Nutritional contribution of plant foods to human diet in evolution

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Citation

Schnorr, S. L. (2016, March 22). *Nutritional contribution of plant foods to human diet in evolution*. Retrieved from https://hdl.handle.net/1887/38835

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Title: Nutritional contribution of plant foods to human diet in evolution
Issue Date: 2016-03-22

CHAPTER 1

INTRODUCTION

The study of nutrition and the research on human diets have historically blazed remarkably different trails on the subject of food and nutrition in human health. The former most notably deals with the relationships between food composition, physiology, and disease while the latter may be considered a more anthropological perspective on the role of food in socio-cultural, biological, and evolutionary aspects of human life. However, their paths have obvious overlap, especially when it comes to human biological adaptation to nutrition, but this has not always been fully appreciated. Nutritionists are largely concerned with applications in public health whereas anthropologists may find controlled dietary studies too restrictive or specific to modern Western society to have evolutionary significance. Diet is one of the most profound factors of influence on an organism′s physiology and behavior. In human evolution specifically, whole genera of archaic hominins are identified on the basis of morphological variations to the masticatory apparatus that may be suggestive of divergent dietary patterns. Indeed, diet is considered one of the main vectors for early hominid differentiation and dispersal across the Plio-Pleistocene. Colossal effort is dedicated to elucidating the diets of these early groups because we believe this information holds vital clues to how and why the human lineage evolved, what led to its successes, and what led to its dead ends. Eventually, highly derived groups within Homo emerged such as H. erectus, H. heidelbergensis, Neanderthals, Denisovans, and modern humans. These highly intelligent, social, and geographically widespread groups show further reduction in masticatory robusticity coincident with cranial expansion (excluding Denisovans, for whom we lack cranio-dental remains), traits highly suggestive of a significant biological response to dietary changes sometime after the emergence of Homo (Organ et al., 2011).

But how do we investigate ephemeral events in the past and, more importantly, how do we quantify the influence of these events? The combined efforts of anthropological sub-disciplines – archaeology, archaeological science, ethnography, and morphology – construct our knowledge base surrounding the history and evolution of human diet, while nutritional science provides the necessary quantitative or mechanistic information about food and digestion. Together, both fields stand to gain tremendous collective insight about human nutrition and adaptive physiology. But reaching this idealized goal of cross-disciplinary cooperation towards a realized mutual outcome has taken considerable time and evolution in both fields. It is perhaps fortuitous that the present zeitgeist is a strong public interest in evolutionary health, effectively forcing a cross-disciplinary response to health research and policy. The explosion of interest in evolutionary medicine, evidenced by the current popularity of “Paleo-diets” or alternative medicine, may (in the most optimistic view) speak to a progressive undercurrent of realization that the factors affecting human health are immutably dictated by millions of years of human evolutionary history. Even our distinctly human characteristic within Primates, a big brain, reaches far back in time, built upon foundations laid out in the Cambrian explosion when intracellular complexity, driven by membrane lipid synthesis, arose and established the precursors for the nervous system (Crawford et al., 2008). As a result, we have likely crossed a cognitive threshold in awareness of who we are as humans and irrevocably formalized that anthropology is the necessary partner to all endeavors in human biology. Correspondingly, as anthropological studies continue to dig deeper within an evolutionary framework, their topics become unambiguously intertwined with the relevant sub-disciplines of biology. However, this was not always the case as both fields experienced a long, non-overlapping, parallel evolution since their inception roughly 200 years ago. The precedence for this is understandable given the age and origin of both fields.

1.1 Chemical revolution and nutritional science history

The setting for the formal beginnings of food and nutritional science is late eighteenth century France, in which the "Chemical Revolution" spawned an era of investigation and elucidation of [periodic] elements in organic matter (Carpenter, 2003). Prior to this, the pioneering work in nutrition amounted to systematic trials of different therapies recommended for scurvy. Progress towards understanding the composition of animal tissue jumped forward when ammonia emanating from decomposing animal matter was determined as three parts hydrogen and one part nitrogen. Nitrogen, it was soon found, resided in abundance in other nutritional plant foods such as wheat and legumes as well as meat, so that these foods were thought to be especially "animalizing" (Carpenter, 2003). People were interested in the paradox of how grazing animals could convert plant food, particularly plant food considered to be deplete of nitrogen, into nitrogen-rich animal tissue. Such knowledge had relevance even at the political level of society, particularly because it could inform about how best to sustain rapid population growth in expanding nations and colonies with a cheap mass-produced staple crop. And so it was that by trying to understand the "animalizing" property of food that the study of how animals internalize and utilize different nutrients (i.e. nutritional composition and digestion physiology) became an empirical scientific endeavor. These efforts were not limited to food composition and intake, but also looked at how heat production and respiration (metabolism) figured into the mass balancing equation (Carpenter, 2003).

The early strides in chemical and nutritional research by many European physicians, chemists, and scholars throughout the mid to late nineteenth century provoked enough action from the medical establishment so as to set off a wave of medical science devoted to the study of the dietary etiology of disease (Taubes, 2007, pp ix-xxv). By the late nineteenth century, nutrition scientists and physicians were keen to establish a cause, and thus a therapy, for obesity and its associated diseases at that time-diabetes, gout, and hypertension. Claude Bernard, the famous French physiologist, made especially pivotal revelations about liver function that yielded an initial understanding of the mechanisms of obesity and adult onset diabetes. More modern iterations on this theme began nearly a century later in the U.S. after WWII with clinical investigations into the relationship between infectious disease and malnutrition (Keusch, 2003), and the treatment of progressive manifestations of 'diseases of civilizations'. The latter was pursued ardently by clinical investigators, with six major conferences and symposia devoted to obesity research by 1973. The medical and by this point U.S. government regulated nutritional policies, however, insisted on a different agenda that aligned with corporate economics. This brought the focus away from discovering the dietary factors deemed essential to health, a pursuit that naturally appeals to evolutionary principles, to instead isolating dietary components arbitrarily considered to be unhealthy. The result was the promotion of certain foods and food groups over others. These contrasting research strategies essentially codified the formal distinction between 'biological science' and 'dietary health research'. The notion of diet, or specifically foods, as a factor in the holistic cultivation of health or etiology of disease fell quite out of favor. By the time mainstream medical establishments were entrenched in the diet-heart hypothesis of the last 50 years, demonstrating their own appalling attempts at empirical science, Bernard's "milieu intérieur" or stability and equilibration of the internal environment was antiquated and long forgotten. Certainly there has been a pressing need for the re-establishment of an evolutionary-based perspective in nutritional science.

1.2 Anthropological study of human diet

Leaving behind this brief history of clinical and medical diet research, we can turn to the seemingly unrelated field of anthropology at the end of the nineteenth century. Although formative exploratory work with native communities had already captured the interests of nineteenth century evolutionists such as Herbert Spencer, Edward B. Tylor, and Lewis H. Morgan 50 years earlier, this era of sociological work focused on religion was still the relative dark ages for anthropology (Tylor, 1871; Orlove, 1980). The end of the nineteenth century was a turning point for the field from the murky, century-old, ethnological societies stuck on reifying long-held racist convictions about European superiority, to more comprehensive approaches towards documenting social institutions of so-called primitive societies (Boas, 1911; McGee and Warms, 2008).

The rebirth of ethnography was mostly dominated by early British-trained social anthropologists working in unindustrialized colonial Africa and the South Pacific (Messer, 1984). As both researchers and explorers, these people incidentaly gave some of the first dedicated accounts of food culture in traditional societies, out of the broader goal to understand the origins of "modern" (the industrialized West) cultural institutions. When the first fossil discoveries of Neanderthals and ancient hominins put western civilization face to face with the enigmatic traces of human prehistoric ancestry, suddenly isolated traditional cultures became a convenient analogy and easy point of reference to bridge the gap between modern and savage "man". Ethnography, it was then thought, was an opportunity to witness "living fossils" and define a kind of socio-behavioral spectrum (Orlove, 1980). At the bottom was primitivism, exemplified by indigenous tribes and attributable to earlier hominins, with radiating linear stages of cognitive progression towards Western civilized society, thought to mirror the biological stages of human evolution (Orlove, 1980). Though still deeply flawed and mired in the institutionally presiding dualism of savagery and barbarism versus civilization and enlightenment, for the first time there was an emerging systematic process to the field of ethnography (Firth, 1934; Orlove, 1980; Messer, 1984).

The A. C. Haddon expedition to the Torres Straits in 1898 was a pinnacle event for anthropology thanks to Haddon's penchant for meticulous detail and scholarship. Haddon's published accounts of the expedition demonstrated the importance of attending to cultural edifices as a whole rather than observing aspects such as religion and ritual in isolation (Richards, 1932). This ideology was soon pushed into the doctrine of social anthropology as "participant observation" through the work of Bronisław Malinowski, who asserted that cultures are to be wholly understood through contact and observation of daily life (Malinowski, 1920). Soon, American anthropology, led by Franz Boas, began to unravel social evolution from biological evolution, in which Boas stated that all humans had the same intellectual capacity and that this was the basis for all human culture (Boas, 1911). Ethnography could finally come to understand cultural systems as the suite of cognitive and behavioral adaptations to the myriad of social and environmental pressures, including subsistence, rather than how these were emblematic of cognitive deficiencies (Firth, 1934).

The work of F.L.S. Bell (1931) and Audrey I. Richards (1932) independently demonstrated that diet is not merely biological, but that the social structure and bonds of family and community are tied to food (Bell, 1931; Richards, 1932). Thus, anthropology rounded another pivotal theoretical premise in the study of diet, that understanding society required an understanding of its subsistence. Soon, the recognition of diet as a powerful evolutionary force necessarily penetrated the interpretive strategies of paleoanthropology. In order to describe and differentiate rapidly emerging hominid fossils, especially on the basis of cranial morphological features in a single specimen, dietary behavior must be invoked (Pilbeam and Gould, 1974). Therefore, dietary ecology research is also ancillary to the needs of paleoanthropologists (Teaford and Ungar, 2000). In the landmark "Man the Hunter" symposium at the 1966 Conference on Hunting and Gathering Societies, influential researchers of that time brought forward a comprehensive dialog about how ethnographic research can inform other areas of anthropology (Devore and Lee, 1968). In both the title and content of the meeting, diet ecology was recognized as the most salient arbiter in the relationship between known and unknown modes of human existence. It was one of the first attempts to bring together anthropology, ethnography, biology, and archaeology under the auspice of establishing a formative theory of subsistence for past humans and societies. Similarly, the sub-discipline of primatology improves our understanding of the niche participation patterns among extant hominoids, and helps us to infer where we might draw the line among extinct hominids for inclusion, or not, in the human family lineage (Isaac, 1978). At the cross-roads of classical social anthropology and a new ecologically motivated mindset, the anthropological and archaeological study of diet in and of itself was thus formally established.

1.3 Why the synthesis of nutrition and anthropology is important

Presently, diet specific studies in anthropology are quite common. Ethnological data and dietary specimens from modern human populations are assembled and assayed to understand the strategic factors that enable a particular mode of human subsistence in a particular region. Archaeology is also a crucial voice towards understanding past dietary behaviors because it provides direct evidence for human activity from ancient remains or deposits that are in anthropogenic association. We live in a time when our Western industrialized modes of subsistence have probably never been more dissimilar to those of our past, the Neolithic farmers or Paleolithic hunter-gatherers, prompting a thrum of academic and public curiosity about the prospects of revisiting these older, more enduring, lifeways. Subsistence impacts diet and health by determining the type foods we eat, how we procure them, and how this affects our overall well-being. Longevity is at a relative peak, but life expectancy for U.S. adults past the age of 60 has only marginally increased in the last 100 years (Arias, 2014). But although we are living longer lives, most people over the age of 60 live with pervasive chronic illness in spite of enormous advances in medicine in the last century (CDC, 2011). It stands in direct contradiction to the fact that we attribute our health and longevity to modern medicine that populations without access to medical care were and are still capable of similarly long lifespans (Hawkes, 2003; Gurven and Kaplan, 2007). One main difference, however, is that while the industrialized West succumbs to noncommunicable diseases and chronic conditions, those in more traditional non-industrial societies are more prone to parasitic or infectious disease. In fact, for these individuals, avoiding infectious disease and physical trauma almost guarantees a life unencumbered by obesity, diabetes, cancer, cardiovascular disease, stroke, or Alzheimer's disease. Instead, a natural senescence eventually concludes their life, something only experienced by less than a quarter of U.S. adults over the age of 65 (WHO, 2011).

The fact that advance in modern medicine parallels an increasing burden of chronic illness in Western society has not escaped public notice, and whether by fad or genuine concern, people are increasingly turning to diet and lifestyle interventions. One of the more popular and increasingly pervasive trends is to emulate ancestral human diets, presumably and arbitrarily targeting the

Paleolithic era, which is supposedly informed by the fertile fields of anthropological research. Though the accuracy of scientific research that is distilled into the public arena certainly leaves much to be desired, there is no doubt now that the world is listening, and anthropology stands to become a potent informant of human health policy for years to come. Therefore, dietary research in anthropology is necessarily an umbrella for nutritional science. Anthropologists should respond by developing and executing research that can unravel the cultural, ecological, and physiological factors that impinge our understanding of how food affects growth, development, and reproduction. We can reduce the complexity by eschewing major technological advances to food production and processing and focus on the technologically simpler subsistence practices of the few remaining hunter-gatherers, subsistence farmers, horticulturists, and pastoralists. Even further, we can develop models of ancient human and hominin ecology by retracing the developmental underpinnings of our own modern physiology and disease etiology.

Throughout my research that is described in the following chapters, I was mindful of the historical trajectory of anthropology and nutritional science, if only to help make my contribution more broadly applicable to both fields. While my work has been largely proof-of-principle, it does open theoretical avenues to future research that can build a more deductive knowledge base for the complex story of what human ancestors ate, how they ate it, and whether this related to the events that made us human.

1.4 The importance and contribution of plant foods to the human diet in evolution

Understanding the dietary ecology of ancient hominins, which accounts for both behavioral and physiological parameters, is a difficult prospect. The main hurdle is the need for preserved material that unambiguously associates with anthropogenic activity and that also informs about dietary or ecological conditions. However, the circumstance of these two requirements, namely preservation, unfortunately leads to a bias in the type information provided by recovered fossil material and artifacts. Specifically, mineralized and inorganic materials from bones and stone tools are found in abundance, whereas organic matter from plants is usually completely degraded or decomposed long before fossilization or imprinting can occur. As a result, the evidence for animal consumption is much better represented than evidence for plant consumption. Therefore, it has been the objective of the Plant Foods Research Group at Max Planck Institute for Evolutionary Anthropology (MPI-EVA) to develop novel investigations specifically aimed at reconstructing the dietary habits relating to plant food consumption and ecology of early humans and human ancestors. In this endeavor, the group has undertaken three main investigative strategies that work from opposite but complementary angles towards a central goal of understanding the role played by plant foods in hominin evolution: 1. Recovery of plant microfossils and artifacts that give direct evidence of anthropogenic plant use and ancient environments; 2. Modeling technology, behavior, and physiology using extant hunter-gatherers as a proxy for Paleolithic human lifestyles; and 3. Exploring new methods or novel application of existing techniques that are sensitive to "invisible" evidence such as organic residues, DNA, and isotopic signatures. As a member of the Plant Foods Group, my research falls mainly in line with the second strategy, which is to model the digestive physiology and plant cooking techniques of the Hadza hunter-gatherers of Tanzania. However, as part of studying digestive physiology, my work bisects the third of these strategies with a study of the composition and function of the Hadza gut microbiota, effectively incorporating the new field of microbiome research within the anthropological study of the relationship between human physiology and diet. In the following paragraphs, I give an overview of what we currently know about the study of plant foods in the human diet throughout evolution. The first sections focus on the plant food ecology of modern human hunter-gatherers in different parts of the world, as well as that of extant great apes. In the following section, I incorporate information about archaeological evidence for ancient hominin plant food ecology, focusing especially on the East African fossil hominins and ecological evolutionary context. The final section describes what we know about the nutritional value of plant foods as it relates to human nutritional requirements. These requirements are driven by physiological constraints on brain growth and energy allocation, especially in more derived members of *Homo*.

1.4.1 Plants in the diets of extant great apes

Humans are a derived ape whose history extends far back in time with the origin of Hominoidea, roughly 35 million years ago. Much of what we can discern about the original ape diet comes from tooth-wear analysis, and is highly suggestive of frugivory (Teaford et al., 1996). Furthermore, the folivorous and frugivorous diets of extant great apes and the considerable evidence for various plant-based diet regimes among the australopiths (Teaford and Ungar, 2000; Hohmann, 2009; Ungar and Sponheimer, 2011) makes it fairly assured that humans are an omnivorous ape derived from a deeply herbivorous ancestral past (Milton, 1999).

Most modern non-human primates (herein referred to simply as 'primates') are technically omnivores, taking advantage of food resources from more than one trophic level, but within that classification are a wide-range of strategies to meet a similar suite of nutritional needs (Milton, 1987). The difference in feeding strategy among primates mainly depends on digestive capacity of the gut, niche selection, body size, and sociality (Hohmann, 2009). However, extant primates are neither pure carnivores nor strict herbivores. Instead, primates have diversified to exploit mostly arboreal forest resources such as fruits, nuts, seeds, young leaves, flowers, and small mammals or invertebrates, but also occasionally terrestrial resources such as tubers or honey. Some small-bodied primates (members of *Loris*, *Tarsius* and *Galagos*) are an exception and feed almost exclusively on insects. Perhaps this insectivorous adaptation is dimly reminiscent of the ancestral mammalian precursor to all primates, but regardless, it serves as a good reminder that the diet composition and niche radiation of primates is surprisingly diverse (Milton, 1987; Hohmann, 2009).

As forest feeders that almost universally target fruits and leaves of dicotyledonous plants, most extant primates, including the Anthropoideae great apes – gorillas, chimpanzees, and orangutans – have a C_3 isotopic signature. The C_3 designation refers to the process of single carbon fixation during photosynthesis from CO_2 into 3-phosphoglycerate in most dicot herbs and trees, while C4 plants fix atmospheric carbon initially into 4-carbon organic acids before continuing on with the Calvin cycle (Grine et al., 2012). As expected, $\delta^{13}C$ values (the difference of the $^{13}C/^{12}C$ ratio from an international standard) for both New World monkeys and Old World apes are highly depleted, falling in range with environmental canopy or forest flora (~ between -31‰ and -23‰) (Schoeninger et al., 1997, 1999; Oelze et al., 2011; Fahy et al., 2013). Early hominins however deviate from the fruit and leaf-eater pattern and consistently present a stronger C_4 signature, indicating both a mixed C_3/C_4 diet and one that increasingly specialized in C_4 resources (Ungar and Sponheimer, 2011; Sponheimer et al., 2013). As a result, the earlier and especially robust hominins appear curiously similar to a grazer isotopic profile (Schoeninger et al., 1999; Cerling et al., 2013). This evidence certainly indicates a resource shift from the tropical forest foods, favored by extant African apes, to those of mixed grassland or semideciduous woodlands. It is unknown to what extent these C_4 signatures signify exploitation of grasses, sedges, or underground storage organs (USOs) by early hominins, but dietary and isotopic information from the gelada baboon (*Papio spp.*), savanna chimpanzee, and African mole rat provide support for diets consisting of candidate C_4 roots, grass seeds, gums, flowers, leaves, fruit, or even termites (Schoeninger et al., 1999; Peters and Vogel, 2005; Sponheimer et al., 2005; Yeakel et al., 2007; Cerling et al., 2013). Yet, only one of the robust australopithecine forms, *Paranthropus boisei*, seems to have even approached a near 100% C_4 based diet (Ungar and Sponheimer, 2011; Sponheimer et al., 2013), owing in large part to extreme masticatory adaptations, perhaps for grinding sedges, grasses, and seeds.

1.4.2 Plants in the diets of contemporary hunter-gatherers

Human diets today are mostly sustained by plant food staple crops and their derivatives (Fuller, 2007; Khoury et al., 2014), though these are primarily from monocot grass seeds that require extensive processing to be edible. As Richard B. Lee concluded in, ironically, “Man the Hunter” (1968), the cumulative picture of the human diet among extant hunter-gatherers based on a variety of ethnographic accounts is thus; over the long-term, gathered plant and marine resources are far more contributive to daily calories than hunted game animals (Lee, 1968; Kelly, 1995). When considered in broad view, a logical pattern comes to light in which hunter-gatherer diets tend to be centered on the routinely available and reliable resources. Such resources typically exclude hunted game meat, for which return rates can vary seasonally, geographically, or in other unpredictable ways (O'Connell et al., 2002). Despite the title, one of the major initiatives that sprung to life as a result of the preeminent 'Man the Hunter' conference was to codify women's contributions in a foraging society by analyzing the collection and distribution of plant foods. However, swapping one narrow ideology for another is missing the point that an inclusive rather than hard-lined interpretive approach is necessary to accurately characterize human dietary ecologies. Some work has since made in-roads towards improving our resolution of hunter-gatherer subsistence strategies, but we are still a long way from making sound predictions about diet and social organization of Pleistocene human ancestors across their expanse of occupied ecological zones (Kelly, 1995).

Contemporary full-time subsistence by way of hunting and gathering has almost completely vanished. Aside from a handful of isolated villages in the impenetrable Amazon rain forest, aboriginal inhabitants of the Andaman Islands, and a few ephemeral foraging camps who self-identify as part of larger, well-known, mixed-subsistence, ethnic groups (meta-populations), most hunter-gatherer societies have had to shed their traditional "aboriginal affluence" (Sahlins, 1968). These groups have thus adopted a more cosmopolitan mode of existence, often relying on government rations, trade, and tourism to offset displacement from their original habitats and economies. The Hadza of Tanzania, the group with whom I worked, are likely one of the only remaining full-time hunter-gatherer societies known today (Marlowe, 2010). The last handful of primarily foraging groups profiled in Man the Hunter (Lee and DeVore, 1969) and in the Ethnographic Atlas (Murdock, 1967), namely the Ache, Agta, Efe, Hiwi, !Kung, Mikea, Tsimane, and others listed in Table 9 of Lee (1968), eventually succumbed to a final spurt of encroachment that removed them from the already marginal territories they occupied. Displacement from their traditional territories effectively terminated their traditional means of subsistence. The lasting result has meant a compression of world-wide foraging populations to essentially two or three groups that still supply the majority of their diet from wild foods. In fact, the ethnographic lists accumulated by Lee (1968) and Murdock (1967) were already more of a historical archive rather than a modern reference at their time of publication. Indeed, many of the entries were societies who no longer engaged in full-time hunting and gathering (having been long ago relocated, settled, and provisioned), or who had already vanished (Kelly, 1995). Consideration of this discrepancy in the primary ethnographic collation of hunter-gatherer societies leads to the realization that post-hoc and observer bias is impossible to escape. Nevertheless, these records are the sole legacy of original first-hand accounts of contemporary traditional communities and their subsistence strategies that at one time existed across all major occupied continental regions (Europe excluded): North and South America, Africa, Siberia, continental and oceanic Asia, and Australia.

The stereotyped hunter-gatherer society, inspired by R.B. Lee's description of the Kalahari Bushmen (Lee, 1968), rests on the image of a highly mobile, non-territorial, materially indifferent, egalitarian group, which is banded together in a harmonious male-female partnership driven by the relative parity in the perceived value of men's and women's labor. Although this sounds endearingly "noble savage", it is accurate to the extent that most hunter-gatherer societies are usually organized by a split between the activities of men and women, utilizing sexual division of labor for the procurement and handling of food, with some notable exceptions (Estioko-Griffin and Griffin, 1981). While there is a large degree of variability, the division of labor matches a biological constraint in which, for women, the burden of reproduction is greater than for men (Trivers, 1972; Hawkes, 1996; Bird, 1999). Therefore, women's foraging activities to acquire plants and occasionally small game are more accommodating to the constraints imposed by pregnancy and infant care. Thus, tracing the labor and activity of women in hunter-gatherer societies is usually a good proxy for the overall group reliance on plant food resources (Isaac, 1978; Hurtado et al., 1985; Hawkes et al., 1989).

The environment is highly predictive of gross foraging strategy and general trends become apparent based on temperature, biomass, rainfall, and territory size patterns. As the effective temperature (a predictive measure of solar radiation and its distribution) increases, so too does the percent of food derived from plants (Kelly, 1995; Binford, 2001), however, a discrepancy exists depending on whether measurements were made based on kilograms of wet weight brought to camp or on kilocalories consumed. Put another way, male contribution to the diet decreases linearly as effective temperature increases. Following this pattern, several well documented African hunter-gatherer groups, including Hadza, Efe, G/wi, Ju/'hoansi, Baka, Mbuti, Gwi, and Dorobo, are cited as having obtained their primary subsistence from gathering [plants – but this is not necessarily independent of small animal resources], often upwards of 70 or 80% of total subsistence (Lee, 1968; Woodburn, 1968; Hart and Hart, 1986; Kelly, 1995; Dounias, 2001). The distribution of solar radiation is in part related to the amount of primary biomass that an environment is capable of producing, and is a significant factor in the energy investment strategy of the vegetation, and by extension, the foraging strategy of resident humans. In high biomass production zones (a function of the effective temperature and total rainfall), plants invest in producing and maintaining structural tissues such as leaves and stems, which are low quality foods. However, in areas of low primary biomass, plants divert solar energy to the production of reproductive tissues such as nuts and seeds and to storage organs such as tubers (Andersen, 1987). Therefore, primary biomass production is counter-intuitively inversely related to the abundance of human consumable plant resources (Kelly, 1995).

The "wild yam question" (Headland, 1987), which asked whether human populations living in a tropical rainforest ecosystem were sustainable prior to agriculture, encapsulates one of the major dilemmas of human subsistence in high primary biomass zones; namely that the edible vegetation may be too low-quality and energy-poor to sustain a large-bodied and large-brained hominin (Leonard et al., 2003). The viability of high-biomass zones for an encephalized hominin may have only been possible after a certain technological threshold was reached, or through intensive exploitation of higher trophic-level resources. This is seemingly consistent with the ethnographic accounts of the traditional subsistence patterns of tropical-forest hunter-gatherers. These groups reportedly relied, to varying degrees, on agricultural products, horticulture, or intensive hunting and fishing as a supplement to pure foraging of wild plant foods, as many groups still do today. Examples span world-wide equatorial tropical forests, including groups such as the Ache [high hunting return rates (Hill et al., 1987)], Mbuti [heavy reliance on agriculture (Hart and Hart, 1986)], Baka [paracultivation (Dounias, 2001)], Aka [heavy reliance on hunting (Bahuchet, 1999)], Hiwi [stable reliance on hunting but with extreme seasonality of net incoming energy (Hurtado and Hill, 1990)], Yanomamo [use of gardens and agriculture (Lizot, 1977)], Matses [intensive hunting and horticulture (Morelli, 2013)], and Agta [male and female hunting (Estioko-Griffin and Griffin, 1981)]. If the implications of the wild yam question can be trusted, as the evidence implies, then niche diversification from tropical forests to more open woodland or savanna-mosaic ecosystems may have offered an immediate upgrade in the diet quality for our early herbivorous ape ancestors. Therefore, arid environments with high effective temperatures, such as the East African savanna-mosaic Rift Valley ecosystem and the more southern Kalahari Desert, may have paradoxically been better suited for hungry large-brained hominins (and modern humans) subsisting chiefly on plant foods. Curiously, the known geographical distributions of early australopiths and members of *Homo* encompass these key areas in Eastern and Southern Africa. Therefore, the human lineage likely experienced a long evolutionary gestation in relatively arid, high-temperature, and low primary-biomass zones where plants are ideally suited to provide for the majority of subsistence. The coalescence of archaeological as well as ethnographic evidence presents an extremely compelling argument that plants have long occupied a central place in the human diet and were implicit within the circumstances that promoted hominin encephalization.

1.4.3 Archaeological evidence for plant food consumption by humans

The archaeological evidence for plant food consumption in prehistory has improved substantially just in the last decade of research. Prior to the more recently established interrogation of dental calculus from archaeological remains, Paleolithic plant consumption was difficult to determine because most plant organic material simply does not preserve well. Occasionally, an archaeological golden ticket appears, treating our investigative palates to the barest taste of information about ancient plant use, such as rock art drawings of plants (Welch, 2003). Some sites have, in fact, contained preserved macrobotanical remains such as seeds and legumes, which give direct evidence of the types of plants targeted by early humans (Lev et al., 2005). These tiny glimpses portend an unimaginably deep well of botanical cultural knowledge hidden beneath our scant superficial awareness (Hardy et al., 2012). Yet the evidence offers little means for an empirically or quantitatively driven experimental approach. Plant microfossils and microremains such as pollen, phytoliths, and starches, however, are more resistant to degradation, preserve over very long times (Prasad et al. 2005), and can provide reliable indicators about ancient environment and diet (Piperno, 1995, 2006; Henry and Piperno, 2008; Henry et al., 2014). I focus the following discussion on starch and phytolith recovery since these two microremains more directly inform about plant use for consumption. Starches are semi-crystalline structures composed of amylose and amylopectin, which are long-chain polymers of glucose, and are used by plants to store energy (Hoover, 2001). Starches and starch containing plant parts, such as USOs, are direct sources of food for humans, and their presence in archaeological remains is usually attributed to food. Phytoliths are the silica bodied metabolic by-products found in plant structural tissue, produced from monosilicic acid-rich water drawn from the soil by plant root systems, and are useful for paleoenvironment reconstructions (Piperno, 1988; Hunt et al., 2008). However, information from plant microfossils about the diet and environment is still biased by the fact that only some plants are starch or phytolith producing, and the presence of these microremains would lead to very different inferences about plant use: phytoliths are only found in the structural plant tissues, which are not typically consumed, whereas starches are found in the non-structural reproductive or storage tissues most highly prized for food. Starches from ancient wild plants have been found on grinding stones recovered in a number of Mid-Upper Paleolithic sites, evidencing that plant processing technology was widespread across Northeastern Europe and the Mediterranean (Revedin et al., 2010). These findings suggest that grinding, such as for making flour, was already common practice in the Paleolithic, and hints at a much earlier origin for the technological refinement of plant foods for human consumption, perhaps even prior to the first wave of human migrations out of Africa (Stahl, 1984; Wrangham and Conklin-Brittain, 2003; Organ et al., 2011).

Improving analytical techniques to detect plant microremains (including starches, phytoliths, and pollen) and residues (fatty acids and aromatic compounds) has successfully brought archaeology into the next research frontier. What began as a histological basis for identification of microremains embedded in dental calculus (Henry et al., 2011, 2014; Power et al., 2014), has transformed into a technically complex workflow designed to maximize the capture of dietary and environmental information that can be inferred both from foreign (trapped food particles, residue, DNA and microorganisms) and endemic (digestive and immunological proteins) artifacts (Salazar-García et al., 2013; Warinner et al., 2014, 2015; Hardy et al., 2015). The prospects of what we will learn from these new techniques are tantalizing. In essence, we finally have the ability to detect "invisible" preservation that may inform about plant food ecology to a degree that is eventually commensurate with our knowledge about ancient animal resource use.

Aside from the rare fortuitous preservation of macrobotanical remains and the more recent exploration of plant microremains, tooth microwear analysis has been one of the most fruitful investigative endeavors for inferring about the diets of early hominins. Tooth microwear analysis is the morphological observation and quantitation of microscopic marks left by food or use wear on the teeth (and the shape of the teeth themselves), such as pits, abrasions, scratches, and striations (Teaford and Walker, 1984; Grine and Kay, 1988). The type of mark and patterning is directly related to oral processing, either from diet, tool-making, or some other type of abrasive wearing imposed on the dentition. Material properties of plant foods inflict pronounced and often diagnostic macro- and microwear on teeth, which along with tooth size, shape, and enamel thickness, signal important dietary adaptations to particular food properties (Daegling and Grine, 1999; Teaford and Ungar, 2000). To briefly summarize this immense body of work, it is understood that Australopithecines had fairly selective diets, unlike the late Miocene apes, but with a suite of dental characteristics that were well suited to gallery forest and grassland resources (Teaford and Ungar, 2000). These species most likely focused on soft fruits, seeds, some abrasive foods requiring incisoral stripping (possibly tubers with bark-like peridermal tissue), and hard but brittle foods such as nuts and corms (Dominy et al., 2008; Grine et al., 2012). The especially powerful combination of stable isotope and dental microwear analysis further supports the notion that C_4 resources, particularly USOs, were a major factor in the divergence of early hominins from late Miocene apes (Grine et al., 2012; Lee-Thorp et al., 2012). Previous work depicts the East African Pleistocene setting and constituent hominins with the following conclusions: an expansion of arid savanna-mosaic environments gave rise to prolific USO producing habitats (Vincent, 1985; Cerling, 1992), while contemporaneous but divergent mammals acquired comparable C_4 enrichment signatures by presumably targeting mixed C_3/C_4 resources, including USOs (Yeakel et al., 2007), and finally, the complex microwear patterns for Australopithecines fall between the profile of a hard-food and tough-food specialist, implicating a diet requiring some grinding and notably with more brittle components than pure foliage (Ungar and Sponheimer, 2011). Furthermore, since USOs are a universally important component of early and modern human diets, the most parsimonious explanation is that this behavior is a relic of the continued pattern of USO exploitation by later *Homo* in savanna-mosaic habitats, including wetlands. This also happens to be supported by mounting evidence that arid and lacustrine habitats were the key areas that could nutritionally support hominin brain growth, owing to the abundance of hydrophilic sedge and small fauna associated with these environments (Laden and Wrangham, 2005; Braun et al., 2010; Organ et al., 2011; Dominy, 2012; Zink et al., 2014). In sum, the evidence weighs heavily in favor of the significant role that plant foods have played, particularly USOs, throughout human evolution.

1.4.4 Nutritional value of plants, processing techniques, and human physiology

The expansion of nutritional and immunological research in the wake of the infectious disease/malnutrition synthesis 60 years ago (Keusch, 2003) is mirrored by a similar advancement in genomics and computing of the last decade, both of which worked to reinvigorate research on mammalian physiology. With specific regard to digestive physiology, we can look at effects from the biochemical, to cellular, to multi-cellular and microbiological levels of interaction, which offer exciting venues to test for yet unseen dietary adaptations.

Early work in the 1980's by Katherine Milton on digestive physiology and kinematics in primates (Milton, 1987; Milton and Demment, 1988) was prescient in its recognition that not only is the gut a bottleneck to nutritional acquisition for all mammals, but also that enteric microbiota enhance the nutritional value of resistant foods, even in the relatively unspecialized anthropoid gut. This work set the stage for Aiello and Wheeler's enduring paradigm on gut-brain energetic tradeoffs, termed the expensive tissue hypothesis (Aiello and Wheeler, 1995). Notably, Milton and Demment (1988) found that humans have a similar digestive response to high concentration (10-15%) neutral detergent fiber (NDF) as that of chimpanzees and other extant hominoids, and the ability to degrade cellulose and hemicellulose via fermentation. Several factors affect this process, including rate of passage through the gut, particle size, lignification, food source, and the level of fiber purification from the native food matrix (Cummings, 1984). Humans have experienced a severe reduction in colon volume relative to the other great apes and therefore a greatly reduced capacity to ferment insoluble fiber (Popovich et al., 1997; Milton, 1999). Chimpanzee diets include on average 33.6% fiber (Conklin-Brittain et al., 2002), whereas the minimum recommendations for fiber consumption in modern human diets are only 20-30g, or about 6% of kcals consumed for a 2000 kcal diet (Papazian, 1997). Humans are incapable of rapid passage of ingesta typical of a carnivore-like digestion pattern (Milton, 2000), but do have marginally shorter mean gut transit times than chimpanzees (Milton and Demment, 1988). Digestive rate along with differences in the gut proportions for humans relative to other great apes (high volume small intestine and low volume colon) clearly indicate that the human dietary strategy at some point shifted away from processing copious amounts of low-quality fibrous plant foods, and instead focused on high quality, easily digestible foods. Presumably, much like today, early humans and hominins were able to utilize sophisticated food processing techniques to initiate an "externalized" digestive phase, as well as target high energy fruits, USOs, nuts, meat, and possibly honey (Crittenden, 2011). Humans and great apes collectively are inefficient degraders of highly lignified foods that have a greater cellulose-to-hemicellulose ratio such as monocot cereal fibers or plant fibers. Instead, relatively unlignified fiber from dicot vegetables, such as from cabbage or carrots, are more compatible with hominoid digestive physiology and gut microbiota (Milton, 1999). Even the fecal microbiota from the ape grazer specialist, *Papio spp.* (baboons), seems to be no better than human gut microbiota at fermenting grass-derived fibers, suggesting that other characteristics such as energetic trade-offs and social structure may enable *Papio* to exploit grassland ecosystems rather than an increased capacity for grass fermentation (Frost et al., 2014). Therefore, a high-breadth plant-based diet must have posed insurmountable barriers to encephalization until sufficient technological innovations for external plant food processing, such as mechanical processing, thermal processing, fermentation, and germination, could enhance the nutritional value of these foods. In fact, use-wear analysis and experiments determined that, of a subsample of 2.0 Ma Oldowan lithics from the Kanjera South site in Kenya, 70% are attributable to plant tissue processing (Lemorini et al., 2014). These results push back our previous estimations of conclusive plant-related tool use by another 1.5 million years, closing in on the putative origin of Oldowan stone tools (Semaw et al., 2003). A decrease in cranial and mandibular robusticity, as well as reductions in the masticatory structures such as mandible size, zygomatic flare, molar size, prognathism, and occlusal relief in early *Homo* all indicate a gracilization process, presumably from reduced reliance on prolonged chewing of tough or hard foods (Teaford et al., 2002). Reduced chewing stress could be the result of targeting softer foods, developing tools and processing technologies, or both. Either way, naturally high-energy yielding plant foods such as nuts, fruits, and USOs are undoubtedly rooted in hominin diet evolutionary history, extending as far back as two million years and likely beyond.

On account of having an extremely large brain relative to body size, humans have notably rigid dietary requirements that are not experienced by the rest of the extant hominoids. In addition to requiring a consistent supply of energy for the brain (either from glucose, ketones, or lactate) (Zilberter et al., 2010), brain growth and maintenance for anatomically modern humans (AMH) is predicated on the availability of several [periodic] elements, such as iron, iodine, selenium, and magnesium, and other complex molecules, such as folate, antioxidants, and omega-3 fatty acids, that are necessary for structural and functional maintenance (Chen and Berry, 2003). Many of these substrates are found exclusively or in sufficient quantities in plants. Wild plants in particular, such as tree nuts and USOs, harbor high quantities of plant oils, starch, protein, and vital micronutrients (Bradbury and Holloway, 1988; Alasalvar and Shahidi, 2008). Furthermore, as a vestige of our deep herbivorous and frugivorous ancestry, humans, like all primates, are incapable of producing vitamin C, and must instead obtain it from plant foods such as fruits or leaves (Milton, 1999).

There is a curious pattern in the relationship between the potential for vitamin toxicity and the primary source of that vitamin in the diet. Vitamins that are found in high abundance in most vegetables typically lack an upper limit for ingestion (which is not necessarily the same as absorption) (Hathcock, 1997). Vitamins that come from primarily animal foods or those that are synthesized into an active form from precursor provitamins, such as vitamins A, D, niacin, B6, folate, selenium, and choline, however, can induce toxicity symptoms from overconsumption (Hathcock, 1997). A logical explanation is that for millions of years, human ancestors consumed large amounts of wild plants for a significant portion of their daily caloric needs, and in the process ingested extremely high quantities of plant-derived vitamins and minerals. Most of these vitamins function as antioxidants and are deficient in today's diet of highly processed and domesticated foods (Milton, 2000). As one of the thirteen essential vitamins, vitamin A is necessary for maintenance of epithelial cells, visual acuity, immune system function, and brain development (Goodman, 1984). Too much vitamin A, though, can induce a toxic and fatal state of hypervitaminosis, as well as cause profound developmental malformations by disrupting patterns of retinoid-induced gene expression in-utero (Lammer et al., 2010). Evidence of chronic hypervitaminosis A is seen in a *Homo erectus* individual known as KNM-ER 1808, and it is believed that acute toxicity eventually resulted in its death (Walker et al., 1982). Preformed vitamin A, called retinol, is physiologically active, potentially toxic, and found in high concentration in animal liver, especially that of carnivores. However, provitamin A, which is the carotenoid precursor to retinol (primarily betacarotenes), is found instead in plant foods and can be used by the body to manufacture the active vitamin. There is no designated upper limit to the consumption of carotenoids, while an excess of 100,000 IU of retinol can induce acute toxicity (Hathcock et al., 1990). Therefore, plant foods have probably adequately supplied the human need for precursor provitamin A over millions of years of evolution, and did so without the danger of hypervitaminosis due to the physiological control over retinol conversion.

Plants resist consumption through a variety of mechanical and chemical means, such as with protective peridermal tissue, resistant fibrous parenchymatous tissue, or through secondary compounds called "antinutrients" (Johns, 1996). Curiously, extant human foragers tend to eschew above-ground, tannin rich, leafy green plant parts in favor of the plant root systems that are vital energy and micronutrient reservoirs. Not only are roots a nutritionally rich resource, but their defense against consumers is often purely physical (residing deep underground or covered in thick peridermal tissue). In fact, a survey of edible USO-bearing plants concluded that at least 65% of species from savanna areas are reportedly consumed raw, compared with only 9% of tropical rainforest plants (Laden and Wrangham, 2005). When chemical toxins or anti-nutrients do appear in edible roots, such as alkaloids, saponins, raphides, glycosides, and enzyme inhibitors (cholinesterase inhibitors and protease inhibitors), they are easily deactivated by simple thermal or mechanical processing (Stahl, 1984; Johns, 1996).

Low nutritional bioavailability, an abundance of antinutrients, and an imbalance in the concentration of certain essential nutrients makes purely vegetarian diets sometimes problematic for modern humans. This is especially so when the diet is dominated by intensively farmed staple monocrops such as maize, wheat, rice, soy, cassava, potatoes, sorghum, and millet, and less inclusive of diverse plant species or wild foods (Eaton and Konner, 1985). In some cases, simply eating a wide variety of plant foods enables the consumer to overcome the burden of anti-nutrients or meet nutritional needs, and is the typical strategy of most non-human primates (Hohmann, 2009). However, humans in particular have adopted advanced processing technologies, considered by some to be biologically essential (Wrangham and Conklin-Brittain, 2003), to mitigate or deactivate antinutrients, while at the same time enhancing nutritional absorption and energy acquisition. Control of fire for use in cooking is undoubtedly a significant consumer advantage because it enables dietary niche expansion, and is proposed to be the catalyst for phylogenetic rate shifts in feeding time between early *Homo* (*H. habilis* and *H. rudolfensis*) and *H. erectus* (Organ et al., 2011). The advantage is three-fold: 1) humans are spared the physiological burden required of detoxification by the liver and kidneys and can thus funnel more resources to other metabolically expensive tissues like the brain, 2) dietary breadth and flexibility is increased by technology, which promotes niche diversification, and 3) environmental buffering using technology unshackles adaptation from the meandering processes of natural selection, thus sparing the need for genetic changes to occur. Additionally, technologies, unlike genetic traits, are highly transmissible, broadly applicable, and do not constrain an organism to genetic specializations or fixations that may be maladaptive in a different environment. Regardless of the importance of animal foods in the human diet, the near endless iterations of culturally and environmentally specific processing techniques for plant foods is a testament to the rich and vital history that plants have played throughout human evolution and migration. Therefore, plant processing technology was likely a great ecological leveler in the adaptive radiation of humans across highly variable environments, quite possibly unlocking the gateway to global colonization.

1.4.5 Concluding remarks

The material presented in this cross-sectional overview of scholarly work in the arena of diet in human evolution has hopefully provided ample evidence for the importance of plant foods in past and present human diets. The results of research from wide ranging fields such as ethnography, primatology, archaeology, and human biology, are surprisingly concordant in reinforcing the notion that plant foods made a significant contribution to human evolution. The research described within this thesis has thus endeavored to open and contribute to the well-established yet under-appreciated discourse about whether plant foods stand in parity with meat as catalysts in the genesis of the human lineage. Importantly, this work attempts to bridge past and present research by focusing on the biological relevance and limitations involved with plant food nutrition and human physiology.

1.5 Theoretical background to the central thesis

The following chapters entail three discreet project papers united by a common theme to understand the nutritional contribution of plant foods in the human diet. The core subject matter revolves around the dietary ecology of Hadza hunter-gatherers from Tanzania. The Hadza are powerful informants for the adaptive strategies of a foraging human population in the East African savanna-mosaic environment, however they are just one example amongst the myriad of past and present human populations. The conclusions we can draw from work with the Hadza are still no less valuable. We gain insight about the necessary depth of behavioral or physiological specializations that must coincide with a human hunter-gatherer subsistence on wild foods using a basic level of technology – our best present-day representation of what human life may have been like for African Paleolithic hunter-gatherers (Marlowe, 2010).

The Hadza are a tribe of people living around Lake Eyasi in northwestern Tanzania, of which approximately 200-300 members still live exclusively by hunting and gathering (Marlowe, 2010). Bush camps comprise usually between five to 30 people throughout the year, and camp membership and location is fluid. Labor is divided amongst men and women where the men hunt game meat and obtain wild honeycomb while the women mainly dig for tubers or collect baobab fruit. When in season, berries are collected by all members of the camps. Hunters use bow and arrows with poison tips or axes to obtain the foods they target, and the women fashion a digging stick out of long brush, which is tapered to a fire-hardened point. The dominant foods in their diet fall into five main categories: meat, berries, honey, baobab, and tubers. Of these foods, tubers stand out as the most consistently available and consumed food resource, with several edible species known and targeted.

Image 1. Hadza women, from young mother to elder grandmother, dig for tubers in the morning while younger children look on.

Tubers, or more generally, underground storage organs (USOs) are central to key theories about hominin evolution and brain growth (Laden and Wrangham, 2005); most notably the grandmothering hypothesis posited by Hawkes and O'Connell (Hawkes et al., 1998) and the cooking hypothesis championed by Richard Wrangham (Wrangham et al., 1999). USOs are also staple foods for many modern populations throughout the world (Oke, 1990), and it stands to reason that these resources have been exploited by human groups for a very long time. Many favorable qualities of USOs lend great support to this concept. Such qualities include: a high nutritional content in the form of vitamins, minerals, and carbohydrates (Finglas and Faulks, 1984; Bradbury and Holloway, 1988); the hidden and protected nature of their below-ground location, thus reducing competition with other species for access (Coursey, 1976; Vincent, 1985); a widespread growth across diverse ecosystems (Vincent, 1985);

an often high moisture value (Schoeninger et al., 2001; Schoeninger and Bunn, 2009); and finally, that their acquisition by women, unlike game meat, is possible even with the burden of pregnancy and lactation (O'Dea, 1991; Hawkes, 1996). The USOs targeted by Hadza are all technically root tubers, which are lateral enlargements of the root that store nutrients during plant inactivity, and so I will refer to Hadza USO's as tubers throughout this text.

Image 2. Collection of three different species of tuber by Hadza women in one morning's forage.

Under the premise of the cooking hypothesis, which says that cooking foods made nutrients more readily available to human ancestors and fostered the rapid brain growth seen at a transitional period approximately 2.5 million years ago coincident with emergence of *Homo erectus* (Carmody and Wrangham, 2009; Organ et al., 2011), cooked tubers should be especially more nutritious than uncooked tubers. Heat reduces the physical structure of complex nutritional and structural components of plants, including starch, inulin, cellulose, and arabinoxylans (Kakade and Liener, 1973; Stahl, 1984). Of note is the effect of heat and moisture on semi-crystalline starch grains, which are polymers of amylose and amylopectin. Heating beyond a certain temperature, typically ≥50-60° C, in the presence of moisture reduces the integrity of the semi-crystalline structure and allows water molecules to enter the starch structure, eventually dissociating its polymers and bursting the granule in a process called gelatinization (Hoover and Vasanthan, 1994). Since gelatinized starch has exposed amylose, this makes it much more susceptible to digestion by amylase enzymes from human saliva or pancreatic fluid (Butterworth et al., 2011). However, critically, whether the gelatinization of starch in tuber foods is the goal of cooking has not previously been tested, it is merely assumed, in the context of various cooking techniques used by modern populations.

1.6 Summary of projects

1.6.1 Brief roasting on starch gelatinization

In my first study I look at the relationship between roasting time and starch gelatinization using an experimental model based on Hadza roasting behavior. Hadza briefly roast tubers directly over a high-flame surface fire, which has been likened to "light roasting" (Tomita, 1966). In this work, I aim to understand the effect of heat application on starch gelatinization in a generalized starchy tuberous food. I model the high-flame fires using an outdoor fire-pit and use this to roast a variety of whole, unmodified, starchy plant organs and record the percent of gelatinized starch in cross-sectioned specimens. The data demonstrate that brief roasting is not adequate for starch gelatinization, implying that this type of cooking serves an alternative purpose. Additionally, my work calls attention to the fact that there are many broad untested assumptions about the roles of cooking across human culture that deserve much more focused examination. Awareness of the simple fact that "cooking" is a blanket term for an incalculable number of methods should also encourage stricter delineations in future studies to specify crucial details such as time, temperature, and technique. Otherwise, results can have no bearing or interpretive power on the topic of the effect of cooking in changing food properties and how this modulates human biology.

1.6.2 Bioaccessibility of Hadza tubers

Pursuing this further, the next logical step towards understanding the contribution of plant foods, and specifically Hadza tubers, to human nutritional requirements is to quantify exactly how much of these foods are absorbed by the gut. This is termed the bioactive, bioavailable or bioaccessible fraction of a food, and is an important metric for ranking the actual biological value of a food resource. While nutritional composition work can tell us the potential contribution, it is not able to account for the resistant, refractory, and inaccessible components. Therefore, bioaccessibility is an especially important evaluation for plant foods, particularly tubers, which can contain a high proportion of fibers and anti-nutrients. The second paper chapter depicts a study to measure the bioaccessibility of glucose in four species of Hadza tuber, collected by the author in cooperation with Hadza women, using a dynamic *in-vitro* model of the stomach and small intestine. The results show that tubers are especially resistant to digestion, and that brief roasting does not appreciably affect absorption. The conclusions offer insight not only about the importance of forager strategy in finding the highest quality resources, but also suggest that low bioaccessibility might be overcome by the sheer abundance of tuber resources across the foraging landscape.

1.6.3 Contributions of Hadza gut microbiota to nutritional acquisition

The last paper chapter in this manuscript entails a slightly different topic and approach, but with the same end goal of understanding how plant foods can contribute to human nutritional needs. In the course of digestion, food particles that are not absorbed in the small intestine enter the colon, and once there, digestion is continued by the trillions of co-resident microorganisms, collectively referred to as the gut microbiota. Earlier work established that commensal bacteria in the human gut can specialize in the breakdown of resistant polysaccharides, and that the metabolic products of this fermentation (namely short chain fatty acid but also other essential compounds) can be a source of energy used by the host (den Besten et al., 2013). Therefore, the gut microbiota contribute, in a secondary fashion, to host metabolism. The findings of Hehemann et al. (2010) showed that horizontal gene transfer from environmental bacteria to enteric bacteria provided the gut microbiota of some Japanese the ability to efficiently breakdown raw seaweed regularly consumed as a part of the traditional diet (Hehemann et al., 2010). This proof of concept study was formative to my initial interest about the potency of the gut microbiota to assist in human digestion of refractory foods and facilitate nutritional acquisition throughout human evolution. These are not new ideas, and with the inception of the National Institutes of Health (NIH) funded Human Microbiome Project in 2008, many scientists have recognized that humans and their resident microbiota form a kind of supraorganism with a collective hologenome (Turnbaugh et al., 2007; Zilber-Rosenberg and Rosenberg, 2008). When comparing the number of human cells to the number of microbial cells, the difference is an order of magnitude in favor of the microbiota. However, when comparing genomic information, the disparity propels beyond our comprehension at a factor of 150 times more unique bacterial genes than human genes (~3,300,000 versus 22,000) (Gill et al., 2006; Warinner et al., 2015). Therefore, our microbial partners are an extra-somatic means of both functional activity and evolutionary selection. In order to begin to understand the microbial landscape, the first task is to assess “who” is present, or in other words, analyze the phylogenetic diversity and taxonomic profile of the microbiome. I hypothesized that the gut microbiota have a major role in the digestive physiology of the Hadza, especially with their unique diet and status as one of the last remaining truly foraging populations. As a result, I applied for the permission to conduct fecal sampling among the groups I would stay with in Tanzania so that for the first time, the gut microbiome of a human hunter-gatherer population could be identified. The final paper chapter is thus the end product of my original, slightly non-traditional, specimen sampling proposal to study the diet related effects on the gut microbiota of the Hadza hunter-gatherers. With this work, we can begin to understand the plant polysaccharide degradation potential of this enteric ecosystem and demonstrate that colonic activity is also substantially contributive to human health, nutrition, and evolution.

1.7 Description of scholarly contributions to research projects

1.7.1 Brief Roasting on Starch Gelatinization

My role as author of this paper was inclusive at all stages of the work. I developed the main hypothesis and designed the experimental processes with input from my two co-author advisors, A.G. Henry and A.N. Crittenden. I conducted the experimental roasting trials with help and support from the Plant Foods lab group, and carried out all subsequent processing, staining, and histological analysis for the count-based methods. A tailored random coordinate generator was generously created by A. Strauss for this project. For the semi-quantitative analysis of gelatinization kinetics, I developed and executed the methods with initial discussions and training with C. Debono-Spiteri. I performed the data analysis with initial help from R. Mundry to design an appropriate mixed effects model. All subsequent model improvements and additional analyses were conducted independently. The paper was researched and written by me with input and revisions from A.N. Crittenden and A.G. Henry.

1.7.2 Bioaccessibility of Hadza Tubers

Successful completion of this study required two major phases; first a field work component and then a lab component. I helped design the study, which was initially conceptualized by A.G. Henry with significant input from K. Venema and A.N. Crittenden. A.N. Crittenden organized the field work itinerary and logistics and I carried out the acquisition, handling, and transportation of field samples from Tanzania while working with the Hadza. I conducted all sample pre-processing at the MPI Plant Foods lab in Leipzig, Germany independently. Plant Foods group members provided help and support for the roasting trials. I conducted the *in-vitro* digestion trials under the supervision of K. Venema at the TNO Department of Pharmacokinetics and Human Studies in Zeist, NL. The sample aliquots were analyzed for glucose and amino acids by an external specialist. I compiled all results of the trials with help from K. Venema and analyzed the data independently. I wrote and researched the paper with extensive feedback and revisions from A.G. Henry and A.N. Crittenden.

1.7.3 Hadza Gut Microbiota

This project and paper was a multi-disciplinary collaboration with a specialist group in human microbiome studies from the University of Bologna Department of Pharmacy and Biotechnology (Unibo) in Bologna, Italy. I conceived of and designed the project with input from A.G. Henry. M. Candela provided expert oversight and revision of the proposed research design and methods. I conducted fecal sample collections from the Hadza cohort in Tanzania, Africa with oversight and organization by A.N. Crittenden. Italian cohort samples were collected by Unibo and DNA extraction, amplification, and sequencing were carried out by Unibo and members of the Institute of Biomedical Technologies at the Italian National Research Council in Milan, Italy. 16S rDNA reads were curated by S. Rampelli, who also conducted analysis and statistical reporting of results for the beta-diversity and cross-study comparative analyses. I conducted taxonomic assignment and alpha-diversity analysis, as well as analysis of dietary data. Metabolomic analysis was conducted by J. Fiori with Unibo. I co-wrote the paper with M. Candela with extensive discussions, revising, and editing contributed by A.G. Henry and A.N. Crittenden.

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