Sex Differences in Food Preferences of Hadza Hunter-Gatherers

Julia Colette Berbesque, Department of Anthropology, Florida State University, Tallahassee, USA. Email: jcb03c@fsu.edu (Corresponding author).

Frank W. Marlowe, Department of Anthropology, Florida State University, Tallahassee, USA.

Abstract: Food preferences are important for understanding foraging choices. In studying human foragers rather than other animals, we have the advantage of being able to ask them which foods they prefer. Yet surprisingly, no studies of systematically collected data exist on human forager food preferences. The Hadza of Tanzania are full-time foragers in an area where the hominin record extends back to 3-4 million years ago, so their diet is very relevant for understanding the paleo-diet. Here, we report on their food preferences, elicited with photographs of species within the five major food categories in their diet: honey, meat, berries, baobab, and tubers. There were sex differences in the ranks of two food categories: meat and berries. While male and female ranks agreed on the other three food categories, females ranked berries second and meat fourth, whereas males ranked meat second and berries fourth. These similarities and differences are interesting in light of the fact that the sexes target different foods. We discuss the implications of Hadza food preferences for the origin of the uniquely human sexual division of foraging labor.

Keywords: food preferences, Hadza, hunter-gatherers, paleo-diet, sexual division of labor.

Introduction

Food preferences, regardless of how genetically or culturally influenced, are an integral part of maintaining an adequate diet in any particular environment. Despite substantial variation across societies there are broad categories of nutritional needs that apply to all humans. These include: carbohydrates, protein, lipids, and micronutrients (vitamins and minerals). If taste is the means by which humans (and other species) gauge the nutritional benefits of their foods, then food preferences should largely map onto nutritional requirements. If food A is always taken when foods A and B are both equally available, then we might assume that food A is higher in nutritional value than food B. However, the adaptive forager should target the food with a higher net value after subtracting the energetic cost of acquiring it. Food A might then be chosen even if it has lower nutritional value if it requires so little energy to obtain that it yields a higher net
Hadza Food Preferences

intake of energy. On the other hand, if we offer the forager both foods free of cost, we should find that the forager then chooses food B, the food with higher nutritional value.

The term preference has different meanings in economics and psychology. In economics and Optimal Foraging Theory (OFT), “preference” refers to a choice made after the cost has been subtracted from the benefit. In the mate preference literature in psychology, on the other hand, the term “preference” refers to the mate one would like to have, independent of the cost (presumably the perceived inherent value for one’s own reproductive success) (Symons, 1979). In the case of foods we call this perceived inherent value the nutritional value (or cost-free benefit). Here, we use the term preference in the latter sense only. We use the term choice, rather than preference, for foods actually taken just as mate choice is used to address real life mate acquisition. In contrast to the literature on mate preferences, the evolutionary literature on food preferences is surprisingly small. But just as with mate preferences, natural selection should have shaped our food preferences, that is, our ability to evaluate the cost-free nutritional value of foods. The evolved preferences for foods high in fat (Booth, 1982) and sugar (Meiselman, 1977) are often cited cases of “mismatch.” Preferences for these energy dense foods were presumably adaptive in an environment where it was nearly impossible to get too much of these foods. However, these same food preferences are now responsible for the obesity epidemic in industrialized countries where access to these foods is virtually limitless.

There are a number of studies involving the actual food choices of foragers (and therefore preference in the economic sense) (c.f. Ginane and Petit, 2005; Hawkes, Hill, and O’Connell, 1982; Hayward, O’Brien, Hofmeyr, and Kerley, 2007; O’Connell and Hawkes, 1984). There are others that describe general preferences in a given population, such as the following quote, “The most highly prized components of the Aboriginal hunter-gatherer diet were the relatively few energy-dense foods: depot fat, organ meats, fatty insects and honey” (O’Dea, Jewell, Whiten, Altmann, Strickland, and Oftedal, 1991, p. 238), see also Hladik and Simmen (1997). Ethnographic accounts of food preferences are often based on statements made by key informants. To the best of our knowledge, there are no previous reports on the expressed preferences of foragers measured in a systematic study.

The Hadza are foragers who live in Tanzania and their diet still consists mainly of wild foods (>90% by kilocalories among those we study) (Marlowe, 2003). They eat foods that are widely available in East Africa today and were present throughout the span of our species and before, such as baobab, honey, large game, and tubers (Baum, Small, and Wendel, 1998; Danforth, Sipes, Fang, and Brady, 2006; Stollhofen et al., 2008; Thulin, Lavin, Pasquet, and Delgado-Salinas, 2004). There must be less mismatch between their current diet and that often referred to as the paleo-diet (Cordain, 2002; Cordain, Eaton, Miller, Mann, and Hill, 2002; Eaton, 2006; Irons, 1998). The Hadza rarely mix foods, but instead eat single component foods, while western populations often consume multiple component foods (e.g. hamburgers). Though there are data on the American preferences of these multiple component foods relative to each other (for example pizza ranked against a hamburger), it is unclear how they relate to any one particular nutritional component (e.g. the meat versus the tomato versus the bun of the hamburger). This problem does not exist with the Hadza diet.

One straightforward prediction is that the higher the calories per kilogram of food, the more that food would be preferred. However, other nutritional properties such as protein or fat or certain micronutrients may also partly predict preferences. It is also possible that the preference rank of a particular food may fluctuate. For example, after one has eaten one food for several days running, one may crave a different food. A one food diet does not supply all of the nutrients
that we need as omnivores, and seeking different foods helps us get the other nutrients we need. The pursuit of a varied diet may mean that a food preference is relatively ephemeral, so that a person craves the essential nutrients that they are most lacking at the time. This, for example, might explain a craving for salty foods (Morris, Na, and Johnson, 2008). Finally, we analyze whether individuals would rank foods in line with their own dietary needs or acquisition abilities (which may vary depending on reproductive status for females). This might mean that males and females may rank foods differently, and children may rank foods differently from adults. Below we interpret our results to see if these or other expectations are supported. We also analyze the preference ranks in relation to the actual acquisition of these foods across the full year and per foray.

Materials and Methods

The Hadza

The Hadza are hunter-gatherers who number approximately 1000. They live in a savanna-woodland habitat that encompasses about 4000 km$^2$ around Lake Eyasi in northern Tanzania. They live in mobile camps which average 30 individuals (Marlowe, 2006). Camp membership often changes as people move in and out of camps (Blurton Jones, Hawkes, and O’Connell, 2005). These camps move about every 6 weeks on average. Hadza feel free to move wherever they like, although most tend to stay in the region where they grew up.

Hadza men usually go foraging alone. They hunt birds and mammals using only bow and arrows – poisoned arrows in the case of larger game. They use no snares, traps or nets. 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 (description of Hadza foods below). 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 90% of medium to large game. Grown men rarely dig tubers.

Hadza women go foraging in groups of 3-8 adults plus nurslings and often some older children. They mainly collect baobab, gather berries (and berry like fruit which we will refer to as berries), and dig tubers of several species. They use simple, fire-hardened, sharpened branches as digging sticks to dig tubers almost every day. They roast and eat some of their tubers once they finish digging and take the remainder (~ 70% of their haul) back to camp to feed others (Marlowe, 2006). Although men and women mostly target different foods, roles are not strict. Women do occasionally get honey (without men’s help), and do opportunistically scavenge meat.

Hadzaland receives considerable rain (300-600mm) during the months of December through May, and almost no rain from June through November, so there is a marked contrast between the rainy season and the dry season. Most foods vary seasonally, with the exception of some tubers and some game animals.

The Hadza diet can be conveniently categorized into five main food types: honey, meat, berries, baobab, and tubers (plus Marula nuts in one region only). Honey is the most energy-dense food in nature (Skinner, 1991), and is highly prized by the Hadza. Honey combs often contain small amounts of bee larvae, which the Hadza consume along with the comb. The berries in Hadzaland are much drier than the berries we are familiar with and they are mostly seed, but what little pulp there is has a high sugar content. Also, when in season, berries are super-abundant. Baobab fruit is common across much of Africa. Baobab fruit has a chalky pulp that is
high in vitamin C, and hard seeds that are high in fat. The seeds are only eaten when baobab is taken back to camp to pound into flour. Many Hadza tubers are continuously available throughout the year, and are a source of carbohydrates. Tubers vary much more in relation to region than season. 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 but must spit out the quid after chewing it for a while. Figure 1 shows three species of berries (Ngwilape, Embilipe, and Congolobe), baobab, and the tuber //ekwa. Table 1 shows basic macronutrient contents of Hadza foods, although it must be noted that the nutritional value of most foods vary by region, season, and in the case of meat by age and sex of the animal as well.

**Figure 1.** Examples of Hadza foods.

![Examples of Hadza foods](image)

**Table 1.** Composition of Hadza foods

|       | Fat       | Protein   | Carbs (starch) | Sugars | Kcal      |
|-------|-----------|-----------|----------------|--------|-----------|
| Honey | <8.0<sup>1</sup> | <4.0<sup>1</sup> | Trace<sup>1</sup> | 87.7<sup>2</sup> | 403-439<sup>1</sup> |
| Meat  | 1.3-9.0<sup>4</sup> | 57.3-68.2<sup>4</sup> | Trace<sup>5</sup> | 96.0<sup>1</sup> | 216<sup>6</sup>-609<sup>7</sup> |
| Tuber | 0.6<sup>3</sup>-<sup>4</sup> | 2.3<sup>2</sup>-10.4<sup>3</sup> | 19.4<sup>2</sup>-61.3<sup>3</sup> | 62<sup>2</sup>-48.3<sup>2</sup> | 73-85<sup>5</sup>, 146-298<sup>2</sup>, 177-279<sup>3</sup> |
| Berries | <2.0<sup>1</sup> | 7.1<sup>1</sup>-15.2<sup>1</sup> | Trace | 61.1-72.7<sup>1</sup> | 108-145<sup>5</sup>,318-342<sup>1</sup> |
| Baobab* | 15.0<sup>1</sup> | 19.4<sup>1</sup> | 5.5<sup>1</sup> | 23.4<sup>1</sup> | 328.5<sup>1</sup> |

<sup>1</sup> (Murray et al., 2001) 2 (Schoeninger et al., 2001) 3 (Vincent, 1985) 4 (Van Zyl and Ferreira, 2004) 5 (Cordain et al., 2002) 6 (Weiner, 1973) 7 (McCullough and Ullrey, 1983) 8 (Galvin et al., ND)

All values based on grams per 100 grams dry weight. All values are averages; foods vary by species, location, and season. Meat macronutrient values large based on springbok, blesbok, and impala samples. Meat kilocalories are based on deer species.

* Baobab composition is based on a ratio of 50% pulp and 50% seed by weight of a pod.

**Note.** Bold numbers indicate which food has the highest value for each macronutrient.
Food taboos among the Hadza are sex specific. Hadza men who have become “real men” by virtue of killing one of the very large game animals (or else are over about 30 years of age) take particular portions of meat from large game animals. This consists primarily of organs including the genitals, kidney, heart, throat, and tongue. The men eat these portions hidden away from the women and children, and it is considered dangerous for women or children to eat these parts. Perhaps a less stringent taboo (FM has witnessed a violation of this taboo) is the eating of tortoises by men. Men say that the poison on their arrows will become weak and not work if they eat tortoise. Women and children, however, eat the tortoise without any repercussions. Both men and women avoid eating fish and reptiles. This avoidance does not rise to the level of a taboo, but when some food does not taste good to them they say that it “tastes like snake,” which is what they say about fish and all reptiles (except for tortoise).

Materials and Procedure

Design
We interviewed individuals one-on-one in the privacy of a Land Rover in the morning. The Hadza were never interviewed after a meal, because being sated by a particular food might affect their preferences. We used photographs of foods on index cards for visual aids. Photographic methods have been used in Western populations to elicit emotions about complex foods as well as food preferences (Corney, Eves, Kipps, and Lumbers, 2001; Hinton, Holland, Gellatly, Soni, and Owen 2006; Rousset, Deiss, Juillard, and Schlich, 2005), and two studies found that photographic methods were very concordant with taste test preference ranks (Guinard, 2000; Guthrie, Rapoport, and Wardle 2000).

We attempted to get at cost-free preferences by specifically stating that the foods should be considered as if they were already in front of the subject, ready to eat, pre-processed, and the subject could eat as much of that food as they wanted at one sitting. This was a two tiered process. The first tier was the ranking of five species from each of three of the food categories: tubers, berries, and game. Only the five species photographs within a particular food category (e.g. tubers) were shown at one time. The first tier species level sorting was done primarily to ensure that any individual’s bias against a particular species within a category did not affect their overall ranks of the five broader food categories (see Figure 2).
**Figure 2.** Forced-choice preference ranking of Hadza foods.

*Note.* This schema shows an individual that selected species A for meat, C for berries, and E for tubers in tier 1. Other individuals may rank different species as “favorites” in the three categories in tier 1. Once they have chosen the favorite in the three categories in tier 1, we asked them to rank those species against baobab and honey in tier 2.

The second tier included the favorite species from the three previous categories, plus a picture of honey, and a picture of baobab. Presumably if this were not a two tiered sort, three species of berries could be ranked before any other food type. The nutritional differences between those berry species is small compared to the differences between those berry species and any other food category. Because we wanted to investigate whether preferences mapped onto different nutritional attributes, we were interested in the overall ranks of these nutritionally distinct categories which are salient to the Hadza and comprise approximately 95% of their diet.

Honey was represented by a single picture (of ba’alako) because recognizing the honey from the different species of bees by photograph would be difficult. In addition, ba’alako (the honey from the African bee—*Apis unicolor adansonii*) is the most common, provides the most kilograms of honey, and is highly prized. A single photograph of baobab was used because there is only one species, but it is such a major fruit in terms of kilograms in the Hadza diet that it deserves a category unto itself. In addition, the Hadza do not refer to it with the same term “fruit” as they use for all species of berries. Animal pictures were used for their recognizability over pictures of meat itself. The species chosen for the categories tuber, berries, and meat are by no means comprehensive because we wanted to keep the interviews relatively brief. All of the species chosen for each of these categories are very well represented in FM’s acquisition data, and were well-known across regions. We chose game animals ranging from small to large to capture the range taken. The food species used can be seen in Table 2.
Table 2. Hadza food species used in this study.

| Category | Hadzane name (English name) | Scientific name |
|----------|-----------------------------|-----------------|
| Tuber    | Matukwayako/Coccinea surantiaca or aurantiaca | Vigna sp. (Papilionoidea Leguminosae) |
|          | Penzepenze/Vigna frutescens |                |
|          | //Ekwa hasa/Vigna macrorhyncha |                |
|          | Do’aiko/Shakeako |                |
|          | Shumuwako/Vatoraea pseudolablab |                |
| Berry    | Embilipe/Grewia flavescens Juss., Grewia platyclada |                |
|          | Congolobe/Grewia bicolor Juss. |                |
|          | K’alahaibe/Opilia campestris Engl. |                |
|          | Undushipi/Cordia gharaf Engl. |                |
|          | Ngwilape/Grewia similis K. Schum. |                |
| Meat     | Nakomako/Syncerus caffer (Buffalo) |                |
|          | Gewedako/Madoqua kirkii (Dikdik) |                |
|          | Komati (Eland)/Taurotragus oryx (Jackal) |                |
|          | Molola (Jackal)/Canis adustus (Warthog) |                |
|          | Kwa’i (Warthog)/Phacochoerus aethiopicus |                |
| Baobab   | N//obabe/Adasonia digitata L. |                |
| Honey    | Ba’alako/Apis unicolor adansonii (bee species) |                |

Food Acquisition

Data on food acquisition were obtained by dividing the kilocalories of each food returned when those foods were acquired by the total time spent foraging out of camp on those forays. Because the Hadza are opportunistic foragers and will rarely search for a particular item to the exclusion of other possibilities, it is very difficult to categorize the targeted item and calculate a search time on any given foray for this item. Hourly kilocalories does not perfectly capture the time necessary to acquire a particular food, but is probably the best possible proxy. Because Hadza men usually forage alone, it takes years of focal individual follows to calculate a percentage of diet eaten out of camp for males. FM has estimated from preliminary data analysis that roughly 30% of the diet is eaten out of camp. We use acquisition of foods brought back to camp as a proxy for the complete diet. Data on kilocalories per hour of foraging were collected from six camps in 1995-96 on adults (ages 18 and older). We also show the percentage of the diet that each food category constitutes. Data on percentage contribution to diet were collected from 16 camps from 1995-2005. We present both kilocalories per hour of foraging and percentage contribution to the diet because our data on kilocalories per hour of foraging are not affected by food availability (which varies by region and season), whereas percentage contribution to the diet is. For instance, because honey is available seasonally, percentage contribution to diet is probably less relevant to taste preferences than hourly kilocalories. If honey is not often available, it will not constitute a high percentage of the diet. Nevertheless when it is available it provides men with their highest return per hour.

Although food preference data were acquired in 2007-2008 in three regions, we do not believe that there were significantly different foraging patterns in those years than in the years in
which other data on kcal/hour acquisition (1995-1996) or percentage contribution to the diet (1995-2005) were collected. All three datasets were collected in the same three regions in camps where the residents were foraging full-time; many of them were also in the food preference data.

**Results**

The total sample consisted of 94 individuals. Males ranged in age from 16-70 years with a mean age of 38.73 (SD = 13.15, n = 45). Females ranged in age from 19-78 years with a mean age of 37.16 (SD = 16.98, n = 49). The foods were ranked from first to fifth by the total sample as follows: honey, meat, baobab, berries, and tubers.

Both males and females ranked honey first, baobab third, and tubers last. There was no significant age variation in preference ranks within sex when analyzed by ten year age cohorts. Because our data are ranked, we used non-parametric Mann-Whitney tests to see if there were sex differences. Although honey was ranked first by both sexes, males had a higher mean rank for it (4.51) than females (3.67) (Mann-Whitney U = 753, p = .003, n₁ = 45, n₂ = 49) (see Table 3). Females ranked berries second and meat fourth, while males ranked meat second and berries fourth (Fig. 3). The mean rank of meat was higher by males than females, but significant only with a one-tailed test (U = 889, p = .099, n₁ = 45, n₂ = 49). Females ranked berries significantly higher than males (U = 679.5, p = .001, n₁ = 45, n₂ = 49). Women who were noticeably pregnant (n = 4) did not have different preferences than other females, nor did nursing women (n = 13).

**Figure 3.** Hadza food preference ranks by sex.
Hadza Food Preferences

Table 3. Descriptive statistics of food preference rankings by sex.

| Sex      | Honey | Meat  | Baobab | Berries | Tubers |
|----------|-------|-------|--------|---------|--------|
|          | Rank 1 | Rank 2 | Rank 3 | Rank 4 | Rank 5 |
| Males n=45 |       |       |        |         |        |
|          | Mean Score | Mean Score | Mean Score | Mean Score | Mean Score |
|          | 4.51 | 3.40 | 2.67 | 2.38 | 2.04 |
|          | SD   | 0.84 | 1.27 | 1.23 | 1.07 |
| Females n=49 |       |       |        |         |        |
|          | Rank 1 | Rank 4 | Rank 3 | Rank 2 | Rank 5 |
|          | Mean Score | Mean Score | Mean Score | Mean Score | Mean Score |
|          | 3.67 | 2.92 | 3.06 | 3.20 | 2.14 |
|          | SD   | 1.44 | 1.46 | 1.33 | 1.21 |
| Total n=94 |       |       |        |         |        |
|          | Rank 1 | Rank 2 | Rank 3 | Rank 4 | Rank 5 |
|          | Mean Score | Mean Score | Mean Score | Mean Score | Mean Score |
|          | 4.07 | 3.15 | 2.87 | 2.81 | 2.10 |
|          | SD   | 1.26 | 1.38 | 1.29 | 1.21 |

Both sexes ranked the five species of berries the same: 1) Ngwilape, 2) Undushupe, 3) Congolobe, 4) Embilipe, and finally 5) K’alahaibe. It is worth noting that during certain berry seasons, men and women often forage for berries together, and even when foraging separately men also feed on berries, though it is women who tend to gather enough to take back to camp. Baobab is the other food that both sexes gather in substantial quantities and they both ranked it third. In contrast, males and females ranked the five tuber species differently, and grown men very rarely dig tubers. Women and men also ranked the five animal species differently, which women rarely take.

The concordance, or inter-rater agreement in this scale for the entire population was tested with Kendall’s W ($W = .205$, $df = 4$, $p = .000$). Males were more concordant in their ranking ($W = .385$, $df = 4$, $p = .000$) than were females ($W = .124$, $df = 4$, $p = .000$) (for tests of concordance for particular food categories by sex, see Appendix 1).

Males ranked higher those foods that they tend to target (see Table 4 for acquisition by sex). Male hourly kilocalorie acquisition by food type perfectly predicts male food preference ranks ($r = .993$, $n = 5$, $p = .001$). Females ranked male acquired foods lower than males ranked them (significantly lower for honey). Female hourly kilocalorie acquisition by food type (Table 4) does not predict their stated food preferences. Honey, meat, and tuber foraging returns deviate from this pattern in female food preferences. Females get little honey but prefer it most, but they also get very little meat (it yields the lowest kcals/hour for them) and yet they do not rank meat high. Women get great quantities of tubers but prefer them least.

Table 4. Hourly acquisition and percentage contribution to diet of Hadza men and women.

|                  | Honey | Baobab | Meat  | Berry | Tuber |
|------------------|-------|--------|-------|-------|-------|
| Male mean Kcal/hour | 229.7 | 81.3   | 163.6 | 65.8  | 40.3  |
| SD               | 201.9 | 77.5   | 189.8 | 66.3  | 50.0  |
| N                | 38    | 32     | 32    | 18    | 6     |
| Male % contribution to diet (n=101) | 12.29% | 13.14% | 71.83% | 1.86% | 0.88% |
| Female mean Kcal/hour | 94.3  | 125.5  | 66.6  | 224.7 | 257.7 |
| SD               | 84.6  | 106.7  | 102.9 | 246.0 | 182.1 |
| N                | 6     | 43     | 6     | 54    | 56    |
| Female % contribution to diet (n=112) | 0.18% | 14.17% | 7.92% | 43.33% | 34.40% |
| Total % contribution to diet (n=232) | 5.02% | 13.76% | 33.49% | 26.75% | 20.99% |
Discussion

Our results call into question some common assumptions about human foragers. In humans, males and females forage apart and target different foods much of the time (Kelly, 1995). Jochim (1988) points out that OFT models have been developed for species in which the generic forager is analyzed, rather than two very different foragers (one male and one female). Yet despite the distinct costs for males and females in acquiring certain foods (due to strength, size, or risk), the preferences of males and females are often assumed to be the same. We found, however, there are sex differences in food preferences among the Hadza. In addition, ethnographers often claim that meat is the most preferred food among foragers (including the Hadza) (Bunn, 2001), yet our empirical data on individual preferences demonstrates that honey is more preferred than meat among the Hadza.

Caloric value predicted the most preferred (honey) and least preferred foods (tubers) for the Hadza. The macronutrient differences in male preferred foods and female preferred foods may be characterized as males preferring protein (meat) more and females preferring sugar (berries) more. What an individual had recently eaten did not seem to substantially affect preference ranks because there was a high degree of concordance in several food category ranks. If recent consumption affected preferences we would have expected a difference in preference ranks from one season or region to the next due to changes in the availability of each food item. For example, because we collected the data in three different regions over two years (one year without any berries available and one with several species of berries available), we would not expect the significant agreement that we found on berry preference ranks in both years. This consistency in preference ranks leads us to conclude that preferences for a food item are not heavily dependent on the availability of that food item.

It is interesting that men bring back to camp more calories of honey per hour gone from camp than any other food type, followed by meat, baobab, berries, and finally tubers. This happens to be exactly the same as their preference ranking. This suggests that men might devote more effort to getting the foods that they like the most. Women’s acquisition, on the other hand, does not match their preference ranks.

Both sexes ranked tubers last, which is what we would expect if they are fallback foods that are taken when more preferred foods are not available in sufficient quantities (Marlowe and Berbesque, in press). Although meat and honey are calorically much more valuable than female foods, females did not place the premium on them that males did, ranking honey first but significantly less frequently than men and ranking meat 4th. Females ranked berries high (2nd), despite their relatively low caloric value per kilogram (as compared with meat). In addition, tubers yield the highest kilocalories per female hour of foraging and yet females ranked tubers last.

It is not clear what we should expect female preferences to be if they are constrained in their foraging. If females had the same dietary requirements as males we might expect both sexes to have the same preferences regardless of who acquires the food. According to one view, the risk aversion of females to the less reliable, higher variance foods (such as honey or meat) may be due to constraints related to infant care (Brown, 1970; Jochim, 1988; Marlowe, 2007).

The view that males and females are pursuing different foraging strategies for the benefit of the household has been challenged in the past two decades. Females may simply avoid hunting and honey collection in favor of more predictable returns which are better for provisioning children. Males may target high variance foods to increase their number of mating
opportunities via food sharing and its signaling value (Bird, 1999; Hawkes, 1990; Smith, 2004). However, Hill (1988) has argued that hunting may be important for supplying particular macronutrients, and may require a great deal of time to learn (Kaplan, Hill, Lancaster, and Hurtado, 2000; Walker, Hill, Kaplan, and McMillan, 2002). One might expect females would still prefer meat most if male hunting were very important for female mate choice. Hadza females, however, ranked meat 4th out of five food types. While it is possible that the female exclusion from eating certain organ meat from big game may bring down their meat ranks, women preferred large game animals over smaller game animals. Organ meat is only tabooed for females in large game animals, so one might expect that women would rank small game higher if organ meat were highly prized for them since they are allowed to eat organ meat in the smaller animals.

We propose two possible explanations for the sex differences in Hadza food preferences. The first is that it was not possible for subjects to fully separate the nutritional value of a food from its net value (i.e. after subtracting costs). For example, males and females can have different costs for acquiring a particular food, and these different costs are often invoked to explain sex differences in food acquisition. If optimal food choices were the only factor for food preferences, we would expect the preferences of males and females to differ significantly. However, there is good reason to think that taste preferences (or perceived nutritional benefits) can be evaluated even when cost can not be assessed. A recent study found that chimpanzees prefer cooked meat to raw meat despite the inability to access cooked meat in an ecologically salient context (Wobber, Hare, and Wrangham, 2008).

The second possible explanation for sex differences in food preferences is that males and females might have different dietary requirements. Though the constraints on foraging stemming from the direct costs of reproduction are often cited as a reason for the evolution of the sexual division of foraging labor, another possibility is that the nutritional benefits of a particular foraging strategy would not be equal for males and females even if the costs were held constant. This could be due to the distinct body composition of males versus females as a consequence of the differential allocation of resources to muscle (in males) and fat (in females). Size dimorphism often results in male-female dietary niche separation in primates (Kamilar and Pokempner, 2008). Given that body composition (e.g. in muscle and fat) is more sexually dimorphic in humans than most mammals (Pond, 1992; Power and Schulkin, 2008), more attention should be paid to dietary sex differences.

One possible area where the optimal diet of males and females may differ is in the dietary requirements of particular macronutrients. There is evidence that in athletes, males derive a greater portion of energy (during exercise) from carbohydrates and protein, while females derive more from fat (Bloomer and Fisher-Wellman, 2008; Chevalier, Marliss, Morais, Lamarche, and Gougeon 2005; Tarnopolsky, MacDougall, Atkinson, Tarnopolsky, and Sutton 1990; Tarnopolsky, 2008; Volek, Forsythe, and Kraemer, 2006). Another possible dietary sex difference may simply be that females require regular calories to maintain body fat (and thereby fecundity). It may be more important for females to have a very regular caloric intake (eat more often), even if this means eating lower quality foods. Evidence from Hadza consumption data indicate that Hadza females are eating significantly more often than males in camp (Berbesque, Marlowe, and Crittenden, n.d.). The aforementioned and often cited reasons for the female foraging strategy of risk aversion and provisioning may only be a part of the picture. Before women have children to provision, they must be fecund. Maintaining fecundity may be another reason female foraging is aimed at foods with an acceptably low variance of daily kilocalories.
In an environment of plenty (like that of most post-industrial societies), perhaps no real deficit occurs if males and females eat the same diet. However, when foragers are expending great amounts of energy to acquire food (like the Hadza are) and are constrained to a subsistence diet, the sex differences in dietary needs could be quite important. Though there is a great deal of overlap in the nutritional needs of men and women, any differences might be very important for understanding the origin and development of the sexual division of foraging labor in human evolution.

Acknowledgements: We wish to thank Kirk Miller for helping us get photos of some of the Hadza foods. Thanks to Johannes and Lene Kleppe for providing us with a base camp in Tanzania and Audax Mabulla for help with research permission and logistics. We thank Daudi Peterson for assistance and innumerable favours, Costech for permission to conduct research and finally the Hadza for their enduring tolerance and hospitality. We thank Martin Muller, Coren Apicella, Brian Wood, two anonymous reviewers, and Edward Hagen for their comments. This research was supported by NSF grants 0544751, 0242455, and 0650574 to F.W. Marlowe. To be able to show the relationship between foods across all four regions of Hadzaland, we have ignored one important food, the marula nut, which is available only in Dunduiya, the region to the West of Lake Eyasi (with the exception of a tiny area of Mangola). We conducted our research in regions where this food is not available, and hope to incorporate this later into the study.

Received 18 August 2009; Revision submitted 24 October 2009; Accepted 19 November 2009

References

Baum, D.A., Small, R.L., and Wendel, J.F. (1998). Biogeography and floral evolution of Baobabs (Adansonia, Bombacaceae) as inferred from multiple data sets. *Systematic Biology*, 47, 181-205.

Berbesque, J.C., Marlowe, F.W., and Crittenden, A.N. (n.d.). Sex differences in the Hadza diet. *Evolutionary Anthropology*, 8, 65-75.

Bird, R. (1999). Cooperation and conflict: The behavioral ecology of the sexual division of labor. *Evolutionary Anthropology*, 8, 65-75.

Bloomer, R.J., and Fisher-Wellman, K.H. (2008). Blood oxidative stress biomarkers: Influence of sex, exercise training status, and dietary intake. *Gender Medicine*, 5, 218-228.

Blurton Jones, N.G., Hawkes, K., and O’Connell, J.F. (2005). Older Hadza men and women as helpers: Residence data. In B.S. Hewlett and M.E. Lamb (Eds.), *Hunter-gatherer childhoods: Evolutionary, developmental and cultural perspectives* (pp. 214-236). New Brunswick: Transaction.

Booth, D.A. (1982). How nutritional effects of foods can influence people’s dietary choices. In L.M. Barker (Ed.), *The psychobiology of human food selection* (pp. 67-84). Westport, CT: AVI Publishing.

Brown, J.K. (1970). A note on the division of labor by sex. *American Anthropologist*, 72, 1073-1078.
Hadza Food Preferences

Bunn, H.T. (2001). Hunting, power scavenging, and butchering by Hadza foragers and by Plio-Pleistocene homo. In C.B. Stanford and H.T. Bunn (Eds.), Meat-eating and human evolution (pp. 199-218). New York: Oxford University Press.

Chevalier, S., Marliss, E.B., Morais, J.A., Lamarche, M., and Gougeon, R. (2005). The influence of sex on protein anabolic response to insulin. Metabolism Clinical and Experimental, 54, 1529-1535.

Cordain, L. (2002). The Paleo diet. Hoboken, NJ: Wiley.

Cordain, L., Eaton, S.B., Miller, J.B., Mann, N., and Hill, K. (2002). The paradoxical nature of hunter-gatherer diets: meat based, yet non-atherogenic. European Journal of Clinical Nutrition, 56, S42-52.

Corney, M., Eves, A., Kipps, M., and Lumbers, M. (2001). School meals: Primary schoolchildren’s perceptions of the healthiness of foods served at school and their preferences for these foods. Health Education Journal, 60, 102-119.

Danforth, B.N., Sipes, S., Fang, J., and Brady, S.G. (2006). The history of early bee diversification based on five genes plus morphology. Proceedings of the National Academy of Sciences U.S.A., 103, 15118-15123.

Eaton, S.B. (2006). The ancestral human diet: What was it and should it be a paradigm for contemporary nutrition? Proceedings of the Nutrition Society, 65, 1-6.

Galvin, K., Hawkes, K., Maga, J.A., O’Connell, J.F., and Blurton-Jones, N. (n.d.). The composition of some wild plant foods used by East African hunter-gatherers. MS.

Ginane, C., and Petit, M. (2005). Feeding behaviour and diet choices of cattle with physical and temporal constraints on forage accessibility: an indoor experiment. Animal Science, 81, 3-10.

Guinard, J.-X. (2000). Sensory and consumer testing with children. Trends in Food Science and Technology, 11, 273-283.

Guthrie, C.A., Rapoport, L., and Wardle, J. (2000). Young children’s food preferences: A comparison of three modalities of food stimuli. Appetite, 35, 73-77.

Hawkes, K. (1990). Why do men hunt? Some benefits for risky strategies. In E. Cashdan (Ed.), Risk and Uncertainty in Tribal and Peasant Economies (pp. 145-166). Boulder: Westview.

Hawkes, K., Hill, K., and O’Connell, J.F. (1982). Why hunters gather: Optimal foraging and the Ache of eastern Paraguay. American Ethnologist, 9, 379-398.

Hayward, M. W., O’Brien, J., Hofmeyr, M., and Kerley, G.I.H. (2007). Testing predictions of the prey of lion derived from modeled prey preferences. Journal of Wildlife Management, 71, 1567-1575.

Hill, K. (1988). Macronutrient modifications of optimal foraging theory: an approach using indifference curves applied to some modern foragers. Human Ecology, 16, 157-197.

Hinton, E.C., Holland, A.J., Gellatly, M.S.N., Soni, S., and Owen, A.M. (2006). An investigation into food preferences and the neural basis of food-related incentive motivation in Prader–Willi syndrome. Journal of Intellectual Disability Research, 50, 633-642.

Hladik, C.M., and Simmen, B. (1997). Taste perception and feeding behavior in nonhuman primates and human populations. Evolutionary Anthropology, 5, 58-71.

Irons, W. (1998). Adaptively relevant environments versus the environment of evolutionary adaptedness. Evolutionary Anthropology, 6, 194-204.

Jochim, M.A. (1988). Optimal foraging and the division of labor. American Anthropologist, 90, 130-136.
Hadza Food Preferences

Kamilar, J.M., and Pokempner, A.A. (2008). Does body mass dimorphism increase male-female dietary niche separation? A comparative study of primates. *Behaviour, 145*, 1211-1234.

Kaplan, H., Hill, K., Lancaster, J., and Hurtado, A. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology, 9*, 156-185.

Kelly, R. L. (1995). *The foraging spectrum*. Washington D.C.: Smithsonian Institution Press.

Marlowe, F.W. (2003). A critical period for provisioning by Hadza men: Implications for pair bonding. *Evolution and Human Behavior, 24*, 217-229.

Marlowe, F.W. (2006). Central place provisioning: The Hadza as an example. In G. Hohmann, M. Robbins and C. Boesch (Eds.), *Feeding ecology in apes and other primates* (pp. 357-375). Cambridge: Cambridge University Press.

Marlowe, F.W. (2007). Hunting and gathering: The human sexual division of foraging labor. *Cross Cultural Research, 41*, 170-195.

Marlowe, F.W., and Berbesque, J.C. (in press). Tubers as fallback foods and their impact on Hadza hunter-gatherers. *American Journal of Physical Anthropology*.

McCullough, D.R., and Ullrey, D.E. (1983). Proximate mineral and gross energy composition of white-tailed deer. *Journal of Wildlife Management, 47*, 430-441.

Meiselman, H. L. (1977). The role of sweetness in the food preference of young adults. In J.M. Weiffenbach (Ed.), *Taste and development* (pp. 269-281). Bethesda, MD: Department of Health, Education, and Welfare.

Morris, M.J., Na, E.S., and Johnson, A.K. (2008). Salt craving: The psychobiology of pathogenic sodium intake. *Context Sensitive Links, 94*, 709-721.

Murray, S.S., Schoeninger, M.J., Bunn, H.T., Pickering, T.R., and Marlett, J.A. (2001). Nutritional composition of some wild plant foods and honey used by Hadza foragers of Tanzania. *Journal of Food Composition and Analysis, 14*, 3-13.

O’Connell, J.F., and Hawkes, K. (1984). Food choice and foraging sites among the Alyawara. *Journal of Anthropological Research, 40*, 504-535.

O’Dea, K., Jewell, P.A., Whiten, A., Altmann, S.A., Strickland, S.S., and Oftedal, O.T. (1991). Traditional Diet and Food Preferences of Australian Aboriginal Hunter-Gatherers. *Philosophical Transactions: Biological Sciences, 334*, 233-241.

Pond, C.M. (1992). An evolutionary and functional view of mammalian adipose tissue. *Proceedings of the Nutrition Society, 51*, 367-377.

Power, M.L., and Shulkin, J. (2008). Sex differences in fat storage, fat metabolism, and the health risks from obesity: possible evolutionary origins. *British Journal of Nutrition, 99*, 931-940.

Rousset, S., Deiss, V., Juillard, E., and Schlich, P. (2005). Emotions generated by meat and other food products in women. *British Journal of Nutrition, 94*, 609-619.

Schoeninger, M.J., Bunn, H.T., Murray, S.S., and Marlett, J.A. (2001). Composition of tubers used by Hadza foragers of Tanzania. *Journal of Food Composition and Analysis, 14*, 15-25.

Skinner, M. (1991). Bee brood consumption—an alternative explanation for hypervitaminosis-A in KNM-ER 1808(Homo erectus) from Koobi Fora, Kenya. *Journal of Human Evolution, 20*, 493-503.

Smith, E.A. (2004). Why do good hunters have higher reproductive success? *Human Nature, 15*, 343-364.

Stollhofen, H., Stanistreet, I.G., McHenry, L.J., Mollle, G.F., Blumenschine, R.J., and Masao, F.T. (2008). Fingerprinting facies of the Tuff IF marker, with implications for early
Hadza Food Preferences

hominin palaeoecology, Olduvai Gorge, Tanzania Palaeogeography, Palaeoclimatology, Palaeoecology, 259, 382-409.
Symons, D. (1979). The evolution of human sexuality. Oxford: Oxford University Press.
Tarnopolsky, L.J., MacDougall, J.D., Atkinson, S.A., Tarnopolsky, M.A., and Sutton, J.R. (1990). Gender differences in substrate for endurance exercise. Journal of Applied Physiology, 68, 302-338.
Tarnopolsky, M.A. (2008). Sex differences in exercise metabolism and the role of 17-beta estradiol. Medicine and Science in Sports and Exercise, 40, 648-654.
Thulin, M., Lavin, M., Pasquet, R., and Delgado-Salinas, A. (2004). Phylogeny and biogeography of Wafira (Leguminosae): A monophyletic segregate of Vigna centered in the horn of Africa region Systematic Botany, 29, 903-920.
Van Zyl, L., and Ferreira, A.V. (2004). Physical and chemical carcass composition of springbok (Antidorcas marsupialis), blesbok (Damaliscus dorcas phillipsi) and impala (Aepyceros melampus). Small Ruminant Research, 53, 103-109.
Vincent, A.S. (1985). Plant foods in savanna environments, a preliminary report of tubers eaten by the Hadza of Northern Tanzania. World Archaeology, 17, 131-148.
Volek, J.S., Forsythe, C.E., and Kraemer, W.J. (2006). Nutritional aspects of women strength athletes. British Journal of Sports Medicine, 40, 742-748.
Walker, R., Hill, K., Kaplan, H., and McMillan, G. (2002). Age-dependency in hunting ability among the Ache of Eastern Paraguay. Journal of Human Evolution, 42, 639-657.
Weiner, J. (1973). Dressing percentage, gross body composition and caloric value of the roe deer Acta Theriologica, 18, 209-222.
Wobber, V., Hare, B., and Wrangham, R. (2008). Great apes prefer cooked food. Journal of Human Evolution, 55, 340-348.

Appendix 1. We used binomial tests with each of the five food categories having a 20% chance of having a particular rank according to the null assumption of random ranking. For example, given there are five categories the null assumption is that honey was ranked first in approximately 20% of the cases for males, females, and then all subjects (see Table A1). Berries and meat were the only two food categories with different modal rank by sex, so the assumption that these ranks were significantly different was tested for males using a rank of 2nd for meat and 4th for berries. Females were tested for concordance in ranking berries 2nd and meat 4th. Male concordance in rank was high across all food categories except baobab. Female concordance was significant only for honey, berries, and tubers (Table A1). It appears that females really do prefer berries over meat because more females ranked berries at 2nd than expected from the null assumption. On the other hand, the ranking of baobab as the 3rd most preferred food by both sexes appears to result from ranking other foods higher or lower than chance.

Table A1. Concordance in Hadza food preference ranking by sex.

|          | Honey | Meat | Baobab | Berries | Tubers |
|----------|-------|------|--------|---------|--------|
| Males observed (n = 45) | .688** | .311* | .222   | .311*   | .444** |
| Females observed (n = 49) | .449** | .244  | .184   | .306*   | .449** |
| Total observed (n = 94) | .564** | .213  | .202   | .245    | .447** |

**p < .001, *p < .05

Observed proportion refers to number of subjects that ranked the food type the same as the mode rank of their sex, or overall modal rank (for totals). For example, a rank of second best for berries for females was observed in 30.6%
Hadza Food Preferences

of cases. The null expectation is that each of the 5 food categories would be named 20% of the time, adding up to 100%. P-values were from Binomial tests with an assumed .20 proportion for each of the five food categories.