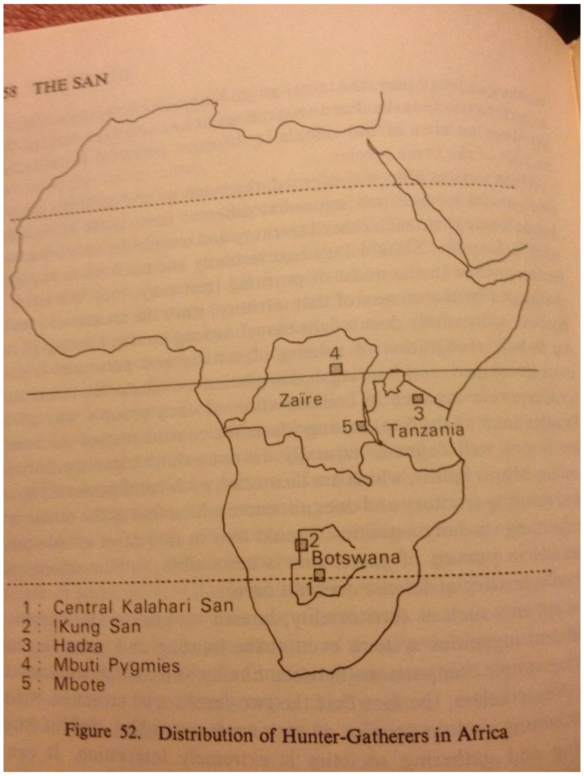
Hunter-Gatherers of Africa-Foodways

Overview of Hunter-Gatherers of Africa



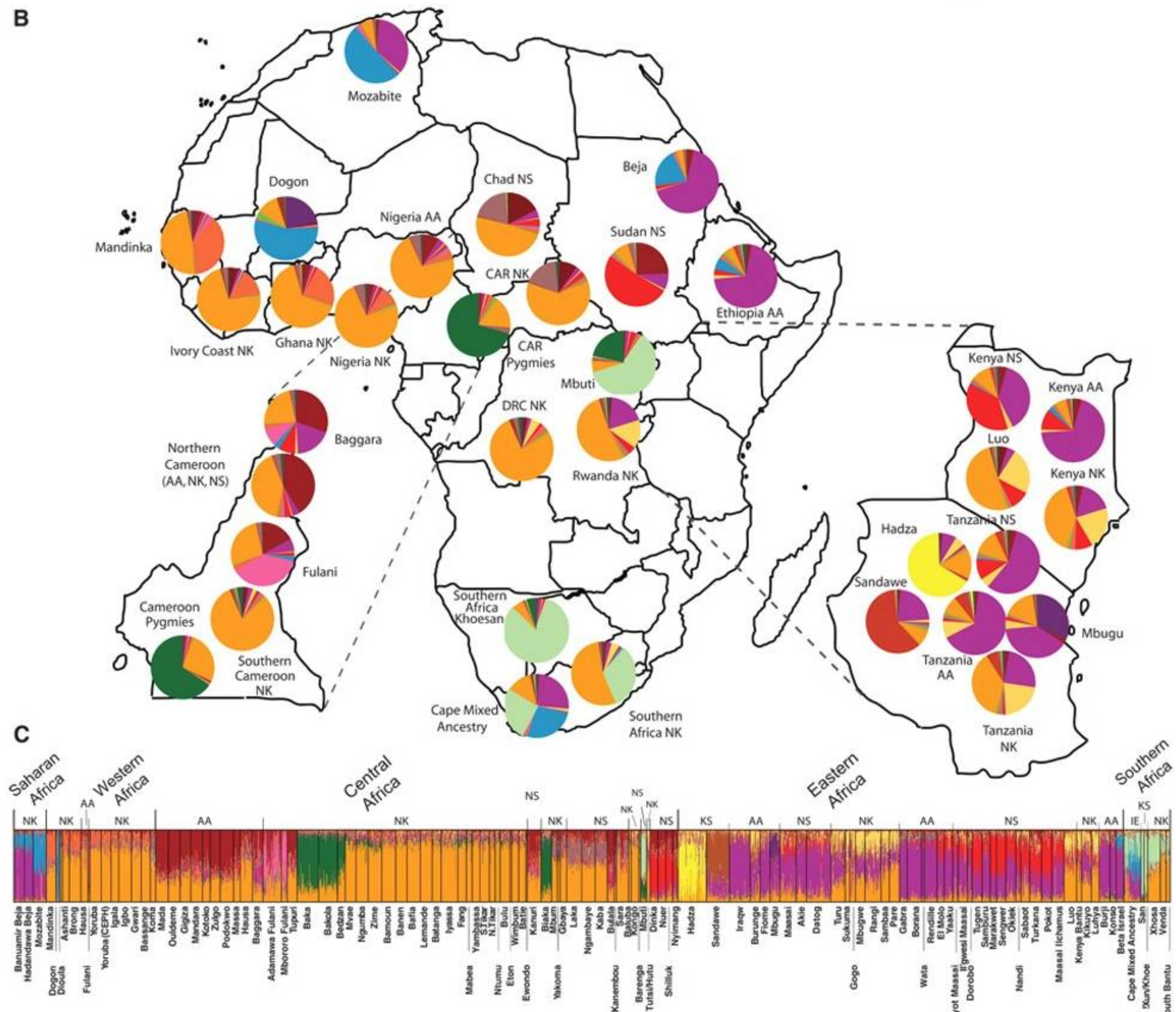
(Tanaka, 1980)(p.158)

Ancestors to modern humans originated in Africa about 200,000 years ago, later spreading across the globe. The long history of humans in Africa has resulted in within-population genetic diversity and more than 2000 distinct ethnolinguistic groups (Tishkoff et al., 2009). The vast majority of the populations of African hunter-gatherers have disappeared in the past 5,000 years through either assimilation into farming and herding groups or by extinction. The only hunter-gatherer groups left include the forest Pygmy populations of central Africa such as the Mbuti, isolated click-speaking populations of Tanzania such as the Hadza, and the San "Bushmen" of the Kalahari Desert region of southern Africa (Henn et al., 2011)(p.5154). All of these groups have ancient genetic lineages.

Hadza People

The Hadza, also known as the Hadzabe, are indigenous to north-central Tanzania and live in the central Rift Valley near Lake Eyasi, which is a salt-water lake that typically dries up during the dry season. This area that is thought to have been inhabited by humans and their hominin ancestors throughout the entire 6 or 7 million years of hominin evolution as evidenced by the many fossils of hominins found there. Fossils of *Paranthropus boisei, Homo habilis*, and *Homo ergaster* were discovered at Olduvai Gorge just 50 km northwest of the Hadza's main region of inhabitance. Even closer at approximately 40 km to the north is the site Laetoli where 3.6 million year old hominin footprints were found. A 130,000 year old skull possibly of the hominin *Homo erectus* was also discovered in the area. While it is unclear how long the Hadza ancestors have inhabited this area, data, including the high density of lithic material and the presence of rock shelters with evidence of consistent occupation, suggest that the Eyasi Basin has continuously been occupied since the Middle Stone Age (280,000 years ago) (Marlowe, 2010)(pp.17-18)(Marlowe, 2002).

The Hadza are unique in that they have maintained genetic and cultural distinctions from other groups (Tishkoff et al., 2009). Genetic data suggest that the Hadza are not closely related to other African populations, and they diverged from a common ancestor with the Sandawe more than 15,000 years ago. This finding is interesting because both the Hadza and Sandawe speak click-based languages, so it was originally thought that these two groups would be closely related genetically. However, some linguists state that the Hadza language is genealogically unrelated to other click languages (Tishkoff et al., 2007). DNA data have revealed 72 significant principal components (PC) of human DNA worldwide, with specific components distinguishing groups. For example, PC1 accounts for 19.5% of variation in humans and distinguishes Africans from non-Africans. Interestingly, PC3 specifically distinguishes Hadza hunter-gatherers from others, accounting for 3.5% of variation. Within Africa, there are 43 significant PCs and the second PC distinguishes the Hadza from other Africans, accounting for 6.1% of variation. Overall, the Hadza are considered genetically distinct from other groups, as indicated by the figure below in which they are the sole constituents of one of the six genetic clusters in Africa (the yellow cluster). All of these data support the idea that the Hadza are not closely, genetically related to other groups (Tishkoff et al., 2007; Tishkoff et al., 2009).



As previously mentioned, the Hadza speak their own language, known as the Hadza language, which is click-based. However, the vast majority of Hadza speak fluent Swahili as their second language, though this is a relatively recent phenomenon, even as recently as 1960 few Hadza spoke Swahili (Marlowe, 2002). Currently, 1200-1300 Hadza people live in Tanzania.

General Societal Structure. The Hadza have no political structure of any kind, at either the camp or tribal level (Marlowe, 2010)(p.40). They are also a strongly egalitarian and individualistic society that promotes independence, making it rather difficult to boss around a Hadza and making them resistant to any rules that might be imposed by chiefs, kings, or presidents (Marlowe, 2010)(p.248)(Berbesque et al., 2012). Both Hadza men and women are encouraged to speak their mind in an independent manner (Marlowe, 2010)(p.172). By being extraordinarily self-reliant, the Hadza are able to form a society relatively free of any sort of social hierarchy. Indeed, while males may practice some level of dominance over females, older adults may be afforded a little more respect, and adults may hold a degree of power over adolescents, these differences in status are marginal compared to other, more complex societies. Importantly, such differences do not affect access to resources (Marlowe, 2010)(p.46). While some Hadza will naturally try to control others, Hadza have been raised to resist or rather just simply avoid domination (Marlowe, 2010)(p.248). Despite promoting independence, there are no specialized roles in the Hadza society. The only dictated roles found within Hadza society arise from the sexual division of labor that assigns hunting to men and foraging to women (Marlowe, 2010)(p.46). Besides these basic specializations between sexes, every Hadza learns how to do everything he or she needs to survive without being dependent upon anyone else. This even applies to medicine so that each adult Hadza has knowledge of what plants to pick for different ailments, requiring no assistance in the form of a shaman or witch doctor (Marlowe, 2010)(p.46).

The Hadza's egalitarian, individualistic society has enable them to resist domination from outside groups, and despite efforts by colonial administrations, the Tanzanian government, and Christian missionaries to make the Hadza embrace farming, leaving their hunting and gathering lifestyle behind, the Hadza continue to live as they have always done (Marlowe, 2010)(pp.32-38).

<u>Side-Note:</u> It is the presence of baboons who are thought to have evolved in the same habitats as the modern day human's hominin ancestors, along with the plentiful supply of archaeological evidence pointing to a consistent hominin presence within this region of Eastern Africa, that makes the Hadza a particularly interesting group of hunter-gatherers to study in the context of human evolution (Berbesque & Marlowe, 2009)(p.756)(Marlowe, 2010)(p.1). A continuous plant and animal record also helps to confirm that the environment of the Hadza may be considered to be similar enough to its ancient past to make general comparisons between the present day Hadza and their East African hominin ancestors (Marlowe, 2010)(p.1).

Diet

Hadzaland and Diet

Many of the plant and animal foods of Hadzaland have been around since the origination of *Homo sapiens*, making it likely that the Hadza ancestors exploited many of the same general foods as the present-day Hadza (Marlowe, 2010)(p.17). Some of the species hunted and consumed by the Hadza would have been present in East Africa even farther back into man's evolutionary past, possibly existing side by side with man throughout the whole time span of his evolution (Marlowe, 2010)(p.126). The mosaic of habitats found within Hadzaland support a variety of large animals. The vast savanna woodland environment with its highly seasonal rainfall has dominated the landscape of East Africa for at least the last three million years (O'Connell, Hawkes, & Jones, 1988a)(p.360). While the primary habitat is savanna woodland, the region is also composed of open grassy plains, rocky hills, scrub brush, wooded riverbeds, palm forest, marshland, as well as gallery forest restricted to areas near permanent water (Marlowe, 2010)(p.13)(Murray, Schoeninger, Bunn, Pickering, & Marlett, 2001)(p.3). Hadzaland provides ample supply of water in the form of rivers and lakes including Lake Eyasi which can typically provide the Hadza with water even during the driest times of the year (Marlowe, 2010)(p.13). The Hadza experience both a wet and a dry season living in what is considered to be a semi-arid climate (Murray et al., 2001)(p.3). Hadzaland's wet season is December through May, at which time they receive 300-600mm of rain. In contrast, there is almost no rain between June and November. Not surprisingly, this seasonal rainfall affects food availability (Berbesque & Marlowe, 2009)(p.603).

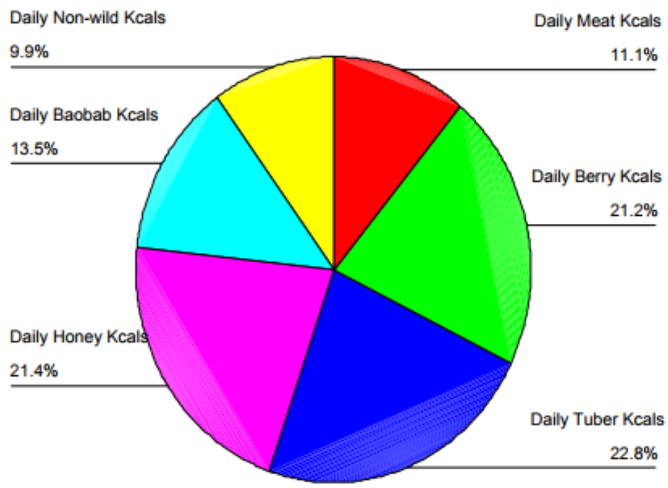
Traditional Hadza Diet

The Hadza diet is essentially omnivorous and consists of five major foods including honey, meat, berries, baobab, and tubers (Berbesque & Marlowe, 2009)(p.603). Of these foods, berries contribute the most overall calories followed by meat, baobab, tubers, and honey (Marlowe, 2010)(p.128). The majority of the meat comes from mammals or birds. Similar to basically all human populations, the Hadza are particular about what foods they eat. Protein in the Hadza diet instead comes from meat, honey (from the larvae and the comb) (Murray et al., 2001)(p.9), and baobab seeds (Nnam & Obiakor, 2003)(pp.266-267), all of which hold great value among the Hadza.

Regarding daily food intake, Marlowe's observations during 1995-96 suggested that the Hadza consume about 30% of their daily Calories while they are foraging and, in the figure below, he shows the percent of daily kilocalories represented by different foods brought to the camp. As shown, the typical day of a Hadza diet would consist of eating equal amounts of berries, honey, and tubers, and smaller proportions of baobab and meat. It's safe to suppose that the Hadza eat honey, berries, and baobab pulp while they are foraging (accounting for Marlowe's 30% of Calories mentioned above), and they bring meat, tubers, and baobab seeds back to the camp for processing before consumption (Marlowe, 2002). Marlowe's findings regarding the relative percent of kcals from various foods in the Hadza diet are consistent with other studies.

When specifically examining the relative contribution of various foods to daily caloric intake, Kaplan et al. found that the Hadza consume approximately 4030 kcals/day and, of these kcals, 1940 kcals/day (48%), 1214 kcals/day (30%), 621 kcals/day (15%), and 255 kcals/day (6%) come from meat, roots, fruits, and invertebrates (bee larvae), respectively (Kaplan, Hill, Lancaster, & Hurtado, 2000)(p.166).

Figure 2. Hadza diet showing daily Kilocalories brought into camp by type of food. Data collected over a 9 month period in 5 different camps in 1995-96 (2,733 person-days). All categories are foraged wild foods except “Daily Non-wild Kcals,” which is mostly maize (5%) and millet (4.2%) gained as gifts from a missionary, or in trade with neighboring agro-pastoralists. This 9.9% of food entering camp equals about 6.93% of total diet, since about 30% of the diet is consumed while out foraging.



Honey. Honey is the most highly-valued food in the Hadza diet, valued even more highly than baobab, and is also the most energy-dense food in nature. The Hadza consume honey from seven different bee species, with the largest quantity of honey from three particular species ba'alako, nateako, and kanoa (Marlowe, 2010)(p.116).

Tubers. Tubers are vital to the Hadza, acting as a kind of staple fallback food that is available and consumed year round. While tubers are almost always on the Hadza menu, they never form more than 31% by weight of the overall diet (Berbesque & Marlowe, 2009)(p.756). The Hadza consume at least ten different species of tubers (Marlowe, 2010)(p.109&113). The most common species of which is Vigna frutescens, known as ekwa (Berbesque & Marlowe, 2009)(p.604). Another common tuber is panjuako (*Ipomoea transvaalensis*) (Marlowe, 2010)(p.120).

Berries. Berries contribute the largest amount of calories of any food in the Hadza diet. This may seem surprising, especially since berries are not available year round, as are other foods such as tubers; however, when berries are in season, they may entirely dominate the diet. Berries are so important to the Hadza diet that the Hadza will commonly place their camp within the berry bushes themselves (Marlowe, 2010)(pp.114-115).

Baobab. Baobab (*Adasonia digitata L.*) is another very important food for the Hadza and several other foraging and agricultural groups across eastern and southern Africa (Murray et al., 2001)(p.4). Baobab is indigenous to the savannas and savanna woodlands of sub-Sahara Africa, and can only live in hot, semi-arid regions, dry woodland and stony places with low amounts of rainfall. Standing prominently along the open savanna, baobab is massive, and is generally regarded as the largest succulent plant in the world with a diameter of 10-12 meters and a height of at least 23 meters (Kamatou, Vermaak, & Viljoen, 2011). With such an enormous size, baobab is a conspicuous source of food that can be easily seen from afar. This massive tree provides an important source of food and shelter for other primates besides humans, offering its fruits to both savanna-dwelling chimpanzees and baboons who are capable of breaking open baobab pods (Chadare, Linnemann, Hounhouigan, Nout, & Van Boekel, 2008)(p.254).

Meat. The Hadza eat big game and predominantly focus on hunting big game to the exclusion of smaller animals. As such, there is great variability in the availability of big game meat, due to inconsistent returns when hunting big game. In one report, Whitten and Widdowson stated that "Species more commonly taken were giraffe (*Giraffa camelopardalis*), zebra (*Equus burchelli*), impala (*Aepyceros melampus*), and warthog (*Phaecochoerus aethiopicus*)" (*Foraging Strategies of Monkeys, Apes, and Humans*, 1992)(p.84). Colette Berbesque reported that the Hadza prefer to hunt and consume bigger animals with quantitatively large amounts of body fat (like Elands or buffalo) due to large amount of potential calories. As such, the Hadza prefer a 300kg buffalo with 10% body fat over a 5k rock hydrax with 40% body fat: "They're both hard to catch, so you go for whatever you see...but you dream big about the amount of fat on a buffalo" (Berbesque, 2014).

Marlowe reported that there are currently less game than there were in the past, leading him to believe that there was more meat in the diet during the early 1900s; however, despite the lower prevalence of elephants, rhinos, and hippos, there are still impalas, kudus, and giraffes (Marlowe, 2010)(p.36). More recent reports also suggest that the availability of meat has decreased: "It's very important to go to work and hunt, but now, you can just walk from morning to night and if you're lucky, you might come back with a dik-dik," he sighed, referring to an animal that is embarrassingly small for someone who once slew two zebras, an antelope and a buffalo in a single day. "But there's always an alternative. The baobab. Together with the herbs" (McCrummen, 2007).

Other foods. Along with their five predominant food sources, the Hadza will eat other foods when available. For instance, the red-billed Quelea (*Quelea quelea*) bird species has a massive synchronized reproduction for 2-3 weeks every year. When this occurs, the Hadza will predominantly eat the baby chicks during this time period (Marlowe, 2010)(p.139). The Hadza occasionally eat tortoises, large land snails, and other small mammals (Marlowe, 2010)(p.118).

<u>Seasonality of the Hadza diet</u>

The Hadza are well-accustomed to seasonal changes in their diet. Most foods in the Hadza diet are available only seasonally, with the exception of tubers and certain game animals (Berbesque & Marlowe, 2009)(p.603). The predominant foods available during the dry season (June-November) include tubers, baobab pulp and seeds, large animals, a little honey, and a few berries (Murray et al., 2001)(p.4). Berries will increase at the end of the dry season and are available in greatest abundance at the end of the dry period through to the first part of the wet season (Marlowe, 2010)(p.108). Besides berries, other foods available during the rainy (December-May) season are tubers, baobab seeds, most fruits, and small animals (Murray et al., 2001)(p.4). Honey is only available in appreciable quantities for a few months each year (Murray et al., 2001)(p.12), and may become scarce or entirely absent during the dry seasons (i.e. July and November) (Berbesque & Marlowe, 2009)(p.756)(Murray et al., 2001)(p.4).

Within these general patterns of foods available with each season are a series of opportunistic feedings that focus upon the consumption of one food in large quantities. For instance, when a big animal is killed the Hadza will gorge for days. During the two month season of their favorite berry, 'undushipi,' the Hadza consume predominantly berries. Similarly, as mentioned above, during the red-billed quelea's annual synchronized reproduction, the Hadza will eat nothing but the chicks for weeks (Marlowe, 2010)(p.139). Despite taking advantage of opportunities to gorge on specific foods, the Hadza still desire variety in their diet. As such, they share meat and other foods among members of a camp, which minimizes individual variance in daily consumption of these items (Marlowe, 2010)(p.139).

Intelligence and Sensing used for finding food

One of the most interesting ways in which the Hadza use intelligence and sensing to find food is through their symbiotic relationship with the honey-guide bird. As detailed under Capture, the Hadza and honey guide bird appear to have co-evolved such that, the bird will fly up to a Hadza man and make noise to get his attention. After this, the Hadza and bird communicate via whistles until the bird successfully guides the man to the hive. At this point, the man uses smoke to subdue the bees and retrieves the honey comb, the contents of which are shared with the honey-guide bird. This relationship requires the Hadza's intelligence in understanding the honey-guide bird's communication, the knowledge of which has been passed down through generations (in part via Hadza mythology). Additionally, the Hadza's hearing abilities are essential to their sensing the presence of the honey-guide bird, and of the hive when they arrive near it (Marlowe, 2010)(p.117)(Crittenden, 2011). Finally, the Hadza's understanding of the use of smoke for subduing bees prior to stealing a hive is critical to their success in obtaining honey. It can be assumed that this knowledge has been passed down through generations, likely through oral communication.

The Hadza technique for scavenging prey from other predatory mammals also requires substantial intelligence and visual and auditory sensory capabilities. The Hadza have learned, likely over thousands of years, that the presence of vultures and predatory mammals, such as lions or hyenas, are likely indicative of recently killed animals. As such, the Hadza intentionally watch for vultures in the sky and listen for the sounds of lions and other predatory mammals at night as indicators of a recent kill. Using this information gained from their auditory and visual senses, they then seek out the recently killed animal and scavenge it for their own source of food (O'Connell, Hawkes, & Jones, 1988b)(p.357).

Another example of the Hadza's use of intelligence is related to their hunting techniques. They specifically wait near watering holes at night, particularly during the dry season, in order to hunt animals on their way to the watering hole. This technique reveals substantial intelligence in understanding the physiological needs of the animals and their patterns for fulfilling those needs (Marlowe, 2010)(p.119)(Berbesque & Marlowe, 2009)(p.756).

Hadza women use their auditory and visual sensory abilities to find tubers. Specifically, they find tubers by identifying the lianas growing up and around a bush or tree. Then, they use their digging sticks, the women will tap the ground and listen for a sound that suggests a large tuber before they begin to dig (Marlowe, 2010)(p.109).

Despite their use of intelligence and sensory capabilities for hunting, scavenging, and gathering honey, the Hadza do not demonstrate the use of any particularly sophisticated weapons and tools for obtaining food. The primary weapon used by Hadza men is a bow and arrow, with the arrow often having a poisoned-tip. Men also carry axes, which they use to cut bee hives out of trees. Among women, the primary tool is a fire-hardened digging stick, used for acquiring tubers and, occasionally, for scaring lions or other predators away from their kills. They also have baskets for carrying berries and non-food items. Overall, the weapons and tools used by the Hadza are not particularly sophisticated. In some ways, this is not surprising, as many of their food sources are relatively easy to access, such as baobab, which simply falls from trees and can be gathered from the ground. Baobab trees are also massive, so they are easy to spot from long distances. However, it is surprising that men have not started using more effective weapons, such as guns, for hunting game.

Locomotion

The primary form of locomotion used by the Hadza is walking. Considering their status as hunter-gatherers, this is not surprising. However, it is interesting that the Hadza rarely choose to run and, when they do, it is specifically for the purpose of obtaining food. They will run briefly for another chance at killing game, to cut animals off before they reach their burrow, or to scavenge a kill from a lion or other predator (Marlowe, 2010)(p.118)(O'Connell et al., 1988b)(p.357). Despite the fact that walking is their primary form of locomotion, the Hadza do participate in a very specific movement pattern, known as the Lévy walk pattern. This pattern is a random walk search strategy specifically used during foraging and is characterized by groups of short steps interspersed with longer movements in between the short steps. “Modeling studies have shown that this step length distribution is advantageous when searching for resources that are patchily distributed and can be profitably revisited (i.e., resources that are not depleted after a given visit)” (Raichlen et al., 2014)(p.728). Raichlen et al. specifically studied the Hadza to determine whether they used Lévy walks when foraging and determined that they do use these walking patterns. This is important because it suggests that this walking pattern may be a fundamental feature of human landscape use, regardless of the cultural or physical environment, and that the Lévy walk “may have played an important role in the evolution of human mobility” (Raichlen et al., 2014)(p.278).

Despite the Hadza’s use of walking as their primary form of locomotion, researchers have found that, while Hadza’s physical activity levels are higher than that of their Western counterparts, the metabolic costs of walking and resting, as well as the average daily energy expenditure of the Hadza, were not significantly different than that of Westerners. Additionally, there was no correspondence between total energy expenditure in the Hadza and their daily walking distance. These findings are important from both an obesity prevention and evolutionary perspective, Indeed, the results of this study led the researchers to “hypothesize that TEE may be a relatively stable, constrained physiological trait for the human species, more a product of our common genetic inheritance than our diverse lifestyles." They also stated that "A growing body of work on mammalian metabolism is revealing that species' metabolic rates reflect their evolutionary history, as TEE responds over evolutionary time to ecological pressures such as food availability and predation risk" (Pontzer et al., 2012).

Territory

As previously mentioned, the Hadza live around Lake Eyasi in Tanzania, with about 25% of the Hadza living west of lake and the other 75% living east of Lake Eyasi in an area about 2,500 km^2 (Marlowe, 2002). The Hadza do recognize five regions within their country (Mangola, Han!abi, Tli'ika, Sipunga, and Dunduiya); however, despite their recognition of these general regions, they are not considered territories and do not divide Hadza groups (Hadzafund.org). Hadza live in camps that range in number from as little as 2 people to over 100 (Marlowe, 2010)(p.40), with the numbers fluctuating greatly from the rainy season when they are the smallest to the dry season when they are the largest (Marlowe, 2010)(p.264). Amidst this variation, the average camp population is around 30 people (Berbesque et al., 2012). During the dry season, the Hadza are forced into congregating into larger groups surrounding the limited number of permanent water sources (Marlowe, 2010)(p.264). Thus, these camps are highly mobile in terms of location as well as their individual composition. The camps will typically move about every 6 weeks to be closer to berries in season, or to move away from a location depleted of a critical resource such as tubers or drinking water (Marlowe, 2010)(p.41)(Berbesque et al., 2012). Camps are always located near a water hole, rarely farther than a 10 minute walk away. During the rainy season, drinking water may be acquired from the tops of big flat rocks or from nearby streams (Marlowe, 2010)(p.41). As mentioned, the individual makeup of the camps are in a state of constant flux with people continually moving in and out. Couples may live with kin of either the husband or the wife, or with neither, although couples most commonly live in the same camp as the wife's kin (Berbesque & Marlowe, 2009)(p.752).

The freedom of migration from one camp to another is reflective of the Hadza's lack of territoriality. Hadza would never be worried of invading another Hadza group's area just as they would never consider whether or not they would be allowed to move to another camp. They simply move to whatever camp they so please. The Hadza will move camp for a number of reasons, including conflict. When there is conflict, a Hadza typically choose to move away from the other Hadza man or woman who is the source of conflict (Marlowe, 2010)(p.249). The Hadza will also abandon a camp if someone gets sick or dies, as illness is associated with the location where the person became ill. Finally, seasonal migration occurs to move to better hunting grounds, closer to water, or closer to other seasonal foods, such as berries.

The Hadza do not consider ownership or control of any area of Hadzaland, making them appear rather extreme in their non-territoriality, even in the context of other hunter-gatherer societies (Marlowe, 2010)(p.43). Thus, as one might expect, it would be extremely unlikely for any one group of Hadza to attack another Hadza group. The only warfare the Hadza occasionally engage involves their pastoralist neighbors who initiate the conflict, sometimes killing Hadza for hunting their livestock (Marlowe, 2010)(p.268).

In the recent past, neighboring people, such as the Datoga herders, have tried to encroach upon the Hadza's territory in order to provide pasture for their cattle and goats. The clearing of land by the Datoga destroys the honey, berries, and tubers the Hadza rely on, as well as drying up watering holes (Marlowe, 2010)(pp.286-287). Additionally, the western Hadza lands are part of a private hunting reserve, and the Hadza are restricted to a reservation within the reserve, though they are prohibited from hunting. Finally, in 2007, the government who controlled the Hadza lands near the Yaeda Valley leased the entire 6,500 km^2 to the royal family of the United Arab Emirates. The purpose of this lease was to supply the royal family with a "personal safari playground" (McCrummen, 2007). As a result of this lease, the Hadza were evicted; however, thankfully, negative press coverage and Hadza protests resulted in the deal being rescinded almost immediately ("Hadzabe celebrate a land victory," 2007).

Ownership of items. Similar to the Hadza's lack of territoriality there are few items they consider to be private property. For example, each women's digging stick, cooking pot, clothes, and jewelry are her private property. Women may lend their property to others, but there is no risk of them being stolen. A man's bow and arrows, clothes, jewelry, and tools are also considered his property. Objects of ritual importance, such as a plume of ostrich feathers, are also considered personal property. The land and the resources it provides are owned by no one, and are available to anyone. A lack of personal property is also related to the Hadza's mobile lifestyle (Marlowe, 2010)(p.253)(Jelliffe, Bennett, Jelliffe, & Woodburn, 1962)(p.908).

Capture

In general, about 75% of the food in the Hadza diet is gathered and the remaining 25% consists of hunted food. This distinguishes the Hadza from other 'warm-climate foragers', as typical foragers obtain 53%, 26%, and 21% of their food from gathering, hunting, and fishing, respectively. However, the Hadza are relatively similar to African foragers, whose median distribution of food is 67% from gathering, 32% from hunting, and 1% from fishing. Similar to other African groups, the Hadza avoid fish. Interestingly, chimpanzees, bonobos, and gorillas also avoid fish (Marlowe, 2010)(p.260).

Overall, men provide a mean of 7248 kcals/day from meat (7248 kcals) and other foods, like honey (841 kcals). This represents about 64.8% of total adult calories and 94.1% of total adult protein. Women provide a mean of 4397 kcals/day from tubers (3093 kcals) and fruits, like baobab and berries, (1304 kcals). This represents 35.2% and 5.9% of total adult calories and protein. Overall, about 48% of daily Calories in the Hadza come from hunting, 36% are extracted (this includes foods, like tubers, that are difficult to extract), and 15% are collected (this includes foods, like berries and honey, that can be obtained and eaten by gathering them from the environment) (Kaplan et al., 2000)(p.162).

Hunting

Big game. Hadza men hunt for big game using bows with poisoned arrows. The poison on the arrows is made from the branches of a shrub (*Adenium coetaneum).* Along with their use of bows and arrows for hunting big game, the Hadza will also scavenge game from lion kills.

Importantly, the Hadza do not use guns, traps, pits, or snares to hunt or capture game (Lee & Daly, 1999)(pp.201-202). Typically, the Hadza are solitary hunters and it is uncommon for them to hunt in a group of several males (Marlowe, 2010)(p.268). Hadza men always carry their bow and arrows, so they are prepared to hunt any time they are away from the camp (O'Connell et al., 1988a)(p.117). According to Whitten and Widdowson, the use of poisoned, metal-tipped arrows likely increased the Hadza's efficiency in hunting big game, thus reflecting the advantages conferred by greater intelligence and better technology (*Foraging Strategies of Monkeys, Apes, and Humans*, 1992)(p.89).

The Hadza take advantage of animals' need for water during the dry season by waiting to ambush animals at night when they come to drink at watering holes (Marlowe, 2010)(p.119). They will often build blinds constructed of branches, typically in combination with living plants and boulders, where they will lie in wait for the animals (Bunn, Bartram, & Kroll, 1988)(p.425). Men may wait for up to 12 hours for an animal to pass by on their way to the watering hole. Not surprisingly, large game is easier to kill by waiting to ambush them during the dry season and, thus, more animals are killed during the dry season than the wet season (Marlowe, 2010)(p.119)(Berbesque & Marlowe, 2009)(p.756).

The Hadza also effectively scavenge meat by monitoring the flight of vultures and listening for the lions, leopards, hyenas, and other carnivores (O'Connell et al., 1988b)(p.357). If Hadza men spot a kill made by a carnivore, they will run to the location to scavenge the meat, which is risky and sometimes results in injury by a predator. In fact, O'Connell et al. found that about 85% of scavenged animal carcasses were seized from lions while they were still feeding on the carcass (O'Connell et al., 1988b)(p.358)! Groups of Hadza women may also run other animals away from their kill using digging sticks (Marlowe, 2010)(p.119). In addition to the physical dangers posed by other predators, the scavenged meat is sometimes rotten and may give the Hadza stomach-aches, though the problem isn't sufficient to discourage them from eating the scavenged meat (Marlowe, 2010)(p.141). Scavenging contributes a significant amount of meat to the Hadza diet, with various reports suggesting that scavenging accounts for about 20% of all medium/large mammal carcasses the Hadza acquire and that scavenging accounts for about 25 grams of meat per camp resident per day (O'Connell et al., 1988b)(pp.356-357)(Marlowe, 2010). The Hadza's success with scavenging is in part due to their prioritizing scavenging over other activities: "Since scavenging opportunities are recognizable at distances of up to several miles, and since the Hadza watch for and eagerly seize every opportunity they see, we think that they are about as successful at scavenging as they can be in this habitat" (O'Connell et al., 1988b)(p.359).

The reported rate of return on hunting large animals is varied, with some researchers suggesting that they average only one kill every thirty days of hunting (O'Connell et al., 1988a)(p.145), and others stating that the Hadza average about one animal every 3.6 days, killing or scavenging 72 animals (*Foraging Strategies of Monkeys, Apes, and Humans*, 1992)(p.84). Hunters may go for weeks between kills, even if there are several men in a hunting group (O'Connell et al., 1988a)(p.145). Importantly, the Hadza almost exclusively hunt big game, ignoring smaller animals. This focus on big game results in large variability in the availability of meat; however, sharing meat reduces some of the variability in meat availability and consumption (*Foraging Strategies of Monkeys, Apes, and Humans*, 1992). In general, men bring about 90% of their kills of medium-to-large game back to the camp (Berbesque & Marlowe, 2009)(p.603).

Small game. As previously stated, the Hadza almost exclusively hunt big game; however, they will occasionally hunt small animals. They use their bow and arrows to hunt small animals and birds (though the arrows may not have poisoned tips if they are hunting smaller animals). While Hadza men rarely run, when hunting small animals, such as a hyrax, they may run to cut the animal off before it can reach its home in a rock crevice or burrow. Additionally, women, while they do not hunt big game, occasionally kill small mammals and birds. Women may also acquire tortoises and large land snails for consumption (Marlowe, 2010)(p.118).

Plant Gathering

Tubers. Women typically dig up tubers every day except for during times when berries are most in season and overly abundant, or for 2 or 3 days when large amounts of meat have been brought into camp (Berbesque & Marlowe, 2009)(p.756). Conversely, when berries are out of season and are least abundant, the Hadza women will put forth the efforts required to dig up greater amounts of tubers (Berbesque & Marlowe, 2009)(p.751). The tubers can be rather deep, up to 2 feet or more underground (Berbesque & Marlowe, 2009)(p.751). Most tubers are found about a 10-30 minute walk from camp. Women find the tubers by identifying the lianas growing up and around a bush or tree. Then, they use their fire-hardened digging sticks, the women will tap the ground and listen for a sound that suggests a large tuber before they begin to dig (Marlowe, 2010)(p.109). With their fire-hardened, sharp digging sticks, the Hadza women will usually devote around 2-3 hours of digging to acquire a hefty pile of tubers. Women typically eat some of the tubers they've gathered immediately and take about 70% of what they've gathered back to the camp to feed others. Men rarely dig up tubers (Marlowe, 2010)(p.109).

Berries. When berries are in season, large groups comprised of all ages and both sexes will set out early to forage. Berries are picked all morning, followed by a rest in the shade at midday, and then continuing on with picking and eating throughout the afternoon, finally returning to camp with overflowing basketfuls of berries. Thus, during the berry season, berries compose the bulk of the diet (Marlowe, 2010)(pp.114-115).

Baobab. Unlike berries, baobab is available throughout most of the year. Generally, baobab is so abundant throughout Hadzaland that the Hadza will simply gather the baobab pods that have fallen to the ground when they happen to pass by them (Marlowe, 2010)(pp.115-116). Hadza women will also collect baobab seeds from baboon dung piles when the opportunity presents itself (Murray et al., 2001)(p.12). (Note that baboons cannot digest these seeds as the Hadza since they lack an ability to pound the seeds into an edible flour).

Honey. The most important honey, ba'alako, may be found very high up in the tall baobab trees. Thus, acquiring honey is commonly a more dangerous activity that is generally performed by men. Falling from the tall trees can lead to serious injury or death (Berbesque & Marlowe, 2009)(p.756). The Hadza men will climb up the tree while carrying a torch and will use the smoke to stun the bees so they can reach in and take out the honeycomb (Marlowe, 2010)(p.116). They will also use small axes to chop into bee hives (Bunn et al., 1988)(p.424). Other varieties of honey are acquired from hives lower in Commiphora trees, and one kind of honey, lulindi, is located underground and requires extensive digging to excavate. Women may help with obtaining these honeys as there is less risk involved of falling or being stung (Marlowe, 2010)(p.117). When men gather honey, they eat a lot of it on the spot and only take about half of it back to the camp (Berbesque & Marlowe, 2009)(p.603).

Interestingly there appears to be some co-evolution between birds and Hadza both in search of honey. A particular bird appropriately referred to as the "honey-guide bird" (*Indicator indicator*) is known to seek out Hadza men in order to guide them to a tree with a hive of the *Apis mellifera* bees in it. The honey-guide bird approaches the man and makes noise to get his attention. Once the man whistles back to the bird and starts following it, the bird and the hunter will continue communicating via chatters and whistles until the man arrives at the tree and sees the hive. After the man opens up the hive and takes the honey, the bird will clean up the leftovers, specifically focusing on consuming the wax and the bees (Marlowe, 2010)(p.117)(Crittenden, 2011).

Storing

The Hadza are sufficiently successful at hunting, scavenging, and gathering food year-round that they do not need to store food. Additionally, the year-round availability of tubers as a fallback food protects the Hadza from starvation (Berbesque & Marlowe, 2009)(p.756). As such, the Hadza do not process foods for storage. The Hadza have been characterized by anthropologists as an immediate-return society, because they do not plan for the future. The year-round availability of food reinforces this behavior and, as such, makes it unnecessary for the Hadza to store food (Marlowe, 2010)(p.254). Marlowe stated that “The Hadza do not value saving the way people in societies that must delay gratification do” and this attitude towards saving explains why they do not make alcohol (Marlowe, 2010)(p.253). In fact, the Hadza do not ferment any foods for storage (Berbesque, 2014), despite the fact that they know how to make alcohol (from honey) and they like alcohol (Marlowe, 2010)(p.253). Their rapid consumption of honey actually precludes them from having sufficient honey to ferment to make alcohol (Marlowe, 2010)(p.253). Similarly, while the Hadza know how to dry and smoke meat for storage, they rarely do so because they eat the meat so quickly after killing an animal (Marlowe, 2010)(p.253)(Berbesque, 2014).

Refining

Meat. The Hadza also eat their meat cooked, predominantly roasting their meat, and eat most of the meat immediately after the kill. After killing an animal, the Hadza will build a fire under the nearest source of shade. Then, as they butcher the animal, they will roast small bits of flesh and warm marrow-containing bones over the fire before cracking them. Marrow-bearing bones are typically cracked at midshaft using a rock or the handle of a wooden knife and the marrow is immediately consumed (O'Connell et al., 1988a)(pp.118-120). The marrow rich bone tissue present on the ends of some of the long bones may also be partly gouged out with a knife and eaten. In contrast to meat, marrow is eaten raw (Marlowe, 2010)(p.120). The Hadza consume most parts of the animal, including tough parts like tendons and ligaments. Tendons and ligaments are roasted, similar to other meat, and the Hadza will eat as much as they can, while spitting out the chewier parts. Not surprisingly, the toughness of these foods has resulted in a great deal of dental wear (Berbesque, 2014). They will also chew on large bones and eat small bones (Berbesque et al., 2012). The brain is regularly consumed, and is cooked similarly to other meats, by roasting them over an open fire (Berbesque, 2014).

The Hadza will split hooves with a knife so that the fatty tissue around the phalanges may be dug out (O'Connell et al., 1988a)(p.120). Ribs are sometimes cracked in half, and the broken ends are gnawed and sucked upon. Skulls are always stripped of their meat right on the spot of the kill after which the skull and mandible are thoroughly shattered, and everything edible is consumed. Skulls may be broken with axes, rocks, or with the hard and dense ends of long bones. Alternatively, skulls may be grasped by the muzzle and swung against a tree or an outcrop of a rock, an efficient way of shattering skulls that is also practiced by chimpanzees (O'Connell et al., 1988a)(p.120).

In contrast to other parts of the animal, vertebrae are often boiled. First, vertebrae containing large amounts of meat are cut into small sections, and then severed laterally with an axe to expose the cancellous, marrow-rich tissue that will provide plenty of fat when boiled. After boiling, the vertebrae will be removed from the pot, methodically shattered with rocks, and then picked clean of all edible tissue before being thrown away. Considerable pieces of hide from sizable animals such as zebra, giraffe, warthog, and eland are brought back to camp, pounded with rocks, lightly roasted, and then eaten after all of the animal's other edible tissue including the meat and marrow are consumed. The hides of the Alcelaphine antelope and impala, on the other hand, are used to make clothing, bags, and ground coverings (O'Connell et al., 1988a).

As previously stated, the Hadza primarily roast their meat and it is never buried and cooked underground with embers, nor do the Hadza typically smoke meat or make broths or sausages. This is primarily because they do not want to waste time processing meat and because meat is typically eaten within a small time frame after it is killed, reducing the need for processing that would enhance the ability to store meat. Rarely, the Hadza may smoke meat for the purposes of trade, but this is unusual. The Hadza may unintentionally produce a meat broth in the process of cooking meat, but do not intentionally boil meat or bones to make broth (Berbesque, 2014).

Tubers. After digging up the tubers, the women will immediately roast and eat some of the tubers, taking the remaining 70% or so back to camp to share with others (Marlowe, 2010). Tubers are typically roasted for about five minutes, but the Hadza are also willing to eat the tubers raw (Berbesque & Marlowe, 2009)(p.751). Roasting tubers may make it easier to peel them. One species, panjuako (*Ipomoea transvaalensis*), is normally consumed in its raw form and tastes like a jicama or a raw potato (Marlowe, 2010)(p.120). Whether they are roasted or not, Hadza men and women will puncture the tuber's skin with their teeth and then proceed to peel the tuber and dice up the inside into chunks before eating it (Berbesque et al., 2012). Ekwa is a tuber with such a high fiber content that it cannot be swallowed, but must be chewed and sucked on for 30 seconds to 3 minutes before the remaining fibrous mass is spat out (Berbesque & Marlowe, 2009)(p.604)(Schoeninger, Bunn, Murray, & Marlett, 2001)(p.71).

Berries. Many berries are eaten raw when they are at their ripest, while some are commonly eaten after they have dried on the brush into a raisin-like food. Some fresh berries may also be dried toward the end of the berry season (Marlowe, 2010)(p.120). Of course, the berries eaten by the Hadza are naturally drier than the cultivated berries we are familiar with in the developed world (Berbesque & Marlowe, 2009)(p.603). The berries of Hadzaland also have much larger seeds, more fiber, and far less pulpy flesh so that the Hadza must consume huge quantities of them in order to satisfy their hunger (Marlowe, 2010)(pp.114-115). The seeds are commonly swallowed (Murray et al., 2001)(pp.9-10), but the Hadza will make at least some efforts to spit out many seeds as well. The seeds they do swallow will pass through the digestive tract unscathed. One particular berry, the pawe, is similar to an apricot in that it has soft flesh that surrounds a hard nut and the Hadza eat the flesh from the nut (Murray et al., 2001)(p.6).

Baobab. The edible parts of baobab lie inside the pod in the form of a yellowish-white, acidic and chalky pulp that surrounds some large, hard seeds. Once the Hadza have cracked open the pod with a good whack, they may immediately scoop out the pulp and eat it (Marlowe, 2010)(pp.115-116). The seeds, however, must be taken back to camp to pound into a flour before eating (Berbesque & Marlowe, 2009)(pp.603-604). If they don't eat the pulp immediately, it may be brought back to camp and mixed with water, honey, or berries (if they're available). The combination of the tart pulp, sweet berries, and honey results in a sweet, tart drink the Hadza like to consume (Marlowe, 2010)(p.120). Hadza women also prepare a flour with the baobab seeds. The first step in preparing the flour is crushing the seeds with a stone, then winnowing the crushed seeds on the surface of a dried animal hide in order to remove the seed coats. The flour is often eaten dry or mixed with water. In a similar process, women will make porridge from baobab by pounding the pulp and seeds with a stone, and then cooking the mixture with water. This porridge is eaten by all Hadza but is especially important as the main weaning food for infants (Marlowe, 2010)(p.120). (Woodburn, 1970)(pp.40-42).

The Hadza may also process the baobab seed in a way that increases the amount of protein that can be readily absorbed. Through the removal of the seed coat by winnowing, the Hadza reduce the levels of trypsin inhibitor present in the flour, thus making the protein more easily digestible (Murray et al., 2001)(p.10). The baobab seeds and pulp may become even more digestible with the addition of either cold or hot water. This simple addition significantly reduces the tannic acid concentrations making the protein, minerals, and other nutrients more readily available for absorption (Chadare et al., 2008)(p.265). Additionally, by mixing the seeds in with the pulp, such as when making porridge, the Hadza add in a hefty dose of protein and fat to the calcium, carbohydrate and vitamin C rich pulp (Nnam & Obiakor, 2003)(pp.266-267).

Honey. Honey is typically eaten raw by the Hadza and, as mentioned, is sometimes mixed with baobab (Marlowe, 2010)(p.234). The Hadza consume the entire honey comb, with bee larvae still present (Berbesque & Marlowe, 2009)(p.603).

The presence of bee larvae adds much nutritional value in the form of fat, protein, and minerals. This may partly be the reason why honeys eaten by the Hadza have been found to contain greater amounts of protein, fat, and ash in relation to larvae and comb free American honeys (Murray et al., 2001)(p.9).

Sharing

Communal sharing. In general, the Hadza share their food on a daily basis with other members of the camp (Marlowe, 2010)(p.252-253). Although, when the chance arises for food to be hidden and smuggled into their individual household, the Hadza may do just that (Marlowe, 2010)(p.249). Honey is one of the most commonly smuggled foods due to its high energetic value and to the fact it does not need to be cooked out on an open fire where other members of the camp can see (Marlowe, 2010)(p.234).

In the case of meat, it is shared widely among members of a camp, which is important, as it minimizes individual variance in daily consumption of meat in particular (Marlowe, 2010)(p.139). In fact, it is expected that meat is shared by everyone and it cannot be reserved for just a hunter and/or his family (Lee & Daly, 1999). Sharing meat is also important due to the Hadza's relatively risky big-game hunting strategies. By sharing meat from kills, the Hadza reduce the risk than particular individuals or members of a camp will go without meat if a hunting trip doesn't pay off. Whiten and Widdowson report that the sharing of carcasses is common among hunter-gatherers and that such sharing, which is ancient in origin, has been crucial to human evolution (*Foraging Strategies of Monkeys, Apes, and Humans*, 1992)(p.84).

Rituals and sex differences related to meat-*Epeme*. While the Hadza generally share their food, one exception to this rule is related to *epeme* meat. The term *epeme* refers to a ritual dance "for the unity, balance and restoration of the significant family ties of the people within the camp", to a group of initiated men, and to fatty meat from hunted animals that is considered sacred (Skaanes, 2015)(p.2600. This *epeme* meat may only be eaten by *epeme* initiates and there are strong taboos against non-initiates eating this meat. Only men can become *epeme* initiates, and they become initiates by killing a large game animal (Berbesque & Marlowe, 2009)(p.605). According to Skaanes, the term *epeme* "marks the semi-godlike quality of the *epeme* collective, which is manifested in their ability to eat the sacred meat, 'supposedly reserved for "god"' (Skaanes, 2015)(p.260). *Ep*eme meat includes the genitals, kidney, heart, lung, throat, and tongue of the largest animals hunted by the Hadza. *Epeme* men consume the meat in separate areas from women and children because they consider it dangerous for women and children to eat these specific parts of the animal. There most serious taboo among the Hadza is against a non-*epeme* man seeing *epeme* meat eaten or eating the *epeme* meat themselves. There are also strong taboos against females or children eating *epeme* meat, such that, the Hadza believe they make get sick, develop a deformity (like missing teeth or a mangled hand), or die if they consume the *epeme* meat (Marlowe, 2010)(pp.63&66). It should be noted that the dance rituals and beliefs surrounding *epeme* meat are at the heart of the Hadza religion (Marlowe, 2010)(p.61).

These beliefs related to *epeme* impact the Hadza women's meat intake, preventing them from having equal access to organ meats of big game animals. Hadza women may eat the organs of the smaller animals that are not considered to have "epeme" meat; however, they often don't have equal access to these animals since many of the smaller animals are eaten outside of camp before they are brought back to share. Thus, overall, women are consuming less meat than men in terms of organ meat and also muscle meat. Meat provides the lowest kcals/hour of any food for the Hadza women. Despite less access to meat, the Hadza women appear to be healthy based upon the medical exams focused on the presence of anemia or blood pressure abnormalities (Berbesque & Marlowe, 2009)(p.609)(Berbesque, 2014).

Other food taboos and preferences. Along with taboos against women and children eating *epeme* meat, there are taboos against mean eating tortoises. Specifically, the Hadza believe that if a man eats a tortoise, the poison on his arrows will weaken and fail to work. Women and children, on the other hand, are free to eat tortoises without concern (Berbesque & Marlowe, 2009)(p.605).

Somewhat similar to tortoises, men do not eat land snails; whereas, women and children do; however, there are not taboos against men eating land snails (Marlowe, 2010)(pp.102-13). There are other foods the Hadza do not eat, typically because it doesn't taste good to them. For example, men and women avoid eating fish and reptiles, saying that it 'tastes like snake' (Berbesque & Marlowe, 2009)(p.605). Indeed, Marlowe reported that one year the weather conditions resulted in a lake in the Yaeda valley being filled with giant catfish. As a result, the "some Hadza men took to walking out in the lake and whacking the fish on the head with their bows. They ate the catfish but complained that they did not taste good. They say that fish is bad, "like snake," which they do not eat" (Marlowe, 2010)(p.63). This anecdote suggests that the Hadza simply do not like the taste of fish. Finally, the Hadza do not Termites are not eaten even though they are abundant.

The Hadza reject other foods in their environment despite their edibility and abundance including almost all insects such as termites, reptiles including snakes and lizards, fish, and fresh-water mollusks (Lee & Daly, 1999)(p.202). Snakes and termites may be avoided for fear of being bitten, which is appropriate as many snake species in Hadzaland are quite dangerous (Marlowe, 2010)(p.102).

Sex differences in food preferences and amounts consumed. Hadza men and women rank honey, baobab, and tubers similarly based on preference, namely, first, third, and fifth, respectively; however, they differ in their preferences for meat and berries. Specifically, men preferentially rank meat second and berries fourth; whereas, women's rankings are reverse that of men (Berbesque & Marlowe, 2009)(pp.601&608). Importantly, the Hadza consistently demonstrate their preference for honey over meat, which is contrary to ethnographers' claims that foragers (including the Hadza) prefer meat over all other foods (Berbesque & Marlowe, 2009)(p.610). Food preference rankings are sometimes related to the types of foods Hadza men and women hunt or gather, such that, men preferentially rate meat (which they hunt/scavenge) over berries (which women gather). Additionally, women rank male-acquired foods, like meat, lower than males rank them. However, women still rate honey first despite the fact that men acquire honey (Berbesque & Marlowe, 2009)(p.610). Food preferences are also related to the caloric value and macronutrients in foods. For example, the most preferred (honey) and least preferred (tubers) foods are the most and least calorie dense, respectively. Men's reference for meat appears to be related to a preference for greater amounts of protein in the diet; whereas, women's preference for berries may reflect a preference for more carbohydrates (Berbesque & Marlowe, 2009)(p.610).

Unfortunately, food preferences do not always align with food consumption. Rather, food consumption patterns tend to relate more strongly to the foods men and women hunt or gather. For example, Hadza men consume more honey than Hadza women, despite women's stated preference for honey over all other foods. Men's greater consumption of honey is likely due to the fact that they are the primary foragers of honey, and will often eat considerable quantities (about half on average) of the honey before bringing it back to camp. Similarly, women consume more tubers (which they gather) than the Hadza men, despite tubers being their least preferred food (Berbesque & Marlowe, 2009)(p.609).

The preferences and overall consumption patterns of the Hadza women appear to favor foods higher in sugars that may be lacking in protein; however, the baobab provides considerable amounts of protein for the Hadza women. This may help to compensate for their lower meat intake relative to the Hadza men. Baobab seeds contain a lot of protein and, despite the fact that they are an incomplete protein due to being inadequate in three essential amino acids, women would only need to consume small quantities of meat to complete their amino acid requirements. The seeds are also high in fat, making them roughly equivalent to honey in terms of energy yield. The consistent availability of baobab and the ease of obtaining baobab makes it a more dependable food source than honey (Murray et al., 2001)(p.12).

Researchers have several hypotheses regarding the sex-differences in food preferences among the Hadza. One hypothesis is that women prefer foods that are more consistently available due to a need for more regular caloric intake than men to maintain adequate body fat levels for fertility. Thus, women may rank "lower-quality" food such as berries higher because of their abundance and availability relative to meat. Indeed, Hadza women have been observed eating significantly more frequently than the Hadza males in camp (Berbesque & Marlowe, 2009)(p.611). Women may also simply be content with targeting foods that are compatible with caring for infants, allowing men to get preferred foods (like honey and meat) because they are more dangerous to acquire and less predictable in their availability (Berbesque & Marlowe, 2009)(p.756).

Another possible reason for sex-differences in food preferences is related to differential fat distribution and body composition of males and females. Specifically, men likely require greater allocation of nutrients to muscle mass (protein), whereas, women require greater allocation of nutrients to fat (carbohydrates or lipids). Data indeed suggest that size dimorphism leads to dietary niche separation between males and females (Kamilar & Pokempner, 2008), and body composition is more sexually dimorphic in humans compared to other mammals (Bellisari, 2016) (Berbesque & Marlowe, 2009)(p.611).

Other Related to Food

Spiritual/Religious Beliefs. When an animal is obtained either through scavenging or hunting, the Hadza aren't supposed to speak about the dead animal until it has been dismembered, because they believe that this puts the animal's fat at risk, which the Hadza value much more highly than the lean meat of the animal (Gowdy, 1998)(p.98).

Division of Labor: Typically, Hadza men are responsible for hunting game and retrieving honey to bring back to the camp, though they occasionally gather baobab, as it is easy for them to gather on the trip home from hunting. Hadza women are primarily responsible for digging up tubers and for gathering baobab. Berries are gathered by both men and women (Berbesque & Marlowe, 2009)(p.603). While there is a division of labor among the Hadza in regards to gathering/capturing food, these roles re not absolute. For example, women may occasionally gather honey without men's help and will scavenge meat from other predators or kill small animals if the opportunity presents itself. Similarly, the Hadza men have knowledge on how to obtain all of the foods females forage on a daily basis, although grown men will rarely dig up tubers. Men more commonly forage for berries and baobab, which they will use to feed themselves when they are hunting (Marlowe, 2010)(p.269). Despite these patterns of crossover in foraging behavior, there is a distinct division of labor between Hadza males and females. A division may also be seen in the preparation of food, and females spend more time preparing and processing food (Marlowe, 2010)(p.97).

This division of labor is likely beneficial to Hadza women. Specifically, regardless of region or season, women in camps where men successfully obtained greater quantities of meat had a higher percent of body fat compared to women in camps where greater quantities of tubers were gathered. While women are able to supply a continuous supply of tubers, they provide fewer nutrients than meat. Dividing labor so that mean can hunt and obtaining a higher quality, albeit much more variable food source, ultimately increases women's body fat to higher levels than could be reached via tubers alone (Berbesque & Marlowe, 2009)(p.751). The division of labor among married Hadza is relatively equal, with males providing approximately 50% of the diet (Marlowe, 2010)(pp.279-280).

Side note: The division of labor among the Hadza may be somewhat likened to that of chimpanzees. For instance, female chimpanzees learn how to use tools for processing or obtaining foods earlier and will use them more often than males, gaining greater proficiency overall. Furthermore, male chimpanzees do the majority of the hunting, performing 71-90% of the hunting. These patterns perhaps suggest that these patterns of labor among males and females have long been intact (Marlowe, 2010)(pp.97 &268).

Trade. The Hadza do not participate in much trade; however, there is evidence of them trading with other groups. For instance, the Hadza's oral history suggests that their ancestors who first came in contact with non-foraging people traded with them for iron to make knives and arrowheads. The Hadza will trade with their neighbors (i.e. the Datoga or Isanzu) for meat, tobacco, alcohol, iron, cloth, clay pots, etc. (Marlowe, 2010)(p.253). The Hadza, while not typically smoking meat, will do so in order to trade with the Datoga (Berbesque, 2014). They may also save honey for the purposes of trade. Only about 9.9% of the Calories in the Hadza diet come from food they acquired via gifts or trade with agro-pastoralist neighbors (Marlowe, 2002).

Mating, Marriage, and Divorce. Unlike in industrialized countries where a person's anthropomorphic characteristics, such as height, weight, BMI, and percent body fat, as well as size and strength, may be important variables for choosing a mate, these characteristics are not particularly important to the Hadza. Hadza women do not show a preference for taller or larger men, as is often found in the societies of the developed world. This may be due to the potential disadvantages involved in having to maintain a larger body size during food shortages. Overall, mating within the Hadza society seems to be random with respect to any of the size variables (Sear & Marlowe, 2009)(pp.606-608).

The Hadza often marry at a young age, may marry more than once, and are often married to a partner who is significantly older or younger than themselves. For example, an 18-year-old man may marry an older widow. If this is the case, the young man will move in with the woman, as she is able to cook for him. However, if a young woman (i.e. 13 or 14-year-old), marries an older man, the girl will stay with her mother and receive help from her, with the husband paying for the mother's help with the meat he shoots. It should also be noted that many of the Hadza practice levirate marriage, in which the brother of a deceased man is obligated to marry his brother's widow (Jelliffe et al., 1962)(pp.908-909). There is no marriage ceremony among the Hadza, rather, only public recognition of a man and women cohabitating is needed to signify a marriage (Redd, 1998).

Divorce rates among the Hadza are relatively high, with 49 divorces per 1000 years of marriage. This relatively high divorce rate may be related to their subsistence based lifestyle and that men and women feel freer and experience less risk when they decide to change partners (Redd, 1998). Despite this apparently low-key approach to marriage and divorce, the main source of conflict within Hadza society is competition for mates. Indeed, almost all of the murders among the Hadza are rooted in male jealousy (Marlowe, 2010)(p.175).

Reproduction. Hadza women reach menarche much later than American women. Specifically, Hadza women reach menarche at about 16-17 years of age, whereas American women reach menarche at around 12.5 years of age. Earlier age of menarche among women in affluent industrialized societies have been reported for some time and is related to diet. Women in industrialized societies eat whenever they are hungry and they foods they eat are higher in fat and calories. This results in women growing larger faster and reaching menarche earlier (Marlowe, 2010)(p.134).

Age of menarche, however, does not negatively affect fertility among the Hadza women. Hadza women are quite fertile, and primary among them is quite rare, with the rate of sterility as low as 3%. Additionally, despite having a later age of menarche, Hadza women are typically younger than the average American woman at the time of their first birth. The median age at first birth is 19 and 24.2 years among Hadza and U.S. women, respectively (Marlowe, 2010)(pp. 151-152). The average number of children born to a Hadza woman during her lifetime (formally known as the Total Fertility Rate) is 6 (i.e. 6.2), and the mean interval between births is 3.4 years. The TFR of Hadza women is slightly higher than the median for all warm-climate foragers of 5.4. This relatively high TFR suggests that Hadza women obtain sufficient energy from their food to support reproduction (Marlowe, 2010)(pp.149&159).

In regards to diet, data among the Hadza reveal that a greater male contribution to the diet is predicted of higher TFR (Marlowe, 2010)(p.149). This is consistent with other foraging societies in which higher male contribution to the diet is predictive of younger age at weaning, greater female reproductive success (which is the mean number of children surviving to age 15), and a higher TFR. However, reproductive success is only correlated with TFR, not with mortality rates, which suggests that women use food provided by mean to speed up their reproduction rates (Marlowe, 2010)(p.271). This is likely why Hadza women place more importance on men being good foragers than they do on physical characteristics. When controlling for age, men who have better reputations as hunters have more children born and more children who survive (Marlowe, 2010)(p.187).

Child-bearing/birth/rearing. Child-bearing and childbirth do not significantly affect Hadza women's ability to forage for food. Women often forage until the day they give birth and return to good shape within a few days after delivery, at which point they return to foraging and carry the newborn on their back (Marlowe, 2010)(pp.64-65). While women can easily manage their daily foraging activities with one newborn in tow, this would be difficult with two children, making the mean birth interval of 3.4 years ideal for Hadza women. However, some Hadza women have birth intervals as short as one year, posing a problem when it comes to keeping with their daily foraging activities (Marlowe, 2010)(p.159).

Women often breastfeed for a long time, likely several years, in order to prolong the amount of time until another pregnancy (though it should be noted that breast-feeding is not a 100% effective method of contraception). Women may paint their breasts with a bitter herbal concoction in order to force cessation of breast-feeding. As previously stated, the Hadza prefer a porridge-like food made of baobab mixed with water as an infant-weaning food and will start to introduce this food early in the infant's life. Once infants have 2 to 4 teeth their mother will feed them pre-chewed meat and by 18 months, most infants are consuming the full range of adult foods (Jelliffe et al., 1962)(pp.909-910).

Hadza children learn essential life skills early on from their parents. For example, 10-year-old boys are fully capable of shooting enough birds and small game to feed themselves and it is not unusual for such a boy to leave his parents and join another group of Hadza (Jelliffe et al., 1962)(p.908). Young children are quite capable of foraging and collecting considerable amounts of food, though older children are more successful at foraging, and some children are capable of collecting enough food to meet their daily caloric needs (For example: A 10-year-old Hadza female exceeded 10,000 kcals in her daily foraging returns). However, child age is not a significant predictor of how much food children bring back to the camp to share, only of the total amount of food collected. Many researchers embrace the "embodied capital model which argues that prolonged investment in growth and delayed reproduction evolved because a long training period is required to learn difficult foraging tasks and become a self-sufficient forager". However, these data suggest that, despite increases in foraging efficiency with age, the relative foraging success of even young children is quite high. This supports the idea that the provision of food by juveniles, combined with food sharing, may have allowed for increased brain growth during hominin evolution AND improved survival rates of children and adults, contributing to longer lifespans (Crittenden, Conklin-Brittain, Zes, Schoeninger, & Marlowe, 2013).

The high number of children Hadza women typically bear may also be related to the fact that the cost of bearing and raising children is lower than in other societies, as Hadza children are able to begin foraging for food (and thus providing, in part, for their own caloric needs) early in life. The ease of navigating Hadzaland and the relatively large amounts of food and water available supports children's ability to being foraging at a young age (Redd, 1998).

Male parenting and food provisioning. Marlowe studied the care provided by Hadza fathers, with particular emphasis on the amount of food fathers brought back to camp in order to determine whether Hadza men's behavior is focused on provisioning their children or on increasing their mating opportunities. Generally, he found that Hadza men with only stepchildren brought significantly less food back to the camp (877 kcals per child) compared to men with only biological children (1901 kcals per child). Additionally, biological fathers provided more calories from meat (349 kcals/child) than stepfathers (63 kcals/child). Marlowe also found that

Hadza men provided more direct care to their children than to their stepchildren. Marlowe's findings were mixed, suggesting that Hadza men are likely more motivated by caring for their children than by increasing their mating opportunities; however, they may trade off parenting effort for mating effort if greater mating opportunities present themselves (Marlowe, 1999a, 1999b). (Note: Marlowe has several caveats related to the relative skillfulness of stepfathers compared to biological fathers in regards to hunting. Let me know if you want more information on these caveats or on male provisioning of food for biological and/or step-children).

Sex and food. Some data from Frank Marlowe suggests that Hadza men believe that providing meat for women may increase the odds of successful sexual exploits; though it is not clear whether this belief plays out in reality: "When I asked men if they could increase their chances of having an affair on safari by offering meat to a woman, several men said yes. And I have observed them trying. Yet it is rare that a man can exchange meat for sex directly because, once in camp, he cannot keep meat hidden and so must share it with everyone. Of course, the inability to make direct exchanges is precisely why a man must show off by sharing with everyone. Once meat is shared out, however, he loses his leverage. If a woman repays him with sex, she is providing a public good others can free-ride on. Because the showoff provides more meat, other men may have to show greater tolerance of his affairs with their wives. Or perhaps single women might pay him back. But which woman and why her? It might be more plausible that, if women are choosing to have affairs with the best hunters, it is because they are gene shopping and hunting success is a good genes indicator. I assume men try to show off, but it is not yet clear if it pays, because it is not clear whether in return for their meat, men gain additional extramarital mating opportunities or better treatment of their children" (Marlowe, 1999b)(p.403).

Competition for food. The Hadza are not the only primates to thrive in this region. The baboon *Papio anubis*, one of the other African primates known to successfully inhabit savanna woodland habitats, also lives in the area. Since baboons eat many of the same foods as the Hadza, the Hadza are often forced into competing with the baboons for resources such as berries, baobab, some small species of game, certain types of honey, and even several species of shallow tubers (Berbesque & Marlowe, 2009)(p.756).

<u>Ingestion</u>

The Hadza actually have dentition distinct from the majority of humans today. Specifically, they typically have 20 back teeth, in comparison to the typical 16 back teeth among modern humans. The Hadza also have a tip-to-tip bite between their upper and lower front teeth, with the edges of their lowers aligning to form a perfect arch. This perfect arch is indicative of the fact that the sizes of Hadza teeth and jaws match perfectly, contract to modern humans, whose teeth are often do not fit properly in our jaws. The Hadza's teeth and jaws are much more similar to humans' ancestors, monkeys, and apes, than to modern humans. The fact that Hadza's jaws fit their teeth and those of most modern humans don't, is related to their diet. The size of the jaw changes with heavy use during childhood, such that, greater use related to higher chewing strains (such as when eating fibrous tubers) results in a longer jaw, which is more able to fit teeth than a shorter jaw. Most humans today feed children foods that have been processed to a fair degree and this processing reduces the strain on the jaw, resulting in the teeth not fitting properly (and subsequent dental bills) (Ungar, 2017). (Funny quote from Ungar: "I remember asking my wife not to cut our daughters' meat into such small pieces when they were young. 'Let them chew,' I begged. She replied that she'd rather pay for braces than have them choke. I lost that argument.")

As previously mentioned, the Hadza's diet, particular the consumption of tubers, results in a greater amount of wear on their teeth, particularly their anterior dentition, compared with most agricultural populations. This pattern of wear is consistent with other hunter-gatherer populations (Berbesque et al., 2012). While some people may believe this wear is a bad thing, according to Peter Ungar, "teeth are evolved to wear in a way that keeps or makes them functionally efficient." He specifically refers to the Hadza and that, though their teeth are more worn than most humans' teeth, the wear on their teeth occurs in such a way (i.e. by creating sharp edges) that makes the teeth more efficient (Zhang, 2017).

The wear patterns among the Hadza vary by sex. Hadza women have more heavily worn anterior dentition than do males. This variation is likely related to differences in diet and the use of teeth as tools. Specifically, Hadza women eat more tubers (as has been mentioned) and they use their anterior teeth as tools, such as when peeling the tough skin off of tubers. Men use their teeth less for the purposes of eating tubers because they: a) eat tubers less often and b) are more likely to carry a knife and use a knife to peel the tuber instead of their teeth. Males exhibit greater asymmetry in their dental wear, with heavier wear on the left compared to the right. This is likely related to their use of teeth as tools for working arrows and tightening bow strings. The men likely stabilize the object with the left side of their mouth and then pull it away from the face on the right side (Berbesque et al., 2012).

Digestion

Tubers. The ekwa tuber frequently consumed by the Hadza contains up to 80% inedible material and the absolute amount of digestible carbohydrates (such as starch, mono- and di-saccharides) is much lower than typically agricultural tubers. A result of the lower amounts of digestible carbohydrates is that the Hadza tubers provide, at best, half of the energy of cultivated tubers (Schoeninger et al., 2001)(p.24).

Berries. In contrast to the tubers, the common berries consumed by the Hadza actually have higher amounts of digestible carbohydrates than American agricultural berries, such as blackberries and raspberries (Murray et al., 2001)(pp.9-10).

Note: Really no data in the Hadza in this regard.

Macronutrients in a traditional Hadza diet

Kuipers et al. attempted to reconstruct Paleolithic diets using different foraging strategies, one of which is relatively similar to the Hadza's modern-day strategies. According to Kuipers' model, this type of diet would consist of approximately 39%, 40%, and 25% of calories from fats, carbohydrates, and protein, respectively (R. S. Kuipers et al., 2010) (see table on next page). This model seems fairly to similar to what might be expected based on Kaplan et al.'s review of the

Hadza diet, in which they examined the daily calories from different foods sources, such as meat, roots, and fruits (Kaplan et al., 2000).

As previously stated, when examining the contribution of various foods to daily caloric intake, Kaplan et al. found that the Hadza consume approximately 4030 kcals/day and 1940 kcals/day (48%), 1214 kcals/day (30%), 621 kcals/day (15%), and 255 kcals/day (6%) come from meat, roots, fruits, and invertebrates (bee larvae), respectively (Kaplan et al., 2000)(p.166).

The macronutrient composition of the traditional Hadza diet varies by sex. Berbesque et al. specifically examined sex differences in the mean percent eating frequency among the Hadza by food type. They found that 38.1%, 30.8%, 13.8%, 5.1%, 5.1%, and 7.2% of the time, males ate berries, meat, tubers, honey, baobab, and traded foods. In females, 31.7%, 26.4%, 23.5%, 7.4%, 6.8%, and 4.2% of the time, females at berries, tubers, meat, traded foods, baobab, and honey. Males at significantly more meat than females; whereas, females at significantly more tubers than males (Berbesque, Marlowe, & Crittenden, 2011)(p.343).

The three tables below show the proposed macronutrient composition of a typical Hadza diet, along with the nutrient compositions of traditional Hadza foods, including honey, baobab, berries, and tubers.

Table 4. Reconstructed Paleolithic diets at different foraging strategies*

(Medians and ranges)

Nutrient	Meat based (non-selective; Eaton *et al.*[26])	Meat based (non-selective; Cordain *et al.*[27])	Meat based (selective; Model 1)		Fish/meat based (non-selective; Model 2)		Fish/meat based (selective; Model 3)		Fish based (non-selective; Model 4)	
	Median	Median	Median	Range	Median	Range	Median	Range	Median	Range
Animal/plant subsistence ratio										
Plant/animal (en%/en%)	65/35†	45/55‡	50/50	70–30/30–70	50/50	70–30/30–70	55/45	70–30/30–70	57/43	70–30/30–70
Meat/fish (en%/en%)	100/0	100/0	100/0		60/40	0–100/100–0	58/52	0–100/100–0	0/100	
Muscle/marrow/brain (en%/en%)	–	–	30/56/14	98/1/1–0/60/20	–	–	20/64/16	50/40/10–0/80/20		
Plants (g/d)	1653§	988	1607	804–1875	1257	539–1875	1078	539–1257	1257	534–1875
Meat (g/d)	890§	1031	695	288–1213	360	0–1028	128	0–411	0	–
Fish (g/d)	0	–	0		381	0–1243	681	357–952	867	533–1243
Macronutrients										
Energy (kJ/d)	12 500†	12 500‡	12 500		12 500		12 500		12 500	
Protein (en%)	37‖	30‡	25	8–35	29	22–35	27	16–35	29	22–35
From plants	9·2	5·4	8·4	4–10	8·4	4–10	7·0	4–10	7·7	4–10
From animals	29	25	16·9	0–32	21	14–40	19	6–29	22	13–31
Carbohydrate (en%)	41‖	34‡	40	20–47	40	19–48	40	20–47	39	19–48
Fat (en%)	22‖	36‡	39	21–72	30	20–46	34	25–62	34	20–46
Protein (g/d)	236	191	160	51–223	185	140–223	172	102–223	185	140–223
From plants	60¶	–	54	26–64	54	27–63	45	27–63	49	26–64
From animals	191¶	–	108	0–204	134	92–253	119	38–185	140	83–198
Carbohydrate (g/d)	294	243	267	144–337	287	136–345	287	144–337	280	136–344
Fat (g/d)	70	114	124	67–229	95	64–146	108	79–197	108	64–146
Essential fatty acids										
ALA (18 : 3*n*-3, g/d)	12·6§	15·0	11·9	7·73–13·4	13·5	6·57–18·5	14·8	8·63–17·4	12·6	6·57–17·0
EPA (20 : 5*n*-3, g/d)	0·39§	0·71	0·38	0·14–0·59	1·74	0·56–6·61	1·41	0·30–2·80	3·45	1·41–6·61
DPA (22 : 5*n*-3, g/d)	0·42§	0·96	0·52	0·20–0·90	1·53	0·66–4·71	1·03	0·20–1·93	2·36	0·89–4·71
DHA (22 : 6*n*-3, g/d)	0·27§	0·41	1·35	0·29–2·84	4·30	0·32–21·7	4·36	0·81–8·79	10·8	3·93–21·7
EPA + DHA (g/d)	0·66§	1·12	1·70	0·87–2·98	6·10	0·88–28·3	5·83	1·38–11·6	14·2	5·34–28·3
LCP *n*-3 (g/d)	1·61	2·01	2·26	1·53–3·52	7·64	1·47–33·9	6·89	1·76–13·8	17·0	6·33–33·9
n-3 (g/d)	17·5	20·3	16·6	12·2–18·5	25·9	16·0–44·4	25·2	14·3–31·9	34·1	22·1–44·4
LA (18 : 2*n*-6, g/d)	8·84§	14·3	9·98	8·60–11·2	11·3	5·53–19·8	9·83	7·20–12·2	7·46	5·53–9·96
AA (20 : 4*n*-6, g/d)	1·81§	2·41	1·81	1·15–2·77	3·65	1·69–10·7	2·84	1·15–4·61	5·46	2·14–10·7
LCP *n*-6 (g/d)	2·23	2·81	2·54	2·03–3·99	5·09	2·00–17·4	4·51	1·91–7·64	8·84	3·41–17·4
n-6 (g/d)	14·8	17·9	13·4	11·7–15·6	17·9	10·9–25·9	15·2	12·9–16·2	17·6	10·9–24·2
LCP (g/d)	3·75	4·70	4·75	3·46–7·46	12·5	3·38–51·3	11·2	3·77–21·2	25·8	9·74–51·3
ALA/LA (g/g)	0·70	1·04	1·12	0·70–1·56	1·25	0·61–1·79	1·47	0·93–1·75	1·64	1·19–1·79
(EPA + DHA)/AA (g/g)	0·49	0·47	0·95	0·49–1·41	1·82	0·36–2·66	2·13	0·78–2·58	2·60	2·45–2·66
LCP *n*-3/LCP *n*-6 (g/g)	0·72	0·72	0·84	0·74–0·92	1·56	0·67–1·96	1·86	0·22–3·07	1·92	1·83–1·96
n-3/*n*-6 (g/g)	1·19	1·13	1·22	0·79–1·59	1·50	0·66–2·05	1·69	1·01–2·01	1·94	1·82–2·05
ALA (18 : 3*n*-3, en%)	4·0	4·7	3·7	2·4–4·2	4·2	2·1–5·8	4·7	2·7–5·5	4·0	2·1–5·3
LCP *n*-3 (en%)	0·5	0·6	0·7	0·5–1·1	2·4	0·5–11	2·9	3·9–4·9	2·9	3·9–4·9
LA (18 : 2*n*-6, en%)	2·8	4·5	3·1	2·7–3·5	3·6	1·7–6·2	3·1	2·3–3·8	2·3	1·7–3·1
LCP *n*-6 (en%)	0·7	0·9	0·8	0·6–1·3	1·6	0·6–5·5	1·4	0·6–2·4	2·8	1·1–5·5
Other fatty acids and cholesterol										
SFA (g/d)	31·7	38·8	36·3	23·0–56·1	38·1	21·8–59·1	36·4	31·6–51·6	38·0	21·8–53·9
MUFA (g/d)	23·4	29·2	58·8	11·5–124	23·6	9·90–50·1	41.3	14·5–109	17·9	9·90–26·5
PUFA (g/d)	29·8	34·4	27·2	25·7–26·2	40·2	26·9–66·6	36·4	26·4–43·9	48·3	29·5–66·6
P/S ratio (g/g)	1·40‖	1·10	0·75	0·46–1·23	1·07	0·68–1·37	1·05	0·58–1·34	1·30	1·23–1·37
Cholesterol (mg/d)	480‖	830	3138	651–6910	498	321–748	914	430–3107	523	321–748

TABLE 1

Nutritional composition of foods consumed by Hadza foragers

Sample[1]	Moisture[2] %	Crude protein (g/100 g dry wt.)	Fat (g/100 g dry wt.)	Starch[3] (g/100 g dry wt.)	Simple sugars[4] (g/100 g dry wt.)	Dietary fiber[5] (g/100 g dry wt.)	Ash (g/100 g dry wt.)	Energy[6] (kJ (kcal) /100 g dry wt.)
Honey								
Ba'alako-1	17.8	3.8	8.1	tr	87.7	—	0.4	1835 (439)
Ba'alako-2	12.4	2.7	6.2	tr	90.5	—	0.6	1793 (429)
N!ateko-1	23.5	3.2	5.1	tr	90.8	—	0.9	1764 (422)
N!ateko-2	—	3.1	1.3	tr	94.8	—	0.8	1685 (403)
Kanoa-1	21.6	3.1	6.2	tr	89.9	—	0.8	1789 (428)
Kanoa-2	—	1.7	1.5	tr	96.0	—	—[7]	1689 (404)
Baobab								
Ground seed	4.8	36.3	29.3	tr	11.2	14.1	9.1	1898 (454)
Pulp	4.7	2.5	0.7	11.0	35.6	45.1	5.1	849 (203)
Non-baobab fruit								
Kisinubi (*Cordia* cf *sinensis*)	73.0	12.6	1.8	—	68.8	11.6	5.2	1430 (342)
Undushibi (*Cordia* cf *sinensis*)	71.0	15.2	—[7]	—	61.4	13.6	7.8	1354 (324)
Masakapi (*Cordia* cf *crenata*)	69.0	12.7	1.9	—	62.5	17.8	5.1	1329 (318)
Hlukayebe (*Grewia villosa*)	24.0	7.1	—[7]	—	72.7	13.4	4.8	1409 (337)
Kongolubi (*Grewia bicolor*)	26.0	12.0	2.0	—	66.1	13.2	6.7	1379 (330)
Pawe (*Sclerocarya birrea*)	83.0	3.6	—[7]	—	49.9	37.7	6.8	970 (232)

Note: tr is $< 0.5\%$; — is not determined.

[1] All samples were collected during the 1994 wet season, except Ba'alako-2, which was collected during the dry season of 1993, and Pawe which was collected during the dry season of 1997. The two samples of N!ateko were collected at different locations in the 1994 wet season.

[2] Non-baobab fruit moisture was measured in the field (see text) and is reported with seeds intact, except for Pawe where the nut-like seed was removed prior to weight determination.

[3] Based on carbohydrate analyses in other East African fruits (Conklin–Brittain *et al.*, 1998), we assume that the berries contain only a trace of starch.

[4] The fraction containing monosaccharides and disaccharides was calculated by difference.

[5] Based on commercial honeys (Gojmerac, 1981), we assume that dietary fiber in the honeys is virtually absent.

[6] Energy was calculated using 16.7 kJ (4 kcal)/g for protein and carbohydrate and 37.6 kJ (9 kcal)/g for fat.

[7] Assumed level equivalent to that in similar samples.

TABLE 4

Edible portion and macronutrients of selected tubers from East Africa

Hadza name[1] *Genus species*	Moisture %	Edible portion[2] (g/100 g dry, peeled tuber)	Crude protein (g/100 g dry, peeled tuber)	Starch (g/100 g dry, peeled tuber)	Simple sugars[3] (g/100 g dry, peeled tuber)	Pectin (g/100 g dry, peeled tuber)	Ash (g/100 g dry, peeled tuber)	Energy[4] (kJ (kcal) /100 g dry wt.)
//ekwa	77.7	42.5	4.5	26.0	6.2	0.8	5.1	610 (146)
Vigna frutescens	± 3.8	± 20.9	± 1.1	± 18.2	± 3.1	± 0.8	± 1.6	± 322 (± 77)
Makaritako	79.9	56.9	6.9	19.6	23.2	1.3	5.9	832 (199)
Eminia entennulifa								
Panjuko	85.9	91.8	2.3	23.9	48.3	11.8	5.5	1246 (298)
Ipomoea transvaalensis								

Note: [1] Data are the mean of duplicate analyses, except for //ekwa data which are mean ± standard deviation of the analyses of five different tubers (see Table 3).

[2] Edible portion is that fraction of the tuber solubilized by stomaching hydrated sample in the presence of salivary amylase.

[3] The fraction containing monosaccharides and disaccharides was determined by difference.

[4] Energy was calculated using 16.72 kJ (4 kcal)/g dry wt. for protein and digestible carbohydrate.

Fatty acid composition of traditional Hadza diets. In the previously mentioned reconstruction of Paleolithic diets, Kuipers et al. estimated the fatty acid composition of such a diet, estimating a consumption of 36.3 grams/day, 58.8 grams/day, 27.2 grams/day, 16.6 grams/day, and 13.4 grams/day of saturated fatty acids, monounsaturated fatty acids (MUFAs), polyunsaturated fatty acids (PUFAs), omega-3 fatty acids, and omega-6 fatty acids. Additionally, they estimated the ratio of poly- and mono-unsaturated fatty acids to SFAs as 0.75 and the ratio of omega-3 to omega-6 fatty acids as 1.22 (R. S. Kuipers et al., 2010).

Baobab seeds contain the largest amount of fat per 100 grams of dry weight of any of the Hadza's plant-based foods. Specifically, ground baobab seeds contain 29.3 grams of fat per 100 grams dry weight (<2% of kcals from fat). In comparison, baobab pulp contains negligible amounts of fat (0.7g/100g dry weight) (Murray et al., 2001)(p.8). The primary fatty acids found in baobab seed include the two unsaturated fatty acids oleic acid (18:1) and linoleic acid(18:2) as well as the saturated fatty acid, palmitic acid, each of which contribute 35.8%, 30.7%, and 24.2% of calories, respectively. Overall, baobab seed oil is approximately 31.7% saturated fatty acid, 37% monounsaturated fatty acids, and 31.7% polyunsaturated fatty acids (Osman, 2004)(p.31). Smaller amounts of linolenic acid (an omega-3 fatty acid), stearic acid (a saturated fatty acid), and arachidonic acid (an omega-6 fatty acid), are all present in the oil of the baobab seed (Kamatou et al., 2011). The fat content in the baobab seeds is great enough to raise the energy yield from the seeds to a level roughly equivalent to that of honey, making this an important energy source for the Hadza, as baobab seeds are a more dependable energy source than honey (Murray et al., 2001)(p.12).

Due to the fact that the Hadza eat honey with the bee larvae present, honey contributes more fat to the Hadza diet than would typically be expected. However, overall fat content in honey is still low. The ba'alako, nateko, and kanoa honeys contain 6.2-8.1, 1.3-5.1, and 1.5-6.2 grams of fat per 100 grams of dry weight (Murray et al., 2001)(p.8).

Tubers contribute negligible amounts of fat to the Hadza diet. For example, the four commonly consumed varieties of tubers, ekwa, makalidako, shumuko, and do-aiko, contain approximately 1.1, 0.6, 2.6, and 3.4 grams of fat per 100 grams of dry weight. Meaning that fat accounts for a small percentage of the total calories in wild tubers (i.e. less than 10%) (Schoeninger et al., 2001)(p.3). Berries also contribute few, if any, calories from fat to the diet, with only a few berries containing and fat at all. For example, the kisinubi, masakapi, and kongolubi berries contain 1.8, 1.9, and 2.0 grams of fat per 100 grams of dry weight (Murray et al., 2001)(p.8).

The fat content of the game consumed by the Hadza varies based on the type of animal. For example, roasted antelope contains about 2.7 grams of fat per 100 grams. Of this fat, 1.0g, 0.6g, and 0.6g are saturated, monounsaturated, and polyunsaturated, respectively. Additionally, antelope contains 100mg of omega-3 and 330 mg of omega-6 fatty acids per 100g, after roasting. Buffalo contains 5.4g of total fat, with 2.3g, 2.1g, and 0.3g of saturated, monounsaturated, and polyunsaturated fat, per 100g roasted meat. Buffalo also contains 29.0mg omega-3 fatty acids and 197mg of omega-6 fatty acids per 100g roasted.

Note: I cannot find any articles about the game meat consumed by Hadza in regards to either the macronutrient or micronutrient composition of the game meat. My guess is that this data is not around because of the large variability in the types of game the Hadza eat and in the amounts and availability of game meat. I looked for a while but did not want to waste time, as the data did not appear to exist. So, I just used nutritiondata.com to pull some representative animals, such as antelope. Let me know if you'd like for me to continue looking into this. FYI-Rebecca did not have any information about game nutrient composition in her articles and had very little data on the micronutrients in Hadza foods.

Protein. As previously mentioned, it is estimated that the Hadza consume about 25% of their daily Calories from protein, with 8.4% from plant sources and 16.9% from animal sources (Remko S. Kuipers et al., 2010). Protein is highly valued by the Hadza due to its relatively limited availability. Meat, of course, is the optimal source of protein, followed by baobab seeds.

Of the plant sources of protein, baobab seeds contribute the largest proportion of protein to the Hadza diet. Similar to fat, baobab seeds contain the largest amount of protein per 100 grams dry weight of any of the Hadza's plant-based foods. Ground baobab seeds contain 36.3 grams of protein per 100 grams dry weight. The pulp contains negligible amounts of protein (2.5g/100g dry weight) (Murray et al., 2001)(p.8). Both the seeds and the fruit pulp of the baobab contain protein with appreciable amounts of the amino acids glutamine, aspartic acid, and arginine. The seeds also contains notable amounts of the amino acids leucine, glycine, proline, serine, phenylalanine, and lysine. The seeds' essential amino acid content is appreciable, especially for a plant seed, but is not entirely complete. Both the seed and the fruit pulp are limited in the sulfur-containing amino acids, particularly methionine. Lysine, an amino acid that is commonly available in limited amounts in plant seed proteins such as those in cereals, is present in significant quantities in baobab seeds. This makes baobab seed a very valuable protein source (Osman, 2004)(pp.30-31)(Chadare et al., 2008)(p.265). Since baobab seeds are close to containing sufficient amounts of all essential amino acids, supplementing seed consumption with small amounts of meat is sufficient to provide adequate intake of essential amino acids (i.e. to create an complete protein) (Murray et al., 2001)(p10). (Side Note: This has important implications for the Hadza women who consume less meat than the Hadza men, and are thus more reliant upon plants for their protein.)

Overall, baobab seeds contain a significantly greater percent of calories from protein (28.4%) than many other local plants, including sorghum, millet, and manioc, which contain 11.4%, 11.0%, and 0.9% of calories from protein, respectively. Compared to the World Health Organization's standard amino acid composition for an ideal complete protein, baobab seed contains a more complete amino acid content than all of the other local agricultural plants, except for beans. Interestingly, despite this, the Hadza do not trade for beans or eat any of the wild beans present in Hadzaland (Murray et al., 2001)(p.10).

Tubers, berries, and honey contribute relatively small proportions of protein to the Hadza diet. The ekwa, makaritako, and panjuko tubers contain 4.5, 6.9, and 2.3 grams of protein per 100 grams of dry weight (Schoeninger et al., 2001). The kisinubi, undushibi, masakapi, and kongolubi berries contain 12.6, 15.2, 12.7, and 12.0 grams of protein per 100 grams dry weight. The hlukayebe and pawe (a drupe, not a berry) contain less protein, with only 7.1 and 3.6 grams of protein per 100 grams dry weight. The berries of the Hadzaland are higher in protein content than typical American berries. Honey contributes even small amounts of protein to the diet.

However, similar to the fat in honey consumed by the Hadza, there is a larger amount of protein than would normally be consumed because of the concomitant consumption of bee larvae. The typical varieties of honey consumed contain between 1.7 and 3.8 grams of protein per 100 grams dry weight (Murray et al., 2001)(p.8).

Antelope contains about 29.4g of protein per 100g (after roasting), which contributes substantially to daily protein needs. Buffalo also contributes substantially to protein needs, providing 33.8g/100g.

Carbohydrates. As previously mentioned, the Hadza likely consume about 39% of their Calories from carbohydrates.

Sugars. Honey provides the largest amount of simple sugars to the Hadza diet. The honey consumed by the Hadza predominantly consists of simple sugars, with amounts ranging from 87.7 to 96.0 grams per 100 grams dry weight and contributing 80-95% of the energy in the honey. Fruits and berries also contribute significantly to the amount of simple sugars in the Hadza diet. Hlukayebe, kisinubi, and kongolubi contain the largest quantity of simple sugars, at 72.7, 68.8, and 66.1 grams per 100 grams dry weight. Compared to cultivated American blackberries and raspberries, the berries eaten by the Hadza are slightly higher in digestible carbohydrate (sugars) (61-73g versus 54g/100g dry wt.). The berries of the Hadzaland are also higher in total overall energy yield (318-342 kcal/100 g dry wt. vs. 288 kcal & 282 kcal/100 g dry wt. for Rubus sp.). Thus, the berries provide the Hadza with a good source of sugars and calories (Murray et al., 2001)(pp.9-10). The berries provide more calories than baobab pulp, but not quite as much as baobab seeds or honey (Murray et al., 2001)(p.9). Pawe contains the smallest amount of simple sugars, at 49.9 grams per 100 grams dry weight. Baobab pulp also contributes a fair amount of simple sugars, containing 35.6 grams of simple sugars per 100 grams dry weight. In contrast to baobab pulp, baobab seeds contribute few simple sugars to the Hadza diet, containing only 11.2 grams per 100 grams dry weight (Murray et al., 2001)(p.8).

With regards to tubers, there is a great deal of variability in the relative amounts of simple sugars. For example, ekwa contains only 6.2g/100g dry weight, whereas makaritako and panjuko contain 23.2 and 48.3g of simple sugars per 100g dry weight, respectively. Along with simple sugars, tubers contain starch. With ekwa, makaritako, and panjuko containing 26.0g, 19.6g, and 23.9g of starch per 100g dry weight, respectively. Overall, the absolute amounts of digestible carbohydrate including starch, monosaccharides, and disaccharides in the wild tubers consumed by the Hadza is significantly lower than that present in agricultural tubers (Schoeninger et al., 2001)(pp.8&24). The lower amounts of digestible carbohydrate available from the wild tubers yield lower amounts of calories overall. While cultivated tubers may yield on average around 400 kilocalories per 100 grams dry weight, the wild tubers of the Hadza provide less than 300 kilocalories per 100 grams dry weight on average, dropping to as low as 150-200 kilocalories per 100 grams of dry weight for some other commonly eaten tubers (Schoeninger et al., 2001)(pp.21-23). It has been suggested that the Hadza's wild tubers provide approximately half of the energy of cultivated tubers, and this does not even account for the tremendous amount of energy the Hadza women must put forth in order to acquire these tubers. Thus, it should not be surprising that tubers supply the fewest calories per weight of any food in the Hadza diet (Berbesque & Marlowe, 2009)(p.756).

In regards to mono- and disaccharides, the content of American and Hadza honeys are relatively similar. Honey contains highest levels of mono- and disaccharides (up to 96% of dry weight), followed by berries (60-70% dry weight), pawe fruit (50% dry weight), baobab pulp (36% dry weight), and baobab seeds (11% dry weight) (Murray et al., 2001)(pp.8-9). In tubers, there is a great amount of variation in the amount of mono- and disaccharides. Ekwa, makaritako, and panjuko have 6, 23.2, and 50g/100g dry weight of mono- and disaccharides, respectively (Schoeninger et al., 2001)(p.9).

The game consumed by the Hadza contains no carbohydrates, as they cook their meat, and any carbohydrates would be broken down prior to consumption due to the roasting process.

Fiber. Honey does not provide any dietary fiber to the Hadza's diet. The berries consumed by the Hadza contain anywhere from 11.6 to 17.8 g of dietary fiber per 100 grams dry weight (12-18% fiber by dry weight); whereas, pawe contains substantially more fiber, at 37.7g of dietary fiber per 100 grams dry weight (40% fiber by dry weight). Baobab seed provides small amounts of fiber (14.1g/100g dry weight); whereas, baobab pulp may provide a substantial amount of fiber. Murray et al. reported that baobab pulp contains 45.1g of fiber per 100g dry weight (45% fiber by dry weight). The high amount of fiber in baobab pulp means that it does not provide as many calories as baobab pulp.

Tubers such as ekwa frequently consumed by the Hadza contain as much as 80% inedible material. Other tubers that have more edible material may still have significant soluble fiber contents. Wild tubers differ more in their fiber content than do cultivated tubers (Schoeninger et al., 2001)(p.24). The amount of fiber in Hadza tubers varies based on whether the tuber is raw or cooked, as well as by species. With regards to ekwa, fiber in raw ekwa ranges from 13.5-41.4%; whereas, in cooked ekwa it ranges from 10.6-42.6%. Overall, the range of fiber content in raw tubers commonly consumed by the Hadza ranges from 13.3-56.9% and, in cooked tubers, from 10.6-43.0% (Crittenden, 2009)(pp.45-46).

Interestingly, the Hadza actually try to avoid consuming fiber. Fiber is in such large quantities, much larger than the highest fiber foods eaten in the developed world that the Hadza need to avoid fiber because it does not provide Calories to the diet and can inhibit the absorption of vital nutrients. This need to avoid fiber is one reason that the Hadza spit out part of the fibrous mass of tubers when consuming them (Marlowe, 2010)(p.130).

Micronutrients

Notes: I could not find vitamin and mineral information on the species of tubers consumed by the Hadza. I was able to find a book with micronutrient information about tubers and selected a tuber of the same genus as one of the traditional Hadza tubers. The tuber I selected is essentially an American sweet potato and is in the same genus, *Ipomoea,* as the Hadza tuber panjuako.

I also couldn't find specific vitamin and mineral information on the pawe fruit consumed by the Hadza. I used apricots to represent pawe. I used *Cordia africana* as a substitute for the berries consumed by the Hadza, as these berries are in the same class as that of the berries consumed by the Hadza, such as *Cordia sinensis.*

Vitamins in a Traditional Hadza Diet

Vitamin A. Carotenoid content of baobab pulp is fairly low, at 0.17ug of beta-carotene per gram of dry weight (Chadare et al., 2008). Sweet potatoes (comparison tuber) vary in their beta carotene content from about 0.14-1.4mg/100g, which is about 14185 IUs of vitamin A, well above the RDA (Food and Agricultural Organization of the United Nations, 1990). Apricots (comparison for pawe fruit) contains 674 IUs of vitamin A per piece of fruit, in the form of beta-carotene. The berries consumed by the Hadza (as represented by *Cordia africana*) contain 1063IUs/100g of vitamin A in the form of beta-carotene (El Reheem Mohamed, 2016). Antelope and buffalo meat do not contain any vitamin A.

Vitamin C. Data on the vitamin C content of baobab pulp is interesting, which some data suggesting that there is great variability in the vitamin C content by the tree on which the baobab grows, with a range from 150-500mg/100g (Chadare et al., 2008)(p.264). However, the majority of data suggests that baobab pulp is high in vitamin C, which in part explains its tart flavor. The vitamin C content of baobab pulp is likely 7-10 times higher than that of oranges (Kamatou et al., 2011), and data suggest that baobab pulp has the highest vitamin C content of any known natural fruit, containing 373 mg/100 g wet weight, whereas citrus fruits typically contain 30-50mg/100g (Chadare et al., 2008). Sweet potatoes contain a small amount of vitamin C, at 2.4mg/100g. Apricots contain 3.5mg of vitamin C per piece of fruit. Other than vitamins A and C pawe does not contain appreciable amounts of other nutrients. *Cordia africana* berries contain 8.9mg/100g of vitamin C (El Reheem Mohamed, 2016). Antelope and buffalo meat do not contain any vitamin C.

B Vitamins. Baobab pulp contains niacin and riboflavin, with data suggesting a range of 1.8-2.7mg/100g and 0.07mg-0.14mg/100g dry weight, respectively. Similar to baobab pulp, the seeds contain niacin and riboflavin, at averages of 1.0mg/100g and 0.14mg/100g of dry weight. The seeds also contain thiamine, with an average of 0.25mg/100g of dry weight (Chadare et al., 2008; Kamatou et al., 2011). Sweet potatoes contain small amounts of the B vitamins per 100g: thiamin-0.1mg, riboflavin-0.1mg, niacin-0.6mg, B6-0.2mg, folate-11.0mcg, and pantothenic acid-0.8mg. *Cordia africana* berries contain 0.018mg/100g of riboflavin, 0.313mg/100g of B6, and 0.055mcg/100g of folate (El Reheem Mohamed, 2016). Antelope meat contains 0.3mg, 0.7mg, and 9.0mcg/100g of thiamin, riboflavin, and folate, respectively. This contributes substantially to daily riboflavin requirements, providing 43% of daily needs per 100g. Buffalo meat provides a substantial amount of riboflavin, niacin, B6, B12, and pantothenic acid, at 0.5mg, 4.8mg, 0.5mg, and 2.4mcg/100g meat. It also contains small amounts of thiamin and folate, 0.1mg/100g and 21.0mcg/100g, respectively.

Other Vitamins. Sweet potatoes contain negligible amounts of vitamins E and K, 0.3mg/100g and 1.8mcg/100g, respectively. *Cordia africana* berries do not contain any vitamin E (El Reheem Mohamed, 2016). Buffalo contains a very small amount of vitamin E-0.2mg/100g.

Minerals in a Traditional Hadza Diet

Calcium. Baobab pulp contains an average of 301.8mg of calcium per 100g dry weight. Baobab seeds contain an average of 252mg of calcium per 100g dry weight (Chadare et al., 2008). Sweet potatoes contain a negligible amount of calcium-30mg/100g dry weight. *Cordia africana* berries contain a negligible amount of calcium-1.19mg/100g (El Reheem Mohamed, 2016). Antelope and buffalo contain negligible amounts of calcium at 4.0mg and 7.0mg/100g, respectively.

Phosphorus. Estimates of phosphorus content of baobab pulp range from 0.04mg/100g dry weight to 425mg/100g dry weight. There has not been any resolution regarding the average of amount of phosphorus in baobab pulp due to this wide range. Baobab seeds contain an average of 453mg of phosphorus per 100g dry weight (Chadare et al., 2008). Sweet potatoes contain only 47mg of phosphorous per 100g dry weight. *Cordia africana* berries contain 95mg/100g of phosphorous (El Reheem Mohamed, 2016). Antelope meat contains a reasonable amount of phosphorus, at 210mg/100g, which is quite a small serving, still contributing to 21% of daily needs. Buffalo meat also contains a decent amount of phosphorus, at 239mg/100g, 24% of daily needs.

Magnesium. Baobab pulp contains an average of 195.1mg of magnesium per 100g dry weight. Baobab seeds have an average of 402mg of magnesium per 100g of dry weight (Chadare et al., 2008). Sweet potatoes only contain 25mg/100g dry weight of magnesium. Antelope and buffalo meat contain 28.0mg and 26.0mg/100g of magnesium, respectively.

Sodium. Baobab pulp contains an average of 14.8mg of sodium/100g dry weight. Baobab seeds contain an average of 2.3mg of sodium/100g dry weight (Chadare et al., 2008). Sweet potatoes only contain about 55mg of sodium/100g dry weight. *Cordia africana* berries contain a strangely large quantity of sodium, at 957.8mg/100g (El Reheem Mohamed, 2016). Antelope and buffalo meat contain negligible amounts of sodium, at 54.0mg and 57.0mg/100g, respectively.

Potassium. Baobab pulp contains an average of 1793.8mg of potassium/100g dry weight; however, the range of potassium contain is quite wide, from 726mg/100g dry weight to 3272mg/100g dry weight. Baobab seeds contain an average of 908mg of potassium per 100g dry weight (Chadare et al., 2008). Sweet potatoes contain 337mg of potassium per 100g dry weight (I found this somewhat surprising since I assumed they would have more than this.). Antelope and buffalo meat contain 372mg and 316mg/100g of potassium, respectively.

Other minerals. Along with the minerals listed above, baobab pulp contains an average of 0.9mg/100g dry weight of copper, 0.7mg/100g of manganese, 1.7mg/100g of zinc, and iron content ranges from 1.1mg/100g to 10.4mg/100g dry weight. Baobab seeds contain average of 2.3mg/100g dry weight of copper, 1.1mg/100g of manganese, 5.0mg/100g of zinc, and 5.1mg/100g of iron (Chadare et al., 2008). Sweet potatoes also contain 0.2mg/100g of copper, 0.3mg/100g of manganese, 0.3mg/100g of zinc, and 0.6mg/100g of iron. *Cordia africana* berries contain 1.8mg/100g of iron and do not contain appreciable amounts of any other minerals (El Reheem Mohamed, 2016). Antelope meat contributes significantly to iron, zinc, and selenium needs, containing 4.2mg, 1.7mg, and 12.9mcg per 100g. Antelope meat also contains 0.2mg/100g of copper. Buffalo meat contributes substantial amounts of iron, zinc, and selenium to the diet, containing 4.9mg, 8.6mg, and 41.7mcg/100g, respectively. Buffalo meat also contains 0.2mg/100g of copper.

Anti-nutrients

Baobab pulp and seeds both contain anti-nutritional factors. The primary anti-nutritional factor in baobab pulp is tannins, though the levels of tannins are too low to be harmful (at 0.0051-0.0062%). Baobab seeds contain trypsin inhibitor, phytic acid, and tannins, at 5.7 Trypsin Inhibitor Activity/mg sample, 73mg/100g, and 23%, respectively. As previously mentioned, food processing techniques, such as treating baobab seeds with cold or hot water, hot alkali or hot acid treatments reduce tannic acid concentrations. Removing the hull of baobab seeds or treating with cold water or hot alkali treatments significantly reduces amylase inhibitors (Chadare et al., 2008). Also, while fermentation reduces the phytate and tannin contents of baobab seeds, the Hadza do not typically ferment foods (Nnam & Obiakor, 2003).

Gut Microbiota

Recent studies have examined the Hadza's gut microbiome and compared it to other, non-hunter-gatherer groups (Italians). These studies showed many differences in the gut microbiome of the Hadza compared to other groups. Specifically, the Hadza demonstrated greater abundance of Bacteroidetes and lower abundance of Firmicutes compared to Italians. The Hadza gut microbiome is also enriched in Prevotella and contains many bacteria from the Clostridiales genus, with many of these bacteria unclassified to date, suggesting an unusual arrangement of Clostridiales in the Hadza. Additionally, the Hadza have Proteobacteria and Spirochaetes in their gut microbiome, whereas, these bacteria were extremely rare in the Italians. In contrast, Actinobacteria is an important subcomponent of the Italian gut microbiome but these bacteria are rare among the Hadza gut microbiome. *Bifidobacterium* is also completely absent in the Hadza gut microbiome. This absence of *Bifidobacterium* distinguishes the Hadza from other humans, as no other human groups, to date, have demonstrated a complete absence of bifidobacteria. The Hadza's lack of consumption of dairy products and livestock animals likely explains their lack of bifidobacteria. Finally, the Hadza gut microbiome is characterized by some opportunistic organisms, including *Succinovibrio, Treponema*, and Proteobacteria. Researchers conclude that the differences in the Hadza microbiome compared to that of the Italians is likely an adaptation that enhances their ability to digest and extract nutrients from fibrous plant-based foods, like ekwa (Schnorr et al., 2014).

Along with similarities and differences in the composition of the gut microbiome between the Hadza and Italians, there are similarities and differences in the functionality of their respective microbiomes. Both groups have comparable functions, with the majority of genes responsible for metabolism, genetic information processing, and environmental information processing. Additionally, the genes responsible for metabolism are dominated by amino acid and carbohydrate metabolism. However, the Hadza have a greater proportion of genes in their gut microbiome with unknown functionality. Overall, the Hadza gut microbiome is enhanced in genes that aid in their processing of the unique foods in their diet. For example, their gut microbiomes are adapted for metabolizing complex polysaccharides, degrading branched-chain amino acids, and for synthesizing aromatic amino acids. The Hadza also have a greater ability to handle excess amino acids via fermentation to short-chain fatty acids or conversion to glucose, which is likely an adaptive response to meat intake. Italians, on the other hand, had genes for metabolizing xenobiotics, likely due to exposure to toxic chemicals or foreign compounds often found in industrialized environments. Whereas, the Hadza did not have these genes (Rampelli et al., 2015).

Comparisons between Hadza and other African populations suggests that both groups have gut microbiomes enriched in *Treponema, Prevotella,* and *Succinivibrio.* Overall, it appears that African populations, regardless of lifestyle, "possess an overall more similar gut microbiome to each other than to western populations" (Schnorr et al., 2014).

There are also sex differences in the gut microbiome of the Hadza. Specifically, women have a greater abundance of *Treponema* and men have greater abundance of *Eubacterium* and *Blautia.* These differences are attributed to the sexual division of labor among the Hadza (with men having a more mobile lifestyle and women staying closer to the camp) and to sex differences in food consumption. Specifically, greater *Treponema* in women is likely related to their greater consumption of tubers and may be an adaptation to help in digesting large amounts of fiber (Schnorr et al., 2014).

Finally, the Hadza demonstrate seasonal variations in their gut microbiomes related to changes in their diets. These variations are cyclical, with some bacteria disappearing during the dry season, only to reappear the following dry season. Overall, the gut microbiome of the Hadza for a given season, is indistinguishable from that same season measured several times, whereas, there are obvious distinctions between the seasons. During the dry season, the Hadza have more phylogenetic diversity in their gut microbiome and more unique operational taxonomic units (OTUs) than during the wet season. Bacteriodetes was one of the OTUs that varied significantly between seasons, declining during the wet season. Some Firmicutes OTUs also vary between wet and dry seasons. Succinivibrionaceae, Paraprevotellaceae, Spriochaetaceae, and Prevotellaceae families were particularly variable across seasons. One of the dietary reasons for these changes is the greater consumption of meat during the dry season, which leads to an enrichment in enzymes related to animal carbohydrates. Increased berry consumption during the wet season is associated with enriched fructan utilization. In general, the microbiota of the Hadza during the wet season is characterized by fewer plant, animal, and mucin carbohydrate active enzymes. Interestingly, the taxa that are undetectable during the wet season correspond with the same tax that are rare or completely absent in industrialized populations, regardless of the season, which is related to decreased diet variability during the wet season (Smits et al., 2017).

<u>Hadza Health</u>

Growth and Stature. While the nutritional content of the Hadza diet may be adequate enough to support good overall health, the Hadza show a slowed pattern of growth compared to individuals in industrial countries including America. The Hadza growth pattern starts out at a fast rate when they are nursing on demand, but after weaning, they grow slower than Americans. Hadza stature peaks at 24 years and 25 years in females, and males, respectively, which is later than developed countries. Additionally, the adolescent growth spurt in the Hadza is minor. This is interesting, as it was previously assumed that the adolescent growth spurt was universal in humans. It may, in fact, be an artifact of the agricultural and industrial revolutions. Indeed, Hadza growth is more similar to other mammals, particularly chimpanzees, than that of most humans. However, their overall growth velocity is also similar to other foragers (Marlowe, 2010)(pp.134-143).

The Hadza also exhibit sexual dimorphism in their statures, with the average Hadza male and female statures being 5’3” (162cm) and 4’9” (150.48cm), respectively. This degree of sexual dimorphism closely mimics other foraging populations. With regards to weight, however, the Hadza have a lesser degree of sexual dimorphism compared to that of other forages, at 1.14 and 1.20, respectively, Typically, Hadza males weigh 116.9 lbs. and females weigh 102.1 lbs. (Marlowe, 2010).

Like most African hunter-gatherers, the Hadza are relatively thin. The average BMI for male and female Hadza adults is approximately 20kg/m^2, close to ideal BMI for athletes, suggesting that the Hadza are not undernourished. This BMI is also lower than that of Westerners which are 27.5kg/m^2 and 25.6kg/m^2 for women and men, respectively (Marlowe, 2010). Corresponding with this relatively low BMI is a low percent of body fat. Hadza men and women have an average of 13.5% and 20.9% body fat, respectively, also similar to that of athletes (Pontzer et al., 2012). This is also lower than that of Western populations, in which the average percent body fat is 22.5% and 37.9% for males and females, respectively. Hadza males also have plenty of muscles to support the requirements of their hunter-gatherer lifestyle. In contrast to Western populations, the Hadza experience a decline in both BMI and body fat percentage with age (Sherry & Marlowe, 2007)(p.114).

Disease risk. Overall, the Hadza are in very good health, having good eyesight, hearing, and teeth. Additionally, cancers are not common among the Hadza, which is similar to most other foragers. Obesity is also quite unusual. This lack of chronic diseases among the Hadza could potentially be related to their active lifestyles and some of the foods they consume (Marlowe, 2010)(p.150). For instance, berries consumed by the Hadza have antioxidant, anti-inflammatory, and anti-diabetic activities (El Reheem Mohamed, 2016). The most common illness among the Hadza are eye infections related to smoke exposure, scabies, backaches, malaria, and broken bones and wounds from accidents (such as when trying to access to a bee hive high in a tree). The Hadza get lice and, similar to other primates, pick lice out of each other’s hair and then eat the lice (Marlowe, 2010)(p.66).

Despite overall good dental health, recent data suggest that the incidence of periodontal disease, dental caries, and orthodontic disorders have increased in a subset of the Hadza populations. This increased incidence of dental disease is directly related to diet and the adoption of a more agricultural diet. For example, Hadza women who live in villages instead of the bush who consume a diet consisting primarily of agricultural products (such as maize) experience more caries and periodontal disease compared to those Hadza who live in the bush and/or consume a wild-food diet. However, in men, the situation is slightly different, as men who live in the bush and consume a wild-food diet have more caries than those eating a more agricultural diet. This is likely due to the large amount of honey consumed by Hadza men living in the bush (Crittenden et al., 2017).

Hadza children are also quite health and do not exhibit protein-energy malnutrition diseases (such as kwashiorkor) or anemia- which is likely related to prolonged breast-feeding and the introduction of meat into children's diets at as early as 6 months of age. They also have a low incidence of roundworm infections, which could be related to their nomadic existence. The Hadza children to exhibit a high incidence of conjunctivitis (30%), which could be related to smoke or dust exposure, or poor water supply during the dry season (Jelliffe et al., 1962).

Lifespan. A cross-cultural comparison regarding the longevity of hunter-gatherers found that the life-expectancy of the Hadza at any given age is about two years longer than other hunter-gatherer adults at said age. This same study predicted the Hadza modal age (most common) of mortality as 76 years old. Overall, there is great variability in life expectancy among hunter-gatherers.

The results of this study led to an interesting hypothesis that "there is a characteristic life span for our species, in which mortality decreases sharply from infancy through childhood, followed by a period in which mortality rates remain essentially constant to about age 40 years, after which mortality rises steadily in Gompertz fashion. The modal age of adult death is about seven decades, before which time humans remain vigorous producers, and after which senescence rapidly occurs and people die.

We hypothesize that human bodies are designed to function well for about seven decades in the environment in which our species evolved. Mortality rates differ among populations and among periods, especially in risks of violent death. However, those differences are small in a comparative cross-species perspective, and the similarity in mortality profiles of traditional peoples living in varying environments is impressive" (Gurven & Kaplan, 2007).

Mortality. The infant and juvenile mortality rates among the Hadza are much higher than that of Americans'; however, they are similar to other foragers. Specifically, the infant mortality rate (defined as the percentage of infants who die during the first year of life) is 21%. The juvenile mortality rate (defined as the percentage of children who die by the age of 15 years) is 46%. These relatively high mortality rates are actually quite similar to the rate at which chimpanzees die during their first few years of life; however, after age 5, human foragers have lower mortality rates than chimpanzees. The precise cause for high infant mortality rates among Hadza is not clear, though many of these deaths appear to be related to respiratory and diarrheal infections, with measles causing deaths in slightly older children. Malaria is also a common cause of death among the young (Marlowe, 2010)(p.150).

Causes of death among the adult Hadza are varied. Specifically, out of 75 deaths, one researcher found that "16% were attributed to measles, 15% to tuberculosis, pneumonia, or some other respiratory illness, 12% to oldness, 7% to childbirth, 7% to poisoning or bewitching, 5% to homicide, 4% when in the hospital or in a jail, 1% to falling from a tree when collecting honey, and 33% to 'other.'" Other potential causes of death include snakebites and viral diarrhea. It is important to note that compared to the mortality rates seen in industrialized countries, the mortality rates among the Hadza remain very high throughout all ages of life, from the young to the old (Marlowe, 2010)(p.141).

Nutrigenetics. Similar to other populations who consume a high-starch diet, the Hadza have a higher copy number of the salivary amylase gene (AMY1) than that of populations who consume starch-poor diets, like the Inuit! The AMY1 gene codes for the production of salivary amylase, which is the enzyme in the saliva responsible for breaking the bonds between glucose molecules in starch (Kumar & Eng, 2015)(p.189).

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