22). Most archaeologists, however, remain skeptical of this conclusion, and will continue to be so, until we find a concrete way of demonstrating that early hominins possessed some form of lethal weapon.

The interpretive problems extend beyond just determining whether ancient faunal assemblages are the product of human hunting or scavenging. For the sake of argument, let us grant that hominins were able to kill large animals and we are satisfied that we have a number of archaeological sites that demonstrate this capacity. We still need to know the season(s) of the year when the animals were killed. Suppose that all of these kills were made in the dry season, arguably the most difficult time of year. We could say that meat from large animals was important in early hominin diet *at that time of year*, perhaps just as a fallback food (Alemseged and Bobe 2009), but we would still know little or nothing about what these foragers ate over the rest of the year.

We can estimate season of death of the animals from their age which, as already discussed, we determine either by cementum analysis or by examining the stage of eruption and wear of the teeth (Grant 1982; Klein and Cruz-Uribe 1983; Klein et al. 1981). Then, if the species in question has a distinct calving season, for example at the beginning of the rainy season, the age of the animal in months can provide us with a crude estimate of the time of year when the animal was killed (i.e., the number of months that elapsed from the calving season to the time the animal died). Unfortunately, over much of Africa today, and perhaps during the Pleistocene as well, birth seasons are often not tightly constrained, or there may be multiple birth peaks, making accurate assessment of season of death crude at best.

Continuing in this same vein, let us assume we know that the animals in the sites in question were hunted, not scavenged, and let us also assume that we know the season of the year when the animals were killed. We still have no idea what the recurrence interval of these kill events was. Did the hominins hunt big animals daily? Weekly? Once a month? Only during occasional inter-annual periods of resource stress? In other words, is a site like FLK-*Zinj* a surviving example of hominin activities that were carried out frequently in the Olduvai region, or is it instead an unusual occurrence that tells us little about what day-to-day life was like in the African savannas some 1.8 million years ago? This brings to mind a humorous quip that archaeologists often make about elephant kills in the archaeological record: "a hunter probably killed this one elephant and spent the rest of his life talking about it." When it comes to determining recurrence interval, we are in the realm of pure conjecture. In most contexts and circumstances, archaeology still lacks the ability to even crudely approximate recurrence interval. And without some handle on the number of kills per unit time per person, we have no way of determining from the archaeologically recovered animal bones what percentage of the daily or annual diet was provided by big-game hunting. Rather than sampling the "daily fare" of these ancient hominins, as we typically assume, we may instead be observing the remains of infrequent, perhaps even rare, events that happen to be very visible archaeologically.

Finally, there is a critical but seldom-questioned assumption that underlies virtually every study concerned with the role of big-game hunting in human evolution, one that has come in fact to have the status of a truism in paleoanthropological thinking – namely, that hominins hunted big animals because they provided calories and high-quality nutrients in large and very cost-effective packages. This book is an attempt to show that this assumption may be incorrect; *big-game* hunting in our evolutionary history may have been motivated first and foremost by social, political, and demographic forces, and only secondarily as a way of putting food on the table.

One more point, a minor yet necessary jog in the path, before we jump into the substance of the book. I am concerned here with the role of big-game hunting (or scavenging) in the lifeways of hominins in Africa, the land where much of our evolutionary career unfolded. When our ancestors left Africa, sometime after about 2 mya, and began to penetrate into cooler and more markedly seasonal environments, and especially once they entered into the genuinely subarctic to arctic environments of glaciated Eurasia, the seasonal availability of carbohydrates and oil-rich plant foods would have declined, while at the same time the average amount of body fat carried by the larger prey animals would have increased to levels well above the meager values seen in most African ungulates, even those in prime condition (*fat in African ungulates*: Burchell 1822:187; Burton 1860:281; Dane 1921:75; Ledger 1968; McKiernan 1954:99; Ntiamoa-Baidu 1997:65; Owen-Smith 2002:149; Smith 1970:127; *fat in northern latitude birds and mammals*: Boonstra 2004; Castro et al. 1992; Ellison 2003:290; Humphries et al. 2004; King and Farner 1966; McNab 2002:464; Sand et al. 1995:441; Witter and Cuthill 1993:74). These changes are likely to have altered the calculus that guided forager hunting strategies. The social, political, and prestige components of big-game hunting (or scavenging) that I will argue characterized early hominin lifeways in Africa almost certainly would have persisted in these new environs (e.g., Jochim 1976). However, the nutritional value of the meat thus acquired, perhaps the partially digested stomach or rumen contents, *and most especially the animal's fat content*, would have become increasingly critical to survival (Stefansson 1944; Andersen 2005:10; see Eidlitz (1969) for evidence of the importance of rumen contents in the diet of arctic and subarctic foragers). One might in fact argue that the politically and prestige-motivated hunting (and perhaps scavenging) strategies of our African forebears would have preadapted hominins to life in the much colder and more seasonal environments that they would eventually colonize.

# Chapter 3
# Big-Game Hunting in Human Evolution: The Traditional View

> *More than 30 years after the publication of Man the Hunter, the role of meat in the early human diet remains a central topic of human evolutionary research. There is little doubt that meat-eating became increasingly important in human ancestry, despite the lack of direct evidence in the fossil record of how meat was obtained, or how much was eaten, or how often, or how exactly increasing importance of meat-eating may have contributed to the rise of the genus Homo.*
>
> Stanford and Bunn (2001:3)

The "Holy Trinity" of human evolution – hunting, meat-eating, and the animal protein thereby derived – in some form or other has dominated our view of human origins and evolution for well over a century. From Darwin's pioneering look at humans as predators in *The Decent of Man* (1871), to a precocious series of late nineteenth- and very early twentieth-century precursors to Dart's (1957) bone-wielding killer-ape hypothesis (Morris 1886; Campbell 1904; Read 1914; interestingly summarized in Cartmill 1993), to Ardrey's (1961) highly controversial popularization of Dart's ideas, to Washburn and Lancaster's (1968) rather amusing (and sexist) attempt to attribute virtually everything "human" to our zest for hunting, to almost every contemporary textbook treatment in paleoanthropology, the ever-more-effective pursuit of large game stands at the very core of our perceived understanding of how we came to be what we are. True, our views about hunting and meat-eating have shifted and morphed in myriad ways over the decades. Yet, through all of its many transformations and reconfigurations, at times influenced as much by issues of gender and feminism, and even political correctness, as by empirical findings in the fossil and archaeological records (see discussions, for example, in Cartmill 1993; Hart and Sussman 2008; Slocum 1975; Sussman 1999; Wrangham and Peterson 1996; Zihlman 1978), the *Man the Hunter* (or *Man the Scavenger*) focus remains very much alive and well (e.g., Bramble and Lieberman 2004; Bunn 2007a; Larsen 2003; Leonard et al. 2007a, b; Milton 1999, 2003; Pickering and Bunn 2007; Stanford 1999).

When I was a beginning student in anthropology more than four decades ago, human origins seemed remarkably clear and straight-forward: bipedalism, hunting, reliance on tools, canine reduction, and increasing brain size all were explicable as

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part of an elegant feedback system set in motion as our ape-like ancestors ventured out of the forests into the open savannas of Plio-Pleistocene eastern Africa and began to prey on the countless herds of antelope that roamed the grasslands. Darwin predicted it, and the archaeology of Olduvai Gorge seemed to confirm it (Leakey 1971). All that remained for archaeologists and paleoanthropologists to do was to fill in a few fuzzy or missing details.

Then came a shock that reverberated across the length and breadth of paleoanthropology, one of those rare cases when new data truly do upend an established theory. Bipedalism (and perhaps reduced canines) had to be jettisoned from the package. The fossil record showed that our curious form of locomotion had emerged long before the appearance of the other components that till then had been so convincingly interwoven in the fabric of the feedback model. Bipedalism developed not in the Plio-Pleistocene, as we had all assumed, but in the early Pliocene or even in the late Miocene, some 5–6 million years ago (mya) or more (Pickford 2006; Shreeve 1996; see also White et al. (2009) and Lovejoy (2009) for recent and somewhat surprising insights on the origins of bipedalism as revealed by Ethiopian fossils of *Ardipithecus ramidus*). And the first step toward bipedalism may have been taken, not in the savannas, as the feedback model predicted, but in much more enclosed woodlands and forests where game was comparatively scarce and could hardly have been the major impetus for our origin.

But through all this theoretical turmoil, the perceived importance of meat-eating hardly wavered an iota from its position of primacy. Though bipedalism now had to be explained by some other means, much of the remaining hunting/meat-eating package was simply shifted forward in time to the origins of the genus *Homo*, roughly 2.0–2.5 mya. Bunn (1995:453) nicely articulates the ease with which this shift was made:

> …the hunting hypothesis was developed in paleoanthropology to account for the behavior of australopithecines. But…the australopithecine hunting hypothesis can usefully be reformulated to examine the evolution and behavior of the genus *Homo*, as researchers have done since the 1970s. On present evidence, hunting, scavenging, and meat eating might not have made us hominids but might have contributed significantly to making us human.

Thus, while hunting and meat-eating could not explain why hominins first rose up on their hind limbs, a meat-based diet could at least be counted upon to explain the speciation event that gave rise to the first big-brained members of our own genus, as well as the beginnings of an eminently visible bone-and-stone-based archaeological record – the so-called Oldowan (Toth and Schick 2009).

Other theoretical forces were afoot at roughly the same time. Beginning in earnest in the 1980s, archaeologists began to challenge the view that early *Homo* was actually a hunter. Presumably lacking thrusting spears or projectile weapons, archaeologists began to see these early members of our genus as scavengers rather than effective predators, at least in so far as large game was concerned. Thus began a long foray into taphonomy, one that continues unabated today, in an attempt to determine whether these early denizens of the savannas had to wait for dinner until the real predators – the lions and hyenas – had satiated themselves (passive scavenging), or instead already possessed the requisite wherewithal to drive these fearsome carnivores off the carcasses while there was still more than table scraps left to pilfer (active, power, or confrontational scavenging) (e.g., Behrensmeyer 1975; Binford 1981; Blumenschine 1986; Blumenschine et al. 2007; Brain 1981; Bunn 1983; Bunn and Kroll 1986; Domínguez-Rodrigo 2002; Domínguez-Rodrigo and Barba 2007; Domínguez-Rodrigo et al. 2007; Lupo 1994; Lyman 1987; Marean and Cleghorn 2003; Njau 2006; O'Connell et al. 1988a; Oliver 1994; Pickering and Wallis 1997; Pobiner and Braun 2005; Potts 1983; Selvaggio 1994; Shipman 1983).

The hunting-scavenging debate, as it is commonly dubbed, for a time was a hotbed of exciting new ideas and a springboard for new methods and approaches, though in recent years it has become increasingly myopic, losing sight of the forest for its preoccupation with the trees. Few involved in this debate back away from the minutiae – the gashes, pits, and grooves on the bones – to question the role of meat in hominin evolution, regardless of how it was acquired; the concern is seldom with why these early hominins ate what they did, but with how they went about getting it (for interesting exceptions, see O'Connell et al. 1988b, 2002; see also the interesting argument offered recently by Alemseged and Bobe 2009).

While most paleoanthropologists agree that meat from larger animals increased in importance more or less hand-on-hand with the appearance of the genus *Homo*, and most would also probably agree that these animals were scavenged, not hunted, there is less agreement about when humans actually began to hunt larger animals (see Tooby and DeVore 1987:221 for an interesting discussion of why scavenging is unlikely to have been a genuine "stage" in human evolution; similar doubts are expressed by O'Connell et al. 2002). There seems little question that Eurasian Neanderthals and their hominin contemporaries in Africa were effective hunters by at least 250,000–300,000 years ago, killing (occasionally? frequently?) a broad spectrum of animals – prime adults, not just the more vulnerable young and old – up to and including some of the largest and most dangerous species on the landscape (Stiner 2002). But when this shift took place is less clear. Stiner (2002:22) suggests that it occurred sometime during the Middle Pleistocene, perhaps on the order of 500,000 years ago, as humans began to successfully colonize the colder latitudes of temperate Eurasia and the meat component of the diet became increasingly important to winter survival. Others, such as Domínguez-Rodrigo et al. (2007), and perhaps Bunn (2007a, b), see this shift occurring much earlier in sub-Saharan Africa, by at least 1.8 mya, and hence in contexts that were far less seasonally variable than Middle Pleistocene Eurasia.

Over the decades, several other lines of argument have emerged that continue and reinforce our focus on meat and animal protein as prime-movers in the story of our origins and evolution. Most of these are so well known that I will only briefly allude to them here. One such line of argument is provided, of course, by archaeology. Cutmarked and humanly battered and broken animal bones obviously provide some of the clearest direct evidence that early members of the genus *Homo* were very much interested in animals, including many quite large ones. One need only look at the exploding taphonomic literature on the Olduvai site of FLK-*Zinj* (e.g., Binford 1981; Bunn 1981, 2007a; Capaldo 1997; Domínguez-Rodrigo 1997; Egeland 2007; Fernández-Jalvo et al. 1998; Marean et al. 1992; Njau and Blumenschine 2006;

O'Connell et al. 2002; Oliver 1994; Potts 1988; Selvaggio 1994) to see how clearly large animal remains had taken front and center position in the lives of early *Homo* (or at least in the eyes of most paleoanthropologists who study the archaeological record of early *Homo*, according to a provocative but intriguing view being put forth recently by Domínguez-Rodrigo et al. 2007; Domínguez-Rodrigo 2009; Egeland 2008; and Mora and de la Torre 2005; these authors are suggesting that the bones, as well as the stone tools, at many of the classic Bed I and Bed II Olduvai localities have little or nothing to do with carcass processing, and may instead be linked to pounding nuts, fruits, or other plant foods). Of course, sites like FLK-*Zinj* have not told us yet what percentage of the annual diet was actually composed of meat, nor does it tell us why early hominins were so interested in meat (Alemseged and Bobe 2009), but they do at least suggest an increasing importance of larger-sized animals in the activities of early hominins after about 2.0 mya.

Optimal foraging theory (OFT), while not providing hard evidence of early hominin behavior, nevertheless provides a rigorous, theoretically grounded, and hence very compelling logic to explain why large game *should be* the ever-increasing focus of hominin interest (Krebs and Davies 1991; Smith and Winterhalder 1992; Winterhalder and Smith 1981, 2000; but see Bird et al. 2009; Hawkes and O'Connell 1992; Hill et al. 1987:20–21; and Koster 2008 for the kinds of circumstances where such a direct equation of rank and size may not hold). When looked at in terms of caloric returns, the preferred "currency" of most theorists, diet breadth models show us that large game should almost invariably assume the paramount position in the food choices made by human foragers, their technological know-how permitting of course, while the remainder of the potentially available foods enter or drop out of the "optimal" diet, not as their own abundance waxes or wanes, but in response to the rates at which foragers encounter the chosen few. Archaeology confirms theory, a match of expectations and observations that can hardly be ignored.

Ethnography also adds its own support to the picture. The primacy of hunting was certainly emphasized by Euroamerican explorers, colonialists, and ethnographers, in part because many of the observers were males with their own cultural biases and baggage, and in part because the people they were observing often expressed similar values – hunting was definitely where the action was (e.g., Reiter 1975; see also Milton 1979).

Recent theoretical looks at human evolution by physical or biological anthropologists reinforce the primacy of hunting (or scavenging) and meat-eating in our explanatory frameworks (e.g., Larsen 2003; Leonard et al. 2007a, b; Milton 1999, 2003). Perhaps the most influential of these is the so-called expensive tissue hypothesis. Aiello and Wheeler (1995; see also Leonard et al. 2007a, b) note that the resting metabolism of humans today is pretty much what one would predict from our body size, yet our brain, a very costly organ to build and run, is vastly enlarged (encephalized) compared to those of other primates and other nonprimate mammals. To account for this energetic enigma, they posit that some other costly organ must have undergone comparable reduction in order to preserve the metabolic *status quo*. They show that the candidate that best seems to fulfill this expectation is the size of the human digestive tract, which is significantly smaller than expected by comparison to the gut size of our nearest primate relatives. But given the comparatively large body size of humans, a decline in gut size is thought to imply a concomitant increase in overall diet quality. In other words, the impressive encephalization seen in humans, a trend that began with early *Homo*, must have been accompanied by a substantial increase in the overall quality of the foods these hominins consumed. Aiello (2007; see also Aiello and Wells 2002) clearly recognizes that there are different ways that early *Homo* could have improved the quality of their diet without relying solely on meat, cooking of course being paramount among them, a point recently emphasized by Wrangham (2009:40):

> Evolutionary benefits of adapting to cooked food are evident from comparing human digestive systems with those of chimpanzees and other apes. The main differences all involve humans having relatively small features. We have small mouths, weak jaws, small teeth, small stomachs, small colons, and small guts overall. In the past, the unusual size of these body parts has mostly been attributed to the evolutionary effects of our eating meat, but the design of the human digestive system is better explained as an adaptation to eating cooked food than it is to eating raw meat.

However, given the lack of unequivocal evidence for the control of fire in the Plio-Pleistocene (Brain and Sillen 1988; de Lumley 2006; Goren-Inbar et al. 2004; Gowlett 2006; James 1996; Rolland 2004; Rowlett 2000), and given the near universal acceptance in our profession that meat is the quintessential "high-quality" food in our larder, it is perhaps not surprising that most contemporary paleoanthropologists focus their sights on meat-eating as the principal nutritional engine that drove much of our evolution: increasing reliance on animal foods, particularly the meat of large mammalian prey, is basically what made us human:

> So the question of our origins concerns the forces that sprung *Homo erectus* from their australopithecine past. Anthropologists have an answer. *According to the most popular view since the 1950s* there was a single supposed impetus: the eating of meat.
>
> Wrangham (2009:5–6), emphasis added

While scholars debate the strengths and weaknesses of the expensive tissue hypothesis (Hladik et al. 1999; Pasquet and Hladik 2005; Snodgrass et al. 2009; a few, such as Isler and van Schaik 2006, 2009, even question whether an increase in diet quality was necessary), only a few studies have begun to challenge the primacy of meat as the critical "high-quality" food (Alemseged and Bobe 2009). Some focus on alternative foods, such as tubers, corms, and bulbs (often dubbed USO's or underground storage organs), a curious choice given that many of the species that are likely to have been available to early hominins may have been relatively energy-poor compared to other plant resources (e.g., Schoeninger et al. 2001), or on new methods of preparing foods, particularly cooking, as the key shifts in hominin lifeways that gave rise to our evolutionary lineage (see, for example, Laden and Wrangham 2005 and O'Connell et al. 1999; see also Lee-Thorp and Sponheimer 2006; Yeakel et al. 2007). Others continue to see meat as a particularly high-quality food, but are turning their attention increasingly to social forces (e.g., costly signaling) that may have compelled humans and higher primates to hunt (Bliege Bird and Smith 2005;

Bliege Bird et al. 2001; Hawkes and Bliege Bird 2002; Mitani and Watts 2001; O'Connell et al. 2002; Smith et al. 2003). For most paleoanthropologists, however, it is business as usual – meat is the food among foods, and human evolution is largely about how we came to be so good at acquiring it.

So where are we heading in the coming pages? First, I will lay out several lines of evidence to show that animal protein is not invariably the nutritional elixir that paleoanthropologists have so often assumed it to be. More is not invariably better. Second, I will attempt to show that the fats that one can glean from muscle tissue, marrow, and brain are neither adequate to warrant the time and effort that goes into hunting big game nor are they needed, given the protein and oils *that are available to African foragers from plants, insects, and other nonhunted resources at more or less the same time that they engage in much of their hunting*. Third, I will add my vote to the minority but growing view that sees social and political factors as important, perhaps critical, components of the hunting story (e.g., Hawkes and Bliege Bird 2002; Hawkes et al. 2001). By questioning the widely assumed *nutritional* importance of the protein and fat acquired by big-game hunting, paleoanthropology may be in a better position to recognize and come to grips with the role played by social and political forces in the emergence and evolution of our species.

# Chapter 4
# The Other Side of Protein

> *Certainly, throughout most of history and prehistory, and among the less developed countries today, the problem has always been that of too little, rather than too much, protein.*
>
> Harris (1979:32)

> *Let's answer that last question with a categorical piece of provocation: that of all the disasters caused by the mis-application of science in this century, including the development of the atom bomb, none has caused more human misery, or a greater misuse of resources, or a more pernicious perversion of policy and action, than the nutritionists' exaggeration of protein requirements.*
>
> Tudge (1977:50)

Paleoanthropologists commonly see animal protein as the best of the best when it comes to nutrients. It has all the amino acids in just the right proportions (Williams 2007) and, as OFT has so eloquently shown us, given the right technology the hunting of larger mammals can provide the successful hunter with meat and animal protein in large, convenient, and efficiently acquired packages. So, stripped to its essence, much of the human story can be reduced to our increasing prowess at acquiring meat.

As simple, forthright, and compelling as this perspective might seem, there are a number of niggling facets of protein nutrition that should make us hesitate before we wholeheartedly sign on to the party line. Let us take a look at a few of these.

## 4.1 The Great Protein Fiasco

> *…demoralising to the profession was the 'great protein fiasco': the massive recalculation of human protein requirements in the 1970s which 'at the stroke of a pen' closed the 'protein gap' and destroyed the theory of pandemic 'protein malnutrition'.*
>
> Cannon (2005:704)

I think it is fair to say that the western industrial world has been having a love affair with protein for a great many years. Paleoanthropologists are in good company; they are far from alone in placing protein upon its own lofty pedestal. McLaren

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(1974, 2000) and Newman (1995); see also Schürch 1995 provide us with a fascinating history of how this love affair came about, one that paleoanthropologists would do well to read:

> The concept of the much-publicised world protein "gap", "crisis", or "problem" arose from the description of kwashiorkor in Africa in the 1930s and the assumption, which has turned out to be wrong, that malnutrition in children takes this form throughout the world. As a result, measures to detect protein deficiency and treat and prevent it by dietary means have been pursued until the present time. The price that has had to be paid for these mistakes is only beginning to be realised.
>
> McLaren (1974:93)

As outlined by McLaren (1974) and Newman (1995), kwashiorkor was first clearly recognized and formally named in the early to mid-1930s by Williams (1933, 1935), a British medical officer in the Gold Coast (now Ghana). Williams made a convincing argument that the disease occurred in young children who were weaned early and put on a maize-based diet that was deficient in protein. And time has shown her to be correct. Problems arose after World War II, however, not from questions about Cicely Williams' original diagnosis of kwashiorkor, but from two influential reports, one by Brock and Autret (1952) published through the UN's World Health Organization (WHO), the other by Trowell et al. (1954). In an oft-quoted statement, Brock and Autret (1952), representing the position of WHO, maintained that kwashiorkor, or protein malnutrition as it came to be called, was the principal source of childhood malnutrition throughout the world: kwashiorkor "is the most serious and widespread nutritional disorder known to medical and nutritional science" (Brock and Autret 1952; quoted in McLaren 1974:93 and Schürch 1995:2255S). Only since the 1970s has protein malnutrition come to be seen as a comparatively rare deficiency syndrome which is now subsumed under the much more inclusive rubric of "protein-calorie" or "protein-energy" malnutrition (PCM or PEM). In other words, as it turns out inadequate protein intake is seldom the root cause of childhood malnutrition. The cause is usually the result of inadequate overall food intake, compounded by pathogens and other factors often associated with poverty and unsanitary living conditions.

Newman (1995:239–240) provides a detailed overview of what transpired from the early 1950s onward, and it is worth quoting his treatment in some detail (I have omitted most of the author's citations from within the quoted text to economize on space).

> The fact that kwashiorkor was the first of PEM's (protein-energy malnutrition's) syndromes to receive widespread attention by the medical profession meant that intervention was aimed at providing more protein to infants and young children. That protein was the centerpiece of early preventive policies during the 1950s is evident in the formation of a Protein Advisory Group of the United Nations. The various reports of this Group emphasized the widespread nature of a protein supply crisis. The international community soon came to regard this "protein gap" as a serious threat to the survival of many nations and possibly even to world peace.
>
> One widely supported solution was to expand the use of cow's milk, especially in those areas where it was not readily available. Williams (1933) had found skim milk to be efficacious in

> the treatment of kwashiorkor, and she recommended its use along with other dairy products as a preventive measure as well. The influential work by Trowell, Davies, and Dean (1954) seconded her opinion, labeling cow's milk as the "ideal transition diet." Other experts agreed, and theory soon became practice during the 1950s and early 1960s. Powdered skim milk, derived largely from surplus stocks in the United States, was made available in large quantities, and when reconstituted, it served as the backbone of many early efforts aimed at dealing with kwashiorkor and other PEM syndromes. Often the skim milk was distributed under U.S. Public Law. 480, better known as the "Food for Peace" program that Congress passed in 1954. P.L. 480 had three primary goals: 1) to dispose of expensive U.S. food surpluses; 2) to combat Communist influences in Asia, Africa, and Latin America; and 3) to provide humanitarian assistance. This mixture is an interesting one that clearly reflects Washington's efforts to use food in the power struggles of the Cold War era. These milk-based strategies of international development agencies soon encountered difficulties, however. As the 1960s progressed, American milk surpluses began running low, and the establishment of dairy industries proved more difficult and expensive than first thought, especially in economically poor tropical settings where dairy husbandry confronts both unfamiliar livestock diseases, heat stress, and infrastructural inadequacies.
>
> Another widely advocated strategy for increasing protein involved fish. But the strategy of modernizing fisheries confronted problems of high costs and environmental limitations; few countries could afford the investment in fishing necessary for attacking PEM.
>
> Others jumped on the bandwagon of "commerciogenic nutritious foods", that is, of specially formulated products enriched with protein from a variety of sources, including oil seeds, soya beans, and fish meal as well as milk products. By the early 1970s, a wide array of these "foods" had been formulated and made available to the public, mainly through market channels. Distributed under such names as Incaparina, Superamine, Nutribun, Pronutro, Uniprotin, and Vitasoy, they served as breast milk substitutes, special weaning foods, general purpose flours, beverages, or snacks. Manufactured locally under the auspices of multi-national food firms and/or various aid donors, commerciogenic foods were touted as means of alleviating the burden of PEM while stimulating economic development through job creation.
>
> Critics soon countered that the responses to the supposed "protein gap" had, in fact, created a "protein fiasco". These critics had the best of it since the "gap" proved to be largely a statistical artifact of the standards then in use – standards which substantially overestimated human protein needs some analysts claim that this continues to be the case even today for infant protein requirements. According to critics, the "fiasco" produced by these miscalculations was the result of a preoccupation with protein that diverted attention away from more important dietary deficiencies of energy. The real "gap" was one of food quantity, not of protein….

McLaren (1974:95) minces few words when he summarizes the general tenor of the period from about 1950 to 1970:

> The undue emphasis put on protein deficiency and on the measures related thereto is clearly documented. After the establishment of the Protein Advisory Group in 1955 the approach became phrenetic, reaching its zenith with an unsuccessful attempt to set up a world council on protein and an abortive effort to convince the U.N. that there was an impending protein crisis.
>
> United Nations (1968)
>
> The entire edifice was built upon erroneous worldwide generalisations made from correct but limited observations in atypical situations such as rural Africa.
>
> Lack of nutriment in general with an energy gap rather than a protein gap is the crux of the matter.

Since the 1970s, attitudes and policies toward the role of protein in undernutrition and malnutrition have gradually shifted as the complex, multivariate nature of these health conditions has come to be more fully appreciated. It is now widely recognized that malnutrition in children may involve inadequacies, not just in protein or amino acids, but in a wide spectrum of macro- and micronutrients, including vitamins, minerals, fatty acids, fiber, and, most importantly, total energy intake. Moreover, numerous studies have shown that the effects of these deficiencies are compounded by unsanitary living conditions, smoking and alcohol consumption, and other factors that commonly go hand-in-hand with poverty. Thus, while the nutrition community remains far from consensus on the role of protein in human nutrition and health, these fields over the past two to three decades have come to focus much less on protein as the panacea for all of the nutritional woes of the so-called underdeveloped world (reviewed in Scherbaum and Furst 2000).

Curiously, in the 1970s, just as the "great protein fiasco" in the nutritional realm was beginning to heave its final gasps, cultural anthropology, particularly that corner of the sub-discipline referred to as "cultural ecology" or "ecological anthropology," got caught up in the same frenzy. Nowhere could this be clearer than in the vitriolic debates that surrounded the putative role of protein as *the* critical limiting variable in the development of Amazonian cultures (e.g., Chagnon and Hames 1979; Diener 1984; Diener et al. 1980; Gross 1975; Harris 1979, 1984). Marvin Harris was unquestionably the most prolific and outspoken champion of protein in cultural ecology:

> Certainly, throughout most of history and prehistory, and among the less developed countries today, the problem has always been that of too little, rather than too much, protein. Individuals and populations are therefore well advised to pursue a production strategy aimed at maximizing protein intake and at resisting any lowering of per capita norms. When one does not know what is a safe minimum, it is best to strive for the highest sustainable rate of consumption possible under given ecological circumstances. For populations subject to periodic crises of war, epidemics, and other calamities, such as storms and floods, there really is no minimum safe protein ration.
>
> Harris (1979:32)

However, by the mid- to late 1980s, shifts in perspective within cultural ecology began to give rise to more complex, nuanced models that no longer placed protein center stage, and extreme "protein-determinist" positions, such as those advanced most emphatically by Marvin Harris, have largely faded from the anthropological scene.

On the other hand, in paleoanthropology many contemporary accounts of hominin origins and evolution still see animal protein as the engine that drove the process. This assertion is easily supported by a cursory look at the literature of our field. Both scholarly and popular accounts of human origins and evolution, recent and not so recent, are peppered with statements suggesting that hunting (or scavenging) by our hominin ancestors had the primary objective of acquiring "high-quality" *protein*. In the past few years, fat (especially from marrow and brain) and a variety of social and political factors (e.g., costly signaling) have begun to appear on paleoanthropology's radar screen but, whether explicitly stated or merely implied, the "meat-equals-protein" perspective still remains very widespread (I will defer discussing these alternative perspectives until later). Also interwoven throughout the literature on human evolution is the commonplace (and mistaken, as we will see later) notion that *protein* is what our ancestors needed to underwrite the development of our species' uniquely large brain. I provide a few examples here, not to criticize the authors who wrote them, for many have since modified their views, but to illustrate the pervasiveness in our evolutionary scenarios of the idea that meat and protein are more or less one and the same thing, and that protein was the critical nutrient underwriting hominin encephalization.

Nearly three decades ago, Holloway (1981:300), a leading expert on the evolution of the brain, articulated the widespread assumption in paleoanthropology at the time that animal protein was the engine that drove the encephalization of the human brain: "as the brain increases in size in the fossil record, there are also the first intimations of the use of protein-rich foods, i.e., animal flesh."

The classic "feedback" model, which has been with us in various guises since Darwin, explicitly links animal protein with other key facets of hominin evolution, including encephalization, as clearly stated in this recent quote from Ungar et al. (2006:214):

> Hominins began to incorporate more meat into their diets, with improved hunting abilities following from an expanding toolkit and increasing intelligence. A feedback loop followed, as the new high-protein diet allowed for larger brains, and hunting strategies led to a division of labor, more complex social systems, and selection for yet greater intelligence….

Ragir (2000:154–155), in her discussion of early hominin diet, also sees meat primarily in terms of its protein content, which she likewise links directly to encephalization:

> The existence of this year-round supply of protein that is essential for the growth of a large brain and body not only supported changes in fetal and postnatal development, but also fueled population expansion and the dispersal of *H. erectus* out of Africa. The enormous cranial volumes found in archaic *Homo sapiens* and the reduction of size dimorphism to modern proportions in late *Homo erectus* may be explained in part by an animal protein component in the female and juvenile diet comparable to that of modern high-latitude hunters. This last significant episode of encephalization, the one that catapulted presapiens to *Homo sapiens,* may best be understood as the result of intensive hunting of large game and a cultural revolution that intensified with the use of fire for cooking.

Antón et al. (2001:91), while emphasizing the *energy* needs of bigger-bodied and bigger-brained hominins as they first dispersed out of Africa, nonetheless squarely focus on the protein content of their hunted (or scavenged) animal resources as the primary fuel for the enlarged brain of early *H. erectus*:

> Although the timing of the first hominid dispersal pre-dates significant technological advances, the energy required by larger hominid body/brain sizes suggest a shift to exploitation of high-protein packages….

Larsen (2003:3893S), in a recent review of the role of animal foods in human evolution written for the nutrition community, also zeros in on a single macronutrient – the protein content of meat: "The hunting of large prey by a group of cooperating adults provided humans with a regular and predictable access to protein and micronutrients."

In a recent and widely read textbook on human evolution, Lewin and Foley (2004) point out that the meat-as-protein view is actually on the ascendancy in contemporary paleoanthropological thinking:

> To some extent the last 40 or 50 years have seen a full circle in hypotheses – from the "Man the Hunter" of the 1960s, through the rejection of meat being important in the 1970s, to a view of scavenging in the 1980s, and more recently to an emphasis on the nutritional importance of protein and the significance of hunting for primates….

Bramble and Lieberman (2004) provide another recent example, emphasizing the importance of endurance running (ER) as a means by which our early hominin ancestors succeeded in obtaining protein:

> One possibility is that ER played a role in helping hominids exploit protein-rich resources such as meat, marrow and brain first evident in the archaeological record at approximately 2.6 Myr ago, coincident with the first appearance of *Homo*.

Finally, it is interesting to see how scholars in other disciplines characterize paleoanthropology's perception of the pivotal role of protein in hominin encephalization. Although many examples can be culled from the literature, which nowadays is so readily accessible and searchable at one's fingertips on the Web, there is no need to belabor the point; a single example will suffice. Rosenberg and Linquist (2005), two philosophers of science, put it very matter-of-factly:

> It is true that the accepted view among biological anthropologists has it that almost everything that is distinctively different between humans and other primates stems from the adoption of hunting as a strategy of protein provision: the large brain, the need for relatively high protein diet to support it….

Since it seems reasonably clear from the archaeological record that hunting, especially the hunting of large game, does in fact increase over the course of human evolution, it has long been the tradition in paleoanthropology to assume that this trend reflects our increasing need for "high-quality" protein to support the nutritional demands of a rapidly enlarging brain. Although a number of paleoanthropologists now recognize the importance of fat in meat, not just its protein content, our brief perusal of recent literature suggests that many in the discipline are still squarely focused on the latter. In light of the rather dramatic change in the position held by protein in the health and nutrition fields, perhaps it is time for our discipline to entertain seriously the possibility that the evolution of *big-game* hunting was driven at least in part, if not in large part, by forces outside, or beyond, the nutritional domain. This of course is not a new idea (as reflected, for example, by the current popularity of "costly signaling" models in behavioral or evolutionary ecology); it just remains trapped on the margins of theorizing in paleoanthropology.

## 4.2 Excess Protein and the Importance of Fat

> *…the Patagonian believes in a future life – a life much on the lines of his earthly one, but abounding in those things which he most desires, and which here he finds in short measure. I only know that the land he is going to after death is a land flowing, not with milk and honey, but with grease.*
>
> Patagonia, South America, Prichard (1902:99)

> *The sun, by some of the people of this benighted land, is considered to be a mass of fat, which descends nightly to the sea, where it is laid hold of by the chief of a white man's ship, who cuts a portion of tallow off it, and giving it a kick, it bounds away, sinks under the wave, goes round below, and then comes up again in the east next morning, its fat having again grown.*
>
> Southern Africa, Alexander (1838:168)

> *There are few things which a Bechuana prizes so highly as fat of any description; they will go an amazing distance for a small portion of it. They use it principally in cooking their sun-dried biltongue* [biltong]*, and they also eat it with their corn.*
>
> Southern Africa, Gordon-Cumming (1851:303)

> *But neither Griquas nor Hottentots are at all adapted for travelling in this country, where fever rages; their manner of living being too gross, as they eat scarcely anything but flesh, consuming immense quantities of fat from one year's end to the other.*
>
> Southern Africa, Chapman (1868:142)

> *Eating or drinking fat is a Ju/'hoan euphemism for sex….*
>
> Southern Africa, Power and Watts (2003)

There is universal agreement among nutritionists and health professionals that protein is an important macronutrient that we must consume in sufficient quantities on a regular basis for optimum growth, health, and well-being. As one might expect, however, there is less agreement over just how much we need (compare, for example, Millward 1999a; Young and Pellett 1994), and a long history of research in attempts to establish sufficient yet safe daily allowances for infants, children, young adults, and the elderly (for discussion and additional references see, for example, Fontana et al. 2008; Jackson 2001; Mertz 2000; Pellet 1990; Rand et al. 2003; Reeds and Garlick 2003; Scrimshaw and Young 1976; as well as almost any recent textbook on human nutrition).

On the other hand, the health and nutrition fields have paid scant attention over the years to the possibility that one could consume too *much* protein. One gets the distinct impression from the literature that too little protein can lead to serious health consequences, whereas too much protein simply provided additional calories. As so clearly articulated by McLaren (1974) and Newman (1995), concern well into the 1970s was almost totally focused on a supposed worldwide "protein gap" or "shortage"; the idea that one could consume too much protein was seldom explicitly considered, since such a situation seemed to have no practical applicability in the "real" world. But in the world of hunters and gatherers, explorers, traders, fur-trappers, nineteenth-century "sports" hunters and adventurers, and frontier military leaders who had to survive the rigors of the "wild" for extended periods with little or no access to agricultural products, the problems that could be posed by sustained reliance on "lean meat" were very real and widely recognized. A handful of quotes (out of literally hundreds that can readily be drawn from eighteenth and nineteenth-century travelers' accounts) will suffice to show how cognizant these early explorers and military personnel were about the threat of "protein poisoning" or "rabbit starvation" as it came to be known in ethnohistoric lore and literature (e.g., Speth 1983; Speth and Spielmann 1983; Noli and Avery 1988; Stefansson 1944).

## 4.3 Historic Accounts of "Protein Poisoning"

An interesting early nineteenth-century discussion of the shortcomings of a lean-meat diet, based on late eighteenth-century writings, is provided by an anonymous author identified only as "Epicuri de grege porcus."

> Of all the parts of an animal, the lean is the least and the fat the most nutritive.... "I experienced," says M. De Pages [Pierre Marie François de Pagès], (in his travels on the Red river and thence to Natchitoches) "the truth of what is said of hunters who live entirely on animal food, but which I used to find difficult to be believed, namely, that besides their desiring [sic; "deriving" in the original] little nourishment from the leaner part, it soon becomes offensive to the taste, whereas the fat is both more nutritious ["nutritive"], and continues to be agreeable to the palate."
>
> Anonymous (1814:460–461); see de Pagès (1793:89–90) for the original statement

> The late judge Henry in his account of the campaign against Quebec in 1775, p. 46 says, "We feasted till noon, and in the intermediate moments culled the entrails *for the fat*. We broke the bones and extracted the marrow, under the full persuasion that food of an oily nature, is one of strongest main stays of human life. Of this principle if we had a doubt we were shortly afterwards most irrefragably convinced." Again, "By this time the fat and marrow of the animals we had killed were exhausted, and our stock of salt expended. One who has never been deprived of bread and salt, nor known the absence of oleaginous [oily or greasy] substances in his food, cannot make a true estimate of the invaluable benefits of such ingredients in the sustentation of the bodily frame."
>
> Anonymous (1814:461), italics in original; see Henry (1812:46–47) for the original statement

> Every person who has been conversant with Indians, or with the labouring class of people among the whites, or with surveyors who are much in the woods, knows the uniform and universal preference given by them to fat substances as food.
>
> Anonymous (1814:461)

> Capt. Lewis on his return from his expedition over this continent to the Pacific ocean twice related to me, that when their salt provisions were exhausted, although they sometimes killed deer, yet no quantity that the stomach could bear of the flesh of venison, would enable his people to go through a day's journey without great and exhausting fatigue, sometimes they would eat lean food when they could get it in plenty, from 6 to 7 lb. of venison per man; but it did not suffice to sustain the strength of the company. A beaver's

> tail of a pound or a pound and a half weight, afforded much more nutriment as a meal for two people. All persons who have eaten this article of food in the woods, speak of it as a great luxury. "An agreable [sic] barter ensued" (says Judge Henry [p. 23]) "we gave salted pork in exchange for two fresh Beaver-tails, which when boiled, renewed ideas of the May butter of our own country."
>
> Anonymous (1814:461–462)

Marcy (1863:16), based on his experiences in the winter of 1857–1858, provided one of the most explicit nineteenth-century accounts of the problems posed by a diet comprised largely of lean meat:

> We tried the meat of horse, colt, and mules, all of which were in a starved condition, and of course not very tender, juicy, or nutritious. We consumed the enormous amount of from five to six pounds of this meat per man daily, but continued to grow weak and thin, until, at the expiration of twelve days, we were able to perform but little labor, and were continually craving for fat meat.

A similar experience with a lean-meat diet is echoed by Jedediah Smith, who led a group of trappers along the Klamath River in California in May 1828. According to Dale Morgan (cited in Allen 1979:457):

> …the party made only 3 miles on the 18th, which taxed their strength to the utmost. 'The men were almost as weak as the horses, for the poor [spring] venison of this country contained little nourishment.'

Others had similar experiences. Thus, for example, Warren A. Ferris, while trapping in the Bear River Valley of Utah in 1830, bemoaned the poor sustenance provided by lean buffalo (Phillips 1940:42):

> We killed here a great many buffalo, which were all in good condition, and feasted, as may be supposed, luxuriously upon the delicate tongues, rich humps, fat roasts, and savoury steaks of this noble and excellent species of game. Heretofore we had found the meat of the poor buffalo the worst diet imaginable, and in fact grew meagre and gaunt in the midst of plenty and profusion. But in proportion as they became fat, we grew strong and hearty….

Lewis and Clark in their diary entries for February 1805 report a similar experience with fat-depleted game (Coues 1893:233):

> Captain Clark returned last evening with all his hunting party. During their excursion they had killed 40 deer, 3 buffalo, and 16 elk; but most of the game was too lean for use…

Likewise, Jacob Fowler (Coues 1898:97), during his expedition to the Rocky Mountains, commented in his journal for February 1822 that:

> Hunters out Early-Killed one Cow Buffelow With In four Hundred yards of Camp-but so Poor the meat Was not Worth Saveing….

Charles Larpenteur (1898), a nineteenth-century fur-trapper on the Upper Missouri, had a similar experience subsisting on lean elk meat:

> For about six weeks I lived on nothing but jerked elk meat…. There is little substance in elk meat. I became so weak that I could scarcely get up the river bank with a bucket of water; my knees felt like giving way.

Fridtjof Nansen's expedition to Greenland provides another clear example of the nutritional problems that can arise when subsisting on lean meat in the absence of an adequate supply of fat:

> This amount would have proved sufficient if we had only had the proper quantities of each kind of food [lean meat and fat], but, owing to a misunderstanding, there was a want of fatty stuffs, which caused us a good deal of inconvenience. Herr Beauvais of Copenhagen, who was to provide our pemmican, informed me that he was accustomed to prepare it in the usual way. I had no opportunity of seeing him personally, but supposing that his pemmican, like the ordinary preparation, would consist of dried meat and fat in equal quantities, or would contain at least a third part of the latter, I ordered the necessary amount of him. As I was passing through Copenhagen just before we started I learned that his pemmican was carefully purified of all fat. This was an unpleasant surprise; but, as we had a certain quantity of butter, as well as some liver "pâte" of a very fatty nature, I thought we should get on well enough. However, it proved a very short supply, and in the end we suffered from a craving for fat which can scarcely be realised by anyone who has not experienced it.
>
> Nansen (1892:38–39)

John Richardson offers an interesting comment regarding the limited nutritional value of caribou meat when the animal is fat-depleted:

> The flesh of the caribou is very tender, and its flavour when in season is, in my opinion, superior to that of the finest English venison; but when the animal is lean it is very insipid, the difference being greater between well-fed and lean caribou than anyone can conceive who has not had an opportunity of judging. The lean meat fills the stomach but never satisfies the appetite, and, scarcely serves to recruit the strength when exhausted by labour.
>
> Richardson (1829:244)

William T. Hamilton, a seasoned trader and trapper on the North American Great Plains, provides a very insightful look at just how important fat was to people who had to subsist for extended periods on lean meat:

> Another important article of food, the equal of which is not to be had except from the buffalo, is "depuyer" (dépouille). It is a fat substance that lies along the backbone, next to the hide, running from the shoulder-blade to the last rib, and is about as thick as one's hand or finger. It is from seven to eleven inches broad, tapering to a feather edge on the lower side. It will weigh from five to eleven pounds, according to the size and condition of the animal. This substance is taken off and dipped in hot grease for half a minute, then is hung up inside of a lodge to dry and smoke for twelve hours. It will keep indefinitely, and is used as a substitute for bread, but is superior to any bread that was ever made. It is eaten with the lean and dried meat, and is tender and sweet and very nourishing, for it seems to satisfy the appetite. When going on the war-path the Indians would take some dried meat and some depuyer to live on, and nothing else, not even if they were to be gone for months.
>
> Hamilton (1905:33)

> I have been asked many times regarding depuyer by different ones who have been astonished when told of its merits as a substitute for other food, and surprised that it was so little known except by mountain men and Indians. Trappers would pay a dollar a pound for it, and I do not believe that bread would bring that price unless one were starving. As I have said, it is a substitute for bread; and when you are invited to an Indian lodge your host will present you with depuyer just as you would present bread to a guest. You may be sure should they fail to present you with depuyer that you are an unwelcome guest.
>
> Hamilton (1905:33–34)

David Hanbury's observations are also of interest. He noted that female caribou after they have given birth are so fat-depleted that they are best ignored as a source of sustenance.

> In the afternoon I hunted for bull caribou and looked for musk-oxen, but without success. It seemed as if we should have to fall back on the wretchedly lean meat of the cow caribou, which, after the calves are dropped, is not worth eating.
>
> Hanbury (1904:231)

Numerous other nineteenth-century traveler accounts make similar observations regarding the impact of the seasonal changes in the animal's reproductive status and concomitant body condition on its suitability as food (Godman 1836:133–134; Pike 1892:48–52; Ripley and Dana 1869:296; Ross 1856:262; Ruxton 1848:254). Osborne Russell's account provides an excellent example:

> We lived on fat mutton until the snow drove us from the mountains in February. Our party then dispersing, joined Mr. Bridger's company, who were passing the winter on Blackfoot Creek, about fifteen miles from the fort, where we staid until the latter part of March. Mr. Bridger's men lived very poor and it was their own fault, for the valley was covered with fat cows when they arrived in November, but instead of approaching and killing their meat for the winter they began to kill by running on horseback, which had driven the buffalo all over the mountain to the head of the Missouri, and the snow falling deep, they could not return during the winter. They killed plenty of bulls, but they were so poor that their meat was perfectly blue, yet this was their only article of food, as bread and vegetables were out of the question in the Rocky Mountains, except a few kinds of roots of spontaneous growth, which the Indians dig and prepare for food.
>
> Russell (1921:43)

Warburton M. Pike offers another insightful look at the selectivity that hunters may be forced to exercise, particularly when they are facing shortages:

> The best swimming-places are known and carefully watched, and woe betide a herd of caribou if once surrounded in a lake by the small hunting-canoes. One thrust of the spear, high up in the loins and ranging forward, does the work. There is no idea of sparing life, no matter what the age or sex of the victim may be; the lake is red with blood and covered with sometimes several hundred carcasses, of which fully one-half are thrown away as not fat enough to be eaten by men who may be starving in a month.
>
> Pike (1892:48)

Captain Benjamin Bonneville's observations provide another nineteenth-century example of the importance to a hunter of an animal's sex and reproductive state when considering whether to pursue and kill it; and, upon making a successful kill, which parts of the carcass to keep and which to discard:

> Cows are considered more delicate eating than bulls, especially during the rutting season, when the latter assume a rank and strong flavour. This was the case about the time that our party saw them. We had no opportunity of killing cows, and as the bulls were lean, we ate principally the tongue and liver of those that we killed. These, together with the hump, hump ribs [thoracic vertebral spines], marrow bones, heart, tender loin, and hunter's roast (fillet near the shoulder blade) constitute the choice pieces; and when buffaloes are plenty, are the only parts that are eaten.
>
> Irving (1837:275)

Like the previous examples, Frederick Wislizenus's 1839 account of an overland journey to the Rocky Mountains briefly, though clearly, stresses the importance to the hunter of the fat on the animals that are being pursued:

> The meat of the cows is usually tenderer and fatter than that of the bulls, and particularly deserves the preference in summer, when the bulls are lean and unpalatable.
>
> Wislizenus (1912:51)

Incidentally, given the near wanton slaughter of animals so amply and "colorfully" described in many of these explorer and traveler accounts, it is quite clear that avoidance of females was seldom if ever done for reasons of conservation but because the lean meat of these animals around the time of the spring calving season was often too poor to eat.

John Palliser, leader of the "British North American Exploring Expedition," traveled extensively in western North America between 1857 and 1860 seeking a route for the Canadian Pacific Railway. During his travels he made some interesting comments about the difficulties of subsisting on lean meat:

> This morning we got our female friends to slice and dry the meat over fires. All of it was very lean, and we could not get any fat or grease to trade from the Indians, which was a bad look out, as it is nearly as hard to live on the dried meat of a lean animal alone without grease, as it is to starve altogether.
>
> Palliser (1863:108)
>
> The hunters had been unsuccessful, and we were now limited to the dry lean moose meat, which has not much more nourishment in it than chips of parchment.
>
> Palliser (1863:111)

John Richardson provides a brief but interesting comment on the need for fat among Russian sailors in the early nineteenth century wintering on an all-meat diet in the arctic:

> …when people have fed for a long time solely upon lean animal food, the desire for fat meat, becomes so insatiable, that they can consume a large quantity of unmixed, and even oily fat, without nausea.
>
> Russian sailors, Richardson (1829:35)

Similar observations were made by arctic explorer John Ross who, like Richardson, was fully cognizant of the dangers of an all-meat diet in the absence of adequate supplies of fat.

> It would be very desirable indeed if the men could acquire the taste for Greenland food; since all experience has shown that the large use of oil and fat meat is the true secret of life in these frozen countries, and that the natives cannot subsist without it; becoming diseased, and dying under a more meagre diet.
>
> Ross (1835:135)

Ludwig Leichhardt's journal of an overland expedition in Australia in 1844–1845 provides another interesting observation concerning the importance of fat when subsisting on lean meat, and in this case from a part of the world well removed from cold temperate or arctic environments:

> In consequence of the additional fatigues of the day, I allowed some pieces of fat to be fried with our meat. Scarcely a fortnight ago, some of my companions had looked with disgust on the fat of our stews, and had jerked it contemptuously out of their plates; now, however, every one of us thought the addition of fat a peculiar favour, and no one hesitated to drink the liquid fat, after having finished his meat. This relish continued to increase as our bullocks became poorer; and we became as eager to examine the condition of a slaughtered beast, as the natives, whose practice in that respect we had formerly ridiculed.
>
> Leichhardt (1847:168–169)

Another Australian explorer, George Henry Haydon, eloquently describes the difficulties he and his party faced when they were reduced to subsisting on just beef that was virtually devoid of fat:

> Arriving at a large creek, we camped, trusting supplies might soon reach us, for although we had now a plentiful supply of beef, we still felt most severely the want of the other necessaries of life. The meat too, as will be readily believed, was not of a description to remind one of the "Roast beef of old England." There was not so much as an ounce of fat on the whole beast, we had no salt to render it more palatable, and I can assure the admirers of roast beef, that let it be ever so good, if they should be reduced to the necessity of living on that *alone* for a few days, they would never relish it so much afterwards.
>
> Haydon (1846:148), emphasis in original

William John Wills, surveyor and astronomical observer on the ill-fated Burke and Wills Expedition of 1860–1861, the first to cross Australia from Melbourne in the south to the Gulf of Carpentaria in the north, left this telling record of the deprivations they suffered owing to the lack of fat in the resources that were accessible to them:

> Certainly, fat and sugar would be more to one's taste, in fact, those seem to me to be the great stand by for one in this extraordinary continent; not [t]hat I mean to depreciate the farinacious food, but the want of sugar and fat in all substances obtainable here is so great that they become almost valueless to us as articles of food, without the addition of something else.
>
> Burke and Wills (1861:31)

Peter Warburton led another expedition into the interior of Australia between 1872 and 1874. Enroute, the party ran out of food, forcing Warburton to kill several of their near-starving camels. His poignant journal entries show that the jerky his men made from the lean camel meat provided them very little sustenance.

> We cut up and jerked the camel-meat; it is surprising how little nourishment there is in this food; it appears to do us no good.
>
> Warburton (1875:275)

> For the last three days we have been living on fresh meat, but none of us find ourselves a bit stronger, in fact we are falling off day by day, and if this continue, the strongest will be unequal to the least exertion.
>
> Warburton (1875:277)

> Our detention will most probably extend over this week. Lewis, who is to start to-night in quest of the river, can scarcely get back under five days, if so soon, and when he returns, the camels must have two or three days' rest. It is thus we are so dreadfully delayed, whilst a close approach to starvation is continually urging us forward. We have scarcely any meat, and that of the worst possible quality, part the old scarecrow camel. She was very old, completely worn out and shrunk, so her meat can only last us a few days, and gives us no nourishment.
>
> Warburton (1875:264)

Africa provides a very similar record concerning the critical importance of fat to hunters who are forced to subsist for extended periods on lean meat. There are many such observations recorded in the journals of African explorers, colonial officers, missionaries, and "sports" hunters. Gerald McKiernan's diaries and notes of five years of travel in southern Africa between 1875 and 1879 contain an excellent example:

> …I will back a tropical negro against an Esquimau for fat eating. I think the propensity is the result of the savage mode of life rather than that of climate. Most of the game-meat is very lean….
>
> McKiernan (1954:99)

Samuel Teleki's 1887–1888 exploring expedition in eastern Africa, as documented by Ludwig von Höhnel, echoes the somewhat earlier observations made by McKiernan, providing another particularly compelling description of how important fat becomes to people who are forced to rely heavily on a diet of lean meat, again in an environmental setting far removed from the arctic. Interestingly, von Höhnel's observations, like those of McKiernan, also stress the generally lean nature of African game, an important point that I will return to again later.

> We felt this the more as the game of Africa is very lean. In fact, we craved as eagerly for fat or grease as do the Esquimaux. We could have eaten pounds of it, and we gloated over the thought of the fat humps of the oxen days before we ate them. They were to us the daintiest tid-bits, and we would not have exchanged them for all the triumphs of European culinary arts.
>
> von Höhnel (1894:24)

Aurel Schulz, in a memoir describing his late nineteenth-century expedition with fellow explorer August Hammar to the Chobe and Okavango Rivers in southern Africa, echoes the same sentiments, even down to a reference much like von Höhnel's to the fat-eating proclivities of the Eskimo:

> All hunters will agree with me how gruesome the daily meal is without any fat; for game at this season of the year is especially dry, while it is almost impossible to transport fat on an extensive trip like ours – rather would we depend upon replenishing our stock from time to time from occasional hippo or eland that might fall to our guns.
>
> Schulz and Hammar (1897:69–70)

> When, however, we obtained a supply of hippo or eland fat, the jubilation in camp might have led an onlooker to conclude that something 'stronger' was answerable for the gaiety prevalent amongst us…. The fat-absorbing qualities of a native, especially of Hottentot

> blood, under hunting conditions are such that even an Esquimaux might tremble for his reputation in a contest.
>
> Schulz and Hammar (1897:70)

### 4.3.1 Fat in the Hippopotamus and Eland

It is interesting that the two species specifically targeted by Schulz and Hammar, the hippo and eland, are the two principal exceptions to the general rule that African larger mammals carry very little body fat (Ledger et al. 1967; Ntiamoa-Baidu 1997:65; Smith 1970:127; see also Mitchell 2005:40). Both hippos and eland, most especially the male eland, often have a substantial amount of fat, making these animals prime targets of hunters (Figs. 4.1 and 4.2).

The fat in the bull eland, in fact, is so striking that it is a feature frequently noted in the literature concerning San (Bushman) belief systems and rock art (see Fig. 4.3; Dowson 1988:122; Lewis-Williams 1987:171; Lewis-Williams and Biesele 1978:119):

> The Bushmen say the heart of an old bull eland is encased in so much fat that a man cannot put his arms around it; melted down, the fat requires the entire eland skin for a suitable container. The Bushmen themselves are very impressed by all these distinctive qualities and talk a great deal about them.
>
> Lewis-Williams (1983:44)

Numerous eighteenth, nineteenth, and early twentieth-century explorers, travelers, and “sports” hunters in Africa offer similar comments concerning the unique properties of both eland and hippo meat. For example, Andrew (Anders) Sparrman

**Fig. 4.1** Eland (*Taurotragus oryx*). Photograph taken July 2009 by Riaan van den Berg in the Dube Nature Reserve, South Africa. ©Riaanvdb/Dreamstime.com. The photograph is reproduced here under “royalty free license” from Dreamstime LLC, Brentwood, TN

**Fig. 4.2** Hippopotamus mother and baby (*Hippopotamus amphibius*). Photograph taken July 2009. ©Smellme/Dreamstime.com. The photograph is reproduced here under "royalty free license" from Dreamstime LLC, Brentwood, TN

**Fig. 4.3** Depictions of eland in San (Bushman) rock paintings found in Game Pass Shelter, Kamberg Nature Reserve, Drakensberg, KwaZulu-Natal, South Africa. Photograph taken in April 2006. ©Wcpmedia/Dreamstime.com. The photograph is reproduced here under "royalty free license" from Dreamstime LLC, Brentwood, TN

(1785), a Swedish naturalist, provides an interesting and fairly detailed early description of the importance of the male eland as a rich source of fat:

> This animal ["Cape-elk" or eland] has a great deal of fat, especially about the heart: from an old male which we gave chase to and shot, we got such a quantity of fine and tender fat, as we could with difficulty get into a box that would hold about ten pounds of butter. As at the commencement of our journey homewards through the desert, the hounds we had with us had unluckily devoured our stock of butter, a farmer, who still accompanied us, showed us how to prepare the fat from about the heart of the elk, and to use it for dressing victuals with,

> and for eating on bread in the same manner as is generally practised with goose-grease and hogs-lard. The taste of it also was very similar to these, and to the full as good; and, indeed, if I may be supposed to have been able to form any judgment of the matter at a time when we were so sharp set, and in absolute want of any thing else of the kind, it was rather better. The breast is likewise extremely fat, and is always looked upon as a great delicacy. The flesh is universally of a finer grain, more juicy and better tasted than that of the *hart-beest*.
>
> Sparrman (1785:207–208)

> The male elks [elands], which are rather aged; and consequently slow and tardy keep apart from the rest of the herd; and are generally so fat and heavy, as, in case of being chased, to tire immediately on the first onset. And indeed, of the elk species, the males are always the fattest and largest in the herd, and have evidently a fuller neck than the others; it is likewise these, that the hunter singles out and is sure to come up with first. I have been assured by several people, that some of the younger and fleeter, but at the same time fatter sort of bucks, will sometimes, when they are hard run, drop down dead during the chase; and, that melted fat, as it were, together with the blood, would at that time gush out of their nostrils.
>
> Sparrman (1785:209)

William Burchell in 1822 provides another informative comment regarding the special role of the eland as a source of fat and the generally lean nature of the meat from other African antelopes:

> Within the colony, this animal is becoming daily more scarce; the boors, as well as the Hottentots, preferring its meat to that of any other antelope, and therefore, on every occasion, hunting it with the greatest eagerness. The principal cause of this preference, and at the same time, a very remarkable circumstance, is, its being the only one of the antelope genus, on which any considerable quantity of fat is ever to be found….
>
> Burchell (1822:311)

Another example, in this case from 1851, is provided by Roualeyn Gordon-Cumming, who says of the eland that:

> This magnificent animal is by far the largest of all the antelope tribe, exceeding a large ox in size. It also attains an extraordinary condition, being often burdened with a very large amount of fat. Its flesh is most excellent, and is justly esteemed above all others. It has a peculiar sweetness, and is tender and fit for use the moment the animal is killed.
>
> Gordon-Cumming (1851:218)

A few years later, in 1859, an anonymous writer again singles out the eland, in this case focusing specifically on the bull, commenting on its extraordinary size and extolling the virtues of its fatty meat:

> All travellers and sportsmen agree that in the quality of his flesh the eland is unapproached by any ruminant in South Africa – that the males grow to enormous size, and lay on fat with as great facility as a true short-horn, while in texture and flavor they are infinitely superior.
>
> Anonymous (1859:256)

In a short article written in 1863, William Chambers and Robert Chambers describe at some length the desirable taste and fattiness of meat from both hippo and eland upon which they feasted while in South Africa:

> To dine on a hippopotamus's ribs and an eland steak was certainly novel, and we were in such a state of hunger that we were not disposed to be critical. The very good and savoury

> odour that arose as we entered the Dutchman's house, induced us to believe that both the articles mentioned were not to be despised. We selected as a commencement a portion of the eland steak, and this without doubt was excellent; it was tender, juicy, and with a sort of venison-flavour; and we at once decided that it would be a most popular dish in England were the eland introduced; as it might be, in sufficient numbers to be killed and sold as food. It having been our fate at a future period to live entirely on eland's flesh during a fortnight, we can affirm that, even with the rough cooking of the bivouac, and the absence of flavour-giving condiments, still eland beef or venison is admirable eating. And now for a slice of hippopotamus. Hippo is usually boiled, and then tastes like a mean proportion between boiled beef and boiled pork. It would be very probable that a person might eat a piece of hippopotamus, and fail to discover that it was not a slice from a prize ox. The hippopotamus seems to possess a contented mind, and accumulates fat rapidly, it being a very unusual thing to find one of these creatures thin, or even deficient in plumpness.
>
> Chambers and Chambers (1863:367)

William Cornwallis Harris, another in a long list of adventurers and travelers, fully recognized the leanness of most African game animals, and the unique gustatory qualities of the meat and fat that one could acquire from an eland bull:

> The flesh [of the male eland] is esteemed by all classes in Africa, above that of any other animal; in grain and colour it resembles beef, but is better tasted, and more delicate, possessing a pure game flavour, and the quantity of fat with which it is interlarded is surprising, greatly exceeding that of any other game quadruped with which I am acquainted.
>
> Harris (1839:73–74)

Somewhat later in the nineteenth century, both Frederick Selous and Emil Holub offer quite similar opinions regarding the value of meat from the male eland (see also Farini 1886:465; Hutchinson:157):

> I had not ridden a couple of miles after leaving my boys when I came upon a herd of some sixty or seventy elands, with three enormous old bulls amongst them. An eland bull is not an animal that an African hunter likes to pass by, as the fat that can be obtained in large quantities from one in good condition is most useful in cooking the dry meat of the smaller antelopes.
>
> Selous (1893:439)

> Of all the antelopes the eland, especially the male, is the most lusty and well-fed, its heart having been known to be imbedded in a mass of fat weighing twenty-five pounds; the animal is consequently generally so short-breathed that it can be readily overtaken and speared. The Masarwas [older term for Bushmen] are very fleet-footed and skilful in hurling their assegais so as mortally to wound the heart or lungs.
>
> Holub (1881:49)

Alfred St. Hill Gibbons, as well as Henry Charles Howard (the Earl of Suffolk and Berkshire), and Baron Frederick John Dealtry Lugard, also extol the virtues of eland fat, echoing the sentiments expressed by many other nineteenth-century African explorers and hunters (e.g., Lichtenstein 1812:24; Wood 1882:129; Ward 1896:212):

> I decided therefore to once more devote my energies to them [the eland], as their flesh is better eating, and their fat – a luxury seldom found in any other African antelope – is soft, and does not stick to the roof of the mouth.
>
> St. Gibbons (1898:256)

> Although so frequently found in purely desert country, the Eland puts on flesh and fat in a quite amazing way. Even in the dry season of the South African winter the writer has hunted and killed these antelopes in the waterless recesses of the North Kalahari, and found them fat and in high condition. The flesh is excellent; tender, juicy, and partaking of the flavour of young, game-like beef – if such a combination can be imagined.
>
> Howard (1911:161)

> The flesh of the eland is extremely good, being like good English beef. The eland is generally so fat that I have more than once succeeded, with my boots off, in running one down, when disabled by a wound.
>
> Lugard (1893:529)

Loring (1914), a zoologist on the 1909–1910 Smithsonian-Theodore Roosevelt African Expedition, makes a similar observation about the fattiness of both eland and hippo meat, and the generally lean and "dry" nature of meat from other African game species. Roosevelt, himself, expresses essentially the same view in an article published at about the same time in *Scribner's Magazine*:

> Speaking generally, the game of British East Africa does not compare with the meat of our American game animals; for, with the exception of the eland and the hippo, it is dry, though tender when young, and lacks the fat necessary to give it the delicious, palatable flavour possessed by our deer, antelope, and mountain-sheep.
>
> Loring (1914:203)

> The eland is by preference a grass-eater, and is usually fat, which makes him a godsend in the African land of lean animals.
>
> Roosevelt (1913:690)

This is an opportune moment to take another brief detour into the realm of archaeology, this time to look at views about the hunting capabilities of hominins who occupied sub-Saharan Africa between about 300,000 years ago and roughly 40,000 years ago, give or take a few millennia. For those not too familiar with archaeology, in Africa this period of the Paleolithic is known as the *Middle Stone Age* (MSA). During more or less the same period of time, Europe and western Asia were inhabited by Neanderthals, and in these more northerly latitudes of the Old World the comparable part of the archaeological record is referred to as the *Middle Paleolithic* (MP). Richard Klein has written extensively about the hunting strategies of MSA peoples, focusing particularly on the faunal record from two well-preserved and widely known cave sites located east of Cape Town along South Africa's Indian Ocean coast – Klasies River Mouth and Die Kelders.

Klein has argued for many years that MSA hominins lacked not only the technological know-how of the people who followed them during the ensuing *Later Stone Age* (LSA), but they also lacked the cognitive wherewithal. Interestingly, eland remains in these caves are central to his line of thinking, and hence the reason for this detour. And, as I have been doing throughout the book, I will let Klein speak for himself.

> In contrast to the other ungulates, the eland in MSA sites include a large proportion of prime-age adults, and the age profile has a catastrophic shape…. The most likely explanation is that

> MSA people had learned that, unlike most other large African bovids, eland can be easily driven, without much personal risk. An eland herd caught in the right position could be forced over a cliff or into a trap….
>
> However, MSA people could not have driven eland herds to their death very often or the species would have become extinct, since its reproductive vitality would have been sapped by the continuing loss of a large proportion of the available prime adults. Not only did the eland survive, but there is no evidence that it became less numerous during the long MSA time span….
>
> Thus, MSA people were probably not very successful at hunting eland, and this makes it especially interesting that eland is the most abundant ungulate in the MSA faunas. The clear implication is that MSA people must have been even less successful at hunting other species that are less common in the sites but were more common in the environment. In short, MSA impact on the large mammal fauna was negligible. By extension, it may be argued that LSA peoples, in whose sites eland and other species are represented more in proportion to their live abundance, probably took a higher proportion of game overall. In short, LSA people were almost certainly more proficient hunters.
>
> Klein (1987:36–37)

I think this argument needs to be turned on its head. Judging by the many quotes from historic accounts that I have already presented, all of which extol the virtues of the eland as the "game-of-game" in a land of fat-poor animals, the eland is precisely the animal that one *should* target if the animal is available and the hunters possess the means. If anything the abundance of prime-adult elands in MSA sites is testimony to just how good, and successful, they were as hunters, not evidence of their impoverished cognitive capacity. It is the LSA hunters that should be the focus of interest here. Why were they (as it would seem) compelled to concentrate more on the far leaner and smaller game, the prey that explorer after explorer considered inferior food, especially when they were short of adequate sources of carbohydrates or alternative means of acquiring fat? It seems far more likely that the hunters of the LSA were under some level of stress, either because they managed to overhunt the elands, or perhaps because environmental changes reduced the numbers of elands. All of this remains speculative, of course, but I think the one conclusion we can safely draw from this is that the presence or absence of eland in archaeological sites tells us nothing about innate cognitive capacities.

Incidentally, the abundance of prime adults, evidence that led Klein to postulate that MSA hunters may have driven groups of eland over cliffs or into traps (the "catastrophic" age profile that Klein refers too – that is, an age structure that resembles what one would observe in a living population) need not imply mass kills. Since the faunal assemblages are aggregates or palimpsests of countless individual hunting episodes, the abundance of adult animals in their prime is what one might expect if hunters often deliberately sought out animals that were at their peak in condition, but also now and then killed whatever eland came within their sights, regardless of age. It would be interesting to know what proportion of the adult eland at Klasies and Die Kelders were males….

Now let us return from our little foray into Middle Stone Age archaeology and turn to the hippo. As is evident from some of the previous quotes, the hippo, like the eland, was clearly highly prized for its fat (e.g., Andersson 1857:414; St. Gibbons 1898:9). While hippos may have been too difficult and too dangerous for Paleolithic hunters to kill, it is perhaps not surprising that (presumably) scavenged hippo remains, with clearly cutmarked bones, often show up in some of our earliest archaeological sites in East Africa, such as the famous *HAS* ("Hippo and Artefact") Site immortalized in a stamp issued jointly in 1975 by Kenya, Tanzania, and Uganda (see Fig. 4.4; Isaac and Harris 1997; for additional early cases, see also Bunn 1994; Clark 1987; Fiore et al. 2004; Harmand et al. 2009; Johanson and Wong 2009:255; Leakey 1996:70–71; Plummer et al. 1999; Pobiner et al. 2008).

William Burchell in 1822 provides a concise but useful description of hippo fat, noting both its quantity and its somewhat unusually low melting point:

> The ribs [of the hippo] are covered with a thick layer of fat, celebrated as the greatest delicacy; and known to the colonists as a rarity by the name of '*Zeekoe-spek*' (Seacow-pork). This can only be preserved by salting; as, on attempting to dry it in the sun in the same manner as the other parts of the animal, it melts away. The rest of the flesh consists entirely of lean; and was, as usual with all other game, cut into large slices, and dried on the bushes; reserving only enough for present use.
>
> Burchell (1822:411)

**Fig. 4.4** 3-shilling stamp, issued jointly by Kenya, Tanzania, and Uganda in 1975 on the occasion of the second World Black and African Festival of Arts and Culture, to commemorate the discovery of *HAS* ("Hippo and Artefact Site" or FxJj3). The site is located in Koobi Fora (northern Kenya), near the eastern shore of modern Lake Turkana. Excavation of *HAS* revealed a series of stone tools associated with the butchered remains of a single hippopotamus carcass that very likely had been scavenged by early hominins (Isaac and Harris 1997). The stamp is affixed to a first-day-cover envelope signed by Glynn Ll. Isaac. The envelope and stamp were loaned to the author by Robert Whallon of the University of Michigan. The photograph was taken by Katherine Clahassey, Museum of Anthropology, University of Michigan, Ann Arbor, Michigan

Schweinfurth's (1878) interesting narrative provides additional insights into the amount of fat that one can obtain from a single hippo carcass; he also comments on the low melting point of the fat, and notes additionally that the fat does not go rancid easily:

> We were hard at work on the following day in turning the huge carcass of the hippopotamus to account for our domestic use. My people boiled down great flasks of the fat which they took from the layers between the ribs, but what the entire produce of grease would have been I was unable to determine, as hundreds of natives had already cut off and appropriated pieces of the flesh. When boiled, hippopotamus-fat is very similar to pork-lard, though in the warm climate of Central Africa it never attains a consistency firmer than that of oil. Of all animal fats it appears to be the purest, and at any rate never becomes rancid, and will keep for many years without requiring any special process of clarifying….
>
> Schweinfurth (1878:192)

Reginald Charles Fulke Maugham provides an estimate of the actual quantity of fat that one could expect to obtain from an adult hippo carcass:

> The great carcase yields a large quantity of excellent fat, which is much prized for cooking purposes. It is wholly free from any unpleasant flavour or odour, and very similar in appearance and consistency to that of the ox. A full-grown animal in good condition would probably yield considerably more than 1 cwt. [centum weight or hundredweight, ~50 kg] of this valuable substance.
>
> Maugham (1906:167)

Dane (1921:75), another experienced "sport" hunter, also notes that: "the hippo and the eland appear to be the only animals in Africa which have any fat, and the three hippos we shot provided a series of banquets, which were much appreciated."

Finally, Richard Tjader, writing in the early years of the twentieth century, not only echoes the observations made by countless hunters and explorers before him that most African big-game animals yield limited amounts of fat, but also adds the intriguing suggestion that even the game birds of Africa lack the amounts of fat that one would find on temperate latitude species.

> The meat of these antelopes [hartebeest] is, as a rule, very good, although they have hardly any fat, in which respect they are like most all other African antelopes, with the exception of the eland and oryx.
>
> Tjader (1910:196)

> There are also a great number of game birds in the Protectorate. The meat of these constitutes a most palatable variation from that of the antelopes, but, strange to say, even the birds seem to be somewhat "dryer," and more devoid of fat than the kindred game birds of northern regions, just as the antelope meat is, as a rule, less juicy and fat than that of deer, elk, or moose.
>
> Tjader (1910:238–239)

### *4.3.2 Fat in the Giraffe and Zebra*

The hippo and eland, particularly the bull eland, are clearly the most highly prized large-game species in southern and eastern Africa, in part because of their size, but especially because of their reliability and productivity as sources of fat. Obviously, they weren't the only animals from which a hunter could obtain fat; this critical nutrient could be obtained from other game species as well, but typically on a more seasonal and much less reliable basis, and generally in lesser amounts. Nonetheless, two other African species are repeatedly mentioned in early traveler's accounts as desirable sources of fat – the giraffe (Fig. 4.5) and especially the zebra – although the latter often seems to have been considered unattractive to the European palate (Fig. 4.6). Even today's Hadza show a decided preference for zebra (Fig. 4.7): "Similarly, the 'good taste' of zebra meat and marrow compared to that of wildebeest may in fact have an as yet unrecognized nutritional basis" (Oliver 1993:217). [As I noted in the *Preface*, Selous (1907:220), a nineteenth-century African explorer, offered a fairly straightforward explanation for why wildebeest meat might not be considered a particularly desirable source of sustenance: "Though the meat of these antelopes [tsessebe] is tolerably good, the fat, like that of the wildebeest, turns hard, unless very hot, and sticks to the palate in a most disagreeable manner."] In zebra, the most desirable fat is found beneath the skin (i.e.,

**Fig. 4.5** Giraffe. Photograph taken in South Africa in October 2009. ©Neal Cooper/Dreamstime.com. The photograph is reproduced here under "royalty free license" from Dreamstime LLC, Brentwood, TN

**Fig. 4.6** Zebra. Photograph taken in Kruger National Park, South Africa in July 2009. ©Vatikaki/ Dreamstime.com. The photograph is reproduced here under "royalty free license" from Dreamstime LLC, Brentwood, TN

**Fig. 4.7** "Cutting zebra." Photograph taken October 1985 (late dry season) by James F. O'Connell, Sanola locality, at south end of Eyasi Basin, northern Tanzania. The hunter shot this zebra with a poisoned arrow from a blind overlooking a water point, then tracked it several kilometers the following morning to the point where he found it dead. Butchery proceeded at the recovery location as described for zebra in O'Connell et al. (1988a). In this photo, the hunter and others are removing a long strip of meat from the ribs and vertebrae. This is probably carcass 22 in O'Connell et al. (1988a:152, their Table A). ©James F. O'Connell. The photograph is reproduced here by permission of James F. O'Connell, Department of Anthropology, University of Utah, Salt Lake City, Utah

subcutaneous fat); these equids in fact are quite poor producers of marrow fat: "Zebra bones yield only slightly more energy (about 220 kcal more) than the… Thomson's gazelle adult, even though adult zebra body weight is 17 times greater" (Blumenschine and Madrigal 1993:568).

A few examples drawn from the diaries and accounts of early African travelers and explorers underscore the value of both giraffes and zebras as sources of fat, and a marvelous 1992 painting by Jay H. Matternes captures the likely importance of zebras to early hominins (Fig. 4.8):

> They [Bakalahari or Bakgalagadi] wandered continually under a burning sun, over the heated sands of the Kalahari, without any fixed habitation, and ever and always engaged in a terrible struggle for existence; living on berries and bulbs and roots, on snakes and toads and tortoises, with an occasional glorious feast on a fat eland, giraffe, or zebra….
>
> Selous (1893:112)

> The flesh of young giraffes and of fat cows especially is excellent; there is the least musky flavour perhaps, but it is not unpleasant. The tongue and marrow-bones are great delicacies, the latter, particularly, furnishing the rarest and most delicious banquet of the African hunter. Old bulls, on the contrary, are rank and excessively strong in scent and flavour, and their flesh is only eatable by half-starved Bushmen.
>
> Bryden (1893:330)

> Swahilis are very fond of zebra meat, especially when fat (and they do get very fat), so there was great rejoicing in camp at the news of my success….
>
> Neumann (1898:271)

> During the rainy season, when giraffes are able to obtain without much exertion a plentiful supply of sweet and nourishing food, the full-grown cows get into very good condition, and are sometimes so fat in the early part of the dry season – May and June – that they

**Fig. 4.8** A marvelous 1992 painting by artist Jay H. Matternes, entitled "*Homo habilis* using volcanic-cobble debitage to rend a carcass," depicts the likely value of zebras, whether obtained by hunting or by scavenging, to the earliest members of the genus *Homo*. ©Jay H. Matternes. The painting is reproduced here by permission of Jay H. Matternes, Fairfax, Virginia

probably never get into bad order for the remainder of the year. I have shot giraffe cows whose sides when the hide was peeled off them were covered with a thick layer of white fat, from half an inch to over two inches in thickness from shoulder to rump. There is no finer meat to be got in the whole world than that of a fat giraffe cow, and the soft white fat when rendered out is equal to the best lard. The tongue and marrow-bones are also great delicacies….

Selous (1908:216–217)

Of wild flesh, the favourite is that of the zebra; it is smoked or jerked, despite which it retains a most savoury flavour. Of the antelopes a few are deliciously tender and succulent; the greater part are black, coarse, and indigestible.

Burton (1860:281)

Soft succulent fat is what the lion probably considers most toothsome, and zebras supply this in a higher degree than any other animal save the rhinoceros and the hippopotamus….

Drummond (1875:281)

The zebra is one of the few animals of East Africa that possesses a considerable quantity of fat, which often lies in thick, yellowish layers under the skin. As the natives are extremely fond of this “mafuta,” or fat, they enjoy zebra meat very much; and if the animal is young and in good condition it is not at all an unpalatable dish even for the sportsman.

Tjader (1910:205)

My men, however, were glad enough to have the zebra, especially as they are among the few wild animals on which there is any fat, of which they are, almost without exception, inordinately fond.

Dracopoli (1914:211)

In parts of Africa, where they are still numerous, hundreds of these zebras may be seen grazing upon a single wide plain – a truly magnificent spectacle, interspersed as they are with other game. The flesh of this, as of other kinds of zebra, while unpalatable to Europeans, is in much esteem among natives. To the Englishman the rich, yellow fat and sweet flavour of the meat, added to the equine nature of the animal, are sufficient obstacles to an enjoyable meal, and the stomach usually rather rebels against this food.

Hutchinson (1905)

The porters were very annoyed when the heard what they had missed, as they love zebra-meat, because it is so fat.

Stigand (1910:180)

African animals exhibit little or no neutral fat. The animal that would perhaps be inclined to show the most fat is the zebra. The lions showed little fat. As a consequence of the absence of fat, incidentally, the natives crave it.

Crile (1941:107)

…my Kikuyu workmen found a partially eaten carcass of a Burchell’s zebra that had been killed by a lion. They eagerly set to work to recover every tiniest scrap of the orange-yellow subcutaneous fat; they then rendered it into lard and bottled it. A few months later, when we went to examine fossil beds at Kendu Bay on Lake Victoria, I found them selling this fat to the local Luo people, charging ten shillings….

Leakey (1969:83)

## 4.4 Ethnographic Accounts of "Protein Poisoning"

> *My white woollen blanket provoked their greatest admiration, which they* [Australian Aborigines] *expressed by smacking with their tongues, and exclaiming in ecstasy: Tamin, tamin! – that is, Fat, fat! The idea of "excellent" is expressed by the natives, as in certain European languages, by the word "fat."*
>
> Lumholtz (1889:225)

As the many quotes just presented amply document, fat was extremely important to explorers, trappers, adventurers, "sports" hunters, and military personnel, and all were fully cognizant of the problems posed by diets high in lean meat in the absence of adequate amounts of fat or alternative inputs of carbohydrates. For explorers and others, this was basic survival knowledge. As the following examples will show, similar observations abound in the ethnographic and ethnohistoric literature on "modern" hunter–gatherers as well, and from all latitudes and across a wide range of different environments.

> The quantity of food consumed at one meal naturally varies according to the amount of fat it contains. Men and dogs will half-starve on a diet of lean caribou meat, however plentiful, whereas half the quantity of blubbery seal-meat will satisfy their desires and keep them well nourished.
>
> Copper Eskimo, Canada; Jenness (1923:100)

> If people had only rabbits at such times they would probably starve to death, because these animals are too lean. The same might be true if they could get only thin moose. People cannot live on lean meat alone, but if they have enough fat they can survive indefinitely.
>
> Kutchin, Alaska; Nelson (1973:142)

> The Pitjandjara consider the best meats to be Kangaroo and Euro, making little distinction between them. They are selective with such animals. When killed they immediately feel the body for evidence of the presence of caul fat. If the animal is njuka, fatless, it is usually left, unless they are themselves starving.
>
> Australian Aborigines, Tindale (1972:248)

> …the Gaucho in the Pampas, for months together, touches nothing but beef. But they eat, I observe, a very large proportion of fat, which is of a less animalised nature; and they particularly dislike dry meat, such as that of the Agouti.
>
> South American Gauchos, Darwin (1890b:123)

> Had the guanaco a reasonable amount of fat upon it, the life of the [Patagonian Tehuelche] Indians would be idyllic, but in this the guanaco fails. Of lean meat he supplies plenty, for he is a large beast, but though he lives in a land where sheep grow fat and well-liking, the long-necked Patagonian llama retains his leanness and his running condition.
>
> Prichard (1902:107)

> In the winter and in the spring the country [Patagonia], as far as wild life is concerned, is but a thin and gaunt place. Nothing that wanders carries any fat, for the food has been reduced to a minimum.
>
> Prichard (1902:192)

> By inference one can see that the Patagonian believes in a future life – a life much on the lines of his earthly one, but abounding in those things which he most desires, and which here he finds in short measure. I only know that the land he is going to after death is a land flowing, not with milk and honey, but with grease. On the pampas of life here below the guanaco is lean and seldom yields an ounce of fat, and as I myself have experienced the craving for fat, or fat-hunger, I know it to be a very real and uncomfortable demand of the human system. But in the Patagonian Beyond the guanaco herds will be plump and well provided with supplies of suet….
>
> Prichard (1902:99)

## 4.5 The Stefansson Experiments

Perhaps the best-known discussion of the nutritional problems that can arise from a diet that is heavily based on lean meat is found in the work of Vihljalmur Stefansson, an arctic explorer and anthropologist who published extensively on this topic in the 1940s and 1950s (e.g., Stefansson, 1944, 1946, 1956). Stefansson (1944:234) provided what is undoubtedly the best known description of "rabbit starvation" or "protein poisoning":

> If you are transferred suddenly from a diet normal in fat to one consisting wholly of rabbit you eat bigger and bigger meals for the first few days until at the end of about a week you are eating in pounds three or four times as much as you were at the beginning of the week. By that time you are showing both signs of starvation and of protein poisoning. You eat numerous meals; you feel hungry at the end of each; you are in discomfort through distention of the stomach with much food and you begin to feel a vague restlessness. Diarrhoea will start in from a week to 10 days and will not be relieved unless you secure fat. Death will result after several weeks.

Since Stefansson's experience was in the arctic among Eskimos or Inuit, many scholars have drawn the erroneous conclusion that high-protein intakes are primarily a problem of life near the poles. Quite the contrary; the prospect of having to subsist for extended periods on a diet composed largely of lean meat was a problem that repeatedly confronted mobile foraging peoples wherever the climate was markedly seasonal, whether due to annual shifts in temperature, as in temperate and arctic environments, or to marked changes in rainfall over the course of the year, as in the semiarid to arid environments of sub-Saharan Africa or the interior of Australia; that is, where there were times of year when edible plant resources became scarce or unavailable or of poor nutritional quality, and where prey animals underwent seasonal cycles of fat build-up and depletion.

## 4.6 Pemmican

Stefansson (1946, 1956) clearly recognized the broader implications of "rabbit starvation," as indicated, for example, by his long-term interest in the nature and importance of pemmican (powdered dried or jerked lean meat mixed with rendered fat) to Native Americans, fur-trappers, explorers, and colonists throughout the plains and boreal forests of North America (see also Allen 1877:567–568; Back 1836:501–502; Baldwin 1896:10; de Wolf Brownell 1856:435–436; Cook 1911:134–135; Dennett 1835:420; Dunn 1844:75; Ellis 1889:18; Godman 1836:133–134; Hind 1860:312; Keating 1824:428; Milton 1866:60–61; Nansen 1892:38–39; Parry 1824:415; Richardson 1829:245; Robinson 1879:162–165; Wissler 1910:22–24).

Interestingly, the Old World apparently had its own version of pemmican which, like its North American counterpart, was used when traveling (Burton 1860; see also Burton 1884:246, text and footnote):

> They also jerk their stores by exposing the meat upon a rope, or spread upon a flat stone, for two or three days in the sun; it loses a considerable portion of nutriment, but it packs into a conveniently small compass. This jerked meat, when dried, broken into small pieces, and stored in gourds or in pots full of clarified and melted butter, forms the celebrated *travelling provision* in the East called *kavurmeh*: it is eaten as a relish with rice and other boiled grains.
>
> Burton (1860:282), italics added

Stefansson demonstrated that traditional pemmican, as described for example by Robinson (1879), Mair (1891), and polar explorer Cook (1911), was not just a haphazard mix of ingredients but a carefully prepared staple food that typically contained, in terms of calories, not more than about 25% protein and at least 75% fat.

> Each bag weighs one hundred pounds, the quantity of fat being nearly half the total weight, the whole composition forming the most solid description of food that man can make.
>
> Robinson (1879:163)

> From the dried meat and tallow of the buffalo the famous pemmican was made, at once the most portable and sustaining of foods. Pemmican was the device of the plain [sic] Indians, and has been made by them from time immemorial. It is first mentioned in the narrative of Coronado's New Mexican expedition of 1541, and the last bag of it was probably eaten on the banks of the Saskatchewan in 1882. I mean, of course, the buffalo pemmican, for it has been made occasionally since by the half-breeds from domestic beef. A sack or "toreau" of pemmican, as it was called, consisted of nearly equal quantities of tallow and dried meat, the latter being pounded on bull hides with stone hammers, axe heads or flails. From the siftings of the dried meat the "fine pemmican" was made in which marrow-fat was used instead of tallow; and the "berry" pemmican, the most highly valued of all, consisted of these two and a due proportion of saskatoon berries, or of choke-cherries, if the other could not be had. The single toreau weighed about 100 lbs., a double sack being over twice that weight. In making it the pounded meat and fat were constantly stirred in a bull-hide trough till they "set," and the mixture was then run into bags made of buffalo hide, sewed with sinew, with the hair side out, and pounded down with a mallet till they were full and compact. The ends were then sewed up, and a sack of this food, when properly made and stored in a dry place, would keep for years. Its value as compared with fresh meat was in the ratio of four to one, eight pounds of the latter being the customary daily ration, which was all eaten, whilst two pounds of pemmican were sufficient.
>
> Mair (1891:104)

> The Eskimo is ever hungry, but his taste is normal. Things of doubtful value in nutrition form no part his dietary. Animal food, consisting of meat and fat, is entirely satisfactory as

> a steady diet without other adjuncts. His food requires neither salt nor sugar, nor is cooking a matter of necessity. Quantity is important, but quality applies only to the relative proportion fat. With this key to gastronomics, pemmican was selected as the staple food, and it would also serve equally well for the dogs. We had an ample supply of pemmican, which was made of pounded dried beef, sprinkled with a few raisins and some currants, and slightly sweetened with sugar. This mixture was cemented together with heated beef tallow and run into tin cans containing six pounds each. This combination was invented by the American Indian, and the supply for this expedition was made by Armour of Chicago after a formula furnished by Captain Evelyn B. Baldwin. Pemmican had been used before as part of the long list of foodstuffs for Arctic expeditions, but with us there was the important difference that it was to be almost entirely the whole bill of fare when away from game haunts.
>
> Cook (1911:134–135); see also Baldwin (1896:10)

The kind of fat that was used to make pemmican was not left to chance, because some fats at room temperature provided a better and longer-lasting seal against moisture, they could be mixed more readily and uniformly with the dried and pounded meat (often called "beat meat"), and they were less susceptible to rancidity. There were also clear differences in taste, with "soft" fats being greatly preferred over "hard" fats. In order to assure that the right fat was used, many of the early descriptions of pemmican making are very explicit about where on an animal the appropriate fat was to be found, with the "flakes" of fat along the base of the spine over the ribs and the "fleece" of fat over the rump area being the deposits of choice.

Stefansson and fellow explorer, Karsen Anderson, conducted an experiment in New York City, in which they both subsisted for an entire year, always under close medical supervision, on a diet consisting solely of meat, with the proportions of protein and fat closely matching what one typically found in pemmican, with no evident long-term health problems (e.g., Lieb 1929; McClellan and DuBois 1930; McClellan et al. 1930, 1931). Stefansson's goal was to convince the military that an all-meat diet, so long as at least 75% of the calories came from fat, was safe, light weight, easy to store and transport, and could be used effectively as emergency rations. His experiment demonstrated the viability of an all-meat diet, which in hindsight is not all that surprising given that Eskimos presumably had been doing it for millennia (e.g., Heinbecker 1928; Krogh and Krogh 1914; Rodahl 1952; Shaffer 1921). Moreover, arctic explorers like Richardson (1829:35) and Ross (1835:135) were already writing on the topic a century before the Stefansson experiment, and a vast literature existed on the preparation and use of pemmican, a carefully prepared mix of lean meat and fat, by Native Americans, fur trappers, explorers, and others. Alexander Mackenzie and David Thompson, quoted at some length here, provide excellent late eighteenth- and early nineteenth-century descriptions of what pemmican consisted of and how it was made. Nonetheless, despite the extensive eighteenth- and nineteenth-century literature on pemmican, as well as the fairly substantial and rapidly growing body of knowledge about Eskimo diet, Stefansson's experiment did little to convince the army that it should use pemmican to feed its soldiers (see, for example, Drury et al. 1959; Hamilton 2003; Hannon and Vaughan 1958; Henschel 1961; Kark et al. 1945; Vaughan et al. 1959).

> The provision called pemmican, on which the Chepewyans, as well as the other savages of this country, chiefly subsist in their journeys, is prepared in the following manner: The lean parts of the flesh of the larger animals are cut in thin slices, and are placed on a wooden grate over a slow fire, or exposed to the sun, and sometimes to the frost. These operations dry it, and in that state it is pounded between two stones; it will then keep with care for several years. If, however, it is kept in large quantities, it is disposed to ferment in the spring of the year, when it must be exposed to the air, or it will soon decay. The inside fat, and that of the rump, which is much thicker in these wild than our domestic animals, is melted down and mixed, in a boiling state with the pounded meat, *in equal proportions*: it is then put in baskets or bags for the convenience of carrying it. Thus it becomes a nutritious food, and is eaten, without any further preparation, or the addition of spice, salt, or any vegetable or farinaceous substance. A little time reconciles it to the palate. There is another sort made with the addition of marrow and dried berries, which is of a superior quality.
>
> Mackenzie (1903:clxxvii–clxxviii), originally published in 1801, emphasis added.

> [The Hudson's Bay Company trading post] serves as the general Depot for all the dried Provisions made of the meat and fat of the Bison under the name of Pemican, a wholesome, well tasted nutritious food, upon which all persons engaged in the Furr Trade mostly depend for their subsistence during the open season; it is made of the lean and fleshy parts of the Bison dried, smoked, and pounded fine; in this state it is called Beat Meat: the fat of the Bison is of two qualities, called hard and soft; the former is from the inside of the animal, which when melted is called hard fat (properly grease) the latter is made from the large flakes of fat that lie on each side [of] the back bone, covering the ribs, and which is readily separated, and when carefully melted resembles Butter in softness and sweetness. Pimmecan is made up in bags of ninety pounds weight, made of the parchment hide of the Bison with the hair on; the proportion of the Pemmecan [sic] when best made for keeping is *twenty pounds of soft and the same of hard fat, slowly melted together, and at a low warmth poured on fifty pounds of Beat Meat*, well mixed together, and closely packed in a bag of about thirty inches in length, by near twenty inches in breadth, and about four in thickness which makes them flat, the best shape for stowage and carriage…. I have dwelt on the above, as it [is] the staple food of all persons, and affords the most nourishment in the least space and weight, even the gluttonous french canadian that devours eight pounds of fresh meat every day is contented with one and a half pound [per] day: it would be admirable provision for the Army and Navy.
>
> Thompson (1916:434–435), emphasis added

What this discussion demonstrates is that hunter-gatherers, explorers, fur-trappers, colonists, military personnel, and others have long been well aware of the potentially detrimental health consequences that can arise from extended high-protein intakes. This was essential survival knowledge for anyone who had to live in the wilderness, far removed from the supermarket and who, particularly in late winter and early spring (or late dry season–early rainy season), had to rely largely or entirely on hunted foods. The only ones who seemed unaware that high-protein intakes might pose a health risk were the nutritionists and health professionals during the period of the "great protein fiasco." For them the problem was always too little protein, not too much.

Fortunately, awareness of the potential problems posed by high-protein intakes is slowly entering mainstream consciousness as nutritionists begin to take a closer look at the various high-protein, low-carbohydrate diets that are currently in vogue (e.g., Atkins 1973, 1997; Denke 2001; St. Jeor et al. 2001; Westerterp-Plantenga et al. 2004).

There is also a growing interest in traditional hunter-gatherer diets as the medical and nutrition sciences come to realize that human reliance on grain-based diets is, in fact, a comparatively recent development (i.e., within the last 10,000–20,000 years) and that for some 98% of human existence we lived as foragers without the benefits of agriculture (Cordain et al. 2000, 2005; Cordain et al. 2002a; Eaton 2006; Eaton et al. 1988, 1997). One major impetus for this growth of interest in hunter-gatherer diets was the discovery, beginning with work in Greenland, that traditional Eskimos (Inuit) ate tremendous quantities of fat (typically on the order of 70% of total calories, or more) and yet suffered few strokes, heart attacks, or other so-called diseases of civilization (Allport 2006; Bang et al. 1976; Crawford et al. 2000; Horrocks and Yeo 1999; Innis and Kuhnlein 1988; Kuhnlein et al. 1991; Simopoulos 2003). This contributed to the explosion of interest in omega-3 ($n$-3 or $\omega$-3) fatty acids, which were abundant in the marine mammals eaten by the Inuit but are comparatively sparse in many western diets. Studies of diabetes, hypertension, colon cancer, and many other diseases are also benefiting from closer looks at the traditional diets of foraging peoples (e.g., Cordain et al. 2000; Eaton et al. 1988, 1997; O'Dea 1991; O'Dea and Sinclair 1983; O'Dea et al. 1988).

## 4.7 What Constitutes an Excessive Intake of Protein?

So what constitutes an excessive intake of protein and why is it problematic? The amino acids from ingested proteins are catabolized (deaminized) in the liver, and the nitrogenous wastes that result from this process are converted to urea and largely excreted in the urine (Morris 1992, 2002b; Powers-Lee and Meister 1988; Saheki et al. 1977, 1980). Dimski (1994) provides a concise description of how the urea cycle works; she also outlines the major differences between obligate carnivores, such as cats, and non-carnivorous mammals, such as rats, dogs, and humans, in the way they synthesize urea (see also Morris 2002a; Nuzum and Snodgrass 1971; Schimke 1962). According to Rudman et al. (1973) (see also Cordain et al. 2000; Jackson 1999; Mann 2000; Bilsborough and Mann 2006), the ability of the liver to upregulate one or more of the five key enzymes involved in the synthesis of urea (*carbamyl phosphate synthetase-I*, *ornithine transcarbamylase*, *argininosuccinate synthetase*, *argininosuccinate lyase*, *arginase*) is rate limited, such that at protein intakes above this limit the liver can no longer effectively deaminize the amino acids, leading to a build-up of ammonia (*hyperammonemia*) and excess amino acids (*hyperaminoacidemia*) in the blood (Dimski 1994; Husson et al. 2003; Morris 1992, 2002b; Powers-Lee and Meister 1988; Ratner 1977; Ratner and Petrack 1951). Presumably these are the conditions, exacerbated by low carbohydrate intake, ketosis, and concomitant impairment of kidney function (Denke 2001; Cordain et al. 2002b; Loren Cordain, personal communication, 2009), that Stefansson and other explorers recognized as "protein poisoning" or "rabbit starvation."

The mean maximum rate of urea synthesis (MRUS) observed in Rudman et al.'s (1973) experiments is about 65 mg of nitrogen (N) per hour per kg body weight (commonly written as 65 mg $\mathrm{N\,h^{-1}\,kg^{-1}}$ ($\mathrm{BW^{0.75}}$)), where BW is the metabolic body weight or $\mathrm{BW^{0.75}}$; range 55–76 mg $\mathrm{N\,h^{-1}\,kg^{-1}}$ ($\mathrm{BW^{0.75}}$). These rates can be used to estimate the approximate upper limit to the amount of protein that an individual can safely consume on a daily (i.e., 24-h) basis. Assuming that protein averages about 16% nitrogen, a widely used value to estimate total or "crude" protein (see, for example, Conklin-Brittain et al. 1999), a 70 kg (154 lb) adult can consume approximately 236 g of protein per day (range 200–276 g), and an 80 kg (176 lb) adult can consume about 261 g of protein per day (range 221–305 g) (Cordain et al. 2000; Mann 2000; Bilsborough and Mann 2006) (Table 4.1).

Though widely cited in discussions of hunter–gatherer diets, this protein threshold is based on modern individuals weighing 70 or 80 kg, figures that are reasonable for non-overweight western adult males (and possibly for at least some Middle and Late Pleistocene hominins as well; see Ruff et al. 1997). Most modern hunter-gatherers, however, are smaller (see Jenike 2001:223, 226; Walker et al. 2006:300), with adult males and females generally falling between about 40 and 60 kg. We therefore need to recalculate the protein thresholds for smaller individuals (Table 4.1). For 40 kg (88 lb) individuals, the mean is 155 g with a range from 131 to 181 g; for 50 kg (110 lb) individuals, the mean is 183 g with a range from 155 to 214 g; and for 60 kg (132 lb) individuals, the mean is 210 g with a range from 178 to 246 g. For simplicity, we will take the values for the 50 kg individual as an estimate for the "typical" or "average" forager. Nevertheless, for many hunter–gatherers, especially women, these protein figures are still somewhat too high.

We can express the mean protein limit for the 50 kg forager (183 g) as a percentage of total daily calorie intake. Data provided by Jenike (2001:212) for non-arctic groups, which are probably the most informative given our focus on hominins in Africa, range from a low of 1,600 kcal (Anbarra, Australia) to a maximum of 3,800 kcal (Ache, Paraguay). Most of the groups documented by Jenike fall in the mid-2,000 kcal. Assuming that each gram of protein yields ~4 kcal, then for individuals consuming 183 g of protein and who need 1,600 kcal per day, protein would constitute about 46% of calories. For non-arctic hunter–gatherers at the high end of daily energy intake (3,800 kcal), the protein limit would be about 19% of total energy. As a rule of thumb, a reasonable working figure would be somewhere between these two extremes, perhaps on the order of 30–35% of calories, approximately the value one would obtain for a daily caloric intake of 2,500 kcal and reasonably close to the value suggested by Cordain et al. (2000).

It should be kept in mind that expressing the safe upper limit to total protein intake as a percentage of total energy may be misleading. It implies that a forager will be fine so long as he or she keeps adding fat or carbohydrate to the diet in order to keep the concentration of protein below about 35% of total calories. But the threshold, whatever the current uncertainties about its actual value, appears to be an absolute amount of protein, expressed in gram per kilogram body weight, that the body can safely deaminize and excrete within a 24-h period. Once that amount has been exceeded, and allowing for a certain (but unknown) degree of adaptation, augmenting one's intake of fat or carbohydrate is not likely to result in a significant upward displacement of the protein limit. *In other words, the maximum amount of*

**Table 4.1** Safe upper limit to total daily protein intake by body weight, expressed in grams and as a percent of total calorie intake. Limits are calculated using the minimum (55 mg N), mean (65 mg N), and maximum (76 mg N) values of the MRUS (maximum rate of urea synthesis)

| Body weight (kg) | Protein limit (g) | | | 2,000 kcal (%) | | | 2,500 kcal (%) | | | 3,000 kcal (%) | | | 3,500 kcal (%) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 55 mg N | 65 mg N | 76 mg N | 55 mg N | 65 mg N | 76 mg N | 55 mg N | 65 mg N | 76 mg N | 55 mg N | 65 mg N | 76 mg N | 55 mg N | 65 mg N | 76 mg N |
| 40 | 131 | 155 | 181 | 26 | 31 | 36 | 21 | 25 | 29 | 17 | 21 | 24 | 15 | 18 | 21 |
| 50 | 155 | 183 | 214 | 31 | 37 | 43 | 25 | 29 | 34 | 21 | 24 | 29 | 18 | 21 | 24 |
| 60 | 178 | 210 | 246 | 36 | 42 | 49 | 28 | 34 | 39 | 24 | 28 | 33 | 20 | 24 | 28 |
| 70 | 200 | 236 | 276 | 40 | 47 | 55 | 32 | 38 | 44 | 27 | 31 | 37 | 23 | 27 | 32 |
| 80 | 221 | 261 | 305 | 44 | 52 | 61 | 35 | 42 | 49 | 29 | 35 | 41 | 25 | 30 | 35 |

*lean meat that a forager can safely consume from a kill is finite, irrespective of how much fat he or she can glean from the carcass.*

Let us look more closely at the meat-eating proclivities of the two best-documented hunter-gatherer groups in sub-Saharan Africa – the Kalahari San in Botswana and the Hadza in Tanzania. According to Lee (1979:271), the per capita daily meat intake of the Ju/'hoansi averages only about 0.23 kg, or about 48.3 g of protein, well below the 183 g safe upper limit suggested earlier. However, Lee (1982:40), emphasis in original, makes the interesting observation that:

> …in late-spring and early-summer [late-dry-season and early-rainy-season] hunting camps the proportion of meat may sharply rise. In one study, the four hunters of a small camp of 12 killed 29 animals in 17 days for a *per capita* consumption of almost two kilos of meat per day.

This is an astoundingly high meat intake, amounting to nearly 420 g of protein (1,680 kcal or more than 75% of an individual's total daily calories). Such gorging leads to an intake of protein that is more than double the 183 g safe upper limit suggested earlier. Interestingly, according to Wilmsen (1978, 1982) (see also Truswell and Hansen 1976; Truswell 1977), the San lose nearly 6% of their body weight (males and females combined) each year during more or less the same period that Lee observed them gorging on meat (i.e., during the late dry season and early rainy season). Unfortunately, the weight data are not presented separately by sex. I would expect the loss to be greater in men than in women if, as seems likely, the men consume greater quantities of meat (e.g., by snacking directly at the kill). Wilmsen (1978) attributes the weight loss to food shortages in the late dry season and early rainy season. I wonder if that's the whole story….

Many African ungulates are among the leanest large mammals on the planet, a fact commented upon by many nineteenth-century explorers (e.g., McKiernan 1954:99; von Höhnel 1894:24). Sinclair (1974, 1975, 1977), for example, shows that virtually all ungulates in the Serengeti subsist on submaintenance diets throughout the dry season. He attributes this to poor forage quality during the stressful period:

> …Sinclair (1975) examined the effects of grass quality (protein content) on the survival of wildebeest in the Serengeti of Tanzania. Despite selecting protein-rich plants and plant parts…, the wildebeest consumed food in the dry season that contained well below the level of protein necessary even for maintenance (5–6% of crude protein); and to judge by the depleted fat reserves of deal males…, this was an important cause of mortality. Moreover, it is highly relevant that the protein requirements of females during late pregnancy and lactation (December–May in the wildebeest) are three to four times higher than the normal…. It is therefore clear that the shortage of high-quality food (and not just food shortage per se) can have a drastic effect on the growth, survival and fecundity of a consumer. In the case of herbivores especially, it is possible for an animal to be apparently surrounded by its food whilst still experiencing a food shortage. We can see the problem if we imagine that we ourselves are provided with a perfectly balanced diet – diluted in an enormous swimming-pool. The pool contains everything we need, and we can see it there before us, but we may very well starve to death before we can drink enough water to extract enough nutrients to sustain ourselves.
>
> Begon et al. (1996:332)

The average carcass fat content in 15 different species of wild African herbivores is only 3.9% (Table 4.2; Ledger 1968; Eaton and Konner 1985:285; Hoffman and Wiklund 2006; see also Smith 1970:126, his Table 1). Ntiamoa-Baidu (1997:65; emphasis added) provides an even lower overall estimate: "In terms of actual protein production, the value of game is even higher than that indicated by the carcass yield since cattle could have up to 40% fat content in dressed carcasses *compared with 2.5% in wild* [African] *ungulates*." Thus, most African large-game species yield values that are lower than the level of body fat found in many North American ungu-

**Table 4.2** Percentage of carcass fat in East African larger mammals (data from Ledger 1968)

| | | | Liveweight (kg) | | % Carcass fat | |
|---|---|---|---|---|---|---|
| Common name[a] | Sex | *N* | Mean ± SD | Range | Mean ± SD | Range |
| 1. Hippopotamus | M | 4 | 1,489.8 ± 224.9 | 1,177.8–1,714.3 | 7.0 ± 2.7 | 4.3–10.7 |
| | F | 4 | 1,277.2 ± 101.5 | 1,185.1–1,400.8 | 10.9 ± 2.0 | 7.9–12.3 |
| 2. Buffalo | M | 8 | 753.0 ± 69.6 | 660.6–849.2 | 5.6 ± 1.0 | 4.8–7.5 |
| 3. Eland | M | 5 | 508.1 ± 63.2 | 411.1–549.0 | 4.2 ± 2.4 | 2.0–8.2 |
| 4. Zebu bulls | M | 10 | 483.9 ± 65.1 | 408.6–585.2 | 13.7 ± 3.3 | 8.8–19.8 |
| 5. Zebu steers | M | 70 | 469.8 ± 66.8 | 278.8–570.2 | 28.6 ± 4.6 | 17.2–41.6 |
| 6. Zebu fat cows | F | 4 | 394.8 ± 41.1 | 353.7–419.9 | 32.9 ± 3.3 | 28.3–36.9 |
| 7. Zebu thin cows | F | 9 | 298.4 ± 48.6 | 224.0–390.7 | 13.4 ± 5.9 | 7.3–25.2 |
| 8. Wildebeest (K) | M | 10 | 243.3 ± 14.6 | 221.8–254.2 | 6.8 ± 2.1 | 2.0–10.0 |
| | F | 10 | 192.0 ± 9.3 | 178.7–208.7 | 7.3 ± 3.5 | 3.8–12.0 |
| 9. Waterbuck | M | 10 | 237.7 ± 18.3 | 206.6–266.9 | 1.0 ± 0.4 | 0.7–1.5 |
| | F | 10 | 181.0 ± 11.2 | 200.3–162.3 | 4.0 ± 1.9 | 1.0–7.0 |
| 10. Wildebeest (S) | M | 10 | 203.0 ± 11.4 | 180.2–221.0 | 2.7 ± 3.0 | 1.8–4.1 |
| | F | 10 | 160.3 ± 12.6 | 140.8–185.0 | 6.4 ± 3.0 | 3.0–11.6 |
| 11. Oryx | M | 10 | 176.4 ± 12.1 | 167.8–209.4 | 2.9 ± 1.2 | 2.1–5.3 |
| | F | 10 | 161.5 ± 20.3 | 116.0–188.4 | 7.1 ± 3.5 | 3.1–11.8 |
| 12. Kongoni (hartebeest) | M | 5 | 142.5 ± 11.1 | 129.0–199.8 | 2.2 ± 0.3 | 1.7–2.6 |
| | F | 5 | 126.2 ± 7.7 | 116.0–135.0 | 3.9 ± 1.6 | 1.9–5.6 |
| 13. Topi | M | 10 | 130.8 ± 9.1 | 113.6–141.0 | 2.3 ± 0.8 | 1.3–3.5 |
| | F | 10 | 103.9 ± 8.0 | 90.6–116.3 | 1.9 ± 0.8 | 1.3–3.9 |
| 14. Kob | M | 10 | 96.7 ± 5.8 | 92.8–107.7 | 2.6 ± 1.1 | 0.43–3.9 |
| | F | 10 | 62.1 ± 4.2 | 59.1–66.4 | 4.0 ± 1.5 | 1.5–5.4 |
| 15. Lesser kudu | M | 10 | 92.1 ± 14.4 | 56.3–108.4 | 3.3 ± 1.5 | 1.0–5.9 |
| 16. Warthog | M | 10 | 87.8 ± 7.5 | 71.9–99.6 | 1.8 ± 0.2 | 1.3–2.8 |
| | F | 10 | 60.2 ± 7.9 | 62.2–70.7 | 1.8 ± 0.7 | 1.1–3.2 |
| 17. Grant's gazelle | M | 6 | 60.1 ± 6.2 | 53.2–68.8 | 2.8 ± 0.6 | 2.0–3.4 |
| | F | 5 | 41.3 ± 1.5 | 40.0–43.7 | 5.1 ± 4.2 | 2.5–12.2 |
| 18. Impala | M | 10 | 56.7 ± 2.6 | 52.6–60.9 | 1.9 ± 0.5 | 1.0–3.1 |
| | F | 10 | 42.0 ± 2.6 | 38.9–45.7 | 2.0 ± 1.2 | 0.9–4.7 |
| 19. Gerenuk | M | 5 | 31.2 ± 2.1 | 28.5–34.2 | 2.0 ± 0.1 | 1.4–2.6 |
| 20. Thomson's gazelle (N) | M | 10 | 25.3 ± 1.6 | 24.0–28.7 | 2.0 ± 1.3 | 0.8–5.0 |
| | F | 10 | 18.4 ± 1.2 | 16.6–20.2 | 2.2 ± 5.6 | 0.2–5.4 |
| 21. Thomson's gazelle (S) | M | 10 | 20.3 ± 1.7 | 17.5–21.7 | 2.0 ± 0.8 | 1.0–3.2 |
| | F | 10 | 16.9 ± 1.3 | 15.0–19.9 | 5.1 ± 2.2 | 2.7–8.8 |

[a] *K* Kajiado, Kenya, *S* Serengeti, Tanzania, *N* Naivasha, Kenya

lates in the spring (compare, for example, Ledger's data with values cited in Speth and Spielmann 1983:10–11). By the end of the dry season or beginning of the rainy season, total carcass fat in many African ungulates drops to levels lower than those found in severely malnourished and starving northern latitude animals (i.e., less than 2–3%; Loren Cordain, personal communication, 2009, notes that Ledger's figures probably underestimate the actual quantity of fat in the carcasses because they were derived by dissection rather than by whole-carcass chemical extraction; early hominins without boiling technology, however, would experience even lower returns). Comparably low dry-season fat levels are commonly found in the marrow of African ungulates (cf. Sinclair and Duncan 1972; Brooks et al. 1977; Brooks 1978). To gorge on such excessive quantities of extremely lean meat, the San are either in trouble nutritionally or, as seems more likely given the diversity of fall-back plant foods available in their environment, there must be social or other non-nutritional factors that push their pursuit of large game well beyond the point where the nutritional consequences remain positive. I will return to this issue again.

Robert Hitchcock notes that the Tyua, a Bushman group in northern Botswana, also gorge on massive amounts of meat during the dry season, paralleling Lee's observations for the Ju/'hoansi. Unfortunately, Hitchcock does not have seasonal body weight data for the Tyua, but he implies that they too probably lose weight (Hitchcock 1988:65). He also makes the same assumption that Richard Lee made, namely that the weight loss is due primarily or entirely to a shortage of calories at that time of year exacerbated by the strenuous labor needed to dig up tubers and other resources. Again, I suspect that the high lean meat intake by itself is a significant contributor to the weight loss experienced by the Tyua.

> One way in which the Tyua coped with dry season subsistence stress was to gorge themselves on lean meat. Some early travelers remarked on what they called the "raw meat feasts" of the Basarwa. While Tyua stated categorically that they did not eat their meat raw, they did admit that they often ate prodigious amounts of cooked meat at single sittings. In one two-day period in the late dry season of 1975, a group of five men consumed 27.6 kilograms of meat [2.76 kg or 6.1 lbs/person/day] while on an expedition hunt near Gum//gabi, north of the Nata River. Some Tyua said that much of their diet during the dry season consisted of lean meat, which they supplemented with the marrow from long bones and Grewia berries.
>
> Hitchcock (1988:73)

Recent work on the Hadza reveals a similar pattern of meat-gorging accompanied by significant weight loss. James O'Connell and colleagues' observations on this are worth quoting in full:

> Large herbivores are often in poor condition at this time of year [late dry season]; and, as Speth (1987, 1989) has shown, humans eating them are likely to sustain a net nutritional deficit as a result. Data from the Hadza underline this point: despite acquiring more than 30 large-bodied prey over a period of 47 days in the late dry season of 1985, the 50-odd members of our study group on average *lost* weight during that period (Hawkes *et al.*, 1991, 1995, 1997), presumably because at least some of the animals they took were in marginal condition. Without access to other resources, mainly underground plant storage organs, they would not have been able to operate in that habitat at that time, the very high rate of carcass access, representing an average of *>1 kg of meat/consumer-day*, notwithstanding (Hawkes *et al.*, 1995, 1997). In other dry seasons in our sample, when large

> carcass acquisition rates were lower, this pattern of weight loss is absent (Hawkes *et al.*, 1997), probably because consumers were eating less lean meat.
>
> O'Connell et al. (2002:858); emphasis in original

The Ache are another example of foragers who consume substantial amounts of meat (~1.15 kg/person) each day, but who nonetheless lose weight in the process (Hill 1982:524; see footnote in their Table 1 for computing edible meat weights; see also Hawkes et al. 1982:385–86; note that their total figure of 150 g of meat per person per day is undoubtedly a misprint and recalculation of their data indicates that the result should read 1,150 g):

> Analysis of six foraging trips ranging from 6–14 days using a paired t-test showed that weight change was not significant for the population as a whole…. This would suggest that Ache caloric needs are as high as the levels of consumption we observed. Within the population, however, there were some interesting differences. Men lost weight on all but one trip and pooling all data, their weight loss is very significant…. Women, in contrast, gained weight on all but one trip, and the results when pooled were also significant….
>
> Hill et al. (1984:132)

Hill et al. (1984) see the weight loss in Ache males as a post-contact phenomenon, stemming from comparatively recent alterations in their overall diet or foraging patterns. They do not consider the possibility that the weight loss is a direct consequence of their very high-protein intakes (probably on the order of 240–250 g), and could well be a consumption pattern that predates contact and missionization.

> Since body weights were observed to change during foraging trips, we must also conclude that either current body weights at the mission, or male and female consumption and energy expenditure in the forest, are not perfectly representative of precontact times.
>
> Hill et al. (1984:132)

Thus, the San, Hadza, and Ache appear to consume excessive amounts of protein for extended periods with the result that they lose rather than gain weight. In essence, their heavy reliance on meat may be putting them on what amounts to a high-protein weight-loss program somewhat akin to an Atkins diet (1973, 1997). And while such a dieting scheme may make sense for the overweight in western industrial societies, and may have little in the way of negative consequences for the more robust and comparatively well-fed Ache, this hardly seems like a desirable goal for African hunter–gatherers, particularly the San, who are already noteworthy for being exceedingly lean (Hiernaux and Hartono 1980: 342; Howell 1986:167).

> …the hunter-gatherer adaptation is based upon a balance between preventive checks and positive checks…which leans to an unexpected degree in the direction of the preventive checks. We can refine our understanding of this achievement by recognizing that hunter-gatherers tend to be thin not because they have exhausted the food in their environment, but because they have evolved a culture which gives them security, leisure and egalitarianism at a price of chronic hunger and undernutrition.
>
> Howell (1986:184)

Interestingly, there are even hints that European Neanderthals and quasi-contemporary modern humans of the mid-Upper Paleolithic may have had to rely repeatedly on excessive amounts of animal protein. This evidence, coming from isotope studies of the fossil human remains themselves, shows that the collagen of these Late Pleistocene humans is more enriched in $^{15}N$ than that of contemporary carnivores (Lee-Thorp and Sponheimer 2006:137; Robbins et al. 2005:538; Sponheimer and Lee-Thorp 2007; see also Schoeninger 1995). The reason for such high levels of $^{15}N$ remains far from clear, but Sponheimer and Lee-Thorp (2007:565–566) (see also Sponheimer et al. 2003; Zhao et al. 2006:476) offer an intriguing possibility:

> …why are both hominins [Neanderthals and mid-Upper Paleolithic humans] enriched by more than 5‰ compared to associated herbivores when an enrichment of about 3‰ would be expected for a carnivore? Stated otherwise, why is their $\partial^{15}N$ significantly higher than that of associated carnivores? As discussed earlier, this may be partially, but not satisfactorily, explained by the consumption of herbivores with unusually high $\partial^{15}N$, such as mammoths, or even by the consumption of omnivores and/or aquatic resources. Another possibility, however, is that there is some physiological explanation for their extremely high $\partial^{15}N$. Experimental studies have shown that when herbivores are fed diets with crude protein contents that are much greater than their nutritional requirements, their diet-tissue spacing can become much greater than 3‰…. This implies that if the prevailing environment forced Neanderthals to consume high-protein diets that considerably exceeded their crude protein requirements, their diet-tissue spacing might have exceeded 3‰, thus artificially increasing their $\partial^{15}N$ compared to other taxa.

There is an alternative explanation for the elevated $^{15}N$ levels observed in European Neanderthals and in their mid-Upper Paleolithic successors. Studies in fish, birds, and mammals have shown that severe nutritional stress can lead to similar increases in $\partial^{15}N$ (e.g., Fuller et al. 2005; Hobson et al. 1993; Kelly 2000; Mekota et al. 2006). Whatever the cause – excessive protein intake or hunger – the nitrogen isotope data available to us thus far suggest that the nutritional problems facing Upper Paleolithic foragers may not have been all that different from those confronting their "archaic" predecessors.

Thus, there is a fair amount of evidence, admittedly mostly historical and anecdotal, that there is an upper limit to the total amount of protein that one can safely consume per day, a limit that was widely recognized by eighteenth- and nineteenth-century explorers and military officers, and one that is gradually coming to be recognized by modern-day nutritionists as well (Cordain et al. 2000; Mann 2000; Bilsborough and Mann 2006). But, as is so often the case, there are potential complexities lying just below the surface that have not been adequately explored. For example, several authors, in attempting to replicate Rudman et al.'s (1973) experiments, found no clear evidence of a fixed cap or limit to the rate of urea synthesis (MRUS), but instead observed that the liver was capable of considerable adaptation (e.g., Boon et al. 1999; Morris 2002a:155; Mouillé et al. 2004; Petersen et al. 1990; Rafoth and Onstad 1975; Rypins et al. 1980; van de Poll et al. 2007; and Vilstrup 1980):

> The most striking finding in this study was a linear relationship between serum amino acid concentration and the urea production rate. Within the range of serum amino acid concentration achieved, that concentration, rather than the liver's synthetic ability, was the limiting factor in urea production. These results stand in clear conflict with the conclusions of

> Rudman et al. [1973] who reported a maximum rate of urea synthesis which could not be exceeded by increasing oral protein ingestion. Even though urea synthetic rates one and one-half times higher than the maximum rate reported by Rudman et al. were achieved in normal subjects in the present study, no plateau in production was reached.
>
> Rafoth and Onstad (1975:1172–1173)

> The linear relation between urea synthesis rate and a-amino acids indicates that saturation of the urea synthesis did not take place.
>
> Vilstrup (1980:994)

> A different kinetics was presumed by Rudman et al. [1973] for estimation of 'maximal rate of urea synthesis' (MRUS), implying saturation of the urea synthesis rate at plasma a-amino concentrations above 11 mmol/1.... However, the calculated urea synthesis rate in that study, assumed to be maximal, is only 50% of the highest synthesis rate seen in the present investigation.
>
> Vilstrup (1980:994)

It would seem, therefore, that determining whether there is a safe upper limit to total daily protein intake, and fixing a value for that limit, is not an easy or straightforward task. Not only is the body capable of adapting to changes in consumption by upregulating the enzymes involved in protein metabolism and urea synthesis, but the process of adaptation may take up to two or three weeks to complete, a period longer than the duration of many of the nutritional studies designed to explore the effects of high-protein intakes (Institute of Medicine 2005:693–694). An entry in the diary of Lt. Frederick Schwatka, head of the 1878–1880 arctic expedition in search of the lost Franklin expedition, provides one of the earliest explicit records of just how long this period of adaptation can be. Forced to switch to an all-meat ("Inuit") diet once his basic provisions were used up, Schwatka observed that:

> When first thrown wholly upon a diet of reindeer meat, it seems inadequate to properly nourish the system, and there is an apparent weakness and inability to perform severe exertive fatiguing journeys. But this soon passes away in the course of two or three weeks.
>
> Stackpole (1965); quoted in Phinney (2004:2–3)

Vihljalmur Stefansson's more detailed observations closely parallel those of Schwatka:

> Novices on the Stefansson expeditions were usually broken to meat when traveling over the sea ice and therefore living on seal. Speaking generally and roughly, they got along very well for the first day or two, eating square meals, for they were already as fond of that meat as the average American is of beef. On the second or third day the appetite would begin to fail, and in from 3 to 5 days, especially with those who believed or feared the diet was going to hurt them, appetite would almost or quite cease. Then there might be nausea at the name, sight, and thought of meat. Some would nibble a little every day. Others would go without food for 2 or 3 days, but then they, too, began to nibble. In 2 to 3 weeks from the last tasting of a vegetable element the whole party, of whatever size, was eating square meals, though in some cases under a good deal of protest.
>
> Stefansson (1944:283–284)

Recently, Phinney (2004) came to conclusions very similar to Schwatka's and Stefansson's earlier observations. Physically active men, including several trained endurance athletes (bicyclists), were switched from a baseline diet providing 67% of non-protein energy as carbohydrate to a ketogenic "Inuit" diet consisting almost entirely of protein (15%) and fat (83%). The participants' performance and metabolic state declined noticeably for the first week or two on the "Inuit" diet, but then returned to normal levels by the third to fourth week (see also Phinney et al. 1983a, b:766, Phinney 1995:305–306).

Finally, Kim Hill (personal communication, 2008), who has worked for many years with Ache hunter–gatherers in Paraguay, noted that it took him several weeks to adjust to their daily high meat intakes.

In sum, while the historic records of explorers, hunters, trappers, and military officers provide ample first-hand evidence for the existence of an upper limit to the amount of protein that one can safely consume on a daily basis, evidence seemingly bolstered by observations among several contemporary foraging groups, the medical and nutritional research that has addressed this issue is less abundant and also much less certain in its conclusions, with Rudman et al.'s (1973) widely cited study finding such a limit, but several more recent ones failing to do so. In fact, contemporary nutritional literature makes it abundantly clear that the pros and cons of high-protein intakes remain to be definitively established. For example, L'Heureux-Bouron et al. (2004:1512) note that "the benefits or adverse health consequences of a long-term or chronic high-protein diet are puzzling and not well understood, despite being increasingly employed in weight loss therapy." Petzke et al. (2005:414) come to a similar conclusion, pointing out that "the tolerable upper level of chronic protein or amino acid intake under various conditions not leading to health risks is still a matter of discussion and remains to be clearly defined." There are even recent discussions exploring possible links between long-term high-protein intakes, elevated serum IGF-1 (insulin-like growth factor 1) levels, and the pathogenesis of tumors in humans:

> These findings demonstrate that, unlike in rodents, long-term severe CR [calorie restriction] does not reduce serum IGF-1 concentration and IGF-1:IGFBP-3 [insulin-like growth factor binding protein 3] ratio in humans. In addition, our data provide evidence that protein intake is a key determinant of circulating IGF-1 levels in humans, and suggest that reduced protein intake may become an important component of anticancer and anti-aging dietary interventions.
>
> Fontana et al. (2008:681)

The amount of protein that one can safely consume on a long-term basis is clearly a topic that remains in need of much more study, for it has important implications, both for modern-day health issues, and for our understanding of the behavior and evolution of ancestral hominins.

# Chapter 5
# Were Big-Game Hunters Targeting Fat?

> *...human and chimpanzee hunters are nevertheless alike in important ways. Both would rather eat meat than anything else, even though meat makes up a minority of both their diets. Both seem more eager for the fat content of meat than either its protein or calories....*
>
> Stanford (2001c:55)

> *Consideration of nutrient requirements has clearly been dominated by protein and calories. Foods are described as protein-rich or rich in energy. …it is suggested that other nutrients could be as, if not more, important than protein and that the emphasis on protein is misplaced.*
>
> Crawford and Rivers (1975:235)

> *In tropical animals which are not subjected to cold stress, subcutaneous deposition of fat would probably serve as a physiological embarrassment during their critical season, which is characterized in most cases by extreme heat. This assumption is supported by the examination of many East African ungulates which have very little, if any, fat under the skin.*
>
> Smith (1970:127)

While our focus in the preceding discussion has been on paleoanthropology's preoccupation with protein, over the past decade or so perspectives in the field have begun to shift, and a growing number of researchers now accept the potential shortcomings of a diet that is heavily based on the fat-poor muscle tissues typical of most African ungulates. As a result, a number of paleoanthropologists are now emphasizing the importance of the fat that early hominins could glean from the marrow bones and brains of hunted (or scavenged) large game. Thus, while *nutritionally motivated* meat-eating and big-game hunting still retain their position of prominence in most contemporary evolutionary scenarios, animal-derived *fat* obtained mostly from marrow and brain is now seen as an essential part of the picture (e.g., Bunn and Ezzo 1993; Cordain et al. 2001; see also arguments and counter-arguments in Blumenschine and Caro 1986:275; Blumenschine and Madrigal 1993; Lupo 1998; Madrigal and Blumenschine 2000).

But as already alluded to, most African ungulates have low average levels of body fat by comparison to levels found in larger mammals elsewhere in the world, including the Neotropics (e.g., Ledger 1968; Hill et al. 1984:111). Norman Smith (1970:127) notes that "…many East African ungulates…have very little, if any,

J.D. Speth, *The Paleoanthropology and Archaeology of Big-Game Hunting*,
Interdisciplinary Contributions to Archaeology, DOI 10.1007/978-1-4419-6733-6_5,

fat under the skin.” Not only isn’t there much fat on African game animals *in prime condition*, at any given point during the year many individuals may be nutritionally stressed and partially to severely fat depleted (e.g., males during the rut, females carrying a full-term fetus or nursing, older animals whose teeth are wearing out, injured or sick animals that have difficulty obtaining sufficient food, very young individuals, animals under drought conditions, and so forth). Thus, on any chunk of African real estate, the number of animals that are in reasonably good condition is likely to be much smaller than the total number of animals in the population.

## 5.1 Hadza Hunting Success

Moreover, the likelihood that an early hominin would encounter a scavengeable carcass, or make a successful kill, of a large ungulate, regardless of the animal’s condition, was probably quite low, judging by the surprisingly low success rates reported in the ethnographies of contemporary African hunter–gatherers. The Hadza provide a striking case in point. Even with unusually high-powered bows, having draw weights of 45 kg (100 lbs) or more (Bartram 1997; Henrich 2008:187–188; Neuwinger 1996:90; O’Brien 1994:89; Woodburn 1970), and arrow points smeared with poison, “individual hunters…fail to kill (or scavenge) large game on 97% of all hunting days” (Hawkes et al. 1997:573).

Lupo and O’Connell (2002) provide a fuller account of just how often Hadza hunters fail in acquiring game:

> Observations over more than 2000 hunter-days show an overall average acquisition rate of only one large animal every 30 hunter-days. Periods of more than ten days in which no hunter in a local cohort of 5-6 took a large carcass are not uncommon in this sample. Scavenging alone produced about 20% of this total—on average, *one animal every 140 hunter-days, just over one per cohort-month*. During 1985-88, several periods longer than a month passed during which our co-resident study population (30-50 people) had no scavenging opportunities of any kind.
>
> Lupo and O’Connell (2002:104), emphasis in original

Even more eye-opening is Kristen Hawkes’ (2000:64) comparison of Hadza hunting success with the return rates that hunters might expect if they instead devoted their efforts to other subsistence pursuits. Hadza men, on average, devote more than 4 h per day to hunting, and yet take home only about 0.12 kg/h of meat. Hawkes concludes that, in terms of caloric returns, adult Hadza men would enjoy higher return rates by gathering:

> The rates for large game can also be compared with gathering plant foods by converting kilograms of meat to calories. If large animals are estimated at 1500 Cal/kg live weight (following Lee 1979), a rate of .12 kg/hr (live weight) gives 180 Cal/hr. This rate is lower than all but the very youngest children earn gathering…. In the long run, big-game hunting is inferior to available alternative strategies for provisioning families.
>
> Hawkes (2000:65)

The tremendous day-to-day variance in hunting success, in which an "average hunter can expect a full month of failures for every day he scores," would be devastating as a family provisioning strategy, especially for children (Hawkes 2000:65).

O'Connell et al. (2002) take this line of reasoning a step further, concluding that prestige, rather than nutrition, underlies the Hadza's focus on big-game hunting:

> If Hadza men were primarily concerned with feeding their wives and children, they would do better by pursuing a broader range of resources, including small game and plant foods, both of which are much more reliably acquired and far more readily defended against the claims of others than are large animal carcasses…. The fact that they rarely adopt this strategy indicates another goal for big game hunting, the most likely candidate being prestige, which affects their status relative to that of other men….
>
> O'Connell et al. (2002:836)

Thus, just in terms of success rates, big-game hunting by the Hadza seems like a very inefficient and unreliable way of putting food on the table.

## 5.2 Bushman (San) Hunting Success

Bushmen or San hunters also have low success rates, particularly for large game (Hitchcock et al. 1996:175). For example, Richard Lee documented the hunting activities of Ju/'hoansi (!Kung San or Bushmen) over 28 days in July–August, 1964, a period that fell squarely within the dry season. During that period, seven men put in a total of 78 person-days of hunting, with an overall success rate of only 23% (Lee 1979:267; Hitchcock et al. 1996:182).

A few years later, in 1968, John Yellen observed the Ju/'hoansi for a period of 80 days. Unlike Lee's earlier work, Yellen's study spanned part of the wet season as well as a portion of the subsequent dry season. During this period, men made no attempt to hunt on 14 days and failed to procure anything on an additional 25 days, indicating that on nearly 50% of the days the hunters made no successful kills. Moreover, most of what they caught were small animals, especially porcupines and springhare, as well as a number of birds (Hitchcock et al. 1996:175). If one considers only the ungulates, their success rate was much lower.

Not only do the San frequently fail in their attempts to kill big game, but the way they go about it is truly perplexing. When I was a graduate student in the late 1960s, publication of the *Man the Hunter* symposium was like a shot of adrenalin for those of us who were interested in hunters and gatherers (Lee and DeVore 1968). Almost overnight the Ju/'hoansi (in those days referred to as the !Kung) became the gold standard by which we viewed and interpreted the hunter–gatherer past. Almost everything came to be seen "through Bushman eyes." Thus, the way the Ju/'hoansi hunted was the way all good hunters, past or present, must have hunted – with uncanny stealth (Stander et al. 1996) and amazing skill as trackers (Biesele and Barclay 2001; Liebenberg 1990, 2008).

Yet, at more or less the same time, I was influenced by one of my fellow graduate students at the University of Michigan, George Frison, an expert on hunting, whose insights stemmed from vast archaeological expertise combined with years of experience as a hunter in his own right. According to Frison (1978:366), big-game hunters whose livelihood depended on the outcome of the hunt would leave as little to chance as possible: "there was careful consideration…as to where animals were killed; nothing was killed where the effort of recovery exceeded the value of the meat…."

A good hunter would also choose a weapon that was appropriate for the behavior and size of the prey, and direct a shot at the animal that would either kill it on the spot or at least immobilize it:

> The ideal location of penetration…is the rib cage forward of the diaphragm and high enough to penetrate the lungs. The heart is a bad choice because it is protected by the ribs that widen and flatten distally. The experienced hunter tries to avoid flesh and/or stomach wounds, which nearly always result in time and effort wasted in trailing wounded animals.
>
> Frison (1998:14579)

Contrast Frison's observations with Bushman hunting. They use tiny bows, not shock weapons, despite the fact that shock weapons – recurved bows – were clearly present in southern Africa prior to contact (Manhire et al. 1985; Noli 1992; but see Hromník 1993 for a different perspective). Marylène Patou-Mathis (2007:121) provides a succinct characterization of the "undersized" Bushman bow: "la faiblesse de leur arme, l'arc ayant peu de puissance et une courte portée, contraint les San à s'approcher le plus près possible du gibier traqué" (see Figs. 5.1 and 5.2).

A few years earlier, writer Alf Wannenburgh and photographers Peter Johnson and Anthony Bannister (1999) arrived at a similar assessment of the Bushman bow:

> The Bushman bow that shoots [their] unflighted projectiles is appropriately light…. With a pull of less than ten kilograms, it is capable of sending such an arrow 100 metres, but the effective range is only a quarter of that…. In all save exceptional instances, such light weaponry would be hopelessly inadequate without poison for either hunting or war.
>
> Wannenburgh et al. (1999:37)

Robert Hitchcock, an anthropologist who has worked for many years among the San, together with colleague Peter Bleed, make a similar statement regarding the nature of San bows and poisoned arrows:

> Poisoned arrows have neither knock-down power nor the ability to open a serious bleeding wound.... Their intended function is simply to introduce the poison. They are most effective against relatively small game and, in any case, they kill relatively slowly; in addition, animals, once hit, must be tracked by the hunters. Often tracking goes on for long distances.
>
> Hitchcock and Bleed (1997:354)

Over a century earlier, Longman and Walrond (1901:101), two late nineteenth-century experts on archery, put it even more bluntly: "The Bushmen rely entirely on their poisoned arrow-heads, as they could kill neither man nor beast merely by the penetration of the arrow from their weak little bows."

Perhaps the most disparaging comment of all concerning the worth of the Bushman bow was made by Sir John Lubbock, eminent nineteenth-century biologist

**Fig. 5.1** Crooked/Qui, a Bushman (San) man with his bow and arrow. Photograph taken in 1955. ©Documentary Educational Resources (DER). Photo from the Marshall Family Collection, courtesy Documentary Educational Resources. The image's Marshall Family Collection original catalog number is 2001.29.430., and it is titled "Man with Bow and Arrow"

**Fig. 5.2** Bushman (San) man drawing his bow. Photograph taken by Marylène Patou-Mathis in 1985. ©Marylène Patou-Mathis. The photograph is reproduced here by permission of Marylène Patou-Mathis, Muséum National d'Histoire Naturelle, Institut de Paléontologie Humaine, Paris, France

and archaeologist: "...the North Americans had good bows and arrows, the Society Islanders and Bushmen had bad ones..." (Lubbock 1869:542).

We have to wait until the latter half of the twentieth century, however, to find actual quantitative assessments of the power [or lack thereof] of Bushman bows. Thus, according to Bartram (1997:325), Kua San bows are less than a meter in length and have an average draw weight of only 8–10 kg (18–22 lbs). Silberbauer (1981:206) provides a similar estimate for the diminutive bow of the Central Kalahari G/wi San – about 9 kg (20 lbs). For San (Ju/wasi or Ju/'hoansi) in Nyae Nyae, Namibia, Thomas (2006:128) gives a slightly higher pull of about 11 kg (25 lbs), but adds that: "to kill a deer-sized animal with an unpoisoned arrow requires a much heavier, longer arrow and a much more potent bow—one with a 50 or 60 lb. pull, minimally."

By comparison, most traditional Native American bows were substantially longer, many backed or recurved, and most had draw weights of 18–23 kg (40–50 lbs) and often considerably more (e.g., Hamilton 1982; Cattelain 1997; Pope 1923; Stephenson et al. 2001:130). Hamilton (1982:138–139) lists draw weights for bows from 17 different North American tribes; these yield a mean weight of 21 kg (47 lbs) and a median weight of 20 kg (45 lbs), double that of Kua bows. The range was from 13 to 36 kg (28–80 lbs).

How do Bushman bows stack up against what modern archers would consider appropriate for a hunting weapon? Sparano (2000:692) in *The Complete Outdoors Encyclopedia* recommends a draw weight of 9 kg (20 lbs), or less, for *children* between the ages of 6 and 12, and at least 23 kg (50 lbs) for deer hunting. In other words, the draw weight of Bushman bows falls within the range of weights that modern bowyers recommend for children! This is hardly a shock weapon and clearly not one designed to deliver a lethal or immobilizing shot to a large animal.

Early travelers in southern Africa didn't think much of Bushman bows or arrows either, although they had considerable respect for the poisons which coated the tips of the arrows:

> Their bows are remarkably small; and, in the hands of anyone but of a Bosjesman [San or Bushman], would be entirely useless.
>
> Barrow (1806:243)

> In the chase, artifice and dexterity must supply all that is wanted from the imperfection of these weapons [bows]....
>
> Lichtenstein (1812:199)

> They do not direct the bow on a level, as might be supposed, but inclining, like Sagittarius in the Zodiac: they hold it in the middle with the left hand, the arrows rest on the thumb, and with the right hand they draw the arrow back at the same time upon the string. This is all done at a commodious height below the eye, so that the direction of the arrow may be perfectly calculated, but not its inclination. For this reason they often fail in the height at which they aim, but never in the direction, and can hit to a certainty the stem of any given tree of some height, and half a foot in thickness, while they would almost always shoot over a hedge three feet high, or perhaps not reach it.
>
> Lichtenstein (1812:199)

> The bow itself is small and weak, nor, judging by their efforts to strike a hat which I once placed as a target, are they very extraordinary marksmen. They generally creep up within thirty yards before shooting at any creature.
>
> Mithune (1847:30)

> Besides the above method of capturing game the Bushman also uses the bow and arrows. This is a weapon in which he is greatly skilled; and although both bow and arrows are as tiny as if intended for children's toys, they are among the deadliest of weapons.

> [T]heir fatal effect lies not in the size of the wound they are capable of inflicting, but in the peculiar mode in which the barbs of the arrows are prepared. I need hardly add that they are dipped in poison;—for who has not heard of the poisoned arrows of the African Bushmen? Both bow and arrows are usually rude enough in their construction, and would appear but a trumpery affair, were it not for a knowledge of their effects.
>
> Reid (1866:24)

> Their bows are but toys, and their arrows only slender reeds. But they arm these apparently insignificant weapons with poison so potent, that even the brave and bellicose Kafir warrior does not like to fight a Bosjesman, though he be protected by his enormous shield.
>
> Wood (1877:63)

> The bow is a very insignificant affair, seldom much exceeding two feet in length when strung. Any stick seems to answer as a bow, provided that it will bend. It is not held perpendicularly, but horizontally, so that no very accurate aim can be taken. This, however, is of little consequence, as the range is very short, thirty yards being quite a long shot for a Bosjesman.
>
> Wood (1886:248)

> Ses armes, qui semblent insignifiantes, sont des plus redoutables: c'est un petit arc et de mignonnes flèches qu'on prendrait pour des joujoux d'enfant, mais qui portent un poison terrible dans le sang de l'ennemi, poison si foudroyant que celui-ci expire un instant après, quelles que soient sa taille et sa force. La portée de l'arc du Bushman n'excède pas quinze mètres: aussi que de ruse, que de savoir, que de patience il consomme pour ramper et se rapprocher insensiblement de la bête si méfiante dont l'ouïe en éveil perçoit les moindres bruits et dont l'oeil découvre les moindres détails à de grandes distances!
>
> Foà (1901:126)

> Their bows are very small and weak-looking, and their arrows are unfeathered, being made of light reeds into the ends of which bone heads are inserted.
>
> Selous (1908:341)

A particularly picturesque but remarkably accurate description of the feeble Bushman bow appeared anonymously in a literary magazine, *All the Year Round: A Weekly Journal,* founded and edited for many years by renowned author, Charles Dickens, and subsequently managed and edited by his son, Charles Dickens, Jr. Although the individual who actually penned the article is nowhere indicated in the magazine, it was almost certainly Frederick Boyle (1882:60), a worldwide traveler and writer, who reproduced the identical paragraph a year later in a curious collection of essays entitled *Legends of My Bungalow*.

> They [the Bushmen] use a little weak bow, a little arrow, and they shoot delicately. The wild beast roars and bounds with pain, but his wound is no more than skin deep. He tears out the slender reed, looks about him, roars again, and drinks quietly, for he credits that a thorn has pricked him.
>
> Dickens Jr (1881:34)

Not only are Bushman bows weak and ineffective, they use very slow-acting poisons that, according to Lee (1979:219), take "an average of 6–24 h or more to work." Thomas (2006:126) indicates that the poison may take even longer to achieve the desired effect: "the poison is the lethal factor, but the process is slow –

one to four days, more or less, largely depending on the size of the victim – during which time the injured party could inflict a tremendous amount of damage on its tormentors." As a result, Bushman hunters have to invest inordinate amounts of time tracking wounded animals across the landscape, animals that they frequently lose to other predators (e.g., Hitchcock and Bleed 1997:354; Liebenberg 2006:1022). More than 150 years ago, Henry Mithune (1847:26) noted this peculiar aspect of Bushman hunting, commenting that "it is astonishing to what a distance they will run in pursuit of the animal which has received the fatal arrow."

> The recovery rate for the ambush hunting activities was 88% and the mean number of man-days spent tracking wounded animals was 1.5. We suspect that this figure is high. The average recovery rate for animals shot with poisoned arrows by the Ju/'hoansi is closer to 50% due to the frequency with which predators and scavengers reach the animal before those trailing it do and the numbers of times that the animal evades its pursuers.
>
> Hitchcock et al. (1996:185)

> John Yellen estimates that perhaps as high a proportion as 50 percent of all the animals wounded by the !Kung are allowed to escape and are never eaten. They either recover from their wounds and survive or run so far away that the hunters decide not to pursue them. In the latter case, the animals die eventually and are eaten by the lions, hyenas, and vultures.
>
> Lee (1979:221)

Though less precise than the observations of trained anthropologists in the twentieth century, Lewis Leslie, a soldier attached to the South African Cape Cavalry in the early nineteenth century, nonetheless, makes a very insightful comment about the ineffectiveness of San arrow poison when used for hunting large and potentially dangerous prey:

> The Bushmen I have frequently seen practise with their bows, but I have very little faith in the correctness of their aim or the strength of their poison. The most authentic relations I could obtain of their shooting even the smallest species of the antelope, prove that the poison is not at all immediate in its effect; the wounded animal, with the barbed and poisoned arrow in his side, will bound along the plain, where he is traced by the Bushman's eagle eye until he staggers and falls when the poison has been absorbed. If such is the case with a weak and timid animal, what would it be with the powerful, bold, and fiery lion? destruction of the daring Bushman who would attempt to meet him. I am well aware that they assert their being able to kill the lion, but am confident it is for the purpose of imposing on the credulous boor to magnify the power of their favourite weapon. In nine months that we were encamped within a mile of a numerous craal of Bushmen, they appeared to live almost wholly on roots, locusts, and ants, and what they obtained from the neighbouring farmers, or from our station.
>
> Leslie (1833:64)

In other words, in stark contrast to Frison's perspective of what an economically motivated hunter must do in order to make ends meet, the San leave a great deal to chance, fail frequently, and invest a huge amount of time and effort doing so. This is hardly a strategy designed to maximize returns of calories, protein, or fat, nor is it an effective way to minimize time, or opportunity costs, unless the payoff lies in some domain other than food (e.g., Winterhalder 1996:48).

Interestingly, these conclusions were anticipated in the early 1990s by Dieter Noli in a difficult-to-find but very interesting dissertation on Bushman archery. While perhaps overstating his conclusions somewhat, Noli's arguments were based on a close look at Bushman bows and arrows housed in the South African Museum, as well as those described in ethnographies and traveler's accounts and depicted in local rock art. He also conducted archery experiments using replicated bows and arrows of different sizes, designs, materials, and draw weights. Based on the combined results of these various lines of evidence, Noli concludes that:

> …the Bushmen are inferior archers using inadequate equipment in a cruel and wasteful manner for an activity for which it was not intended, and which is irrelevant for their survival.
>
> Noli (1992:187)

> [The Bushman bow] was *not* a means of acquiring as much meat as possible in as little time as possible, as that would have led them to adopt the power bow. What they wanted was something which would require great skill, endurance and patience when used for hunting, and which would make the hunt as long as possible. These requirements have all the hallmarks of a recreation activity, indulged in mainly for non-economic benefits such as personal gratification and social prestige.
>
> Noli (1992:196), italics in original

The Bushman strategy becomes even more perplexing if one considers the number of years (actually, decades) that it takes a hunter to master the skills needed to successfully locate, pursue, and kill large game. According to Walker et al. (2002:639), hunters don't attain their peak level of performance until they are well into their thirties or even later, long after they pass their physical prime (see also Blurton Jones and Marlowe 2002; Gurven et al. 2006; MacDonald 2007).

> While many foraging activities may be complicated, hunting is potentially the most skill- and strength-intensive foraging activity. This is indicated by the fact that hunting return rates peak later in life than most other food acquisition activities. Hunting return rate curves peak in the early 30s for the Hiwi (Kaplan et al., 2000), 40 for the Machiguenga and Piro (Gurven & Kaplan, [2006]), early or mid-40s to mid-50s for the Etolo (Dwyer, 1983), 35-45 for the Gidra (Ohtsuka, 1989), 45-50 for the Hadza (Marlowe, 2000) and 37-42 for the Ache....

If, as Kristen Hawkes (2000:65) so aptly put it, "in the long run, big-game hunting is inferior to available alternative strategies for provisioning families," one has to wonder why hunters invest so much of their life, starting already as children, honing these particular skills?

## 5.3 Alternative Foods Available to the San

Thus, for our two classic African foragers, the Ju/'hoansi and the Hadza, big-game hunting does not appear to be an effective or reliable way to go about getting fat. Take away their capacity to render grease from bones by boiling, as would likely have been the case for early hominins, and African big game would be even less attractive. Moreover, both groups have much more reliable access to fat from sources other than big game, particularly from nuts (mongongo and baobab), although other plant foods, as well as small mammals, reptiles, birds and birds' eggs, and various insects, also provide fat, sometimes in bountiful quantities (e.g., termites and caterpillars; see Nonaka 1996:33–34).

Let us begin with a brief look at the nutritional value of some of the alternative foods that are available to the Ju/'hoansi. Through Richard Lee's (1968, 1973, 1979) seminal work among the San in the 1960s, we know that the Ju/'hoansi relied heavily on mongongo nuts (Fig. 5.3; also called manketti, mangetti, nongongo) (*Schinziophyton rautanenii* or often *Ricinodendron rautanenii*; see Graz 2002:19; Tchoundjeu et al. 2006:9). In the area where Lee did his field work, groves of mongongo trees were extremely productive in most years, and according to his input–output studies provided, on average, about 40% or more of the Ju/'hoansi's daily energy intake. The actual percentage varied seasonally from a low of about 10% in the late summer rainy season to as high as 90% in the fall and early winter (dry season) months when the fruits ripened and dropped to the ground (Büschel 2002:11, 30; Lee 1973:320; Peters 1987a, 1987b; Sih and Milton 1985:399).

Processing the mongongo is labor-intensive and takes a fair amount of skill (see Bock 2005:119–121), but return rates are substantial, especially during the major fall/early winter harvest season; at that time families often camp in or close to the groves in order to minimize transport costs (Büschel 2002:11, 30; Blurton Jones et al. 1994; Hawkes and O'Connell 1981; Lee 1968, 1973, 1979; Peters 1987a; Sih and Milton 1985). Mongongo nuts are available throughout much of the year, since considerable numbers remain edible long after they have fallen to the ground

**Fig. 5.3** Mongongo nuts (*Schinziophyton* or *Ricinodendron rautanenii*), one of the staple foods of the Ju/'hoansi (San) in the Kalahari Desert region of Southern Africa. ©Royal Botanic Gardens, Kew, UK. Media ID 1887057; filename "EBC_44489_050607AM002.jpg"

(Lee 1968, 1973; Keegan 1982). However, as groves close at hand are progressively harvested out, families have to visit more distant groves, increasing overall travel time and hence transport costs.

Mongongo nuts contain very high levels of fat (45–58 g/100 g) and are very rich in protein as well, averaging between 26 and 29 g/100 g (Chivandi et al. 2008:31; Lee 1973:311, 1979; Peters 1987a, 1987b:494; Saxon and Chidiamassamba 2005; Silberbauer 1981:274; Tanaka 1980:55–74; Wehmeyer et al. 1969; Yellen and Lee 1976:40–41). They also contain fairly high concentrations of polyunsaturated fatty acids, particularly linoleic (Chivandi et al. 2008; Engelter and Wehmeyer 1970; Peters 1987a:345; Wehmeyer 1971, 1986). Lee (1979:270) observed that Ju/'hoansi during the harvest season ate about 300 nuts per person per day, which according to Duke (2000:258) would contain "the caloric equivalent of 1,134 g of cooked rice and the protein equivalent of 396.9 g lean beef" (see also Lee 1968:33). In addition, Duke (2000:258), citing Adrian et al. (1955; see also Smith et al. 1959:136), provides information on the amino acid composition of mongongo nuts, which turns out to be quite respectable: 2.6% histidine, 4.1% cysteine, 7.9% isoleucine, 6.2% leucine, 5.1% lysine, 2.0% methionine, 4.6% phenylalanine, 7.9% threonine, 1.2% tryptophan, and 7.1% valine.

What is perhaps most intriguing about mongongos in the context of the present discussion is the fact that they are most abundant in the months of April, May, and June, precisely the months when the Ju/'hoansi also bring the most meat into camp (Fig. 5.4; see also Hitchcock et al. 1996:201). Tsin beans (originally *Bauhinia esculenta*, now

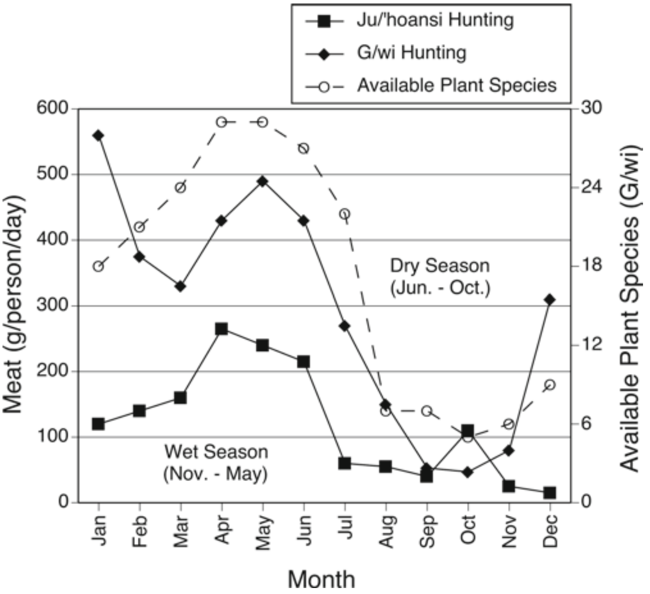

**Fig. 5.4** Seasonal changes in the average amount of meat (gram/person/day) available to Ju/'hoansi and G/wi San foragers. Adapted from Hitchcock et al. (1996:201, their Fig. 5)

*Tylosema esculentum*; see Castro et al. 2005:99), another very important source of protein and fat for many San groups, ripen at this same time of year (Figs. 5.5–5.7; Story 1958:25). In other words, Ju/'hoansi hunting activities peak at more or less

**Fig. 5.5** Tsin or marama (*Tylosema esculentum*) pods with unripe beans. ©Aase Solvej Hansen. The photograph is reproduced here by permission of Aase Solvej Hansen, Department of Food Science, Faculty of Life Sciences, University of Copenhagen, Denmark

**Fig. 5.6** Tsin or marama (*Tylosema esculentum*) beans (ripe). ©Aase Solvej Hansen. The photograph is reproduced here by permission of Aase Solvej Hansen, Department of Food Science, Faculty of Life Sciences, University of Copenhagen, Denmark

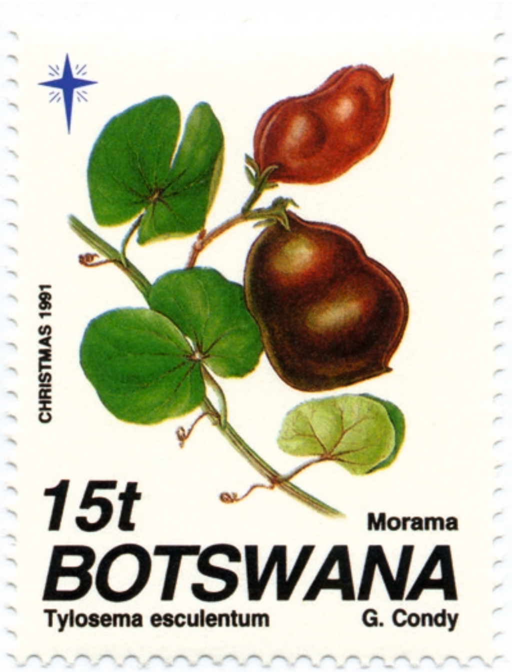

**Fig. 5.7** Tsin or marama plant and pods (*Tylosema esculentum*) illustrated on a 15-*thebe* Christmas stamp issued in 1991 by the Republic of Botswana. The original stamp is in the author's possession. The photograph was taken by Katherine Clahassey, Museum of Anthropology, University of Michigan, Ann Arbor, Michigan

the same time that the return rates from harvesting and processing mongongo nuts (and tsin beans) also peak (~1,300 kcal/h for the mongongo according to Sih and Milton 1985:399). If there were any time of the year when the Ju/'hoansi would *not* need to hunt large game for fat, or for that matter for protein, this would be it.

Figure 5.4 shows that the same pattern also holds for the G/wi, San foragers who occupy Botswana's arid Central Kalahari region (Silberbauer 1973, 1981). While the G/wi do not have mongongo nuts as a staple, the availability of other plant foods reaches its maximum during the rainy season, at more or less the same time that their hunting returns also peak, whether measured in grams of meat per person per day, as in the figure, or in total number of kills per month (for syntheses of Silberbauer's plant and animal data, arrayed by season, see Deacon and Deacon 1999:142, their Fig. 8.11, and Speth and Davis 1976:443, Table 2).

Thus, while not all San have access to mongongo nuts, most groups, like the G/wi, have alternative wild plant foods that serve as more or less comparable staples:

> …resources such as the mongongo nut, which in some months provides 70-80 percent of the diet in the /xai/xai area…, are completely absent in other *n!ores* 50 km to the west in the centre of the Nyae Nyae area and are not a staple food for any of the Nyae Nyae !Kung (Marshall, 1976). In this latter area the Tsin bean replaces the mongongo as a staple. In the N/umsi (Dobe)-/xai/xai areas, even adjacent *n!oresi* are known to specialize in resources at given times of the year, with some being known for mongongo nuts (*Ricinodendron rautanenii*), others for

> tsin beans (*Tylosema esculenta* [sic]), others for baobab fruits (*Adansonia digitata*), and so on, all of which are rich in protein, minerals and vitamins.
>
> Wiessner (1981:644)

Although Polly Wiessner emphasizes the protein content of these foods, as is so often the case in ethnographically oriented nutritional studies, tsin (marama or morama) beans (*Bauhinia esculenta* or *Tylosema esculentum*) and marula nuts (*Sclerocarya caffra* or *S. birrea* or sometimes *Poupartia birrea*), in particular, are not only high in protein (30–38% and 23–36%, respectively), they also are rich in fat (33–42% and 42–63%, respectively), making them extremely important staples (Amarteifio and Moholo 1998:331; Arnold et al. 1985; Bower et al. 1988; Burger et al. 1987; Eromosele and Eromosele 1993; Francis and Campbell 2003:9; Glew et al. 2004:105–107; Gouwakinnou et al. 2009; Jideani et al. 2009:1213; Keegan and Van Staden 1981; Keith and Renew 1975; Ketshajwang et al. 1998; Mmonatau 2005; Mojeremane and Tshwenyane 2004; Monaghan and Halloran 1996; Ojewole et al. 2010; Powell 1987; Tanaka 1980:71; Thiong'o et al. 2002:242; Wehmeyer 1971, 1986; Wehmeyer et al. 1969:1529–1530; Weinert et al. 1990; Yellen and Lee 1976:40–41).

The tsin bean deserves particular note because of its considerable nutritional value. Not only is it high in protein, but its protein quality is excellent as well, and the fat provides essential fatty acids, including approximately 19–23% linoleic acid and 2.0–2.7% α-linolenic acid (Bower et al. 1988:535; Francis and Campbell 2003:9).

> Protein quality of marama bean seeds, i.e., essential amino acid composition, is slightly better than that for soybeans and is comparable to that of casein or milk protein…. The oils of marama beans are reported to contain 31% unsaturated fatty acids…. Strong trypsin inhibition is found in raw seeds, but this negative nutritional factor is averted by cooking them.
>
> Powell (1987:217)

The Tyua San in northern Botswana provide another interesting case in which the timing of big-game hunting coincides quite closely with the peak production of other more reliable and productive foods. And again these are foods that are rich in fat as well as protein. The principal large-game species hunted by Tyua are kudu and wildebeest, with most kills, according to Hitchcock (1988), occurring in the rainy season, particularly in January and February. The wet season is also the time when nutrient-dense marama beans become available. But the Tyua have another extremely important resource as well, in this case an insect, the mopane worm (also called phane, mophane, madora, and in some of the earlier literature lopane), that becomes available at this same time of year, and often in prodigious quantities (generally classified as *Imbrasia belina* or *Gonimbrasia belina* but occasionally also as *Acanthocampa belina*; Glew et al. 1999; Ohiokpehai 2006).

> Informants told me that they intentionally ate large amounts of food that was high in fats and oils during the wet season in order to build up body fat and add weight. They did this, they said, because work requirements in the dry season were high and because the variety of plants and animals that they could depend on was low. Special emphasis was placed on insects, in part because of their high fat content. There were sometimes outbreaks of

> termites and flying ants during the rainy season, and people concentrated their efforts on them, capturing and consuming large amounts in short time periods. Another important food item in the Nata area was the *mopane* worm (*Gonimbrasia belina*). These worms, which are between 5 and 10 cm long, appear twice a year, first in about December and then again in March or April. During the summer [December], groups would camp in belts of *mopane* forest for as long as three to four weeks, subsisting almost entirely on caterpillars.
>
> Hitchcock (1988:73)

The mopane "worm" is actually the instar or larval stage (caterpillar) of the Emperor moth (Fig. 5.8). Normally, there are two "outbreaks" or generations of caterpillars each year, the principal one occurring in the early months of the rainy season between November or December and January, and a second more minor one between March or April and May (Ditlhogo 1996; Frears et al. 1997; Gaston et al. 1997:22; Morris 2004:83; Stack et al. 2003; Styles 1996). In Namibia, however, there is only a single generation, which becomes available in March and April (Marais 1996). Mopane worms are highly prized in southern Africa, and have become the focus of a thriving commercial industry, both as a much sought-after delicacy for human consumption and for use as a feed for livestock (Illgner and Nel 2000; Quin 1959). According to Ekpo et al. (2008:8), "thousands of tons of *Imbracia* [sic] *belina* larvae are eaten by people in Africa. Almost all known

**Fig. 5.8** Mopane "worms" (Emperor moth caterpillars or larvae; *Imbrasia* or *Gonimbrasia belina*) feeding on leaves of the mopane tree (*Colophospermum mopane*). Photograph taken in Botswana. ©Anthony Bannister/NHPA/Photoshot. Filename "ZB980_TBA004266A.jpg"

cooking techniques have been tried on the larvae. It can be eaten fried, dried, raw grilled and boiled." In fact, their importance in Southern Africa is such that the Republic of Botswana, in 2000, inaugurated a series of five *pula* (meaning "rain") coins with the mopane worm shown on the reverse (see Fig. 5.9; Gewald 2001:557; Morris 2004:84).

Given their economic importance, it is not surprising that mopane worms have been the subject of an array of nutritional studies. While most of these have emphasized the caterpillar's high (crude) protein content, which typically falls between about 48 and 62%, mopane worms are also rich sources of fat (average 15–19%), with unsaturated fatty acids making up as much as 65% of the fat, and the omega-3 fatty acid, α-linolenic, comprising around 30% (Dreyer and Wehmeyer 1982; Headings and Rahnema 2002, 2007; Madibela et al. 2007, 2009; Motshegwe et al. 1998; Ohiokpehai 2006; Onigbinde and Adamolekun 1998; Pharithi et al. 2004; Quin 1959; Sekhwela 1989; Yeboah and Mitei 2009; Zinzombe and George 1994). In terms of total energy, mopane worms provide about 450 kcal/100 g (Illgner and Nel 2000:346–347). Dreyer and Wehmeyer (1982) discuss the digestibility and assimilability of mopane protein and conclude that it compares favorably with protein from other sources:

> ...a major advantage of the moisture-free mopanie caterpillar products is their high protein content. In comparison with the protein from the other products of animal origin, digestibility of this protein was found to be relatively low. However, the above weakness was compensated for to a considerable degree by an assimilability index which compares favourably with those of the high-class products such as casein and beef. The net effect of the digestibility and assimilability, as given by the NPU [net protein utilization] values, is such that, quality-wise, the mopanie product protein occupies a position well above the midpoint between the bottom end (gluten, 27%) and the uppermost point on the scale of natural proteins as exemplified by whole hen's egg protein (85%).
>
> Dreyer and Wehmeyer (1982:35)

**Fig. 5.9** Five *pula* (meaning "rain") coin, issued by the Republic of Botswana in 2007, showing the mopane worm on the reverse side. The original coin is in the author's possession. The photograph was taken by Katherine Clahassey, Museum of Anthropology, University of Michigan, Ann Arbor, Michigan

Thus, it would appear that Bushman groups throughout the Kalahari have access to a number of nutrient-dense and often quite abundant plant (e.g., Tanaka 1982:3), animal, and insect resources that become available at more or less the same time of year that they undertake much of their big-game hunting. This intriguing temporal convergence raises the possibility that the San hunt these animals for reasons other than fat or protein. *Perhaps, instead, it is precisely because of the reliability and high fat and protein content of mongongos, baobabs, tsin beans, marula nuts, mopane worms, and others that Bushman hunters are able to afford the "luxury" of engaging in such a time-consuming, failure-prone, and costly activity* (see also Wilmsen 1982:105, 108). In other words, an explanation for their hunting behavior may well lie beyond the strictly nutritional realm.

I should interject a word of explanation here, lest my intent be seen to imply something quite unintended. By talking about an abundance of nutrient-dense resources, such as mongongos, baobabs, or mopane worms, I am not trying to resurrect the once popular but now long-outmoded notion of an "original affluent society," as eloquently and persuasively put forth many years ago by Marshall Sahlins (1968):

> If economics is the dismal science, the study of hunting-gathering economies must be its most advanced branch. Almost totally committed to the argument that life was hard in the Paleolithic, our textbooks compete to convey a sense of impending doom, leaving the student to wonder not only how hunters managed to make a living, but whether, after all, this was living? The specter of starvation stalks the stalker in these pages. His technical incompetence is said to enjoin continuous work just to survive, leaving him without respite from the food quest and without the leisure to "build culture." Even so, for his efforts he pulls the lowest grades in thermo-dynamics—less energy harnessed per capita per year than any other mode of production. And in treatises on economic development, he is condemned to play the role of bad example, the so-called subsistence economy. It will be extremely difficult to correct this traditional wisdom. Perhaps then we should phrase the necessary revisions in the most shocking terms possible: that this was, when you come to think of it, the original affluent society.
>
> Sahlins (1968:85)

There is ample evidence that calorie intakes for Kalahari hunter–gatherers were often marginal, particularly during the long dry season, and that seemingly inexhaustible staples like the mongongo might in some years fail utterly (Hitchcock 1986; Hitchcock et al. 1989; Howell 1986; Truswell and Hansen 1976; Wiessner 2002:415–416; Wilmsen 1978, 1982; Wilmsen and Durham 1988). Drought is the most obvious cause of such shortfalls and failures, but unusual storms can also have devastating effects. Droughts not only reduce or eliminate critical plant resources relied upon by hunter–gatherers, they may also reduce the amount and quality of forage available to larger game, reducing their body condition and rendering them even less attractive as sources of fat (e.g., Mduma et al. 1999; Spinage and Matlhare 1992).

> African herbivores typically gain weight and accumulate stores of both fat and muscle during the wet season, and these are gradually depleted as the dry season progresses. This decline of condition is associated with increased mortality. In addition, interannual mortality often is highly episodic, concentrated in years of extended dry seasons.
>
> McNaughton and Georgiadis (1986:54)

The impressive gorging of meat by San that occurs under such circumstances is almost certainly a sign of serious stress, not plenty or "affluence":

> For example, figures from 17 months of subsistence studies between 1996 and 1998 in the Nyae Nyae area show that during two "hungry months" when food was scarce, large kills provided more than 80% of the diet....
>
> Wiessner (2002:416)

## 5.4 Alternative Foods Available to the Hadza

Now let us shift our focus to the Hadza in Tanzania. For these East African foragers baobab fruits and seeds (*Adansonia digitata*) assume much the same role that mongongo nuts do for the Ju/'hoansi (Figs. 5.10–5.13). Baobab seeds contain almost 30% fat by dry weight, up to a third of which is linoleic acid, and a similar or even

**Fig. 5.10** Baobab tree (*Adansonia digitata*), a reliable source of nutrient-rich fruit pods and seeds for Hadza foragers in Tanzania. ©Royal Botanic Gardens, Kew, UK. Media ID 1887049; filename "EXP_MALI-03-119.jpg"

**Fig. 5.11** "Baobab fruit pods." Photograph taken July 1986 (early dry season) by James F. O'Connell, at south end of Eyasi Basin, northern Tanzania. Adult Hadza man collects fruit pods knocked from a tree and bundles them for carrying back to camp. ©James F. O'Connell. The photograph is reproduced here by permission of James F. O'Connell, Department of Anthropology, University of Utah, Salt Lake City, Utah

**Fig. 5.12** Partially opened Baobab fruit pod. ©Anthony Hall/Dreamstime.com. The photograph is reproduced here under "royalty free license" from Dreamstime LLC, Brentwood, Tennessee

higher concentration of protein (up to 36%). The raw pulp, which contains surprisingly little moisture for a ripe fruit, is rich in carbohydrate (80% by dry weight), and has high levels of several B vitamins, vitamin C, calcium, and iron (Addy and Eteshola 1984; Amarteifio and Mosase 2006; Boukari et al. 2001; Chadare et al. 2009; Cisse et al. 2009; Crittenden et al. 2009; De Caluwé et al. 2009a, 2009b;

**Fig. 5.13** Baobab (*Adansonia digitata*) seeds. Photograph taken in Kenya in 2009 by Spencer Woodard. ©Spencer Woodard. The photograph is reproduced here by permission of Spencer Woodard, Mill Valley, California (http://www.anthrome.wordpress.com)

Engelter and Wehmeyer 1970; Eteshola and Oraedu 1996; Ezeagu et al. 1998; Gebauer et al. 2002; Glew et al. 1997; Manfredini et al. 2002; Murray et al. 2001; National Research Council 2008; Nour et al. 1980; Odetokun 1996; Osman 2004; Prentice et al. 1993; Sena et al. 1998; Sidibe and Williams 2002; Vertuani et al. 2002; Wehmeyer 1971; Yellen and Lee 1976:40–41). According to Murray et al. (2001:9), baobab seeds in fact yield about the same amount of energy per 100 g dry weight as honey.

One of the surprising aspects of baobab seeds is their protein content – they contain substantially more protein than agricultural plants like sorghum (11.4%), millet (11.9%), and manioc (0.9%) (data from Murray et al. 2001, but see also Gross 1975 and Leung 1968 for additional values). Moreover, the amino acid profile of the protein is better than in most of the local crops, with the exception of beans, and is especially noteworthy for its high amount of lysine (De Caluwé et al. 2009b:62). Even the fruit pulp may at times contain a fair amount of protein (a few studies report concentrations as high as 5%; Murray et al. 2001:10; National Research Council 2008; but see Amarteifio and Mosase 2006).

Thus, baobab fruit pulp and seeds together provide a substantial and highly reliable source of fat, protein, and carbohydrate. The fruits ripen during the late dry season and/or early wet season, but remain edible for several months after they form (Marlowe 2006: 363; National Research Council 2008:50, 57). According to Murray et al. (2001:12), Hadza "women consistently returned with dozens of baobab fruits or with significant quantities of seeds over the majority of months of the year either through direct fruit collection or through collection of seeds in baboon dung piles."

How does Hadza hunting covary with baobab availability? The Hadza engage in two principal types of hunting – intercept hunting at night from blinds during the late dry season when animals are concentrated close to major waterholes, and daytime encounter hunting which occurs throughout the year whenever hunters are out of camp. Curiously, despite their much more powerful bows, the Hadza, like the San, rely on slow-acting poison (which O'Brien 1994:90 suggests may in fact be of dubious reliability) and frequently have to track their prey for several hours or longer after they have been wounded (O'Connell et al. 1992; Hawkes et al. 1991, 2001). In the studies conducted by Kristen Hawkes and colleagues in the mid-to-late 1980s, the Hadza made 52 kills just in the last 3 months of the dry season – August, September, and October – compared to a total of only 19 kills during the remaining seasons (O'Connell et al. 1992:320–321). And the late dry season is precisely when the baobabs come into fruit. It is therefore tempting to conclude that Hadza big-game hunting, like Bushman big-game hunting, was only possible *because* it was underwritten by the availability of other productive, dependable, and cost-effective food sources. With baobabs, mongongos, tsin beans, marula nuts, and mopane worms as staples, the Hadza and Ju/'hoansi certainly don't need to hunt big game for either protein or fat. And in the Hadza case the late dry season also happens to be the worst possible time of year to pursue African ungulates for fat.

# Chapter 6
# Protein and Pregnancy

> *In 1980, the publication of the results of a controlled, randomized, partially double-blind trial of prenatal nutritional supplementation in low income pregnant women in New York City indicated the need for a reassessment of the role of dietary protein during pregnancy. That study found a 73 gram decrement (n.s.) in the mean birth weight of infants whose mothers received a high protein, high energy supplement compared to those who received a low protein, moderate energy supplement. Reviews of other prospective, controlled studies of women with sufficient energy intake showed consistent deficits in infant birth weight associated with high levels of dietary or supplemental protein.*
>
> Sloan et al. (2001:130)

From the 1950s to the 1970s, during the heyday of the "great protein fiasco," public health officials, concerned about health and nutrition in America's urban ghettos, routinely recommended high-protein supplements, sometimes together with restricted calorie intakes, for undernourished pregnant women in order to improve birth outcome (i.e., birth weight, perinatal mortality and morbidity, and cognitive development). Such programs went on for years with few systematic attempts to evaluate their effectiveness or consequences.

Not until the late 1970s did nutritionists begin to examine retrospectively the results of these programs, finding that in many cases the benefits proved to have been negligible and at times even the opposite of what had been anticipated (Campbell et al. 1996; Campbell-Brown et al. 1986; Kramer and Kakuma 2003; Merialdi et al. 2003; Pereira et al. 1982; Rush 1982, 1986, 1989, 2001; Rush et al. 1980; Sloan 1985; Sloan et al. 2001; Stein et al. 1979). In terms of the present discussion, perhaps the most interesting finding of these studies was that when protein supplements exceeded about 20% of total energy, their impact on birth outcome was decidedly negative (Rush 2001:S248; see also Sloan et al. 2001; Axelsson 2006):

> There is repeated and consistent evidence that high-density protein supplements (those in which protein supplies over 20% of energy) are toxic: birth weights are consistently lower than those among unsupplemented women. This may be mediated by the anorectic effect of high-density protein, since, typically, maternal weight gains are also lowered. As this review goes to press, another confirmation of this finding by Sloan et al. has been published in Nutrition Research 2001:129–139.

J.D. Speth, *The Paleoanthropology and Archaeology of Big-Game Hunting*,
Interdisciplinary Contributions to Archaeology, DOI 10.1007/978-1-4419-6733-6_6,

Recent research on infertility in both animals (cattle, sheep, pigs, and rodents) and humans is providing intriguing insights into at least one aspect of protein's potentially deleterious effects on pregnancy outcome. These studies show that high-protein maternal diets (or amino-acid-enriched culture media used for in vitro fertilization) can become toxic through the buildup of ammonia that ultimately reduces the viability of the developing blastocyst and embryo and compromises fertility (e.g., Gardner and Lane 2005; Gardner et al. 2004:190; Meza-Herrera et al. 2006; Lane and Gardner 2003, 2005; Thompson et al. 2006; Zander et al. 2006; see also Chavarro et al. 2008).

> These data show that consumption of a high protein [25%] diet results in the excess accumulation of ammonium in the fluid of the female reproductive tract of mice. These high levels of ammonium subsequently impair the formation of the fetal progenitor cells and increase cell death at the blastocyst stage. These data from in vivo-developed mouse blastocysts are similar to those for blastocysts developed in culture in the presence of 300 μM ammonium. Therefore, it is not advisable to maintain mice on a high protein diet. These data have significant implications for animal breeding, and for patients attempting IVF treatment.
>
> Gardner et al. (2004:190)

> …amino acid inclusion, especially that of glutamine, significantly increases the level of ammonia within embryo culture media systems. It was shown that the benefits of amino acid addition could be annulled by the effect of ammonia build-up, partly from degradation of glutamine over the course of embryo culture, and partly as a result of deamination of amino acids during metabolism. Early embryos appear to be sensitive to levels of ammonia as low as 100 μM and levels above 300 μM yield significant detrimental effects.
>
> (Thompson et al. (2006:62)

If elevated protein intakes can be deleterious to pregnant women, how much *meat* can they securely afford to eat on a daily basis? For hunter-gatherers consuming a diet that provides 2,500 kcal per day, the safe upper limit for pregnant women (~20%) would amount to about 500 kcal or about 125 g of protein per day, considerably less than the limit (183 g) noted earlier for a 50 kg forager.

One of the striking features of both the ethnographic and medical/health science literature about food taboos and food aversions in pregnancy is how commonly meat tops the list (Fessler and Navarrete 2003; Flaxman and Sherman 2000; Spielmann 1989).

> Pregnant women most often reported aversions to "meat, fish, poultry, and eggs." Per capita aversions to these animal products (0.28/woman) were nearly double those of the second most aversive food category, "nonalcoholic beverages" (0.16 aversions/woman), and more than triple the aversions to "vegetables" (0.08/woman). Per capita aversions to "alcoholic beverages" and "ethnic, strong and spicy foods" were only 0.04/woman, and aversions to "dairy and ice cream," and "sweets, desserts, and chocolate" were even less frequent. Aversions to "grains and starches" and "fruit and fruit juice" were very rare (<0.02/woman).
>
> Flaxman and Sherman (2000:125)

While there are alternative explanations for why meat is so often tabooed or avoided by pregnant women, such as the likelihood that meat may harbor dangerous pathogens or teratogenic substances that can interfere with embryonic development (e.g., Fessler 2001; Flaxman and Sherman 2000; Profet 1988, 1992; Sherman and Flaxman 2002; Speth 1990), problems for both mother and fetus posed by intakes of protein in excess of about 20% of calories may be a critical dimension that anthropologists have not yet adequately considered.

Perhaps not surprisingly, elevated protein concentrations may not only be toxic to pregnant mothers, leading to premature births and low-birth-weight newborns, but if protein is then fed to such infants at concentrations exceeding the extremely low values found in human breast milk (see discussion below), the short- and long-term health consequences for the infant can be very serious indeed (Goldman et al. 1974:764; see also Axelsson 2006; Goldman et al. 1969; Jackson 1999):

> A follow-up study was carried out on 304 infants of birth weight below 2000 gm. While in the premature nursery these infants were randomly assigned to either a 2% or a 4% protein diet in amounts to provide either 3.0-3.6 or 6.0-7.2 gm/kg/day of protein. Approximately 80% of the infants were recalled for pediatric, psychometric, and ophthalmologic evaluation at 3 and 5-7 years of age. The incidence of medical, surgical, and neurologic sequelae was approximately equal in both diet groups. However, in the group which had received the 4% protein diet, a significantly increased incidence of low IQ scores was found in infants of birth weight below 1,300 gm and a significantly increased incidence of strabismus in infants of birth weight below 1,700 gm. These data suggest that intakes of cow's milk protein in excess of 6 gm/kg/day should not be used for low-birth-weight infants.

Finally, high maternal protein intakes during pregnancy may impact the health and well-being of the offspring later in life, regardless of whether or not the offspring was a low-birth-weight baby, through a process known as "fetal programming" (Daenzer et al. 2002; Hermanussen and Tresguerres 2008; Herrick et al. 2003; Koletzko 2006; Metges 2005; Rolland-Cachera et al. 2006; Samaras and Elrick 2005). The poor in utero environment arising from maternal under- or over-nutrition can significantly increase the susceptibility of the offspring later in life, perhaps in a sex-dependent manner (Thöne-Reineke et al. 2006), to high blood pressure, obesity, cardiovascular disease, and diabetes, a cluster of diseases often referred to as the "metabolic syndrome."

> There is increasing evidence that raised blood pressure and related conditions, including glucose intolerance and the metabolic syndrome, may originate from adverse influences during intrauterine life that lead to permanent alterations in fetal structure and physiology. This process is known as fetal programming. Although the hypothesis originated in studies showing associations between low birthweight and these conditions in adult life, more recent studies suggest that fetal programming may occur in the absence of changes in fetal size. Recent research therefore has sought to identify the nature of the adverse maternal influences that raise blood pressure and alter levels of cardiovascular risk factors in the offspring.
>
> Herrick et al. (2003:3554)

Specifically with regard to maternal protein intake during pregnancy, Herrick et al. (2003) conclude that their:

> …findings provide the first human evidence that an unbalanced high-meat/fish, low-green-vegetable diet during pregnancy may present a metabolic stress to the mother and program the HPA [hypothalamic-pituitary-adrenal] axis of the offspring, leading to lifelong hypercortisolemia.
>
> Herrick et al. (2003:3560)

Reynolds et al. (2007) also report long-term detrimental consequences for the health of offspring resulting from a maternal diet high in protein during the latter half of pregnancy:

> Salivary cortisol concentrations were measured during a modified Trier Social Stress Test in 70 men and women aged 36.3 yr whose mothers had taken part in a dietary intervention in which they were advised to eat 1 pound (0.45 kg) of red meat daily during pregnancy and to avoid carbohydrate-rich foods.
>
> Reynolds et al. (2007:2208)

> The offspring of women who reported greater consumption of meat and fish in the second half of pregnancy had higher cortisol concentrations during the Trier Test. Compared with the offspring of mothers who had reported eating no more than 13 meat/fish portions per week, the average cortisol concentrations were raised by 22%…and 46%…in the offspring of those eating 14-16 and at least 17 portions per week, respectively.
>
> Reynolds et al. (2007:2208)

And perhaps not surprisingly, high-protein intakes may continue to have detrimental effects when fed to infants during and following the period when they transition from breastfeeding to a diet-based wholly on family foods:

> To our knowledge, this is the first study to indicate that early protein intakes are associated not only with a higher BMI [body mass index] but also with a higher %BF [body fat] in mid-childhood. As suggested by our results, a high protein intake at 12 mo of age may be unfavorably related to later adiposity if high protein intakes are maintained throughout the second year of life….
>
> Günther et al. (2007:1631)

# Chapter 7
# Other Problems with High-Protein Intakes

> *Defining optimal intakes of protein in the human diet requires indicators of adequacy which are unequivocal and quantifiable, and it is clear that progress in identifying such indicators is painfully slow.*
>
> Millward (1999b:411)

## 7.1 Water Balance

There are at least four other problems associated with diets high in protein that are worth noting here. The first of these concerns water consumption. As already alluded to, high-protein intakes step up the rate of urea synthesis and excretion, a process that may necessitate an increase in water intake (e.g., Bankir et al. 1996; Bankir and Kriz 1995; Denke 2001; Jackson 1999; but see Luft et al. 1983:605; and Martin et al. 2006 for a contrasting view). The impact of high-protein intakes on water requirements and renal function, like so many other issues in nutrition, still remains controversial (Lowery and Devia 2009). Experiments vary in the amount of protein ingested, the duration of the studies, the age and sex of the participants, and even the mix of proteins from animal versus vegetable sources (e.g., Bernstein et al. 2007:648). And, perhaps not surprisingly, there are differences between the conclusions drawn by medical and nutrition science researchers and the first-hand experience of explorers and ethnographers living among, and observing, hunters and gatherers.

> Their high-protein diet imposed on Eskimos a need to dispose of an unusually large metabolic load of urea, a potentially toxic nitrogenous compound formed during the conversion of amino acids to glucose. Animals fed high-protein diets exhibit diuresis and an increase in water consumption, and it is of interest that early explorers commented on the high water intake of Eskimos.
>
> Draper (1977:312)

In many habitats occupied by foraging peoples, water was so ubiquitous and abundant that it hardly would have posed a problem. However, in the semi-arid habitats

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of Plio-Pleistocene eastern and southern Africa, water may have been seasonally scarce and patchily distributed. If so, it may have become an increasingly important constraint for early hominins as they incorporated greater quantities of animal protein into their diet.

## 7.2 Calcium

The second problem concerns the relationship between protein intake and calcium balance. Numerous studies in the past have shown that as protein intake increases, calcium from bone is increasingly mobilized to buffer the acid that results from metabolism of the protein (e.g., Barzel and Massey 1998; Hegsted and Linkswiler 1981; Johnson et al. 1970; Linkswiler 1976; Massey 2003; Sellmeyer et al. 2001; Walker and Linkswiler 1972; see also Mazess and Mather 1974). While various plant foods can lessen the calcium loss, high-protein diets can lead to excretion of substantial amounts of calcium in the urine.

A spate of newer research, summarized in recent papers by Cordain (2007), Heaney and Layman (2008), and Conigrave et al. (2008), is beginning to question this once seemingly well-established relationship, however, showing instead that elevated protein intakes may not lead to the serious calcium imbalance that earlier research had claimed (Arjmandi et al. 2003; Dawson-Hughes et al. 2004; Kerstetter et al. 2005, 2006; Pannemans et al. 1997; Roughead et al. 2003; Spencer et al. 1978). Thus, Pannemans et al. (1997:728), in a detailed study of calcium balance in two different age groups, found that:

> ...there were no differences between the two age groups with respect to the interaction between protein intake and Ca excretion, absorption and balance. Moreover urinary Ca excretion was increased in young and elderly subjects (whole group) when changing from 12 to 21 % total energy as protein. This increase in Ca excretion in urine was compensated by an increased apparent Ca absorption (whole group). For the elderly this resulted in a less negative Ca balance during the higher protein intake whereas for the young adults there was no effect of protein intake on Ca balance.... It can be concluded that the present study confirms the hypercalciuretic effects of dietary protein but does not support the view that an increased protein intake has adverse effects on Ca balance, either in young or in elderly people.

In a more recent study, Kerstetter et al. (2005:26) come to similar conclusions, again finding that elevated protein intakes do not seem to negatively impact bone calcium:

> The high-protein diet caused a significant reduction in the fraction of urinary calcium of bone origin and a nonsignificant trend toward a reduction in the rate of bone turnover. There were no protein-induced effects on net bone balance. These data directly demonstrate that, at least in the short term, high-protein diets are not detrimental to bone.

Interestingly, Iwaniec (1997; see also Cho and Stout 2003:214), in a study that compared histological patterns evident in bones of Inuit and Southwestern (U.S.)

Pueblo Indians, groups that traditionally had vastly different average protein intakes, failed to find convincing differences between the two samples that could be attributed confidently to the level of protein in their diet:

> …since significant differences between Inuits and Pueblo agriculturists were detected in females only, a dietary hypothesis based on differential protein intake is not concordant with the human data, as both Inuit males and females consumed high protein, high acid diets. Based on the histomorphometric pattern observed and the sex and age groups affected, it is proposed that the effects of pregnancy and lactation in association with the probable fluctuations in food availability and variables associated with the Inuit diet best account for the observed variation in cortical bone remodeling patterns.
>
> Iwaniec (1997:159)

Thus, what in older research seemed like a fairly clear-cut detrimental consequence of consuming high-protein diets may turn out not to have a negative impact on calcium balance. Ongoing research should clarify this issue.

## 7.3 Specific Dynamic Action

The third problem stems from the rise in metabolism that accompanies the ingestion of food (Barnes 1976:12–13; Bigwood 1972:xxii; Briggs and Calloway 1979:32; Brundin and Wahren 1994; Chaney and Ross 1971:45; Guthrie 1975:94–95; Houssay et al. 1955:455–456; Johnston et al. 2002; Rothwell and Stock 1979; Taylor and Pye 1966:39–40). This increase in metabolic costs is often referred to as the specific dynamic action (SDA) of food, or diet-induced thermogenesis (DIT), which Secor (2009) characterizes as "...the accumulated energy expended (or heat produced) from the ingestion, digestion, absorption, and assimilation of a meal...." The SDA of a diet that consists largely of fat is about 0–3%, while that of a diet high in carbohydrates is about 5–10% (Snodgrass and Leonard 2009:226). In striking contrast, the SDA of a diet that consists largely of protein may be as high as 20–30%, or higher (Crovetti et al. 1998; Snodgrass and Leonard 2009:226; Tappy 1996; Westerterp-Plantenga et al. 2006:S18). The SDA of protein varies with source (plant vs. animal), timing of ingestion, other foods ingested at the same time, rate of digestion, and amino acid composition, such that animal protein produces a higher thermogenic response than an equivalent amount of protein from plant sources (Bos et al. 2003; Dangin et al. 2001, 2002; Fouillet et al. 2008; Mikkelsen et al. 2000; Secor 2009; Tessari et al. 2003; Veldhorst et al. 2008; Westerterp-Plantenga 2008; Westerterp-Plantenga et al. 2006:S21).

The branched-chain amino acids (BCAA), leucine, isoleucine, and valine, which are far more abundant in meat, fish, and eggs than in most plant foods (Cordain and Friel 2005:4–5, 53, their Table 4.1), may play a key role both in the degree of assimilation and in the high thermogenic response produced by the ingestion of animal protein (e.g., Anthony et al. 1999; Donato et al. 2006; Dreyer et al. 2008; Kimball and Jefferson 2006; Manninen 2006; McCue et al. 2005;

Shimomura et al. 2004; Tsujinaka et al. 1996; Tipton and Wolfe 2004; Yamaoka 2008; Zhang et al. 2007), a phenomenon that is now even exploited in order to elevate core body temperature in patients undergoing surgery:

> The present study...demonstrated that the inhibitory effect of AAs [amino acids] on hypothermia during surgery was affected by the composition of the AA mixture and suggested that branched AAs are necessary, but do not solely prevent hypothermia.
>
> Yamaoka (2008:311)

DIT has an important bearing on the efficiency of protein as a source of energy. For every 100 calories of protein ingested, up to 30 additional calories are needed to compensate for the increased metabolic costs. Thus, persons who consume a diet that is high in animal protein experience higher metabolic costs than those whose diet is composed primarily of carbohydrates or fat, or protein from vegetable sources (Pannemans et al. 1998:68; see van Milgen 2002 and Westerterp-Plantenga et al. 2006:S18, for an alternative way of expressing the metabolic efficiency of macronutrients in terms of the cost of ATP synthesis). For example, members of Eskimo populations, at least 90% of whose caloric needs were traditionally met by meat and fat (Draper 1980:263; Høygaard 1941), had basal metabolic rates 13–33% above the so-called DuBois standard, which is based on the metabolic rates of populations consuming western diets (Itoh 1980:285). Stefansson and a colleague experienced similar rises in metabolism when they subsisted for an entire year on an all-meat diet. When their intake was only lean meat (ca. 3% fat), the increase in their metabolic rate varied from 14.6 to 25.0% above basal levels, with one test yielding an increase of over 45%. When they subsisted on a diet that was similar in composition to traditional pemmican, in which fat provided about 75% of the calories, the SDA ranged from 8.6 to 22.3% (McClellan et al. 1931; McClellan and DuBois 1930; see also Snodgrass and Leonard 2009:226; Rodahl 1952). Thus, in comparison to diets rich in carbohydrates or fat, a high-protein diet is a comparatively inefficient source of energy, obviously a key factor in the popularity of contemporary protein-rich dieting regimes, but not ideal for hunter-gatherers who can ill-afford to lose weight (Johnston et al. 2002). The high SDA of animal protein needs to be factored into models that see meat as the principal "high-quality" food underwriting the dramatic increase in early hominin brain size. In fact, the SDA of animal protein would have been highest at that stage in our evolution, because raw meat is much tougher and energetically more costly to ingest and digest than cooked meat (see Boback et al. 2007; see also Murakami et al. 2007; Oka et al. 2003; Wrangham 2009).

## 7.4 Core Body Temperature

Finally, high-protein intakes not only elevate SDA or DIT, they also increase core body temperature. In studies by Brundin and Wahren (1994) and Johnston et al. (2002), body temperature increased significantly following ingestion of protein.

And, as already noted, BCAA, which are particularly abundant in animal protein, may play a key role in the production of body heat (Yamaoka 2008:311). Added heat of this sort, together with elevated water needs that accompany a diet high in protein, while of little or no consequence to hunter-gatherers in temperate or northern latitudes, would likely compound the nutritional problems confronting early hominins subsisting on large quantities of meat and plant protein in the hot, semi-arid habitats of Plio-Pleistocene eastern and southern Africa.

# Chapter 8
# Protein and Taste

*…raw meat has little flavor and only a blood-like taste…*

Shahidi (1989:188)

If the high-quality protein that meat yields up to the successful hunter or scavenger were the "nutrient among nutrients" in our evolutionary climb to modernity, one might reasonably assume that we should have developed some clear-cut, hardwired taste for it. Curious, then, that study after study characterizes uncooked fresh meat as essentially tasteless (Bender and Ballance 1961; Calkins and Hodgen 2007; Cambero et al. 2000; Crocker 1948; Cross et al. 1986; Farmer 1994; Geay et al. 2001:12; Landmann and Batzer 1966; Macleod and Ames 1986; Mottram 1998; Mottram et al. 2004; Ramarathnam et al. 1991; Rhee 1989; Shahidi et al. 1986; Stetzer et al. 2008; Wang et al. 1996; see also Hart and Sussman 2008:228). One of the first scientific studies to demonstrate the tasteless character of fresh raw meat was published over half a century ago by Crocker (1948:180):

> a piece of raw beef chuck of good quality, with pH of 6, was trimmed of fat and examined for odor and taste after various treatments. While cold, it had only a weak odor of blood or serum type, strongest where there was obvious blood. The taste was also weak, sweetish, salty, and generally blood-like.

Crocker's characterization is echoed in countless subsequent studies. Two recent examples will suffice. Coggins (2007:92) describes the flavor of uncooked meat as "bloodlike and metallic." Mottram et al. (2004:463–464) (see also Mottram 2007) offer a similar characterization, and provide a succinct overview of the critical role that cooking plays in producing the aromas and flavors that we usually associate with meat:

> Meat flavor is thermally derived, as uncooked meat has little or no aroma and only a blood-like taste. During cooking, a complex series of thermally induced reactions between nonvolatile components of lean and fatty tissues occur, resulting in a large number of reaction products. The volatile compounds formed in these reactions are largely responsible for the characteristic flavors associated with cooked meat. An examination of the literature relating to the volatile compounds found in meat indicates that more than 1000 volatile compounds have been identified.

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> The thermally induced reactions occurring during heating that provide meat flavor are principally the Maillard reaction, between amino acids and reducing sugars, and the degradation of lipid. Both types of reaction involve complex reaction pathways, leading to a wide range of products, which account for the large number of volatile compounds found in cooked meat. Heterocyclic compounds, especially those containing sulfur, are important flavor compounds produced in the Maillard reaction; they provide savory, meaty, roast, and boiled flavors. Lipid degradation produces compounds that give fatty aromas to cooked meat and compounds that determine some of the aroma differences between meats from different species.

Interestingly, with a few notable exceptions, many of the amino acids that make up the proteins in meat are also either tasteless or bitter (Berg 1953; Birch and Kemp 1989; Friedman 1999; Glaser 1999; Haefeli and Glaser 1990; Haefeli et al. 1998; Kaneko 1938, 1939; Meister 1965; Mori et al. 1991; Schiffman et al. 1981; Shallenberger 1993; Solms 1969; Solms et al. 1965; Stone 1967).

> All essential L-amino acids except L-threonine (Thr) are generally bitter, whereas nonessential ones and Thr are sweet. The acidic L-amino acids, L-glutamic and L-aspartic acid (Glu and Asp), are sour, yet the sodium salt of both define a unique taste, which is called "umami" in Japanese. The term "umami" is usually translated as "delicious" or "savory"…
>
> Mori et al. (1991:987)

Again, the characteristic meaty flavor that makes meat so appealing to many diners today does not stem from the taste of its amino acids. Instead, the desirable tastes that we associate with meat are largely a product of cooking, fermenting, smoking, ageing, seasoning, or other treatment applied to the meat; they are not a built-in feature of fresh raw meat. So it would seem that humans may not possess a hardwired predilection for fresh meat in its uncooked form. But what then is *umami*?

## 8.1 Umami

Our gustatory system has evolved to recognize four distinctive tastes – sweet, sour, salty, and bitter. There now seems to be reasonable consensus that there is a fifth taste as well, known as *umami*, a Japanese term that best translates as "delicious" or "savory" (Beauchamp and Pearson 1991; Bellisle 1999; Chaudhari et al. 2002; Hellekant and Ninomiya 1991; Kurihara and Kawamura 1991; Lindemann 2000; Pritchard and Norgren 1991; Rouhi 2003; Shi and Zhang 2006; Torii et al. 1987; Yamaguchi 1991; Yamaguchi and Ninomiya 2000). While umami has been known since 1908, when it was first recognized by Kikunae Ikeda, a chemist at Imperial University of Tokyo (Ikeda 1909, 2002), western scholars only came to accept this additional taste in the past few decades. Umami is very different from the other four basic tastes, a fact that has contributed to the slowness with which scientists accepted umami as a genuine taste in its own right. While sweet, sour, salty, and bitter are discrete tastes that can easily be isolated and identified, umami is more like a flavor quality that becomes manifest when *free* L-glutamate (Bigiani

2005:129–130), the basic component of monosodium glutamate (MSG), or the ribonucleotides Inosine 5′-monophosphate (IMP) and guanosine monophosphate (GMP), are present in foods or are added as flavor or palatability enhancers.

> Umami makes a variety of foods palatable, although umami by itself is not particularly palatable. For example, a solution of MSG is not very palatable, but MSG added to soup greatly enhances its palatability…
>
> Yamaguchi and Ninomiya (2000:923S)

The umami taste is most notably associated with meat and seafood, but is also very evident in aged cheeses, a variety of fermented foods, milk (including human breast milk), and in a number of vegetables, such as tomatoes and mushrooms (Lindemann 2000; Rouhi 2003; Yamaguchi and Ninomiya 2000). Much of the research on umami supports the view that it provides a taste signal allowing humans, primates, and other mammals to identify foods that are rich in protein. And in recent years an L-glutamate taste receptor has been identified, clinching the view that umami is a genuine taste and not simply the product of combining the other four tastes in some fashion (Bigiani 2005; Chaudhari et al. 2002; Nelson et al. 2002; Yamaguchi and Ninomiya 2000). One might therefore conclude that umami is what made meat so attractive to early hominins and to our closest primate relative, the chimpanzee, regardless of whether or not it was cooked.

There are two problems with this perspective, however. First, there is nothing that I have been able to find in the literature that shows the presence of umami in fresh raw meat. As already noted, uncooked meat is essentially tasteless. Umami in meat emerges when it has been cooked, seasoned, marinated, fermented, aged, or otherwise altered from its fresh state. Thus, unless we allow early hominins the regular control of fire and some degree of “haute cuisine,” it is doubtful that umami played much of a role in attracting our early ancestors, or chimpanzees, to meat.

The second problem concerns what umami actually signals concerning dietary protein status. Thus, Beauchamp and Pearson (1991:1011) state that, contrary to expectations, umami preference is not enhanced when protein intake is deficient:

> Our initial research on MSG in malnourished infants was predicated upon the idea that, as Ikeda… had originally suggested, MSG might be a taste signal for the presence of amino acids and protein. In this teleological sense it was argued that MSG taste was also a basic taste, like sweet, salty, bitter and sour, serving a basic nutritional need. We have found no enhancement of preference for MSG in infants… or adults… who are protein depleted. In fact, Torii and his colleagues… and Kimura and colleagues report the opposite responses in rats made protein or lysine deficient… Thus there is no evidence for a craving or hunger for MSG following protein depletion in the same way that a desire for sweets or salt may follow extreme calorie or sodium depletion.

Kurihara and Kawamura (1991:1029–1030) make a similar observation concerning the relationship between umami and protein:

> In the rat, a preference for umami was observed when dietary protein was within normal limits. A preference for umami did not occur during a deficiency of dietary protein. When lysine (Lys)-deficient animals consumed a solution and began to grow normally, they started to prefer MSG.

Likewise, Mori et al. (1991:994) come to the same notion regarding umami and its relationship to dietary protein status:

> When an animal is faced with prolonged essential nutrient deficiency, such as that for essential L-amino acids, certain signals may be elicited from the brain or the periphery that indicate insufficient control of homeostasis. In this case, the animal under anorexia may seek out and develop a strong preference for the deficient nutrient, e.g., lysine. Once normal growth and maintenance has been reachieved, preference for umami taste substance is reestablished.

Kimura et al. (1991:997) also reach essentially the same conclusion regarding umami preference and the level of protein intake:

> We also observed that a preference for umami, especially for monosodium L-glutamate (MSG), was induced in animals fed a moderate- or high-protein diet and consumption of the umami solution had a reducing effect on sodium chloride intake. However, no preference for the MSG solution was induced and there was no reducing effect on sodium chloride in animals fed a low-protein diet… The results suggested that an elevated threshold of taste sensation occurred in rats fed a low-protein diet.

Finally, Bellisle (1999:431), like the previous examples, suggests that umami is not a signal of protein deficiency or need, but a taste that becomes desirable only once protein or amino acid homeostasis is achieved:

> It has been well established that the preference of laboratory rats for the Umami taste is dependent on nutritional status. A deficiency in one of the essential amino acids in an ingested protein restricts the utilization of this protein to the level of the limiting amino acid… which can compromise growth. Rats fed a diet deficient in one essential amino acid (e.g. lysine) do not prefer MSG solutions. They present a clear preference for NaCl solutions and for solutions which contain the deficient amino acid… In severe protein malnutrition, rats prefer NaCl as well as glycine sources… After animals are refed a balanced amino acid diet, and recover from amino acid deficiency, the preference for Umami tasting substances reappears.

Thus, while umami may signal a food that is rich in protein, if we grant that it is present at all in fresh uncooked meat (which is doubtful), it seems to come into play as a desirable taste only after dietary protein or amino acid concentrations have achieved a normal level; umami seems not to be a signal that an individual is deficient in, or needs, amino acids or protein. Umami therefore hardly accounts for early hominins' pronounced interest in meat.

## 8.2 Raw Meat: Steak *Tartare* and Frozen Meat

Meat is eaten raw in two specific contexts that may at first glance seem to contradict the view that uncooked meat is essentially devoid of taste – steak *tartare*, a delicacy made from raw ground meat, often beef, and frozen meat as traditionally consumed by Inuit (Eskimo) peoples. A brief search of the Web, or perusal of any number of cookbooks, will show that steak *tartare* is not simply a serving of raw meat, but a carefully concocted dish that often involves seasonings such as Worcestershire sauce, as well as onions, capers, and a variety of other additions.

> The classic "raw" meat dish of Western cuisine is steak tartare. The name alludes to the ferocious medieval reputation of the Mongols, also known, from the particular name of one group of Mongol tribes, as Tatars. The word reminded medieval ethnographers of Tartarus, the classical hell, and made it seem especially appropriate to demonize these enemies. The dish as it is known today, however, is a focus of civilized overcompensation. The meat is ground into soft, curling, vermicular twists of bright flesh. As if to make up for its rawness, its preparation is usually turned into a table-side restaurant ritual, when the waiter ceremoniously folds in, one by one, flavor-stretching ingredients which might include seasoning, fresh herbs, spring onions and onion shoots, capers, bits of anchovy, pickled peppercorns, olives and egg. Vodka is an unorthodox but immeasurably improving addition. The other raw meat and fish dishes licensed by civilization are equally removed from nature – their nakedness heavily dressed, their savagery sanitized by elaboration. "Raw" ham is heavily cured and smoked. Carpaccio is sliced with courtly finesse into delicate slivers and no one thinks of eating it until it has been drizzled with olive oil and bedecked with pepper and Parmesan.
>
> Fernández-Armesto (2002:6–7)

And in the case of the Inuit and other peoples who traditionally consumed uncooked frozen meat (e.g., Starks 2007:47–48), even this involved an interesting form of "preparation" before it was eaten:

> Both coastal and inland villagers also used another, far less complicated, freezing method. Raw meat was simply cut into usable sections and frozen, uncovered, in cold cellars, to be eaten at a later date. This frozen raw meat is known as *koowahk* (sometimes spelled *kwak*). For centuries, throughout the coldest months of the year – up to eleven months in some areas of the Arctic – *koowahk* provided an important source of protein, and it was served at all three daily meals. It is still eaten today.
>
> Spray (2002:39)

> Timing and texture are crucial to the dish. The frozen meat is allowed to thaw just to the point when a finger pressed against its surface leaves a slight indentation. Biting into solidly frozen meat would be like biting into an ice cube, but thawed meat is equally undesirable. When the meat has reached the perfect, partially thawed consistency, the head woman of the house quickly slices it paper-thin, not unlike Carpaccio. But there's more to *koowahk* than the taste: the ice crystals in the meat crackle, then burst, in the mouth before quickly melting, affording a sophisticated sensory experience. Once the meat has defrosted and grown flaccid, its texture and taste are no longer pleasing. At this point, diners quickly dip their meat slices into the ever-burning seal-oil lamp to cook, and *koowahk* becomes a communal dish, much like Beef Fondue or the Chinese Chrysanthemum Pot.
>
> Spray (2002:39)

Moreover, as recently discussed in some detail by Wrangham (2009:28–31), for the main meal of the day, in contradistinction to snacks consumed while traveling or hunting, meat was usually prepared by thorough cooking (mostly by boiling) and it was clearly preferred that way. Blubber and various soft organs such as brain, liver, kidneys, and intestines of caribou and other game were often eaten raw at the kill, and fish were commonly eaten raw as well, but generally after they had been allowed to rot or ferment (see descriptions in Pálsson (2001) and Stefansson (1913)).

> I have heard of Eskimo merely warming meat to eat it. These always comment unfavorably on a piece that is a trifle rare and I have not seen one eaten that would not be considered "medium" or "well done" if a beefsteak in a grillroom. In fact I have never seen Eskimo

> eat partly cooked meat so bloody as many steaks I have seen devoured in cities – when they cook, they usually cook well.
>
> Stefansson in Pálsson (2001:210)

> I am strongly inclined to believe that the very name by which we know these people owes its origin to a similar case of hasty generalization. "Eskimo," according to the best authorities, means "eater of raw flesh," and most people believe that all Eskimos habitually eat their food raw, devouring enormous quantities of reeking flesh and blubber… Nevertheless, most observations indicate that this habit is exceptional, and the writings of all the original observers, from the time of Egede and Crantz, are full of accounts of the cooking of food, even when the oil-lamps furnished the only fire for this purpose.
>
> Murdoch (1887:15)

Interestingly, even our closest living relatives, chimpanzees, consistently prefer cooked over raw meat (Wobber et al. 2008; Wrangham 2009). While these pioneering studies did not determine whether the preference was a response to changes in taste that result from heating raw flesh, or merely a reflection of the greater ease of masticating and ingesting meat once it has been cooked (or both), it is certainly possible that uncooked fresh meat is as tasteless to chimpanzees as it is to humans.

It is interesting in this regard that chimpanzees sometimes abandon a kill after eating only the softer parts of the animal or not eating it at all. Wrangham (2009) attributes this curious behavior to the difficulty in chewing the tough uncooked muscle tissue, but one wonders whether the taste (or lack thereof) of uncooked meat, and the fat content of organs like the brain, might also be important factors:

> …chimpanzees sometimes decline the opportunity to eat meat despite their usual enormous enthusiasm for it. After chewing meat for an hour or two, a chimpanzee can abandon a carcass and relax or eat fruit instead. Chimpanzees of the Kanyawara community in Kibale National Park, Uganda, occasionally forgo meat-eating opportunities without chewing muscle at all.
>
> Wrangham (2009:117)

> When chimpanzees kill a prey animal, they normally eat such parts as the guts, liver, and brain first. They can swallow those quickly. But when eating muscle, chimpanzees are forced to chew it slowly, taking as much as an hour to chew one-third of a kilogram (three-quarters of a pound). They can get as many calories per hour by chewing fruits as they can by chewing meat. The habilines [the earliest hominins assigned by many, though not all, paleoanthropologists to the genus *Homo*] would have faced the same challenge. If they had relied on unprocessed meat for as much as half their calories and had eaten their meat as slowly as chimpanzees, with certain cuts of meat they would have had to spend several hours a day chewing it. The digestive costs likewise would have been high, since the gut would have been busy digesting for many hours.
>
> Wrangham (2009:117–118)

> My work on carcass consumption… indicated that Gombe chimpanzees seek fat from the brain and from limb-bone marrow over other body parts after a kill.
>
> Stanford (1998:195)

> Thus the sequence of carcass consumption, which has been seen as important in interpreting the fossil hominid record…, suggests that chimpanzees seek fat in colobus prey above other nutrients and also above calories.
>
> Stanford (1996:103)

If uncooked meat is, in fact, tasteless, as I have suggested, and it takes so long to chew, as suggested by Wrangham (2009), why is it so actively sought by chimpanzees and (presumably) by our early hominin ancestors in the days before they gained control over fire? Unfortunately, I don't have a very convincing answer to this critically important question, and all I can do at the moment is speculate. I suspect the basis for such carnivory in early hominins stems not from a need for protein or fat or some missing micronutrient such as vitamin B-12 (e.g., Hamilton and Busse 1978), as these would likely have been available to them from other sources at less cost and less risk. Instead, as already suggested on several occasions earlier in this endeavor, I suspect the answer lies somewhere in the political domain, perhaps as a display of sheer power or dominance that was directed at other male conspecifics, perhaps as a more subtle demonstration of the hunter's ability or reliability as a provider or ally that was aimed more broadly at other members of the social group. Whatever its ultimate cause, I don't think we will understand the evolution of big-game hunting if we continue to assume the "obvious" – that the principal reason one hunts *large game* is to acquire protein and energy. Outside of the arctic, where fat is a comparatively scarce commodity, and in the days before hominins could render grease from bones, I suspect this was generally not the case.

## 8.3 Prey Body Size and Total Fat Content

One other issue with a bearing on the taste and desirability of meat, particularly the meat from larger animals, is worth pointing out here. While lean, raw muscle tissue has little or no taste, one critical factor that would enhance its gustatory appeal is the presence of fat, both intra- and intermuscular. It is well known that the quantity of fat in an animal varies with its age and sex, its reproductive state, its overall health, and the season of the year (Speth and Spielmann 1983). Less well known, at least in paleoanthropological circles, is Pitts and Bullard's (1968) (see discussion in Cordain et al. 2000:685–686) study showing that, all other things being equal, the amount of fat is a nonlinear function of the animal's body size or fat-free body weight ($\mathrm{FFBW}^{0.2}$). In other words, the larger the animal, the more fat it possesses, both relatively and absolutely. If this relationship holds, it may, as Cordain et al. (2000, 2001) have suggested, be one of the reasons why hunters are especially attracted to *large game*.

The Pitts–Bullard relationship is actually part of a much larger debate in ecology, often referred to as the "fasting endurance hypothesis" or FEH (e.g., Lindstedt and Boyce 1985; Millar and Hickling 1990). As succinctly described by Dunbrack and Ramsay (1993:337): "…among mammal species the proportion of body mass allocated to fat stores appears to scale with a mass exponent well in excess of the generally accepted 0.75 scaling for metabolic rate…, implying that the length of fast that could be supported by fat stores will increase with body mass." The relationship is complicated, however, because fat-free body weight and total fat weight vary, at least to some extent, independently of each other, and are often not clearly distinguished in studies of fasting endurance. Moreover, there are numerous confounding factors, stemming both from the nature of the environment and local habitats to which animals are adapted, as well as the strategies different taxa employ to cope with seasonally variable and unpredictable resources (e.g., Dunbrack and Ramsay 1993; Speakman 1992).

Moreover, interesting as the Pitts–Bullard study may be, given the nature of the data that were used to generate the relationship, I am skeptical of its usefulness for interpreting the human predilection for big-game hunting. There are several reasons for my hesitancy. First and foremost, the data used in the original study are very heterogeneous, a fact openly acknowledged by the authors (Pitts and Bullard 1968:46). Their sample sizes for most taxa are small; most of their samples are a mix of both males and females; aside from being “adult,” the age and reproductive status of the animals they analyzed are not indicated; the study specimens were collected in different seasons of the year (e.g., those from Virginia and Brazil in winter; those from Alaska and Wisconsin in summer); and biogeographically they represent a striking range of environments, some arctic or subarctic (Alaska), others mild-temperate (Virginia), still others Neotropical (Brazil).

There are other reasons for skepticism as well. The vast majority of their sample is comprised of very small mammals, mostly rodents or rodent-sized animals, including 11 species of bats (almost 20% of the entries). Out of a total of 58 entries, fully 50 (86%) of the taxa weigh less than 10 kg (22 lb), hardly qualifying as medium mammals, let alone large ones. Of the seven genuinely larger animals, two are huge marine mammals (whales), one is *Homo sapiens*, and two are domestic animals (horse and cattle).

Inclusion of whales in the study is problematic. Not only are whales gargantuan in comparison to everything else in the database, but as marine mammals they are also warehouses of blubber, thereby guaranteeing a significant correlation when they are stuck on the upper end of a distribution which is largely comprised of rodent-sized animals.

The inclusion of domestic animals in the relationship is also less than ideal. Numerous studies have shown that domestic animals have very different quantities and types of fat than wild animals (e.g., Crawford 1968; Cordain et al. 2002b), so again they will contribute to a correlation that might be weaker, perhaps considerably so, had wild ungulates been used instead.

Mixing both non-arctic and arctic animals in the same relationship is also troublesome, since northern latitude animals commonly have more body fat, at least seasonally, than is characteristic of taxa living in temperate or tropical environments (Pond 1978:552). And, since most of the larger-bodied mammals in the Pitts–Bullard database are from Alaska, this adds an additional bias at the heavier end of the distribution toward animals with higher body-fat levels.

Finally, the inclusion of humans as one of the few larger mammals in the database increases the potential for bias, since *H. sapiens* is “…atypical among mammals, not only with respect to the quantities of fat deposited, but also to its location on the body and to the very marked changes in its distribution with age, sex, and race” (Pond 1978:560; see also Wells 2006).

Given the extreme mix of environments in the database, the clear underrepresentation of medium to large body sizes, the inclusion of a large number of bats, the mix of animals from terrestrial and aquatic habitats, and the use of domestic animals, whales, and humans to represent the larger mammals, the Pitts–Bullard body size–fatness relationship hardly seems a reliable basis upon which to explain a human preference for the meat of larger mammals. In order to see if the relationship really holds, the study needs to be redone, this time focusing on a much more restricted set of environments; looking only at wild, not domestic, animals; truly spanning the size range from small to large mammals; and sticking to terrestrial forms of the kinds that would have been targets of ground-based foragers. It would also be useful to include a seasonal dimension in such a study, one that looks at the availability of fat across different body-size classes at times when animals are in peak condition and at times when they are stressed and mobilizing their fat reserves. In order to do this, it will be necessary to examine each sex separately, not mixed together as in the Pitts–Bullard study, since the annual body–fat cycles of males and females are likely to be out of synch with each other (Speth 1983; Speth and Spielmann 1983). Until such a reanalysis is undertaken, it is probably premature to conclude that the meat of larger prey, on average, would have rewarded hunters with proportionately more fat than they could obtain from the meat of smaller animals.

# Chapter 9
# Protein and Breast Milk

> *Human milk has the lowest protein concentration (about 7% of energy) of any primate milk that has been studied. In general, it appears that primates produce small daily amounts of a relatively dilute milk.... Thus the protein and energy demands of lactation are probably low for primates by comparison to the demands experienced by many other mammals.*
>
> Oftedal (1991:167)

I think it is reasonable to assume that early hominin infants, like those of modern hunter-gatherers, would have depended on breast milk for sustenance during the critical first year following birth, and very likely for some considerable time beyond (Kennedy 2005; Sellen 2007). If high-quality protein was the "nutrient among nutrients" underwriting the astounding encephalization that we see in our Plio-Pleistocene ancestors, one would expect that importance to be resoundingly reflected in the composition of human breast milk. This is patently *not* the case, however (Robson 2004; Sellen 2007). In fact, human breast milk is one the lowest-protein milks in the mammalian world, right along with the milks of the great apes and many other primates (Amen-Ra 2007:1149; Bell 1928; Ben Shaul 1962; Darragh and Moughan 1998; Davis et al. 1994; Goedhart and Bindels 1994; Hambraeus 1994; Hinde 1986; Jelliffe and Jelliffe 1978; Jenness 1985, 1986; Jenness and Sloan 1970; Lönnerdal 2003; Malacarne et al. 2002; McCullagh and Widdowson 1970; Milligan 2007; Milligan and Bazinet 2008; Milligan and Oftedal 2007; Milligan et al. 2008; Oftedal 1981, 1984; Oftedal and Iverson 1995; Patiño and Borda 1997; Power 2006; Power et al. 2002; Schmidt-Nielsen 1986; Siewert 2003:173). For example, according to Davis et al. (1994:1126):

> The protein concentration of milk varies more than 10-fold among species, with that of human milk at the low end of the range (~8 g protein/L, Jenness and Sloan 1970).

The same authors go on to point out that great apes, and primates more generally, have low protein milk when compared to the milk of other mammalian taxa:

> Among the primates, the human, chimpanzee and gorilla, on average, had significantly lower concentrations of total amino acids in their milks than did the lower primates.... The total amino acid concentration of human milk did not differ significantly from those of

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> milks from the great apes. Thus, a low total amino acid concentration in milk does not seem to be peculiar to the human or the great apes, but to primates generally.
>
> Davis et al. (1994:1128)

Patiño and Borda (1997:8–12) similarly emphasize the low protein concentrations in primate breast milk:

> In general, milk of the order Primates, compared with that of other orders, is characterized by moderate amounts of solids and fats, low levels of proteins, and high levels of sugar…. In fact, human milk has the lowest concentration of proteins (1.0%) of all the species of primates.

According to Lönnerdal (2003:1538S), the protein content of human milk is somewhat elevated at the onset of lactation, but then falls off quite rapidly over the next several months:

> The true protein content of breast milk…is 14-16 g/L during early lactation, 8-10 g/L at 3-4 mo of lactation, and 7-8 g/L at 6 mo and later….

Interestingly, the low concentrations of protein commonly reported in studies of human and other primate milks, on the order of 1–2%, may in fact be over-estimates of the true values:

> Commonly quoted values for the protein content of human milk are around l-2%, but the true protein content is lower. This is because the protein content has been calculated from total nitrogen analysis without adequate consideration of the considerable fraction (up to 25%) of the nitrogen content of human milk that is nonprotein nitrogen.
>
> Schmidt-Nielsen (1986:141)

The exceedingly low protein concentrations in human milk pose a serious conundrum for those paleoanthropologists who see protein as the high-quality nutrient underwriting the phenomenal encephalization that transformed pea-brained early hominins into brainy humans (e.g., Kennedy 2003:564; "…because rapid brain growth occurs during 'childhood'…, high-quality protein is especially crucial."). We have seen that protein can be toxic to the fetus when it exceeds about 20% of calories in the mother's diet. We have also seen that elevated concentrations of protein in the diet of low-birth-weight infants can produce deleterious outcomes, including reduced IQ. We have also seen that among nutrients, protein offers the most inefficient way to supply energy to mother and baby because of its high SDA or DIT. And we now see that the most encephalized mammals on the planet – humans and great apes – have the least amount of protein in their milk.

Jackson (1999:S48–S49) nicely summarizes the shifting perception among nutritionists as to how much protein an infant needs for normal growth and development:

> In considering the protein requirements during early life, approaches have been dominated by a logic which suggests that because protein is required for normal growth and development, improved growth and enhanced development can be best achieved on higher protein intakes. There is a deep-rooted belief that this is so, but the evidence suggests that this may not be correct.

> The consumption of human milk has been taken to represent the intake required for normal patterns of growth and development during the newborn period and the first six months of life. Human milk has a composition which is low in nitrogen and extremely low in protein. The consumption of relatively high protein formulations based upon cow's milk has been associated with serious complications leading on occasion to death. Over recent years there has been a progressive reduction in the nitrogen and protein content of formulae to achieve adequate patterns of growth together with minimal metabolic stress…. *This can best be achieved with formulations in which the protein content is very low, compared with what was thought to be desirable ten years ago*. When the requirements for protein during early life have been assessed based upon a factorial approach, with the metabolic demand for nitrogen and amino acids being used as the objective, the recommendations for optimal protein intakes are very much lower than they have been in the past…. (emphasis added)

Jackson (2000) makes another very interesting point concerning the nature of the fetus's protein needs that paleoanthropologists might well keep in mind when they envision meat as the quintessential food for the pregnant or nursing mother:

> In nutrition, the amino acids have classically been divided into two groups; those that need to be provided preformed in the diet, essential amino acids, and those which can be synthesised in adequate amounts by the host, non-essential amino acids. Even for adults, this division is less sharp than previously recognised, but for the fetus all amino acids have to be provided preformed either from the mother or from the placenta until the pathways for de novo formation are adequately developed and mature. The time and pace of this maturation varies, with some pathways not achieving significant or adequate function until after birth, for example the ability to synthesis adequate amounts of cysteine and taurine. *The pattern of amino acids required by the developing fetus is very different to that found in dietary protein, the "goodness of fit" is poor. Therefore there must be considerable modification to produce an appropriate pattern, either by maternal metabolism or placental formation.*
>
> Jackson (2000:45); emphasis added

Perhaps, the low concentration of protein in breast milk is actually not all that surprising. According to Singh (2005:240), the human "…brain is the fattiest organ of the body. Almost two-third[s] of the weight of the human brain is accounted [for] by phospholipids." Large quantities of protein are needed for building and maintaining muscle tissue, and for other structural and functional needs within the body; the human brain's protein needs, by comparison, are modest. Moreover, as many scholars have pointed out over the years, the growth rate in human infants is very slow (e.g., Foley and Lee 1991; Wells 2006). As a consequence, human breast milk need not contain large amounts of protein (see Robson 2004).

In a detailed review of the nature, distribution, quantities, and function of adipose tissue in infancy and childhood, Christopher Kuzawa reaches a very similar conclusion:

> Data on the mass and chemical composition of the human brain are available for the first year of life, allowing calculation of substrate deposition in the growing brain during this period of rapid cerebral expansion (Schulz et al. 1961[sic 1962]; White et al., 1991). These figures reveal that the requirements of brain growth are trivial relative to cerebral energy needs and account for a small fraction of the body's total growth expenditure during this period. …most of the mass of the brain is water, with fat and protein accounting for only about 9.4% (44.5 g) and 10.1% (47.7 g), respectively, of brain growth during the first year

> of life. This represents only 3% of the 1,740 g of lipid and 6% of the 804 g of protein deposited in the growing infant body between birth and 12 months of age (male/female average from Fomon et al. 1982). Even in the adult, roughly 12% of brain weight is lipid, suggesting that the lifetime lipid requirement for brain growth contributes minimally to total body lipid deposition.
>
> Kuzawa (1998:188)

The elephant offers a particularly interesting counterpoint to the assumption common among paleoanthropologists that a large brain requires a diet rich in protein for its growth and maintenance (see also Langdon 2006:13):

> Among terrestrial mammals elephants share the unique status, along with great apes and humans, of having large brains, being long-lived and having offspring that require long periods of dependency. *Elephants not only have the largest brains but also the greatest volume of cerebral cortex of all terrestrial mammals.*
>
> Hart et al. (2008:87), emphasis added

and yet…

> *Elephants, in nature, customarily consume a diet with the lowest concentration of calories and protein of any mammalian species* and their digestive system is adapted for the ingestion of large volumes of forage with low nutritive value.
>
> Hart et al. (2008:87), emphasis added

Perhaps, it is time that paleoanthropologists reexamine some of their long-held beliefs regarding encephalization. As Kuzawa (1998:185) notes, "…the infant's massive brain is estimated to consume 50–60% of total metabolic expenditure…." What the infant's brain needs in spades, therefore, is energy to build, run, and maintain itself, not protein.

# Chapter 10
# Fat in Infancy

> *Humans diverge from most mammals, including nonhuman primates, by depositing significant quantities of body fat in utero and are consequently one of the fattest species on record at birth.*
>
> Kuzawa (1998:177)

> *Despite the similarity in brain size at birth, a major difference between humans and chimpanzees (or other non-human primates) is the virtual absence of body fat in the chimpanzee infant.*
>
> Cunnane and Crawford (2003:21)

One interesting way the newly born infant assures a stable supply of energy to both body and brain, aside from breast milk, is through its reserves of body fat. Human newborns are the fattest babies in the mammalian world, fatter in fact than seals and sea lions (Kuzawa 1998:181, Table 1; see also Wells 2006). This is one area in which humans differ dramatically from their nearest primate relative, the chimpanzee, whose babies are thin, gaunt, and very wrinkled – almost prune-like – in appearance. Over the years, paleoanthropologists have commonly attributed the human infant's plumpness to its hairlessness and concomitant need for insulation, but a number of more recent studies suggest instead that the primary purpose of such thick deposits of adipose tissue in infancy is to provide a stable and predictable supply of energy to the developing infant (Kuzawa 1998; Pond 1978, 1991, 1997; Robson 2004; Wells 2006). This is clearly the implication of Kerr et al.'s (1978) study of severe undernutrition in infants:

> While preservation of body protein is essential for survival of starvation, it is apparent that this is efficiently achieved. The normal reserves of fat, on the other hand, would be depleted after about 3 wk of fasting. Availability of energy, specifically fat, appears to be the limiting factor in survival of starvation by infants.
>
> Kerr et al. (1978:432)

> These conclusions support recent recommendations that availability of energy is of prime importance in prevention and treatment of malnutrition and should not be overshadowed by exaggerated attention to protein requirements.
>
> Kerr et al. (1978:432)

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> These studies emphasize the flexibility of energy homeostasis in maintaining requirements for vital functions during fasting even in severely wasted infants. This ability to make a rapid conversion from oxidation of glucose to oxidation of fat with a minimal change in glucose concentration and without utilization of very much protein is presumably a general phenomenon.
>
> Kerr et al. (1978:432)

Of particular interest in the present context, the infant's substantial reserves of body fat serve as a critical source of ketones that can be used to fuel its energy-guzzling brain during periods between feeds when adequate supplies of glucose are not available:

> …the brain can oxidize ketones but it does not oxidize the fatty acids they come from. In adults, glucose is the main fuel for the brain. If food is restricted, body glucose stores (glycogen) last less than 24h. Without ketones, brain function would be rapidly compromised or muscle protein would need to be degraded to release amino acids that can be converted to glucose. Hence, ketones are an essential alternative fuel to glucose for the brain. Healthy human infants have a large store of fat that is available to make ketones. In infants, slightly elevated blood ketones are present all the time (mild ketonemia) regardless of feeding status. This is not the case with fed adults. In human fetuses at mid-gestation, ketones are not just an alternative fuel but appear to be an essential fuel because they supply as much as 30% of the energy requirement of the brain at that age….
>
> Cunnane and Crawford (2003:22)

# Chapter 11
# DHA and the Developing Brain

> *Docosahexaenoic acid (DHA; 22:6n-3) is the major n-3 fatty acid in the central nervous system and retina. The most rapid rates of brain DHA accumulation occur during the last intrauterine trimester and the first year of life. These stages of development may be influenced directly by the nutritional status of the mother….*
>
> Carlson (2009:678S)

> *One such nutrient-based approach has focused on the n-3 long-chained polyunsaturated fatty acid docosahexaenoic acid (DHA), which is a primary constituent of membrane phospholipids within the synaptic networks of the brain essential for optimal cognitive functioning. As biosynthesis of DHA from n-3 dietary precursors (alpha-linolenic acid, LNA) is relatively inefficient, it has been suggested that preformed DHA must have been an integral dietary constituent during evolution of the genus Homo to facilitate the growth and development of an encephalizing brain.*
>
> Carlson and Kingston (2007a):132

Thus, protein is hardly the engine that drove the dramatic encephalization of the human brain over the course of the Plio-Pleistocene. A number of nutritionists, recognizing this fact, have focused instead on an omega-3 fatty acid (often written 22:6*n*-3 or 22:6$\omega$-3) known as DHA (an abbreviation for docosahexaenoic acid), a long-chain polyunsaturated fatty acid (LC-PUFA) that forms a critical component of the central nervous system (Al et al. 2000; Arterburn et al. 2006; Bakewell et al. 2006; Bourre 2006; Brenna 2002; Brenna et al. 2007; Broadhurst et al. 2002; Burdge 2006; Burdge and Calder 2005; Burdge and Wootton 2002; Burdge et al. 2006; Carlson and Kingston 2007a, b; Carnielli et al. 2007; Childs et al. 2008; Clandinin 1999; Cordain et al. 2001; Crawford et al. 1993, 1999, 2001; Cunnane and Crawford 2003; Cunnane et al. 2007; Goyens et al. 2006; Green and Yavin 1993, 1996, 1998; Haggarty 2002, 2004; Herrera et al. 2006; Hibbeln et al. 2006; Innis 2000a, b, 2005, 2007a, b; Jensen et al. 2000; Langdon 2006; Lefkowitz et al. 2005; Muskiet et al. 2004, 2006; Peng et al. 2007; Rioux et al. 2008; Robson 2004; Rosell et al. 2005; Sauenvald et al. 2000; Simopoulos 2001; Singh 2005; Su et al. 2000; Williams and Burdge 2006). The essence of the "DHA model" is that humans are very inefficient at biosynthesizing DHA de novo from its precursor, $\alpha$-linolenic acid, in quantities

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sufficient to supply the needs of the developing fetus and newborn infant. Instead, the mother must obtain *preformed* DHA through the foods in her diet.

There are two principal ways that a prehistoric forager might have obtained preformed DHA in sufficient quantity. One way, often dubbed the "aquatic hypothesis," is to target aquatic resources, most especially marine-derived foods such as molluscs, fish, and seals. Though present in animal foods from freshwater habitats, the concentration of DHA is generally lower, and values may range widely among species, at different seasons of the year, and in response to changing levels of competition among animals that utilize overlapping sets of resources. By contrast, DHA is absent in terrestrial plant foods such as vegetable fats and oils, including nuts, grains, and seeds (Innis 2007a; Koussoroplis et al. 2008). It is also almost entirely absent from most terrestrial insects and, unfortunately, is not widely reported in aquatic species (Brett and Müller-Navarra 1997; Cartland-Shaw et al. 1998; Ghioni et al. 1996; Gladyshev et al. 2009; Hanson et al. 1985; Nor Aliza et al. 2001; Speake et al. 2004; Stanley-Samuelson 1994; Stanley-Samuelson and Dadd 1983; Stanley-Samuelson et al. 1988; Stanley-Samuelson and Nelson 1993).

> It is notable in this context that the insects studied here, and the range of aquatic insects studied previously, effectively lack 22:6n-3 [DHA]. It can be inferred that the role fulfilled in vertebrate neural and retinal tissue (and other body tissues) by 22:6n-3 is readily fulfilled in insect neural and retinal tissue by 20:5n-3, which may account for the abundance of C20 PUFA in the retina of the butterfly and the spermatophores of the cricket….
>
> Ghioni et al. (1996:167)

And DHA is present in small but variable amounts in the muscle tissues, liver, and other organs of terrestrial animals (Cordain et al. 2001; Cordain et al. 2002b; Hoffman and Wiklund 2006:203; Koussoroplis et al. 2008).

The other way a prehistoric forager might acquire preformed DHA is to go after the brains of large mammals, whether by hunting or by scavenging (Broadhurst et al. 2002; Cordain et al. 2001; Crawford et al. 1993, 1999, 2001; Cunnane and Crawford 2003; Cunnane et al. 2007). Though this strategy does not have as convenient a label as the "aquatic hypothesis," it is the one of particular concern to us in the present discussion because it offers paleoanthropology a way to maintain its traditional focus on nutrition in the evolution of big-game hunting, albeit with a shift in the tissue of interest from muscle to brain.

If one accepts the aquatic hypothesis, one would expect evidence for the use of marine or freshwater resources to become prominent in the archaeological record by the late Pliocene or beginning of the Pleistocene when the first clear signs of encephalization in early *Homo* become evident (i.e., ca. 2.0–2.5 mya). Unfortunately, with the possible exception of some fish remains from Olduvai's FLK-*Zinj* site at about 1.8 million years ago and a few other rather meager and taphonomically uncertain occurrences (e.g., Stewart 1994; Erlandson 2001; Erlandson and Moss 2001), there really is no compelling evidence for regular early hominin use of aquatic resources. Admittedly, preservation in this remote time period is often quite poor, and notoriously perishable remains such as fish bones may simply no longer be visible. However, some resources such as molluscs have a reasonably good chance of surviving the vicissitudes of time and, if they were used in any significant quantity, we should have little difficulty in finding their remains. But we don't, not until a much later date, long after encephalization had been underway for hundreds of thousands of years (e.g., Fa 2008; Hu et al. 2009; Klein 1999; Marean et al. 2007; Parkington 2001; Richards et al. 2005; Richards and Trinkaus 2009).

On the other hand, based on what we know about the Plio-Pleistocene archaeological record, it is certainly within the realm of possibility that early hominins obtained DHA by targeting the brains of large mammals (they may have taken marrow bones at the same time, not as a source of DHA, but as a concentrated though limited source of nonprotein energy; see discussion in Cordain et al. (2001) (see also Blumenschine and Madrigal 1993; Bunn 1981, 2007a; Domínguez-Rodrigo 1997; Fernández-Jalvo et al. 1998; Marean et al. 1992; O'Connell et al. 2002; Oliver 1994; Potts 1988; Stiner 2002).

However, both DHA scenarios seem rather unlikely. In the first place, one does not need to hunt big game in order to get DHA, as the brains of the many varieties of smaller mammals that were exploited by hunter-gatherers, as well as lizards, snakes, and other easy-to-catch prey, and bird eggs, may well have provided an adequate supply at a fraction of the cost and risk. Nor does one need to envision foragers painstakingly picking out diminutive brains from the crania of rodents and other small mammals, in a manner akin to extracting tiny pieces of nutmeat stubbornly encased within the tough, compartmentalized shells of walnuts, in order to cobble together the needed fat. Well-preserved prehistoric human coprolites (feces) recovered in large numbers from dry caves throughout western North America are full of pulverized bone fragments, including pieces of broken skulls, as well as fur and feathers, indicating that rodents, rabbits, birds, lizards, snakes, and amphibians were often cooked whole, pounded in a wooden mortar or on a milling stone, and then consumed in their entirety – bones, fur, feathers, and all, including the precious DHA in the brains (Reinhard et al. 2007; Sobolik 1993; Yohe et al. 1991).

> Small game was broiled on coals; sometimes, too, venison and rabbits. The two latter were also cooked in an earth oven, whatever was not immediately eaten being crushed in a mortar – bones included in the case of rabbits – dried, and stored. The pounding of flesh is a habit common to most of the California Indians.
>
> Kroeber (1925:652)

> We used to eat rats, mice, lizards, and some snakes, but I don't remember what kinds…. The little things were pounded on a rock, bones and all and then stewed.
>
> Shipek (1970:32–33), cited in Yohe et al. (1991:660)

And, for the many reasons outlined below, an external supply of preformed DHA may not have been necessary at all (see Carlson and Kingston 2007a, b; Langdon 2006 for comprehensive, point-by-point critiques of the aquatic hypothesis; see also Robson 2004 for an earlier look at DHA and human brain growth).

First, though admittedly a rather subjective point, there are many religious and ethnic groups throughout the world today whose members are vegetarians (or vegans), consuming little or no meat or fish, and yet they seem to have little difficulty, aside perhaps from the constraints imposed by poverty, to produce viable children who grow up to lead what would seem to be quite normal lives (e.g., Langdon 2006). This view is not totally without empirical support, however. For example, in studies of pregnant baboons on a "vegan-like" diet devoid of preformed DHA, fetal brain development nonetheless appeared to progress normally:

> …this study shows that LNA [α-linolenic] and DHA are transferred to the fetus from the mother, and preformed DHA is incorporated into fetal tissues at least one order of magnitude higher than is LNA-derived DHA. About 0.075 and 1.6% of the dose of LNA and DHA, respectively, was incorporated into the brain as DHA. Based on this level of DHA brain accretion, we estimate that LNA provided as 0.45%en in an LCP-free [long-chain polyunsaturated fatty acid] diet would support DHA requirements of the brain. Future investigations focusing on fetal conversion of LNA to DHA are required to determine whether the mother is the sole source of DHA in the latter half of gestation.
>
> Greiner et al. (1997:832)

Similarly, Cheon et al. (2000) found that pregnant rats fed diets that contained no preformed DHA, but adequate amounts of its precursor, α-linolenic acid, synthesized sufficient amounts of DHA to produce healthy, behaviorally normal pups:

> However, our result [sic] show that rats except those in the LA1 group, fed with diets containing 1–3% LNA and 8.7–11.2% LA of total dietary calories with 2–10 LA/LNA ratio, could synthesize an appropriate amount of DHA and have normal behavioral activity without dietary supplementation of DHA.
>
> Cheon et al. (2000:2295)

Second, animal studies provide evidence that the enzymes in the liver involved in the bioconversion of the essential fatty acid α-linolenic acid (α-LNA) to DHA may be upregulated substantially in the presence of a diet containing α-LNA but lacking in preformed DHA.

> Our kinetic and enzyme data show that the liver can maintain brain DHA composition when DHA is absent from the diet but a sufficient amount (4.6% of total fatty acid) of α-LNA is present and when dietary α-LNA is reduced to some extent (which has yet to be determined). This ability is attributable to high baseline liver converting enzyme activities and to increases in these activities in response to *n*-3 PUFA deprivation.
>
> Igarashi et al. (2007:2468)

Third, recent work by Graham Burdge and colleagues (Burdge and Calder 2006; Burdge and Wootton 2002; Burdge et al. 2002; Williams and Burdge 2006; see also Childs et al. 2008) points out that many of the studies looking into the rate at which humans are capable of biosynthesizing DHA have focused on male subjects, or on unspecified mixtures of males and females, a curious bit of sexism in the medical/nutrition fields if the concern is with the *mother's* ability to provide adequate nutrition to her developing fetus or nursing infant. These studies are showing, perhaps not surprisingly, that women have a greater capacity than men to biosynthesize DHA:

> Two reports have specifically studied α-LNA conversion in women of reproductive age. Burdge & Wootton (2002) showed that conversion of α-LNA to EPA and DHA in women aged about 28 years was substantially greater (2.5-fold and >200-fold, respectively) than in a comparable study of men of similar age (Burdge et al. 2002)…. This finding is strongly supported by kinetic analysis, which showed that the rate-constant coefficient for the

> conversion of DPA to DHA was approximately 4-fold greater in women compared with men…. This may reflect a greater availability of α-LNA for conversion in women than in men that may perhaps, in part, be due to lower partitioning towards b-oxidation. However, since the rate-constant coefficient for the conversion of DPA to DHA was greater in women than men…, it is likely that there is a sex-related difference in the activity of the desaturation–elongation pathway.
>
> Burdge and Calder (2006:35–36)

> One possible explanation for the greater synthesis of EPA and DHA from α-LNA in women compared with men is the action of oestrogen. DHA synthesis was almost 3-fold greater in women using an oral contraceptive pill containing 17a-ethylnyloestradiol than in those who did not (Burdge & Wootton (2002)). The suggestion that oestrogen may increase the activity of the desaturation–elongation pathway is consistent with the finding that oestrogen-based hormone replacement therapy in postmenopausal women resulted in greater plasma dihomo-g-linolenic and arachidonic acid concentrations than before treatment….
>
> Burdge and Calder (2006:36)

Giltay et al. (2004a, b) have come to conclusions that are very similar to those reached by Burdge (see also Alessandri et al. 2008; Welch et al. 2006, 2008):

> …our data suggest that biosynthesis of DHA is greater in women than in men because of the effects of sex hormones, presumably estrogens. A strong stimulus with estrogens induced an increase in DHA status, whereas a testosterone stimulus induced a decrease in DHA.
>
> Giltay et al. (2004b:1173)

> From an evolutionary perspective, it seems plausible that an increase in endogenous maternal DHA biosynthesis during pregnancy and lactation enabled optimal fetal and neonatal growth and brain development…. Vegetarian and non-fish-eating mothers may depend totally on this biosynthetic pathway to acquire DHA from ALA….
>
> Giltay et al. (2004b:1173)

Many other studies, directly or indirectly, point to similar conclusions regarding the greater capacity of women to accumulate and biosynthesize DHA. For example, in a study of the proportions of *n*-3 (omega-3) polyunsaturated fatty acids in serum lipids of male and female New Zealanders consuming broadly similar diets, Crowe et al. (2008) found that women had higher concentrations of DHA than men. Similarly, Dewailly et al. (2001a) observed that, while men in a sample of Quėbecers regularly consumed considerably more fish than women, women nonetheless maintained significantly higher concentrations of DHA. And in a parallel study among Canadian Nunavik Inuit, Dewailly et al. (2001b) again found much higher levels of DHA in women, even though both sexes appeared to consume broadly comparable diets.

Interestingly, a woman's capacity to synthesize DHA appears to be adversely affected by the availability of preformed DHA in the diet. Pawlosky et al. (2003a, b), for example, observed that women produced more DHA when they consumed beef, a food that contains little or no DHA, than when they ate fish, an excellent source of preformed DHA. Similar observations are offered by Barceló-Coblijn et al. (2005), Burdge (2003), Cho et al. (1999:37338), DeMar et al. (2008), Morise et al. (2004), and Sinclair et al. (2002:1117).

Moreover, the low levels of DHA in breast milk and adipose tissue that one commonly observes today in American and European women may not be typical of the levels that would have been found in earlier hominin foragers, whose diets would have encompassed a far more diverse range of wild plant foods than is the norm nowadays. The amount of DHA that the mother can synthesize de novo is heavily influenced by the absolute amounts, and ratio, of the two essential fatty acids, linoleic and α-linolenic acid, and these amounts have been steadily shifting over the past half century or more in favor of linoleic acid, to the detriment of the mother's capacity to produce DHA (Boudreau et al. 1991; Goyens et al. 2006; Leece and Allman 1996).

> …the content of LA [linoleic acid] in mature breast milk of US women, a reflection of their fat intake, has steadily increased from 6–7 to 15–16% of total fatty acids between 1945 and 1995 and has stayed at around 16%, whereas the percentage of LNA [α-linolenic acid] has remained essentially unchanged (approximately 1.0%). So, the ratio of LA to LNA has progressively increased to reach a mean value of 16. Very similar values have been obtained recently for the fatty acid composition of adipose tissue in US women, a parameter which is also considered to be a fair reflection of dietary lipid intake…. Such an imbalance in the dietary n-6/n-3 ratio could favour the bioconversion of LA to AA to the detriment of that of LNA to DHA.
>
> Ailhaud and Guesnet (2004:24)

> Although a great variation of PUFA content is reported in the breast milk of European women, it should be noted that LA and LA to LNA ratios in mature breast milk of US women are higher than those of European women…. Furthermore, it is also interesting to note that the ratio of AA to DHA is twofold higher in the breast milk of US women because of its lower DHA content….
>
> Ailhaud and Guesnet (2004:24)

If the absolute amounts of linoleic (LA) and α-linolenic (LNA) acid in the diet, and their ratio, affect the ability of the mother to biosynthesize DHA, then contemporary Western women, whose diets typically are heavily based on foods made from cereal grains (or meat, eggs, and even fish from animals commercially raised on cereals), may be rather poor models for examining the capacity of forager women in the past to produce their own DHA. Using data from contemporary hunter-gatherers in various parts of the world, a number of nutrition studies over the past two decades have attempted to estimate what the ratio of LA to LNA might have been in prehistoric forager diets – the so-called Paleolithic diet (e.g., Cordain 1999, 2002; Cordain et al. 2000, 2005; Eaton et al. 1988), concluding that the value probably would have been somewhere in the vicinity of 1–2:1. During the "Neolithic," however, with the onset of cereal domestication (Bere 2007; Morrison 1978; Price and Parsons 1975; Slavin 2003; Welch 1975), and especially in areas where fish or other aquatic resources did not form a major component of the diet, the ratio is thought to have been much higher, much like present-day Western values that often fall in the range of 15–20:1 (Simopoulos 2001, 2002a, b, 2004, 2008; Sinclair 1979; van der Walt et al. 2009). If this striking contrast between foragers and farmers in the ratio of LA to LNA is basically correct, and if premenopausal women build up substantial stores of both LA and LNA in their body fat reserves (to be discussed shortly), then contemporary studies designed to estimate the capacity of women to biosynthesize DHA may underestimate, perhaps substantially, that capacity in prehistoric forager women subsisting on a "Paleolithic diet."

It may be useful here to digress briefly to comment on the way nutritionists often (mis)conceptualize the "Neolithic" when they make comparisons between our modern "unhealthy" diet and the "healthy" diet of foragers who lived prior to the advent of agriculture. Contrary to the way it is often portrayed, the "Neolithic" was not a uniform transformation of broad-based foraging economies into narrowly focused, field-based agricultural systems such as our own, as forever immortalized in *America the Beautiful* by the unforgettable allusion to "amber waves of grain." It is true that cereals (e.g., wheat, barley, oats, maize, etc.) became increasingly important during the early to mid-Holocene in many parts of the world, and in fact we now know, based on recent work at the Epipaleolithic site of Ohalo II (Israel), that wild cereals, at least in this part of the Near East, were already being incorporated into the diet in quite substantial quantities some 23,000 years ago (Piperno et al. 2004; Weiss et al. 2004, 2008). But this was not the case over most of the globe, nor over most of the Holocene (Smith 2001). As counterintuitive as it may seem, most tribally organized (i.e., small-scale) farming societies, right up to European contact in many places, were horticulturalists or "gardeners," not field agriculturalists, and (here comes the counterintuitive part) they consumed a *greater* diversity of wild plant taxa than did our archetypal foragers – the Bushman (San), Australian Aborigines, Hadza, Pygmies, and others.

This surprising inversion of what most of us would take to be so intuitively obvious was beautifully documented many years ago in a paper by Cecil Brown (1985). In a global cross-cultural look at ethnographically documented hunter-gatherer and small-scale farming societies, Brown showed that it is the farmers, not the foragers, who recognize, classify (using a genuine binomial taxonomy), and exploit by far the greatest range of wild plant foods (these "foods" include a variety of medicinal plants, many of which contribute nutrients as well as pharmacological properties, and hence their separation from other food plants is arbitrary). Brown outlined some of the likely reasons for this rather unexpected revelation, noting that farmers, through their constant disturbance of the landscape by cultivation and fallowing practices, create a diversity of closely juxtaposed habitats which support a considerable variety and density of edible wild plants (many are what we would classify as "pioneer annuals," weedy species that colonize disturbed habitats; see, for example, Smith 1989). Though not cultivated (planted), many of these, in fact, were deliberately tended and managed by weeding and other techniques to protect them from pests and to enhance their productivity (for an example, see Casas et al. 1996).

In addition, Brown suggests that farming systems are often more vulnerable to failure than foraging systems, both because cultivated crops are more susceptible to destruction or pilfering by insect and mammalian pests, untimely frosts, droughts or excessive rainfall, and because village-based farmers have fewer mobility options than foragers do when things get tough. In order to buffer such periods of resource stress, farmers incorporate a much wider range of "fall-back" or "famine" foods into their larder than foragers do.

And finally, semisedentary or sedentary village life, which often goes hand-in-hand with larger numbers of people living in close proximity for extended periods of time, increases the likelihood of diseases stemming from poor sanitation, earlier weaning, and a variety of other causes. As a consequence, farmers have a much more extensive plant-based pharmacopeia than is typical of hunter-gatherers.

Thus, when nutritionists compare what they perceive to be the typical "unhealthy" diet of "Neolithic" farmers against a putatively "healthier" Paleolithic diet, they are not comparing a diet that was the norm for most of humanity for most of the last 10,000 years, but a diet that was characteristic of only some parts of the farming world for only a portion of the last 10,000 years.

Now, steering this digression back to the topic at hand, if the ratio of linoleic to α-linolenic acid has been shifting in an undesirable direction, this is likely not a universal characteristic of the last 10,000 years, but a consequence of a shift from small-scale, horticulturally based economies to field-based agricultural systems by a subset of the world's farming populations, such as those in the Near East, South Asia, and China, and probably not until the Bronze Age or even later.

Continuing now with our discussion of reasons why the "aquatic hypothesis" and its variants may ultimately prove to be unnecessary for understanding the evolution of human braininess, a fourth consideration is the apparent enhancement of the endogenous biosynthesis of DHA in the presence of modest concentrations of myristic acid (MY), a fatty acid (FA) typically found in human breast milk (Jan et al. 2004; Jensen et al. 1990; Rioux et al. 2005):

> …these results suggest that increasing long-chain (*n*-3) PUFA dietary intake is not the exclusive way to increase long-chain (*n*-3) PUFA cellular levels. Although the conversion of ALA to DHA is low, the presence of a nutrient like MY can help to reach this goal by modulating both the level of cellular ALA and its conversion to DHA. From a nutritional point of view, myristic acid should therefore be considered for its potential beneficial effect on (*n*-3) FA cellular availability….
>
> Rioux et al. (2008:644)

Fifth, not only can DHA be stored in body fat, but women seem to have a significantly greater capacity than men to do so (e.g., Garland et al. 1998; Herrera et al. 2006; Hodson et al. 2008; Leaf et al. 1995; Lin and Conner 1990; Plakke et al. 1983; Tavendale et al. 1992).

> If cycling of DHA between adipose tissue and the liver was an important pathway, it would be anticipated that DHA concentration in the adipose tissue would be greater in women than men. This suggestion is supported by the observation that young women have a higher concentration of DPA *n*-3 and DHA in adipose tissue compared with men….
>
> Bakewell et al. (2006:97–98)

When the mother is nursing, some dietary fatty acids, including DHA, are transferred directly to breast milk where they become available to the suckling infant. However, most of the DHA (some 60–80%) reaches the infant less immediately and less directly, by first accumulating in the mother's adipose tissue and only subsequently becoming mobilized and incorporated into breast milk (Hachey et al. 1987; Demmelmair et al. 1998; Del Prado et al. 2001; Fidler et al. 2000; Lassek and

Gaulin 2006; Lefkowitz et al. 2005; Sauenvald et al. 2000). Thus, it would appear that the baby is buffered from day-to-day variability in the concentrations of nutrients in the mother's diet, and instead is more heavily dependent on the stores of PUFA, and their long-chain derivatives, that have accumulated in the mother's body fat prior to, and during, the course of the pregnancy.

> Although maternal diet clearly affects the composition of human milk, these studies using stable isotope methodology show that only a minor proportion of dietary fatty acids is directly transferred into milk, whereas maternal body pools are the major contributors to milk fatty acids, including PUFA and LC-PUFA. Hence, short-term variations of dietary fat composition are buffered to some extent by intermediate incorporation into storage pools, and the PUFA and particularly LC-PUFA content in human milk as well as the supply to the breastfed infant remains relatively constant. It is tempting to speculate that this metabolic buffer benefits the breast-fed infant by reducing the variability in dietary supply of these essential substrates with great biological relevance for early human development.
>
> Demmelmair et al. (2001:187–188)

Women also store and mobilize their body fat in ways specifically designed to enhance the availability of DHA and other polyunsaturated fatty acids to the nursing infant. Not only do premenopausal women have more body fat than men, their body fat accumulates primarily in subcutaneous deposits, to some extent in the abdomen but especially in the buttocks and thighs ("gluteal–femoral" fat). Fat in men, on the other hand, accumulates in visceral or intra-abdominal deposits (Blaak 2001; Das 2006; Koutsari et al. 2008; Lassek and Gaulin 2006, 2007, 2008; Leibel et al. 1989; Mittendorfer 2005; Power and Schulkin 2008; Rebuffé-Scrive et al. 1985; Shadid et al. 2007; Trujillo and Scherer 2006; Wajchenberg 2000; Williams 2004). This difference gives rise to the classic contrast between the "apple" or android body shape in obese men versus the "pear" or gynoid body shape in obese women. Excess fatty acids stored as visceral fat are readily mobilized in overweight and obese men and have been implicated in the development of a number of diseases, including type 2 diabetes, hypertension, atherosclerosis, and coronary heart disease. In contrast, the gluteal–femoral adipose deposits in women actively accumulate throughout pregnancy but remain highly resistant to being mobilized, except toward the end of pregnancy and especially during lactation (Bird 2003; Blaak 2001; Frayn et al. 2005; Hamdy et al. 2006; Horowitz 2003; Jensen 1997; O'Sullivan et al. 2001; Power and Schulkin 2008; Snijder et al. 2003, 2006; Tan et al. 2004; Wahrenberg et al. 1989; Williams 2004; Yim et al. 2008).

> Changes in adipose tissue metabolism occur at these times that favor fat deposition during pregnancy and mobilization during lactation. Adipose tissue fatty acid synthesis increases in midpregnancy, decreases at term, and remains low throughout lactation. Adipose tissue lipoprotein lipase (LPL) activity follows a similar pattern; levels are high in midpregnancy, drop at term, and decrease further as long as suckling continues.
>
> Steingrimsdottir et al. (1980:837)

> As discussed above, women have more fat and larger fat cells than men in the femoral region. One reason for this particular accumulation of adipose tissue in women could be that the femoral region subserves a specific function. To test this hypothesis, lipolysis and LPL activity were examined in adipocytes from the femoral and abdominal regions in

> women during the menstrual cycle, pregnancy, and lactation. The results clearly show that the femoral fat cells change their metabolic pattern and become lipolytic during lactation, supporting the concept of a specialized function.
>
> Rebuffé-Scrive et al. (1985:1973)

> …it is possible that the femoral adipose tissue may serve a specialized function in women, i.e., it is utilized as an important source of energy supply during lactation. This possibility is also supported by the characteristic preponderance of the femoral depots in women and by the fact that men usually only have a small femoral depot.
>
> Rebuffé-Scrive et al. (1985:1976)

Moreover, the gluteal–femoral deposits typical of women contain significantly more monounsaturated (MUFA) and polyunsaturated (PUFA) fatty acids, including the long-chain fatty acids (LC-PUFA), arachidonic (AA) and DHA, and their essential fatty acid precursors, linoleic (LA) and α-linolenic acid (α-LNA), whereas the intra-abdominal adipose tissue typically found in men is far more saturated.

> The present study showed that there was a general tendency for nearly all unsaturated FA to be present in greater proportions in the thigh than in either the abdomen or the arm. This was clearly demonstrated by the significant differences in the total amount of saturated and unsaturated FA (and their ratios) presented in Table 1.
>
> Pittet et al. (1979:60)

> Our study not only confirms that the fatty acid composition differs between deep-seated (perirenal) and subcutaneous (abdominal and buttock) adipose tissue but also clearly demonstrates that it varies between the two subcutaneous sites, abdominal and buttock. The results clearly indicate that abdominal adipose tissue is more saturated than buttock adipose tissue.
>
> Malcom et al. (1989:290)

> Whatever the mechanism that establishes this gradient of saturates, monounsaturates, and polyunsaturates between sites, its effect is a significant change in the physical properties of the TG [triglyceride]. The mean melting point data show continuous (and statistically significant) decreases in this temperature variable from abdomen, to inner thigh, and to outer thigh. These data suggest that the composition of human adipose tissue is structured to the specific conditions of its site.
>
> Phinney et al. (1994:728–729)

> A main finding of the present study is that the fatty acid composition of abdominal adipose tissue is less favorable than that of buttock. This is in agreement with adult studies indicating elevated proportions of saturated fatty acids and reduced proportions of monounsaturated and polyunsaturated fat in abdominal as opposed to buttock depots….
>
> Mamalakis et al. (2002:1084)

> Gluteofemoral fat is richer than abdominal and visceral fat in essential LCPUFAs (Phinney et al., 1994; Pittet, Halliday, & Bateman, 1979; Shafer [sic] & Overvad, 1990), and a lower WHR [waist-hip ratio] is associated with higher DHA levels in the blood (Decsi, Molnar, & Koletzko, 1996; Garaulet et al., 2001; Karlsson et al., 2006; Klein-Platat, Davis, Oujaa, Schleinger, & Simon, 2005; Seidell, Cigolini, Deslypere, Charzewska, & Ellsinger, 1991). In contrast, abdominal fat decreases the amount of the enzyme Δ-5 desaturase, which is rate

> limiting for the synthesis of neurologically important LCPUFAs from dietary precursors (Fuhrman et al., 2006; Phinney, 1996), and higher WHRs decrease DHA production (Decsi et al., 2000; Hollmann, Runnebaum, & Gerhard, 1997).
>
> Lassek and Gaulin (2008:28)

Thus, it seems eminently possible that a healthy adult woman, especially a forager woman who consumed a diet containing a diversity of wild plant foods, would have been able, by drawing on her gluteal–femoral fat reserves, to provide her nursing infant with an adequate supply of DHA for normal development of the infant's brain without dietary supplements of preformed DHA obtained from aquatic resources or from the brains of hunted or scavenged animals.

> …the unusual fattiness and fat deposition patterns of reproductive-aged women may be the result of natural selection for the ability to support fetal and infant neurodevelopment – a selection pressure that was much weaker in our close primate relatives. This hypothesis thus unites two derived (evolutionarily novel) features of *Homo sapiens*: sexually dimorphic fat distributions and large brains. On this view, a low WHR [waist-hip ratio] signals the availability of critical brain-building resources….
>
> Lassek and Gaulin (2008:28–29); see also Singh (1993)

Sixth, not just the mother but the fetus, too, builds up stores of DHA in its adipose tissue (e.g., Christensen and Høy 1997). This is discussed at length by Haggarty (2004), who concludes that:

> Although the brain of the newborn has a relatively high concentration of DHA, the absolute accretion during in utero life is small. The striking thing about in utero LCPUFA accretion is the very high concentration of DHA and AA in the fetal adipose tissue compared to maternal adipose tissue and the fact that 50 times more DHA is stored in the adipose tissue than is deposited in the fetal brain during in utero life. Within a few hours of birth, the adipose tissue stores of the newborn begin to turn over at a high rate…and the stored DHA is largely used up in the first 2 months of postnatal life if the diet is devoid of preformed DHA…. Therefore, the purpose of this adipose store of LCPUFA would appear to support processes such as brain and retinal development during the critical first months of postnatal life. This suggests that the in utero requirement for DHA is likely to be complicated by its interaction with postnatal nutritional status. If the baby has a good supply of DHA in the first months of life, then its adipose stores may not be critical, but if it has a poor supply because it is given formula milk without added LCPUFA, or the mother's breast milk is poor in LCPUFA, or the baby does not feed well on any diet, then the availability in utero and the amount already laid down in the adipose tissue of the newborn may be critical.
>
> Haggarty (2004:1560)

> The total in utero accretion of DHA in the fetus is around 10 g. Most of this is deposited in the last 10 weeks of pregnancy and much of it is to be found in the adipose tissue of the newborn.
>
> Haggarty (2004:1560)

Seventh, there is limited and somewhat contradictory but growing evidence that the fetus and developing infant may be capable of biosynthesizing some of their own DHA de novo, a process that may take place particularly in the brain's astrocytes (e.g., Barceló-Coblijn et al. 2005; Carnielli et al. 2007; Green and Yavin 1998; Williard et al. 2001, 2002).

> The fetal gastrointestinal (G-I) tract may be instrumental in supplying DHA to the fetal brain under certain conditions, such as following intra-amniotic administration of ethyl-docosahexaenoate (Et-DHA). In this pathway, DHA is supplied independently of the maternal metabolism, and the fetal liver is apparently involved. The fetal G-I tract may be advantageous for DHA supply in cases of maternal–placental insufficiency resulting in intrauterine growth retardation. The fetal brain itself is capable of metabolizing LnA to DHA, without the participation of the fetal liver, thus contributing to the accumulation of its own DHA during one of the most crucial periods of its development.
>
> Green and Yavin (1998:129)

Another recent study, in this case using the pig as an animal model, found similar evidence regarding the capacity of the neonate to provide endogenously biosynthesized long-chain polyunsaturated fatty acids for brain development.

> …with the exception of the brain, the fatty acid composition of plasma and of different tissues of [neonatal] piglets are strongly influenced by the fatty acid profile of TPN [total parenteral nutrition] emulsions. However, fatty acid composition in brain phospholipids is much less dependent on dietary composition, indicating an active and efficient metabolism that ensures the appropriate composition in this key stage of its development.
>
> Amusquivar et al. (2008:721)

Interestingly, several recent studies show that the amounts of LA and LNA, and their ratio, affect the capacity of infants, not just adults, to biosynthesize DHA (e.g., Blank et al. 2002; Griffin 2008; Makrides et al. 2000; Weiler and Fitzpatrick-Wong 2002). Many of these studies have been done using animal models, particularly rat pups or piglets, as proxies for the human condition. Dropping the LA:LNA [or LA:ALA] ratio from very high levels (i.e., on the order of 15–20:1) to values above about 6–8:1 had little or no effect on DHA synthesis. However, when the ratio fell below 6:1 the amount of DHA accreting in infant tissues increased significantly. Positive responses continued as the ratio was dropped further until reaching a value of approximately 3–4:1, below which the proportion of DHA was no longer significantly enhanced.

> The amount of DHA that an infant can synthesize is limited to some extent by the ratio of LA to ALA (LA:ALA) in dietary fats. We showed in an earlier study that the amount of erythrocyte DHA in formula-fed infants was increased from 53% to 73% of the amount found in breast-fed infants by simply lowering the LA:ALA in formula from 19:1 to 3 or 4:1.
>
> Makrides et al. (2000:120–121)

> …reduction in the (n-6):(n-3) fatty acid ratio from 9:1 to 4.5:1 using flax seed oil as a source of ALA supports normal somatic and bone growth in piglets. The lower ratio appears to be optimal for DHA status.
>
> Weiler and Fitzpatrick-Wong (2002:2671)

> The most significant finding of this study is the complex response of DHA to changes in dietary ratios of LA to ALA. While reducing the LA-ALA ratio from 10:1 to about 2:1 resulted in an increase in the proportion of DHA in all tissues examined, further decreases in the ratio actually resulted in a decrease in the observed proportion of DHA, while at the same time, all other *n*-3 LCPUFAs continued to increase. Thus, ratios of 10:1 and 0.5:1 resulted in similar proportions of DHA in all tissues despite the very different

> levels of dietary ALA. These results are relevant to infant studies in two ways. First, they confirm that the positive effect on DHA status seen in infants fed formula with LA-ALA in the range of 3:1 or 4:1 was maximal. Secondly, we think that the results predict that ratios of LA-ALA below 4:1 would have little further beneficial effect on DHA status.
>
> Blank et al. (2002:1540)

And last but not least, while there is some evidence, albeit inconsistent and at times contradictory, that dietary supplementation with preformed DHA may increase gestation length and hence birth weight (see review by Wathes et al. 2007), recent work in the field of in vitro fertilization suggests that diets supplemented with preformed DHA may actually be detrimental to normal development of the embryo.

> This study demonstrated that exposure of the oocyte during maturation in the ovary to an environment high in *n*-3 PUFA resulted in altered mitochondrial distribution and calcium levels and increased production of reactive oxygen species. Despite normal fertilization and development in vitro following IVF, the exposure of oocytes to an environment high in *n*-3 PUFA during in vivo fertilization adversely affected the morphological appearance of the embryo and decreased developmental ability to the blastocyst stage. This study suggests that high maternal dietary *n*-3 PUFA exposure periconception reduces normal embryo development in the mouse and is associated with perturbed mitochondrial metabolism, raising questions regarding supplementation with *n*-3 PUFAs during this period of time.
>
> Wakefield et al. (2008:E425)

In sum, it would seem that the role of DHA in human evolution and food choice remains far from certain; and it is therefore premature to conclude that the regular use of aquatic resources, or the preferential hunting of big-game animals for the omega-3 fatty acids in their brain, were necessary in order to underwrite the striking encephalization seen in our hominin ancestors over the course of the Plio-Pleistocene:

> The notion that humans require larger amounts of long-chain omega-3 fatty acids than other mammals still awaits solid evidence…. It is also uncertain if humans, as has been suggested, have a lower capacity than rodents and herbivores to convert the predominant omega-3 fatty acid in plants, alpha-linolenic acid, into the long chain omega-3 fatty acid docosahexaenoic acid (DHA)…. Available knowledge of fatty acid requirements, including requirements for brain development, does not give strong hints about the intake of animal versus plant foods during human evolution, nor about the intake of foods like fish, shellfish, meat, insects, eggs, nuts, roots, leaves, or fruits.
>
> Lindeberg (2009:49)

# Chapter 12
# Big-Game Hunting: Protein, Fat, or Politics?

> *Doubt is not a pleasant condition, but certainty is absurd.*
>
> Voltaire [Arouet] (1919:232), in a letter dated 1770
> to Frederick William, Prince of Prussia

> *Essentially, all models are wrong, but some are useful.*
>
> Box and Draper (1987:424)

> *In fact nothing in nature explains the sexual division of labour, nor such institutions as marriage, conjugality or paternal filiation. All are imposed on women by constraint, all are therefore facts of civilisation which must be explained, not used as explanations.*
>
> Meillassoux (1981:21)

I have pulled together a variety of information concerning protein as a nutrient, focusing particularly on protein's costs and potentially undesirable effects when consumed in large amounts. Intakes of protein (plant and animal combined) above about ~200–250 g per day can lead to weight loss, lethargy, and weakness, and, if sustained long enough, death. Such intakes can also be detrimental, even toxic, to the fetus and nursing newborn, lowering birth weight and increasing the chances of cognitive disorders, morbidity, and perinatal mortality. Because of its high-specific dynamic action (SDA), protein is also an inefficient way to provide energy to the body, whether for general metabolic needs or specifically for fueling the brain. It is also not the ideal nutrient for brain growth, which requires considerable inputs of fatty acids, particularly the long-chain polyunsaturated fatty acid, docosahexaenoic acid (DHA). Aside from brain, the meat and organs from wild ungulates, African or otherwise, are limited, costly, and inefficient sources of DHA (see data in Crawford et al. 1969; Cordain et al. 2001, 2002b).

These and other factors suggest that paleoanthropologists are probably making a mistake if they elevate protein conceptually to a unique position of prominence above that of other macronutrients. While protein is obviously important, so too are fat and carbohydrates, not to mention a host of vitamins and minerals. In short, protein, as a nutrient (and lean muscle tissue as a food) is unlikely to have played as pivotal a role as in our origins and evolution as many paleoanthropologists currently assume.

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But even if paleoanthropologists have been misguided in singling out *protein* as a prime mover in human evolution, perhaps those who have looked instead at *meat* rather than protein per se have been closer to the mark. After all, meat can have substantial quantities of fat in it, and hence provide a richer food source without necessarily pushing a forager's intake past the ceiling posed by protein. This idea might be true were it not for the fact that much of human evolution took place in Africa, where the larger mammals upon which our hominin ancestors preyed or scavenged, are (on average) among the leanest known, even when they are in prime condition, and they may be reduced to "walking shoe-leather" when their fat reserves have been mobilized during recurrent periods of seasonal stress. This unusual aspect of the African fauna has been documented in detail by Ledger (1968), Pitts and Bullard (1968), and Hoffman and Wiklund (2006), as well as many earlier African travelers and explorers, and is succinctly put in perspective by Hill et al. (1984:111):

> Based on the body fat measurements of Brazilian specimens...we calculate the caloric value of paca, armadillo, agouti, opossum, and raccoon to be 242, 201,238, 211, and 299 cal/100 g live weight, respectively.... On the other hand, equivalent calculations for the African warthog and the hippopotamus yield 85 and 144 cal/100 g live weight, respectively. Other East African game animals are in this same range.... This points out the little-appreciated fact that many South American game animals are substantially fatter than common African or North American game.

The low fat levels that typify wild ungulates are also discussed by Cordain et al. (2002b:186–187):

> the major difference between domestic meat (muscle tissue) and game meat is in the total amount of fat. ...the total fat (5.63 g) in 100 g of grain-fed beef trimmed of all visible fat is more than double that in the muscle of antelope, deer, elk, cape buffalo and eland (mean = 2.2 g per 100 g tissue). The relatively higher total fat content in beef muscle meat (trimmed of surrounding fat) results from lipid accumulation in interfascicular adipocytes, a trait known as marbling....

There is a little doubt that our African ancestors would have benefitted from including meat in their diet – as a source of calories, some amount of fat, and of course protein. But this begs two critical questions that are seldom addressed head-on by paleoanthropologists: (1) how much meat? and (2) why meat from big animals?

With regard to the first question, most paleoanthropologists seem to assume, for the most part implicitly, that more is better and, as a consequence, that the story of human evolution is largely one of humans' ever-improving prowess as hunters.

Paleoanthropologists generally defer to optimal foraging theory when considering the second question. Put simply, big animals are argued to be the preferred targets because they yield higher return rates than smaller ones (but see Hill et al. 1987; Bird et al. 2009; and Koster 2008 for some interesting caveats pertinent to this commonplace, but sometimes erroneous, assumption, especially when large prey are also highly mobile and hence difficult to capture or kill). Thus, our history over the course of the Plio-Pleistocene, reduced to its barest essence, is typically seen as one of more and more hunting (or scavenging) of bigger and bigger animals until one day there were too many of us to be sustained by the hunt and we became farmers.

We have already dealt at some length with the many problems and shortcomings that would confront hominins relying on a diet based heavily on lean meat. If more is *not* necessarily better, then how much hunting should we expect just in terms of the foragers' protein needs? McGrew (2001:166–167) has already given us an answer and, for those who are life-long members of the protein fan-club, a rather surprising one at that–"not much." He noted some time ago that chimpanzees can collect enough ("high-quality") protein to fulfill their daily protein needs in half an hour of termite fishing. And, unlike the pursuit of large game, with its characteristically high failure rate, termite mounds are the ultimate in spatial and temporal co-operativeness.

The Ache provide further perspective on this issue. Current estimates of the protein requirement for healthy adult humans are about 0.83 g/kg body weight (Rand et al. 2003). For a 60 kg Ache, this amounts to about 50 g. Here, some observations made by Hill (1982) are particularly interesting. He notes that Ache males devote nearly 7 h a day to hunting (Hill and Kintigh 2009:370). According to the data summarized by Jenike (2001) and Sorensen and Leonard (2001), this level of effort places the Ache among the most physically active foragers on the planet, right up there with the Inuit (Eskimos). Yet, Kim Hill says:

> A striking finding...is that Ache hunters in eastern Paraguay obtain 0.27 kg of meat per hour foraging using no weapon or tool but their bare hands and occasionally a digging stick.... The calculation does not subtract out the time that Ache men spend hunting with bow and arrow, and thus an even higher overall rate would result if hunters concentrated only on hand-killed prey while foraging....
>
> Hill (1982:527)

Now, if we assume that meat is about 21% protein, less than 1 h of foraging *without the aid of tools* would yield about 270 g of meat or 56.7 g protein, more than enough to fulfill the hunter's protein needs for the day. Why then do the Ache continue hunting for almost six more hours each day (Hill and Kintigh 2009:370)? Surely, it is not for more protein.

Hill (1988:165) makes some other observations about the Ache that may help us sort out the extent to which nutrition is likely to be the principal force that drives the Ache to hunt as much as they do.

> ...Ache males could significantly increase their mean foraging return rate if they exploited more vegetable resources upon encounter. First, Ache women, on days when they do not spend time moving camp possessions and children, achieve a higher mean energetic foraging return rate than men do on those days, or all other foraging days. This means that men are choosing a lower caloric return foraging strategy than women choose. Second, aerial photos and ground transects suggest that palm densities in Paraguay are high enough that if men foraged for palm fiber alone, all day long, they could achieve a foraging return rate of 2630 calories per hour. This suggests that all resources characterized by return rates lower than 2630 calories per hour should be excluded from the optimal diet. Instead, men opt to hunt almost 7 hours per day at a return rate of only 1340 calories per hour. This number includes some calories due to honey acquisition, but is primarily meat.... Both of these observations suggest that something about hunting or its product, meat, is more attractive than vegetable collecting to Ache men. In fact, they suggest that acquiring half as many calories of meat per hour is more attractive to Ache men than an alternative foraging strategy that would produce twice as many calories in the form of starch.

Hill (1988; see also Bliege Bird and Bird 2008:657; Cronk 1991; Kaplan and Hill 1992:189; Marlowe 2007) notes other cases where quantitative studies have shown that hunting generated lower returns than plant collecting (e.g., the Cuiva or

Hiwi in Venezuela and the Yora or Yaminahua in Peru), and we have already noted at least three possible cases – San (Ju/'hoansi), Hadza, and the Ache – where hunters actually appear to have lost weight in course of their hunting activities. In the Hadza case, at least, such weight loss cannot be attributed entirely to high activity levels during the hunt, since much of the hunting was done from stationary blinds (O'Connell et al. 1988a).

Dwyer (1983) documented another interesting example, in this case from the Highlands of New Guinea, in which the energy expended by men in hunting exceeded the caloric return. Unfortunately, there are no corresponding body weight data to see whether the hunters actually lost weight at the same time.

Though not strictly hunter-gatherers, Ifaluk torch fishing provides another example of a male subsistence pursuit that entails a substantial investment of time and effort on the part of its participants despite its overall negative returns: "as a result of the significant time and energetic costs of preparation, men on average probably suffered a net caloric loss from torch fishing" (Sosis 2000:232).

Hilton and Greaves (2008:151) provide an interesting example drawn from the Pumé of Venezuela in which the high returns from women's plant-gathering activities clearly supported men's costly and unreliable hunting activities:

> Women target highly predictable foods such as roots and mangos that can be collected in large quantities. In contrast, men concentrate on meat, which requires searching and may produce no returns. It appears that the consistent and large returns of female foraging in the wet season underwrite the large energetic effort of men's hunting.

Finally, Cartmill (1993:28) offers an interesting commentary on hunting in present-day American society. While one might easily dismiss the U.S. case as fundamentally different from the situation in more traditional "subsistence" economies, the parallels with the examples already enumerated are interesting enough to be worth including here:

> The importance of hunting lies in its symbolism, not its economics. For a few skilled hunters in rural areas, 'harvesting' wild animals with a gun may still be an efficient way of putting meat on the table; but the average U.S. deer hunter, who expends about five man-hours of labor and $20 in cash to bring home a single pound of venison, would be better off harvesting some roast beef in a good restaurant.

Such trade-offs are not restricted just to whether males hunt or instead gather plant foods; they can also arise from the particular types of animals that men opt to focus on. Thus, among the Meriam (Torres Strait Islands, Australia), Bliege Bird (2007) shows that, by spearing fish, men have chosen a strategy that reduces their foraging efficiency compared with what they could attain where they to do as the women do and collect shellfish or go after small-hook fish:

> All else being equal, household production of food would be greater if men collected shellfish rather than spearing fish, or if men acquired more reef-top and small-hook fish that are less likely to be shared. Meriam men do not specialize in fishing activities that confront women with high child-care trade-offs; they specialize in high-variance fishing activities that are routinely shared. This preference for variance often trades off with the ability to maximize energetic efficiency, as it does for men fishing on the reef. Men prefer variance and unpredictability at a cost to their provisioning efficiency, and this choice further handicaps their ability to adjust subsistence effort to household needs.
>
> Bliege Bird (2007:449)

Bliege Bird and Bird (2008) offer another interesting example, in this case from the Martu, hunter-gatherers of the Western Desert of Australia. Martu women as well as men hunt, women focusing primarily on lizards (goanna), men hunting kangaroos and other large game. Although kangaroos are much bigger than goannas, providing a substantially greater return in meat per successful kill, the failure rate for large game (75%) is so much higher than for goanna (9% failure rate) that "...kangaroo hunters are operating at a cost to themselves – they would have a larger share [of meat] over the long term by remaining in camp and waiting for the goanna hunters to return" (Bliege Bird and Bird 2008:673).

The Barí inhabitants of the Maracaibo Basin along the border between Colombia and Venezuela provide another interesting example (Beckerman 1983):

> The tenet of optimal foraging theory of interest here posits that a forager should exploit a particular resource only when he cannot, on the average, get a better return for his time by exploiting some other resource(s).... That is, it is hardly an efficient use of time and labor to hunt at an average return of 100 g of meat per man-hour when one can fish at an average return of 400 g of meat per man-hour. The problem is that the Barí do just that – they continue hunting even in those seasons when fishing returns are several-fold higher than hunting returns.
>
> Beckerman (1983:269)

Venturing further afield and into the domain of primatology, a recent study by Gilby and Wrangham (2007; see also Watts and Mitani 2002; Matsumoto-Oda and Hayashi 1999; Newton-Fisher 2007:1313) offers an interesting analysis of chimpanzee red colobus monkey hunting, conducted by adult males, that is almost certainly not driven by a need for protein (a point made by the authors), and may not be driven by nutrition at all. This last suggestion is admittedly speculative on my part in the absence of quantitative data documenting the energetic returns from colobus hunting (adjusted for time and energy expended, and the likelihood of failure as well as injury) versus returns that males might obtain if they instead invested their efforts in plant foods, particularly fruits, seeds, and nuts. Nevertheless, Gilby and Wrangham's observations on chimpanzee hunting are intriguing, and dovetail amazingly well with observations I made earlier concerning the synchrony between plant food availability and big-game hunting activity among the San and Hadza:

> ... the Kanyawara chimpanzees were more likely to choose to hunt (a high-risk strategy) during periods when their diet quality was particularly high.
>
> Gilby and Wrangham (2007:1778)

> ...it is possible that chimpanzees hunt in response to shortages of specific macronutrients rather than energy in general. Protein is the most likely candidate, but Conklin-Brittain et al. (1998) demonstrated that protein intake varies little for the Kanyawara chimpanzees and is always high in relation to nutritional needs.
>
> Gilby and Wrangham (2007:1777)

> ...the individuals most at risk of specific macronutrient shortage would presumably be low-ranking females and young. However, meat is eaten mainly by adult males, whereas some females and young eat little or no meat. Thus, it is unlikely that hunting patterns are driven by specific macronutrient deficiencies....
>
> Gilby and Wrangham (2007:1777–1778)

Protein, therefore, is not what these chimps are after when they hunt, and I doubt their hunting reflects a need for fat or calories either. The red colobus monkey is very lean, much like other African mammals, averaging only about 3% fat and yielding <400 kcal/h (Wrangham and Conklin-Brittain 2003:40–41):

> The energy requirements for a *Homo erectus* female have been estimated at 2269-2487 per day.... At 400 cal/h, a *Homo erectus* [female] would therefore have had to chew raw meat for 5.7-6.2 h/day to satisfy her daily energy needs....

Stanford (1996), though talking about a different chimpanzee population, underscores the rather meager fat and energetic returns that these apes can anticipate from monkey hunting by comparison to what they could obtain by focusing just on the nuts of oil palms.

> At least one important food in the chimpanzee diet, the oil palm nut (palmae, *Elaeis guineensis*), is known to have eight times as many calories per kilogram and to be higher in unsaturated fat than monkey meat.... Oil palm trees are abundant and at least some are in fruit year-round at Gombe. Any cost-benefit analysis of foraging decisions by chimpanzees at Gombe or elsewhere must take into account the tradeoff between easily available palm nuts and more energetically expensive hunts for colobus meat.
>
> Stanford (1996:101)

Returning now to the Ache, it seems reasonably clear that neither protein nor calories are the reason why the Ache hunt as much as they do. As I have already indicated, these hunters can fulfill their basic protein needs, on average, in an hour or less. And in terms of calories, males would consistently do better, often substantially so, if they focused on plant foods, or on small or less mobile animals, rather than on hunting large game. To account for this enigma, Hill et al. (1987) suggest that the Ache are especially targeting the comparatively rich supply of fat found in Neotropical mammals such as armadillos and peccaries.

But the acquisition of fat in this manner comes at some considerable cost to Ache hunters:

> Most comparisons of hunting and gathering activities lead to the conclusion that hunting should be avoided when gathering can provide equal amounts of food. For example, hunting seems to be associated with greater risk of injury. In approximately 225 days of foraging with the Ache three serious wounds from animal bites were witnessed, six poisonous snake bites, and several arrow wounds, all of which were incurred while hunting. Hunting seems to be associated with greater exposure to heat, cold, and moisture in the Ache case, as well as greatly increasing the risk of becoming lost (something we observed several times). Because hunting takes place at a greater distance from the social group it may make individuals more vulnerable to hostile attacks from enemies, and means that any serious injury may result in death because of lack of assistance. The results of this greater danger can be demonstrated in the most extreme form by comparing Ache male and female death rates from accidental causes (snake bite, jaguar, falling out of a tree, getting lost, etc.). A sample of 169 adult Ache deaths shows 16% of male deaths and only 4% of female deaths from accidental causes.
>
> Hill (1988:168)

So, one must conclude that most of the Ache's Herculean efforts to acquire game, amounting to nearly seven very strenuous hours each day, not to mention all the accompanying risk from accident, illness, attack, and failure to make a kill, is driven by the need to acquire fat? Hardly, the Ache already have access to a richer supply of fat than foragers do in Africa, so why must they still devote the better part of each day to hunting? Armadillos alone account for 35% by weight of the game animals taken by the Ache. These animals are hunted without the use of weapons and they are quite fat even at the "lean" times of year, varying in fat content "between thin and fat pork" (Hill et al. 1984:127; see also Hill 2002:110; Hill and Hawkes 1983:165; Hill and Hurtado 1996:64).

Palm larvae are another important source of fat for the Ache, and perhaps were even more so prior to contact (26% fat and 9% protein; Hill et al. 1987:13–14; Hill and Hurtado 1996, 1999:93; see also Hawkes et al. 1982:383–386; Hurtado et al. 1985:17). Milton (1991:259) provides even higher fat (35–69%) and protein (22–39%) values for palm larvae exploited by Amazonian foragers in Brazil. Vellard's (1939) account from the 1930s vividly describes the value of palm larvae to the Ache (Guayaki):

> The pindo palm offers yet another alimentary resource for the Guayakis. The fallen, rotting trunks are home to large, white, soft larvae of the Coleoptera [beetles], Passalidae, 10 or 12 cm long and the thickness of a finger. The forestial Indians seem very fond of these larvae or of others analogous to them which live in different wood. Each time that my Mbwiha guides had the chance, they gathered them and, in the evening at camp, grilled them pierced on skewers over the fire. They curled up upon being scorched and a very fluid fat leaked out; browned just right, they emit a not too disagreeable odor. They melt in one's mouth like fat balls and their taste is similar to that of brains....
>
> Vellard (1939:84–85); translation from De Foliart (n.d.)

Clastres (1972), based on field work in the 1960s, provides another interesting description of the considerable importance of palm larvae as a source of fat for the Ache. According to his observations, the Ache deliberately managed and encouraged the resource, in a manner akin to "cultivation," by cutting down trees to provide suitable habitat for the growth of the larvae:

> By far the most important variety for the Guayaki is the one that produces the eggs of the very large coleoptera (*Mynda*). This insect lays its eggs in the trunk of the pindo palm, and the resulting larva (*guchu*) is enormous, sometimes growing to 4 inches in length. It is a sort of flabby sack filled with an oily, yellowish material, extremely rich in fats. The Indians eat it with relish in large quantities, cooked or raw.
>
> Clastres (1972:160)

> The interest in the *guchu* larvae is not limited solely to its food value. The Guayaki consider it more than a food gathered by chance in the forest; rather, it is the product of a sort of cultivation. The Indians knock down the palm tree, leaving a stump about 3 feet high. They then generally cut the fallen trunk into sections 10 or 12 feet long, preparing the wood for the insects, who can then lay their eggs more easily both in the stump and in the round sections on the ground. The larvae then reproduce and grow while feeding on the fibers of the wood. Each man is the owner of his larvae bed, since he alone cut and sectioned a certain number of palm trees. This private property is almost always respected and no one touches the larvae of another. Later, the harvest is divided and eaten collectively. Thus the Guayaki distribute a relatively abundant supply of food, which they can easily gather when returning to the larvae plantation after the beds are judged "ripe."
>
> Clastres (1972:160)

Thus, given the abundance and comparative reliability (at least seasonally) of such valuable sources of both fat and protein, it is difficult to avoid the conclusion that a lot more than nutrition is driving male foraging decisions, not just among the Ache, but also among other hunter-gatherers who devote a significant amount of their time and effort to the pursuit of large game.

And in the case of African ungulates, most of which are notoriously lean throughout the year, does it make nutritional sense to invest substantial amounts of time and energy to acquire large carcasses that are mostly lean muscle tissue? An interesting alternative, one championed by Cordain et al. (2001), is to posit that ancient hominins in Africa, like the modern Ache, were targeting primarily those parts of their larger prey that were particularly rich in fat; in other words, the brain, marrow bones, and perhaps the tongue. But why invest so heavily in what is clearly a laborious, dangerous, and often unsuccessful enterprise, not to mention inefficient and wasteful, just to get fat, when other food sources, such as insect larvae, oily nuts and seeds, eggs, and brains from small animals would have been more abundant, predictable, and "economical"? It really stretches credibility to think that all this time and effort is driven by nutritional needs.

It would seem that our early hominin relatives' apparent fondness for meat, and most especially the meat of large animals, may have far less to do with baseline nutritional needs than we have generally assumed. The million dollar question, of course, is why early hominins would have been so attracted to meat, and especially the meat of large mammals, if (1) in fresh, uncooked form it was essentially tasteless; (2) it was costly to acquire and calorically expensive to metabolize; (3) it offered a poor source of nutriment for the growing brain; (4) its acquisition was unreliable and sometimes dangerous; (5) it was potentially toxic to fetuses and nursing infants; and (6) protein was already widely available in more than adequate quantities in plant foods, insects, and a variety of small animals? Although this was perhaps not what Richard Lee (1968:41) had in mind when he penned these words some 40 years ago, he nonetheless captured the essence of the big-game hunting conundrum when he wrote: "…the Bushmen of the Dobe area eat as much vegetable food as they need, and as much meat as they can."

So, why has *big-game* hunting been so attractive to our hominin ancestors, as well as to our nearest primate relative, the chimpanzee? I suspect nutrition is only part of the answer, and probably not the major one. It seems far more likely (and I am certainly not the first to suggest this) that a key part of the answer to this question lies in the social, political, psychological, and/or reproductive domains, a direction of thinking that is rapidly gaining momentum in ethnology, behavioral ecology, primate studies, archaeology, and gender studies (e.g., Alvard 2002; Betzig 2008; Bird and Bliege Bird 2005; Bird and O'Connell 2006; Bliege Bird and Bird 2005, 2008; Bliege Bird and Smith 2005; Bliege Bird et al. 2001; Broughton and Bayham 2003; Codding and Jones 2007; Fiddes 1994; Gintis et al. 2001; Gomes and Boesch 2009; Gurven et al. 2000a, b; Hawkes et al. 2001; Kuhn and Stiner 2006; Marlowe 1999, 2003, 2004; McGuire and Hildebrandt 2005; Mitani and Watts 2001; O'Connell et al. 2002; Siskind 1973; Smith 2004; Smith et al. 2003; Sobal 2005; Stanford 1996, 1999, 2001a; Watts and Mitani 2002;

Wiessner 1996, 2002; Wood 2006; Wood and Hill 2000; Zahavi and Zahavi 1997; Zeanah 2004).

Ethnologists interested in the division of labor from the perspective of gender politics have been concerned for many years with the important role that big-game hunting and meat might play in establishing and fostering the asymmetries one commonly sees in male–female relations, even in so-called "egalitarian" (a misleading anthropological label if ever there was one!) foraging societies such as the San, Hadza, and Australian Aborigines. These studies make it eminently clear that there is much more to hunting and meat than protein, fat, or calories. Ernestine Friedl articulated this perspective more than three decades ago when she observed that:

> No matter what proportion of the diet it may represent, meat is always the favored food. It is the food believed to taste best, to be the most satisfying. The giving of meat from big game animals always confers prestige on the givers. This situation has important consequences for sex roles among hunters and gatherers.
>
> Friedl (1975:13), cited in Endicott (1981:5)

> First...meat as a scarce resource is valued above all others, second the hunter of meat is correspondingly valued, and third, honor and prestige are accorded the generous giver.
>
> Friedl (1975:22), cited in Endicott (1981:5)

Scattered throughout the voluminous literature on the San or Bushmen, one finds numerous illuminating statements that highlight the centrality of men's hunting activities in the domain of gender politics. For example, some four decades ago, Daniel McCall produced an interesting little monograph with a title that clearly encapsulated the essence of the link between hunting and sex in San ideology (*Wolf Courts Girl: The Equivalence of Hunting and Mating in Bushman Thought*).

> ...both hunting activities and sexual activities are given a magnified place in the ideology of the Bushmen in comparison with the frequency and performance. Both play an important part in the psychic life of these people and furthermore the two have become so intertwined that one symbolizes the other.
>
> McCall (1970:18)

Over the years, Megan Biesele has written extensively on the subject of male hunting and its prominent place in San ideology and gender politics:

> Mediation between the opposite sexual spheres centres around a comprehensive metaphor linking eating with intercourse. Men hunt and 'eat' women as carnivores prey on herbivores. Fat as a liquid solid, the 'cool' result of the union of hot and cold, is used as an alternative mediator. The consumption of fat is metaphoric of the sexual mediation between semen (hot) and menstrual blood (cold).
>
> Biesele (1993:196)

James Woodburn's extensive field work among the Hadza shows that hunting-related gender politics plays a key role among these African hunter-gatherers as well:

> Among the Hadza, the sacred *epeme* meat – certain rigidly prescribed and highly valued joints of meat of most large game animals – has to be eaten communally in secret by all of the co-resident initiated men together until it is finished. Hunters have no control of the

> *epeme* meat of any animal they kill. It is sacred meat belonging jointly to all the initiated men including the hunter, but only if he has already been initiated.
>
> Woodburn (2005:26)

> In comparison with large animals, small animals are less widely shared. None of their meat is *Epeme* meat. An animal the size of a hare or a fox will often be cooked and eaten in the bush by the hunter. Only if he gets a second one will he be likely to bring it back to camp and to share it.
>
> Woodburn (1998:52)

> Hadza women are excluded from hunting the larger animals and from using the most effective weapons but they are thereby protected from the dangers of big-game hunting and warfare. Men control the major sources of meat and their right to do so is manifest in the ritual of 'God's meat' which takes place after the killing of a large animal and from which women and children (including boys) are excluded.
>
> La Fontaine (1981:335)

Hunting-related gender politics is especially pronounced in many Australian Aboriginal societies, but in the interests of space, and the reader's patience, a single example must suffice here. In a group studied by Neville White (1985) in northeast Arnhem Land, women, regardless of their age or reproductive status, generally received smaller shares of meat than did males; and, they often were not permitted to eat animal fat. White's observations are echoed by Basil Hetzel, who comments that the "order of precedence of food distribution – old men, hunting men, children, dogs and women suggest[s] females are the most likely to develop malnutrition ...." (Hetzel 1978:41).

A number of anthropologists, looking across the broad spectrum of foraging societies, argue that the division of labor among such groups stems not from fundamental sex-based biological or physiological differences but from culturally derived, gender-based beliefs that preclude women's access to the essential hunting weapons and associated training needed to hunt big game and from many of the activities connected with the procurement, distribution, and consumption of meat.

> Thus while sex-classification [male/female] is universal, the particular attributes of each sex-class in any society are culturally specific. These attributes are, again universally, deemed intrinsic by association with anatomical features represented as the 'cause' of the other attributes. The terms 'man' and 'woman' therefore are constructs which serve as legitimising principles for, and constraints on, behaviour.
>
> La Fontaine (1981:335)

> The relative value accorded to hunting and to big-game meat and the convertibility of these into prestige and authority are also of near-universal distribution in foraging societies, and it is with these and not with physiological differences that the exclusion of women's hunting can be put into correspondence. The sexual division of foraging labor at once allocates primarily to men both society's most valued labor and opportunities to distribute its most valued foods. Arbitrary in relation to physiological sex differences, the division of labor is thus motivated in relation to gender politics.
>
> Brightman (1996:712)

> Ce n'est pas la chasse qui est interdite aux femmes, ce sont les armes; c'est l'accès aux armes, en tant que telles et en tant que concrétisation d'un développement technologique, qui leur est refusé.
>
> Tabet (1979:28)

> Among modern hunter-gatherers, exclusion of females from the individualistic hunting of larger mammals seems to be closely related to the making and using of hunting weapons and associated economic and/or religious ideas. Women have no weapons of their own which are specially made to hunt animals. If they want to hunt they must do so without weapons or otherwise with some provisional weapons such as sticks. Rarely do they use specially made hunting weapons such as harpoons or spears, although these might be borrowed temporarily from males. Under these restrictions women's hunting activities are confined to small animal hunts in which they take part in driving, and, very rarely, individual hunts of larger mammals. Ethnographic data suggest that perhaps the development of hunting weapons and ideas associated with them is one of the factors relevant to the tendency towards the exclusion of females from hunting.
>
> Watanabe (1968:74–75)

Ideas stemming from evolutionary biology are becoming increasingly prominent in recent literature concerned with why men invest heavily in the unreliable enterprise of big-game hunting and distribute much of the proceeds of the hunt to non-kin rather than to their own families.

> Hawkes and colleagues argue that big-game hunting is often a form of *costly signaling*, a means by which men establish and maintain social position relative to their peers and competitors, not just among the Hadza but among foragers in general.... To the degree the hunter is successful, two ends are achieved. First, because big-game hunting is a risky, skill-intensive undertaking, the good hunter marks himself as a powerful ally and dangerous adversary. His relationships with others are likely to be structured accordingly. Equally important, his successes make available a "public good," one that is of interest to all, unpredictably acquired, readily divisible, and thus likely to be shared widely..., considerations that draw still more favorable attention his way. That attention might include deference to his wishes, support in disputes, positive dealings with his spouse and children, and more frequent mating opportunities....
>
> Bird and O'Connell (2006:164–165), emphasis added

Geoffrey Miller, in a sweeping look at the evolution of human *cultural* productions, concludes that "art, music, myth, ritual and other cultural phenomena" are all forms of costly signaling that developed within the context of sexual selection. From Miller's perspective even male big-game hunting would fit comfortably within the domain of costly signaling:

> A single pattern seems to pervade the age-sex profiles of cultural production across quite different media from different cultures and historical epochs. Human males and females show a virtually identical age profile for cultural production: a rapid rise following late adolescence, a peak around age thirty (plus or minus a few years), and a roughly exponential decline throughout the remainder of life, with the most rapid productivity loss between ages forty and sixty, followed by a more gradual decline until death. This age pattern for cultural production resembles that found for many other domains of display behaviour….
>
> Miller (1999:86)

> …this universal profile will be found for every quantifiable human behaviour that is public (i.e. perceivable by many potential mates) and costly (i.e. not affordable by all sexual competitors) …. If the universal profile is replicated for other genres, other media, other cultures and other historical epochs, it could be interpreted as an evolved, species-typical, sexually dimorphic, life-history adaptation, shaped by sexual selection and fundamental to understanding the distribution of cultural behaviour in our species.
>
> Miller (1999:87)

Gavrilets et al. (2008), in modeling the emergence of egalitarianism in human foraging societies, provide an interesting framework that links the evolution of our species' unique cognitive abilities in the context of within-group competition to the formation of cooperative coalitions that can ultimately expand to encompass all members of a social group. Costly signaling related to men's big-game hunting might well play an important role in this process. Svensson (2009:234) provides a concise summary of the argument:

> …networks of allies ('coalitions') emerge as a result of within-group competition between individuals for resources, social status or mates. Social networks and the high cognitive abilities of humans play a key role in this process. Group members utilize information from within-group conflicts (dyadic interactions), and can then form coalitions based on the information they have obtained from these antagonistic interactions. This leads to a self-reinforcing positive feedback loop, or a 'runaway' process, in which coalitions grow larger and larger, and they might ultimately encompass all or most members of the original group. As the network grows, individuals outside the coalition are at a disadvantage, and at some point it pays to join the coalition and becomes almost impossible to remain outside.

Interestingly, Rebecca Bliege Bird and colleagues, based on extensive fieldwork among the Martu, an Aboriginal people in the Western Desert of Australia, see costly signaling tied to men's big-game hunting successes and subsequent widespread meat-sharing (which they refer to as the successful hunter's "magnanimity") leading in the opposite direction–toward greater inequalities, at least in terms of gender:

> Martu men's foraging goals more often involve political strategies, in which men use hunting for high-variance prey (here, mainly kangaroo) as a way to rise in the ritual hierarchy. Because the acquisition and distribution of high-variance prey ends up being costly, it can serve as an honest signal of a hunter's absolute generosity, and of his or her motivation to work for the public good…. For Martu, this magnanimity demonstrates an honest disengagement with property, …not only one who is a skilled producer, but one who frequently produces public goods…. For Martu, inequalities develop as a function not of who keeps more, but of who produces more, which leads to a sort of competitive magnanimity that provides the basis for both secular and religious hierarchy…..
>
> Bird et al. (2009:122); see also Bird and Bliege Bird (2010)

Costly signaling, though currently very popular in forager studies (and beyond), is not the only explanation on the table nowadays. An earlier though closely related explanation is known as the "show-off hypothesis," persuasively put forward by Hawkes (1990, 1991; see also Gomes and Boesch 2009), which suggests that men's hunting and widespread sharing of meat benefits the successful hunter by gaining greater social attention for himself and his family, with fitness benefits in terms of child care, a variety of other forms of help and support, and increased mating opportunities.

Other recent or current approaches focus more on the benefits of cooperation among individuals in hunting and in other activities (e.g., Gurven et al. 2002; Hill 2002); sharing meat in order to recruit and maintain coalitional support (Patton 2005), an argument akin to the one put forward by Gavrilets et al. (2008); providing meat as a means of establishing a reputation for generosity (Gurven et al. 2000a); and so forth (for an interesting discussion of alternatives, see Codding and Jones 2007).

And, as is so often the case, reality is turning out to be more complex than any one of these models might anticipate, suggesting that it may be necessary to combine approaches. Complexities of this sort are nicely illustrated, for example, by Marlowe's (1999, 2003) work among the Hadza, which suggests that men's hunting and sharing behavior might best be explained as a provisioning strategy when they are feeding their own children, but something more akin to costly signaling when they have stepchildren. Similarly, Wood and Hill (2000) and Wood (2006) propose that men may be more likely to pursue a costly signaling strategy when they are unmarried or widowed, and a provisioning strategy when they are married with children (see also Heath and Hadley 1998). Thornhill and Gangestad (2008) suggest that prey size may enter into the calculus, such that hunting of large game may be directed primarily toward mating effort, while procurement of smaller animals may function more in the realm of provisioning:

> …different hunting endeavors may differentially benefit men through parental investment and mating effort. Hawkes et al. (2001) emphasize that men's large-game hunting is not an effective or efficient means of provisioning offspring. But large-game hunting (in at least some foraging societies) may benefit men substantially in the form of mating effort. By contrast, men in foraging societies have much more control of the distribution of captured small game and may preferentially direct it toward primary partners and offspring, such that hunting of small game functions as an effective means of paternal investment.
>
> Thornhill and Gangestad (2008:66)

Apostolou (2007), based on a cross-cultural look at marriage practices among a wide range of foraging societies, suggests that signaling by a man seeking a marriage partner may be directed not just at the potential mate, but at her parents, and especially at her father, who may play a prominent if not determinant role in choosing the husband.

Finally, Wiessner (2002:429) sees signaling among the Ju/'hoansi as varying in importance at different stages in a man's life, and that "...provisioning, signaling, reciprocity, nepotism, and long-term political objectives were all outcomes achieved by producing and distributing a surplus of meat" (see also Alvard and Gillespie 2004; Gurven et al. 2000b; Gurven and Hill 2009; Gurven and von Rueden 2006; Smith 2004).

Regardless of how these various approaches finally shake out in the end, they all share one appealing feature in common–their emphasis is squarely on the social, political, psychological, and/or reproductive benefits that accrue from big-game hunting and meat-sharing, not solely on the nutritional value of the meat itself. The calories and nutrients one gets from eating meat are certainly not to be dismissed as irrelevant, but they should be seen as added benefits (and, at times, as added costs) of big-game hunting, not its *raison d'être*.

# References

Adams, J. L., 1999. Refocusing the role of food-grinding tools as correlates for subsistence strategies in the U. S. Southwest. *Am. Antiq.* 64(3):475–498.

Addy, E. O., Eteshola, E., 1984. Nutritive value of a mixture of tigernut tubers (*Cyperus esculentus* L.) and baobab seeds (*Adansonia digitata* L.). *J. Sci. Food Agric.* 35(4):437–440.

Adrian, J., Rerat, A., Xabrecas, J., 1955. L'huile et le tourteau de *Ricinodendron rautanenii*: une uouvelle possibilité alimentaire Africaine. *Oleagineux* 10:481–487.

Aiello, L. C., 2007. Notes on the implications of the expensive tissue hypothesis for human biological and social evolution. In: Roebroeks, W. (Ed.), *Guts and Brains: An Integrative Approach to the Hominin Record*. Leiden University Press, Amsterdam, The Netherlands, pp. 17–28.

Aiello, L. C., Wells, J. C. K., 2002. Energetics and the evolution of the genus *Homo*. *Annu. Rev. Anthropol.* 31:323–338.

Aiello, L. C., Wheeler, P., 1995. The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Curr. Anthropol.* 36(2):199–221.

Ailhaud, G., Guesnet, P., 2004. Fatty acid composition of fats is an early determinant of childhood obesity: a short review and an opinion. *Obes. Rev.* 5(1):21–26.

Akey, J. M., Eberle, M. A., Rieder, M. J., Carlson, C. S., Shriver, M. D., Nickerson, D. A., Kruglyak, L., 2004. Population history and natural selection shape patterns of genetic variation in 132 genes. *PLoS Biol.* 2(10):e28. doi:10.1371/journal.pbio.0020286.

Al, M. D. M., Houwelingen, A. C., van, Hornstra, G., 2000. Long-chain polyunsaturated fatty acids, pregnancy, and pregnancy outcome. *Am. J. Clin. Nutr.* 71(Suppl.):285S–291S.

Alemseged, Z., Bobe, R., 2009. Diet in early hominin species: a paleoenvironmental perspective. In: Hublin, J.-J., Richards, M. P. (Eds.), *The Evolution of Hominid Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*. Vertebrate Paleobiology and Paleoanthropology. Springer, Dordrecht, The Netherlands, pp. 181–188.

Alessandri, J.-M., Extier, A., Langelier, B., Perruchot, M.-H., Heberden, C., Guesnet, P., Lavialle, M., 2008. Estradiol favors the formation of eicosapentaenoic acid (20:5*n*-3) and *n*-3 docosapentaenoic acid (22:5*n*-3) from alpha-linolenic acid (18:3*n*-3) in SH-SY5Y neuroblastoma cells. *Lipids* 43(1):19–28.

Alexander, J. E., 1838. *An Expedition of Discovery into the Interior of Africa, Through the Hitherto Undescribed Countries of the Great Namaquas, Boschmans, and Hill Damaras. Performed Under the Auspices of Her Majesty's Government, and the Royal Geographical Society, Vol. 1*. Henry Colburn, London, England.

Allen, D. L., 1979. *Wolves of Minong: Their Vital Role in a Wild Community*. Houghton Mifflin Company, Boston, MA.

Allen, J. A., 1877. *History of the American Bison, Bison americanus*. U.S. Government Printing Office, Washington, DC.

Allport, S., 2006. *The Queen of Fats: Why Omega-3s were Removed from the Western Diet and What We Can Do to Replace Them*. University of California Press, Berkeley, CA.

Alvard, M. S., 2002. Carcass ownership and meat distribution by big-game cooperative hunters. In: Dannhaeuser, N., Werner, C. (Eds.), *Social Dimensions in the Economic Process*. Res. Econ. Anthropol. 21. Elsevier/JAI Press, New York, NY, pp. 99–131.

Alvard, M. S., Gillespie, A., 2004. Good Lamalera whale hunters accrue reproductive benefits. *Res. Econ. Anthropol.* 23:223–245.

Amarteifio, J. O., Moholo, D., 1998. The chemical composition of four legumes consumed in Botswana. *J. Food Compost. Anal.* 11(4):329–332.

Amarteifio, J. O., Mosase, M. O., 2006. The chemical composition of selected indigenous fruits of Botswana. *J. Appl. Sci. Environ. Manag.* 10(2):43–47.

Ambrose, S. H., Katzenberg, M. A. (Eds.), 2001. *Biogeochemical Approaches to Paleodietary Analysis*. Adv. Archaeol. Museum Sci. 5. Kluwer Academic/Plenum Press, New York, NY.

Amen-Ra, N., 2007. How dietary restriction catalyzed the evolution of the human brain: an exposition of the nutritional neurotrophic neoteny theory. *Med. Hypotheses* 69(5):1147–1153.

Ames, B. N., 1983. Dietary carcinogens and anticarcinogens: oxygen radicals and degenerative diseases. *Science* 221(4617):1256–1264.

Amusquivar, E., Sánchez, M., Hyde, M. J., Laws, J., Clarke, L., Herrera, E., 2008. Influence of fatty acid profile of total parenteral nutrition emulsions on the fatty acid composition of different tissues of piglets. *Lipids* 43(8):713–722.

Andersen, S. M., 2005. *Vitamins and Minerals in the Traditional Greenland Diet*. NERI Technical Report 528. Ministry of the Environment, National Environmental Research Institute, Copenhagen, Denmark.

Andersson, C. J., 1857. *Lake Ngami; or, Explorations and Discoveries During Four Years' Wanderings in the Wilds of South Western Africa*. Dix, Edwards and Company, New York, NY.

Anonymous, 1814. Cookery. In: Cooper, T. (Ed.), *The Emporium of Arts and Sciences, Vol. 2(3, New Series)*. Kimber and Richardson, Philadelphia, PA, pp. 456–468 (signed only as "Epicuri de grege porcus").

Anonymous, 1859. The new venison. In: Littell, E. (Ed.), *Littell's Living Age. Vol. 61, Third Series, Fifth Quarterly Volume. From the Beginning*. Littell, Son, and Company, Boston, MA, pp. 255–256.

Anthony, J. C., Anthony, T. G., Layman, D. K., 1999. Leucine supplementation enhances skeletal muscle recovery in rats following exercise. *J. Nutr.* 129(6):1102–1106.

Antón, S. C., Aziz, F., Zaim, Y., 2001. Plio-Pleistocene *Homo*: patterns and determinants of dispersal. In: Tobias, P. V., Raath, M. A., Moggi-Cecchi, J., Doyle, G. A. (Eds.), *Humanity from African Naissance to Coming Millennia. Colloquia in Human Biology and Palaeoanthropology*. Firenze University Press and Witwatersrand University Press, Firenze, Italy and Johannesburg, South Africa, pp. 91–102.

Apostolou, M., 2007. Sexual selection under parental choice: the role of parents in the evolution of human mating. *Evol. Hum. Behav.* 28(6):403–409.

Aranguren, B., Becattini, R., Lippi, M. M., Revedin, A., 2007. Grinding flour in Upper Palaeolithic Europe (25 000 years bp). *Antiquity* 81(314):845–855.

Ardrey, R., 1961. *African Genesis: A Personal Investigation into the Animal Origins and Nature of Man*. Atheneum, New York, NY.

Aristotle, 1897 (350 BC). *History of Animals, Book III*. Cresswell, R. (Trans.). George Bell and Sons, London, England.

Arjmandi, B. H., Khalil, D. A., Smith, B. J., Lucas, E. A., Juma, S., Payton, M. E., Wild, R. A., 2003. Soy protein has a greater effect on bone in postmenopausal women not on hormone replacement therapy, as evidenced by reducing bone resorption and urinary calcium excretion. *J. Clin. Endocrinol. Metab.* 88(3):1048–1054.

Arnold, T. H., Wells, M. J., Wehmeyer, A. S., 1985. Khoisan food plants: taxa with potential for future economic exploitation. In: Wickens, G. E., Goodin, J. R., Field, D. V. (Eds.), *Plants for Arid Lands. Proceedings of the Kew International Conference on Economic Plants for Arid Lands Held in the Jodrell Laboratory, Royal Botanic Gardens, Kew, England, 23–27 July, 1984*. George Allen and Unwin, London, England, pp. 69–86.

Arnqvist, G., Rowe, L., 2005. *Sexual Conflict*. Monographs in Behavior and Ecology. Princeton University Press, Princeton, NJ.

Arterburn, L. M., Hall, E. B., Oken, H., 2006. Distribution, interconversion, and dose response of *n*-3 fatty acids in humans. *Am. J. Clin. Nutr.* 83(6):S1467–1476S.

Atkins, R. C., 1973. *Dr. Atkins' Diet Revolution: The High Calorie Way to Stay Thin Forever*. Bantam Books, New York, NY.

Atkins, R. C., 1997. *Dr. Atkins' New Diet Revolution*. Avon Books, New York, NY.

Axelsson, I., 2006. Effects of high protein intakes. In: Rigo, J., Ziegler, E. E. (Eds.), *Protein and Energy Requirements in Infancy and Childhood*. Nestlé Nutrition Workshop Series, Pediatric Program 58. Karger and Nestlé Nutrition Institute, Basel and Vevey, Switzerland, pp. 121–131.

Back, G., 1836. *Narrative of the Arctic Land Expedition to the Mouth of the Great Fish River, and Along the Shores of the Arctic Ocean, in the Years 1833, 1834, and 1835*. John Murray, London, England.

Bakewell, L., Burdge, G. C., Calder, P. C., 2006. Polyunsaturated fatty acid concentrations in young men and women consuming their habitual diets. *Br. J. Nutr.* 96(1):93–99.

Balaresque, P. L., Ballereau, S. J., Jobling, M. A., 2007. Challenges in human genetic diversity: demographic history and adaptation. *Hum. Mol. Genet.* 16(Rev. Issue 2):R134–R139.

Baldwin, E. B., 1896. *The Search for the North Pole, or Life in the Great White World. A Complete and Connected Story of Arctic Explorations, Superbly Illustrated from Real Scenes. Replete With Anecdote, Incident, Thrilling Adventure, and Intensely Interesting Information. The Book With a Purpose Consecrated to Further Polar Investigation*. Sold Only by Subscription, Chicago, IL.

Baldwin, G. C., 1950. The pottery of the Southern Paiute. *Am. Antiq.* 16(1):50–56.

Bang, H. O., Dyerberg J., Hjøorne, N., 1976. The composition of food consumed by Greenland Eskimos. *Acta Med. Scand.* 200(1–2):69–73.

Bank, A. (Ed.), 1998. *The Proceedings of the Khoisan Identities and Cultural Heritage Conference. Organised by the Institute for Historical Research, University of the Western Cape, Held at the South African Museum, Cape Town, South Africa, 12–16 July 1997*. Institute for Historical Research, University of the Western Cape and InfoSource, Bellville, South Africa.

Bankir, L., Bouby, N., Trinh-Trang-Tan, M.-M., Ahloulay, M., Promeneur, D., 1996. Direct and indirect cost of urea excretion. *Kidney Int.* 49(6):1598–1607.

Bankir, L., Kriz, W., 1995. Adaptation of the kidney to protein intake and to urine concentrating activity: similar consequences in health and CRF. *Kidney Int.* 47(1):7–24.

Barceló-Coblijn, G., Collison, L. W., Jolly, C. A., Murphy, E. J., 2005. Dietary α-linolenic acid increases brain but not heart and liver docosahexaenoic acid levels. *Lipids* 40(8):787–798.

Barlow, K. R., Metcalfe, D., 1996. Plant utility indices: two Great Basin examples. *J. Archaeol. Sci.* 23(3):351–371.

Barnard, A., 2002. Hunter–gatherers: seventeenth or eighteenth-century invention? *Archaeol. Dialogues* 9(2):119–122.

Barnard, A., 2004. Hunter–gatherers in history, archaeology and anthropology: introductory essay. In: Barnard, A. (Ed.), *Hunter–Gatherers in History, Archaeology and Anthropology*. Berg, Oxford, England, pp. 1–13.

Barnard, A., 2007. *Anthropology and the Bushman*. Berg, Oxford, England.

Barnes, R. H., 1976. Energy. In: Hegsted, D. M. (Ed.), *Present Knowledge in Nutrition*. 4th ed. Nutrition Foundation, New York, NY, pp. 10–16.

Barreiro, L. B., Laval, G., Quach, H., Patin, E., Quintana-Murci, L., 2008. Natural selection has driven population differentiation in modern humans. *Nat. Genet.* 40(3):423–436.

Barrow, J., 1806. *Travels Into the Interior of Southern Africa: In Which Are Described the Character and Condition of the Dutch Colonists of the Cape of Good Hope, and of the Several Tribes of Natives Beyond Its Limits: The Natural History of Such Subjects as Occurred in the Animal, Mineral and Vegetable Kingdoms; and the Geography of the Southern Extremity of Africa.* Comprehending Also a Topographical and Statistical Sketch of Cape Colony; With an Inquiry Into Its Importance as a Naval and Military Station, as a Commercial Emporium; as a Territorial Possession, Vol. 1. 2nd ed. T. Cadell and W. Davies, London, England.

Bartram, L. E., 1997. A comparison of Kua (Botswana) and Hadza (Tanzania) bow and arrow hunting. In: Knecht, H. (Ed.), *Projectile Technology*. Interdisciplinary Contributions to Archaeology. Plenum, New York, NY, pp. 321–343.

Barzel, U. S., Massey, L. K., 1998. Excess dietary protein can adversely affect bone. *J. Nutr.* 128(6):1051–1053.

Beauchamp, G. K., Pearson, P., 1991. Human development and umami taste. *Physiol. Behav.* 49(5):1009–1012.

Becker, H., 2003. The least sexist society? perspectives on gender, change and violence among southern African San. *J. South. Afr. Stud.* 29(1):5–23.

Beckerman, S., 1983. Carpe diem: an optimal foraging approach to Bari fishing and hunting. In: Hames, R. B., Vickers, W. T. (Eds.), *Adaptive Responses of Native Amazonians*. Academic Press, New York, NY, pp. 269–299.

Begon, M., Harper, J. L., Townsend, C. R., 1996. *Ecology: Individuals, Populations, and Communities*. 3rd ed. Blackwell Science, Oxford, England.

Behrensmeyer, A. K., 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya. *Harvard University, Museum of Comparative Zoology Bulletin* 146(10):473–578.

Bell, M., 1928. Studies on the composition of human milk. *J. Biol. Chem.* 80(1):239–247.

Bellisle, F., 1999. Glutamate and the umami taste: sensory, metabolic, nutritional and behavioural considerations. A review of the literature published in the last 10 years. *Neurosci. Biobehav. Rev.* 23(3):423–438.

Ben Shaul, D. M., 1962. The composition of the milk of wild animals. *Int. Zoo Yearb.* 4:333–342.

Bender, A. E., Ballance, P. E., 1961. A preliminary examination of the flavour of meat extract. *J. Sci. Food Agric.* 12(10):683–687.

Benison, C. J., 1999. Burned rock complexes, baked clay objects, steatite, and ceramics: evolutionary implications for Plains/Eastern Woodlands cooking technologies. *N. Am. Archaeol.* 20(4):287–317.

Benyshek, D. C., Watson, J. T., 2006. Exploring the thrifty genotype's food-shortage assumptions: a cross-cultural comparison of ethnographic accounts of food security among foraging and agricultural societies. *Am. J. Phys. Anthropol.* 131(1):120–126.

Bere, E., 2007. Wild berries: a good source of omega-3. *Eur. J. Clin. Nutr.* 61(3):431–433.

Berg, C. P., 1953. Physiology of the D-amino acids. *Physiol. Rev.* 33(2):145–189.

Berger, T. D., Trinkaus, E., 1995. Patterns of trauma among the Neandertals. *J. Archaeol. Sci.* 22(6):841–852.

Bernal, V., Novellino, P., Gonzalez, P. N., Perez, S. I., 2007. Role of wild plant foods among late Holocene hunter–gatherers from central and north Patagonia (South America): an approach from dental evidence. *Am. J. Phys. Anthropol.* 133(4):1047–1059.

Bernstein, A. M., Treyzon, L., Li, Z., 2007. Are high-protein, vegetable-based diets safe for kidney function? A review of the literature. *J. Am. Diet. Assoc.* 107(4):644–650.

Betzig, L. L., 2008. Hunting kings. *Cross-Cult. Res.* 42(3):270–289.

Biesele, M., 1993. *Women Like Meat: The Folklore and Foraging Ideology of the Kalahari Ju/'hoan*. Indiana University Press, Bloomington, IN.

Biesele, M., Barclay, S., 2001. Ju/'hoan women's tracking knowledge and its contribution to their husbands' hunting success. *Afr. Study Monogr. Suppl.* 26:67–84.

Biesele, M., Guenther, M. G., Hitchcock, R. K., Lee, R. B., MacGregor, J., 1989. Hunters, clients and squatters: the contemporary socioeconomic status of Botswana Basarwa. *Afr. Study Monogr.* 9(3):109–151.

Biesele, M., Royal/O/oo, K., 1997. *San*. Heritage Library of African Peoples. Rosen Publishing Group, New York, NY.

Bigiani, A., 2005. Glutamate receptors in taste receptor cells. In: Gill, S., Pulido, O. (Eds.), *Glutamate Receptors in Peripheral Tissue: Excitatory Transmission Outside the CNS*. Springer, New York, NY, pp. 129–145.

Bigwood, E. J. (Ed.), 1972. *Protein and Amino Acid Functions*. Pergamon Press, Oxford, England.

Bilsborough, S., Mann, N., 2006. A review of issues of dietary protein intake in humans. *Int. J. Sport Nutr. Exerc. Metab.* 16(2):129–152.

Binford, L. R., 1968. Post-pleistocene adaptations. In: Binford, S. R., Binford, L. R. (Eds.), *New Perspectives in Archaeology*. Aldine, Chicago, IL, pp. 313–342.

Binford, L. R., 1978. *Nunamiut Ethnoarchaeology*. Academic Press, New York, NY.

Binford, L. R., 1981. *Bones: Ancient Men and Modern Myths*. Academic Press, New York, NY.

Binford, L. R., 2001. *Constructing Frames of Reference: An Analytical Method for Archaeological Theory Building Using Hunter–Gatherer and Environmental Data Sets*. University of California Press, Berkeley, CA.

Binford, L. R., 2006. Bands as characteristic of "mobile hunter–gatherers" may exist only in the history of anthropology. In: Sellet, F., Greaves, R. D., Yu, P.-L. (Eds.), *Archaeology and Ethnoarchaeology of Mobility*. University Press of Florida, Gainesville, FL, pp. 3–22.

Birch, G. G., Kemp, S. E., 1989. Apparent specific volumes and tastes of amino acids. *Chem. Senses* 14(2):249–258.

Bird, D. W., Bliege Bird, R., 2005. Mardu children's hunting strategies in the Western Desert, Australia: foraging and the evolution of human life histories. In: Hewlett, B. S., Lamb, M. E. (Eds.), *Hunter Gatherer Childhoods*. Aldine de Gruyter, New York, NY, pp. 129–146.

Bird, D. W., Bliege Bird, R. L., 2010. Competing to be leaderless: food sharing and magnanimity among Martu Aborigines. In: Vaughn, K. J., Eerkins, J., Kantner, J. (Eds.), *The Emergence Of Leadership: Transitions in Decision Making from Small-Scale to Middle-Range Societies*. School of Advanced Research Press, Santa Fe, NM, pp. 21–49.

Bird, D. W., Bliege Bird, R., Codding, B. F., 2009. In pursuit of mobile prey: Martu hunting strategies and archaeofaunal interpretation. *Am. Antiq.* 74(1):3–29.

Bird, D. W., O'Connell, J. F., 2006. Behavioral ecology and archaeology. *J. Archaeol. Res.* 14(2):143–188.

Bird, P. J., 2003. Why does fat deposit on the hips and thighs of women and around the stomachs of men? In: Scientific American (Eds.), *Scientific American's Ask the Experts: Answers to the Most Puzzling and Mind-Blowing Science Questions*. HarperCollins, New York, NY, pp. 125–127.

Bird-David, N., 1990. The giving environment: another perspective on the economic system of gatherer-hunters. *Curr. Anthropol.* 31(2):189–196.

Birdsell, J. B., 1953. Some environmental and cultural factors influencing the structuring of Australian Aboriginal populations. *Am. Nat.* 87(834):171–207.

Birdsell, J. B., 1958. On population structure in generalized hunting and collecting populations. *Evolution* 12(2):189–205.

Blaak, E., 2001. Gender differences in fat metabolism. *Curr. Opin. Clin. Nutr. Metab. Care* 4(6):499–502.

Blank, C., Neumann, M. A., Makrides, M., Gibson, R. A., 2002. Optimizing DHA levels in piglets by lowering the linoleic acid to α-linolenic acid ratio. *J. Lipid Res.* 43(9):1537–1543.

Bliege Bird, R. L., 2007. Fishing and the sexual division of labor among the Meriam. *Am. Anthropol.* 109(3):442–451.

Bliege Bird, R. L., Bird, D. W., 2005. Human hunting seasonality. In: Brockman, D. K., van Schaik, C. P. (Eds.), *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates.* Cambridge University Press, Cambridge, England, pp. 243–266.

Bliege Bird, R. L., Bird, D. W., 2008. Why women hunt: risk and contemporary foraging in a Western Desert Aboriginal community. *Curr. Anthropol.* 49(4):655–693.

Bliege Bird, R. L., Codding, B. F., Bird, D. W., 2009. What explains differences in men's and women's production? Determinants of gendered foraging inequalities among Martu. *Hum. Nat.* 20(2):105–129.

Bliege Bird, R. L., Smith, E. A., 2005. Signaling theory, strategic interaction, and symbolic capital. *Curr. Anthropol.* 46(2):221–248.

Bliege Bird, R. L., Smith, E. A., Bird, D. W., 2001. The hunting handicap: costly signaling in human foraging strategies. *Behav. Ecol. Sociobiol.* 50(1):9–19.

Blumenschine, R. J., 1986. *Early Hominid Scavenging Opportunities: Implications of Carcass Availability in the Serengeti and Ngorongoro Ecosystems*. BAR International Series 283. British Archaeological Reports, Oxford, England.

Blumenschine, R. J., 1995. Percussion marks, tooth marks, and experimental determinations of the timing of hominid and carnivore access to long bones at FLK *Zinjanthropus*, Olduvai Gorge, Tanzania. *J. Hum. Evol.* 29(1):21–51.

Blumenschine, R. J., Caro, T. M., 1986. Unit flesh weights of some East African bovids. *Afr. J. Ecol.* 24(4):273–286.

Blumenschine, R. J., Madrigal, T. C., 1993. Variability in long bone marrow yields of east African ungulates and its zooarchaeological implications. *J. Archaeol. Sci.* 20(5):555–587.

Blumenschine, R. J., Prassack, K. A., Kreger, C. D., Pante, M. C., 2007. Carnivore tooth-marks, microbial bioerosion, and the invalidation of Domínguez-Rodrigo and Barba's (2006) test of Oldowan hominin scavenging behavior. *J. Hum. Evol.* 53(4):420–426.

Blurton Jones, N. G., 2002. The lives of hunter–gatherer children: effects of parental behavior and parental reproductive strategy. In: Pereira, M. E., Fairbanks, L. A. (Eds.), *Juvenile Primates: Life History, Development, and Behavior*. Oxford University Press, Oxford, England, pp. 309–326.

Blurton Jones, N. G., Hawkes, K., Draper, P., 1994. Foraging returns of !Kung adults and children: why didn't! Kung children forage? *J. Anthropol. Res.* 50(3):217–248.

Blurton Jones, N. G., Marlowe, F. W., 2002. Selection for delayed maturity: does it take 20 years to learn to hunt and gather? *Hum. Nat.* 13(2):199–238.

Blurton Jones, N. G., Smith, L. C., O'Connell, J. F., Hawkes, K., Kamuzora, C. L., 1992. Demography of the Hadza, an increasing and high density population of savanna foragers. *Am. J. Phys. Anthropol.* 89(2):159–181.

Boaretto, E., Wu, X., Yuan, J., Bar-Yosef, O., Chu, V., Pan, Y., Liu, K., Cohen, D., Jiao, T., Li, S., Gu, H., Goldberg, P., Weiner, S., 2009. Radiocarbon dating of charcoal and bone collagen associated with early pottery at Yuchanyan Cave, Hunan Province, China. *Proc. Natl. Acad. Sci.* 106(24):9595–9600.

Boback, S. M., Cox, C. L., Ott, B. D., Carmody, R., Wrangham, R. W., Secor, S. M., 2007. Cooking and grinding reduces the cost of meat digestion. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 148(3):651–656.

Bock, J., 2005. What makes a competent adult forager? In: Hewlett, B. S., Lamb, M. E. (Eds.), *Hunter–Gatherer Childhoods: Evolutionary, Developmental, and Cultural Perspectives*. Evolutionary Foundations of Human Behavior. Aldine Transaction, Edison, NJ, pp. 109–128.

Boesch, C., Hohmann, G., Marchant, L. F. (Eds.), 2002. *Behavioural Diversity in Chimpanzees and Bonobos*. Cambridge University Press, Cambridge, England.

Bollong, C. A., Sampson, C. G., Smith, A. B., 1997. Khoikhoi and Bushman pottery in the Cape Colony: ethnohistory and Later Stone Age ceramics of the South African interior. *J. Anthropol. Archaeol.* 16(3):269–299.

Boon, L., Geerts, W. J. C., Jonker, A., Lamers, W. H., Van Noorden, C. J. F., 1999. High protein diet induces pericentral glutamate dehydrogenase and ornithine aminotransferase to provide sufficient glutamate for pericentral detoxification of ammonia in rat liver lobules. *Histochem. Cell Biol.* 111(6):445–452.

Boonstra, R., 2004. Coping with changing northern environments: the role of the stress axis in birds and mammals. *Integr. Comp. Biol.* 44(2):95–108.

Bos, C., Metges, C. C., Gaudichon, C., Petzke, K. J., Pueyo, M. E., Morens, C., Everwand, J., Benamouzig, R., Tomé, D., 2003. Postprandial kinetics of dietary amino acids are the main determinant of their metabolism after soy or milk protein ingestion in humans. *J. Nutr.* 133(5):1308–1315.

Boudreau, M. D., Chanmugam, P. S., Hart, S. B., Lee, S. H., Hwang, D. H., 1991. Lack of dose response by dietary n-3 fatty acids at a constant ratio of *n*-3 to *n*-6 fatty acids in suppressing eicosanoid biosynthesis from arachidonic acid. *Am. J. Clin. Nutr.* 54(1):111–117.

Boukari, I., Shier, N. W., Fernandez R. X. E., Frisch, J., Watkins, B. A., Pawloski, L., Fly, A. D., 2001. Calcium analysis of selected western African foods. *J. Food Compost. Anal.* 14(1):37–42.

Bourre, J.-M., 2006. Effects of nutrients (in food) on the structure and function of the nervous system: update on dietary requirements for brain, part 2. macronutrients. *J. Nutr. Health Aging* 10(5):386–399.

Bower, N., Hertel, K., Oh, J., Storey, R., 1988. Nutritional evaluation of marama bean (*Tylosema esculentum*, Fabaceae): analysis of the seed. *Econ. Bot.* 42(4):533–540.

Box, G. E. P., Draper, N. R., 1987. *Empirical Model-Building and Response Surfaces*. Wiley Series in Probability and Mathematical Statistics 157. John Wiley and Sons, New York, NY.

Boyle, F., 1882. *Legends of My Bungalow*. Chapman and Hall, London, England.

Brace, C. L., Rosenberg, K. R., Hunt, K. D., 1987. Gradual change in human tooth size in the late Pleistocene and post-Pleistocene. *Evolution* 41(4):705–720.

Brain, C. K., 1967. Hottentot food remains and their meaning in the interpretation of fossil bone assemblages. *Namib Desert Research Station Scientific Paper* 32:1–11.

Brain, C. K., 1969. The contribution of Namib Desert Hottentots to an understanding of Australopithecine bone accumulations. *Namib Desert Research Station Scientific Paper* 39:13–22.

Brain, C. K., 1981. *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. University of Chicago Press, Chicago, IL.

Brain, C. K., Sillen, A., 1988. Evidence from the Swartkrans Cave for the earliest use of fire. *Nature* 336(6198):464–466.

Bramble, D. M., Lieberman, D. E., 2004. Endurance running and the evolution of *Homo*. *Nature* 432(7015):345–352.

Brenna, J. T., 2002. Efficiency of conversion of α-linolenic acid to long chain *n*-3 fatty acids in man. *Curr. Opin. Clin. Nutr. Metab. Care* 5(2):127–132.

Brenna, J. T., Varamini, B., Jensen, R. G., Diersen-Schade, D. A., Boettcher, J. A., Arterburn, L. M., 2007. Docosahexaenoic and arachidonic acid concentrations in human breast milk worldwide. *Am. J. Clin. Nutr.* 85(6):1457–1464.

Brett, M. T., Müller-Navarra, D. C., 1997. The role of highly unsaturated fatty acids in aquatic foodweb processes. *Freshw. Biol.* 38(3):483–499.

Briggs, G. M., Calloway, D. H., 1979. *Bogert's Nutrition and Physical Fitness*. 10th ed. W. B. Saunders, Philadelphia, PA.

Brightman, R., 1996. The sexual division of foraging labor: biology, taboo, and gender politics. *Comp. Stud. Soc. Hist.* 38(4):687–729.

Broadhurst, C. L., Wang, Y., Crawford, M. A., Cunnane, S. C., Parkington, J. E., Schmidt, W. F., 2002. Brain-specific lipids from marine, lacustrine, or terrestrial food resources: potential impact on early African *Homo sapiens*. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* 131(4):653–673.

Brock, J. F., Autret, M., 1952. *Kwashiorkor in Africa*. World Health Organization Monograph Series 8, W.H.O. Bull. 5. W.H.O., Geneva, Switzerland.

Brooks, P. M., 1978. Relationship between body condition and age, growth, reproduction and social status in impala, and its application to management. *S. Afr. J. Wildl. Res.* 8(4):151–157.

Brooks, P. M., Hanks, J., Ludbrook, J. V., 1977. Bone marrow as an index of condition in African ungulates. *S. Afr. J. Wildl. Res.* 7(2):61–66.

Broughton, J. M., Bayham, F. E., 2003. Showing off, foraging models, and the ascendance of large-game hunting in the California Middle Archaic. *Am. Antiq.* 68(4):783–789.

Brown, C. H., 1985. Mode of subsistence and folk biological taxonomy. *Curr. Anthropol.* 26(1):43–64.

de Wolf Brownell, C., 1856. *The Indian Races of North and South America. Comprising an Account of the Principal Aboriginal Races; a Description of their National Customs, Mythology, and Religious Ceremonies, the History of their Most Powerful Tribes, and of their Most Celebrated Chiefs and Warriors; their Intercourse and Wars with the European Settlers; and a Great Variety of Anecdote and Description, Illustrative of Personal and National Character*. American Subscription House, New York, NY.

Brundin, T., Wahren, J., 1994. Influence of protein ingestion on human splanchnic and whole-body oxygen consumption, blood flow, and blood temperature. *Metabolism* 43(5):626–632.

Bryden, H. A., 1893. *Gun and Camera in Southern Africa: A Year of Wanderings in Bechuanaland, the Kalahari Desert, and the Lake River Country, Ngamiland, with Notes on Colonisation, Natives, Natural History and Sport*. Edward Stanford, London, England.

Buckland, W., 1824. *Reliquiae Diluvianae, or Observations on the Organic Remains Contained in Caves, Fissures, and Diluvial Gravel, and on Other Geological Phenomena, Attesting the Action of an Universal Deluge*. 2nd ed. John Murray, London, England.

Bunn, H. T., 1981. Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. *Nature* 291:574–577.

Bunn, H. T., 1983. Evidence on the diet and subsistence patterns of Plio-Pleistocene hominids at Koobi Fora, Kenya, and at Olduvai Gorge, Tanzania. In: Clutton-Brock, J., Grigson, C. (Eds.), *Animals and Archaeology, Vol. 1. Hunters and Their Prey*. BAR International Series 163. British Archaeological Reports, Oxford, England, pp. 21–30.

Bunn, H. T., 1994. Early Pleistocene hominid foraging strategies along the ancestral Omo River at Koobi Fora, Kenya. *J. Hum. Evol.* 27(1–3):247–266.

Bunn, H. T., 1995. Review of "A View to a Death in the Morning: Hunting and Nature Through History, by Matt Cartmill. Cambridge: Harvard University Press, 1993, 331 pp." *Am. J. Phys. Anthropol.* 97(4):453–454.

Bunn, H. T., 2007a. Meat made us human. In: Ungar, P. S. (Ed.), *Evolution of the Human Diet: The Known, the Unknown, and the Unknowable*. Human Evolution Series. Oxford University Press, Oxford, England, pp. 191–211.

Bunn, H. T., 2007b. "Ungulate mortality patterns at FLK *Zinj* and their behavioral implications." Unpublished paper presented at the 16th annual meeting of the Paleoanthropology Society, Philadelphia, Pennsylvania, 27–28 March 2007.

Bunn, H. T., Ezzo, J. A., 1993. Hunting and scavenging by Plio-Pleistocene hominids: nutritional constraints, archaeological patterns, and behavioural implications. *J. Archaeol. Sci.* 20(4):365–398.

Bunn, H. T., Kroll, E. M., 1986. Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania. *Curr. Anthropol.* 27(5):431–452.

Burchell, W. J., 1822. *Travels in the Interior of Southern Africa, Vol. 1*. Longman, Hurst, Rees, Orme, and Brown, London, England.

Burdge, G. C., 2003. *n*-3 Fatty acid metabolism in women – reply. *Br. J. Nutr.* 90(5):994–995.

Burdge, G. C., 2006. Metabolism of α-linolenic acid in humans. *Prostaglandins, Leukot. Essent. Fatty Acids* 75(3):161–168.

Burdge, G. C., Calder, P. C., 2005. α-Linolenic acid metabolism in adult humans: the effects of gender and age on conversion to longer-chain polyunsaturated fatty acids. *Eur. J. Lipid Sci. Technol.* 107(6):426–439.

Burdge, G. C., Calder, P. C., 2006. Dietary α-linolenic acid and health-related outcomes: a metabolic perspective. *Nutr. Res. Rev.* 19(1):26–52.

Burdge, G. C., Jones, A. E., Wootton, S. A., 2002. Eicosapentaenoic and docosapentaenoic acids are the principal products of α-linolenic acid metabolism in young men. *Br. J. Nutr.* 88(4), 355–363.

Burdge, G. C., Sherman, R. C., Ali, Z., Wootton, S. A., Jackson, A. A., 2006. Docosahexaenoic acid is selectively enriched in plasma phospholipids during pregnancy in Trinidadian women – results of a pilot study. *Reprod. Nutr. Dev.* 46(1):63–67.

Burdge, G. C., Wootton, S. A., 2002. Conversion of α-linolenic acid to eicosapentaenoic, docosapentaenoic and docosahexaenoic acids in young women. *Br. J. Nutr.* 88(4):411–420.

Burger, A. E. C., De Villiers, J. B. M., Du Plessis, L. M., 1987. Composition of the kernel oil and protein of the marula seed. *S. Afr. J. Sci.* 83:733–735.

Burke, R. O. H., Wills, W. J., 1861. *The Burke and Wills Exploring Expedition: An Account of the Crossing the Continent of Australia, from Cooper's Creek to Carpentaria, With Biographical Sketches of Robert O'Hara Burke and William John Wills*. Wilson and MacKinnon, Melbourne, Australia.

Burton, I., 1884. *The Inner Life of Syria, Palestine, and the Holy Land, From My Private Journal, Vol. 2*. Kegan Paul, Trench and Company, London, England.

Burton, R. F., 1860. *The Lake Regions of Central Africa: A Picture of Exploration, Vol. 2*. Longman, Green, Longman, and Roberts, London, England.

Burton, R. F., Beadle, B. A., Beke, C. T., Royal Geographical Society, 1873. *The Lands of Cazembe: Lacerda's Journey to Cazembe in 1798. Also Journey of the Pombeiros, P. J.*

*Baptista and Amaro José, Across Africa from Angola to Tette on the Zambesi. And a Résumé of the Journey of MM. Monteiro and Gamitto*. John Murray, London, England.

Büschel, D., 2002. *Dependency on a Woodland Resource: Contribution of Non-Timber Forest Products to the Livelihood of San Vakwangali Households in Western Kavango, Namibia*, Unpublished MA Thesis, Department of Rural Development Studies, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Calkins, C. R., Hodgen, J. M., 2007. A fresh look at meat flavor. *Meat Sci.* 77(1):63–80.

Cambero, M. I., Pereira-Lima, C. I., Ordoñez, J. A., García de Fernando, G. D., 2000. Beef broth flavour: study of flavour development. *J. Sci. Food Agric.* 80(10):1510–1518.

Campbell, H., 1904. The evolution of man's diet. *Lancet* 164(4230):909–912.

Campbell, D. M., Hall, M. H., Barker, D. J. P., Cross, J., Shiell, A. W., Godfrey, K. M., 1996. Diet in pregnancy and the offspring's blood pressure 40 years later. *Br. J. Obstet. Gynaecol.* 103(3):273–280.

Campbell-Brown, M., Johnstone, F. D., Kerr Grieve, J. F., 1986. The effect on birthweight of a high-protein, low-carbohydrate diet during pregnancy (abstract). *Proc. Nutr. Soc.* 45(3):90A.

Cannon, G., 2005. The rise and fall of dietetics and of nutrition science, 4000 BCE-2000 CE. *Public Health Nutr.* 8(6A):701–705.

Capaldo, S. D., 1997. Experimental determinations of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (*Zinjanthropus*), Olduvai Gorge, Tanzania. *J. Hum. Evol.* 33(5):555–597.

Carlson, B. A., Kingston, J. D., 2007a. Docosahexaenoic acid, the aquatic diet, and hominin encephalization: difficulties in establishing evolutionary links. *Am. J. Hum. Biol.* 19(1):132–141.

Carlson, B. A., Kingston, J. D., 2007b. Docosahexaenoic acid biosynthesis and dietary contingency: encephalization without aquatic constraint. *Am. J. Hum. Biol.* 19(4):585–588.

Carlson, S. E., 2009. Docosahexaenoic acid supplementation in pregnancy and lactation. *Am. J. Clin. Nutr.* 89(2):678S–684S.

Carmody, R. N., Wrangham, R. W., 2009. The energetic significance of cooking. *J. Hum. Evol.* 57(4):379–391.

Carnielli, V. P., Simonato, M., Verlato, G., Luijendijk, I., De Curtis, M., Sauer, P. J. J., Cogo, P. E., 2007. Synthesis of long-chain polyunsaturated fatty acids in preterm newborns fed formula with long-chain polyunsaturated fatty acids. *Am. J. Clin. Nutr.* 86(5):1323–1330.

Cartland-Shaw, L. K., Cree, A., Skeaff , C. M., Grimmond, N. M., 1998. Differences in dietary and plasma fatty acids between wild and captive populations of a rare reptile, the tuatara (*Sphenodon punctatus*). *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* 168B(8):569–580.

Cartmill, M., 1993. *A View to a Death in the Morning: Hunting and Nature through History*. Harvard University Press, Cambridge, MA.

Casas, A., del Carmen Vázquez, M., Viveros, J. L., Caballero, J., 1996. Plant management among the Nahua and the Mixtec in the Balsas River basin, Mexico: an ethnobotanical approach to the study of plant domestication. *Hum. Ecol.* 24(4):455–478.

Castro, G., Myers, J. P., Ricklefs, R. E., 1992. Ecology and energetics of sandlerlings migrating to four latitudes. *Ecology* 73(3):833–844.

Castro, S., Silveira, P., Coutinho, A. P., Figueiredo, E., 2005. Systematic studies in *Tylosema* (Leguminosae). *Bot. J. Linn. Soc.* 147(1):99–115.

Caton, J. D., 1877. *The Antelope and Deer of America*. Hurd Houghton, New York, NY.

Cattelain, P., 1997. Hunting during the Upper Paleolithic: bow, spearthrower, or both? In: Knecht, H. (Ed.), *Projectile Technology*. Interdisciplinary Contributions to Archaeology. Plenum Press, New York, NY, pp. 213–240.

Chadare, F. J., Linnemann, A. R., Hounhouigan, J. D., Nout, M. J. R., Van Boekel, M. A. J. S., 2009. Baobab food products: a review on their composition and nutritional value. *Crit. Rev. Food Sci. Nutr.* 49(3):254–274.

Chagnon, N. A., Hames, R. B., 1979. Protein deficiency and tribal warfare in Amazonia: new data. *Science* 203(4383):910–913.

Chambers, W., Chambers, R., 1863. Uncommon dinners. *Chambers's Journal of Popular Literature, Science, and Arts* 20(518):367–368.

Chaney, M. S., Ross, M. L., 1971. *Nutrition*. 8th ed. Houghton Mifflin, Boston, MA.

Chapman, J., 1868. *Travels in the Interior of South Africa, Comprising Fifteen Years' Hunting and Trading; With Journeys Across the Continent from Natal to Walvisch Bay, and Visits to Lake Ngami and the Victoria Falls, Vol. 1*. Bell and Daldy, London, England.

Chaudhari, N., Landin, A. M., Roper, S. D., 2002. A metabotropic glutamate receptor variant functions as a taste receptor. *Nat. Neurosci.* 3(2):113–119.

Chavarro, J. E., Rich-Edwards, J. W., Rosner, B. A., Willett, W. C., 2008. Protein intake and ovulatory infertility. *Am. J. Obstet. Gynecol.* 198(2):210.e1–210.e7.

Cheon, S.-H., Huh, M.-H., Lee, J.-S. Park, Y.-B., Sohn, H.-S., Chung, C.-W., 2000. Effect of dietary linoleate/alpha-linolenate balance on the brain lipid composition, reproductive outcome and behavior of rats during their prenatal and postnatal development. *Biosci. Biotechnol. Biochem.* 64(11):2290–2297.

Cheshier, J., Kelly, R. L., 2006. Projectile point shape and durability: the effect of thickness:length. *Am. Antiq.* 71(2):353–363.

Childs, C. E., Romeu-Nadal, M., Burdge, G. C., Calder, P. C., 2008. Gender differences in the *n*-3 fatty acid content of tissues. *Proc. Nutr. Soc.* 67(1):19–27.

Chivandi, E., Davidson, B. C., Erlwanger, K. H., 2008. A comparison of the lipid and fatty acid profiles from the kernels of the fruit (nuts) of *Ximenia caffra* and *Ricinodendron rautanenii* from Zimbabwe. *Industrial Crops and Products* 27(1):29–32.

Cho, H., Stout, S. D., 2003. Bone remodeling and age-associated bone loss in the past: an histomorphometric analysis of the Imperial Roman skeletal population of Isola Sacra. In: Agarwal, S. C., Stout, S. D. (Eds.), *Bone Loss and Osteoporosis: An Anthropological Perspective*. Kluwer Academic/Plenum/Springer, New York, NY, pp. 207–228.

Cho, H. P., Nakamura, M. T., Clarke, S. D., 1999. Cloning, expression, and fatty acid regulation of the human Δ-5 desaturase. *J. Biol. Chem.* 274(52):37335–37339.

Christensen, M. M., Høy, C.-E., 1997. Early dietary intervention with structured triacylglycerols containing docosahexaenoic acid: effect on brain, liver, and adipose tissue lipids. *Lipids* 32(2):185–191.

Churchill, S. E., 1993. Weapon technology, prey size selection, and hunting methods in modern hunter–gatherers: implications for hunting in the Palaeolithic and Mesolithic. In: Peterkin, G. L., Bricker, H. M., Mellars, P. A. (Eds.), *Hunting and Animal Exploitation in the Later Palaeolithic and Mesolithic of Eurasia*. Archeological Paper 4(1). American Anthropological Association, Washington, DC, pp. 11–24.

Churchill, S. E., Rhodes, J. A., 2009. The evolution of the human capacity for killing at a distance: the human fossil evidence for the evolution of projectile weaponry. In: Hublin, J.-J., Richards, M. P. (Eds.), *The Evolution of Hominid Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*. Vertebrate Paleobiology and Paleoanthropology. Springer, Dordrecht, The Netherlands, pp. 201–210.

Cisse, M., Sakho, M., Dornier, M., Mar Diop, C., Reynes, M., Sock, O., 2009. Caractérisation du fruit du baobab et étude de sa transformation en nectar. *Fruits* 64(1):19–34.

Clandinin, M. T., 1999. Brain development and assessing the supply of polyunsaturated fatty acid. *Lipids* 34(2):131–138.

Clark, G. A., 2000. Thirty years of Mesolithic research in Atlantic coastal Iberia (1970–2000). *J. Anthropol. Res.* 56(1):17–37.

Clark, J. D., 1987. Transitions: *Homo erectus* and the Acheulian: the Ethiopian sites of Gadeb and the Middle Awash. *J. Hum. Evol.* 16(7–8):809–826.

Clark, J. E., Gosser, D., 1995. Reinventing Mesoamerica's first pottery. In: Barnett, W. K., Hoopes, J. W. (Eds.), *The Emergence of Pottery: Technology and Innovation in Ancient Societies*. Smithsonian Series in Archaeological Inquiry. Smithsonian Institution Press, Washington, DC, pp. 209–221.

Clastres, P., 1972. The Guayaki. In: Bicchieri, M. G. (Ed.), *Hunters and Gatherers Today*. Holt, Rinehart and Winston, New York, NY, pp. 138–174.

Cochran, G., Harpending, H., 2009. *The 10,000 Year Explosion: How Civilization Accelerated Human Evolution*. Basic Books, New York, NY.

Codding, B. F., Jones, T. L., 2007. Man the showoff? Or the ascendance of a just-so-story: a comment on recent applications of costly signaling theory in American archaeology. *Am. Antiq.* 72(2):349–357.

Coggins, P. C., 2007. Attributes of muscle foods: color, texture, flavor. In: Nollet, L. M. L. (Ed.), *Handbook of Meat, Poultry and Seafood Quality*. Blackwell Publishing, Oxford, England, pp. 89–100.

Conigrave, A. D., Brown, E. M., Rizzoli, R., 2008. Dietary protein and bone health: roles of amino acid-sensing receptors in the control of calcium metabolism and bone homeostasis. *Annu. Rev. Nutr.* 28:131–155.

Conklin-Brittain, N. L., Dierenfeld, E. S., Wrangham, R. W., Norconk, M., Silver, S. C., 1999. Chemical protein analysis: a comparison of Kjeldahl crude protein and total ninhydrin protein from wild, tropical vegetation. *J. Chem. Ecol.* 25(12):2601–2622.

Conklin-Brittain, N. L., Wrangham, R. W., Hunt, K. D., 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance, II. macronutrients. *Int. J. Primatol.* 19(6):971–998.

Cook, F. A., 1911. *My Attainment of the Pole: Being the Record of the Expedition that First Reached the Boreal Center, 1907–1909, With the Final Summary of the Polar Controversy*. Polar Publishing Company, New York, NY.

Cordain, L., 1999. Cereal grains: humanity's double-edged sword. In: Simopoulos, A. P. (Ed.), *Evolutionary Aspects of Nutrition and Health: Diet, Exercise, Genetics and Chronic Disease*. World Rev. Nutr. Diet. 84. Karger, Basel, Switzerland, pp. 19–73.

Cordain, L., 2002. *The Paleo Diet*. John Wiley and Sons, New York, NY.

Cordain, L., 2007. The protein debate: the evolutionary basis for the therapeutic effects of high protein diets. *Performance Menu: J. Nutr. Athl. Excell.* 2007:1–31.

Cordain, L., Brand Miller, J., Eaton, S. B., Mann, N. J., Holt, S. H. A., Speth, J. D., 2000. Plant–animal subsistence ratios and macronutrient energy estimations in worldwide hunter–gatherer diets. *Am. J. Clin. Nutr.* 71(3):682–692.

Cordain, L., Eaton, S. B., Brand Miller, J., Mann, N. J., Hill, K., 2002. The paradoxical nature of hunter–gatherer diets: meat-based, yet non-atherogenic. *Eur. J. Clin. Nutr.* 56(Suppl. 1):S42–S52.

Cordain, L., Eaton, S. B., Sebastian, A., Mann, N. J., Lindeberg, S., Watkins, B. A., O'Keefe, J. H., Brand-Miller, J., 2005. Origins and evolution of the Western diet: health implications for the 21st century. *Am. J. Clin. Nutr.* 81(2):341–354.

Cordain, L., Friel, J., 2005. *Paleo Diet for Athletes: A Nutritional Formula for Peak Athletic Performance*. Rodale, Emmaus, PA.

Cordain, L., Watkins, B. A., Florant, G. L., Kelher, M., Rogers, L., Li, Y., 2002. Fatty acid analysis of wild ruminant tissues: evolutionary implications for reducing diet-related chronic disease. *Eur. J. Clin. Nutr.* 56(3):181–191.

Cordain, L., Watkins, B. A., Mann, N. J., 2001. Fatty acid composition and energy density of foods available to African hominids: evolutionary implications for human brain development. In: Simopoulos, A. P., Pavlou, K. N. (Eds.), *Nutrition and Fitness: Metabolic Studies in Health and Disease*. World Rev. Nutr. Diet. 90. Karger, Basel, Switzerland, pp. 144–161.

Coues, E. (Ed.), 1893. *The History of the Lewis and Clark Expedition, Vol. 1*. Francis P. Harper, New York, NY.

Coues, E. (Ed.), 1898. *The Journal of Jacob Fowler*. Francis P. Harper, New York, NY.

Crawford, M. A., 1968. Fatty-acid ratios in free-living and domestic animals. *Lancet* 291(7556):1329–1333.

Crawford, M. A., Bloom, M., Broadhurst, C. L., Schmidt, W. F., Cunnane, S. C., Galli, C., Ghebremeskel, K., Linseisen, F., Lloyd-Smith, J., Parkington, J. E., 1999. Evidence for the unique function of docosahexaenoic acid during the evolution of the modern hominid brain. *Lipids* 34(Suppl. 1):S39–S47.

Crawford, M. A., Bloom, M., Cunnane, S. C., Holmsen, H., Ghebremeskel, K., Parkington, J. E., Schmidt, W. F., Sinclair, A. J., Broadhurst, C. L., 2001. Docosahexaenoic acid and cerebral evolution. In: Hamazaki, T., Okuyama, H. (Eds.), *Fatty Acids and Lipids: New Findings*. World Rev. Nutr. Diet. 88. Karger, Basel, Switzerland, pp. 6–17.

Crawford, M. A., Cunnane, S. C., Harbige, L., 1993. A new theory of evolution: quantum theory. In: Sinclair, A., Gibson, R. (Eds.), *Essential Fatty Acids and Eicosanoids*. AOCS, Champaign, IL, pp. 87–95.

Crawford, M. A., Gale, M. M., Woodford, M. H., 1969. Linoleic acid and linolenic acid elongation products in muscle tissue of *Syncerus caffer* and other ruminant species. *Biochem. J.* 115(1), 25–27.

Crawford, M. A., Galli, C., Visioli, F., Renaud, S., Simopoulos, A. P., Spector, A. A., 2000. Role of plant-derived omega-3 fatty acids in human nutrition. *Ann. Nutr. Metab.* 44(5–6):263–265.

Crawford, M. A., Marsh, D., 1995. *Nutrition and Evolution: Food in Evolution and the Future*. Keats Publishing, New Canaan, CT.

Crawford, M. A., Rivers, J. P. W., 1975. The protein myth. In: Steele, F., Bourne, A. G. (Eds.), *The Man/Food Equation. Proceedings of a Symposium Held at the Royal Institution, London, September, 1973*. Academic Press, London, England, pp. 235–246.

Crile, G., 1941. *Intelligence, Power and Personality*. McGraw-Hill Book Company, New York, NY.

Crittenden, A. N., Conklin-Brittain, N. L., Marlowe, F. W., Schoeninger, M. J., Wrangham, R. W., 2009. Foraging strategies and diet composition of Hadza children (Abst.). *Am. J. Phys. Anthropol.* 138(S48):112.

Crocker, E. C., 1948. Flavor of meat. *J. Food Sci.* 13(3):179–183.

Cronk, L., 1991. Human behavioral ecology. *Annu. Rev. Anthropol.* 20:25–53.

Cross, H. R., Durland, P. R., Seideman, S. C., 1986. Sensory qualities of meat. In: Bechtel, P. J. (Ed.), *Muscle as Food*. Food Science and Technology Monographs. Academic Press, Orlando, FL, pp. 279–320.

Crovetti, R., Porrini, M., Santangelo, A., Testolin, G., 1998. The influence of thermic effect of food on satiety. *Eur. J. Clin. Nutr.* 52(7):482–488.

Crowe, F. L., Skeaff, C. M., Green, T. J., Gray, A. R., 2008. Serum *n*-3 long-chain PUFA differ by sex and age in a population-based survey of New Zealand adolescents and adults. *Br. J. Nutr.* 99(1):168–174.

Cunnane, S. C., Crawford, M. A., 2003. Survival of the fattest: fat babies were the key to evolution of the large human brain. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 136(1):17–26.

Cunnane, S. C., Plourde, M., Stewart, K., Crawford, M. A., 2007. Docosahexaenoic acid and shore-based diets in hominin encephalization: a rebuttal. *Am. J. Hum. Biol.* 19(4):578–581.

Daenzer, M., Ortmann, S., Klaus, S., Metges, C. C., 2002. Prenatal high protein exposure decreases energy expenditure and increases adiposity in young rats. *J. Nutr.* 132(2):142–144.

Dahlberg, F. (Ed.), 1981. *Woman the Gatherer*. Yale University Press, New Haven, CT.

Damp, J. E., Vargas, L. P., 1995. The many contexts of early Valdivia ceramics. In: Barnett, W. K., Hoopes, J. W. (Eds.), *The Emergence of Pottery: Technology and Innovation in Ancient Societies*. Smithsonian Series in Archaeological Inquiry. Smithsonian Institution Press, Washington, DC, pp. 157–168.

Dane, R. M., 1921. *Sport in Asia and Africa*. Andrew Melrose, London, England.

Dangin, M., Boirie, Y., Garcia-Rodenas, C., Gachon, P., Fauquant, J., Callier, P., Ballèvre, O., Beaufrere, B., 2001. The digestion rate of protein is an independent regulating factor of post-prandial protein retention. *Am. J. Physiol. Endocrinol. Metab.* 280(2):E340–E348.

Dangin, M., Boirie, Y., Guillet, C., Beaufrere, B., 2002. Influence of the protein digestion rate on protein turnover in young and elderly subjects. *J. Nutr.* 132(10):S3228–S3233.

Darragh, A. J., Moughan, P. J., 1998. The amino acid composition of human milk corrected for amino acid digestibility. *Br. J. Nutr.* 80(1):25–34.

Dart, R. A., 1957. *The Osteodontokeratic Culture of Australopithecus Prometheus*. Memoir 10. Transvaal Museum, Pretoria, South Africa.

Darwin, C. R., 1871. *The Descent of Man*. C. A. Watts and Company, London, England.

Darwin, C. R., 1890a. *The Descent of Man, and Selection in Relation to Sex*. 2nd ed. John Murray, London, England.

Darwin, C. R., 1890b. *Journal of Researches into the Natural History and Geology of the Countries Visited During the Voyage Round the World of H.M.S. 'Beagle' Under the Command of Captain Fitz Roy, R.N.* D. Appleton and Company, New York, NY.

Das, U. N., 2006. Aberrant expression of perilipins and 11-b-HSD-1 as molecular signatures of metabolic syndrome X in South East Asians. *J. Assoc. Physicians India* 54(8):637–649.

Davis, T. A., Nguyen, H. V., Garcia-Bravo, R., Fiorotto, M. L., Jackson, E. M., Lewis, D. S., Lee, D. R., Reeds, P. J., 1994. Amino acid composition of human milk is not unique. *J. Nutr.* 124(7):1126–1132.

Dawson-Hughes, B., Harris, S. S., Rasmussen, H., Song, L., Dallal, G. E., 2004. Effect of dietary protein supplements on calcium excretion in healthy older men and women. *J. Clin. Endocrinol. Metab.* 89(3):1169–1173.

Deacon, H. J., Deacon, J., 1999. *Human Beginnings in South Africa: Uncovering the Secrets of the Stone Age*. AltaMira Press, Walnut Creek, CA.

De Caluwé, E., De Smedt, S., Assogbadjo, A. E., Samson, R., Sinsin, B., Van Damme, P., 2009a. Ethnic differences in use value and use patterns of baobab (*Adansonia digitata* L.) in northern Benin. *Afr. J. Ecol.* 47(3):433–440.

De Caluwé, E., Halamová, K., Van Damme, P., 2009b. Baobab (*Adansonia digitata* L.): a review of traditional uses, phytochemistry and pharmacology. In: Juliani, H. R., Simon, J. E., Ho, C.-T. (Eds.), *African Natural Plant Products: New Discoveries and Challenges in Chemistry and Quality*. ACS Symp. Series 1021. American Chemical Society, Washington, DC, pp. 51–84.

Decsi, T., Csábi, G., Török, K., Erhardt, É., Minda, H., Burus, I., Molnár, S., Molnár, D., 2000. Polyunsaturated fatty acids in plasma lipids of obese children with and without metabolic cardiovascular syndrome. *Lipids* 35(11):1179–1184.

Decsi, T., Molnár, D., Koletzko, B., 1996. Long-chain polyunsaturated fatty acids in plasma lipids of obese children. *Lipids* 31(3):305–311.

De Foliart, G. R., n.d., The human use of insects as a food resource: a bibliographic account in progress (online). http://www.food-insects.com/ (downloaded December 30, 2008).

Del Prado, M., Villalpando, S., Elizondo, A., Rodríguez, M., Demmelmair, H., Koletzko, B., 2001. Contribution of dietary and newly formed arachidonic acid to human milk lipids in women eating a low-fat diet. *Am. J. Clin. Nutr.* 74(2):242–247.

de Lumley, H., 2006. Il y a 400 000 ans: la domestication du feu, un formidable moteur d'hominisation. *C. R. Palevol* 5(1–2):149–154.

DeMar Jr., J. C., DiMartino, C., Baca, A. W., Lefkowitz, W., Salem Jr., N., 2008. Effect of dietary docosahexaenoic acid on biosynthesis of docosahexaenoic acid from alpha-linolenic acid in young rats. *J. Lipid Res.* 49(9):1963–1980.

Demmelmair, H., Baumheuer, M., Koletzko, B., Dokoupil, K., Kratl, G., 1998. Metabolism of U$^{13}$C-labeled linoleic acid in lactating women. *J. Lipid Res.* 39(7):1389–1396.

Demmelmair, H., Sauerwald, T., Fidler, N., Baumheuer, M., Koletzko, B., 2001. Polyunsaturated fatty acid metabolism during lactation. In: Hamazaki, T., Okuyama, H. (Eds.), *Fatty Acids and Lipids: New Findings*. World Rev. Nutr. Diet. 88. Karger, Basel, Switzerland, pp. 184–189.

Denham, T., Fullagar, R., Head, L., 2009. Plant exploitation on Sahul: from colonisation to the emergence of regional specialisation during the Holocene. *Quat. Int.* 202(1–2):29–40.

Denke, M. A., 2001. Metabolic effects of high-protein, low-carbohydrate diets. *Am. J. Cardiol.* 88(1):59–61.

Dennett, J. F., 1835. *The Voyages and Travels of Captains Ross, Parry, Franklin, and Mr. Belzoni; Forming an Interesting History of the Manners, Customs, and Characters of Various Nations*. William Wright, London, England.

Dewailly, É., Blanchet, C., Gingras, S., Lemieux, S., Sauvé, L., Bergeron, J., Holub, B. J., 2001a. Relations between *n*-3 fatty acid status and cardiovascular disease risk factors among Quebecers. *Am. J. Clin. Nutr.* 74(5):603–611.

Dewailly, É., Blanchet, C., Lemieux, S., Sauvé, L., Gingras, S., Ayotte, P., Holub, B. J., 2001b. *n*-3 fatty acids and cardiovascular disease risk factors among the Inuit of Nunavik. *Am. J. Clin. Nutr.* 74(5):464–473.

Diab, M. C., 1998. Economic utility of the ringed seal (*Phoca hispidea*): implications for arctic archaeology. *J. Archaeol. Sci.* 25(1):1–26.

Dickens, Jr., C., 1881. A traveller's tales. *All the Year Round: A Weekly Journal* 27(645, New Series):28–34.

di Costanzo, J., 2000. Paleolithic nutrition: a model for the future? *Curr. Opin. Clin. Nutr. Metab. Care* 3(2):87–92.

Diener, P., 1984. Humanism and science in cultural anthropology: the great protein fiasco. *J. Soc. Philos.* 15(1):13–20.

Diener, P., Moore, K., Mutaw, R., 1980. Meat, markets, and mechanical materialism: the great protein fiasco in anthropology. *Dialect. Anthropol.* 5(3):171–192.

Dillehay, T. D., Rossen, J., Maggard, G., Stackelbeck, K., Netherly, P., 2003. Localization and possible social aggregation in the late Pleistocene and early Holocene on the north coast of Perú. *Quat. Int.* 109–110:3–11.

Dimski, D. S., 1994. Ammonia metabolism and the urea cycle: function and clinical implications. *J. Vet. Intern. Med.* 8(2):73–78.

Dirks, R., 1993. Starvation and famine: cross-cultural codes and some hypothesis tests. *Cross-Cult. Res.* 27(1–2):28–69.

Ditlhogo, M. K., 1996. *The Natural History of Imbrasia belina (Westwood) (Lepidoptera: Saturnidae), and Some Factors Affecting its Abundance in North-Eastern Botswana*. Unpublished PhD Dissertation, Ecology, University of Manitoba, Winnipeg, MB.

Dockall, J. E., 1997. Wear traces and projectile impact: a review of the experimental and archaeological evidence. *J. Field Archaeol.* 24(3):321–331.

Domínguez-Rodrigo, M., 1997. Meat-eating by early hominids at the FLK-22 *Zinjanthropus* site, Olduvai Gorge (Tanzania): an experimental approach using cut-mark data. *J. Hum. Evol.* 33(6):669–690.

Domínguez-Rodrigo, M., 2002. Hunting and scavenging by early humans: the state of the debate. *J. World Prehist.* 16(1):1–54.

Domínguez-Rodrigo, M., 2009. Are all Oldowan sites palimpsests? If so, what can they tell us about hominid carnivory? In: Hovers, E., Braun, D. R. (Eds.), *Interdisciplinary Approaches to the Oldowan*. Vertebrate Paleobiology and Paleoanthropology Series. Springer, Dordrecht, The Netherlands, pp. 129–147.

Domínguez-Rodrigo, M., Barba, R., 2007. Five more arguments to invalidate the passive scavenging version of the carnivore-hominid-carnivore model: a reply to Blumenschine et al. (2007a). *J. Hum. Evol.* 53(4):427–433.

Domínguez-Rodrigo, M., Barba, R., Egeland, C. P., 2007. *Deconstructing Olduvai: A Taphonomic Study of the Bed I Sites*. Vertebrate Paleobiology and Paleoanthropology. Springer, Dordrecht, The Netherlands.

Dominy, N. J., Vogel, E. R., Yeakel, J. D., Constantino, P., Lucas, P. W., 2008. Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. *Evol. Biol.* 35(3):159–175.

Donato, J., Pedrosa, R. G., Cruzat, V. F., Santana de Oliveira Pires, I., Tirapegui, J., 2006. Effects of leucine supplementation on the body composition and protein status of rats submitted to food restriction. *Nutrition* 22(5):520–527.

Dowson, T. A., 1988. Revelations of religious reality: the individual in San rock art. *World Archaeol.* 20(1):116–128.

Dracopoli, I. N., 1914. *Through Jubaland to the Lorian Swamp: An Adventurous Journey of Exploration and Sport in the Unknown African Forests and Deserts of Jubaland to the Unexplored Lorian Swamp*. Seeley, Service and Company, London, England.

Draper, H. H., 1977. The Aboriginal Eskimo diet in modern perspective. *Am. Anthropol.* 79(2):309–317.

Draper, H. H., 1980. Nutrition. In: Milan, F. A. (Ed.), *The Human Biology of Circumpolar Populations*. International Biological Programme 21. Cambridge University Press, Cambridge, England, pp. 257–284.

Draper, P., Howell, N., 2006. Changes in co-survivorship of adult children and parents: Ju/'hoansi of Botswana in 1968 and 1988. In: Hitchcock, R. K., Ikeya, K., Biesele, M., Lee, R. B. (Eds.), *Updating the San: Image and Reality of an African People in the 21st Century*. Senri Ethnological Studies 70. National Museum of Ethnology, Osaka, Japan, pp. 81–100.

Dreyer, H. C., Drummond, M. J., Pennings, B., Fujita, S., Glynn, E. L., Chinkes, D. L., Dhanani, S., Volpi, E., Rasmussen, B. B., 2008. Leucine-enriched essential amino acid and carbohydrate ingestion following resistance exercise enhances mTOR signaling and protein synthesis in human muscle. *Am. J. Physiol. Endocrinol. Metab.* 294(2):E392–E400.

Dreyer, J. J., Wehmeyer, A. S., 1982. On the nutritive value of mopanie worms. *S. Afr. J. Sci.* 78:33–35.

Drummond, W. H., 1875. *The Large Game and Natural History of South and South-East Africa. From the Journals of the Hon. W. H. Drummond*. Edmonston and Douglas, Edinburgh, Scotland.

Drury, H. F., Vaughan, D. A., Hannon, J. P., 1959. Some metabolic effects of a high-fat, high-protein diet during semistarvation under winter field conditions. *J. Nutr.* 67(1):85–97.

Duke, J. A., 2000. *Handbook of Nuts: Herbal Reference Library*. Herbal Reference Library, Vol. 4. CRC Press, Boca Raton, FL.

Dunbrack, R. L., Ramsay, M. A., 1993. The allometry of mammalian adaptations to seasonal environments: a critique of the fasting endurance hypothesis. *Oikos* 66(2):336–342.

Dunn, J., 1844. *History of the Oregon Territory and British North-American Fur Trade; with an Account of the Habits and Customs of the Principal Native Tribes on the Northern Continent*. Edwards and Hughes, London, England.

Dwyer, P. D., 1983. Etolo hunting performance and energetics. *Hum. Ecol.* 11(2):145–174.

Eaton, S. B., 2006. The ancestral human diet: what was it and should it be a paradigm for contemporary nutrition? *Proc. Nutr. Soc.* 65(1):1–6.

Eaton, S. B., Eaton III, S. B., Konner, M. J., 1997. Paleolithic nutrition revisited: a twelve-year retrospective on its nature and implications. *Eur. J. Clin. Nutr.* 51(4):207–216.

Eaton, S. B., Konner, M. J., 1985. Paleolithic nutrition: a consideration of its nature and current implications. *N. Engl. J. Med.* 312(5):283–289.

Eaton, S. B., Shostak, M., Konner, M. J., 1988. *The Paleolithic Prescription: A Program of Diet and Exercise and a Design for Living*. Harper and Row, New York, NY.

Eerkens, J. W., 2003. Residential mobility and pottery use in the western Great Basin. *Curr. Anthropol.* 44(5):728–738.

Eerkens, J. W., Neff, H., Glascock, M. D., 1999. Early pottery from Sunga'va and implications for the development of ceramic technology in Owens Valley, California. *J. Calif. Gt. Basin Anthropol.* 21(2):275–285.

Eerkens, J. W., Neff, H., Glascock, M. D., 2002. Ceramic production among small-scale and mobile hunters and gatherers: a case study from the southwestern Great Basin. *J. Anthropol. Archaeol.* 21(2):200–229.

Efremov, I. A., 1940. Taphonomy: new branch of paleontology. *Pan-Am. Geologist* 74(2):81–93.

Egeland, C. P., 2007. *Zooarchaeological and Taphonomic Perspectives on Hominid and Carnivore Interactions at Olduvai Gorge, Tanzania*. Unpublished PhD Dissertation, Indiana University, Bloomington, IN.

Egeland, C. P., 2008. Patterns of early hominid site use at Olduvai Gorge. *Mitteilungen der Gesellschaft für Urgeschichte* 17:9–37.

Ekpo, K. E., Azeke, M. A., Ugbenyen, A. M., 2008. Functional properties of dried *Imbrasia belina* larvae flour as affected by mesh size and pH. *Nigerian Ann. Nat. Sci.* 8(1):6–9.

Ellis, C. J., 1997. Factors influencing the use of stone projectile tips: an ethnographic perspective. In: Knecht, H. (Ed.), *Projectile Technology*. Interdisciplinary Contributions to Archaeology. Plenum Press, New York, NY, pp. 37–74.

Ellis, G. E., 1889. The Hudson Bay Company. In: Winsor, J. (Ed.), *Narrative and Critical History of America, Vol. 8*. Houghton, Mifflin and Company, Boston, MA, pp. 1–64.

Eidlitz, K., 1969. *Food and Emergency Food in the Circumpolar Area*. Studia Ethnographica Upsaliensia 32. Almqvist and Wiksells Boktryckert AB, Uppsala, Sweden.

Ellison, P. T., 2003. *On Fertile Ground: A Natural History of Human Reproduction*. Harvard University Press, Cambridge, MA.

Elton, S., 2008. Environments, adaptation, and evolutionary medicine: should we be eating a stone age diet? In: Elton, S., O'Higgins, P. (Eds.), *Medicine and Evolution: Current Applications, Future Prospects*. Society for the Study of Human Biology. CRC Press, Boca Raton, FL, pp. 9–33.

Emerson, A. M., 1993. The role of body part utility in small-scale hunting under two strategies of carcass recovery. In: Hudson, J. (Ed.), *From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains*. Occasional

Paper 21. Southern Illinois University, Center for Archaeological Investigations, Carbondale, IL, pp. 138–155.

Endicott, K. L., 1981. The conditions of egalitarian male–female relationships in foraging societies. *Canberra Anthropol.* 4(2):1–10.

Engels, F., 1884. *Der Ursprung der Familie, des Privateigentums und des Staats: Im Anschluss an Lewis H. Morgans Forschungen*. Hottingen, Zürich, Switzerland.

Engels, F., 1972. *The Origin of the Family, Private Property, and the State*. Pathfinder Books, New York, NY.

Engelter, C., Wehmeyer, A. S., 1970. Fatty acid composition of oils and some edible seeds of wild plants. *J. Agric. Food Chem.* 18(1):25–26.

Erlandson, J. M., 2001. The archaeology of aquatic adaptations: paradigms for a new millennium. *J. Archaeol. Res.* 9(4):287–350.

Erlandson, J. M., Moss, M. L., 2001. Shellfish feeders, carrion eaters, and the archaeology of aquatic adaptations. *Am. Antiq.* 66(3):413–432.

Eromosele, I. C., Eromosele, C. O., 1993. Studies on the chemical composition and physico-chemical properties of seeds of some wild plants. *Plant Foods Hum. Nutr.* (formerly *Qualitas Plantarum*) 43(3):251–258.

Eteshola, E., Oraedu, A. C. I., 1996. Fatty acid compositions of tigernut tubers (*Cyperus esculentus* L.), baobab seeds (*Adansonia digitata* L.), and their mixture. *J. Am. Oil Chem. Soc.* 73(2):255–257.

Ezeagu, I. E., Petzke, K. J., Lange, E., Metges, C. C., 1998. Fat content and fatty acid composition of oils extracted from selected wild-gathered tropical plant seeds from Nigeria. *J. Am. Oil Chem. Soc.* 75(8):1031–1035.

Fa, D. A., 2008. Effects of tidal amplitude on intertidal resource availability and dispersal pressure in prehistoric human coastal populations: the Mediterranean–Atlantic transition. *Quat. Sci. Rev.* 27(23–24):2194–2209.

Farini, G. A., 1886. *Through the Kalahari Desert. A Narrative of a Journey with Gun and Camera, and Note-Book to Lake N'Gami and Back*. Scribner and Welford, New York, NY.

Farmer, L. J., 1994. The role of nutrients in meat flavour formation. *Proc. Nutr. Soc.* 53(2):327–333.

Fedigan, L. M., 1986. The changing role of women in models of human evolution. *Annu. Rev. Anthropol.* 15:25–66.

Fernández-Armesto, F., 2002. *Near a Thousand Tables: A History of Food*. Simon and Schuster, New York, NY.

Fernández-Jalvo, Y., Denys, C., Andrews, P., Williams, T., Dauphin, Y., Humphrey, L., 1998. Taphonomy and palaeoecology of Olduvai Bed-1 (Pleistocene, Tanzania). *J. Hum. Evol.* 34(2):137–172.

Fessler, D. M. T., 2001. Luteal phase immunosuppression and meat eating. *Riv. Biol.* 94(3):403–426.

Fessler, D. M. T., Navarrete, C. D., 2003. Meat is good to taboo: dietary proscriptions as a product of the interaction of psychological mechanisms and social processes. *J. Cognit. Cult.* 3(1):1–40.

Fiddes, N. 1994. Social aspects of meat eating. *Proc. Nutr. Soc.* 53(2):271–280.

Fidler, N., Sauerwald, T., Pohl, A., Demmelmair, H., Koletzko, B., 2000. Docosahexaenoic acid transfer into human milk after dietary supplementation: a randomized clinical trial. *J. Lipid Res.* 41(9):1376–1383.

Fiore, I., Bondioli, L., Coppa, A., Macchiarelli, R., Russom, R., Kashay, H., Solomon, T., Rook, L., Libsekal, Y., 2004. Taphonomic analysis of the late Early Pleistocene – bone remains from Buia (Dandiero Basin, Danakil Depression, Eritrea): evidence for large mammal and reptile butchering. *Riv. Ital. Paleont. Strat.* 110(1):89–97.

Fischer, A., 1989. Hunting with flint-tipped arrows: results and experiences from practical experiments. In: Bonsall, C. (Ed.), *The Mesolithic of Europe.* John Donald Publishers, Edinburgh, Scotland, pp. 29–39.

Fischler, C., 1980. Food habits, social change and the nature/culture dilemma. *Soc. Sci. Inf.* 19(6):937–953.

Fitzhugh, B., 2003. *The Evolution of Complex Hunter–Gatherers: Archaeological Evidence from the North Pacific*. Interdisciplinary Contributions to Archaeology. Springer, New York, NY.

Fitzhugh, B., Habu, J. (Eds.), 2002. *Beyond Foraging and Collecting: Evolutionary Change in Hunter–Gatherer Settlement Systems*. Springer, New York, NY.

Flannery, K. V., 1969. Origins and ecological effects of early domestication in Iran and the Near East. In: Ucko, P. J., Dimbleby, G. W. (Eds.), *The Domestication and Exploitation of Plants and Animals*. Aldine Publishing Company, Chicago, IL, pp. 73–100.

Flaxman, S. M., Sherman, P. W., 2000. Morning sickness: a mechanism for protecting mother and embryo. *Q. Rev. Biol.* 75(2):113–148.

Foà, E., 1901. *A Travers l'Afrique Centrale du Cap au Lac Nyassa*. 2nd ed. Librairie Plon, Plon-Nourrit et Companie, Imprimeurs-Editeurs, Paris, France.

Foley, R. A., Lee, P. C., 1991. Ecology and energetics of encephalization in hominid evolution. *Philos. Trans. R. Soc. Lond., B. Biol. Sci.* 334B:223–232.

Fomon, S. J., Haschke, F., Ziegler, E. E., Nelson, S. E., 1982. Body composition of reference children from birth to age 10 years. *Am. J. Clin. Nutr.* 35(5):1169–1175.

Fontana, L., Weiss, E. P., Villareal, D. T., Klein, S., Holloszy, J. O., 2008. Long-term effects of calorie or protein restriction on serum IGF-1 and IGFBP-3 concentration in humans. *Aging Cell* 7(5):681–687.

Fouillet, H., Juillet, B., Bos, C., Mariotti, F., Gaudichon, C., Benamouzig, R., Tomé, D., 2008. Urea-nitrogen production and salvage are modulated by protein intake in fed humans: results of an oral stable-isotope-tracer protocol and compartmental modeling. *Am. J. Clin. Nutr.* 87(6):1702–1714.

Francis, C. M., Campbell, M. C., 2003. *New High Quality Oil Seed Crops for Temperate and Tropical Australia*. RIRDC Publication 03/045. Rural Industries Research and Development Corporation, Barton, ACT, Australia.

Frayn, K. N., Fielding, B. A., Karpe, F., 2005. Adipose tissue fatty acid metabolism and cardiovascular disease. *Curr. Opin. Lipidol.* 16(4):409–415.

Frears, S. L., Chown, S. L., Webb, P. I., 1997. Behavioural thermoregulation in the mopane worm (Lepidoptera). *J. Therm. Biol.* 22(4–5):325–330.

Friedl, E., 1975. *Women and Men: An Anthropologist's View*. Holt, Rinehart and Winston, New York, NY.

Friedman, M., 1999. Chemistry, nutrition, and microbiology of D-amino acids. *J. Agric. Food Chem.* 47(9):3457–3479.

Friesen, T. M., 2001. A zooarchaeological signature for meat storage: re-thinking the drying utility index. *Am. Antiq.* 66(2):315–331.

Frison, G. C., 1978. *Prehistoric Hunters of the High Plains*. Academic Press, New York, NY.

Frison, G. C., 1998. Paleoindian large mammal hunters on the plains of North America. *Proc. Natl. Acad. Sci.* 95(24):14576–14583.

Fuhrman, B. J., Barba, M., Krogh, V., Micheli, A., Pala, V., Lauria, R., Chajes, V., Riboli, E., Sieri, S., Berrino, F., Muti, P., 2006. Erythrocyte membrane phospholipid composition as a biomarker of dietary fat. *Ann. Nutr. Metab.* 50(2):95–102.

Fullagar, R. L. K., Field, J., 1997. Pleistocene seed-grinding implements from the Australian arid zone. *Antiquity* 71(272):300–307.

Fuller, B. T., Fuller, J. L., Sage, N. E., Harris, D. A., O'Connell, T. C., Hedges, R. E. M., 2005. Nitrogen balance and □$^{15}$N: why you're not what you eat during nutritional stress. *Rapid Commun. Mass Spectrom.* 19(18):2497–2506.

Garaulet, M., Pérez-Llamas, F., Pérez-Ayala, M., Martínez, P., Sánchez de Medina, F., Tebar, F. J., Zamora, S., 2001. Site-specific differences in the fatty acid composition of abdominal adipose tissue in an obese population from a Mediterranean area: relation with dietary fatty acids, plasma lipid profile, serum insulin, and central obesity. *Am. J. Clin. Nutr.* 74(5):585–591.

Garcea, E. A. A., 2006. Semi-permanent foragers in semi-arid environments of North Africa. *World Archaeol.* 38(2):197–219.

Gardner, D. K., Lane, M., 2005. Ex vivo early embryo development and effects on gene expression and imprinting. *Reprod. Fertil. Dev.* 17(3):361–370.

Gardner, D. K., Stilley, K. S., Lane, M., 2004. High protein diet inhibits inner cell mass formation and increases apoptosis in mouse blastocysts developed in vivo by increasing the levels of ammonium in the reproductive tract (abstract). *Reprod. Fertil. Dev.* 16(2):190.

Garland, M., Sacks, F. M., Colditz, G. A., Rimm, E. B., Sampson, L. A., Willett, W. C., Hunter, D. J., 1998. The relation between dietary intake and adipose tissue composition of selected fatty acids in US women. *Am. J. Clin. Nutr.* 67(1):25–30.

Gaston, K. J., Chown, S. L., Styles, C. V., 1997. Changing size and changing enemies: the case of the mopane worm. *Acta Oecol.* 18(1):21–26.

Gaudzinski, S., 2000. On the variability of Middle Palaeolithic procurement tactics: the case of Salzgitter Lebenstedt, northern Germany. *Int. J. Osteoarchaeol.* 10(5):396–406.

Gaudzinski, S., Roebroeks, W., 2000. Adults only: reindeer hunting at the Middle Palaeolithic site Salzgitter Lebenstedt, northern Germany. *J. Hum. Evol.* 38(4):497–521.

Gavrilets, S., Duenez-Guzman, E. A., Vose, M. D., 2008. Dynamics of alliance formation and the egalitarian revolution. *PLoS One* 3(10):e3293. doi:10.1371/journal.pone.0003293.

Geay, Y., Bauchart, D., Hocquette, J.-F., Culioli, J., 2001. Effect of nutritional factors on biochemical, structural and metabolic characteristics of muscles in ruminants, consequences on dietetic value and sensorial qualities of meat. *Reprod. Nutr. Dev.* 41(1):1–26.

Gebauer, J., El-Siddig, K., Ebert, G., 2002. Baobab (*Adansonia digitata* L.): a review on a multipurpose tree with promising future in the Sudan. *Gartenbauwissenschaft* 67(4):155–160.

Gewald, J.-B. 2001. El Negro, el Niño, witchcraft and the absence of rain in Botswana. *Afr. Aff.* 100(401):555–580.

Ghioni, C., Bell, J. G., Sargent, J. R., 1996. Polyunsaturated fatty acids in neutral lipids and phospholipids of some freshwater insects. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* 114B(2):161–170.

Giardina, M. A., 2006. Anatomía económica de Rheidae. *Intersecciones en Antropología* 7:263–276.

St. Gibbons, A. H., 1898. *Exploration and Hunting in Central Africa 1895–96*. Methuen, London, England.

Gilbert, R. I., Mielke, J. H. (Eds.), 1985. *The Analysis of Prehistoric Diets*. Academic Press, Orlando, FL.

Gilby, I. C., Wrangham, R. W., 2007. Risk-prone hunting by chimpanzees (*Pan troglodytes schweinfurthii*) increases during periods of high diet quality. *Behav. Ecol. Sociobiol.* 61(11):1771–1779.

Giltay, E. J., Duschek, E. J. J., Katan, M. B., Zock, P. L., Neele, S. J., Netelenbos, J. C., 2004a. Raloxifene and hormone replacement therapy increase arachidonic acid and docosahexaenoic acid levels in postmenopausal women. *J. Endocrinol.* 182(3):399–408.

Giltay, E. J., Gooren, L. J. G., Toorians, A. W. F. T., Katan, M. B., Zock, P. L., 2004b. Docosahexaenoic acid concentrations are higher in women than in men through estrogenic effects. *Am. J. Clin. Nutr.* 80(5):1167–1174.

Gintis, H., Smith, E. A., Bowles, S., 2001. Costly signaling and cooperation. *J. Theor. Biol.* 213(1):103–119.

Gladyshev, M. I., Arts, M. T., Sushchik, N. N., 2009. Preliminary estimates of the export of omega-3 highly unsaturated fatty acids (EPA + DHA) from aquatic to terrestrial ecosystems. In: Arts, M. T., Brett, M. T., Kainz, M. J. (Eds.), *Lipids in Aquatic Ecosystems*. Springer, New York, NY, pp. 179–209.

Glaser, D., 1999. The evolution of taste perception. In: Corti, A. (Ed.), *Low-Calorie Sweeteners: Present and Future*. World Rev. Nutr. Diet. 85. Karger, Basel, Switzerland, pp. 18–38.

Glew, R. H., Jackson, D., Sena, L. P., VanderJagt, D. J., Pastuszyn, A., Millson, M., 1999. *Gonimbrasia belina* (Lepidoptera: Saturniidae): a nutritional food source rich in protein, fatty acids and minerals. *Am. Entomol.* 45(4):250–253.

Glew, R. H., VanderJagt, D. J., Lockett, C., Grivetti, L. E., Smith, G. C., Pastuszyn, A., Millson, M., 1997. Amino acid, fatty acid, and mineral composition of 24 indigenous plants of Burkina Faso. *J. Food Compost. Anal.* 10(3):205–217.

Glew, R. S., VanderJagt, D. J., Huang, Y.-S., Chuang, L.-T., Bosse, R., Glew, R. H., 2004. Nutritional analysis of the edible pit of *Sclerocarya birrea* in the Republic of Niger (*daniya*, Hausa). *J. Food Compost. Anal.* 17(1):99–111.

Godman, J. D., 1836. *American Natural History, to Which is Added His Last Work, the Rambles of a Naturalist, with a Biographical Sketch of the Author, Vol. 2*. 3rd ed. Hogan and Thompson, Philadelphia, PA.

Goedhart, A. C., Bindels, J. G., 1994. The composition of human milk as a model for the design of infant formulas: recent findings and possible applications. *Nutr. Res. Rev.* 7(1):1–23.

Goldman, H. I., Freudenthal, R., Holland, B., Karelitz, S., 1969. Clinical effects of two different levels of protein intake on low-birth-weight infants. *J. Pediatr.* 74(6):881–889.

Goldman, H. I., Goldman, J. S., Kaufman, I., Liebman, O. B., 1974. Late effects of early dietary protein intake on low-birth-weight infants. *J. Pediatr.* 85(6):764–769.

Gomes, C. M., Boesch, C., 2009. Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS One* 4(4):e5116. doi:10.1371/journal.pone.0005116.

Gordon-Cumming, R., 1851. *Five Years of a Hunter's Life in the Far Interior of South Africa, with Notices of the Native Tribes, and Anecdotes of the Chase of the Lion, Elephant, Hippopotamus, Giraffe, Rhinoceros, &c., Vol. 1*. Harper and Brothers, New York, NY.

Goren-Inbar, N., Alperson, N., Kislev, M. E., Simchoni, O., Melamed, Y., Ben-Nun, A., Werker, E., 2004. Evidence of hominin control of fire at Gesher Benot Ya'aqov, Israel. *Science* 304(5671):725–727.

Gould, S. J., 2000. The spice of life. *Leader to Leader* 15(Winter):14–19.

Gouwakinnou, G. N., Kindomihou, V., Assogbadjo, A. E., Sinsin, B., 2009. Population structure and abundance of *Sclerocarya birrea* (A. Rich) Hochst subsp. *birrea* in two contrasting land-use systems in Benin. *Int. J. Biodivers. Conserv.* 1(6):194–201.

Gowlett, J. A. J., 2006. The early settlement of northern Europe: fire history in the context of climate change and the social brain. *C. R. Palevol* 5:299–310.

Goyens, P. L. L., Spilker, M. E., Zock, P. L., Katan, M. B., Mensink, R. P., 2006. Conversion of α-linolenic acid in humans is influenced by the absolute amounts of α-linolenic acid and linoleic acid in the diet and not by their ratio. *Am. J. Clin. Nutr.* 84(1):44–53.

Grant, A., 1982. The use of tooth wear as a guide to the age of domestic ungulates. In: Wilson, B., Grigson, C., Payne, S. (Eds.), *Ageing and Sexing Animal Bones from Archaeological Sites*. BAR British Series 109. British Archaeological Reports, Oxford, England, pp. 91–108.

Graz, F. P., 2002. Description and ecology of *Schinziophyton rautanenii* (Schinz) Radcl.-Sm. in Namibia. *Dinteria* 27:19–35.

Green, P., Yavin, E., 1993. Elongation, desaturation, and esterification of essential fatty acids by fetal rat brain in vivo. *J. Lipid Res.* 34(12):2099–2107.

Green, P., Yavin, E., 1996. Fatty acid composition of late embryonic and early postnatal rat brain. *Lipids* 31(8):859–865.

Green, P., Yavin, E., 1998. Mechanisms of docosahexaenoic acid accretion in the fetal brain. *J. Neurosci. Res.* 52(2):129–136.

Greiner, R. C. S., Winter, J., Nathanielsz, P. W., Brenna, J. T., 1997. Brain docosahexaenoate accretion in fetal baboons: bioequivalence of dietary α-linolenic and docosahexaenoic acids. *Pediatr. Res.* 42(6):826–834.

Griffin, B. A., 2008. How relevant is the ratio of dietary n-6 to n-3 polyunsaturated fatty acids to cardiovascular disease risk? Evidence from the OPTILIP study. *Curr. Opin. Lipidol.* 19(1):57–62.

Gross, D. R., 1975. Protein capture and cultural development in the Amazon basin. *Am. Anthropol.* 77(3):526–549.

Günther, A. L. B., Buyken, A. E., Kroke, A., 2007. Protein intake during the period of complementary feeding and early childhood and the association with body mass index and percentage body fat at 7 y of Age. *Am. J. Clin. Nutr.* 85(6):1626–1633.

Gurven, M. D., Allen-Arave, W., Hill, K., Hurtado, A. M., 2000. "It's a wonderful life": signaling generosity among the Ache of Paraguay. *Evol. Hum. Behav.* 21(4):263–282.

Gurven, M. D., Hill, K., 2009. Why do men hunt? A reevaluation of "Man the Hunter" and the sexual division of labor. *Curr. Anthropol.* 50(1):51–74.

Gurven, M. D., Hill, K., Jakugi, F., 2004. Why do foragers share and sharers forage? Explorations of social dimensions of foraging. *Res. Econ. Anthropol.* 23:19–43.

Gurven, M. D., Hill, K., Kaplan, H., 2002. From forest to reservation: transitions in food-sharing behavior among the Ache of Paraguay. *J. Anthropol. Res.* 58(1):93–120.

Gurven, M. D., Hill, K., Kaplan, H., Hurtado, A. M., Lyles, R., 2000. Food transfers among Hiwi foragers of Venezuela: tests of reciprocity. *Hum. Ecol.* 28(2):171–218.

Gurven, M. D., Kaplan, H., 2006. Determinants of time allocation across the lifespan: a theoretical model and an application to the Machiguenga and Piro of Peru. *Hum. Nat.* 17(1):1–49.

Gurven, M. D., Kaplan, H., Gutierrez, M., 2006. How long does it take to become a proficient hunter? Implications for the evolution of extended development and long life span. *J. Hum. Evol.* 51(5):454–470.

Gurven, M. D., von Rueden, C., 2006. Hunting, social status and biological fitness. *Soc. Biol.* 53(1–2):81–99.

Guthrie, H. A., 1975. *Introductory Nutrition*. 3rd ed. C. V. Mosby, St. Louis, MO.

Haaland, R., 1992. Fish, pots and grain: early and mid-Holocene adaptations in the central Sudan. *Afr. Archaeol. Rev.* 10(1):43–64.

Hachey, D. L., Thomas, M. R., Emken, E. A., Garza, C., Brown-Booth, L., Adlof, R. O., Klein, P. D., 1987. Human lactation: maternal transfer of dietary triglycerides labeled with stable isotopes. *J. Lipid Res.* 28(10):1185–1192.

Haefeli, R. J., Glaser, D., 1990. Taste responses and thresholds obtained with the primary amino acids in humans. *Lebenson. Wiss. Technol. (Food Sci. Technol.)* 23(6):523–527.

Haefeli, R. J., Solms, J., Glaser, D., 1998. Taste responses to amino acids in common marmosets (*Callithrix jacchus jacchus*, Callitrichidae) a non-human primate in comparison to humans. *Lebenson. Wiss. Technol. (Food Sci. Technol.)* 31(4):371–376.

Haggarty, P., 2002. Placental regulation of fatty acid delivery and its effect on fetal growth – a review. *Placenta* 23(Suppl. 1):S28–S38.

Haggarty, P., 2004. Effect of placental function on fatty acid requirements during pregnancy. *Eur. J. Clin. Nutr.* 58(12):1559–1570.

Hambraeus, L., 1994. Milk composition in animals and humans: nutritional aspects. In: Serrano Rios, M., Sastre, A., Perez Juez, M. A., Estrala, A., De Sebastian, C. (Eds.), *Dairy Products in Human Health and Nutrition. Proceedings of the 1st World Congress Dairy Products in Human Health and Nutrition, Madrid, June 7–10, 1993*. A. A. Balkema, Rotterdam, The Netherlands, pp. 13–23.

Hamdy, O., Porramatikul, S., Al-Ozairi, E., 2006. Metabolic obesity: the paradox between visceral and subcutaneous fat. *Curr. Diabetes Rev.* 2(4):367–373.

Hamilton, A., 2003. World War II's mobilization of the science of food acceptability: how ration palatability became a military research priority. *Ecol. Food Nutr.* 42(4–5):325–356.

Hamilton, T. M., 1982. *Native American Bows*. 2nd ed. Special Publication 5. Missouri Archaeological Society, Columbia, MO.

Hamilton, W. J., Busse, C. D., 1978. Primate carnivory and its significance to human diets. *Bioscience* 28(12):761–766.

Hamilton, W. T., 1905. *My Sixty Years on the Plains: Trapping, Trading, and Indian Fighting*. Forest and Stream Publishing Company, New York, NY.

Hanbury, D. T., 1904. *Sport and Travel in the Northland of Canada*. Edward Arnold, London, England.

Hannon, J. P., Vaughan, D. A., 1958. Effect of prolonged consumption of pemmican survival ration on some aspects of the intermediary metabolism of rat liver tissue. *Am. J. Physiol.* 193(2):449–454.

Hanson, B. J., Cummins, K. W., Cargill, A. S., Lowry, R. R., 1985. Lipid content, fatty acid composition, and the effect of diet on fats of aquatic insects. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* 80B(2):257–276.

Harmand, S., DeGusta, D., Slimak, L., Lewis, J., Melillo, S., Dohmen, I., Omar, M., 2009. Nouveaux sites paléolithiques anciens en République de Djibouti: bilan préliminaire de prospections récentes dans le Bassin du Gobaad, Afar Central. *C. R. Palevol* 8(5):481–492.

Harris, D. R., Hillman, G. C. (Eds.), 1989. *Foraging and Farming: The Evolution of Plant Exploitation*. Unwin Hyman, London, England.

Harris, M., 1979. The human strategy: our pound of flesh. *Nat. Hist.* 88(7):30–36.

Harris, M., 1984. Animal capture and Yanomamo warfare: retrospect and new evidence. *J. Anthropol. Res.* 40(1):183–201.

Harris, W. C., 1839. *The Wild Sports of Southern Africa: Being the Narrative of an Expedition from the Cape of Good Hope, Through the Territories of the Chief Moselekatse, to the Tropic of Capricorn*. John Murray, London, England.

Harry, K. G., Frink, L., O'Toole, B., Charest, A., 2009. How to make an unfired clay cooking pot: understanding the technological choices made by arctic potters. *J. Archaeol. Meth. Theor.* 16(1):33–50.

Hart, B. L., Hart, L. A., Pinter-Wollman, N., 2008. Large brains and cognition: where do elephants fit in? *Neurosci. Biobehav. Rev.* 32(1):86–98.

Hart, D. L., Sussman, R. W., 2008. *Man the Hunted: Primates, Predators, and Human Evolution*. Expanded ed. Westview Press, Boulder, CO.

Hawkes, K., 1990. Why do men hunt? Benefits for risky choices. In: Cashdan, E. A. (Ed.), *Risk and Uncertainty*. Westview Press, Boulder, CO, pp. 145–166.

Hawkes, K., 1991. Showing off: tests of an hypothesis about men's foraging goals. *Ethol. Sociobiol.* 12:29–54.

Hawkes, K., 2000. Hunting and the evolution of egalitarian societies: lessons from the Hadza. In: Diehl, M. W. (Ed.), *Hierarchies in Action: Cui Bono?* Occasional Paper 27. Southern Illinois University, Center for Archaeological Investigations, Carbondale, IL, pp. 59–83.

Hawkes, K., Bliege Bird, R., 2002. Showing off, handicap signaling, and the evolution of men's work. *Evol. Anthropol.* 11(2):58–67.

Hawkes, K., Hill, K., O'Connell, J. F., 1982. Why hunters gather: optimal foraging and the Ache of eastern Paraguay. *Am. Ethnol.* 9(2):379–398.

Hawkes, K., O'Connell, J. F., 1981. Affluent hunters? Some comments in light of the Alyawara case. *Am. Anthropol.* 83(3):622–626.

Hawkes, K., O'Connell, J. F., 1992. On optimal foraging models and subsistence transitions. *Curr. Anthropol.* 33(1):63–66.

Hawkes, K., O'Connell, J. F., Blurton Jones, N. G., 1991. Hunting income patterns among the Hadza: big game, common goods, foraging goals, and the evolution of the human diet. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 334B(1270):243–251.

Hawkes, K., O'Connell, J. F., Blurton Jones, N. G., 1995. Hadza children's foraging: juvenile dependency, social arrangements, and mobility among hunter–gatherers. *Curr. Anthropol.* 36(4):688–700.

Hawkes, K., O'Connell, J. F., Blurton Jones, N. G., 1997. Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal life spans. *Curr. Anthropol.* 38(4):551–577.

Hawkes, K., O'Connell, J. F., Blurton Jones, N. G., 2001. Hadza meat sharing. *Evol. Hum. Behav.* 22(2):113–142.

Hawks, J. D., Wang, E. T., Cochran, G. M., Harpending, H. C., Moyzis, R. K., 2007. Recent acceleration of human adaptive evolution. *Proc. Natl. Acad. Sci.* 104(52):20753–20758.

Haydon, G. H., 1846. *Five Years' Experience in Australia Felix, Comprising a Short Account of Its Early Settlement and Its Present Position, With Many Particulars Interesting to Intending Emigrants*. Hamilton, Adams, and Company, London, England.

Haynes, G., 2002. Archeological methods for reconstructing human predation on terrestrial vertebrates. In: Kowalewski, M. J., Kelley, P. H. (Eds.), *The Fossil Record of Predation*. Special Papers 8. Paleontological Society, Yale Printing Service, New Haven, CT, pp. 51–68.

Headings, M. E., Rahnema, S., 2002. The nutritional value of mopane worms, *Gonimbrasia belina* (Lepidoptera: Saturniidae) for human consumption (Abst.). Ten-Minute Papers, Section B. Physiology, Biochemistry, Toxicology, and Molecular Biology, The 2002 Entomological Society of America (ESA) Annual Meeting and Exhibition, Fort Lauderdale, Florida, November 20, 2002. http://www.esa.confex.com/esa/2002/techprogram/session_1102.htm.

Headings, M. E., Rahnema, S., 2007. Crude protein composition of sixteen species representing nine orders of insects. Ten-Minute Papers, Section B. Physiology, Biochemistry, Toxicology, and Molecular Biology, 2007 Entomological Society of America (ESA) Annual Meeting and Exhibition, San Diego, California, December 10, 2007. http:www.//esa.confex.com/esa/2007/techprogram/paper_32243.htm.

Heaney, R. P., Layman, D. K., 2008. Amount and type of protein influences bone health. *Am. J. Clin. Nutr.* 87(5):1567S–1570S.

Hearne, S., 1971 [1795]. *A Journey from Prince of Wales's Fort in Hudson's Bay to the Northern Ocean, Undertaken by Order of the Hudson's Bay Company for the Discovery of Copper Mines, A North-West Passage, &c., in the Years 1769, 1771, and 1772*. Charles E. Tuttle, Rutland, VT.

Heath, K. M., Hadley, C., 1998. Dichotomous male reproductive strategies in a polygynous human society: mating versus parental effort. *Curr. Anthropol.* 39(3):369–374.

Heinbecker, P., 1928. Studies on the metabolism of Eskimos. *J. Biol. Chem.* 80(2):461–475.

Heinz, H.-J., 1966. *Social Organization of the !Ko Bushmen*. Unpublished MA thesis, Department of Anthropology, University of South Africa, Pretoria, South Africa.

Hegsted, M., Linkswiler, H. M., 1981. Long-term effects of level of protein intake on calcium metabolism in young adult women. *J. Nutr.* 111(2):244–251.

Hellekant, G., Ninomiya, Y., 1991. On the taste of umami in chimpanzee. *Physiol. Behav.* 49(5):927–934.

Henley, P., 2003. Film-making and ethnographic research. In: Prosser, J. (Ed.), *Image-Based Research: A Sourcebook for Qualitative Researchers*. RoutledgeFalmer Press, London, England, pp. 42–59.

Henrich, J., 2008. A cultural species. In: Brown, M. J. (Ed.), *Explaining Culture Scientifically*. University of Washington Press, Seattle, WA, pp. 184–210.

Henry, J. J., 1812. *An Accurate and Interesting Account of the Hardships and Sufferings of That Band of Heroes, Who Traversed the Wilderness in the Campaign Against Quebec in 1775*. William Greer, Lancaster, PA.

Henschel, A., 1961. Arctic rations. In: Fisher, F. R. (Ed.), *Man Living in the Arctic. Proceedings of a Conference, Quartermaster Research and Engineering Center, Natick, Massachusetts, 1, 2 December 1960*. National Academy of Sciences/National Research Council, Washington, DC, pp. 68–71.

Hermanussen, M., Tresguerres, J. A. F., 2008. Factors influencing body mass index, appetite control, and the role of glutamate and excess nutritional protein during child development: a review. *Curr. Pediatr. Rev.* 4(2):110–119.

Herrera, E., Amusquivar, E., López-Soldado, I., Ortega, H., 2006. Maternal lipid metabolism and placental lipid transfer. *Horm. Res.* 65(Suppl. 3):59–64.

Herrick, K., Phillips, D. I. W., Haselden, S., Shiell, A. W., Campbell-Brown, M., Godfrey, K. M., 2003. Maternal consumption of a high-meat, low-carbohydrate diet in late pregnancy: relation to adult cortisol concentrations in the offspring. *J. Clin. Endocrinol. Metab.* 88(8):3554–3560.

Hesse, M., 2002. *Alkaloids: Nature's Curse or Blessing?* Wiley-VCH, Weinheim, Germany.

Hetzel, B. S., 1978. The changing nutrition of Aborigines in the ecosystem of central Australia. In: Hetzel, B. S., Frith, H. J. (Eds.), *The Nutrition of Aborigines in Relation to the Ecosystem of Central Australia*. Symposium of the Commonwealth Scientific and Industrial Research Organization. CSIRO, Melbourne, pp. 39–47.

Hibbeln, J. R., Ferguson, T. A., Blasbalg, T. L., 2006. Omega-3 fatty acid deficiencies in neurodevelopment, aggression and autonomic dysregulation: opportunities for intervention. *Int. Rev. Psychiatry* 18(2):107–118.

Hiernaux, J., Hartono, D. B., 1980. Physical measurements of the adult Hadza of Tanzania. *Ann. Hum. Biol.* 7(4):339–346.

Hill, J. H., 1978. Language contact systems and human adaptations. *J. Anthropol. Res.* 34(1):1–26.

Hill, K., 1982. Hunting and human evolution. *J. Hum. Evol.* 11(6):521–544.

Hill, K., 1988. Macronutrient modifications of optimal foraging theory: an approach using indifference curves applied to some modern foragers. *Hum. Ecol.* 16(2):157–197.

Hill, K., 2002. Altruistic cooperation during foraging by the Ache, and the evolved human predisposition to cooperate. *Hum. Nat.* 13(1):105–128.

Hill, K., Hawkes, K., 1983. Neotropical hunting among the Ache of eastern Paraguay. In: Hames, R. B., Vickers, W. T. (Eds.), *Adaptive Responses of Native Amazonians*. Academic Press, New York, NY, pp. 139–188.

Hill, K., Hawkes, K., Hurtado, A. M., Kaplan, H., 1984. Seasonal variance in the diet of Ache hunter–gatherers in eastern Paraguay. *Hum. Ecol.* 12(2):101–136.

Hill, K., Hurtado, A. M., 1989. Hunter–gatherers of the new world. *Am. Sci.* 77(5):437–443.

Hill, K., Hurtado, A. M., 1996. *Ache Life History: The Ecology and Demography of a Foraging People*. Foundations of Human Behavior. Aldine de Gruyter, Hawthorne, NY.

Hill, K., Hurtado, A. M., 1999. The Ache of Paraguay. In: Lee R. B., Daly, R. H. (Eds.), *The Cambridge Encyclopedia of Hunters and Gatherers*. Cambridge University Press, Cambridge, England, pp. 92–96.

Hill, K., Kaplan, H., Hawkes, K., Hurtado, A. M., 1987. Foraging decisions among Ache hunter–gatherers: new data and implications for optimal foraging models. *Ethol. Sociobiol.* 8(1):1–36.

Hill, K., Kintigh, K., 2009. Can anthropologists distinguish good and poor hunters? Implications for hunting hypotheses, sharing conventions, and cultural transmission. *Curr. Anthropol.* 50(3):369–377.

Hilton, C. E., Greaves, R. D., 2008. Seasonality and sex differences in travel distance and resource transport in Venezuelan foragers. *Curr. Anthropol.* 49(1):144–153.

Hind, H. Y., 1860. *Narrative of the Canadian Red River Exploring Expedition of 1857 and of the Assinniboine and Saskatchewan Exploring Expedition of 1858, Vol. 1*. Longman, Green, Longman, and Roberts, London, England.

Hinde, R. A., 1986. Can non-human primates help us understand human behavior? In: Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., Struhsaker, T. T. (Eds.), *Primate Societies*. University of Chicago Press, Chicago, IL, pp. 413–420.

Hitchcock, R. K., 1982. *The Ethnoarchaeology of Sedentism: Mobility Strategies and Site Structure Among Foraging and Food-Producing Populations in the Eastern Kalahari Desert, Botswana*. Unpublished PhD Dissertation, Department of Anthropology, University of New Mexico, Albuquerque, NM.

Hitchcock, R. K., 1986. Botswana: impacts of drought upon Kalahari San populations. *International Work Group for Indigenous Affairs Newsletter* (*Copenhagen*) 45:9–14.

Hitchcock, R. K., 1988. Settlement, seasonality, and subsistence stress among the Tyua of northern Botswana. In: Huss-Ashmore, R., Curry, J. J., Hitchcock, R. K. (Eds.), *Coping with Seasonal Constraints*. MASCA Research Papers in Science and Archaeology 5. University of Pennsylvania, University Museum, Museum Applied Science Center for Archaeology (MASCA), Philadelphia, PA, pp. 65–85.

Hitchcock, R. K., Biesele, M., Babchuk, W., 2009. Environmental anthropology in the Kalahari: development, resettlement, and ecological change among the San of southern Africa. *vis-à-vis: Explor. Anthropol.* 9(2):170–188.

Hitchcock, R. K., Bleed, P., 1997. Each according to need and fashion: spear and arrow use among San hunters of the Kalahari. In: Knecht, H. (Ed.), *Projectile Technology*. Interdisciplinary Contributions to Archaeology. Plenum, New York, NY, pp. 345–368.

Hitchcock, R. K., Ebert, J. I., Morgan, R. G., 1989. Drought, drought relief, and dependency among the Basarwa of Botswana. In: Huss-Ashmore, R., Katz, S. H. (Eds.), *African Food Systems in Crisis, Part One. Microperspectives*. Gordon and Breach, New York, NY, pp. 303–336.

Hitchcock, R. K., Yellen, J. E., Gelburd, D. J., Osborn, A. J., Crowell, A. L., 1996. Subsistence hunting and resource management among the Ju/'hoansi of northwestern Botswana. *Afr. Study Monogr.* 17(4):153–220.

Hladik, C. M., Chivers, D. J., Pasquet, P., 1999. On diet and gut size in non-human primates and humans: is there a relationship to brain size? *Curr. Anthropol.* 40(5):695–697.

Hobson, K. A., Alisauskas, R. T., Clark, R. G., 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. *Condor* 95(2):388–394.

Hodson, L., Skeaff, C. M., Fielding, B. A., 2008. Fatty acid composition of adipose tissue and blood in humans and its use as a biomarker of dietary intake. *Prog. Lipid Res.* 47(5):348–380.

Hoffman, L. C., Wiklund, E., 2006. Game and venison – meat for the modern consumer. *Meat Sci.* 74(1):197–208.

Hollmann, M., Runnebaum, B., Gerhard, I., 1997. Impact of waist-hip-ratio and body-mass-index on hormonal and metabolic parameters in young, obese women. *Int. J. Obes.* 21(6):476–483.

Holloway, R. L., 1981. Culture, symbols, and human brain evolution: a synthesis. *Dialect. Anthropol.* 5(4):287–303.

Holt, B. M., Formicola, V., 2008. Hunters of the ice age: the biology of Upper Paleolithic people. *Am. J. Phys. Anthropol.* 137(Suppl. 47):70–99.

Holub, E., 1881. *Seven Years in South Africa: Travels, Researches, and Hunting Adventures, Between the Diamond-Fields and the Zambesi (1872–79), Vol. 2*. Frewer, E. E. (Trans.). Sampson Low, Marston, Searle, and Rivington, London, England.

Hoopes, J. W., 1994. Ford revisited: a critical review of the chronology and relationships of the earliest ceramic complexes in the New World, 6000–1500 B.C. *J. World Prehist.* 8(1):1–49.

Horowitz, J. F., 2003. Fatty acid mobilization from adipose tissue during exercise. *Trends Endocrinol. Metab.* 14(8):386–392.

Horrocks, L. A., Yeo, Y. K., 1999. Health benefits of docosahexaenoic acid (DHA). *Pharmacol. Res.* 40(3):211–225.

Houssay, B. A., Lewis, J. T., Orias, O., Braun-Menendez, E., Hug, E., Foglia, V. G., Leloir, L. F., 1955. *Human Physiology*. 2nd ed. McGraw-Hill, New York, NY.

Howard, H. C. (Earl of Suffolk and Berkshire) (Ed.), 1911. *The Encyclopaedia of Sport and Games, Vol. 2. Crocodile Shooting – Hound Breeding*. New and enlarged ed. J. B. Lippincott, Philadelphia, PA.

Howell, N., 1986. Feedbacks and buffers in relation to scarcity and abundance: studies of hunter–gatherer populations. In: Coleman, D., Schofield, R. (Eds.), *The State of Population Theory: Forward from Malthus*. Basil Blackwell, Oxford, England, pp. 156–187.

Høygaard, A., 1941. *Studies on the Nutrition and Physio-pathology of Eskimos, Undertaken at Angmagssalik, East-Greenland 1936–1937*. Norske Videnskapsakademi i Oslo, Skrifter 1. Matematisk-Naturvidenskapelig Klasse 1940(9).

Hromník, C. A., 1993. The bow of Siva alias Heitsi Eibib in the rock art of the Cape Quena. *Afr. Asian Stud.* 28(3–4):243–252.

Hu, Y., Shang, H., Tong, H., Nehlich, O., Liu, W., Zhao, C., Yu, J., Wang, C., Trinkaus, E., Richards, M. P., 2009. Stable isotope dietary analysis of the Tianyuan 1 early modern human. *Proc. Natl. Acad. Sci.* 106(27):10971–10974.

Humphries, M. M., Umbanhowar, J., McCann, K. S., 2004. Bioenergetic prediction of climate change impacts on northern mammals. *Integr. Comp. Biol.* 44(2):152–162.

Hurtado, A. M., Hawkes, K., Hill, K., Kaplan, H., 1985. Female subsistence strategies among Ache hunter–gatherers of eastern Paraguay. *Hum. Ecol.* 13(1):1–28.

Husson, A., Brasse-Lagnel, C., Fairand, A., Renouf, S., Lavoinne, A., 2003. Argininosuccinate synthetase from the urea cycle to the citrulline-NO cycle. *Eur. J. Biochem.* 270(9):1887–1899.

Hutchings, W. K., 1997. *The Paleoindian Fluted Point: Dart or Spear Armature? The Identification of Paleoindian Delivery Technology Through the Analysis of Lithic Fracture Velocity*. Unpublished PhD Dissertation, Department of Archaeology, Simon Fraser University, Burnaby, BC.

Hutchings, W. K., 1999. Quantification of fracture propagation velocity employing a sample of Clovis channel flakes. *J. Archaeol. Sci.* 26(12):1437–1447.

Hutchinson, H. G. (Ed.), 1905. *Big Game Shooting, Vol. 2*. "Country Life" Library of Sport. Published at the Offices of "Country life," Ltd., London, England.

Hutton, J., 1795. *Theory of the Earth, with Proofs and Illustrations, Vol. 2*. Farther Induction of Facts and Observations, Respecting the Geological Part of the Theory. Cadell, Junior, and Davies, and William Creech, London, England, and Edinburgh, Scotland.

Hutton Estabrook, V., 2009. *Sampling Biases and New Ways of Addressing the Significance of Trauma in Neandertals*. Unpublished PhD Dissertation, Department of Anthropology, University of Michigan, Ann Arbor, MI.

Igarashi, M., Ma, K., Chang, L., Bell, J. M., Rapoport, S. I., 2007. Dietary *n*-3 PUFA deprivation for 15 weeks upregulates elongase and desaturase expression in rat liver but not brain. *J. Lipid Res.* 48(11):2463–2470.

Ikeda, K., 1909. New seasonings [in Japanese]. *J. Chem. Soc. Tokyo* 30:820–836.

Ikeda, K., 2002. New seasonings [in English]. *Chem. Senses* 27(9):847–849.

Illgner, P., Nel, E., 2000. The geography of edible insects in Sub-Saharan Africa: a study of the mopane caterpillar. *Geogr. J.* 166(4):336–351.

Innis, S. M., 2000a. Essential fatty acids in infant nutrition: lessons and limitations from animal studies in relation to studies on infant fatty acid requirements. *Am. J. Clin. Nutr.* 71(Suppl. 1):238S–244S.

Innis, S. M., 2000b. The role of dietary *n*-6 and *n*-3 fatty acids in the developing brain. *Dev. Neurosci.* 22(5–6):474–480.

Innis, S. M., 2005. Essential fatty acid transfer and fetal development. *Placenta* 26(Suppl. A. Trophoblast Research, Vol. 19):S70–S75.

Innis, S. M., 2007a. Dietary (*n*-3) fatty acids and brain development. *J. Nutr.* 137(4):855–859.

Innis, S. M., 2007b. Human milk: maternal dietary lipids and infant development. *Proc. Nutr. Soc.* 66(3):397–404.

Innis, S. M., Kuhnlein, H. V., 1988. Long-chain *n*-3 fatty acids in breast milk in Inuit women consuming traditional foods. *Early Hum. Dev.* 18(2–3):185–190.

Institute of Medicine, 2005. *Dietary Reference Intakes for Energy, Carbohydrate, Fiber, Fat, Fatty Acids, Cholesterol, Protein, and Amino Acids (Macronutrients)*. Institute of Medicine, Panel on Macronutrients, Standing Committee on the Scientific Evaluation of Dietary Reference Intakes. National Academies Press, Washington, DC.

International HapMap Consortium, 2007. A second generation human haplotype map of over 3.1 million SNPs. *Nature* 449(7164):851–861.

Irving, W., 1837. *Adventures of Captain Bonneville, or Scenes Beyond the Rocky Mountains of the Far West*. Baudry's European Library, Paris, France.

Isaac, G. L. (Ed.), 1997. *Koobi Fora Research Project, Vol. 5. Plio-Pleistocene Archaeology*. Koobi Fora Research Project 5. Clarendon Press, Oxford, England.

Isaac, G. L., Harris, J. W. K., 1997. Sites stratified within the KBS tuff: reports. In: Isaac, G. L. (Ed.), *Koobi Fora Research Project, Vol. 5. Plio-Pleistocene Archaeology*. Koobi Fora Research Project 5. Clarendon Press, Oxford, England, pp. 71–110.

Isler, K., van Schaik, C., 2006. Costs of encephalization: the energy trade-off hypothesis tested on birds. *J. Hum. Evol.* 51(3):228–243.

Isler, K., van Schaik, C. P., 2009. The expensive brain: a framework for explaining evolutionary changes in brain size. *J. Hum. Evol.* 57(4):392–400.

Itoh, S., 1980. Physiology of circumpolar people. In: Milan, F. A. (Ed.), *The Human Biology of Circumpolar Populations*. International Biological Programme 21. Cambridge University Press, Cambridge, England, pp. 285–303.

Iwaniec, U. T., 1997. *Effects of Dietary Acidity on Cortical Bone Remodeling: A Histomorphometric Assessment*. Unpublished PhD Dissertation, Department of Anthropology, University of Wisconsin, Madison, WI.

Jackson, A. A., 1999. Limits of adaptation to high dietary protein intakes. *Eur. J. Clin. Nutr.* 53(Suppl. 1):S44–S52.

Jackson, A. A., 2000. Nutrients, growth, and the development of programmed metabolic function. In: Koletzko, B., Fleischer Michaelsen, K., Hernell, O. (Eds.), *Short and Long Term Effects of Breast Feeding on Child Health*. Adv. Exp. Med. Biol. 478. Springer, Dordrecht, The Netherlands, pp. 41–55.

Jackson, A. A., 2001. Human protein requirement: policy issues. *Proc. Nutr. Soc.* 60(1):7–11.

Jackson S. D., 2004. Los implementos de molienda en un campamento estacional del Holoceno medio: implicancias funcionales y contextuales. In: *Simposio Perspectivas Teóricas y Metodológicas en los Estudios Líticos*. Chungará. Revista de Antropología Chilena, Volumen Especial 36 (Tomo 1). Universidad de Tarapacá, Facultad de Ciencias Sociales Administrativas y Económicas, Departamento de Arqueología y Museología, Arica, Chile, pp. 95–103.

James, S. R., 1996. Early hominid use of fire: recent approaches and methods for evaluation of the evidence. In: Bar-Yosef, O., Cavalli-Sforza, L. L., March, R. J., Piperno, M. (Eds.), *The Study of Human Behaviour in Relation to Fire in Archaeology: New Data and Methodologies for Understanding Prehistoric Fire Structures*. International Union of Prehistoric and Protohistoric Sciences. Colloquia of the XIII International Congress of Prehistoric and Protohistoric Sciences, Forli (Italy), 8–14 September 1996. The Lower and Middle Palaeolithic, Vol. 5. Colloquium IX. A.B.A.C.O. Edizioni, Forli, Italy, pp. 65–75.

Jan, S., Guillou, H., D'Andrea, S., Daval, S., Bouriel, M., Rioux, V., Legrand, P., 2004. Myristic acid increases Δ6-desaturase activity in cultured rat hepatocytes. *Reprod. Nutr. Dev.* 44(2):131–140.

Jelliffe, D. B., Jelliffe, E. F. P., 1978. The volume and composition of human milk in poorly nourished communities: a review. *Am. J. Clin. Nutr.* 31:492–515.

Jenike, M. R., 2001. Nutritional ecology: diet, physical activity and body size. In: Panter-Brick, C., Layton, R. H., Rowley-Conwy, P. (Eds.), *Hunter–Gatherers: An Interdisciplinary Perspective*. Cambridge University Press, Cambridge, England, pp. 205–238.

Jenness, D., 1923. *Report of the Canadian Arctic Expedition, 1913–1918 (Southern Party, 1913–1916), Vol. 12*. The Copper Eskimo. F. A. Acland, Ottawa, Ontario.

Jenness, R., 1985. Biochemical and nutritional aspects of milk and colostrum. In: Larson, B. L. (Ed.), *Lactation*. University of Iowa Press, Ames, IA, pp. 164–197.

Jenness, R., 1986. Lactational performance of various mammalian species. *J. Dairy Sci.* 69(3):869–885.

Jenness, R., Sloan, R. E., 1970. The composition of milks of various species: a review. *Dairy Sci. Abstr.* 32(10):599–612.

Jensen, C. L., Maude, M., Anderson, R. E., Heird, W. C., 2000. Effect of docosahexaenoic acid supplementation of lactating women on the fatty acid composition of breast milk lipids and maternal and infant plasma phospholipids. *Am. J. Clin. Nutr.* 71(Suppl. 1):292S–299S.

Jensen, M. D., 1997. Lipolysis: contribution from regional fat. *Annu. Rev. Nutr.* 17:127–139.

Jensen, R. G., Ferris, A. M., Lammi-Keefe, C. J., Henderson, R. A., 1990. Lipids of bovine and human milks: a comparison. *J. Dairy Sci.* 73(2):223–240.

Jideani, V. A., Van Wyk, J., Cruywagen, M. H., 2009. Physical properties of *Tylosemia* [sic] *esculentum* and the effect of roasting on the functional properties of its flour. *Afr. J. Agric. Res.* 4(11):1208–1219.

Jochim, M. A., 1976. *Hunter–Gatherer Subsistence and Settlement: A Predictive Model*. Academic Press, New York, NY.

Johanson, D. C., Wong, K., 2009. *Lucy's Legacy: The Quest for Human Origins*. Random House, New York, NY.

Johns, T. A., Duquette, M., 1991. Detoxification and mineral supplementation as functions of geophagy. *Am. J. Clin. Nutr.* 53(2):448–456.

Johns, T. A., 1990. *With Bitter Herbs They Shall Eat It: Chemical Ecology and the Origins of Human Diet and Medicine*. University of Arizona Press, Tucson, AZ.

Johnson, N. E., Alcantara, E. N., Linkswiler, H., 1970. Effect of level of protein intake on urinary and fecal calcium and calcium retention of young adult males. *J. Nutr.* 100(12):1425–1430.

Johnston, C. S., Day, C. S., Swan, P. D., 2002. Postprandial thermogenesis is increased 100% on a high-protein, low-fat diet versus a high-carbohydrate, low-fat diet in healthy, young women. *J. Am. Coll. Nutr.* 21(1):55–61.

Jones, K. T., Metcalfe, D., 1988. Bare bones archaeology: bone marrow indices and efficiency. *J. Archaeol. Sci.* 15(4):415–423.

Jones, M., 2009. Moving north: archaeobotanical evidence for plant diet in Middle and Upper Paleolithic Europe. In: Hublin J.-J., Richards M. P. (Eds.), *The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*. Vertebrate Paleobiology and Paleoanthropology. Springer, Dordrecht, The Netherlands, pp. 171–180.

Kaneko, T., 1938. Taste and constitution of a-amino acids. *J. Chem. Soc. Japan* 59:433–439.

Kaneko, T., 1939. Taste and constitution of a-amino acids, II. stereochemistry of a-amino acids. *J. Chem. Soc. Japan* 60:531–538.

Kaplan, H., Hill, K., 1992. The evolutionary ecology of food acquisition. In: Smith, E. A., Winterhalder, B. (Eds.), *Evolutionary Ecology and Human Behavior*. Aldine de Gruyter, Hawthorne, NY, pp. 167–201.

Kaplan, H., Hill, K., Lancaster, J., Hurtado, A. M., 2000. A theory of human life history evolution: diet, intelligence, and longevity. *Evol. Anthropol.* 9(4):156–185.

Kark, R. M., Johnson, R. E., Lewis, J. S., 1945. Defects of pemmican as an emergency ration for infantry troops. *War Med.* 7(6):345–352.

Karlsson, M., Mårild, S., Brandberg, J., Lönn, L., Friberg, P., Strandvik, B., 2006. Serum phospholipid fatty acids, adipose tissue, and metabolic markers in obese adolescents. *Obesity* 14(6):1931–1939.

Katz, S. H., 1990. An evolutionary theory of cuisine. *Hum. Nat.* 1(3):233–259.

Keally, C. T., Taniguchi, Y., Kuzmin, Y. V., Shewkomud, I. Y., 2004. Chronology of the beginning of pottery manufacture in East Asia. *Radiocarbon* 46(1):345–351.

Keating, W. H., 1824. *Narrative of an Expedition to the Source of St. Peter's River, Lake Winnepeek, Lake of the Woods, &c. &c. Performed in the Year 1823, by Order of the Hon. J. C. Calhoun, Secretary of War, Under the Command of Stephen H. Long, Major U. S. T. E. Compiled from the Notes of Major Long, Messrs. Say, Keating, and Colhoun, Vol. 1*. H. C. Carey and I. Lea, Philadelphia, PA.

Keating, W. H., 1825. *Narrative of an Expedition to the Source of St. Peter's River, Lake Winnepeek, Lake of the Woods, &c. Performed in the Year 1823, by Order of the Hon. J. C. Calhoun, Secretary of War, Under the Command of Stephen H. Long, U. S. T. E. Compiled from the Notes of Major Long, Messrs. Say, Keating, and Colhoun, Vol. 2*. Geo. B. Whittaker, London, England.

Keegan, A. B., 1982. *Dormancy and Germination of the Manketti Nut, Ricinodendron rautanenii*. Unpublished PhD Dissertation, University of Natal, Pietermaritzburg, South Africa.

Keegan, A. B., Van Staden, J., 1981. Marama bean, *Tylosema esculentum*, a plant worthy of cultivation. *S. Afr. J. Sci.* 77:387.

Keith, M. E., Renew, A., 1975. Notes on some edible wild plants found in the Kalahari. *Koedoe* 18(1):1–12.

Kelly, J. F., 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Can. J. Zool.* 78(1):1–27.

Kelly, R. L., 1995. *The Foraging Spectrum: Diversity in Hunter–Gatherer Lifeways*. Smithsonian Institution Press, Washington, DC.

Kelly, R. L., Thomas, D. H., 2009. *Archaeology*. 5th ed., Revised. Wadsworth, Cengage Learning, Belmont, CA.

Kennedy, G. E., 2003. Palaeolithic grandmothers? Life history theory and early *Homo*. *J. R. Anthropol. Inst.* 9(3):549–572.

Kennedy, G. E., 2005. From the ape's dilemma to the weanling's dilemma: early weaning and its evolutionary context. *J. Hum. Evol.* 48:123–145.

Kent, S., 1996. Hunting variability at a recently sedentary Kalahari village. In: Kent, S. (Ed.), *Cultural Diversity Among Twentieth-Century Foragers: An African Perspective*. Cambridge University Press, Cambridge, England, pp. 125–156.

Kerr, D. S., Stevens, M. C. G., Robinson, H. M., 1978. Fasting metabolism in infants, I. effect of severe undernutrition on energy and protein utilization. *Metabolism* 27(4):411–435.

Kerstetter, J. E., O'Brien, K. O., Caseria, D. M., Wall, D. E., Insogna, K. L., 2005. The impact of dietary protein on calcium absorption and kinetic measures of bone turnover in women. *J. Clin. Endocrinol. Metab.* 90(1):26–31.

Kerstetter, J. E., Wall, D. E., O'Brien, K. O., Caseria, D. M., Insogna, K. L., 2006. Meat and soy protein affect calcium homeostasis in healthy women. *J. Nutr.* 136(7):1890–1895.

Ketshajwang, K. K., Holmback, J., Yeboah, S. O., 1998. Quality and compositional studies of some edible Leguminosae seed oils in Botswana. *J. Am. Oil Chem. Soc.* 75(6):741–743.

Kimball, S. R., Jefferson, L. S., 2006. Signaling pathways and molecular mechanisms through which branched-chain amino acids mediate translational control of protein synthesis. *J. Nutr.* 136(Suppl. 1):227S–231S.

Kimura, S., Kim, C. H., Ohtomo, I. M., Yokomukai, Y., Komai, M., Morimatsu, F., 1991. Nutritional studies of the roles of dietary protein levels and umami in preference response to sodium chloride in experimental animals. *Physiol. Behav.* 49(5):997–1002.

King, J. R., Farner, D. S., 1966. The adaptive role of winter fattening in the white-crowned sparrow with comments on its regulation. *Am. Nat.* 100(914):403–418.

Klein, R. G., 1987. Reconstructing how early people exploited animals: problems and prospects. In: Nitecki, M. H., Nitecki, D. V. (Eds.), The *Evolution of Human Hunting*, pp. 11–46. Plenum Press, New York, NY.

Klein, R. G., 1999. *The Human Career: Human Biological and Cultural Origins*. 2nd ed. University of Chicago Press, Chicago, IL.

Klein, R. G., Cruz-Uribe, K., 1983. The computation of ungulate age (mortality) profiles from dental crown heights. *Paleobiology* 9(1):70–78.

Klein, R. G., Cruz-Uribe, K., 1984. *The Analysis of Animal Bones from Archaeological Sites*. University of Chicago Press, Chicago, IL.

Klein, R. G., Wolf, C. A., Freeman, L. G., Allwarden, K., 1981. The use of dental crown heights for constructing age profiles of red deer and similar species in archaeological samples. *J. Archaeol. Sci.* 8(1):1–31.

Klein-Platat, C., Drai, J., Oujaa, M., Schlienger, J.-L., Simon, C., 2005. Plasma fatty acid composition is associated with the metabolic syndrome and low-grade inflammation in overweight adolescents. *Am. J. Clin. Nutr.* 82(6):1178–1184.

Koletzko, B. V., 2006. Long-term consequences of early feeding on later obesity risk. In: Rigo, J., Ziegler, E. E. (Eds.), *Protein and Energy Requirements in Infancy and Childhood*. Nestlé Nutrition Workshop Series, Pediatric Program 58. Nestec Ltd./S. Karger AG, Vevey and Basel, Switzerland, pp. 1–18.

Konner, M., Shostak, M., 1986. Ethnographic romanticism and the idea of human nature: parallels between Samoa and !Kung San. In: Biesele, M., Gordon, R., Lee, R. B. (Eds.), *The Past and Future of !Kung Ethnography: Critical Reflections and Symbolic Perspectives: Essays in Honour of Lorna Marshall*. Quellen zur Khoisan-Forschung 4. Helmut Buske Verlag, Hamburg, Germany, pp. 69–76.

Koster, J. M., 2008. Hunting with dogs in Nicaragua: an optimal foraging approach. *Curr. Anthropol.* 49(5):935–944.

Koussoroplis, A.-M., Lemarchand, C., Bec, A., Desvilettes, C., Amblard, C., Fournier, C., Berny, P., Bourdier, G., 2008. From aquatic to terrestrial food webs: decrease of the docosahexaenoic acid/linoleic acid ratio. *Lipids* 43(5):461–466.

Koutsari, C., Dumesic, D. A., Patterson, B. W., Votruba, S. B., Jensen, M. D., 2008. Plasma free fatty acid storage in subcutaneous and visceral adipose tissue in postabsorptive women. *Diabetes* 57(5):1186–1194.

Kramer, M. S., Kakuma, R., 2003. Energy and protein intake in pregnancy. *Cochrane Database of Systematic Reviews* 4: CD000032. doi:10.1002/14651858. CD000032.

Krebs, J. R., Davies, N. B. (Eds.), 1991. *Behavioural Ecology: An Evolutionary Approach*. 3rd ed. Blackwell Scientific Publications, Oxford, England.

Kroeber, A. L., 1925. *Handbook of the Indians of California*. Bulletin 78. Smithsonian Institution, Bureau of American Ethnology, Washington, DC.

Krogh, A., Krogh, M., 1914. A study of the diet and metabolism of Eskimos undertaken in 1908 on an expedition to Greenland. *Meddelelser om Grønland* 51(1):1–52.

Kuhn, S. L., Stiner, M. C., 2006. What's a mother to do? The division of labor among Neandertals and modern humans in Eurasia. *Curr. Anthropol.* 47(6):953–980.

Kuhnlein, H. V., Kubow, S., Soueida, R., 1991. Lipid components of traditional Inuit foods and diets of Baffin Island. *J. Food Compost. Anal.* 4(3):227–236.

Kurihara, K., Kawamura, Y., 1991. Overview. *Physiol. Behav.* 49(5):1029–1030.

Kuzawa, C. W., 1998. Adipose tissue in human infancy and childhood: an evolutionary perspective. *Yearb. Phys. Anthropol.* 41:177–209.

Kuzmin, Y. V., 2006. Chronology of the earliest pottery in East Asia: progress and pitfalls. *Antiquity* 80(308):362–371.

L'Heureux-Bouron, D., Tomé, D., Bensaid, A., Morens, C., Gaudichon, C. Fromentin, G., 2004. A very high 70%-protein diet does not induce conditioned taste aversion in rats. *J. Nutr.* 134(6):1512–1515.

Laden, G. T., Wrangham, R. W., 2005. The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and Australopith origins. *J. Hum. Evol.* 49(4):482–498.

La Fontaine, J. S., 1981. The domestication of the savage male. *Man* 16(3):333–349.

Landmann, W. A., Batzer, O. F., 1966. Influence of processing procedures on the chemistry of meat flavors. *J. Agric. Food Chem.* 14(3):210–214.

Lane, M., Gardner, D. K., 2003. Ammonium induces aberrant blastocyst differentiation, metabolism, pH regulation, gene expression and subsequently alters fetal development in the mouse. *Biol. Reprod.* 69(4):1109–1117.

Lane, M., Gardner, D. K., 2005. Understanding cellular disruptions during early embryo development that perturb viability and fetal development. *Reprod. Fertil. Dev.* 17(3):371–378.

Langdon, J. H., 2006. Has an aquatic diet been necessary for hominin brain evolution and functional development? *Br. J. Nutr.* 96(1):7–17.

Larpenteur, C., 1898. *Forty Years a Fur Trader on the Upper Missouri: The Personal Narrative of Charles Larpenteur, 1833–1872*. American Explorers Series 2. F. P. Harper, New York, NY.

Larsen, C. S., 1999. *Bioarchaeology: Interpreting Behavior from the Human Skeleton*. Cambridge University Press, Cambridge, England.

Larsen, C. S., 2003. Animal source foods and human health during evolution. *J. Nutr.* 133(Suppl. 11):3893S–3897S.

Lassek, W. D., Gaulin, S. J. C., 2006. Changes in body fat distribution in relation to parity in American women: a covert form of maternal depletion. *Am. J. Phys. Anthropol.* 131(2):295–302.

Lassek, W. D., Gaulin, S. J. C., 2007. Menarche is related to fat distribution. *Am. J. Phys. Anthropol.* 133(4):1147–1151.

Lassek, W. D., Gaulin, S. J. C., 2008. Waist-hip ratio and cognitive ability: is gluteofemoral fat a privileged store of neurodevelopmental resources? *Evol. Hum. Behav.* 29(1):26–34.

Leaf, D. A., Connor, W. E., Barstad, L., Sexton, G., 1995. Incorporation of dietary *n*-3 fatty acids into the fatty acids of human adipose tissue and plasma lipid classes. *Am. J. Clin. Nutr.* 62(1):68–73.

Leakey, L. S. B., 1969. *Animals of East Africa: The Wild Realm*. National Geographic Society, Washington, DC.

Leakey, M. D., 1971. *Olduvai Gorge, Vol. 3*. Excavations in Beds I and II, 1960–1963. Cambridge University Press, Cambridge, England.

Leakey, R., 1996. *The Origin of Humankind*. Science Masters Series. Basic Books, New York, NY.

Lebzelter, V., 1934. *Rassen und Kulturen in Süd und Südwest Afrika, Band 2. Eingeborenenkultur in Süd- und Südwestafrika. Wissenschaftliche Ergebnisse einer Forschungsreise nach Süd- und Südwestafrika in den Jahren 1926–1928*. Karl W. Hiersemann, Leipzig, Germany.

Ledger, H. P., 1968. Body composition as a basis for a comparative study of some East African mammals. In: Crawford, M. A. (Ed.), *Comparative Nutrition of Wild Animals. Proceedings of a Symposium Held at the Zoological Society of London on 10 and 11 November 1966*. Symp. Zool. Soc. Lond. 21. Academic Press, London, England, pp. 289–310.

Ledger, H. P., Sachs, R., Smith, N. S., 1967. Wildlife and food production. *World Rev. Anim. Prod.* 3(11):13–37.

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

Lee, R. B., 1973. Mongongo: the ethnography of a major wild food resource. *Ecol. Food Nutr.* 2:307–321.

Lee, R. B., 1979. *The !Kung San: Men, Women, and Work in a Foraging Society*. Cambridge University Press, Cambridge, England.

Lee, R. B., 1982. Politics, sexual and non-sexual, in an egalitarian society. In: Leacock, E. B., Lee, R. B. (Eds.), *Politics and History in Band Societies*. Cambridge University Press, Cambridge, England, pp. 37–59.

Lee, R. B., 1992. Art, science, or politics? The crisis in hunter–gatherer studies. *Am. Anthropol.* 94(1):31–54.

Lee, R. B., 2006. Twenty-first century indigenism. *Anthropol. Theor.* 6(4):455–479.

Lee, R. B., Daly, R., 1999. Introduction: foragers and others. In: Lee, R. B., Daly, R. (Eds.), *The Cambridge Encyclopedia of Hunters and Gatherers*. Cambridge University Press, Cambridge, England, pp. 1–19.

Lee, R. B., DeVore, I. (Eds.), 1968. *Man the Hunter*. Aldine, Chicago, IL.

Leece, E. A., Allman, M. A., 1996. The relationships between dietary α-linolenic:linoleic acid and rat platelet eicosapentaenoic and arachidonic acids. *Br. J. Nutr.* 76(3):447–452.

Lee-Thorp, J., Sponheimer, M., 2006. Contributions of biogeochemistry to understanding hominin dietary ecology. *Yearb. Phys. Anthropol.* 49:131–148.

Lefkowitz, W., Lim, S.-Y., Lin, Y., Salem Jr., N., 2005. Where does the developing brain obtain its docosahexaenoic acid? relative contributions of dietary α-linolenic acid, docosahexaenoic acid, and body stores in the developing rat. *Pediatr. Res.* 57(1):157–165.

Leibel, R. L., Edens, N. K., Fried, S. K., 1989. Physiologic basis for the control of body fat distribution in humans. *Annu. Rev. Nutr.* 9:417–443.

Leichhardt, L., 1847. *Journal of an Overland Expedition in Australia, from Moreton Bay to Port Essington, a Distance of Upwards of 3000 Miles, During the Years 1844–1845*. T. and W. Boone, London, England.

Leonard, W. R., Robertson, M. L., Snodgrass, J. J., 2007a. Energetics and the evolution of brain size in early *Homo*. In: Roebroeks, W. (Ed.), *Guts and Brains: An Integrative Approach to the Hominin Record*, Leiden University Press, Amsterdam, The Netherlands, pp. 29–46.

Leonard, W. R., Snodgrass, J. J., Robertson, M. L., 2007b. Effects of brain evolution on human nutrition and metabolism. *Annu. Rev. Nutr.* 27:311–327.

Leslie, L., 1833. Lion-hunting in South Africa. In: Jameson, R. (Ed.), *Edinburgh New Philosophical Journal, Exhibiting a View of the Progressive Discoveries and Improvements in the Sciences and the Arts, Vol. 15*. Adam and Charles Black, Edinburgh, Scotland, pp. 62–68.

Leung, W.-T. W., 1968. *Food Composition Table for Use in Africa*. Food and Agricultural Organization of the United Nations, Nutrition Division, and U.S. Department of Health, Education, and Welfare, Public Health Service, Rome, Italy.

Lewin, R., Foley, R. A., 2004. *Principles of Human Evolution*. 2nd ed. Blackwell Science, Oxford, England.

Lewis, M., Clarke, W., 1815. *Travels to the Source of the Missouri River and Across the American Continent to the Pacific Ocean: Performed by Order of the Government of the United States, in the Years 1804, 1805, and 1806, Vol. 3*. Longman, Hurst, Rees, Orme, and Brown, London, England.

Lewis-Williams, J. D., 1983. *The Rock Art of Southern Africa*. Cambridge University Press, Cambridge, England.

Lewis-Williams, J. D., 1987. A dream of eland: an unexplored component of San shamanism and rock art. *World Archaeol.* 19(2):165–177.

Lewis-Williams, J. D., Biesele, M., 1978. Eland hunting rituals among northern and southern San groups: striking similarities. *Africa* 48(2):117–134.

Lichtenstein, H., 1812. *Travels in Southern Africa, in the Years 1803, 1804, 1805, and 1806*. Plumptre, A. (Trans.). Henry Colburn, London, England.

Lieb, C. W., 1929. The effects on human beings of a twelve months' exclusive meat diet: based on intensive clinical and laboratory studies on two arctic explorers living under average conditions in a New York climate. *J. Am. Med. Assoc.* 93(1):20–22.

Liebenberg, L., 1990. *The Art of Tracking: The Origin of Science*. David Philip Publishers, Claremont, South Africa.

Liebenberg, L., 2006. Persistence hunting by modern hunter–gatherers. *Curr. Anthropol.* 47(6):1017–1025.

Liebenberg, L., 2008. The relevance of persistence hunting to human evolution. *J. Hum. Evol.* 55(6):1156–1159.

Lieberman, D. E., 1994. The biological basis for seasonal increments in dental cementum and their application to archaeological research. *J. Archaeol. Sci.* 21(4):525–539.

Lieberman, D. E., Krovitz, G. E., Yates, F. W., Devlin, M., St. Claire, M., 2004. Effects of food processing on masticatory strain and craniofacial growth in a retrognathic face. *J. Hum. Evol.* 46(6):655–677.

Lin, D. S., Conner, W. E., 1990. Are the *n*-3 fatty acids from dietary fish oil deposited in the triglyceride stores of adipose tissue? *Am. J. Clin. Nutr.* 51(4):535–539.

Lindeberg, S., 2009. Modern human physiology with respect to evolutionary adaptations that relate to diet in the past. In: Hublin, J.-J., Richards, M. P. (Eds.), *The Evolution of Hominid Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*. Vertebrate Paleobiology and Paleoanthropology. Springer, Dordrecht, The Netherlands, pp. 43–57.

Lindemann, B., 2000. A taste for umami. *Nat. Neurosci.* 3(2):99–100.

Lindstedt, S. L., Boyce, M. S., 1985. Seasonality, fasting endurance, and body size in mammals. *Am. Nat.* 125(6):873–878.

Linkswiler, H. M., 1976. Calcium. In: Hegsted, D. M. (Ed.), *Present Knowledge in Nutrition*. 4th ed. Nutrition Foundation, New York, NY, pp. 232–240.

Linton, R., 1944. North American cooking pots. *Am. Antiq.* 9(4):369–380.

Lombard, M., Parsons, I., Van der Ryst, M. M., 2004. Middle Stone Age lithic point experimentation for macro-fracture and residue analyses: the process and preliminary results with reference to Sibudu Cave points. *S. Afr. J. Sci.* 100(3–4):159–166.

Longman, C. J., Walrond, H., 1901. *Archery*. Reissued ed. Longmans, Green, and Company, London, England.

Lönnerdal, B., 2003. Nutritional and physiologic significance of human milk proteins. *Am. J. Clin. Nutr.* 77(Suppl. 6):1537S–1543S.

Loring, J. A., 1914. *African Adventure Stories*. Charles Scribner's Sons, New York, NY.

Lovejoy, C. O., 2009. Reexamining human origins in light of *Ardipithecus ramidus*. *Science* 326(5949):74, 74e1–74e8.

Lowery, L. M., Devia, L., 2009. Dietary protein safety and resistance exercise: what do we really know? *J. Int. Soc. Sports Nutr.* 6(3):doi:10.1186/1550-2783-6-3.

Lubbock, J., 1869. *Pre-historic Times, as Illustrated by Ancient Remains, and the Manners and Customs of Modern Savages*. 2nd ed. Williams and Norgate, Edinburgh, Scotland.

Luca, F., Bubba, G., Basile, M., Brdicka, R., Michalodimitrakis, E., Rickards, O., Vershubsky, G., Quintana-Murci, L., Kozlov, A. I., Novelletto, A., 2008. Multiple advantageous amino acid variants in the NAT2 gene in human populations. *PLoS One* 3(9):e3136. doi:10.1371/journal.pone.0003136.

Lucas, P. W., 2006. Facial dwarfing and dental crowding in relation to diet. In: Bromage, T. G., Vidal, A., Ramón Areces, F., Aguirre, E., Perez-Ochoa, A. (Eds.), *Integrative Approaches to Human Health and Evolution. Proceedings of the International Symposium "Integrative Approaches to Human and Evolution" Held in Madrid, Spain, Between 18 and 20, April 2005*. International Congress Series 1296. Elsevier, Amsterdam, The Netherlands, pp. 74–82.

Lucas, P. W., Sui, Z., Ang, K. Y., Tan, H. T. W., King, S. H., Sadler, B., Peri, N., 2009. Meals versus snacks and the human dentition and diet during the Paleolithic. In: Hublin, J.-J., Richards, M. P. (Eds.), *The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*. Vertebrate Paleobiology and Paleoanthropology. Springer, Dordrecht, The Netherlands, pp. 31–41.

Luft, F. C., Fineberg, N. S., Sloan, R. S., Hunt, J. N., 1983. The effect of dietary sodium and protein on urine volume and water intake. *J. Lab. Clin. Med.* 101(4):605–610.

Lugard, F. J. D., 1893. *The Rise of Our East African Empire: Early Efforts in Nyasaland and Uganda, Vol. 1*. William Blackwood and Sons, Edinburgh, Scotland.

Lumholtz, C., 1889. *Among Cannibals: An Account of Four Years' Travels in Australia and of Camp Life with the Aborigines of Queensland*. John Murray, London, England.

Lupo, K. D., 1994. Butchering marks and carcass acquisition strategies: distinguishing hunting from scavenging in archaeological contexts. *J. Archaeol. Sci.* 21(6):827–837.

Lupo, K. D., 1998. Experimentally derived extraction rates for marrow: implications for body part exploitation strategies of Plio-Pleistocene hominid scavengers. *J. Archaeol. Sci.* 25(7):657–675.

Lupo, K. D., O'Connell, J. F., 2002. Cut and tooth mark distributions on large animal bones: ethnoarchaeological data from the Hadza and their implications for current ideas about early human carnivory. *J. Archaeol. Sci.* 29(1):85–109.

Lyell, C., 1830–1833. *Principles of Geology, Vol. 1–3*. John Murray, London, England.

Lyell, C., 1863. *The Geological Evidences of the Antiquity of Man, with Remarks on Theories of the Origin of Species by Variation*. John Murray, London, England.

Lyman, R. L., 1987. Hunting for evidence of Plio-Pleistocene hominid scavengers. *Am. Anthropol.* 89:710–715.

Lyman, R. L., 1994. *Vertebrate Taphonomy*. Cambridge Manuals in Archaeology. Cambridge University Press, Cambridge, England.

Lyman, R. L., 2004. The concept of equifinality in taphonomy. *J. Taphonomy* 2(1):15–26.

Lyman, R. L., 2008. *Quantitative Paleozoology*. Cambridge Manuals in Archaeology. Cambridge University Press, Cambridge, England.

Lyman, R. L., Savelle, J. M., Whitridge, P., 1992. Derivation and application of a meat utility index for phocid seals. *J. Archaeol. Sci.* 19(5):531–555.

MacDonald, K., 2007. Cross-cultural comparison of learning in human hunting: implications for life history evolution. *Hum. Nat.* 18(4):386–402.

Mackenzie, A., 1903. *Voyages from Montreal Through the Continent of North America to the Frozen and Pacific Oceans in 1789 and 1793 with an Account of the Rise and State of the Fur Trade, Vol. 1*. A. S. Barnes and Company, New York.

Macleod, G., Ames, J. M., 1986. The effect of heat on beef aroma: comparisons of chemical composition and sensory properties. *Flavour Fragr. J.* 1(3):91–104.

Madibela, O. R., Mokwena, K. K., Nsoso, S. J., Thema, T. F., 2009. Chemical composition of mopane worm sampled at three sites in Botswana and subjected to different processing. *Trop. Anim. Health Prod.* 41(6):935–942.

Madibela, O. R., Seitiso, T. K., Thema, T. F., Letso, M., 2007. Effect of traditional processing methods on chemical composition and in vitro true dry matter digestibility of the mophane worm (*Imbrasia belina*). *J. Arid Environ.* 68(3):492–500.

Madrigal, T. C., 2004. The derivation and application of white-tailed deer utility indices and return rates. *J. Taphonomy* 2(4):185–199.

Madrigal, T. C., Blumenschine, R. J., 2000. Preferential processing of high return rate marrow bones by Oldowan hominids: a comment on Lupo. *J. Archaeol. Sci.* 27(8):739–741.

Magalon, H., Patin, E., Austerlitz, F., Hegay, T., Aldashev, A., Quintana-Murci, L., Heyer, E., 2008. Population genetic diversity of the NAT2 gene supports a role of acetylation in human adaptation to farming in Central Asia. *Eur. J. Hum. Genet.* 16(2):243–251.

Mair, C., 1891. The American bison: its habits, method of capture and economic use in the North-West, with reference to its threatened extinction and possible preservation. *Trans. R. Soc. Can.* 8(2, 1890):93–108.

Makrides, M., Neumann, M. A., Jeffrey, B., Lien, E. L., Gibson, R. A., 2000. A randomized trial of different ratios of linoleic to α-linolenic acid in the diet of term infants: effects on visual function and growth. *Am. J. Clin. Nutr.* 71(1):120–129.

Malacarne, M., Martuzzi, F., Summer, A., Mariani, P., 2002. Protein and fat composition of mare's milk: some nutritional remarks with reference to human and cow's milk. *Int. Dairy J.* 12(11):869–877.

Malcom, G. T., Bhattacharyya, A. K., Velez-Duran, M., Guzman, M. A., Oalmann, M. C., Strong, J. P., 1989. Fatty acid composition of adipose tissue in humans: differences between subcutaneous sites. *Am. J. Clin. Nutr.* 50(2):288–291.

Mamalakis, G., Kafatos, A., Manios, Y., Kalogeropoulos, N., Andrikopoulos, N., 2002. Abdominal vs buttock adipose fat: relationships with children's serum lipid levels. *Eur. J. Clin. Nutr.* 56(11):1081–1086.

Manfredini, S., Vertuani, S., Buzzoni, V., 2002. *Adansonia digitata*: il baobab farmacista. *Integratore Nutrizionale* 5(4):25–29.

Manhire, A., Parkington, J. E., Yates, R., 1985. Nets and fully recurved bows: rock paintings and hunting methods in the western Cape, South Africa. *World Archaeol.* 17(2):161–174.

Mann, N., 2000. Dietary lean red meat and human evolution. *Eur. J. Nutr.* 39(2):71–79.

Manne, T. H., Stiner, M. C., Bicho, N. F., 2005. Evidence for bone grease rendering during the Upper Paleolithic at Vale Boi (Algarve, Portugal). In: Bicho, N. F. (Ed.), *Animais na Pré-história e Arqueologia da Península Ibérica. Actas do IV Congresso de Arqueologia Peninsular. Congresso de Arqueologia Peninsular, Faro, 2004*. Promontoria Monográfica 3. Centro de Estudos de Património, Universidade do Algarve, Faro, Portugal, pp. 145–158.

Manninen, A. H., 2006. Hyperinsulinaemia, hyperaminoacidaemia and post-exercise muscle anabolism: the search for the optimal recovery drink. *Br. J. Sports Med.* 40(11):900–905.

Marais, E., 1996. Omaungo in Namibia: *Imbrasia belina* (Saturniidae: Lepidoptera) as a commercial resource. In: Gashe, B. A., Leggett, K., Mpuchane, S. F. (Eds.), *Phane. Proceedings of the First Multidisciplinary Symposium on Phane, 18 June 1996*. University of Botswana, Department of Biological Sciences and Kalahari Conservation Society, Gaborone, Botswana, pp. 23–31.

Marcy, R. B., 1863. *The Prairie Traveler: A Handbook for Overland Expeditions*. Trubner, London, England.

Marean, C. W., Bar-Matthews, M., Bernatchez, J., Fisher, E., Goldberg, P., Herries, A. I. R., Jacobs, Z., Jerardino, A., Karkanas, P., Minichillo, T., Nilssen, P. J., Thompson, E., Watts, I., Williams, H. M., 2007. Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. *Nature* 449(7164):905–908.

Marean, C. W., Cleghorn, N., 2003. Large mammal skeletal element transport: applying foraging theory in a complex taphonomic system. *J. Taphonomy* 1(1):15–42.

Marean, C. W., Spencer, L. M., Blumenschine, R. J., Capaldo, S. D., 1992. Captive hyaena bone choice and destruction, the schlepp effect and Olduvai archaeofaunas. *J. Archaeol. Sci.* 19(1):101–121.

Marlowe, F. W., 1999. Showoffs or providers? The parenting effort of Hadza men. *Evol. Hum. Behav.* 20(6):391–404.

Marlowe, F. W., 2000. The patriarch hypothesis: an alternative explanation of menopause. *Hum. Nat.* 11(1):27–42.

Marlowe, F. W., 2003. A critical period for provisioning by Hadza men: implications for pair bonding. *Evol. Hum. Behav.* 24:217–229.

Marlowe, F. W., 2004. What explains Hadza food sharing? *Res. Econ. Anthropol.* 23:69–88.

Marlowe, F. W., 2006. Central place provisioning: the Hadza as an example. In: Hohmann, G., Robbins, M. M., Boesch, C. (Eds.), *Feeding Ecology in Apes and Other Primates: Ecological, Physical and Behavioral Aspects*. Cambridge Studies in Biological and Evolutionary Anthropology 48. Cambridge University Press, Cambridge, England, pp. 359–377.

Marlowe, F. W., 2007. Hunting and gathering: the human sexual division of foraging labor. *Cross-Cult. Res.* 41(2):170–195.

Marshall, L., 1976. *The !Kung of Nyae Nyae*. Harvard University Press, Cambridge, MA.

Martin, M. K., Voorhies, B., 1975. *Female of the Species*. Columbia University Press, New York, NY.

Martin, W. F., Cerundolo, L. H., Pikosky, M. A., Gaine, P. C., Maresh, C. M., Armstrong, L. E., Bolster, D. R., Rodriguez, N. R., 2006. Effects of dietary protein intake on indexes of hydration. *J. Am. Diet. Assoc.* 106(4):587–589.

Massey, L. K., 2003. Dietary animal and plant protein and human bone health: a whole foods approach. *J. Nutr.* 133(3):862S–865S.

Matsumoto-Oda, A., Hayashi, Y., 1999. Nutritional aspects of fruit choice by chimpanzees. *Folia Primatol.* 70(3):154–162.

Maugham, R. C. F., 1906. *Portuguese East Africa: The History, Scenery, and Great Game of Manica and Sofala*. E. P. Dutton, New York, NY.

Mayr, E., 1963. *Animal Species and Evolution*. Belknap Press, Cambridge, MA.

Mazel, A. D., 1992. Early pottery from the eastern part of southern Africa. *S. Afr. Archaeol. Bull.* 47(155):3–7.

Mazess, R. B., Mather, W. E., 1974. Bone mineral content of northern Alaskan Eskimos. *Am. J. Clin. Nutr.* 27(9):916–925.

McBrearty, S., Brooks, A. S., 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. *J. Hum. Evol.* 39(5):453–563.

McCall, D. F., 1970. *Wolf Courts Girl: The Equivalence of Hunting and Mating in Bushman Thought*. Papers in International Studies, Africa Series 7. Ohio University Center for International Studies, Athens, OH.

McCartney, A. P., 1970. "Pottery" in the Aleutian Islands. *Am. Antiq.* 35(1):105–108.

McClellan, W. S., DuBois, E. F., 1930. Clinical calorimetry, XLV. prolonged meat diets with a study of kidney function and ketosis. *J. Biol. Chem.* 87(3):651–668.

McClellan, W. S., Rupp, V. R., Toscani, V., 1930. Clinical calorimetry, XLVI. prolonged meat diets with a study of the metabolism of nitrogen, calcium, and phosphorus. *J. Biol. Chem.* 87(3):669–680.

McClellan, W. S., Spencer, H. J., Falk, E. A., 1931. Clinical calorimetry, XLVII. prolonged meat diets with a study of the respiratory metabolism. *J. Biol. Chem.* 93:419–434.

McClymont, R. A., Thompson, J. R., Fenton, M., 1977. Developments in meat identification at the University of Alberta. In: *Forensic Science. Symposium Proceedings, April 13–15, 1977, Calgary, Alberta*. Alberta Recreation, Parks and Wildlife, Fish and Wildlife Division, Edmonton, Alberta, pp. 183–211.

McCue, M. D., Bennett, A. F., Hicks, J. W., 2005. The effect of meal composition on specific dynamic action in Burmese pythons (*Python molurus*). *Physiol. Biochem. Zool.* 78(2):182–192.

McCullagh, K. G., Widdowson, E. M., 1970. The milk of the African elephant. *Br. J. Nutr.* 24:109–117.

McGrew, W. C., 2001. The other faunivory: primate insectivory and early human diet. In: Stanford, C. B., Bunn, H. T. (Eds.), *Meat-Eating and Human Evolution*. Oxford University Press, Oxford, England, pp. 160–178.

McGuire, K. R., Hildebrandt, W. R., 2005. Re-thinking Great Basin foragers: prestige hunting and costly signaling during the Middle Archaic period. *Am. Antiq.* 70(4):695–712.

McKiernan, G., 1954. *The Narrative and Journal of Gerald McKiernan in South West Africa, 1874–1879*. Serton, P. (Ed.). Publication 35. Van Riebeeck Society, Cape Town, South Africa.

McLaren, D. S., 1974. The great protein fiasco. *Lancet* 304(7872):93–96.

McLaren, D. S., 2000. The great protein fiasco revisited. *Nutrition* 16(6):464–465.

McNab, B. K., 2002. *The Physiological Ecology of Vertebrates: A View from Energetics*. Comstock Book Series. Cornell University Press, Ithaca, NY.

McNaughton, S. J., Georgiadis, N. J., 1986. Ecology of African grazing and browsing mammals. *Annu. Rev. Ecol. Syst.* 17:39–66.

Mduma, S. A. R., Sinclair, A. R. E., Hilborn, R., 1999. Food regulates the Serengeti wildebeest: a 40-year record. *J. Anim. Ecol.* 68(6):1101–1122.

Meillassoux, C., 1981. *Maidens, Meal and Money: Capitalism and the Domestic Community*. Themes in the Social Sciences. Cambridge University Press, Cambridge, England.

Meister, A., 1965. *Biochemistry of the Amino Acids*. 2nd ed. Academic Press, New York, NY.

Mekel-Bobrov, N., Gilbert, S. L., Evans, P. D., Vallender, E. J., Anderson, J. R., Hudson, R. R., Tishkoff, S. A., Lahn, B. T., 2005. Ongoing adaptive evolution of ASPM, a brain size determinant in *Homo sapiens*. *Science* 309(5741):1720–1722.

Mekota, A.-M., Grupe, G., Ufer, S., Cuntz, U., 2006. Serial analysis of stable nitrogen and carbon isotopes in hair: monitoring starvation and recovery phases of patients suffering from anorexia nervosa. *Rapid Commun. Mass Spectrom.* 20(10):1604–1610.

Mercader, J., Garcia-Heras, M., Gonzalez-Alvarez, I., 2000. Ceramic tradition in the African forest: characterisation analysis of ancient and modern pottery from Ituri, D.R. Congo. *J. Archaeol. Sci.* 27(2):163–182.

Merialdi, M., Carroli, G., Villar, J., Abalos, E., Gülmezoglu, A. M., Kulier, R., Onis, M. de, 2003. Nutritional interventions during pregnancy for the prevention or treatment of impaired fetal growth: an overview of randomized controlled trials. *J. Nutr.* 133(5):1626S–1631S.

Mertz, W., 2000. Three decades of dietary recommendations. *Nutr. Rev.* 58(10):324–331.

Metcalfe, D., Jones, K. T., 1988. A reconsideration of animal body-part utility indices. *Am. Antiq.* 53(3):486–504.

Metges, C. C., 2005. Longterm effects of pre- and postnatal exposure to low and high dietary protein levels. In: Back, N., Cohen, I. R., Kritchevsky, D., Lajtha, A., Paoletti, R., Koletzko, B., Dodds, P., Akerblom, H., Ashwell, M. (Eds.), *Early Nutrition and its Later Consequences: New Opportunities*. Adv. Exp. Med. Biol. 569. Springer, Dordrecht, The Netherlands, pp. 64–68.

Meza-Herrera, C. A., Ross, T., Hawkins, D., Hallford, D., 2006. Interactions between metabolic status, pre-breeding protein supplementation, uterine pH, and embrionic [sic] mortality in ewes: preliminary observations. *Trop. Anim. Health Prod.* 38(5):407–413.

Mikkelsen, P. B., Toubro, S., Astrup, A., 2000. Effect of fat-reduced diets on 24-h energy expenditure: comparisons between animal protein, vegetable protein, and carbohydrate. *Am. J. Clin. Nutr.* 72(5):1135–1141.

Millar, J. S., Hickling, G. J., 1990. Fasting endurance and the evolution of mammalian body size. *Funct. Ecol.* 4(1):5–12.

Miller, G. F., 1999. Sexual selection for cultural displays. In: Dunbar, R., Knight, C., Power, C. (Eds.), *The Evolution of Culture: An Interdisciplinary View*. Rutgers University Press, New Brunswick, NJ, pp. 71–91.

Milligan, L. A., 2007. *Nonhuman Primate Milk Composition: Relationship to Phylogeny, Ontogeny, and Ecology*. Unpublished PhD Dissertation, University of Arizona, Tucson, AZ.

Milligan, L. A., Bazinet, R. P., 2008. Evolutionary modifications of human milk composition: evidence from long-chain polyunsaturated fatty acid composition of anthropoid milks. *J. Hum. Evol.* 55(6):1086–1095.

Milligan, L. A., Oftedal, O. T., 2007. Hominoid milk composition: relationship to phylogeny and ontogeny. Unpublished paper presented at the seventy-sixth annual meeting of the American Association of Physical Anthropologists, Philadelphia, PA, March 28–31, 2007.

Milligan, L. A., Rapoport, S. I., Cranfield, M. R., Dittus, W., Glander, K. E., Oftedal, O. T., Power, M. L., Whittier, C. A., Bazinet, R. P., 2008. Fatty acid composition of wild anthropoid primate milks. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* 149(1):74–82.

Millward, D. J., 1999a. The nutritional value of plant-based diets in relation to human amino acid and protein requirements. *Proc. Nutr. Soc.* 58(2):249–260.

Millward, D. J., 1999b. Optimal intakes of protein in the human diet. *Proc. Nutr. Soc.* 58(2):403–413.

Milton, K., 1991. Comparative aspects of diet in Amazonian forest-dwellers. *Philos. Trans. R. Soc. Lond., B Biol. Sci.* 334B(1270):253–263.

Milton, K., 1999. A hypothesis to explain the role of meat-eating in human evolution. *Evol. Anthropol.* 8(1):11–21.

Milton, K., 2003. The critical role played by animal source foods in human (*Homo*) evolution. *J. Nutr.* 133:3886S–3892S.

Milton, K., 1979. Male bias in anthropology. *Man* 14(1):40–54.

Milton, W. F., 1866. *Voyage de l'Atlantique au Pacifique à Travers le Canada, les Montagnes Rocheuses et la Colombie Anglaise par le Vicomte Milton et le Dr W. B. Cheadle*. Traduit de l'Anglais par J. Belin-de Launay. Librairie de L. Hatchette, Paris, France.

Mitani, J. C., Watts, D. P., 2001. Why do chimpanzees hunt and share meat? *Anim. Behav.* 61:915–924.

Mitchell, P., 2005. *African Connections: An Archaeological Perspective on Africa and the Wider World*. African Archaeology Series. AltaMira Press, Walnut Creek, CA.

Mithune, H. H. (Ed.), 1847. *History of the Bosjesmans, or Bush People: The Aborigines of Southern Africa. With Copious Extracts from the Best Authors, Showing the Habits and Disposition of the Above-Named Extraordinary Race of Human Beings*. Chapman, Elcoate, and Company, London, England.

Mittendorfer, B., 2005. Sexual dimorphism in human lipid metabolism. *J. Nutr.* 135(4):681–686.

Mmonatau, Y., 2005. *Flour from the Morama Bean: Composition and Sensory Properties in a Botswana Perspective*. Unpublished MA thesis, Consumer Science (Foods), Stellenbosch University, Stellenbosch, South Africa.

Mojeremane, W., Tshwenyane, S. O., 2004. The resource role of morula (*Sclerocarya birrea*): a multipurpose indigenous fruit tree of Botswana. *J. Biol. Sci.* 4(6):771–775.

Monaghan, B. G., Halloran, G. M., 1996. RAPD variation within and between natural populations of morama [*Tylosema esculentum* (Burchell) Schreiber] in southern Africa. *S. Afr. J. Bot.* 62:287–291.

Moncel, M.-H., Gema Chacón, M., Coudenneau, A., Fernandes, P., 2009. Points and convergent tools in the European early Middle Palaeolithic site of Payre (SE, France). *J. Archaeol. Sci.* 36(9):1892–1909.

Mora, R., de la Torre, I., 2005. Percussion tools in Olduvai Beds I and II (Tanzania): implications for early human activities. *J. Anthropol. Archaeol.* 24(2):179–192.

Mori, M., Kawada, T., Ono, T., Torii, K., 1991. Taste preference and protein nutrition and L-amino acid homeostasis in male Sprague-Dawley rats. *Physiol. Behav.* 49(5):987–995.

Morise, A., Combe, N., Boué, C., Legrand, P., Catheline, D., Delplanque, B., Fénart, E., Weill, P., Hermier, D., 2004. Dose effect of α-linolenic acid on PUFA conversion, bioavailability, and storage in the hamster. *Lipids* 39(4):325–334.

Morris, B., 2004. *Insects and Human Life*. Berg Publishers, Oxford, England.

Morris, C., 1886. The making of man. *Am. Nat.* 20(6):493–505.

Morris, J. G., 2002. Idiosyncratic nutrient requirements of cats appear to be diet-induced evolutionary adaptations. *Nutr. Res. Rev.* 15(1):153–168.

Morris Jr., S. M., 1992. Regulation of enzymes of urea and arginine synthesis. *Annu. Rev. Nutr.* 12:81–101.

Morris Jr., S. M., 2002. Regulation of enzymes of the urea cycle and arginine metabolism. *Annu. Rev. Nutr.* 22:87–105.

Morrison, W. R., 1978. Wheat lipid composition. *Cereal Chem.* 55(5):548–558.

Morwood, M. J., Trezise, P. J., 1989. Edge-ground axes in Pleistocene greater Australia: new evidence from S.E. Cape York Peninsula. *Queensland Archaeol. Res.* 6:77–90.

Motshegwe, S. M., Holmback, J., Yeboah, S. O., 1998. General properties and the fatty acid composition of the oil from the mophane caterpillar, *Imbrasia belina*. *J. Am. Oil Chem. Soc.* 75(6):725–728.

Mottram, D. S., 1998. Flavour formation in meat and meat products: a review. *Food Chem.* 62(4):415–424.

Mottram, D. S., 2007. The Maillard reaction: source of flavour in thermally processed foods. In: Berger, R. G. (Ed.), *Flavours and Fragrances: Chemistry, Bioprocessing and Sustainability*. Springer, Berlin, Germany, pp. 269–283.

Mottram, D. S., Koutsidis, G., Oruna-Concha, M.-J., Ntova, M., Elmore, J. S., 2004. Analysis of important flavor precursors in meat. In: Deibler, K. D., Delwiche, J. (Eds.), *Handbook of Flavor Characterization: Sensory Analysis, Chemistry, and Physiology*. Marcel Dekker, New York, NY, pp. 463–472.

Mouillé, B., Robert, V., Blachier, F., 2004. Adaptative increase of ornithine production and decrease of ammonia metabolism in rat colonocytes after hyperproteic diet ingestion. *Am. J. Physiol. Gastrointest. Liver Physiol.* 287(2):G344–G351.

Munro, N. D., Bar-Oz, G., 2004. Debating issues of equifinality in ungulate skeletal part studies. *J. Taphonomy* 2(1):1–13.

Murakami, K., Sasaki, S., Takahashi, Y., Uenishi, K., Yamasaki, M., Hayabuchi, H., Goda, T., Oka, J., Baba, K., Ohki, K., Kohri, T., Muramatsu, K., Furuki, M., 2007. Hardness (difficulty of chewing) of the habitual diet in relation to body mass index and waist circumference in free-living Japanese women aged 18–22 y. *Am. J. Clin. Nutr.* 86(1):206–213.

Murdoch, J., 1887. On some popular errors in regard to the Eskimos. *Am. Nat.* 21(1):9–16.

Murray, S. S., Schoeninger, M. J., Bunn, H. T., Pickering, T. R., Marlett, J. A., 2001. Nutritional composition of some wild plant foods and honey used by Hadza foragers of Tanzania. *J. Food Compost. Anal.* 14(1):3–13.

Muskiet, F. A. J., Fokkema, M. R., Schaafsma, A., Boersma, E. R., Crawford, M. A., 2004. Is docosahexaenoic acid (DHA) essential? Lessons from DHA status regulation, our ancient diet, epidemiology and randomized controlled trials. *J. Nutr.* 134:183–186.

Muskiet, F. A. J., van Goor, S. A., Kuipers, R. S., Velzing-Aarts, F. V., Smit, E. N., Bouwstra, H., Dijck-Brouwer, D. A. J., Boersma, E. R., Hadders-Algra, M., 2006. Long-chain polyunsaturated fatty acids in maternal and infant nutrition. *Prostaglandins, Leukot. Essent. Fatty Acids* 75(3):135–144.

Myers, F. R., 1988. Critical trends in the study of hunter–gatherers. *Annu. Rev. Anthropol.* 17:261–282.

Nabhan, G. P., 2004. *Why Some Like It Hot: Food, Genes, and Cultural Diversity*. Island Press, Washington, DC.

Nakazawa, Y., Straus, L. G., González-Morales, M. R., Solana, D. C., Saiz, J. C., 2009. On Stone-boiling technology in the Upper Paleolithic: behavioral implications from an early Magdalenian hearth in El Mirón Cave, Cantabria, Spain. *J. Archaeol. Sci.* 36(3):684–693.

Nansen, F., 1892. *The First Crossing of Greenland*. Gepp, H. M. (Trans.). Longmans, Green, and Company, London, England.

National Research Council, 2008. *Lost Crops of Africa, Vol. III. Fruits*. National Academies Press, Washington, DC.

Neel, J. V., 1962. Diabetes mellitus: a “thrifty” genotype rendered detrimental by “progress”? *Am. J. Hum. Genet.* 14(4):353–362.

Neel, J. V., 1982. The “thrifty genotype” revisited. In: Köbberling, J., Tattersall, R. (Eds.), *The Genetics of Diabetes Mellitus*. Serono Symp. Proc. 47. Academic Press, New York, NY, pp. 137–147.

Neel, J. V., 1999. The “thrifty genotype” in 1998. *Nutr. Rev.* 57(5 Part 2):S2–S9.

Nelson, G., 2002. *My first years in the fur trade: the journals of 1802–1804.* Peers, L. L., Schenck, T. M. (Eds.). Rupert’s Land Record Society Series 8. McGill-Queen’s University Press, Montreal, Quebec, and Kingston, Ontario.

Nelson, G., Chandrashekar, J., Hoon, M. A., Feng, L., Zhao, G., Ryba, N. J. P., Zuker, C. S., 2002. An amino-acid taste receptor. *Nature* 416(6877):199–202.

Nelson, R. K., 1973. *Hunters of the Northern Forest: Designs for Survival Among the Alaskan Kutchin*. University of Chicago Press, Chicago, IL.

Neumann, A. H., 1898. *Elephant-Hunting in East Equatorial Africa: Being an Account of Three Years’ Ivory-Hunting Under Mount Kenia and Among the Ndorobo Savages of the Lorogi Mountains, Including a Trip to the North of Lake Rudolph*. Rowland Ward, London, England.

Neuwinger, H. D., 1996. *African Ethnobotany: Poisons and Drugs – Chemistry, Pharmacology, Toxicology*. Porter, A. (Trans.). Chapman and Hall, Weinheim, Germany.

Newman, J. L., 1995. From definition, to geography, to action, to reaction: the case of protein-energy malnutrition. *Ann. Assoc. Am. Geogr.* 85(2):233–245.

Newton-Fisher, N. E., 2007. Chimpanzee hunting behavior. In: Henke, W., Tattersall, I. (Eds.), *Handbook of Paleoanthropology*. Springer Reference. Springer, Berlin, Germany, pp. 1295–1320.

Nielsen, R., Hellmann, I., Hubisz, M., Bustamante, C., Clark, A. G., 2007. Recent and ongoing selection in the human genome. *Nat. Rev. Genet.* 8(11):857–868.

Njau, J. K., 2006. *The Relevance of Crocodiles to Oldowan Hominin Paleoecology at Olduvai Gorge, Tanzania*. Unpublished PhD Dissertation, Rutgers University, New Brunswick, NJ.

Njau, J. K., Blumenschine, R. J., 2006. A diagnosis of crocodile feeding traces on larger mammal bone, with fossil examples from the Plio-Pleistocene Olduvai basin, Tanzania. *J. Hum. Evol.* 50(2):142–162.

Noli, H. D., 1992. *Archery in Southern Africa: The Evidence from the Past*. Unpublished PhD Dissertation, Department of Archaeology, University of Cape Town, Rondebosch, South Africa.

Noli, D., Avery, G., 1988. Protein poisoning and coastal subsistence. *J. Archaeol. Sci.* 15(4):395–401.

Nonaka, K., 1996. Ethnoentomology of the central Kalahari San. *Afr. Studies Monogr. Suppl.* 22:29–46.

Nor Aliza, A. R., Bedick, J. C., Rana, R. L., Tunaz, H., Hoback, W. W., Stanley, D. W., 2001. Arachidonic and eicosapentaenoic acids in tissues of the firefly, *Photinus pyralis* (Insecta: Coleoptera). *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 128A(2):251–257.

Nour, A. A., Magboul, B. I., Kheiri, N. H., 1980. Chemical composition of baobab fruit (*Adansonia digitata* L.). *Trop. Sci.* 22(4):383–388.

Ntiamoa-Baidu, Y. (Ed.), 1997. *Wildlife and Food Security in Africa*. FAO Conservation Guide 33. Food and Agriculture Organization of the United Nations, Rome, Italy.

Nuzum, C. T., Snodgrass, P. J., 1971. Urea cycle enzyme adaptation to dietary protein in primates. *Science* 172(3987):1042–1043.

Nyerup, R., 1806. *Oversyn over Faedrelandets Mindesmaerker fra Oldtiden*. Oxford Studies in the History of Archaeology. A. og S. Soldin, Copenhagen, Denmark.

O'Brien, C. J., 1994. *Determining Seasonality and Age in East African Archaeological Faunas: An Ethnoarchaeological Application of Cementum Increment Analysis*. Unpublished PhD Dissertation, Department of Anthropology, University of Wisconsin, Madison, WI.

O'Connell, J. F., Hawkes, K., Blurton Jones, N. G., 1988a. Hadza hunting, butchering, and bone transport and their archaeological implications. *J. Anthropol. Res.* 44(2):113–162.

O'Connell, J. F., Hawkes, K., Blurton Jones, N. G., 1988b. Hadza scavenging: implications for Plio/Pleistocene hominid subsistence. *Curr. Anthropol.* 29(2):356–363.

O'Connell, J. F., Hawkes, K., Blurton Jones, N. G., 1992. Patterns in the distribution, site structure and assemblage composition of Hadza kill-butchering sites. *J. Archaeol. Sci.* 19(3): 319–345.

O'Connell, J. F., Hawkes, K., Blurton Jones, N. G., 1999. Grandmothering and the evolution of *Homo erectus*. *J. Hum. Evol.* 36(5):461–485.

O'Connell, J. F., Hawkes, K., Lupo, K. D., Blurton Jones, N. G., 2002. Male strategies and Plio-Pleistocene archaeology. *J. Hum. Evol.* 43(6):831–872.

O'Dea, K., 1991. Traditional diet and food preferences of Australian Aboriginal hunter–gatherers. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 334B:233–241.

O'Dea, K., Sinclair, A. J., 1983. The modern Western diet: the exception in man's evolution. In: Boundy, K. A., Smith, G. H. (Eds.), *Agriculture and Human Evolution*. Australian Institute of Agricultural Science, Melbourne, Australia, pp. 56–61.

O'Dea, K., White, N. G., Sinclair, A. J., 1988. An investigation of nutrition-related risk factors in an isolated Aboriginal community in northern Australia: advantages of a traditionally orientated life-style. *Med. J. Aust.* 148(4):177–180.

Odell, G. H., Cowan, F., 1986. Experiments with spears and arrows on animal targets. *J. Field Archaeol.* 13(2):195–212.

Odetokun, S. M., 1996. The nutritive value of baobab fruit (*Andasonia* [sic] *digitata*). *La Rivista Italiano Delle Sostanze Grasse* 73(8):371–373.

Oftedal, O. T., 1981. *Milk, Protein and Energy Intakes of Suckling Mammalian Young: A Comparative Study*. Unpublished PhD Dissertation, Cornell University, Ithaca, NY.

Oftedal, O. T., 1984. Milk composition, milk yield and energy output at peak lactation: a comparative review. *Symp. Zool. Soc. Lond.* 51:33–85.

Oftedal, O. T., 1991. The nutritional consequences of foraging in primates: the relationship of nutrient intakes to nutrient requirements. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 334B(1270):161–170.

Oftedal, O. T., Iverson, S. J., 1995. Comparative analysis of nonhuman milks, A. phylogenetic variation in gross composition of milks. In: Jensen, R. G. (Ed.), *Handbook of Milk Composition*. Academic Press, San Diego, CA, pp. 749–788.

Ohiokpehai, O., 2006. Expanding the uses of phane, a nutritionally rich local food in southern Africa. *J. Food Agric. Environ.* 4(3–4):26–32.

Ohtsuka, R., 1989. Hunting activity and aging among the Gidra Papuans: a biobehavioral analysis. *Am. J. Phys. Anthropol.* 80(1):31–39.

Ojewole, J. A. O., Mawoza, T., Chiwororo, W. D. H., Owira, P. M. O., 2010. *Sclerocarya birrea* (A. Rich) Hochst. ['marula'] (Anacardiaceae): a review of its phytochemistry, pharmacology and toxicology and its ethnomedicinal uses. *Phytother. Res.* 24(5):633–639.

Oka, K., Sakuarae, A., Fujise, T., Yoshimatsu, H., Sakata, T., Nakata, M., 2003. Food texture differences affect energy metabolism in rats. *J. Dent. Res.* 82(6):491–494.

O'Keefe Jr., J. H., Cordain, L., 2004. Cardiovascular disease resulting from a diet and lifestyle at odds with our Paleolithic genome: how to become a 21st-century hunter–gatherer. *Mayo Clin. Proc.* 79(1):101–108.

Oliver, J. S., 1993. Carcass processing by the Hadza: bone breakage from butchery to consumption. In: Hudson, J. (Ed.), *From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains*. Occasional Paper 21. Southern Illinois University, Center for Archaeological Investigations, Carbondale, IL, pp. 200–227.

Oliver, J. S., 1994. Estimates of hominid and carnivore involvement in the FLK *Zinjanthropus* fossil assemblage: some socioecological implications. *J. Hum. Evol.* 27(1–3):267–294.

Onigbinde, A. O., Adamolekun, B., 1998. The nutrient value of *Imbrasia belina* Lepidoptera: Saturnidae (madora). *Cent. Afr. J. Med.* 44(5):125–127.

Osman, M. A., 2004. Chemical and nutrient analysis of baobab (*Adansonia digitata*) fruit and seed protein solubility. *Plant Foods Hum. Nutr.* (formerly *Qualitas Plantarum*) 59(1):29–33.

O'Sullivan, A. J., Martin, A., Brown, M. A., 2001. Efficient fat storage in premenopausal women and in early pregnancy: a role for estrogen. *J. Clin. Endocrinol. Metab.* 86(10):4951–4956.

Oswalt, W. H., 1955. Alaskan pottery: a classification and historical reconstruction. *Am. Antiq.* 21(1):32–43.

Oswalt, W. H., 1973. *Habitat and Technology: The Evolution of Hunting*. Holt, Rinehart and Winston, New York, NY.

Oswalt, W. H., 1976. *An Anthropological Analysis of Food Getting Technology*. John Wiley, New York, NY.

Outram, A. K., Rowley-Conwy, P., 1998. Meat and marrow utility indices for horse (*Equus*). *J. Archaeol. Sci.* 25(9):839–849.

Owen, R. C., 1965. The patrilocal band: a linguistically and culturally hybrid social unit. *Am. Anthropol.* 67(3):675–690.

Owen-Smith, R. N., 2002. *Adaptive Herbivore Ecology: From Resources to Populations in Variable Environments*. Cambridge University Press, Cambridge, England.

de Pagès, P. M. F. 1793. *Travels Round the World, in the Years 1767, 1768, 1769, 1770, 1771, Vol. 1. Translated from the French*. 2nd ed. John Murray, London, England.

Palliser, J., 1863. *The Journals, Detailed Reports, and Observations Relative to the Exploration, by Captain Palliser, of that Portion of British North America, which, in Latitude, Lies Between the British Boundary Line and the Height of Land or Watershed of the Northern or Frozen Ocean Respectively, and in Longitude, Between the Western Shore of Lake Superior and the Pacific Ocean, During the Years 1857, 1858, 1859, and 1860. Presented to both Houses of Parliament by Command of Her Majesty, 19th May, 1863*. Printed by George Edward Eyre and William Spottiswoode for Her Majesty's Stationery Office, London, England.

Pálsson, G. (Ed.), 2001. *Writing on Ice: The Ethnographic Notebooks of Vilhjalmur Stefansson*. Dartmouth College Press and University Press of New England, Hanover, NH.

Pannemans, D. L. E., Schaafsma, G., Westerterp, K. R., 1997. Calcium excretion, apparent calcium absorption and calcium balance in young and elderly subjects: influence of protein intake. *Br. J. Nutr.* 77(5):721–729.

Pannemans, D. L. E., Wagenmakers, A. J. M., Westerterp, K. R., Schaafsma, G., Halliday, D., 1998. Effect of protein source and quantity on protein metabolism in elderly women. *Am. J. Clin. Nutr.* 68(6):1228–1235.

Parkington, J. E., 2001. Milestones: the impact of the systematic exploitation of marine foods on human evolution. In: Tobias, P. V., Raath, M. A., Moggi-Cecchi, J., Doyle, G. A. (Eds.), *Humanity from African Naissance to Coming Millennia. Colloquia in Human Biology and Palaeoanthropology*. Firenze University Press and Witwatersrand University Press, Firenze, Italy and Johannesburg, South Africa, pp. 327–336.

Parry, W. E., 1824. *Journal of a Second Voyage for the Discovery of a North-West Passage from the Atlantic to the Pacific: Performed in the Years 1821–22–23, in His Majesty's Ships Fury* *and Hecla, Under the Orders of Captain William Edward Parry, R.N., F.R.S., and Commander of the Expedition*. John Murray, London, England.

Pasquet, P., Hladik, C.-M., 2005. Theories of human evolutionary trends in meat eating and studies of primate intestinal tracts. *Estudios del Hombre (Guadalajara, Jalisco, México)* 19:21–31.

Passarge, S., 1907. *Die Buschmänner der Kalahari*. Dietrich Reimer Verlag, Berlin, Germany.

Patin, E., Barreiro, L. B., Sabeti, P. C., Austerlitz, F., Luca, F., Sajantila, A., Behar, D. M., Semino, O., Sakuntabhai, A., Guiso, N., Gicquel, B., McElreavey, K., Harding, R. M., Heyer, E., Quintana-Murci, L., 2006. Deciphering the ancient and complex evolutionary history of human arylamine *N*-acetyltransferase genes. *Am. J. Hum. Genet.* 78(3):423–436.

Patin, E., Quintana-Murci, L., 2008. Demeter's legacy: rapid changes to our genome imposed by diet. *Trends Ecol. Evol.* 23(2):56–59.

Patiño, E. M., Borda, J. T., 1997. The composition of primates' milk and its importance in selecting formulas for hand-rearing. *Lab. Prim. Newsl.* 36(2):8–12.

Patou-Mathis, M., 2007. *Une Mort Annoncée: A la Rencontre des Bushmen, Derniers Chasseurs-Cueilleurs du Kalahari*. Librairie Académique Perrin, Paris, France.

Patton, J. Q., 2005. Meat sharing for coalitional support. *Evol. Hum. Behav.* 26(2):137–157.

Pawlosky, R. J., Hibbeln, J. R., Lin, Y., Goodson, S., Riggs, P., Sebring, N., Brown, G. L., Salem Jr., N., 2003a. Effects of beef- and fish-based diets on the kinetics of *n*-3 fatty acid metabolism in human subjects. *Am. J. Clin. Nutr.* 77(3):565–572.

Pawlosky, R. J., Hibbeln, J. R., Lin, Y., Salem Jr., N., 2003b. *n*-3 fatty acid metabolism in women. *Br. J. Nutr.* 90(5):993–994.

Payne, S., 1987. Reference codes for wear stages in the mandibular cheek teeth of sheep and goats. *J. Archaeol. Sci.* 14(6):609–614.

Pearsall, D. M., 1989. *Paleoethnobotany: A Handbook of Procedures*. Academic Press, San Diego, CA.

Pellet, P. L., 1990. Protein requirements in humans. *Am. J. Clin. Nutr.* 51(5):723–737.

Peng, Y. M., Zhang, T. Y., Wang, Q., Zetterström, R. H., Strandvik, B., 2007. Fatty acid composition in breast milk and serum phospholipids of healthy term Chinese infants during first 6 weeks of life. *Acta Pædiatr.* 96(11):1640–1645.

Pereira, M., Rush, D., Campbell-Brown, M., Rosso, P., Winick, M., Brasel, J., Stein, Z., Susser, M., 1982. Effects of prenatal nutritional supplementation on the placenta: report of a randomized controlled trial. *Am. J. Clin. Nutr.* 36:229–234.

Perry, G. H., Dominy, N. J., Claw, K. G., Lee, A. S., Fiegler, H., Redon, R., Werner, J., Villanea, F. A., Mountain, J. L., Misra, R., Carter, N. P., Lee, C., Stone, A. C., 2007. Diet and the evolution of human amylase gene copy number variation. *Nat. Genet.* 39(10):1256–1260.

Peters, C. R., 1987a. Nut-like oil seeds: food for monkeys, chimpanzees, humans, and probably ape–men. *Am. J. Phys. Anthropol.* 73(3):333–363.

Peters, C. R., 1987b. *Ricinodendron rautanenii* (Euphorbiaceae): Zambezian wild food plant for all seasons. *Econ. Bot.* 41(4):494–502.

Petersen, K. F., Vilstrup, H., Tygstrup, N., 1990. Effect of dietary protein on the capacity of urea synthesis in rats. *Horm. Metab. Res.* 22(12):612–615.

Petzke, K. J., Friedrich, M., Metges, C. C., Klaus, S., 2005. Long-term dietary high protein intake up-regulates tissue specific gene expression of uncoupling proteins 1 and 2 in rats. *Eur. J. Nutr.* 44(7):414–421.

Pharithi, M. T., Suping, S. M., Yeboah, S. O., 2004. Variations of the fatty acid composition in the oil from the larval stages of the emperor moth caterpillar, *Imbrasia belina*. *Bull. Chem. Soc. Ethiop.* 18(1):67–72.

Phillips, Paul C., 1940. *Life in the Rocky Mountains, by W. A. Ferris*. Old West Publishing Company, Denver, CO.

Phinney, S. D., 1995. The functional effects of carbohydrate and energy underconsumption. In: Marriott, B. M. (Ed.), *Not Eating Enough: Overcoming Underconsumption of Military Operational Rations*. National Academy Press, Washington, DC, pp. 303–315.

Phinney, S. D., 1996. Arachidonic acid maldistribution in obesity. *Lipids* 31(Suppl. 1):S271–S274.

Phinney, S. D., 2004. Ketogenic diets and physical performance. *Nutr. Metab.* 1(1):2. doi:10.1186/1743-7075-1-2.

Phinney, S. D., Bistrian, B. R., Evans, W. J., Gervino, E., Blackburn, G. L., 1983a. The human metabolic response to chronic ketosis without caloric restriction: preservation of submaximal exercise capability with reduced carbohydrate oxidation. *Metabolism* 32(8):769–776.

Phinney, S. D., Bistrian, B. R., Wolfe, R. R., Blackburn, G. L., 1983b. The human metabolic response to chronic ketosis without caloric restriction: physical and biochemical adaptation. *Metabolism* 32(8):757–768.

Phinney, S. D., Stern, J. S., Burke, K. E., Tang, A. B., Miller, G., Holman, R. T., 1994. Human subcutaneous adipose tissue shows site-specific differences in fatty acid composition. *Am. J. Clin. Nutr.* 60(5):725–729.

Pickering, T. R., Bunn, H. T., 2007. The endurance running hypothesis and hunting and scavenging in savanna-woodlands. *J. Hum. Evol.* 53(4):434–438.

Pickering, T. R., Wallis, J., 1997. Bone modifications resulting from captive chimpanzee mastication: implications for the interpretation of Pliocene archaeological faunas. *J. Archaeol. Sci.* 24(12):1115–1127.

Pickford, M., 2006. Paleoenvironments, paleoecology, adaptations, and the origins of bipedalism in Hominidae. In: Ishida, H., Tuttle, R., Pickford, M., Ogihara N., Nakatsukasa, M. (Eds.), *Human Origins and Environmental Backgrounds. Developments In Primatology: Progress and Prospects*. Springer, New York, NY, pp. 175–198.

Pickrell, J. K., Coop, G., Novembre, J., Kudaravalli, S., Li, J. Z., Absher, D., Srinivasan, B. S., Barsh, G. S., Myers, R. M., Feldman, M. W., Pritchard, J. K., 2009. Signals of recent positive selection in a worldwide sample of human populations. *Genome Res.* 19(5):826–837.

Pike, W. M., 1892. *The Barren Ground of Northern Canada*. Macmillan, London, England.

Piperno, D. R., 2006. *Phytoliths: A Comprehensive Guide for Archaeologists and Paleoecologists*. AltaMira Press, Lanham, MD.

Piperno, D. R., Weiss, E., Holst, I., Nadel, D., 2004. Processing of wild cereal grains in the Upper Palaeolithic revealed by starch grain analysis. *Nature* 430:670–673.

Pittet, P. G., Halliday, D., Bateman, P. E., 1979. Site differences in the fatty acid composition of subcutaneous adipose tissue of obese women. *Br. J. Nutr.* 42(1):57–61.

Pitts, G. C., Bullard, T. R., 1968. Some interspecific aspects of body composition in mammals. In: Agricultural Board, Division of Biology and Agriculture, National Research Council, *Body Composition in Animals and Man. Proceedings of a Symposium Held May 4, 5, and 6, 1967 at the University of Missouri, Columbia*. Publication 1598. National Academy of Sciences, Washington, DC, pp. 45–70.

Plakke, T., Berkel, J., Beynen, A. C., Hermus, R. J. J., Katan. M. B., 1983. Relationship between the fatty acid composition of the diet and that of the subcutaneous adipose tissue in individual human subjects. *Hum. Nutr. Appl. Nutr.* 37A(5):365–372.

Pluciennik, M., 2002. The invention of hunter–gatherers in seventeenth-century Europe. *Archaeol. Dialogues* 9(2):98–118.

Plummer, T. W., Bishop, L. C., Ditchfield, P., Hicks, J., 1999. Research on late Pliocene Oldowan sites at Kanjera South, Kenya. *J. Hum. Evol.* 36(2):151–170.

Pobiner, B. L., Braun, D. R., 2005. Strengthening the inferential link between cutmark frequency data and Oldowan hominid behavior: results from modern butchery experiments. *J. Taphonomy* 3(3):107–119.

Pobiner, B. L., Rogers, M. J., Monahan, C. M., Harris, J. W. K., 2008. New evidence for hominin carcass processing strategies at 1.5 Ma, Koobi Fora, Kenya. *J. Hum. Evol.* 55(1):103–130.

Pond, C. M., 1978. Morphological aspects and the ecological and mechanical consequences of fat deposition in wild vertebrates. *Annu. Rev. Ecol. Syst.* 9:519–570.

Pond, C. M., 1991. Adipose tissue in human evolution. In: Roede, M., Wind, J., Patrick, J. M., Reynolds, V. (Eds.), *The Aquatic Ape: Fact or Fiction?* Souvenir Press, London, England, pp. 193–220.

Pond, C. M., 1997. The biological origins of adipose tissue in humans. In: Morbeck, M. E., Galloway, A., Zihlman, A. L. (Eds.), *The Evolving Female: A Life-History Perspective*. Princeton University Press, Princeton, NJ, pp. 147–162.

Pope, S. T., 1923. A study of bows and arrows. *Publ. Am. Archaeol. Ethnol.* 13(9):329–414.

Porter, C. C., Marlowe, F. W., 2007. How marginal are forager habitats? *J. Archaeol. Sci.* 34(1):59–68.

Potts, R. B., 1983. Foraging for faunal resources by early hominids at Olduvai Gorge, Tanzania. In: Clutton-Brock, J., Grigson, C. (Eds.), *Animals and Archaeology, Vol. 1. Hunters and Their Prey*. BAR International Series 163. British Archaeological Reports, Oxford, England, pp. 51–62.

Potts, R. B., 1988. *Early Hominid Activities at Olduvai*. Aldine de Gruyter, New York, NY.

Powell, A. M., 1987. Marama bean (*Tylosema esculentum*, Fabaceae) seed crop in Texas. *Econ. Bot.* 41(2):216–220.

Power, C., Watts, I., 1997. The woman with the zebra's penis: gender, mutability and performance. *J. R. Anthropol. Inst.* 3(3):537–560.

Power, C., Watts, I., 2003. First gender, wrong sex. In: Moore, H. L., Sanders, T., Kaare, B. (Ed.), *Those Who Play With Fire: Gender, Fertility and Transformation in East and Southern Africa*. London School of Economics Monographs on Social Anthropology 69. Berg, Oxford, England, pp. 101–132.

Power, M. L., 2006. Sources of variation in milk composition: phylogeny, life history, and maternal condition (abstract). *Am. J. Primatol.* 68(S1):130.

Power, M. L., Oftedal, O. T., Tardif, S. D., 2002. Does the milk of Callitrichid monkeys differ from that of larger anthropoids? *Am. J. Primatol.* 56(2):117–127.

Power, M. L., Schulkin, J., 2008. Sex differences in fat storage, fat metabolism, and the health risks from obesity: possible evolutionary origins. *Br. J. Nutr.* 99(5):931–940.

Powers-Lee, S. G., Meister, A., 1988. Urea synthesis and ammonia metabolism. In: Arias, I. M., Jakoby, W. B., Popper, H., Schachter, D., Shafritz, D. A. (Eds.), *The Liver: Biology and Pathobiology*. 2nd ed. Raven Press, New York, NY, pp. 317–329.

Pratt, J. A. F., 1999. Determining the function of one of the New World's earliest pottery assemblages: the case of San Jacinto, Colombia. *Lat. Am. Antiq.* 10(1):71–85.

Prentice, A., Laskey, M. A., Shaw, J., Hudson, G. J., Day, K. C., Jarjou, L. M. A., Dibba, B., Paul, A. A., 1993. The calcium and phosphorus intakes of rural Gambian women during pregnancy and lactation. *Br. J. Nutr.* 69(3):885–896.

Price, P. B., Parsons, J. G., 1975. Lipids of seven cereal grains. *J. Am. Oil Chem. Soc.* 52(12): 490–493.

Prichard, H. V. H., 1902. *Through the Heart of Patagonia*. D. Appleton and Company, New York, NY.

Pritchard, T. C., Norgren, R., 1991. Preference of Old World monkeys for amino acids and other gustatory stimuli: the influence of monosodium glutamate. *Physiol. Behav.* 49(5):1003–1007.

Profet, M., 1988. The evolution of pregnancy sickness as protection to the embryo against Pleistocene teratogens. *Evol. Theor.* 8:177–190.

Profet, M., 1992. Pregnancy sickness as adaptation: a deterrent to maternal ingestion of teratogens. In: Barkow, J. H., Cosmides, L., Tooby, J. (Eds.), *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. Oxford University Press, Oxford, England, pp. 327–365.

Quin, P. J., 1959. *Foods and Feeding Habits of the Pedi*. Witwatersrand University Press, Johannesburg, South Africa.

Rafoth, R. J., Onstad, G. R., 1975. Urea synthesis after oral protein ingestion in man. *J. Clin. Invest.* 56(5):1170–1174.

Ragir, S., 2000. Diet and food preparation: rethinking early hominid behavior. *Evol. Anthropol.* 9(4):153–155.

Ramarathnam, N., Rubin, L. J., Diosady, L. L., 1991. Studies on meat flavor, 1. qualitative and quantitative differences in uncured and cured pork. *J. Agric. Food Chem.* 39(2):344–350.

Rand, W. M., Pellett, P. L., Young, V. R., 2003. Meta-analysis of nitrogen balance studies for estimating protein requirements in healthy adults. *Am. J. Clin. Nutr.* 77(1):109–127.

Rapp, G. R., Hill, C. L., 2006. *Geoarchaeology: The Earth-Science Approach to Archaeological Interpretation*. 2nd ed. Yale University Press, New Haven, CT.

Ratner, S., 1977. A long view of nitrogen metabolism. *Annu. Rev. Biochem.* 46:1–24.

Ratner, S., Petrack, B., 1951. Biosynthesis of urea, III. Further studies on arginine synthesis from citrulline. *J. Biol. Chem.* 191(2):693–705.

Read, C., 1914. On the differentiation of man from the anthropoids. *Man* 14(91):181–186.

Rebuffé-Scrive, M., Enk, L., Crona, N., Lönnroth, P., Abrahamsson, L., Smith, U., Björntorp, P., 1985. Fat cell metabolism in different regions in women: effect of menstrual cycle, pregnancy, and lactation. *J. Clin. Invest.* 75(6):1973–1976.

Reeds, P. J., Garlick, P. J., 2003. Protein and amino acid requirements and the composition of complementary foods. *J. Nutr.* 133(Suppl. 9):2953S–2961S.

Reid, M., 1866. *Odd People: Being a Popular Description of Singular Races of Man*. Ticknor and Fields, Boston, MA.

Reid, M., 1889. *The Young Voyageurs or the Boy Hunters in the North*. John W. Lovell, New York, NY.

Reinhard, K. J., Ambler, J. R., Szuter, C. R., 2007. Hunter–gatherer use of small animal food resources: coprolite evidence. *Int. J. Osteoarchaeol.* 17(4):416–428.

Reiter, R. R. (Ed.), 1975. *Toward an Anthropology of Women*. Monthly Review Press, New York, NY.

Reynolds, R. M., Godfrey, K. M., Barker, M., Osmond, C., Phillips, D. I. W., 2007. Stress responsiveness in adult life: influence of mother's diet in late pregnancy. *J. Clin. Endocrinol. Metab.* 92(6):2208–2210.

Rhee, K. S., 1989. Chemistry of meat flavor. In: Min, D. B., Smouse, T. H. (Eds.), *Flavor Chemistry of Lipid Foods. Papers Presented at the 79th Annual Meeting of the American Oil Chemists' Society Held May 8–12th, 1988 in Phoenix, AZ.* A.O.C.S. Honored Scientist Series, The Stephen S. Chang Symposium. American Oil Chemists' Society, Champaign, IL, pp. 166–189.

Rhode, D., Madsen, D. B., Jones, K. T., 2006. Antiquity of early Holocene small-seed consumption and processing at Danger Cave. *Antiquity* 80(308):328–339.

Rice, P. M., 1999. On the origins of pottery. *J. Archaeol. Meth. Theor.* 6(1):1–54.

Richards, M. P., Jacobi, R., Cook, J., Pettitt, P. B., Stringer, C. B., 2005. Isotope evidence for the intensive use of marine foods by late Upper Palaeolithic humans. *J. Hum. Evol.* 49(3):390–394.

Richards, M. P., Trinkaus, E., 2009. Isotopic evidence for the diets of European Neanderthals and early modern humans. *Proc. Natl. Acad. Sci.* 106(38):16034–16039.

Richardson, J., 1829. *Fauna Boreali Americana or the Zoology of the Northern Parts of British America*. John Murray, London, England.

Rieder, H., 2000. Die altpaläolithischen wurfspeere von Schöningen, ihre erprobung und ihre bedeutung für die lebensumwelt des *Homo erectus*. *Praehistoria Thuringica* 5:68–75.

Rieder, H., 2003. Der große wurf der frühen jäger: nachbau altsteinzeitlicher speere. *Biologie in Unserer Zeit* 33(3):156–160.

Rioux, V., Catheline, D., Beauchamp, E., Le Bloc'h, J., Pédrono, F., Legrand, P., 2008. Substitution of dietary oleic acid for myristic acid increases the tissue storage of α-linolenic acid and the concentration of docosahexaenoic acid in the brain, red blood cells and plasma in the rat. *Animal* 2(4):636–644.

Rioux, V., Catheline, D., Bouriel, M., Legrand, P., 2005. Dietary myristic acid at physiologically relevant levels increases the tissue content of C20:5*n*-3 and C20:3*n*-6 in the rat. *Reprod. Nutr. Dev.* 45(5):599–612.

Ripley, G., Dana, C. A. (Eds.), 1869. *The New American Cyclopaedia: A Popular Dictionary of General Knowledge, Vol. 3. Beam-Browning*. D. Appleton and Company, New York, NY.

Robbins, C. T., Felicetti, L. A., Sponheimer, M., 2005. The effect of dietary protein quality on nitrogen isotope discrimination in mammals and birds. *Oecologia* 144(4):534–540.

Robinson, H. M., 1879. *The Great Fur Land, or, Sketches of Life in the Hudson's Bay Territory*. Sampson Low, Marston, Searle, and Rivington, London, England.

Robson, S. L., 2004. Breast milk, diet, and large human brains. *Curr. Anthropol.* 45(3):419–425.

Rodahl, K., 1952. Basal metabolism of the Eskimo. *J. Nutr.* 48(3):359–368.

Rolland, N., 2004. Was the emergence of home bases and domestic fire a punctuated event? A review of the Middle Pleistocene record in Eurasia. *Asian Perspect.* 43(2):248–280.

Rolland-Cachera, M. F., Deheeger, M., Maillot, M., Bellisle, F., 2006. Early adiposity rebound: causes and consequences for obesity in children and adults. *Int. J. Obes.* 30(Suppl. 4):S11–S17.

Roosevelt, A. C., Housley, R. A., Imazio da Silveira, M., Maranca, S., Johnson, R., 1991. Eighth millennium pottery from a prehistoric shell midden in the Brazilian Amazon. *Science* 254(5038):1621–1624.

Roosevelt, T., 1913. The life-history of the African buffalo, giant eland, and common eland. *Scribner's Magazine* 54:681–693.

Rosell, M. S., Lloyd-Wright, Z., Appleby, P. N., Sanders, T. A. B., Allen, N. E., Key, T. J., 2005. Long-chain *n*-3 polyunsaturated fatty acids in plasma in British meat-eating, vegetarian, and vegan men. *Am. J. Clin. Nutr.* 82(2):327–334.

Rosenberg, A., Linquist, S., 2005. On the original contract: evolutionary game theory and human evolution. *Analyse and Kritik* 27(1):136–157.

Ross, A., 1856. *The Red River Settlement: Its Rise, Progress, and Present State with Some Account of the Native Races and Its General History, to the Present Day*. Smith, Elder and Company, London, England.

Ross, J., 1835. *Narrative of a Second Voyage in Search of a North-West Passage, and of a Residence in the Arctic Regions During the Years 1829, 1830, 1831, 1832, 1833, Including the Reports of James Clark Ross and the Discovery of the Northern Magnetic Pole*. Baudry's European Library, Paris, France.

Rothwell, N. J., Stock, M. J., 1979. A role for brown adipose tissue in diet-induced thermogenesis. *Nature* 281(5726):31–35.

Roughead, Z. K., Johnson, L. K., Lykken, G. I., Hunt, J. R., 2003. Controlled high meat diets do not affect calcium retention or indices of bone status in healthy postmenopausal women. *J. Nutr.* 133(4):1020–1026.

Rouhi, A. M., 2003. What's that stuff? Monosodium glutamate. *Chem. Eng. News* 81(30):57.

Rowland, M. J., 2002. Geophagy: an assessment of implications for the development of Australian indigenous plant processing technologies. *Aust. Aborig. Stud.* 2002(1):51–66.

Rowlett, R. M., 2000. Fire control of *Homo erectus* in East Africa and Asia. *Acta Anthropol. Sin.* 19(Suppl.):198–208.

Rowley-Conwy, P. A., 2007. *From Genesis to Prehistory: The Archaeological Three Age System and Its Contested Reception in Denmark, Britain, and Ireland*. Oxford Studies in the History of Archaeology. Oxford University Press, Oxford, England.

Rowley-Conwy, P. A., Halstead, P., Collins, P., 2002. Derivation and application of a food utility index (FUI) for European wild boar (*Sus scrofa* L.). *Environ. Archaeol.* 7:77–87.

Rudman, D., DiFulco, T. J., Galambos, J. T., Smith, R. B., Salam, A. A., Warren, W. D., 1973. Maximal rates of excretion and synthesis of urea in normal and cirrhotic subjects. *J. Clin. Invest.* 52(9):2241–2249.

Rudner, J., 1979. The use of stone artefacts and pottery among the Khoisan peoples in historic and protohistoric times. *S. Afr. Archaeol. Bull.* 34(129):3–17.

Ruff, C. B., Trinkaus, E., Holliday, T. W., 1997. Body mass and encephalization in Pleistocene *Homo*. *Nature* 387(6629):173–176.

Rush, D., 1982. Effects of changes in protein and calorie intake during pregnancy on the growth of the human fetus. In: Enkin, M., Chalmers, I. (Eds.), *Effectiveness and Satisfaction in Antenatal Care*. Clinics in Developmental Medicine 81/82. J. B. Lippincott, Philadelphia, PA, pp. 92–113.

Rush, D., 1986. Nutrition in the preparation for pregnancy. In: Chamberlain, G., Lumley, J. (Eds.), *Prepregnancy Care: A Manual for Practice*. John Wiley and Sons, New York, NY, pp. 113–139.

Rush, D., 1989. Effects of changes in protein and calorie intake during pregnancy on the growth of the human fetus. In: Chalmers, I., Enkin, M., Keirse, M. J. N. C. (Eds.), *Effective Care in*

*Pregnancy and Childbirth, Vol. 1. Pregnancy*. Oxford Medical Publications. Oxford University Press, Oxford, England, pp. 255–280.

Rush, D., 2001. Maternal nutrition and perinatal survival. *J. Health Popul. Nutr.* 19(Suppl. 3) :S217–S264.

Rush, D., Stein, Z., Susser, M., 1980. A randomized controlled trial of prenatal nutritional supplementation in New York City. *Pediatics* 65(4):683–697.

Russell, O., 1921. *Journal of a Trapper or Nine Years in the Rocky Mountains, 1834–1843*. Syms-York Company, Boise, ID.

Ruxton, G. F., 1848. *Adventures in Mexico and the Rocky Mountains*. Harper and Brothers, New York, NY.

Rypins, E. B., Henderson, J. M., Fulenwider, J. T., Moffitt, S., Galambos, J. T., Warren, W. D., Rudman, D., 1980. A tracer method for measuring rate of urea synthesis in normal and cirrhotic subjects. *Gastroenterology* 78(6):1419–1424.

Sabeti, P. C., Varilly, P., Fry, B., Lohmueller, J., Hostetter, E., Cotsapas, C., Xie, X., Byrne, E. H., McCarroll, S. A., Gaudet, R., Schaffner, S. F., Lander, E. S., International HapMap Consortium, 2007. Genome-wide detection and characterization of positive selection in human populations. *Nature* 449(7164):913–918.

Saheki, T., Katsunuma, T., Sase, M., 1977. Regulation of urea synthesis in rat liver: changes of ornithine and acetylglutamate concentrations in the livers of rats subjected to dietary transitions. *J. Biochem.* 82(2):551–558.

Saheki, T., Tsuda, M., Takada, S., Kusumi, K., Katsunuma, T., 1980. Role of argininosuccinate synthetase in the regulation of urea synthesis in the rat and argininosuccinate synthetase-associated metabolic disorder in man. *Adv. Enzyme Regul.* 18:221–238.

Sahlins, M. D. 1968. Notes on the original affluent society. In: Lee, R. B., DeVore, I. (Eds.), *Man the Hunter*. Aldine, Chicago, IL, pp. 85–89.

St. Jeor, S. T., Howard, B. V., Prewitt, T. E., Bovee, V., Bazzarre, T., Eckel, R. H., 2001. Dietary protein and weight reduction: a statement for healthcare professionals from the Nutrition Committee of the Council on Nutrition, Physical Activity, and Metabolism of the American Heart Association. *Circulation* 104:1869–1874.

Samaras, T., Elrick, H., 2005. An alternative hypothesis to the obesity epidemic: obesity is due to increased maternal body size, birth size, growth rate, and height. *Med. Hypotheses* 65(4):676–682.

Sand, H., Cederlund, G., Danell, K., 1995. Geographical and latitudinal variation in growth patterns and adult body size of Swedish moose (*Alces alces*). *Oecologia* 102(4):433–442.

Sassaman, K. E., 1993. *Early Pottery in the Southeast: Tradition and Innovation in Cooking Technology*. University of Alabama Press, Tuscaloosa, AL.

Sauenvald, T. U., Demmelmair, H., Fidler, N., Koletzko, B., 2000. Polyunsaturated fatty acid supply with human milk: physiological aspects and in vivo studies of metabolism. In: Koletzko, B., Fleischer Michaelsen, K., Hernell, O. (Eds.), *Short and Long Term Effects of Breast Feeding on Child Health*. Advances in Experimental Medicine and Biology 478. Kluwer Academic/ Plenum Publishers, New York, NY, pp. 261–270.

Savelle, J. M., Friesen, T. M., 1996. An Odontocete (Cetacea) meat utility index. *J. Archaeol. Sci.* 23(5):713–721.

Saxon, G., Chidiamassamba, C., 2005. *Indigenous Knowledge of Edible Tree Products: The Mungomu Tree in Central Mozambique*. Report 40. United Nations, Food and Agricultural Organization, Links Project: Gender, Biodiversity and Local Knowledge Systems for Food Security, Rome, Italy.

Schäfer, L., Overvad, K., 1990. Subcutaneous adipose-tissue fatty acids and vitamin E in humans: relation to diet and sampling site. *Am. J. Clin. Nutr.* 52(3):486–490.

Schaller, G. B., 1972. *The Serengeti Lion*. University of Chicago Press, Chicago, IL.

Scheinfeldt, L. B., Biswas, S., Madeoy, J., Connelly, C. F., Schadt, E. E., Akey, J. M., 2009. Population genomic analysis of ALMS1 in humans reveals a surprisingly complex evolutionary history. *Mol. Biol. Evol.* 26(6):1357–1367.

Scherbaum, V., Furst, P., 2000. New concepts on nutritional management of severe malnutrition: the role of protein. *Curr. Opin. Clin. Nutr. Metab. Care* 3(1):31–38.

Schiffman, S. S., Sennewald, K., Gagnon, J., 1981. Comparison of taste qualities and thresholds of D- and L-amino acids. *Physiol. Behav.* 27(1):51–59.

Schimke, R. T., 1962. Adaptive characteristics of urea cycle enzymes in the rat. *J. Biol. Chem.* 237(2):459–468.

Schmidt-Nielsen, K., 1986. Why milk? *News Physiol. Sci.* 1(4):140–142.

Schmitt, D., Churchill, S. E., Hylander, W. L., 2003. Experimental evidence concerning spear use in Neandertals and early modern humans. *J. Archaeol. Sci.* 30(1):103–114.

Schmitt, E., Stopper, H., 2001. Estrogenic activity of naturally occurring anthocyanidins. *Nutr. Cancer* 41(1–2):145–149.

Schoeninger, M. J., 1995. Stable isotope studies in human evolution. *Evol. Anthropol.* 4(3):83–98.

Schoeninger, M. J., Bunn, H. T., Murray, S. S., Marlett, J. A., 2001. Composition of tubers used by Hadza foragers of Tanzania. *J. Food Compost. Anal.* 14(1):15–25.

Schultze, L. S., 1907. *Aus Namaland und Kalahari. Bericht an die Königlich Preussische Akademie der Wissenschaften zu Berlin über eine Forschungsreise im Westlichen und Zentralen Südafrika, Ausgeführt in den Jahren 1903–1905*. Gustav Fischer, Jena, Germany.

Schulz, A., Hammar, A., 1897. *The New Africa: A Journey Up the Chobe and Down the Okovango Rivers – a Record of Exploration and Sport*. William Heinemann, London, England.

Schulz, D. M., Giordano, D. A., Schulz, D. H., 1962. Weights of organs of fetuses and infants. *Arch. Pathol.* 74:244–250.

Schürch, B., 1995. Malnutrition and behavioral development: the nutrition variable. *J. Nutr.* 125(8):2255S–2262S.

Schweinfurth, G., 1878. *The Heart of Africa: Three Years' Travels and Adventures in the Unexplored Regions of Central Africa from 1868 to 1871, Vol. 2.* Frewer, E. E. (Trans.). 3rd ed. Sampson-Low, Marston, Searle, and Rivington, London, England.

Schweitzer, P. P., 2004. No escape from being theoretically important: hunter–gatherers in German-language debates of the late nineteenth and early twentieth centuries. In: Barnard, A. (Ed.), *Hunter–Gatherers in History, Archaeology and Anthropology*. Berg, Oxford, England, pp. 69–76.

Scrimshaw, N. S., Young, V. R., 1976. The requirements of human nutrition. *Sci. Am.* 235:51–64.

Secor, S. M., 2009. Specific dynamic action: a review of the postprandial metabolic response. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* 179(1):1–56.

Seidell, J. C., Cigolini, M., Deslypere, J.-P., Charzewska, J., Ellsinger, B.-M., 1991. Polyunsaturated fatty acids in adipose tissue in European men aged 38 years in relation to serum lipids, smoking habits, and fat distribution. *Am. J. Epidemiol.* 134(6):583–589.

Sekhwela, M. B. M., 1989. The nutritive value of "mophane bread"-mophane insect secretion (maphote or moaboti). *Botsw. Notes Rec.* 20:151–153.

Sellen, D. W., 2007. Evolution of infant and young child feeding: implications for contemporary public health. *Annu. Rev. Nutr.* 27:123–148.

Sellmeyer, D. E., Stone, K. L., Sebastian, A., Cummings, S. R., 2001. A high ratio of dietary animal to vegetable protein increases the rate of bone loss and the risk of fracture in postmenopausal women. *Am. J. Clin. Nutr.* 73(1):118–122.

Selous, F. C., 1893. *Travel and Adventure in South-East Africa: Being the Narrative of the Last Eleven Years Spent by the Author on the Zambesi and its Tributaries; with an Account of the Colonisation of Mashunaland and the Progress of the Gold Industry in that Country*. Rowland Ward, London, England.

Selous, F. C., 1907. *A Hunter's Wanderings in Africa: Being a Narrative of Nine Years Spent Amongst the Game of the Far Interior of South Africa, Containing Accounts of Explorations Beyond the Zambesi, on the River Chobe, and in the Matabele and Mashuna Countries, With Full Notes Upon the Natural History and Present Distribution of All the Large Mammalia*. 5th ed. Macmillan and Company, London, England.

Selous, F. C., 1908. *African Nature Notes and Reminiscences*. MacMillan and Company, London, England.

Selvaggio, M. M., 1994. *Identifying the Timing and Sequence of Hominid and Carnivore Involvement With Plio-Pleistocene Bone Assemblages from Carnivore Tooth Marks and Stone-*

*Tool Butchery Marks on Bone Surfaces*. Unpublished PhD Dissertation, Rutgers University, New Brunswick, NJ.

Semaw, S., 2000. The world's oldest stone artefacts from Gona, Ethiopia: their implications for understanding stone technology and patterns of human evolution between 2.6–1.5 million years ago. *J. Archaeol. Sci.* 27(12):1197–1214.

Sena, L. P., VanderJagt, D. J., Rivera, C., Tsin, A. T. C., Muhamadu, I., Mahamadou, O., Millson, M., Pastuszyn, A., Glew, R. H., 1998. Analysis of nutritional components of eight famine foods of the Republic of Niger. *Plant Foods Hum. Nutr.* (formerly *Qualitas Plantarum*) 52(1):17–30.

Service, E. R., 1962. *Primitive Social Organization: An Evolutionary Perspective*. Random House, New York, NY.

Service, E. R., 1966. *The Hunters*. Prentice-Hall, Englewood Cliffs, NJ.

Service, E. R., 1971. *Primitive Social Organization: An Evolutionary Perspective*. 2nd ed. Random House, New York, NY.

Shadid, S., Koutsari, C., Jensen, M. D., 2007. Direct free fatty acid uptake into human adipocytes in vivo: relation to body fat distribution. *Diabetes* 56(5):1369–1375.

Shaffer, P. A., 1921. Antiketogenesis, II. the ketogenic antiketogenic balance in man. *J. Biol. Chem.* 47(2):449–473.

Shahidi, F., 1989. Flavor of cooked meats. In: Teranishi, R., Buttery, R. G., Shahidi, F. (Eds.), *Flavor Chemistry: Trends and Developments*. ACS Symposium Series 388. American Chemical Society, Washington, DC, pp. 188–201.

Shahidi, F., Rubin, L. J., D'Souza, L. A., 1986. Meat flavor volatiles: a review of the composition, techniques of analysis, and sensory evaluation. *Crit. Rev. Food Sci. Nutr.* 24(2):141–243.

Shallenberger, R. S., 1993. *Taste Chemistry*. Chapman and Hall, London, England.

Shea, J. H., 1982. Twelve fallacies of uniformitarianism. *Geology* 10(9):455–460.

Shea, J. J., 2006. The origins of lithic projectile point technology: evidence from Africa, the Levant, and Europe. *J. Archaeol. Sci.* 33(6):823–846.

Sherman, P. W., Flaxman, S. M., 2002. Nausea and vomiting of pregnancy in an evolutionary perspective. *Am. J. Obstet. Gynecol.* 186(5 Suppl. 2):S190–S197.

Shi, P., Zhang, J., 2006. Contrasting modes of evolution between vertebrate sweet/umami receptor genes and bitter receptor genes. *Mol. Biol. Evol.* 23(2):292–300.

Shimomura, Y., Murakami, T., Nakai, N., Nagasaki, M., Harris, R. A., 2004. Exercise promotes BCAA catabolism: effects of BCAA supplementation on skeletal muscle during exercise. *J. Nutr.* 134(6):1583S–1587S.

Shipek, F. C., 1970. *The Autobiography of Delphina Cuero, a Diegueño Indian*. Malki Press, Banning, CA.

Shipman, P., 1983. Early hominid lifestyle: hunting and gathering or foraging and scavenging? In: Clutton-Brock, J., Grigson, C. (Eds.), *Animals and Archaeology, Vol. 1. Hunters and Their Prey*. BAR International Series 163. British Archaeological Reports, Oxford, England, pp. 31–50.

Shostak, M., 1981. *Nisa: The Life and Words of a !Kung Woman*. Harvard University Press, Cambridge, MA.

Shreeve, J., 1996. Sunset on the savanna: the evolution of bipedalism. *Discover* 17(7):116–125.

Sidibe, M., Williams, J. T., 2002. *Baobab: Adansonia digitata*. Fruits of the Future 4. University of Southampton, International Centre for Underutilised Crops, Southampton, England.

Siewert, F., 2003. *Entwicklung der Ernährungsforschung bei der Katze (Bis 1975)*. Unpublished PhD Dissertation, Veterinärmedizin, Institut für Tierernährung der Tierärztlichen Hochschule Hannover, Hannover, Germany.

Sih, A., Milton, K. A., 1985. Optimal diet theory: should the !Kung eat mongongos. *Am. Anthropol.* 87(2):395–401.

Silberbauer, G. B., 1973. *Socio-ecology of the G/wi Bushmen*. Unpublished PhD Dissertation, Monash University, Clayton, Australia.

Silberbauer, G. B., 1981. *Hunter and Habitat in the Central Kalahari Desert*. Cambridge University Press, Cambridge, England.

Simopoulos, A. P. (Ed.), 1999. *Evolutionary Aspects of Nutrition and Health: Diet, Exercise, Genetics and Chronic Disease*. World Rev. Nutr. Diet. 84. Karger, Basel, Switzerland.

Simopoulos, A. P., 2001. Evolutionary aspects of diet, essential fatty acids and cardiovascular disease. *Eur. Heart J. Suppl.* 3(D):D8–D21.

Simopoulos, A. P., 2002a. Omega-3 fatty acids in wild plants, nuts and seeds. *Asia Pac. J. Clin. Nutr.* 11(Suppl. 6 [sic, Suppl. 2]):S163–S173.

Simopoulos, A. P., 2002b. The importance of the ratio of omega-6/omega-3 essential fatty acids. *Biomed. Pharmacother.* 56(8):365–379.

Simopoulos, A. P., 2003. Importance of the ratio of omega-6/omega-3 essential fatty acids: evolutionary aspects. In: Simopoulos, A. P., Cleland, L. G. (Eds.), *Omega-6/Omega-3 Essential Fatty Acid Ratio: The Scientific Evidence*. World Rev. Nutr. Diet. 92. Karger, Basel, Switzerland, pp. 1–22.

Simopoulos, A. P., 2004. Omega-3 fatty acids and antioxidants in edible wild plants. *Biol. Res.* 37(2):263–277.

Simopoulos, A. P., 2008. The importance of the omega-6/omega-3 fatty acid ratio in cardiovascular disease and other chronic diseases. *Exp. Biol. Med.* 233(6):674–688.

Sinclair, A. J., Attar-Bashi, N. M., Li, D., 2002. What is the role of α-linolenic acid for mammals? *Lipids* 37(12):1113–1123.

Sinclair, A. R. E., 1974. The natural regulation of buffalo populations in East Africa, IV. The food supply as a regulating factor, and competition. *East Afr. Wildl. J.* 12(4):291–311.

Sinclair, A. R. E., 1975. The resource limitation of trophic levels in tropical grassland ecosystems. *J. Anim. Ecol.* 44(2):497–520.

Sinclair, A. R. E., 1977. *The African Buffalo*. University of Chicago Press, Chicago, IL.

Sinclair, A. R. E., Duncan, P., 1972. Indices of condition in tropical ruminants. *East Afr. Wildl. J.* 10:143–149.

Sinclair, H. M., 1979. The human nutritional advantages of plant foods over animal foods. *Plant Foods Hum. Nutr.* (formerly *Qualitas Plantarum*) 29(1–2):7–18.

Singh, D., 1993. Body shape and women's attractiveness: the critical role of waist-to-hip ratio. *Hum. Nat.* 4(3):297–321.

Singh, M., 2005. Essential fatty acids, DHA and human brain. *Indian J. Pediatr.* 72(3):239–242.

Siskind, J., 1973. *To Hunt in the Morning*. Oxford University Press, New York, NY.

Slavin, J. 2003. Why whole grains are protective: biological mechanisms. *Proc. Nutr. Soc.* 62(1):129–134.

Sloan, N. L., 1985. *Effects of Maternal Protein Consumption on Fetal Growth and Gestation*. Unpublished PhD Dissertation, Public Health, Faculty of Medicine, Columbia University, New York, NY.

Sloan, N. L., Lederman, S. A., Leighton, J., Himes, J. H., Rush, D., 2001. The effect of prenatal dietary protein intake on birth weight. *Nutr. Res.* 21(1–2):129–139.

Slocum, S., 1975. Woman the gatherer: male bias in anthropology. In: Reiter, R. R. (Ed.), *Toward an Anthropology of Women*. Monthly Review Press, New York, NY, pp. 36–50.

Smith, A. J., 2007. Century-scale Holocene processes as a source of natural selection pressure in human evolution: Holocene climate and the human genome project. *The Holocene* 17(5): 689–695.

Smith, B. D., 1989. Origins of agriculture in eastern North America. *Science* 246(4937):1566–1571.

Smith, B. D., 2001. Low-level food production. *J. Archaeol. Res.* 9(1):1–43.

Smith, C. R., Shekleton, M. C., Wolff, I. A., Jones, Q., 1959. Seed protein sources – amino acid composition and total protein content of various plant seeds. *Econ. Bot.* 13(2):132–150.

Smith, E. A., 2004. Why do good hunters have higher reproductive success? *Hum. Nat.* 15(4):343–364.

Smith, E. A., Bliege Bird, R. L., Bird, D. W., 2003. The benefits of costly signaling: Meriam turtle hunters. *Behav. Ecol.* 14(1):116–126.

Smith, E. A., Winterhalder, B. (Eds.), 1992. *Evolutionary Ecology and Human Behavior*. Aldine de Gruyter, Hawthorne, NY.

Smith, N. S., 1970. Appraisal of condition estimation methods for East African ungulates. *East Afr. Wildl. J.* 8(1):123–129.

Snijder, M. B., Dekker, J. M., Visser, M., Yudkin, J. S., Stehouwer, C. D. A., Bouter, L. M., Heine, R. J., Nijpels, G., Seidell, J. C., 2003. Larger thigh and hip circumferences are associated with better glucose tolerance: the Hoorn study. *Obes. Res.* 11(1):104–111.

Snijder, M. B., van Dam, R. M., Visser, M., Seidell, J. C., 2006. What aspects of body fat are particularly hazardous and how do we measure them? *Int. J. Epidemiol.* 35(1):83–92.

Snodgrass, J. J., Leonard, W. R., 2009. Neandertal energetics revisited: insights into population dynamics and life history evolution. *PaleoAnthropology* 2009:220–237.

Snodgrass, J. J., Leonard, W. R., Robertson, M. L., 2009. The energetics of encephalization in early hominids. In: Hublin, J.-J., Richards, M. P. (Eds.), *The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*. Vertebrate Paleobiology and Paleoanthropology. Springer, Dordrecht, The Netherlands, pp. 15–29.

Sobal, J., 2005. Men, meat, and marriage: models of masculinity. *Food Foodways* 13(1–2): 135–158.

Sobolik, K. D., 1993. Direct evidence for the importance of small animals to prehistoric diets: a review of coprolite studies. *N. Am. Archaeol.* 14(3):227–244.

Sobolik, K. D., 2003. *Archaeobiology*. Altamira Press, Lanham, MD.

Solms, J., 1969. Taste of amino acids, peptides and proteins. *J. Agric. Food Chem.* 17(4):686–688.

Solms, J., Vuataz, L., Egli, R. H., 1965. The taste of L- and D-amino acids. *Experientia* 21(12):692–694.

Sorensen, M. V., Leonard, W. R., 2001. Neandertal energetics and foraging efficiency. *J. Hum. Evol.* 40(6):483–495.

Sosis, R., 2000. Costly signaling and torch fishing on Ifaluk atoll. *Evol. Hum. Behav.* 21(4):223–244.

Sparano, V. T., 2000. *The Complete Outdoors Encyclopedia*. Macmillan, New York, NY.

Sparrman, A., 1785. *A Voyage to the Cape of Good Hope, Towards the Antarctic Polar Circle, and Round the World: But Chiefly into the Country of the Hottentots and Caffres, from the Year 1772, to 1776, Vol. 2. Translated from the Swedish Original*. G. G. J. and J. Robinson, London, England.

Speake, B. K., Herbert, J. F., Thompson, M. B., 2004. Comparison of the fatty-acid compositions of prey items and yolks of Australian insectivorous Scincid lizards. *J. Comp. Physiol. B. Biochem. Syst. Environ. Physiol.* 174B(5):393–397.

Speakman, J. R., 1992. Evolution of animal body size: a cautionary note on assessments of the role of energetics. *Funct. Ecol.* 6(4):495–496.

Spencer, H., Kramer, L., Osis, D., Norris, C., 1978. Effect of a high protein (meat) intake on calcium metabolism in man. *Am. J. Clin. Nutr.* 31(12):2167–2180.

Speth, J. D., 1983. *Bison Kills and Bone Counts: Decision Making by Ancient Hunters*. University of Chicago Press, Chicago, IL.

Speth, J. D., 1987. Early hominid subsistence strategies in seasonal habitats. *J. Archaeol. Sci.* 14(1):13–29.

Speth, J. D., 1989. Early hominid hunting and scavenging: the role of meat as an energy source. *J. Hum. Evol.* 18(5):329–343.

Speth, J. D., 1990. Seasonality, resource stress, and food sharing in so-called "egalitarian" foraging societies. *J. Anthropol. Archaeol.* 9(2):148–188.

Speth, J. D., Clark, J. L., 2006. Hunting and overhunting in the Levantine Late Middle Palaeolithic. *Before Farming* 3(1):1–42.

Speth, J. D., Davis, D. D., 1976. Seasonal variability in early hominid predation. *Science* 192(4238):441–445.

Speth, J. D., Spielmann, K. A., 1983. Energy source, protein metabolism, and hunter–gatherer subsistence strategies. *J. Anthropol. Archaeol.* 2(1):1–31.

Speth, J. D., Tchernov, E., 2001. Neandertal hunting and meat-processing in the Near East: evidence from Kebara Cave (Israel). In: Stanford, C. B., Bunn, H. T. (Eds.), *Meat-Eating and Human Evolution*. The Human Evolution Series. Oxford University Press, Oxford, England, pp. 52–72.

Spielmann, K. A., 1989. A review: dietary restrictions on hunter–gatherer women and the implications for fertility and infant mortality. *Hum. Ecol.* 17(3):321–345.

Spinage, C. A., Matlhare, J. M., 1992. Is the Kalahari cornucopia fact or fiction? A predictive model. *J. Appl. Ecol.* 29(3):605–610.

Sponheimer, M., de Ruiter, D., Lee-Thorp, J. A., Späth, A., 2005. Sr/Ca and early hominin diets revisited: new data from modern and fossil tooth enamel. *J. Hum. Evol.* 48(2):147–156.

Sponheimer, M., Dufour, D. L., 2009. Increased dietary breadth in early hominin evolution: revisiting arguments and evidence with a focus on biogeochemical contributions. In: Hublin, J.-J., Richards, M. P. (Eds.), *The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*. Vertebrate Paleobiology and Paleoanthropology. Springer, Dordrecht, The Netherlands, pp. 229–240.

Sponheimer, M., Lee-Thorp, J., 2007. Hominin paleodiets: the contribution of stable isotopes. In: Henke, W., Tattersall, I. (Eds.), *Handbook of Paleoanthropology*. Springer Reference. Springer, Berlin, Germany, pp. 555–585.

Sponheimer, M., Robinson, T., Ayliffe, L., Roeder, B., Hammer, J., Passey, B. H., West, A. G., Cerling, T. E., Dearing, D., Ehleringer, J., 2003. Nitrogen isotopes in mammalian herbivores: hair $\partial^{15}$N values from a controlled feeding study. *Int. J. Osteoarchaeol.* 13(1–2):80–87.

Spray, Z., 2002. Alaska's vanishing arctic cuisine. *Gastronomica* 2(1):30–40.

Stack, J., Dorward, A., Gondo, T., Frost, P., Taylor, F., Kurebgaseka, N., 2003. Mopane worm utilisation and rural livelihoods in southern Africa. Center for International Forestry Research (CIFOR), International Conference on Rural Livelihoods, Forests and Biodiversity, Bonn, Germany, 2003. http://www.mopane.org/.

Stackpole, E. A. (Ed.), 1965. *The Long Arctic Search: The Narrative of Lieutenant Frederick Schwatka, U. S. A., 1878–1880, Seeking the Records of the Lost Franklin Expedition by Frederick Schwatka*. Publication 44. The Marine Historical Association, Mystic, CT.

Stahl, A. B., 1989. Plant-food processing: implications for dietary quality. In: Harris, D. R., Hillman, G. C. (Eds.), *Foraging and Farming: The Evolution of Plant Exploitation*. Unwin Hyman, London, England, pp. 171–194.

Stander, P. E., Ghau, X., Tsisaba, D., Txoma, X., 1996. A new method of darting: stepping back in time. *Afr. J. Ecol.* 34(1):48–53.

Stanford, C. B., 1996. The hunting ecology of wild chimpanzees: implications for the evolutionary ecology of Pliocene hominids. *Am. Anthropol.* 98(1):96–113.

Stanford, C. B., 1998. *Chimpanzee and Red Colobus: The Ecology of Predator and Prey*. Harvard University Press, Cambridge, MA.

Stanford, C. B., 1999. *The Hunting Apes: Meat Eating and the Origins of Human Behavior*. Princeton University Press, Princeton, NJ.

Stanford, C. B., 2001a. A comparison of social meat-foraging by chimpanzees and human foragers. In: Stanford, C. B., Bunn, H. T. (Eds.), *Meat-Eating and Human Evolution*. Oxford University Press, Oxford, England, pp. 122–140.

Stanford, C. B., 2001b. *The Hunting Apes: Meat Eating and the Origins of Human Behavior*. Princeton University Press, Princeton, NJ.

Stanford, C. B., 2001c. *Significant Others: The Ape–Human Continuum and the Quest for Human Nature*. Basic Books, New York, NY.

Stanford, C. B., 2002. The ape's gift: meat-eating, meat-sharing, and human evolution. In: Waal, F. B. M. de (Ed.), *Tree of Origin: What Primate Behavior Can Tell Us About Human Social Evolution*. Harvard University Press, Cambridge, MA, pp. 95–118.

Stanford, C. B., Bunn, H. T. (Eds.), 2001. *Meat-Eating and Human Evolution*. The Human Evolution Series. Oxford University Press, Oxford, England.

Stanley-Samuelson, D. W., 1994. Prostaglandins and related eicosanoids in insects. In: Evans, P. D. (Ed.), *Adv. Insect. Phys.* 24. Academic Press, London, England, pp. 115–212.

Stanley-Samuelson, D. W., Dadd, R. H., 1983. Long-chain polyunsaturated fatty acids: patterns of occurrence in insects. *Insect Biochem.* 13(5):549–558.

Stanley-Samuelson, D. W., Jurenka, R. A., Cripps, C., Blomquist, G. J., de Renobales, M., 1988. Fatty acids in insects: composition, metabolism, and biological significance. *Arch. Insect Biochem. Physiol.* 9(1):1–33.

Stanley-Samuelson, D. W., Nelson, D. R. (Eds.), 1993. *Insect Lipids: Chemistry, Biochemistry, and Biology*. University of Nebraska Press, Lincoln, NE.

Starks, Z. S., 2007. Arctic foodways and contemporary cuisine. *Gastronomica* 7(1):41–49.

Steele, T. E., 2003. Using mortality profiles to infer behavior in the fossil record. *J. Mammal.* 84(2):418–430.

Stefansson, V., 1913. *My Life with the Eskimos*. Macmillan, New York, NY.

Stefansson, V., 1921. *The Friendly Arctic: The Story of Five Years in Polar Regions*. Macmillan, New York, NY.

Stefansson, V., 1944. *Arctic Manual*. Macmillan, New York, NY.

Stefansson, V., 1946. *Not by Bread Alone*. Macmillan Company, New York, NY.

Stefansson, V., 1956. *The Fat of the Land*. Macmillan, New York, NY.

Steguweit, L., 1999. Die recken von Schöningen: 400,000 jahre mit dem speer. *Mitteilungsblatt der Gesellschaft für Urgeschichte* 8:5–14.

Stein, Z. A., Susser, M. W., Rush, D., 1979. Prenatal nutrition and birthweight: experiments and quasi-experiments in the past decade. *J. Reprod. Med.* 21:287–297.

Steingrimsdottir, L., Brasel, J. A., Greenwood, M. R. C., 1980. Diet, pregnancy, and lactation: effects on adipose tissue, lipoprotein lipase, and fat cell size. *Metabolism* 29(9):837–841.

Stephenson, R. O., Gerlach, S. C., Guthrie, R. D., Harington, C. R., Mills, R. O., Hare, G., 2001. Wood bison in late Holocene Alaska and adjacent Canada: paleontological, archaeological and historical records. In: Gerlach, S. C., Murray, M. S. (Eds.), *People and Wildlife in Northern North America: Essays in Honor of R. Dale Guthrie*. BAR International Series S944. Archaeopress, British Archaeological Reports, Oxford, England, pp. 125–159.

Stetzer, A. J., Cadwallader, K., Singh, T. K., Mckeith, F. K., Brewer, M. S., 2008. Effect of enhancement and ageing on flavor and volatile compounds in various beef muscles. *Meat Sci.* 79(1):13–19.

Steward, J. H., 1938. *Basin-Plateau Aboriginal Socio-Political Groups*. Bulletin 120. Smithsonian Institution, Bureau of American Ethnology, Washington, DC.

Stewart, K. M., 1994. Early hominid utilization of fish resources and implications for seasonality and behaviour. *J. Hum. Evol.* 27(1–3):229–245.

Stigand, C. H., 1910. *To Abyssinia Through an Unknown Land: An Account of a Journey Through Unexplored Regions of British East Africa by Lake Rudolf to the Kingdom of Menelek*. J. B. Lippincott, Philadelphia, PA.

Stimmell, C., Stromberg, R. L., 1986. A reassessment of Thule Eskimo ceramic technology. In: Kingery, W. D. (Ed.), *Ceramics and Civilization, Vol. 2*. Technology and Style. American Ceramic Society Columbus, OH, pp. 237–250.

Stiner, M. C., 1990. The use of mortality patterns in archaeological studies of hominid predatory adaptations. *J. Anthropol. Archaeol.* 9(4):305–351.

Stiner, M. C., 1994. *Honor Among Thieves: A Zooarchaeological Study of Neandertal Ecology*. Princeton University Press, Princeton, NJ.

Stiner, M. C., 2001. Thirty years on the "broad spectrum revolution" and Paleolithic demography. *Proc. Natl. Acad. Sci.* 98(13):6993–6996.

Stiner, M. C., 2002. Carnivory, coevolution, and the geographic spread of the genus *Homo*. *J. Archaeol. Res.* 10(1):1–63.

Stock, J. T., 2008. Are humans still evolving? *Eur. Mol. Biol. Organ. (EMBO) Rep.* 9(Spec. Issue 1):S51–S54.

Stone, H., 1967. Gustatory responses to the L-amino acids in man. In: Hayashi, T. (Ed.), *Olfaction and Taste II. Proceedings of the Second International Symposium, Tokyo, September 1965*. Pergamon Press, London, England, pp. 289–306.

Stopper, H., Schmitt, E., Kobras, K., 2005. Genotoxicity of phytoestrogens. *Mutat. Res./ Fundamental and Molecular Mechanisms of Mutagenesis* 574(1–2):139–155.

Story, R., 1958. *Some Plants Used By the Bushmen in Obtaining Food and Water*. Memoir 30. Department of Agriculture, Division of Botany, Botanical Survey of South Africa, Pretoria, South Africa.

Ströhle, A., Wolters, M., Hahn, A., 2009. Die ernährung des menschen im evolutionsmedizinischen kontext. *Wien. Klin. Wochenschr.* 121(5–6):173–187.

Stutz, A. J., 2002. Polarizing microscopy identification of chemical diagenesis in archaeological cementum. *J. Archaeol. Sci.* 29(11):1327–1347.

Styles, C. V., 1996. The biological ecology of *Imbrasia belina* (Saturniinae, Saturniidae) with reference to its behaviour, physiology, distribution, population dynamics, impact within mophane veld and utilization within South Africa. In: Gashe, B. A., Leggett, K., Mpuchane, S. F. (Eds.), *Phane. Proceedings of the First Multidisciplinary Symposium on Phane, 18 June 1996*. University of Botswana, Department of Biological Sciences and Kalahari Conservation Society, Gaborone, Botswana, pp. 9–13.

Su, H.-M., Huang, M.-C., Saad, N. M. R., Nathanielsz, P. W., Brenna, J. T., 2000. Fetal baboons convert 18:3*n*-3 to 22:6*n*-3 in vivo: a stable isotope tracer study. *J. Lipid Res.* 42(4):581–586.

Sugawara, K., 2004. The modern history of Japanese studies on the San hunter–gatherers. In: Barnard, A. (Ed.), *Hunter–Gatherers in History, Archaeology and Anthropology*. Berg, Oxford, England, pp. 115–128.

Sussman, R. W., 1999. The myth of man the hunter, man the killer and the evolution of human morality. *Zygon* 34(3):453–471.

Svensson, E. I., 2009. Understanding the egalitarian revolution in human social evolution. *Trends Ecol. Evol.* 24(5):233–235.

Tabet, P., 1979. Les mains, les outiles, les armes. *L'Homme* 19(3):5–61.

Tan, G. D., Goossens, G. H., Humphreys, S. M., Vidal, H., Karpe, F., 2004. Upper and lower body adipose tissue function: a direct comparison of fat mobilization in humans. *Obes. Res.* 12(1):114–118.

Tanaka, J., 1980. *The San Hunter–Gatherers of the Kalahari: A Study in Ecological Anthropology*. Columbia University Press, New York, NY.

Tanaka, J., 1982. Adaptation to arid environment: a comparative study of hunter–gatherers and pastoralists in Africa. *Afr. Studies Monogr. Suppl.* 1:1–12.

Tappy, L., 1996. Thermic effect of food and sympathetic nervous system activity in humans. *Reprod. Nutr. Dev.* 36(4):391–397.

Tavendale, R., Lee, A. J., Smith, W. C. S., Tunstall-Pedoe, H., 1992. Adipose tissue fatty acids in Scottish men and women: results from the Scottish Heart Health Study. *Atherosclerosis* 94(2–3):161–169.

Taylor, C. M., Pye, O. F., 1966. *Foundations of Nutrition*. 6th ed. Macmillan, New York, NY.

Tchoundjeu, Z., Mpeck, M. L. N., Atangana, A. R., Degrande, A., Momha, C., 2006. *Ndjanssang: Ricinodendron heudelotii (Baill.)*. Fruits for the Future 7. University of Southampton, Southampton Centre for Underutilised Crops, Southampton, England.

Tessari, P., Kiwanuka, E., Zanetti, M., Barazzoni, R., 2003. Postprandial body protein synthesis and amino acid catabolism measured with leucine and phenylalanine–tyrosine tracers. *Am. J. Physiol. Endocrinol. Metab.* 284(5):E1037–E1042.

Thieme, H., 1997. Lower Paleolithic hunting spears from Germany. *Nature* 385(6619):807–810.

Thieme, H., Mania, D., Urban, B., van Kolfschoten, T., 1993. Schöningen (Nordharzvorland): eine Altpaläolithische fundstelle aus dem Mittleren Eiszeitalter. *Archäologisches Korrespondenzblatt* 23(2):147–163.

Thiong'o, M. K., Kingori, S., Jaenicke, H., 2002. The taste of the wild: variation in the nutritional quality of marula fruits and opportunities for domestication. In: Drew, R. (Ed.), *International Symposium on Tropical and Subtropical Fruits*. ISHS Acta Horticulturae 575. International Society for Horticultural Science, Leuven, Belgium, pp. 237–244.

Thomas, E. M., 1959. *The Harmless People*. Alfred A. Knopf, New York, NY.

Thomas, E. M., 2006. The lion/Bushman relationship in Nyae Nyae in the 1950s: a relationship crafted in the old way. In: Solway, J. S. (Ed.), *The Politics of Egalitarianism: Theory and Practice*. Berghahn Books, New York, NY, pp. 119–129.

Thompson, D., 1916. *David Thompson's Narrative of his Explorations in Western America, 1784–1812*. In: Tyrrell, J. B. (Ed.), Publication of the Champlain Society 12. Champlain Society, Toronto, Ontario.

Thompson, J. G., Lane, M., Robertson, S., 2006. Adaptive responses of early embryos to their microenvironment and consequences for post-implantation development. In: Wintour, E. M., Owens, J. A. (Eds.), *Early Life Origins of Health and Disease*. Adv. Exp. Med. Biol. 573. Springer, New York, NY, pp. 58–69.

Thompson, V. D., Stoner, W. D., Rowe, H. D., 2008. Early hunter–gatherer pottery along the Atlantic coast of the southeastern United States: a ceramic compositional study. *J. Island Coastal Archaeol.* 3(2):191–213.

Thoms, A. V., 2009. Rocks of ages: propagation of hot-rock cookery in western North America. *J. Archaeol. Sci.* 36(3):573–591.

Thöne-Reineke, C., Kalk, P., Dorn, M., Klaus, S., Simon, K., Pfab, T., Godes, M., Persson, P., Unger, T., Hocher, B., 2006. High-protein nutrition during pregnancy and lactation programs blood pressure, food efficiency, and body weight of the offspring in a sex-dependent manner. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 291(4):R1025–R1030.

Thornhill, R., Gangestad, S. W., 2008. *The Evolutionary Biology of Human Female Sexuality*. Oxford University Press, New York, NY.

Tindale, N. B., 1972. The Pitjandjara. In: Bicchieri, M. G. (Ed.), *Hunters and Gatherers Today*. Holt, Rinehart and Winston, New York, NY, pp. 217–268.

Tipton, K. D., Wolfe, R. R., 2004. Protein and amino acids for athletes. *J. Sports Sci.* 22(1):65–79.

Tishkoff, S. A., Reed, F. A., Ranciaro, A., Voight, B. F., Babbitt, C. C., Silverman, J. S., Powell, K., Mortensen, H. M., Hirbo, J. B., Osman, M., Ibrahim, M., Omar, S. A., Lema, G., Nyambo, T. B., Ghori, J., Bumpstead, S., Pritchard, J. K., Wray, G. A., Deloukas, P., 2007. Convergent adaptation of human lactase persistence in Africa and Europe. *Nat. Genet.* 39(1):31–40.

Tishkoff, S. A., Varkonyi, R., Cahinhinan, N., Abbes, S., Argyropoulos, G., Destro-Bisol, G., Drousiotou, A., Dangerfield, B., Lefranc, G., Loiselet, J., Piro, A., Stoneking, M., Tagarelli, A., Tagarelli, G., Touma, E. H., Williams, S. M., Clark, A. G., 2001. Haplotype diversity and linkage disequilibrium at human G6PD: recent origin of alleles that confer malarial resistance. *Science* 293(5529):455–462.

Tjader, R., 1910. *The Big Game of Africa*. D. Appleton and Company, New York, NY.

Tooby, J., DeVore, I., 1987. The reconstruction of hominid behavioral evolution through strategic modeling. In: Kinzey, W. G. (Ed.), *The Evolution of Human Behavior: Primate Models*. SUNY Series in Primatology. State University of New York Press, Albany, NY, pp. 183–237.

Torii, K., Mimura, T., Yugari, Y., 1987. Biochemical mechanism of umami taste perception and effect of dietary protein on the taste preference for amino acids and sodium chloride in rats. In: Kawamura, Y., Kare, M. R. (Eds.), *Umami, a Basic Taste*. Marcel Dekker, New York, NY, pp. 481–509.

Toth, N., Schick, K. D., 2009. The Oldowan: the tool making of early hominins and chimpanzees compared. *Annu. Rev. Anthropol.* 38:289–305.

Trowell, H., Davies, J. N. P., Dean, R. F. A., 1954. *Kwashiorkor*. Edward Arnold, London, England.

Trujillo, M. E., Scherer, P. E., 2006. Adipose tissue-derived factors: impact on health and disease. *Endocrine Rev.* 27(7):762–778.

Truswell, A. S., 1977. Diet and nutrition of hunter–gatherers. In: Elliott, K., Whelan, J. (Eds.), *Health and Disease in Tribal Societies*. Ciba Foundation Symp. 49 (n.s.). Elsevier, Amsterdam, The Netherlands, pp. 213–226.

Truswell, A. S., Hansen, J. D. L., 1968. Medical and nutritional studies of !Kung Bushmen in northwest Botswana: a preliminary report. *S. Afr. Med. J.* 42:1338–1339.

Truswell, A. S., Hansen, J. D. L., 1976. Medical research among the !Kung. In: Lee, R. B., DeVore, I. (Eds.), *Kalahari Hunter–Gatherers: Studies of the !Kung San and Their Neighbors*. Harvard University Press, Cambridge, MA, pp. 166–194.

Tsujinaka, T., Sakaue, M., Iijima, S., Ebisui, C., Kan, K., Kishibuchi, M., Morimoto, T., Kido, Y., 1996. Modulation of thermogenic response to parenteral amino acid infusion in surgical stress. *Nutrition* 12(1):36–39.

Tudge, C., 1977. *The Famine Business*. St. Martin's Press, New York, NY.

Ungar, P. S. (Ed.), 2007. *Evolution of the Human Diet: The Known, the Unknown, and the Unknowable*. Human Evolution Series. Oxford University Press, Oxford, England.

Ungar, P. S., Grine, F. E., Teaford, M. F., 2006. Diet in early *Homo*: a review of the evidence and a new model of adaptive versatility. *Annu. Rev. Anthropol.* 35(1):209–228.

Ungar, P. S., Teaford, M. F. (Eds.), 2002. *Human Diet: Its Origin and Evolution*. Praeger, Westport, CT.

United Nations, 1968. *International Action to Avert the Impending Protein Crisis*. United Nations Publications, New York, NY.

van de Poll, M. C. G., Wigmore, S. J., Redhead, D. N., Beets-Tan, R. G. H., Garden, O. J., Greve, J. W. M., Soeters, P. B., Deutz, N. E. P., Fearon, K. C. H., Dejong, C. H. C., 2007. Effect of major liver resection on hepatic ureagenesis in humans. *Am. J. Physiol. Gastrointest. Liver Physiol.* 293(5):G956–G962.

van der Walt, A. M., Ibrahim, M. I. M., Bezuidenhout, C. C., Loots, D. T., 2009. Linolenic acid and folate in wild-growing African dark leafy vegetables (morogo). *Public Health Nutr.* 12(4):525–530.

van Milgen, J., 2002. Modeling biochemical aspects of energy metabolism in mammals. *J. Nutr.* 132(10):3195–3202.

Vaughan, D. A., Drury, H. F., Hannon, J. P., Vaughan, L. N., Larson, A. M., 1959. Some biochemical effects of restricted diets during successive field trials in winter. *J. Nutr.* 67(1):99–108.

Veldhorst, M., Smeets, A., Soenen, S., Hochstenbach-Waelen, A., Hursel, R., Diepvens, K., Lejeune, M., Luscombe-Marsh, N., Westerterp-Plantenga, M., 2008. Protein-induced satiety: effects and mechanisms of different proteins. *Physiol. Behav.* 94(2):300–307.

Vellard, J., 1939. *Une Civilisation du Miel: Les Indiens Guayakis du Paraguay*. Gallimard, Paris, France.

Vertuani, S., Braccioli, E., Buzzoni, V., Manfredini, S., 2002. Antioxidant capacity of *Adansonia digitata* fruit pulp and leaves. *Acta Phytother.* 5(2):2–7.

Villa, P., Boscato, P., Ranaldo, F., Ronchitelli, A., 2009. Stone tools for the hunt: points with impact scars from a Middle Paleolithic site in southern Italy. *J. Archaeol. Sci.* 36(3):850–859.

Villa, P., Lenoir, M., 2006. Hunting weapons of the Middle Stone Age and the Middle Palaeolithic: spear points from Sibudu, Rose Cottage and Bouheben. *Southern African Humanities (Pietermaritzburg, South Africa)* 18(1):89–122.

Villa, P., Lenoir, M., 2009. Hunting and hunting weapons of the Lower and Middle Paleolithic of Europe. In: Hublin, J.-J., Richards, M. P. (Eds.), *The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*. Vertebrate Paleobiology and Paleoanthropology. Springer, Dordrecht, The Netherlands, pp. 59–85.

Vilstrup, H., 1980. Synthesis of urea after stimulation with amino acids: relation to liver function. *Gut* 21(11):990–995.

Voight, B. F., Kudaravalli, S., Wen, X., Pritchard, J. K., 2006. A map of recent positive selection in the human genome. *PLoS Biol.* 4(3):e72. doi:10.1371/journal.pbio.0040072.

Voltaire (Arouet), F.-M., 1919. *Voltaire in His Letters: Being a Selection from His Correspondence.* E. B. Hall (Pseud. Tallentyre, S. G.) (Trans.). G. P. Putnam's Son, New York, NY.

von Höhnel, L., 1894. *Discovery of Lakes Rudolf and Stefanie: A Narrative of Count Samuel Teleki's Exploring and Hunting Expedition in Eastern Equatorial Africa in 1887 and 1888, Vol. 2*. Bell, N. (Trans.). Longmans, Green, and Company, London, England.

Voormolen, B., 2008. Ancient hunters, modern butchers: Schöningen 13II-4, a kill-butchery site dating from the northwest European Lower Paleolithic. *J. Taphonomy* 6(2):71–247.

Waguespack, N. M., Surovell, T. A., Denoyer, A., Dallow, A., Savage, A., Hyneman, J., Tapster, D., 2009. Making a point: wood- versus stone-tipped projectiles. *Antiquity* 83(321): 786–800.

Wahrenberg, H., Lonnqvist, F., Amer, P., 1989. Mechanisms underlying regional differences in lipolysis in human adipose tissue. *J. Clin. Invest.* 84(2):458–467.

Wajchenberg, B. L., 2000. Subcutaneous and visceral adipose tissue: their relation to the metabolic syndrome. *Endocr. Rev.* 21(6):697–738.

Wakefield, S. L., Lane, M., Schulz, S. J., Hebart, M. L., Thompson, J. G., Mitchell, M., 2008. Maternal supply of omega-3 polyunsaturated fatty acids alter mechanisms involved in oocyte and early embryo development in the mouse. *Am. J. Physiol. Endocrinol. Metab.* 294(2):E425–E434.

Walker, R. M., Linkswiler, H. M., 1972. Calcium retention in the adult human male as affected by protein intake. *J. Nutr.* 102(10):1297–1302.

Walker, R. S., Gurven, M., Hill, K., Migliano, A., Chagnon, N., de Souza, R., Djurovic, G., Hames, R., Hurtado, A. M., Kaplan, H., Kramer, K., Oliver, W. J., Valeggia, C., Yamauchi, T., 2006. Growth rates and life histories in twenty-two small-scale societies. *Am. J. Hum. Biol.* 18(3):295–311.

Walker, R. S., Hill, K., Kaplan, H., McMillan, G., 2002. Age-dependency in hunting ability among the Ache of eastern Paraguay. *J. Hum. Evol.* 42(6):639–657.

Wandsnider, L., 1997. The roasted and the boiled: food composition and heat treatment with special emphasis on pit-hearth cooking. *J. Anthropol. Archaeol.* 16(1):1–48.

Wang, K., Maga, J. A., Bechtel, P. J., 1996. Taste properties and synergisms of beefy meaty peptide. *J. Food Sci.* 61(4):837–839.

Wannenburgh, A., Johnson, P., Bannister, A., 1999. *The Bushmen*. Struik, Cape Town, South Africa.

Warburton, P. E., 1875. *Journey Across the Western Interior of Australia, With an Introduction and Additions by Charles H. Eden*. In: Bates, H. W. (Ed.). Sampson Low, Marston, Low, and Searle, London, England.

Ward, R., 1896. *Records of Big Game: Containing an Account of Their Distribution, Descriptions of Species, Lengths, and Weights, Measurements of Horns and Field Notes for the Use of Sportsmen and Naturalists*. Rowland Ward and Company, London, England.

Washburn, S. L., Lancaster, C. S., 1968. The evolution of hunting. In: Lee, R. B., DeVore, I. (Eds.), *Man the Hunter*. Aldine, New York, NY, pp. 293–303.

Watanabe, H., 1968. Subsistence and ecology of northern food gatherers with special reference to the Ainu. In: Lee, R. B., DeVore, I. (Eds.), *Man the Hunter*. Aldine, Chicago, IL, pp. 69–77.

Wathes, D. C., Abayasekara, D. R. E., Aitken, R. J., 2007. Polyunsaturated fatty acids in male and female reproduction. *Biol. Reprod.* 77(2):190–201.

Watts, D. P., Mitani, J. C., 2002. Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. *Int. J. Primatol.* 23(1):1–28.

Wehmeyer, A. S., 1971. The nutritional value of some edible wild fruits and plants. In: Claassens, J. W., Potgieter, H. J. (Eds.), *Proteins and Food Supply in the Republic of South Africa*. A. A. Balkema, Cape Town, South Africa, pp. 89–94.

Wehmeyer, A. S., 1986. *Edible Wild Plants of Southern Africa: Data on the Nutrient Contents of Over 300 Species*. NFRI Report. Council for Scientific and Industrial Research (CSIR), National Food Research Institute, Pretoria, South Africa. http://www.hdl.handle.net/10204/2337.

Wehmeyer, A. S., Lee, R. B., Whiting, M., 1969. The nutrient composition and dietary importance of some vegetable foods eaten by the !Kung Bushmen. *S. Afr. Med. J.* 43:1529–1530.

Weiler, H. A., Fitzpatrick-Wong, S. C., 2002. Modulation of essential (n-6):(n-3) fatty acid ratios alters fatty acid status but not bone mass in piglets. *J. Nutr.* 132(9):2667–2672.

Weinert, I. A. G. , van Wyk, P. J., Holtzhausen, L. C., 1990. Marula. In: Nagy, S., Shaw, P. E., Wardowski, W. F. (Eds.), *Fruits of Tropical and Subtropical Origin: Composition, Properties, and Uses*. Florida Science Source, Lake Alfred, FL, pp. 88–115.

Weiss, E., Kislev, M. E., Simchoni, O., Nadel, D., 2004. Small-grained wild grasses as staple food at the 23 000-year-old site of Ohalo II, Israel. *Econ. Bot.* 58(Suppl.):S125–S134.

Weiss, E., Kislev, M. E., Simchoni, O., Nadel, D., Tschauner, H., 2008. Plant-food preparation area on an Upper Paleolithic brush hut floor at Ohalo II, Israel. *J. Archaeol. Sci.* 35(8):2400–2414.

Welch, A. A., Bingham, S. A., Ive, J., Friesen, M. D., Wareham, N. J., Riboli, E., Khaw, K. T., 2006. Dietary fish intake and plasma phospholipid *n*-3 polyunsaturated fatty acid concentrations in men and women in the European Prospective Investigation into Cancer – Norfolk United Kingdom Cohort. *Am. J. Clin. Nutr.* 84(6):1330–1339.

Welch, A. A., Bingham, S. A., Khaw, K. T., 2008. Estimated conversion of α-linolenic acid to long chain *n*-3 polyunsaturated fatty acids is greater than expected in non fish-eating vegetarians and non fish-eating meat-eaters than in fish-eaters (abstract). *J. Hum. Nutr. Diet.* 21(4):404.

Welch, R. W., 1975. Fatty acid composition of grain from winter and spring sown oats, barley and wheat. *J. Sci. Food Agric.* 26(4):429–435.

Wells, J. C. K., 2006. The evolution of human fatness and susceptibility to obesity: an ethological approach. *Biol. Rev. Camb. Philos. Soc.* 81(2):183–205.

Westerterp-Plantenga, M. S., 2008. Protein intake and energy balance. *Regul. Pept.* 149(1–3):67–69.

Westerterp-Plantenga, M. S., Lejeune, M. P. G. M., Nijs, I., van Ooijen, M., Kovacs, E. M. R., 2004. High protein intake sustains weight maintenance after body weight loss in humans. *Int. J. Obes.* 28(1):57–64.

Westerterp-Plantenga, M. S., Luscombe-Marsh, N., Lejeune, M. P. G. M., Diepvens, K., Nieuwenhuizen, A., Engelen, M. P. K. J., Deutz, N. E. P., Azzout-Marniche, D., Tome, D., Westerterp, K. R., 2006. Dietary protein, metabolism, and body-weight regulation: dose-response effects. *Int. J. Obes.* 30(Suppl. 3):S16–S23.

White, D. R., Widdowson, E. M., Woodard, H. Q., Dickerson, J. W. T., 1991. The composition of body tissues (II): fetus to young adult. *Br. J. Radiol.* 64(758):149–159.

White, N., 1985. Sex differences in Australian Aboriginal subsistence: possible implications for the biology of hunter–gatherers. In: Ghesquiere, J., Martin, R. D., Newcombe, F. (Eds.), *Human Sexual Dimorphism*. Symp. Soc. Study Hum. Biol. 24. Taylor and Francis, London, pp. 323–361.

White, T. D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C. O., Suwa, G., WoldeGabriel, G., 2009. *Ardipithecus ramidus* and the paleobiology of early hominids. *Science* 326(5949):64, 75–86.

Wiber, M. G., 1997. *Erect Men, Undulating Women: The Visual Imagery of Gender, "Race" and Progress in Reconstructive Illustrations of Human Evolution*. Wilfrid Laurier University Press, Waterloo, Ontario.

Wiedenfeld, H., Roeder, E., Bourauel, T., Edgar, J., 2008. *Pyrrolizidine Alkaloids: Structure and Toxicity*. Vandenhoeck and Ruprecht/Bonn University Press, Göttingen, Germany.

Wiessner, P., 1977. *Hxaro: A Regional System of Reciprocity for Reducing Risk Among the !Kung San*. Unpublished PhD Dissertation, Department of Anthropology, University of Michigan, Ann Arbor, MI.

Wiessner, P., 1981. Measuring the impact of social ties on nutritional status among the !Kung San. *Soc. Sci. Inf.* 20(4–5):641–678.

Wiessner, P., 1996. Leveling the hunter: constraints on the status quest in foraging societies. In: Wiessner, P., Schiefenhövel, W. (Eds.), *Food and the Status Quest: An Interdisciplinary Perspective*. Berghahn Books, Oxford, England, pp. 171–192.

Wiessner, P., 2002. Hunting, healing, and Hxaro exchange: a long-term perspective on !Kung (Ju/'hoansi) large-game hunting. *Evol. Hum. Behav.* 23(6):407–436.

Willett, S., 2003. *The Khoe and San: An Annotated Bibliography, Vol. 2*. University of Botswana/ University of Tromsø Collaborative Programme for San/Basarwa Research and Capacity Building (NUFU PRO 20/96). Lightbooks/Lentswe La Lesedi, Gaborone, Botswana.

Williams, C. D., 1933. A nutritional disease of childhood associated with a maize diet. *Arch. Dis. Child.* 8:423–433.

Williams, C. D., 1935. Kwashiorkor: a nutritional disease of children associated with a maize diet. *Lancet* 226(5855):1151–1152.

Williams, C. M., 2004. Lipid metabolism in women. *Proc. Nutr. Soc.* 63(1):153–160.

Williams, C. M., Burdge, G. C., 2006. Long-chain *n*-3 PUFA: plant *v*. marine sources. *Proc. Nutr. Soc.* 65(1):42–50.

Williams, D., 1997. Early pottery in the Amazon: a correction. *Am. Antiq.* 62(2):342–352.

Williams, P., 2007. Nutritional composition of red meat. *Nutr. Diet.* 64(Suppl. 4):S113–S119.

Williamson, S. H., Hubisz, M. J., Clark, A. G., Payseur, B. A., Bustamante, C. D., Nielsen, R., 2007. Localizing recent adaptive evolution in the human genome. *PLoS Genet.* 3(6):e90. doi:10.1371/journal.pgen.0030090.

Williard, D. E., Harmon, S. D., Kaduce, T. L., Preuss, M., Moore, S. A., Robbins, M. E. C., Spector, A. A., 2001. Docosahexaenoic acid synthesis from *n*-3 polyunsaturated fatty acids in differentiated rat brain astrocytes. *J. Lipid Res.* 42(9):1368–1376.

Williard, D. E., Harmon, S. D., Kaduce, T. L., Spector, A. A., 2002. Comparison of 20-, 22-, and 24-carbon *n*-3 and *n*-6 polyunsaturated fatty acid utilization in differentiated rat brain astrocytes. *Prostaglandins Leukot. Essent. Fatty Acids* 67(2–3):99–104.

Wilmsen, E. N., 1978. Seasonal effects of dietary intake on Kalahari San. *Fed. Proc.* 37(1):65–72.

Wilmsen, E. N., 1982. Studies in diet, nutrition, and fertility among a group of Kalahari Bushmen in Botswana. *Soc. Sci. Inf.* 21(1):95–125.

Wilmsen, E. N., 1989. *Land Filled With Flies: A Political Economy of the Kalahari*. University of Chicago Press, Chicago, IL.

Wilmsen, E. N., Durham, D., 1988. Food as a function of seasonal environment and social history. In: de Garine, I., Harrison, G. A. (Eds.), *Coping with Uncertainty in Food Supply*. Clarendon Press, Oxford, England, pp. 52–87.

Winterhalder, B., 1996. Social foraging and the behavioral ecology of intragroup resource transfers. *Evol. Anthropol.* 5(2):46–57.

Winterhalder, B., 1997. Gifts given, gifts taken: the behavioral ecology of nonmarket, intragroup exchange. *J. Archaeol. Res.* 5(2):121–168.

Winterhalder, B., Smith, E. A. (Eds.), 1981. *Hunter–Gatherer Foraging Strategies: Ethnographic and Archaeological Analyses*. University of Chicago Press, Chicago, IL.

Winterhalder, B., Smith, E. A., 2000. Analyzing adaptive strategies: human behavioral ecology at twenty-five. *Evol. Anthropol.* 9(2):51–72.

Wislizenus, F. A., 1912. *Journey to the Rocky Mountains in the Year 1839*. Wislizenus, F. A. (Trans.). Missouri Historical Society, Saint Louis, MO.

Wissler, C., 1910. *Material Culture of the Blackfoot Indians*. Anthropological Paper 5(1). American Museum of Natural History, New York, NY.

Witter, M. S., Cuthill, I. C., 1993. The ecological costs of avian fat storage. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 340(1291):73–92.

Wobber, V., Hare, B., Wrangham, R., 2008. Great apes prefer cooked food. *J. Hum. Evol.* 55(2):340–348.

Wobst, H. M., 1974. Boundary conditions for Paleolithic social systems: a simulation approach. *Am. Antiq.* 39(2 Part 1):147–178.

Wobst, H. M., 1976. Locational relationships in Paleolithic society. *J. Hum. Evol.* 5(1):49–58.

Wobst, H. M., 1977. Stylistic behavior and information exchange. In: Cleland, C. E. (Ed.), *Papers for the Director: Research Essays in Honor of James B. Griffin*. Anthropological Paper 61. University of Michigan, Museum of Anthropology, Ann Arbor, MI, pp. 317–342.

Wobst, H. M., 1978. The archaeo-ethnology of hunter–gatherers or the tyranny of the ethnographic record in archaeology. *Am. Antiq.* 43(2):303–309.

Wobst, H. M., 1993. Mobility and gene flow: some biological and social thoughts on the Paleolithic. In: Krass, D. S., Thomas, R. B., Cole, J. W. (Eds.), *Ela' Qua: Essays in Honor of Richard B. Woodbury*. Research Report 28. University of Massachusetts, Department of Anthropology, Amherst, MA, pp. 283–291.

Wollstonecroft, M. M., Ellis, P. R., Hillman, G. C., Fuller, D. Q., 2008. Advances in plant food processing in the Near Eastern Epipalaeolithic and implications for improved edibility and nutrient bioaccessibility: an experimental assessment of *Bolboschoenus maritimus* (L.) Palla (sea club-rush). *Veget. Hist. Archaeobot.* 17(Suppl. 1):19–27.

Wood, B. M., 2006. Prestige or provisioning? A test of foraging goals among the Hadza. *Curr. Anthropol.* 47(2):383–387.

Wood, B. M., Hill, K., 2000. A test of the "showing-off" hypothesis with Ache hunters. *Curr. Anthropol.* 41(1):124–125.

Wood, J. G., 1882. *The Uncivilized Races of Men in All Countries of the World; Being a Comprehensive Account of their Manners and Customs, and of their Physical, Social, Mental, Moral and Religious Characteristics, Vol. 1*. J. A. Brainerd, San Francisco, CA.

Wood, J. G., 1877. *Nature's Teachings: Human Invention Anticipated By Nature*. Daldy, Isbister and Company, London, England.

Wood, J. G., 1886. *Man and His Handiwork*. Society for Promoting Christian Knowledge, London, England.

Woodburn, J., 1968. An introduction to Hadza ecology. In: Lee, R. B., DeVore, I. (Eds.), *Man the Hunter*. Aldine, Chicago, IL, pp. 49–55.

Woodburn, J., 1970. *Hunters and Gatherers: The Material Culture of the Nomadic Hadza*. British Museum, London, England.

Woodburn, J., 1998. 'Sharing is not a form of exchange': an analysis of property-sharing in immediate-return hunter–gatherer societies. In: Hann, C. M. (Ed.), *Property Relations: Renewing the Anthropological Tradition*. Cambridge University Press, Cambridge, England, pp. 48–63.

Woodburn, J., 2005. Egalitarian societies revisited. In: Widlok, T., Tadesse, W. G. (Eds.), *Property and Equality: Ritualisation, Sharing, Egalitarianism, Vol. 1*. Berghahn Books, Oxford, England, pp. 18–31.

Wrangham, R. W., 2009. *Catching Fire: How Cooking Made Us Human*. Basic Books, New York, NY.

Wrangham, R. W., Conklin-Brittain, N. L., 2003. Cooking as a biological trait. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 136(1):35–46.

Wrangham, R. W., Peterson, D., 1996. *Demonic Males: Apes and the Origins of Human Violence*. Houghton Mifflin, Boston, MA.

Yamaguchi, S., 1991. Basic properties of umami and effects on humans. *Physiol. Behav.* 49(5):833–841.

Yamaguchi, S., Ninomiya, K., 2000. Umami and food palatability. *J. Nutr.* 130(Suppl. 4):921S–926S.

Yamaoka, I., 2008. Modification of core body temperature by amino acid administration. *Asia Pac. J. Clin. Nutr.* 17(Suppl. 1):309–311.

Yeakel, J. D., Bennett, N. C., Koch, P. L., Dominy, N. J., 2007. The isotopic ecology of African mole rats informs hypotheses on the evolution of human diet. *Proc. R. Soc. Lond. B Biol. Sci.* 274B(1619):1723–1730.

Yeboah, S. O., Mitei, Y. C., 2009. Further lipid profiling of the oil from the mophane caterpillar, *Imbrasia belina*. *J. Am. Oil Chem. Soc.* 86(11):1047–1055.

Yellen, J. E., Lee, R. B., 1976. The Dobe-/Du/da environment: background to a hunting and gathering way of life. In: Lee, R. B., DeVore, I. (Eds.), *Kalahari Hunter–Gatherers: Studies of the !Kung San and Their Neighbors*. Harvard University Press, Cambridge, MA, pp. 27–46.

Yengoyan, A. A., 2004. Anthropological history and the study of hunters and gatherers: cultural and non-cultural. In: Barnard, A. (Ed.), *Hunter–Gatherers in History, Archaeology and Anthropology*. Berg, Oxford, England, pp. 57–66.

Yim, J.-E., Heshka, S., Albu, J. B., Heymsfield, S., Gallagher, D., 2008. Femoral–gluteal subcutaneous and intermuscular adipose tissues have independent and opposing relationships with CVD risk. *J. Appl. Physiol.* 104(3):700–707.

Yohe, R. M., Newman, M. E., Schneider, J. S., 1991. Immunological identification of small-mammal proteins on Aboriginal milling equipment. *Am. Antiq.* 56(4):659–666.

Young, V. R., Pellett, P. L., 1994. Plant proteins in relation to human protein and amino acid nutrition. *Am. J. Clin. Nutr.* 59(5):1203S–1212S.

Zahavi, A., Zahavi, A., 1997. *The Handicap Principle: A Missing Piece of Darwin's Puzzle*. Oxford University Press, Oxford, England.

Zander, D. L., Thompson, J. G., Lane, M., 2006. Perturbations in mouse embryo development and viability caused by ammonium are more severe after exposure at the cleavage stages. *Biol. Reprod.* 74(2):288–294.

Zeanah, D. W., 2004. Sexual division of labor and central place foraging: a model for the Carson Desert of Western Nevada. *J. Anthropol. Archaeol.* 23(1):1–32.

Zhang, C., 2002. The discovery of early pottery in China. *Doc. Praehist.* 29:29–35.

Zhang, Y., Guo, K., LeBlanc, R. E., Loh, D., Schwartz, G. J., Yu, Y.-H., 2007. Increasing dietary leucine intake reduces diet-induced obesity and improves glucose and cholesterol metabolism in mice via multimechanisms. *Diabetes* 56(6):1647–1654.

Zhao, L., Schell, D. M., Castellini, M. A., 2006. Dietary macronutrients influence $^{13}$C and $^{15}$N signatures of pinnipeds: captive feeding studies with harbor seals (*Phoca vitulina*). *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 143(4):469–478.

Zihlman, A. L. 1978. Women in evolution, II. subsistence and social organization among early hominids. *Signs* 4(1):4–20.

Zinzombe, I. M., George, S., 1994. Larval lipid quality of Lepidoptera: *Gonimbrasia belina*. *Botsw. Notes Rec.* 26:167–173.

Zvelebil, M., 2002. The invention of hunter–gatherers in seventeenth century Europe? a comment on Mark Pluciennik. *Archaeol. Dialogues* 9(2):123–129.

Zvelebil, M., 2008. Innovating hunter–gatherers: the Mesolithic in the Baltic. In: Bailey, G. N., Spikins, P. (Eds.), *Mesolithic Europe*. Cambridge University Press, Cambridge, England, pp. 18–59.

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