

Tubers as Fallback Foods and Their Impact on Hadza Hunter-Gatherers

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ABSTRACT The Hadza are hunter-gatherers in Tanzania. Their diet can be conveniently categorized into five main categories: tubers, berries, meat, baobab, and honey. We showed the Hadza photos of these foods and asked them to rank them in order of preference. Honey was ranked the highest. Tubers, as expected from their low caloric value, were ranked lowest. Given that tubers are least preferred, we used kilograms of tubers arriving in camp across the year as a minimum estimate of their availability. Tubers fit the definition of fallback foods because they are the most continuously available but least

preferred foods. Tubers are more often taken when berries are least available. We examined the impact of all foods by assessing variation in adult body mass index (BMI) and percent body fat (%BF) in relation to amount of foods arriving in camp. We found, controlling for region and season, women of reproductive age had a higher %BF in camps where more meat was acquired and a lower %BF where more tubers were taken. We discuss the implications of these results for the Hadza. We also discuss the importance of tubers in human evolution. *Am J Phys Anthropol* 140:751–758, 2009. ©2009 Wiley-Liss, Inc.

Natural selection should favor exploitation of low-quality foods when they minimize wasting and starvation during hard times. The term “fallback foods” refers to these lower quality foods that are eaten when more preferred foods are not available. Their importance has been investigated mostly in nonhuman primates (Malenky and Wrangham, 1994; Altmann, 2000; Furuichi et al., 2001; Lambert et al., 2004; Hanya et al., 2006). Primatologists assess food preferences by calculating the probability that an animal takes certain foods, controlled for their availability. When two foods are equally available and an animal routinely chooses one over the other it must be preferred. In the case of humans we can simply ask them which foods they prefer. That is what we did with the Hadza, who are hunter-gatherers in Tanzania. We use their preference rankings and our measures of food availabilities to determine which foods might be fallback foods and show that tubers fit the definition. We then examine which foods best predict the taking of tubers. Next we investigate the impact of tubers and other foods on Hadza physical condition. Finally, we discuss the implications of our results.

Tubers are underground storage organs (USO's), a category that includes corms, bulbs, and rhizomes—plants that store water underground even in the dry season and therefore tend to be available and edible year-round. Tubers are often quite deep (2 feet or more) underground, which makes it difficult for many animals to access them. This means they could have been an important niche for tool using primates to exploit. Even chimpanzees have been observed using sticks to dig shallow tubers (up to 250 mm or about 10 inches deep) at one savanna site (Hernandez-Aguilar et al., 2007). Although we have not observed it, some Hadza say baboons (*Papio anubis*) occasionally use sticks to dig for shallow tubers as well. Our ancestors could have for a very long time possessed a simple but effective digging stick for accessing deep tubers.

A variety of tubers are taken by many foragers described ethnographically (Peters and O'Brien, 1981;

Hladik et al., 1984; Odea, 1991; Kuhn and Stiner, 2001). Tubers are present within the latitudes that hominins have occupied from their inception through the first expansion of Homo out of Africa (O'Connell et al., 1999; Laden and Wrangham, 2005). Some hominins show dental features (e.g., thick enamel) that have been interpreted as adaptations to eating USOs (Hatley and Kappelman, 1980; Teaford and Ungar, 2000; Laden and Wrangham, 2005). Wrangham and Conklin-Brittain (2003) and Wrangham et al. (1999) have argued that tubers are implicated in the transition to Homo and that cooking is also implicated because tubers are usually roasted before eaten. It is still not clear just how important it is to roast tubers. Tubers eaten by the Hadza are usually roasted for about 5 min (Mallol et al., 2007). Nevertheless, they are quite willing to eat them raw. Hadza women often say they roast them because it makes them easier to peel. This reason for roasting is also noted in the film “The Hadza” (Hudson and Woodburn, 1966). However, the Hadza sometimes say roasting tubers makes them taste better (though to us the change in taste is slight).

In the following section, we describe the Hadza. We then explain the methods we used to ask three ques-

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tions: (1) how do the Hadza rank the foods in their diet in terms of taste preference, (2) what are the availabilities of these foods, and (3) what impact do these foods have on Hadza body condition. We evaluate the physical condition of Hadza adults as reflected in their body mass index (BMI) and percent body fat (%BF). If tubers are fallback foods we might see Hadza get leaner and lighter when more of their diet is comprised of tubers. If they do not, tubers must be of sufficient quality to prevent them losing weight and body fat.

THE HADZA

The Hadza are hunter-gatherers who live in a savanna-woodland habitat that encompasses about 4,000 km² around Lake Eyasi in northern Tanzania. The Hadza think of this area in terms of four different regions: Mangola, Dunduiya, Tli'ika, and Sipunga, each with its own character. Roughly, 250 Hadza live in each of the four areas. Hadzaland receives considerable rain (300–600 mm) during the months of December through May, and almost no rain from June through November. There are first the short rains followed by the long rains and we break the year into four seasons: early wet (Dec–Feb), late wet (Mar–May), early dry (Jun–Aug), and late dry (Sept–Nov).

The Hadza live in mobile camps that average 30 individuals (Marlowe, in press). During the late dry season, camps tend to be larger because they need to be near enough to a waterhole and there are only so many permanent waterholes. These camps move about every 6 weeks on average. Hadza feel free to move wherever they like but most tend to stay in the region where they grew up. Camp membership is often changing as people move in and out of camps. Residence is multilocal: couples live with the kin of the wife, the kin of the husband, the kin of both, or with no kin. Living with the wife's kin is most common (Woodburn, 1964; Blurton Jones et al., 2005).

Hadza men usually go foraging alone. They hunt only with bow and arrows, poisoned arrows in the case of larger game. They always have their bow and arrows with them, even when they carry an ax to access honey. While on walkabout they often feed themselves on berries and baobab. They take back to camp mainly meat and honey, as well as some baobab. They may eat much of the honey they find but take back to camp about half of their haul on average, and about 9/10 of their meat. Grown men rarely dig tubers.

Hadza women go foraging typically in groups of three to eight women plus nurslings and some older children. They mainly collect baobab fruit, gather a variety of berries, and dig tubers of several species. They use fire-hardened, sharpened branches as digging sticks to dig tubers almost every day. They usually roast some of their tubers once they finish digging and take the remainder (~ 3/4 of their haul) back to camp to feed others. The species eaten most frequently by the Hadza is //ekwa (*Vigna frutescens*). All of their tubers have high-fiber content but it is so high in //ekwa that one cannot swallow it and must spit out the quid after chewing it for a while.

METHODS

Food preferences

When food A and B are equally available and a forager is regularly choosing to take B over A, we might assume

TABLE 1. The species eaten by the Hadza that were used in the food preference experiments (five species of tubers, five species of berries, five animal species, the main type of honey and baobab)

Category	Hadzane name	Scientific name
Tuber	Matukwayako	<i>Coccinea surantiaca</i> or <i>aurantiaca</i>
	Penzepepe	<i>Vigna</i> sp. (<i>Papilionoidea Leguminosae</i>)
	//Ekwa hasa	<i>Vigna frutescens</i>
	Do'aiko/Shakeako	<i>Vigna macrorhyncha</i>
	Shumuwako	<i>Vatoraea pseudolablab</i>
Berry	Mbilipe	<i>Grewia flavescens</i> Juss., <i>Grewia platyclada</i>
	Congorobe	<i>Grewia bicolor</i> Juss.
	K'alahaipe	<i>Opilia campestris</i> Engl.
	Undushipi	<i>Cordia gharaf</i> Ehrenb.
	Ngwilabe	<i>Grewia similis</i> K. Schum.
Meat	Nakomako	<i>Syncerus caffer</i>
	Gewedako	<i>Madoqua kirkii</i>
	Komati	<i>Taurotragus oryx</i>
	Molola	<i>Canis adustus</i>
	Kwa'i	<i>Phacochoerus aethiopicus</i>
Baobab	N//obabe	<i>Adasonia digitata</i> L.
Honey	Ba'alako	<i>Apis unicolor adansonii</i> (bee species)

B has a higher nutritional value. However, the adaptive forager should go for the food with a higher net value after subtracting the required energy expenditure to acquire it. Food B will be chosen even though it has lower nutritional value when it requires so little energy to acquire that it yields a higher net intake of energy. On the other hand, if we offer the same forager both foods free of cost, we should find that the forager then chooses A, the one with higher nutritional value. If tastes have evolved to gauge nutritional value then food A should taste better. We used a forced-choice experiment and asked the Hadza to rank their foods according to taste.

Table 1 shows the species we used to elicit Hadza preferences. These fall into five food categories (tubers, berries, game, baobab, and honey). All Hadza are completely familiar with these foods and do not need to taste them before deciding which they like best. For this reason, we used separate photos of each of five tuber species, five berry species, five animal species, plus one photo of baobab and one photo of honey. We first had subjects rank the five species in order of preference within the category of tubers, berries, and animal species. Once we had their favorite food within each of these three categories, we added these three photos to the one of baobab and the one of honey. We then had each subject rank the five photos from most favorite (rank = 5) to least favorite (rank = 1). We asked the Hadza to imagine they had as much of the food as they could eat at one sitting right in front of them. They had no problem understanding what we wanted to know and could easily tell us which foods taste best to them.

Food availability

We do not have phenological data on Hadza foods. Measures of food availability therefore come from all foods Hadza brought back to camp (see Appendix A). Foods were weighed using a hanging scale. A sizeable number of camp residents (about 40% at midday) are in camp while others are out foraging (Marlowe, 2006). This means the amount of food arriving in camp cap-

tures the majority of daily consumption. To assess availability we used kilograms of food by type and by season and month. If a food type is brought into camp in every season and every month in substantial quantities this constitutes a minimum estimate of its availability throughout the year. Of course, if a food is ranked lowest in preference then it may be available but not taken because more preferred foods are available and taken first. If the least preferred foods come into camp in substantial amounts throughout the year we can be sure they are available throughout the year in even greater quantities. For each food type, we also asked Hadza whether it was available in the area “at this time of year” before getting them to rank which foods they preferred.

Here we use only kilograms of foods rather than kilocalories. Caloric values of the Hadza diet are still being analyzed and there is some debate over caloric values of some foods, especially tubers with their very high fiber content (Vincent, 1985a,b; Hawkes et al., 1995; Schoeninger, 2001a,c). Another reason we use kilograms is that using calories ignores other qualities of foods such as micronutrients which might be important. To see which foods best predicted how many kilograms of tubers were taken we used multiple linear regression analyses and controlled for region and season.

The measure of food consumption we used to analyze effects of food on body condition is per capita kilograms. This was computed by summing the kilograms of each food type for each camp, then dividing by the number of residents in that camp. We used this rather than individual production of foods arriving in camp because of the considerable amount of food sharing. Adults acquire food to provision children and get food from other adults as well. Because we are looking for the effects of certain foods on body condition our per capita measure should better capture this than individual production. If a man kills a giraffe that everyone in camp eats, for example, it makes little sense to attribute all those kilograms to the hunter to assess its impact on his body condition. Furthermore, we are interested in the effects of tubers on men and meat on women even though tubers are usually only targeted by women and game by men (see Appendix A).

Body condition

In each camp where we work normally for about 6 weeks (the average time Hadza stay in one location), we measured the height of all individuals with a stadiometer and weight with a scale that also measures percent body fat (%BF) using bioelectrical impedance (Tanita BF522). Body mass index (BMI) equals weight (kilograms) divided by height (meters) squared. Because BMI and %BF differ greatly between children and adults and %BF differs between males and females, we used only adults (age ≥ 18 years) and analyzed men and women separately. We use data on food collected by Marlowe's research team from 24 camps between 1995 and 2006. For anthropometry we use data from 49 camps, over a 6-year period during 2001–2006. We feel that these data include enough camps at different times of the year to capture seasonal variation fairly accurately. There are 17 camps in which we have both anthropometry and food data and it is these that we use to report the effects of certain foods on body condition.

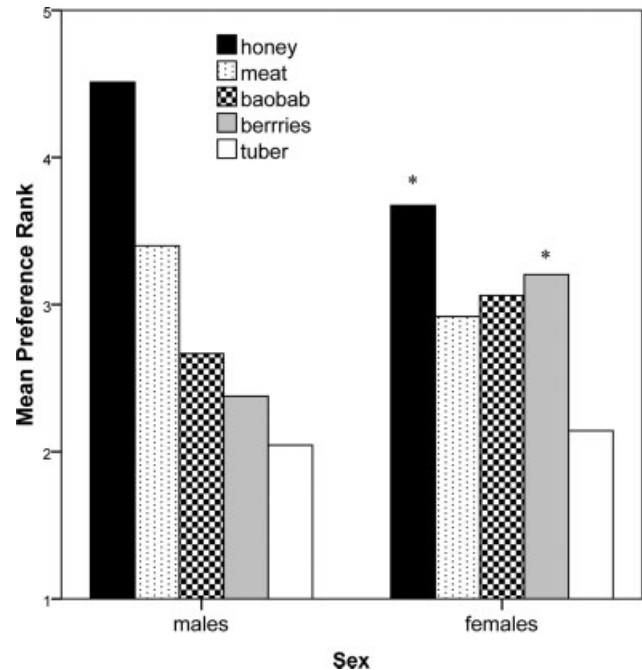


Fig. 1. Hadza food preferences by sex (49 women, 45 men). Rank 5 = high; 1 = low. * $P < 0.05$ using two-tailed Mann–Whitney U tests for sex differences in mean rank.

RESULTS

Food preferences

For both women ($n = 49$) and men ($n = 45$) the most preferred food was honey (mean rank = 4.07) and the least preferred food was tubers (mean rank = 2.10). Baobab was ranked third by women and men. There were sex differences on the other two foods: women ranked berries second and meat fourth, while men ranked meat second and berries fourth. In addition, though both sexes ranked honey first, men did so significantly more often (Mann–Whitney $U = 753$, $P = 0.003$, $n = 94$). Women ranked berries significantly higher than men did ($U = 679.5$, $P = 0.001$, $n = 94$) (see Fig. 1). It appears that men prefer men's foods a bit more than women do and women prefer women's foods a bit more than men do (Berbesque and Marlowe, submitted for publication).

Food availability

In the 24 camps for which we had food acquisition data there were a total of 489 individuals in those camps. Figure 2a shows that tubers varied the least across the four seasons of the year in terms of kilograms taken back to camp, from 18 to 31% of the diet (1.7-fold). Berries varied from 18 to 37% (2.1-fold), baobab from 7 to 15% (2.1-fold), meat from 10 to 35% (3.5-fold), and honey from 1 to 19% (19-fold). Many Hadza tubers are available throughout the year (Fig. 2a). They vary much more in relation to area than season (Fig. 2b). During our food preference experiments subjects said most species of tubers were always available. Men preferred foods in the reverse order of their variability because honey was most variable, followed by meat, baobab, berries, and tubers.

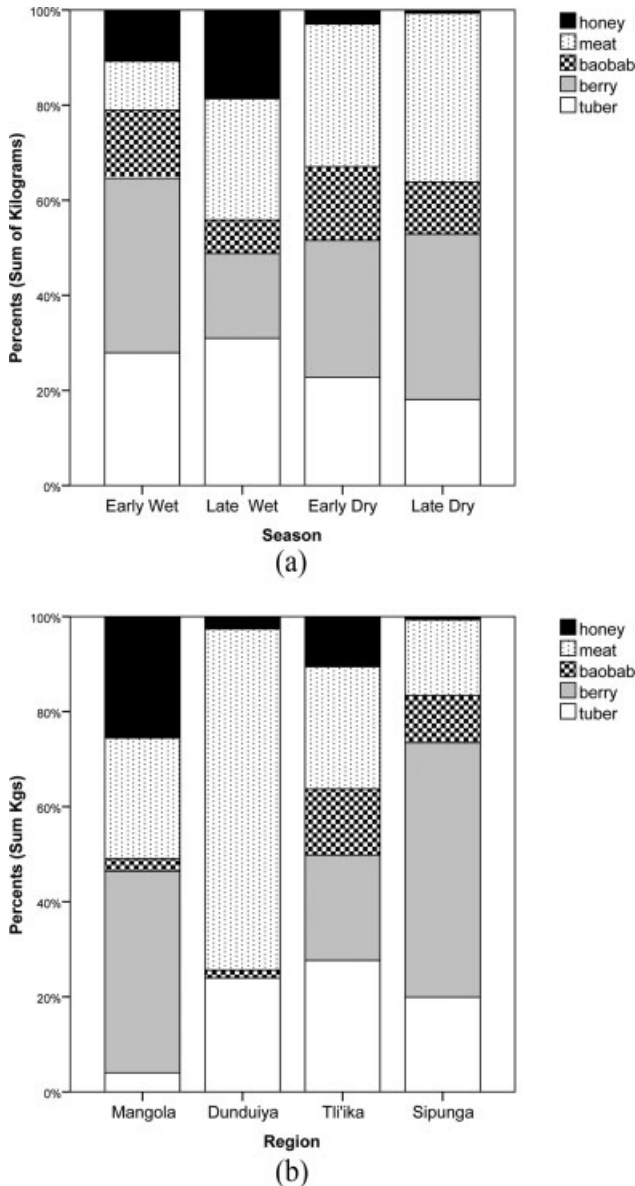


Fig. 2. (a) The five main food types in the Hadza diet by percent of total kilograms brought into camps by season (individuals of all ages). $n = 12,757$ food weight entries. (b) The five main food types in the Hadza diet by percent of total kilograms brought into camps by region (individuals of all ages). $n = 12,757$ food weight entries.

All foods varied significantly across the four seasons (Fig. 2a) and across the four regions (Fig. 2b). For this reason, we controlled for region and season with dummy variables in the following analyses. If tubers are fallback foods they should be taken when more preferred foods are not available so we investigated which food (more than any other) must be lacking for Hadza women to take more tubers. Table 2 shows Pearson correlation coefficients to illustrate the simple relationship between per capita kilograms of tubers and other foods brought back to a camp across all 24 camps with food data. In a multiple linear regression controlling for region and season, the best predictor of per capita kilograms of tubers acquired was the per capita kilograms of berries

TABLE 2. Pearson correlation coefficients between percent of Hadza diet that is tubers against other foods as measured by per capita kilograms brought into camps ($n = 837$ people of all ages)

	Tuber	Berry	Honey	Meat	Baobab
Tuber		-0.807 ^a	-0.030	0.168 ^a	0.251 ^a
Berry			-0.239 ^a	-0.546 ^a	-0.257 ^a
Honey				-0.115 ^a	-0.047
Meat					-0.349 ^a

^a Significant r statistic at $P < 0.0005$.

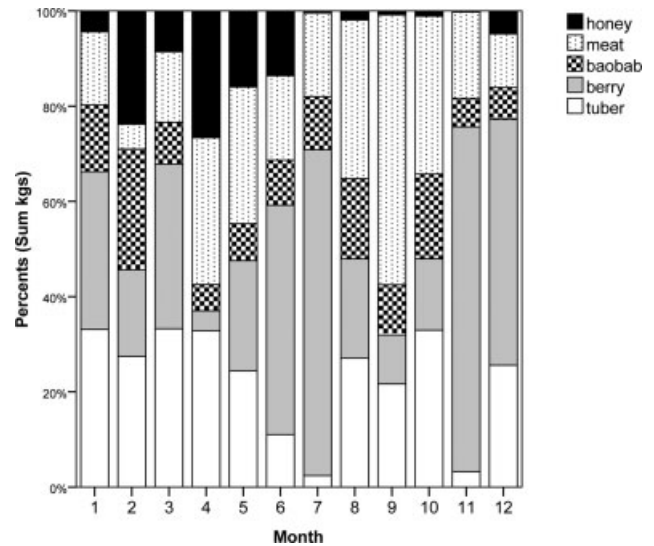


Fig. 3. The five main food types in the Hadza diet by percent of total kilograms brought into camps by month (individuals of all ages). $n = 12,757$ food weight entries.

acquired ($\beta = -.338, P < 0.0005, df = 479$). When more berries were available fewer tubers were taken.

Figure 3 shows how foods varied by month rather than season. Note that tubers varied considerably more by month. Much of this is due to the fact that tubers are mostly absent from the areas around certain camps in one region or another, such as Mangola (Fig. 2b). By month it is easier to see how tubers and berries are related; when berries comprised a larger fraction of the diet tubers usually comprised a smaller fraction.

Body condition

The mean BMI of men was 20.2 (SD = 1.7, $n = 252$) and mean BMI of women was 20.4 (SD = 2.3, $n = 237$). The mean %BF of men was 11% (SD = 3.4, $n = 250$) and mean %BF of women was 20% (SD = 7.3, $n = 232$). Previous analyses revealed that Hadza men and women varied little in BMI and %BF across season, though there was some variation by age-sex groups (prime-age men had higher BMI and %BF than elderly men) and a slight but significant variation within individuals across the year in %BF (Sherry and Marlowe, 2007). Here, in a larger sample that includes all adults for which we have anthropometry data, there are significant differences across the four regions (see Appendix B). We therefore controlled for regions before assessing seasonal effects.

Controlling for region, the early wet season was associated with a lower BMI ($\beta = -0.127, P = 0.026$,

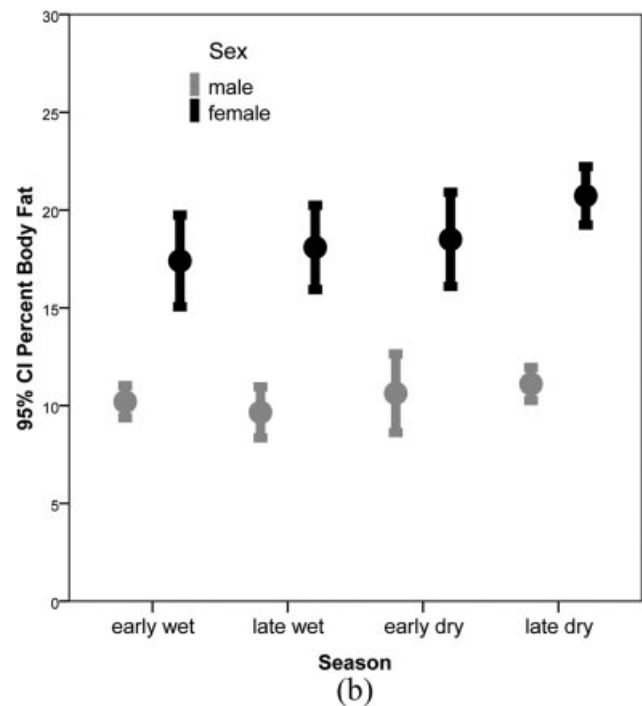
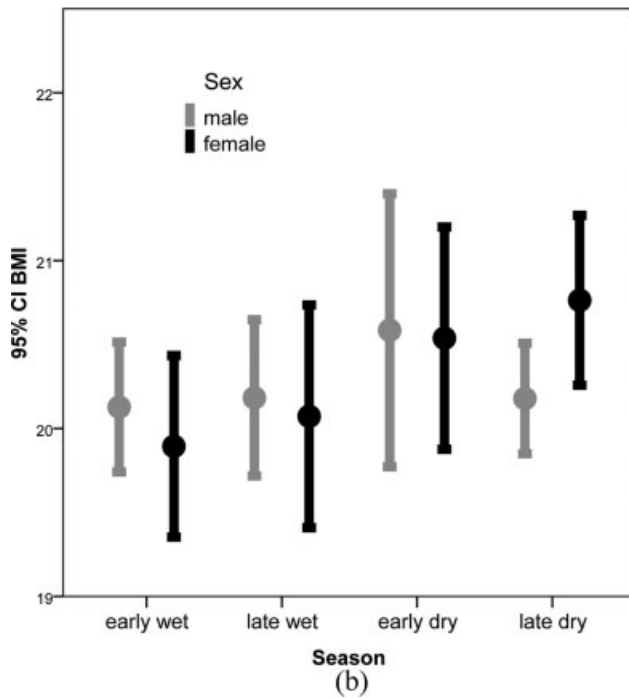
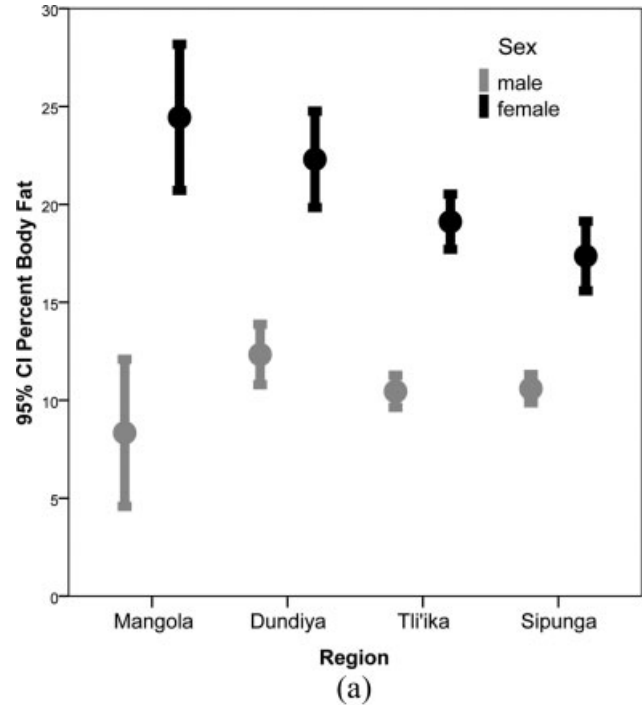
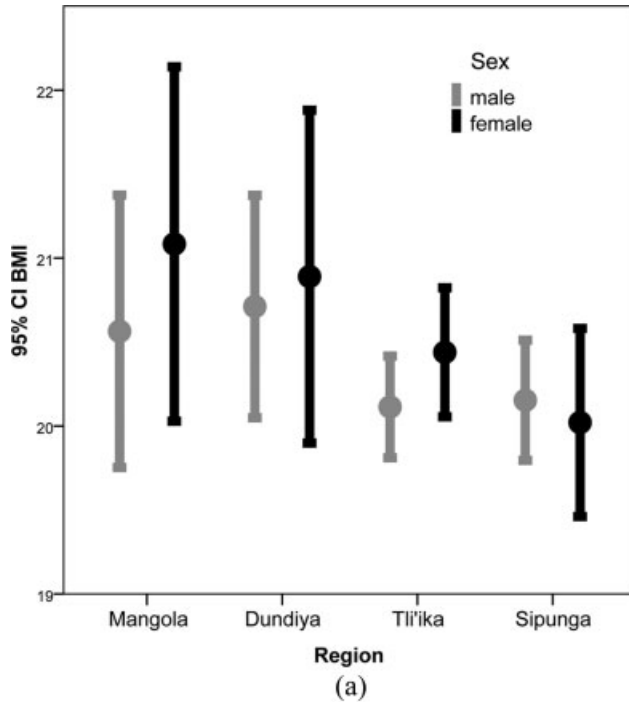


Fig. 4. (a) Hadza adult BMI by region and sex ($n = 234$ women, $n = 227$ men). (b) Hadza Adult BMI by season and sex ($n = 234$ women, $n = 227$ men).

Fig. 5. (a) Hadza adult %BF by region and sex ($n = 226$ women, $n = 222$ men). (b) Hadza adult %BF by season and sex ($n = 226$ women, $n = 222$ men).

$df = 484$) and a lower %BF ($\beta = -0.137$, $P = 0.017$, $df = 473$) in women. Men's BMI did not vary significantly by season, controlling for region, but their %BF was lower during the late wet season ($\beta = -0.108$, $P = 0.032$, $df = 465$).

Using those adults where we have anthropometry and food data (per capita kilograms), men showed no significant difference by region or season in %BF ($n = 203$) or

BMI ($n = 227$). Women's BMI ($n = 234$) and %BF ($n = 216$) did vary by region and season (Figs. 4a,b and 5a,b) (see Appendix B).

For the following results we used stepwise regressions, controlled for region and season. Men's BMI and %BF did not vary in relation to per capita kilograms of any food type. Women's BMI, on the other hand, was higher when more berries were taken ($\beta = 0.226$, $P = 0.003$,

$df = 230$) and lower when more baobab was taken ($\beta = -0.221, P = 0.005, df = 230$).

Women between 18 and 55 years of age (when they are bearing and nursing children) had a higher %BF when more meat was taken ($\beta = 0.320, P < 0.0005, df = 169$). They had a lower %BF when more tubers were taken ($\beta = -0.185, P = 0.003, df = 169$).

DISCUSSION

Honey is the most energy-dense food in nature (Skinner, 1991) and tubers are the foods with the fewest calories in the Hadza diet (Vincent, 1985a,b; Hawkes et al., 1995; Schoeninger, 2001b,c). Tubers were the most continuously available foods and were the least preferred so they fit the definition of fallback foods. Marshall and Wrangham (2007) propose two categories of fallback foods: staples and fillers. Staples are those that are available year-round and are eaten year-round and may seasonally constitute up to 100%, whereas fillers are those that never constitute 100% and may be avoided for weeks at a time. The tubers eaten by the Hadza do not fit neatly into either category. Unlike fillers, tubers are never avoided for weeks at a time and unlike staples they never constitute anywhere near 100% of the diet. For the Hadza, tubers come closer to being staple fallback foods than fillers because they are available year round and eaten year round but never reach more than 31% by kilograms.

The fact that women and men preferred honey most and tubers least implies that caloric value per kilogram is the best single predictor of Hadza preferences, at least at the extremes. Women's preference for berries over meat and men's for meat over berries means each sex slightly prefers the foods they take more of. The sexual division of foraging labor may influence these sex differences. If females are constrained to more reliable foods that are compatible with care of nurslings they may be more motivated to search for those foods. Acquiring tubers is hard work but it is compatible with childcare. Women may be content to target the foods compatible with infant care (Brown, 1970; Marlowe, 2007) and let men get the most preferred food (honey) because it is less predictable, more variable, and more dangerous. The most important honey, ba'alako, of the African honey bee (*Apis unicolor adansonii*) is usually in tall baobab trees and a fall can result in serious injury or death. It is interesting that men liked more variable foods because, unlike women, they also target more variable foods.

Women's %BF declined when more baobab was taken. Given that baobab is high in vitamin C and the seeds are high in fat, this must be because baobab is more available at times when other important foods (berries and meat) are less available. Table 2 shows that all other foods except for tubers are negatively correlated with baobab. Women's %BF would be much lower at such times but for the benefits of baobab. When more tubers are acquired, the %BF of reproductive-aged women declines. This could mean that women are suffering during times of more tubers or that at other times women are buffering themselves by adding more fat so as to weather the worse times without suffering.

Men's body condition varied less than women's in relation to foods taken. This might be because women have less access to foods or work harder. Although we cannot rule this out, it seems more likely that women vary

more than men simply because the demands of reproduction mean women add more fat in good times to draw on in lean times, something seen in other mammals (Stirling and Derocher, 1993; Parker et al., 2007) and primates as assessed by energy balance (Sherry, 2002; Thompson and Knott, 2008; Thompson and Wrangham, 2008). Women in most human populations have about twice the body fat of men and this is true of the Hadza. Women draw on this fat to support pregnancy and lactation (Ellison, 2003) and we suspect this explains their greater variation in body condition.

There is a dramatic change in the Hadza habitat between the dry and wet seasons yet the physical condition of the Hadza does not change dramatically. Their ability to cope with seasonality is partly due to replacement of one disappearing preferred food with another that is coming into season. In Figure 3, we see that the Hadza take some species of berry throughout the year and some baobab in every month in one region or another. Only honey is virtually absent at certain times of the year (July and November). The types of honey that come in small amounts rather than one large hive are often eaten out of camp, so the low amounts from July through November slightly underestimate the amount eaten by men.

Variation in body condition is also minimized by extensive food sharing, especially of large game, which is easier to kill by ambush hunting at waterholes in the dry season (Marlowe, 2006; Sherry and Marlowe, 2007). It is interesting that increased meat consumption is associated with greater %BF in women. This implies the sexual division of foraging labor is beneficial to women. If women share their reliable tubers with men then males can specialize in the risky endeavor of hunting, which should increase their hunting success, resulting in greater consumption of meat than would otherwise be possible.

Another reason the Hadza are able to avoid serious wasting is their ability to fall back on tubers. Women normally dig tubers every day though they may ignore tubers for an extended period when berries come into season since berries are superabundant. In addition to being more highly preferred (ranked 2nd by women), berries are easy to acquire. Children as young as 2 or 3 years old can simply feed themselves all day on berries and need little provisioning (Hawkes et al., 1995). Hadza women also occasionally skip digging for tubers for 2 or 3 days running when there is a lot of meat in camp. During the Plio-Pleistocene hunting was likely much less efficient so tubers would have been even more important to fall back on.

The use of USOs by most tropical foragers implies they were probably part of the diet at least since the appearance of modern humans. The Hadza occupy a habitat quite relevant for a long span of hominin evolution. It is also home to baboons, the other successful group of African savanna/woodland primates. The Hadza experience intense competition with savanna baboons (*Papio anubis*) for many of the same foods including all the berries, baobab, some small game, some honey, and even some shallow tubers. It is fortunate for the Hadza then that the baboons cannot take the deep tubers that Hadza women get. The only serious competitors for deeper tubers are the naked mole rats (*Heterocephalus glaber*) and the warthogs (*Phacochoerus africanus*). The C3/C4 ratios of these two animals overlap with those of Australopithecine and *Homo ergaster* specimens (Yeakel

et al., 2007) suggesting our earlier ancestors may also have been consuming significant amounts of tubers. If Homo-Pan speciation was triggered by receding forest leaving hominins in more open habitats then accessing deeper USOs would have given them a competitive advantage over sympatric species. The benefits of exploiting this large store of reliable food underground should have selected for more persistent tool use among hominins than was typical of their rainforest relatives (Hernandez-Aguilar et al., 2007; McGrew, 1992). With a simple digging stick early hominins could have exploited tubers as fallback foods to great advantage.

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APPENDIX A

We have also collected data on actual individual food consumption including the foods eaten out of camp, which are volume estimates by sight rather than actual weights and these are still being analyzed. From a very preliminary analysis it appears that about one-third of all food consumed by the Hadza is consumed out of camp and 2/3 in camp. Men appear to consume a slightly larger fraction of their diet out of camp than women do. A large share of berries (which are eaten as they are picked) are consumed out of camp, while only a small proportion of meat (especially larger game) is eaten out of camp. Still, the relative contribution of the five main food categories to the overall diet is probably fairly reflected in our data on foods arriving in camp.

To be able to show the relationship between foods across all four regions of Hadzaland, we have ignored one important food, the marula fruit, which is available only in Dunduiya, the region to the West of Lake Eyasi (with the exception of a tiny bit of Mangola). In Dunduiya, the baboons eat the fruit before it even gets fully ripe to preempt the Hadza. They then pass the large seeds on top of large rocks where they sleep. The Hadza go and collect these seeds after they have dried and then pound them open with hammerstones. We omit this food only because it would make comparisons across regions and seasons more difficult to interpret.

APPENDIX B

Women's BMI varies by region ($F = 3.64$, $P = 0.013$, $df = 3$, $n = 490$) as does their %BF ($F = 6.02$, $P < 0.0005$, $df = 3$, $n = 479$) (Figs. 4a and 5a). Mens %BF does not vary significantly by region (Fig. 5a) but their BMI does ($F = 3.32$, $P = 0.020$, $df = 3$, $n = 473$) (Fig.

4a). Women's %BF varies significantly by region ($F = 4.88$, $P = 0.003$, $df = 3$, $n = 226$) and by season ($F = 2.75$, $P = 0.043$, $df = 3$, $n = 226$).

We excluded those adults with %BF <5% or >35% on the grounds that they are outliers, possibly because the scale failed to record their fat correctly. This seems likely given that their BMI was not extremely low and because the bio-impedance scale sometimes returns an error message when it can not give a reading because of dirty feet. This amounted to 10 women and 19 men (only two had %BF over 35% and both were women).

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