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Sex Differences in Food Preferences, Eating Frequency, and Dental Attrition of the Hadza

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SEX DIFFERENCES IN FOOD PREFERENCES, EATING FREQUENCY, AND DENTAL ATTRITION OF THE HADZA

By

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In memory of N. Ruth Patterson and Jacques E. Berbesque:

Great souls have wills; feeble ones have only wishes.
Chinese Proverb
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ABSTRACT

This dissertation focuses on a few possible causes and consequences of the sexual division of foraging labor in the Hadza, hunter-gatherers of Tanzania. I present three separate studies; the investigation of foraging goals as reflected in food preferences, the extent of cross-sex food sharing as reflected in consumption, and the consequences as reflected in evidence of the sexual division of foraging labor that would be detectable in the archaeological record.

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. The first study reports 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. Theses similarities and differences are interesting in light of the fact that the sexes target different foods.

My second study uses eating frequency data from instantaneous scan observations of the Hadza, hunter-gatherers of Tanzania, to see to how much sharing of foods taken back to camp compensates for the targeting of different foods by each sex while out foraging. I find that eating in camp differs by sex in terms of overall eating frequency, as well as in terms of diet composition (frequencies of eating each food type). I also control for sex-differences in time spent in camp and still find sex-differences in eating frequencies—women are observed eating significantly more frequently than men. There are also sex-differences in the eating frequencies of particular food types both with and without controlling for presence in camp. Finally, I use data on acquisition of each food type by sex and find that both sexes are more frequently observed eating women’s foods in camp than men’s foods.

My third study investigates the relationship between patterns of attrition across age and sex cohorts with behavioral data on diet composition in a contemporary hunter-gatherer population, the
Hadza of Tanzania. Despite the targeting of different foods by males and females among hunter-gatherers, the sharing of male and female foods is usually assumed to result in virtually the same diet for males and females. Despite the widespread sharing of foods among the Hadza, hunter-gathers of Tanzania, women were observed eating significantly more frequently than Hadza men, and were eating more of some foods than others. Casts of the upper dentition (full arcade) were made from molds taken from 126 adults (71 women and 55 men) and scored according to the Murphy dental attrition scoring system. Females demonstrated significantly greater anterior occlusal wear than males controlling for age. Males demonstrated greater asymmetry in wear, with greater wear on the left side in canines, first premolars, and first molars. I believe that these sex differences in wear patterns reflect the sex differences seen in eating frequency, as well as differences in the use of teeth as tools.
CHAPTER # 1
INTRODUCTION

This dissertation focuses on a few possible causes and consequences of the sexual division of foraging labor in the Hadza, hunter-gatherers of Tanzania. I present three separate studies. The first study on food preferences tells us something about the forager’s decision-making. In particular, food preferences tell us about the constraints on a forager. By knowing what foods a forager prefers, then measuring what he or she gets, we can see how and where trade-offs were made. After the Hadza (and other hunter-gatherers) acquire food, much of it is brought back to camp and shared. My second study investigates the observed eating patterns of each sex in camp. My third study builds on the observed eating to determine how these patterns might be detected in archeological contexts through an analysis of dental wear. I use the term hunter-gatherers and foragers interchangeably to refer to those societies whose diet is acquired from wild foods rather than any form of horticulture, agriculture, or pastoralism.

Why are foragers important? Before ten thousand years ago, all humans were foragers. Foraging was the only mode of subsistence in East Africa until approximately two thousand years ago and continued to be the only mode in some places (such as Australia) until AD 1788 AD when the British arrived. The eventual spread of agriculture was slow and halting in many areas of the world. Most human adaptations are a consequence of selection in the pre-agricultural past. Our best chance of understanding what selected for these adaptations is by studying people still occupying the foraging niche. While all foragers may inform our understanding of human evolution, the Hadza are particularly relevant for several reasons. The Hadza are foragers that live in a region that has a record of hominin occupation dating back approximately 4 million years. They eat wild foods that have been in the region even longer. The foods that the Hadza target are relevant for understanding human evolution, and relevant over a longer period than the foods targeted by foragers in many other habitats, such as arctic foragers.
Food Sharing and the Sexual Division of Foraging Labor

Food sharing occurs in a number of mammalian species, for example wild dogs (*Lycaon pictus*) (Goodall & van Lawick, 1970). Males and females are not targeting different foods however, so they share the same kinds of foods. Other species have slight dinichism, for example chimpanzees (*Pan troglodytes*), where each sex targets slightly different foods. Females eat more insects and males more vertebrates (McGrew, 1992). However, there is little sharing of these foods with the exception of some meat sharing among the group of hunters (Mitani & Watts, 2001). What is unique to human foragers is that men and women seek different foods and share them. Hadza mothers take their infants with them when they go foraging but leave their weanlings in camp. This requires acquiring surplus food to take back to camp for provisioning those who remain in camp. The Hadza are central place provisioners, men and women go foraging and return to a central place (camp) with foods to share (Marlowe, 2006).

Whether human mate bonds evolved to further cooperation or not is unclear. Once such bonds exist, however, they create the potential for cooperation between mates. One view of the sexual division of foraging labor emphasizes cooperation between males and females (husbands and wives) to further the interests of the household (Lancaster & Lancaster, 1980; Lancaster & Lancaster, 1983). By targeting a limited range of foods males and females might become more efficient foragers. This foraging specialization might benefit the household in terms of more food and more varied foods. Because females target low-variance foods that can be depended on, males have the option of targeting less reliable high value but high variance foods like large game. This could provide the household with a better diet and relieve women from the costs of high risk, dangerous foraging strategies that may be incompatible with pregnancy or childcare (Brown, 1970a; Marlowe, 2007a). Since both the wife and husband should have overlapping interests in providing for their children to some degree, hunting and honey collection may be mainly a family and kin provisioning strategy.

A different view of the sexual division of foraging labor sees hunting as primarily a male mating effort strategy that benefits successful hunters, not necessarily their households (Hawkes & Bliege Bird, 2002). Sexual conflict has been defined by Chapman et al. (2003) as ‘differences in the evolutionary interests between males and females’. With different levels of cooperation and conflict, we might make different predictions about the types and overall quantity of ‘help’ that husbands and wives supply each other. Given that males have a higher potential reproductive rate, they have the potential to gain more than females from increased mating effort (Clutton-Brock, 1991). Females have far less variation in
their reproductive rate. It pays females to invest in parenting effort for two reasons. First, they do not have as much of a trade off in mating versus parenting effort due to the lower variance in reproductive rate. Second, unlike males, a female can always be sure that she is the mother of her child. As a result, males may often be interested in extra mating rather than being purely interested in investing in their current mate or household. From an evolutionary perspective we expect each individual to maximize their own reproductive success.

The motivation underlying meat sharing among hunter-gatherers is hotly debated. Hadza men share meat not only with their wives and children, but often with every other person in camp (Hawkes, 2001; Hawkes, O'Connell, & Jones, 2001a; Marlowe, 2004; Woodburn, 1998). Some see this sharing as delayed reciprocity, which may be an effective means of reducing the variation in meat eating (Gurven, 2004; Kaplan & Hill, 1985). This would still benefit the wives of the hunters substantially by providing more regular calories and protein. Others have presented this sharing as ‘forced sharing’ or tolerated theft, wherein the goal of each hunter may be to return the entire carcass to his household, but loses much of the carcass to other camp members demanding shares (Blurton Jones, 1984; Isaac, 1978). Each unit of a large food package item has diminishing returns to the acquirer who has eaten the first unit. Additional units will most benefit those who have not eaten yet, so hungry camp members are more willing to fight for them. Consequently, it pays the owner to share additional units rather than fight to keep them (Blurton Jones, 1984; Jones, 1987; Winterhalder, 1996).

A third hypothesis concerning meat sharing is that the successful hunter is effectively signaling his mate quality because hunting requires great skill (Bird, 1999; Hawkes & Bird, 2002). If men could expend the same time and energy acquiring the foods women target, fruit for example, and deliver to their household more nutritional benefit than they do by hunting, we might conclude that hunting is not an effective household provisioning strategy. Alternatively, if men provide more nutritional benefit to their household by hunting and collecting honey, then there is no reason to invoke costly signaling theory to explain why men hunt.

With all of this at stake, food acquisition has been widely investigated across several forager populations. Surprisingly, who is actually eating what (and how frequently) is rarely reported. This is mainly because it is very difficult to measure actual food consumption by many individuals without being very intrusive. Extensive food sharing in camp is often observed and has often led researchers to assume the diets of men and women are similar as a result. Often individual consumption is estimated by dividing the kilograms of each food arriving in camp by the total camp population (Blurton Jones,
Hawkes, & O’Connell, 1997; Hurtado & Hill, 1990b; Jones, Hawkes, & O’Connell, 1997; Marlowe & Berbesque, 2009). This per capita analysis assumes perfect sharing in camp. The in-camp diet is likely an under-estimate of sex-differences in the total diet because each sex eats some of their targeted foods (and sometimes, but rarely the other sex’s foods) while out foraging.

In most models of foraging decisions, each forager represents the ideal optimal forager. However, in human foragers there are typically two different foraging strategies—that of women and that of men (Jochim, 1988), reflecting a trade-off between high-variance, but high-quality foods and low-variance but low-quality foods. What this means is that it is not sufficient to focus solely on what men should be targeting for maximum household benefit. Rather the focus should be on what men should be targeting given what women are targeting. The only reason that men are able to target high variance foods is that women target low variance foods. Women’s foods insure there will be some food acquired every day while men’s foods offer the less reliable but highly prized bonanza of meat or honey.

**Nutrition**

Human nutritional requirements are far more hotly contested than is usually appreciated (Cordain et al., 2000; Wrangham, 2009). If we use the great apes (Chimpanzees, Bonobos, Gorillas, and Orangutans) to help us sketch out the evolution of the human diet, we see there are some sex differences in diet composition even among other apes (Ganas & Robbins, 2004; McGrew, 1979). They certainly do not differ nearly as much as the foods targeted by men and women among human foragers before sharing occurs. Because there is considerable sex difference in the body composition of men and women we might expect them to have different nutritional needs due to distinct energetic demands. The cost of reproduction in female primates may be large enough to require energy levels that are equivalent to that of males 30-50% larger in body size (Key & Ross, 1999). Sexually dimorphic traits such as size might produce slight to pronounced separation in the diet of single species (Bean, 1999; Kamilar & Pokempner, 2008a). Sex differences in diet composition have also been recorded in many primate species (dininichism) (Clutton-Brock, 1977). In addition, females tend to spend more time feeding than males, especially when supporting infants.

Body composition is more sexually dimorphic in humans than most mammals (Pond, 1992; Power & Schulkin, 2008b). This sex difference in body composition is the result of the greater male allocation of resources to muscle and greater female allocation of resources to fat. 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 & Fisher-Wellman, 2008; Chevalier, Marliss, Morais, Lamarche, & Gougeon, 2005; Tarnopolsky, MacDougall, Atkinson, Tarnopolsky, & Sutton, 1990; Tarnopolsky, 2008; Volek, Forsythe, & Kraemer, 2006a). If it is more efficient to allocate particular types of nutrients to muscle or fat than others, one might expect that the optimal diet of males and females are not the same. When foragers are expending great amounts of energy to acquire food (like the Hadza are) and are constrained to a subsistence diet, any sex differences in dietary needs could be quite important.

**Foragers and Archaeology**

Contemporary foragers provide us with an invaluable opportunity to advance our understanding of archaeological data (O'Connell, 1997; O'Connell, Blurton-Jones, & Hawkes, 1992; Yellen, 1977). Analyzing the dentition of contemporary foragers allows us to make inferences about the diet of our pre-agricultural hominin ancestors. The environments occupied by hominins throughout their evolution are not monolithic. There are different relevant environments for understanding different human adaptations. The relevant environment for nursing dates to the origin of mammals while that for bipedalism dates to 6-7 millions years ago and that for our exceptionally large brains 2.5 million years (Irons, 1998b). Contemporary foragers are especially relevant when we are reconstructing the period from the beginning of modern sapiens, less so as we go further back in time. Still, certain aspects of Hadza foraging such as use of hammerstones to crack nuts or digging sticks to acquire tubers may well extend back to the last common ancestor we share with chimpanzees and bonobos. Radical changes in technology, language capacity, and behavioral complexity appeared later and contemporary foragers can help us understand these uniquely human traits.
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.

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 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 & Petit, 2005; Hawkes, Hill, & O'Connell, 1982; Hayward, O'Brien, Hofmeyr, & Kerley, 2007a; O'Connell & 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 et al., 1991 p.238, p. 278), 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, & Wendel, 1998; Danforth, Sipes, Fang, & Brady, 2006;
Stollhofen et al., 2008; Thulin, Lavin, Pasquet, & 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, & Hill, 2002; Eaton, 2006; Irons, 1998a). 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, & 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, & 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 2.1 shows three species of berries (Ngwilape, Embilipe, and Congolobe), baobab, and the tuber //ekwa. Table 2.1 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 2.1. Examples of Hadza foods
Table 2.1. Composition of Hadza foods

<table>
<thead>
<tr>
<th></th>
<th>Fat</th>
<th>Protein</th>
<th>Carbs (starch)</th>
<th>Sugars</th>
<th>Kcal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Honey</td>
<td>&lt;8.0¹</td>
<td>&lt;4.0¹</td>
<td>Trace¹</td>
<td>87.7¹</td>
<td>403-439¹</td>
</tr>
<tr>
<td>Meat</td>
<td>1.3-9.0³</td>
<td>57.3-68.2²</td>
<td>Trace³</td>
<td>Trace³</td>
<td>216⁶-609⁷</td>
</tr>
<tr>
<td>Tuber</td>
<td>0.6³-3.4³</td>
<td>2.3³-10.4¹</td>
<td>19.4³-61.3³</td>
<td>6.2²-48.3²</td>
<td>73-85³</td>
</tr>
<tr>
<td>Baobab*</td>
<td>15.0¹</td>
<td>19.4¹</td>
<td>5.5¹</td>
<td>23.4¹</td>
<td>328.5¹</td>
</tr>
</tbody>
</table>


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 witness 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, & Lumbers, 2001; Hinton, Holland, Gellatly, Soni, & Owen, 2006; Rousset, Deiss, Juillard, & Schlich, 2005), and two studies found that photographic methods were very concordant with taste test preference ranks (Guinard, 2000; Guthrie, Rapoport, & 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 2.2).
Figure 2.2. Forced-choice preference ranking of Hadza foods

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 2.2.

### Table 2.2. Hadza food species used in this study

<table>
<thead>
<tr>
<th>Category</th>
<th>Hadzane name (English name)</th>
<th>Scientific name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tuber</td>
<td>Matukwayako</td>
<td><em>Coccinea surantiaca or aurantiaca</em></td>
</tr>
<tr>
<td></td>
<td>Penzepenze</td>
<td><em>Vigna sp. (Papilionoidea Leguminosae)</em></td>
</tr>
<tr>
<td></td>
<td>//Ekwa hasa</td>
<td><em>Vigna frutescens</em></td>
</tr>
<tr>
<td></td>
<td>Do'aiko/Shakeako</td>
<td><em>Vigna macrorhyncha</em></td>
</tr>
<tr>
<td></td>
<td>Shumuwako</td>
<td><em>Vatoraea pseudolablab</em></td>
</tr>
<tr>
<td>Berry</td>
<td>Embilipe</td>
<td><em>Grewia flavescens Juss., Grewia platyclada</em></td>
</tr>
<tr>
<td></td>
<td>Congolobe</td>
<td><em>Grewia bicolor Juss.</em></td>
</tr>
<tr>
<td></td>
<td>K'alahaibe</td>
<td><em>Opilia campestris Engl.</em></td>
</tr>
<tr>
<td></td>
<td>Undushipi</td>
<td><em>Cordia gharaf Ehrenb.</em></td>
</tr>
<tr>
<td></td>
<td>Ngwilape</td>
<td><em>Grewia similis K. Schum.</em></td>
</tr>
<tr>
<td>Meat</td>
<td>Nakomako (Buffalo)</td>
<td><em>Syncerus caffer</em></td>
</tr>
<tr>
<td></td>
<td>Gewedako (Dikdik)</td>
<td><em>Madoqua kirkii</em></td>
</tr>
<tr>
<td></td>
<td>Komati (Eland)</td>
<td><em>Taurotragus oryx</em></td>
</tr>
<tr>
<td></td>
<td>Molola (Jackal)</td>
<td><em>Canis adustus</em></td>
</tr>
<tr>
<td></td>
<td>Kwa’i (Warthog)</td>
<td><em>Phacochoerus aethiopicus</em></td>
</tr>
<tr>
<td>Baobab</td>
<td>N//obabe</td>
<td><em>Adasonia digitata L.</em></td>
</tr>
<tr>
<td>Honey</td>
<td>Ba’alako</td>
<td><em>Apis unicolor adansonii</em> (bee species)</td>
</tr>
</tbody>
</table>
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 the summers of 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, \( p = .003, n_1 = 45, n_2 = 49 \)) (see Table 2.3). Females ranked berries second and meat fourth, while males ranked meat second and berries fourth (Fig. 2.3). The mean rank of meat was higher by males than females, but significant only with a one-tailed test (\( U = 889, p = .099, n_1 = 45, n_2 = 49 \)). Females ranked berries significantly higher than males (\( U = 679.5, p = .001, n_1 = 45, n_2 = 49 \)). Women who were noticeably pregnant (n=4) did not have different preferences than other females, nor did nursing women (n=13).

**Figure 2.3.** Hadza food preference ranks by sex
Table 2.3. Descriptive statistics of food preference rankings by sex

<table>
<thead>
<tr>
<th>Sex</th>
<th>Honey</th>
<th>Meat</th>
<th>Baobab</th>
<th>Berries</th>
<th>Tubers</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean Score</td>
<td>SD</td>
<td>Mean Score</td>
<td>SD</td>
<td>Mean Score</td>
</tr>
<tr>
<td>Males</td>
<td>Rank</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>n = 45</td>
<td>Mean Score</td>
<td>4.51</td>
<td>3.40</td>
<td>2.67</td>
<td>2.38</td>
</tr>
<tr>
<td></td>
<td>SD</td>
<td>0.84</td>
<td>1.27</td>
<td>1.23</td>
<td>1.07</td>
</tr>
<tr>
<td>Females</td>
<td>Rank</td>
<td>1</td>
<td>4</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>n = 49</td>
<td>Mean Score</td>
<td>3.67</td>
<td>2.92</td>
<td>3.06</td>
<td>3.20</td>
</tr>
<tr>
<td></td>
<td>SD</td>
<td>1.44</td>
<td>1.46</td>
<td>1.33</td>
<td>1.21</td>
</tr>
<tr>
<td>Total</td>
<td>Rank</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>n = 94</td>
<td>Mean Score</td>
<td>4.07</td>
<td>3.15</td>
<td>2.87</td>
<td>2.81</td>
</tr>
<tr>
<td></td>
<td>SD</td>
<td>1.26</td>
<td>1.38</td>
<td>1.29</td>
<td>1.21</td>
</tr>
</tbody>
</table>

Both sexes ranked the 5 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 A1).

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 2.4) 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 2.4.** Hourly acquisition and percentage contribution to diet of Hadza men and women.

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

**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 & 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, 1970b; Jochim, 1988; Marlowe, 2007b).

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, & Hurtado, 2000a; Walker, Hill, Kaplan, & 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 4\textsuperscript{th} 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, & 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 & Pokempner, 2008b). Given that body composition (e.g. in muscle and fat) is more sexually dimorphic in humans than most mammals (Pond, 1992; Power & Schulkin, 2008a), 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 & Fisher-Wellman, 2008; Chevalier et al., 2005; Tarnopolsky et al., 1990; Tarnopolsky, 2008; Volek, Forsythe, & Kraemer, 2006b). 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, & Crittenden, ND). 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.
CHAPTER # 3
SEX DIFFERENCES IN HADZA EATING FREQUENCY BY FOOD TYPE

Abstract

The diets of contemporary foragers can provide insights into the nutritional ecology of our pre-agricultural ancestors as well as our current nutritional needs. Measuring the actual consumption of each individual, however, is very problematic: it is often difficult to get a large enough sample-size using individual focal follow observations, and it is intrusive. Consequently, researchers have often used total camp food acquisition divided by camp population as a proxy for consumption. This per capita proxy for consumption obscures any possible sex-differences in eating patterns. Here we use eating frequency data from instantaneous scan observations of the Hadza, hunter-gatherers of Tanzania, to see to how much sharing of foods taken back to camp compensates for the targeting of different foods by each sex while out foraging. We find that eating in camp differs by sex in terms of overall eating frequency, as well as in terms of diet composition (frequencies of eating each food type). We also control for sex-differences in time spent in camp and still find sex-differences in eating frequencies—women are observed eating significantly more frequently than men. There are also sex-differences in the eating frequencies of particular food types both with and without controlling for presence in camp. Finally, we use data on acquisition of each food type by sex and find that both sexes are more frequently observed eating women’s foods in camp than men’s foods.

Introduction

The sexual division of foraging labor in humans involves two major components: the targeting of different foods by each sex, and the sharing of those foods (generally back at a central place) (Marlowe, 2007a). This trait is rare in the animal kingdom. Some species have slight to pronounced dinichism, where each sex targets different foods, but there is no substantial sharing of these foods. Food sharing
exists in many species, but they typically target and share the same food types. Here, we investigate sex differences in frequencies of adults eating in a foraging population—the Hadza of Tanzania.

Men and women acquire and eat different types of foods while on foray. These differences in diet are minimized by the sharing of those foods with the opposite sex when they are brought back to camp. The portion of diet eaten in camp should therefore be an underestimate of the total dietary sex differences. The targeting of different foods has received the majority of attention in the literature on the sexual division of foraging labor. Because the sexual division of foraging labor implies food sharing (otherwise it would be called dinichism), this study focuses on in-camp consumption to investigate how much sharing offsets differences in acquisition.

Sex-differences in the actual diet (in terms of amounts eaten or in diet composition) of foraging groups is rarely reported because measuring the foods going to each mouth is difficult and intrusive and because sharing is often tacitly assumed to even things out. Hadza food acquisition has been reported (Blurton Jones et al., 1997; Hawkes, Blurton Jones, & O'Connell, 1995; Marlowe, 2003) and these measures have been used as proxies for Hadza consumption. Acquisition data divided by camp population have been used for an overall estimate of kilocalories per individual (Blurton Jones et al., 1997; Marlowe & Berbesque, 2009). Some reports of consumption in other foragers are also calculated as a per capita measure (with perfect sharing assumed) (Hurtado & Hill, 1990a; Kaplan, Hill, Lancaster, & Hurtado, 2000b; Lee, 1979). Some have reported on the portions of foods given to the household of the producer versus other households (Hawkes, O'Connell, & Jones, 2001b; Kaplan, Hill, Hawkes, & Hurtado, 1984; Wood & Marlowe, ND). These studies are informative for investigating the producer’s control of food (and inform the debate about who hunts and why) (Bird & Bird, 2008; Gurven & Hill, 2009). Other descriptive ethnographies of human foragers comment anecdotally on consumption, and indicate sex-differences (Hewlett, Koppel, & Koppel, 1985; Walker & Hewlett, 1990b). Hames and McCabe (2007) analyzed eating frequencies to investigate food sharing across households among the Ye’kwana, but do not report on sex differences in consumption. Our study appears to be the first to analyze actual frequencies of eating by sex across food types.

We might expect the diets of men and women to differ due to the distinct energetic demands on human males versus females. These differences do not entirely map onto what would be expected by body-size. The cost of reproduction in female primates may be large enough to require energy levels that are equivalent to that of males 30-50% larger in body size (Dufour & Sauther, 2002; Key & Ross, 1999). Dimorphic traits such as size produce slight to pronounced separation in the diet of the sexes in
some species (Bean, 1999; Kamilar & Pokempner, 2008a). Sex differences in diet composition have also been recorded in many primate species (dinichism) (Clutton-Brock, 1977). In addition, in brown lemurs (Eulemur fulvus) females tend to spend more time feeding than males, especially when supporting nursing infants (Tarnaud, 2006). Among howler monkeys (Alouatta palliata), time budgets show males average 14% of the day feeding and females 18%, despite males having larger body sizes than females (Smith, 1977).

Using instantaneous scan sampling data, we focus on Hadza eating in camp to see how much food sharing compensates for the targeting of different foods by each sex. We investigate whether eating in camp differs by sex in terms of overall eating frequency and in terms of diet composition (frequencies of eating each food type). We also examine whether eating frequency by men and women differs after controlling for amount of time spent in camp. Finally, we investigate which sex is more often observed eating the foods acquired by the other sex.

**Materials and Methods**

*Study Population*

The Hadza are hunter-gatherers who number approximately 1000. They live in a savanna-woodland habitat that encompasses about 4000 km² 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 et al., 2005). These camps move about every 6 weeks on average.

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 mainly take meat and honey, as well as some baobab, back to camp. They may eat much of the honey they find, but take about half of their haul of honey, on average, and about 90% of medium to large game back to camp. 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 dig tubers of several species but will opportunistically pick up a tortoise or kill small mammals or scavenge larger game. They use simple, fire-hardened, sharpened branches as digging sticks to dig tubers almost every day. They roast some of their tubers once they finish digging and take the remainder (~70% of their haul) back to camp to feed others (Marlowe, 2006).

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). Nonetheless, Hadza BMI and percent body fat (%BF) does not vary greatly with season, though it does vary a bit in women (Marlowe & Berbesque, 2009).

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). See Table 3.1 for a list of common foods. The berries (or berry-like fruit which we will refer to as berries) in Hadzaland consist mostly of seed with a small amount of dry pulp that is high in sugar. When in season, several species of berries are super-abundant. Baobab is only one species, but is such a major fruit in terms of kilocalories or kilograms contributed to the Hadza diet that it deserves a category unto itself. Baobab is common across much of Africa. The 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 (Marlowe & Berbesque, 2009). 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. Table 3.2 shows basic macronutrient contents of Hadza foods, although it must be noted that most foods vary by region, season, and in the case of meat by age and sex of the animal as well.
Table 3.1. Numbers of species by type of food in Hadza diet.

<table>
<thead>
<tr>
<th></th>
<th>Frequency</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Domestics</td>
<td>7</td>
<td>.8</td>
</tr>
<tr>
<td>Berries</td>
<td>26</td>
<td>3.0</td>
</tr>
<tr>
<td>Fruits</td>
<td>8</td>
<td>.9</td>
</tr>
<tr>
<td>Mammals</td>
<td>56</td>
<td>6.4</td>
</tr>
<tr>
<td>Tubers</td>
<td>18</td>
<td>2.1</td>
</tr>
<tr>
<td>Honeys</td>
<td>7</td>
<td>.8</td>
</tr>
<tr>
<td>Birds</td>
<td>741</td>
<td>84.4</td>
</tr>
<tr>
<td>Reptiles</td>
<td>2</td>
<td>.2</td>
</tr>
<tr>
<td>Invertebrates</td>
<td>1</td>
<td>.1</td>
</tr>
<tr>
<td>berry or fruit</td>
<td>2</td>
<td>.2</td>
</tr>
<tr>
<td>fruit/nut</td>
<td>3</td>
<td>.3</td>
</tr>
<tr>
<td>Greens</td>
<td>1</td>
<td>.1</td>
</tr>
<tr>
<td>Insects</td>
<td>1</td>
<td>.1</td>
</tr>
<tr>
<td>Vegetables</td>
<td>2</td>
<td>.2</td>
</tr>
<tr>
<td>Eggs</td>
<td>1</td>
<td>.1</td>
</tr>
<tr>
<td>roots (other)</td>
<td>2</td>
<td>.2</td>
</tr>
<tr>
<td>Total</td>
<td>878</td>
<td>100.0</td>
</tr>
</tbody>
</table>

Table 3.2. Composition of Hadza foods

<table>
<thead>
<tr>
<th></th>
<th>Fat</th>
<th>Protein</th>
<th>Carbs (starch)</th>
<th>Sugars</th>
<th>Kcal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Honey</td>
<td>&lt;8.0(^1)</td>
<td>&lt;4.0(^1)</td>
<td>Trace(^3)</td>
<td>87.7(^1)-96.0(^1)</td>
<td>403-439(^1)</td>
</tr>
<tr>
<td>Meat</td>
<td>1.3-9.0(^4)</td>
<td>57.3-68.2(^4)</td>
<td>Trace(^5)</td>
<td>Trace(^5)</td>
<td>216(^6)-609(^7)</td>
</tr>
<tr>
<td>Tuber</td>
<td>0.6(^3)-3.4(^3)</td>
<td>2.3(^2)-10.4(^3)</td>
<td>19.4(^2)-61.3(^3)</td>
<td>6.2(^2)-48.3(^2)</td>
<td>73-85(^8), 146-298(^2), 177-279(^3)</td>
</tr>
<tr>
<td>Berries</td>
<td>&lt;2.0(^1)</td>
<td>7.1(^1)-15.2(^1)</td>
<td>Trace</td>
<td>61.1-72.7(^1)</td>
<td>108-145(^8), 318-342(^1)</td>
</tr>
<tr>
<td>Baobab*</td>
<td>15.0(^1)</td>
<td>19.4(^1)</td>
<td>5.5(^1)</td>
<td>23.4(^1)</td>
<td>328.5(^1)</td>
</tr>
</tbody>
</table>

1 (Murray et al., 2001) 2 (Schoeninger et al., 2001) 3 (Vincent, 1985) 4 (Van Zyl & Ferreira, 2004) 5 (Cordain et al., 2002) 6 (Weiner, 1973) 7 (McCullough & 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 are 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.

Data Collection

Behavioral observations were conducted using instantaneous scans once per hour during the day in camp, with a maximum of 13 scans from 7 AM (sunrise) to 7 PM (sunset) performed per day. During each observation the behavior of all people present was recorded. Eating was one of the behaviors recorded and the type of food eaten was recorded. The Hadza diet was broken into the aforementioned categories (honey, meat, baobab, berries, and tubers) with two additional categories. One category was “traded” foods. This category includes both animal and plant products ranging from beef to millet. This is a category primarily used to designate non-wild foods that were not acquired through foraging, but by trading with non-Hadza neighbors who are pastoralists or agro-pastoralists. There was also a category labeled “other.” This included “marula,” which is the nut of a fruit that is important but only in one of the four regions of Hadzaland, and for this reason it was lumped into the final category which also includes observations of eating where food type could not be determined as well as food items that constitute a very small percentage of the Hadza diet such as leaves, figs, etc.

While scan data are not ideal for measuring exact consumption amounts, they do have some real benefits that observations of focal individuals who are followed continuously over some time period do not have. Scan data capture all camp members present, which would be impossible with focal follows. Scan data provide a more thoroughly random sampling of all Hadza, and a very large sample of all food types. There are some limitations since this method does not measure package-size and processing time. Small package items that require no processing may be less likely to be captured by an instantaneous scan. On the other hand, food items that are processed and eaten almost simultaneously (such as peeling and eating a tuber bit by bit) may be over-represented in terms of time spent by quantity eaten. However, here we are investigating sex differences and there is no obvious reason why this should apply to one sex more than the other.

To assess the reliability of our scan data with respect to overall consumption, we analyzed eating frequency by food type in relation to amount of foods brought into camp for each camp separately. We
ran paired t-tests by camp to test whether the percent of each food type brought into camp (by kilograms) correlated with camp-wide eating frequencies of that food type in the same camp. Our data came from a total of 239,924 person-scans that were collected over a period of 11 non-sequential years (in 16 different camps). People in fewer than 20 scans were dropped from the analyses. This was done to prevent skew stemming from few observations of particular individuals (for example, a visitor could be seen eating 100% of the time due to a single observation).

Results

The total sample consisted of 318 people over the age of 15 (152 males and 190 females). Mean age of females was 38.7 years, and for males 39.1 years. The mean number of observations per individual was 85.1 for males and 108.3 for females. The mean number of observations of eating was 5.1 for males and 10.0 for females.

The percentage of the in-camp diet contributed by each food type was significantly correlated with adult eating frequencies of that food type in those camps (see Table 3.3), giving us confidence that the scan data are reliable (even with smaller package items such as honey).

Table 3.3. Paired correlations of Hadza eating frequencies against acquisition by food type

<table>
<thead>
<tr>
<th>Paired Samples Correlations</th>
<th>N</th>
<th>Correlation</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pair 1 Frequency of eating honey &amp; per capita honey acquisition</td>
<td>16</td>
<td>.611</td>
<td>.012</td>
</tr>
<tr>
<td>Pair 2 Frequency of eating meat &amp; per capita meat acquisition</td>
<td>16</td>
<td>.529</td>
<td>.035</td>
</tr>
<tr>
<td>Pair 3 Frequency of eating berries &amp; per capita berry acquisition</td>
<td>16</td>
<td>.744</td>
<td>.001</td>
</tr>
<tr>
<td>Pair 4 Frequency of eating baobab &amp; per capita baobab acquisition</td>
<td>16</td>
<td>.728</td>
<td>.001</td>
</tr>
<tr>
<td>Pair 5 Frequency of eating tubers &amp; per capita tuber acquisition</td>
<td>16</td>
<td>.819</td>
<td>.000</td>
</tr>
</tbody>
</table>

Females were observed eating far more frequently than males (t = -6.101, p < .0005, df = 323.126, n₁ = 152, n₂ = 190). However, due to females’ greater time spent in camp, this is not entirely surprising. Figure 1 below demonstrates that females were eating more frequently (t = -7.040, p = .003,
df = 339.679, \( n^1 = 152, n^2 = 190 \) even when presence in camp is controlled for by dividing observations of a person seen eating by total observations of that person seen in camp.

Figure 3.1. Hadza eating frequencies controlled for presence in camp. Midlines indicate medians, bars indicate first to third quartiles, whiskers indicate maximum excluding outliers, which are shown as circles and extremes as stars.

In terms of absolute eating frequencies (not controlled for presence in camp), females were eating significantly more of every food category than were males (see table 3.4). This trend is more pronounced with tuber consumption than any other food category. Figure 3.2 shows the total number of observations of individuals eating each type of food divided by the total number of observations recorded per individual (to control for time spent in camp). Females were observed eating every food
category more frequently than males but only significantly more tubers ($t = -5.288$, $p < .0005$, $df = 325.933$, $n^1 = 152$, $n^2 = 190$).

Table 3.4. Sex differences in Hadza eating frequency (raw counts) by food type

<table>
<thead>
<tr>
<th></th>
<th>T</th>
<th>Df</th>
<th>sig (2-tailed)</th>
<th>$n^1$</th>
<th>$n^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Honey</td>
<td>-2.210</td>
<td>335.671</td>
<td>.028</td>
<td>152</td>
<td>190</td>
</tr>
<tr>
<td>Meat</td>
<td>-2.329</td>
<td>335.911</td>
<td>.020</td>
<td>152</td>
<td>190</td>
</tr>
<tr>
<td>Berries</td>
<td>-2.106</td>
<td>332.279</td>
<td>.036</td>
<td>152</td>
<td>190</td>
</tr>
<tr>
<td>Baobab</td>
<td>-2.176</td>
<td>297.368</td>
<td>.030</td>
<td>152</td>
<td>190</td>
</tr>
<tr>
<td>Tuber</td>
<td>-2.176</td>
<td>288.246</td>
<td>.000</td>
<td>152</td>
<td>190</td>
</tr>
</tbody>
</table>

Figure 3.2. Observations of Hadza eating frequencies by sex and food type.
Another way to look at consumption is the contribution of each food category to the overall percentage of eating observations of each sex including the ‘other’ category so that all eating observations are counted. For example, how many times were males observed eating meat as a proportion all eating events by males? Are these frequencies different from that of females? Figure 3.3 shows that males were observed eating relatively more meat, berries, and honey, while females were eating relatively more baobab and tubers. Men were observed eating meat significantly more often as a percentage of their overall observed eating than women ($t = 2.271$, $p = 0.024$, $df = 259.131$, $n_1 = 152$, $n_2 = 190$). Women ate significantly more tubers as a percentage of their overall eating observations ($t = -2.733$, $p = .007$, $df = 318$, $n_1 = 152$, $n_2 = 190$).

Figure 3.3. Hadza eating observations by food type divided by total eating observations.
The previous analyses include the eating of foods that don’t fall into one of the five main categories, because the ‘other’ category is included in the denominator (hence, bars in Figure 3 do not add up to 100%). Figure 3.4 below shows the percentage eaten of each of the five main food types of interest divided by all observed eating and scaled to represent 100% of the diet of each sex. These five categories constitute approximately 95% of the diet by weight (Marlowe & Berbesque, 2009).

Figure 3.4. Hadza mean eating frequencies by sex.

To find out which sex is more frequently eating the other sex’s foods we added all observations of eating foods that are commonly acquired by females (berries, and tubers), and subtracted from those the total number of observations of eating foods that are commonly acquired by males (meat and honey). Baobab is more difficult to categorize, being brought into camp by both sexes (36% by males and 64% by females by kilograms). We allocated .36 of all baobab eating instances to “male acquired foods” and
.64 of baobab eating instances to “female acquired foods” so the production of each sex was represented. The other food categories were dominantly acquired by one sex more than the other, with little variance. This categorization of male acquired versus female acquired foods allows for an analysis of whether one sex is benefiting more from the production of the other sex (although this may be far closer to an estimate by weight than by kilocalories). Seventy-one percent of eating observations of females are of female acquired foods, while 63.1% of male eating observations are of female acquired foods. Figure 3.5 shows that both sexes are eating female acquired foods more frequently than male acquired foods. If male foods were eaten more than female foods this would push the mean into negative numbers.

Twenty-nine percent of eating observations in females are of male acquired foods, while 36.9% of eating observations of males are of male acquired foods. While both sexes are more frequently eating female acquired foods, as a percentage of each sex’s eating observations, males are eating male acquired foods significantly more often than females (t = 2.387, p = .018, df = 264.449, n₁ = 138, n₂ = 184). Females are not eating significantly more of their own foods.

Due to females’ more frequent eating overall, it is not surprising that in terms of absolute counts of eating, without correcting for the number of all observations (i.e. presence in camp), females are eating significantly more of both male acquired foods (t = -2.951, p = .003, n₁ = 152, n₂ = 190) and female acquired foods (t = -4.836, p < .0005, n₁ = 152, n₂ = 190).
Table 3.5 summarizes all of the previous results of eating frequencies by food type. The results are divided into three categories of analysis: 1) raw frequencies of eating (counts) by sex, 2) frequencies of eating divided by number of observations by sex, 3) frequencies of eating as a percentage of the total diet for each sex.
Table 3.5. Summary of Hadza eating frequency results by food type

<table>
<thead>
<tr>
<th>Food Type</th>
<th>Raw #</th>
<th>women &gt; men</th>
<th>p</th>
<th>Divided by observations</th>
<th>women = men</th>
<th>p</th>
<th>As % of diet</th>
<th>women &gt; men</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Meat</td>
<td></td>
<td>women &gt; men</td>
<td>p = .020</td>
<td>women = men</td>
<td>NS</td>
<td></td>
<td>women &gt; men</td>
<td>p = .024</td>
<td></td>
</tr>
<tr>
<td>Tuber</td>
<td></td>
<td>women &gt; men</td>
<td>p &lt; .0005</td>
<td>women &gt; men</td>
<td>p &lt; .0005</td>
<td></td>
<td>women &gt; men</td>
<td>p = .007</td>
<td></td>
</tr>
<tr>
<td>Berries</td>
<td></td>
<td>women &gt; men</td>
<td>p = .036</td>
<td>women = men</td>
<td>NS</td>
<td></td>
<td>women = men</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Baobab</td>
<td></td>
<td>women &gt; men</td>
<td>p = .030</td>
<td>women &gt; men</td>
<td>NS</td>
<td></td>
<td>women = men</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Honey</td>
<td></td>
<td>women &gt; men</td>
<td>p = .028</td>
<td>women = men</td>
<td>NS</td>
<td></td>
<td>women = men</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>women &gt; men</td>
<td>p &lt; .0005</td>
<td>women &gt; men</td>
<td>p = .003</td>
<td></td>
<td>NA</td>
<td>NA</td>
<td></td>
</tr>
</tbody>
</table>

NS- Not significant

The only analysis in which males are eating significantly more than females is in bold.
Discussion

All of these results are meaningful. However, in terms of the sexual division of foraging labor we believe it is the raw eating counts that most accurately measure the outcome of food sharing with the other sex in camp. Hadza women eat more of every food category than do men. This is partly due to the fact that women spend more time in camp than men. Without controlling for time spent in camp, both men and women are eating women’s foods more frequently than men’s foods. However, women are eating their own foods as well as men’s foods more frequently than men are.

When presence in camp is controlled for, women are still observed eating significantly more frequently than are men. There are sex differences in the in-camp diet composition. If the in-camp diet is considered as a whole, men are eating more meat as a proportion of their in-camp diet than women, and women are eating more tubers. Women also eat tubers out of camp (whereas men do not), so overall, women are eating tubers far more frequently than men.

Berbesque and Marlowe (2009) found that Hadza men’s and women’s food preferences were significantly different. While they agreed on honey as most preferred, baobab as third, and tubers as least preferred, men ranked meat second and berries fourth, while women ranked berries second and meat fourth. So, while men are eating less frequently than women, they are eating more of the foods that they prefer (honey and meat) as a proportion of their overall diet. In contrast, women are eating more of the food they least prefer—tubers. This may be largely due to the fact that men eat far less frequently in camp than do women, and thus they are eating high quality foods (such as meat and honey) both in and out of camp. While females are eating meat more often than men in absolute terms, this constitutes a smaller percentage of their in-camp diet. Women are probably eating a significantly higher proportion of their overall diet in camp, and their out of camp diet is probably lower quality than men’s out of camp diet.

Sherry & Marlowe (2007) reported on the nutritional homogeneity among the Hadza as measured by percent body fat (%BF) and body mass index (BMI). The results here reveal that there are significant sex differences in the Hadza diet in camp (as measured by eating frequencies). Differences in the in-camp diet are likely to be an underestimate of total dietary sex differences. Marlowe and Berbesque (2009) analyzed a larger sample of all foods brought into camp by region and season, and found that men’s body condition did not vary. On the other hand, the relative contributions of different foods significantly affected female body condition as measured by percent body fat (%BF) and body
mass index (BMI). Hadza women of reproductive age had a higher %BF in camps where more meat was acquired and a lower %BF where more tubers were acquired. Women’s BMI, on the other hand, was higher when more berries were acquired.

If meat matters for female %BF could men provide more? Men are eating only slightly less (not significantly less) of their own foods that they have taken back to camp to share. Because men often eat some of their own foods before bringing the remainder back to camp, one might expect that men would eat much less of those foods in camp (and eat more of women’s foods instead). In addition, men reserve some particular portions of large game, which is not captured by our scan data because it is eaten in private. Hadza men who have become ‘real’ (epeme) 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 (epeme meat). 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. Hadza men have far lower overall absolute eating frequencies than females, and without controlling for presence in camp roughly equal eating frequencies of high quality foods (such as honey and meat). In terms of absolute number of eating observations the sharing of men’s foods appears to be fairly equitable in camp. However preliminary estimates reveal that a higher portion of men’s (than women’s) diet is eaten while on walkabout (Marlowe, 2010). If this were not true men would be eating far less than women even though they are about 13% heavier. Hadza women also have on average 20% BF, while males have only 9%.

Hadza men are eating a higher quality diet than are women, but women are able to eat far more frequently, and spend less time foraging than men (4.1 hours a day for women versus 6.1 hours a day for men). Similar observations have been made anecdotally about “snacking” by the Aka pygmy women (Walker & Hewlett, 1990b). Maintaining adequate body fat and a positive energy balance are important factors for female fertility (Ziomkiewicz, Ellison, Lipson, Thune, & Jasienska, 2008). It is not yet clear whether a regular caloric intake of lower quality foods would be more beneficial for maintaining fecundity than a more variable diet consisting of higher quality foods. It has been pointed out that the regular caloric intake (as well as sedentism) of agricultural populations may be responsible for their increase in fertility, even when overall measures of health are not improved (or even decline) (Lambert, 2009; Lukacs, 2008).

Women in foraging societies may do less hunting than men because it is incompatible with childcare (Brown, 1970a). However, if female fertility is significantly enhanced from regular caloric
intake (even at the expense of overall health) female foragers may maximize their RS by pursuing a much more reliable diet even if it consists of relatively lower quality foods.

Estimates of the degree of reliance on plant foods versus animal foods in the ‘paleo-diet’ (or the forager diet) may be premature. At least in the case of the Hadza, we see pronounced sex differences in the in-camp diet. The proportion of the diet eaten in camp should yield an underestimate of the total dietary sex-differences because about 1/4 to 1/3 of the diet is eaten out of camp. The vast majority of food sharing occurs in camp (Marlowe, 2006). Even though we find significant sex differences in the Hadza diet, it is important to note that food sharing in camp does lessen the difference in the diet of the sexes. For example, almost 30% of women’s in-camp diet consists of meat and honey and almost 100% of these two foods are produced by men (Figure 4). Likewise, 55% of men’s in camp diet consists of tubers, berries, and baobab and 88% of these three foods were acquired by women (Figure 4). In the future we will analyze the total diet (including consumption while on forays as well as in-camp consumption). This will likely demonstrate sex-differences that are more pronounced than those presented in this analysis.
CHAPTER # 4
SEX DIFFERENCES IN DENTAL WEAR PATTERNS OF HADZA HUNTER-GATHERERS

Abstract

This study investigates the relationship between patterns of attrition across age and sex cohorts with behavioral data on diet composition in a contemporary hunter-gatherer population, the Hadza of Tanzania. Despite the targeting of different foods by males and females among hunter-gatherers, the sharing of male and female foods is usually assumed to result in virtually the same diet for males and females. Despite the widespread sharing of foods among the Hadza, hunter-gathers of Tanzania, women were observed eating significantly more frequently than Hadza men, and were eating more of some foods than others. Casts of the upper dentition (full arcade) were made from molds taken from 126 adults (71 women and 55 men) and scored according to the Murphy dental attrition scoring system. Females demonstrated significantly greater anterior occlusal wear than males controlling for age. Males demonstrated greater asymmetry in wear, with greater wear on the left side in canines, first premolars, and first molars. We believe that these sex differences in wear patterns reflect the sex differences seen in eating frequency, as well as differences in the use of teeth as tools.

Introduction

Dental wear can be used to reconstruct diet, local ecology, health, and cultural practices both within and across populations. Much of the focus on tooth wear has been focused on tracking differences across subsistence patterns, in particular the timing and consequences of transitions to agriculture in various populations (McKee & Molnar, 1988; Sciulli, 1997). A decline in rates of dental wear has been correlated with the transition to agriculture or food production. Deter (2009) suggests that there may be attrition differences in “big game hunters” versus broad spectrum hunter-gatherers. Food preparation technologies, such as cooking in pots or boiling foods may also lead to lesser degrees
of attrition because these techniques soften food (Deter, 2009; Scott & Turner, 1988). Dental attrition is also used to establish age at death for individuals in archaeological contexts (Arnold, Naumova, Koloda, & Gaengler, 2007; Mays, 2002). Here, we analyze the patterns of dental wear by age and sex in a contemporary East African hunter-gatherer population, the Hadza. We test hypotheses based on our previous results on sex differences in the Hadza diet and the use of their teeth as tools.

Tooth wear can result from physical abrasion or chemical erosion. Physical abrasion can result from consumption of particular abrasive foods, from food processing (e.g. from grinding or pounding with stone), tooth-on-tooth contact, and from using the dentition for purposes other than eating (using the teeth as tools, or extramasticatory use). Chemical erosion most typically results from the consumption of acidic foods. Another factor affecting dental wear is the developmental timing of eruption. Age of eruption is different for each tooth class, and this is a critical factor in its relative degree of wear between tooth classes (even within one individual) (Molnar, 1971). Those teeth that erupt earlier tend to show greater wear because they have been used longer.

Studies on wear patterns among hunter-gatherers and agriculturalists often report greater wear in hunter-gatherer dentition than agriculturalists dentition, particularly in the anterior teeth (Deter, 2009; Hinton, 1981). Gender and status are two major factors that often affect within population variation. The Hadza are egalitarian (and have very little differential access to resources), so we should not expect status differences. On the other hand, the sexual division of foraging labor is essentially gendered roles in the context of foraging and food processing. Because of this we focus on sex differences in dental wear in the Hadza. Studies of other populations (from various subsistence strategies) present various findings with regard to sex differences in attrition rates. Some studies find no sex differences in attrition (Deter, 2009; Kieser & Groeneveld, 1985; Lovejoy, 1985), while others find greater rates of attrition in males (e.g. Greenland natives and modern Igaloolik Eskimos) (Davies & Pederson, 1955; Tomenchuk & Mayhall, 1979). Others report higher rates of attrition in females (prehistoric American Indian and Australian aborigines) (Molnar, 1971; Richards, 1984).

There are few studies of the dental attrition of contemporary foragers (van Reenen, 1992; Walker & Hewlett, 1990a). Hewlett and Walker (1990) found that both the Aka and Mbuti (Congo) men had greater attrition than their female counterparts. Hewlett and Walker were not convinced their result reflected a real sex-difference because the mean female age was younger than the mean male age in the sample. We are not aware of any other studies finding sex-differences in the dental wear of contemporary foragers.
In a previous study of the Hadza, Berbesque & Marlowe (ND) have found that there are sex differences in the in-camp eating frequencies of different food types. Hadza women are eating far more tubers than are Hadza men. Hadza men are eating more meat as a proportion of their diet. Tubers are very fibrous and tough (Dominy, Vogel, Yeakel, Constantino, & Lucas, 2008). They are perhaps the most abrasive food that the Hadza eat. Therefore, we would expect that Hadza females should have greater wear than males, particularly in the older age cohorts. Because the Hadza often use their teeth as tools we also discuss how this could explain some of the patterns of dental wear.

Subject Population

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 et al., 2005). These camps move about every 6 weeks on average.

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 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 mainly take meat and honey, as well as some baobab, back to camp. They may eat much of the honey they find, but take about half of their haul of honey, on average, and about 90% of medium to large game back to camp. 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 dig tubers of several species. They use simple, fire-hardened, sharpened branches as digging sticks to dig tubers almost every day. They roast some of their tubers once they finish digging and take the remainder (~ 70% of their haul) back to camp to feed others (Marlowe, 2006).

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 available seasonally and is the most preferred food for the Hadza (Berbesque & Marlowe, 2009). Though honey consumption may result in
higher caries rates (and perhaps subsequent antemortem tooth loss), it is not likely a factor in dental attrition. Meat in the Hadza diet is also unlikely to produce much wear, however the Hadza eat most of the animal (including tendons, ligaments, etc.). They also gnaw on the bones, and eat smaller bones.

The berries in Hadzaland consist mostly of seed with a small amount of dry pulp that is high in sugar. Also, when in season, berries are super-abundant. The berries are most commonly swallowed whole (seed and all), and probably contribute little to tooth wear. However, we have heard anecdotes of Hadza cracking or chipping teeth on berry seeds.

Baobab fruit is common across much of Africa and 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. Inclusions of rock particles in the baobab flour may result from the process of pounding of baobab seeds, especially since they use big open rock surfaces as their anvils. If this is the case it could be another significant factor in Hadza dental attrition.

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 the species //ekwa that one cannot swallow it but must spit out the quid after chewing it for a while.

Figure 4.1 shows the in-camp diet considered as a whole. This is the number of observations of an individual person eating a particular food type divided by the total number of observations of the person seen eating (scaled to 100%), so that the composition of the male and female diet can be compared, despite more frequent female eating (and more frequent presence in camp). This shows the in camp diet only (which is 100%). Men are more frequently eating meat as a proportion of their in-camp eating observations than women, and women are eating more tubers. Women also eat tubers out of camp (whereas men do not), so overall women are eating tubers far more frequently than men (Berbesque & Marlowe, ND)
The Hadza frequently use their teeth as tools. Men use their teeth to work arrows (see Figure 4.2), tighten bow strings, and strip bark off of branches to make twine. Women use their teeth to cut beading string, and chew both leather hides and bow strings to make them supple. Both Hadza men and women use their teeth to puncture tuber “skin” and then continue holding onto the outer layer with their teeth to peel the tuber before eating it. Both men and women occasionally use small sticks as toothpicks to clean their teeth.
Methods

These data were collected over three summers (2007-2010) across 9 camps. Molds of Hadza maxillary dentition were made (President Jet molding material), and converted to epoxy casts (Epotek 301). The Hadza are not accustomed to dentistry, so to avoid causing them any discomfort we used shorter dental trays that extend only through the first molar on most Hadza. Second molar impressions were captured in some cases (most commonly when the individual had lost some of their other teeth), but dropped from analyses due to the small sample size for this tooth class. Each tooth present in the casts was then scored for attrition. Attrition rates were scored based on the Murphy scoring system (1959b) as modified by Smith (1984) for incisors, canines, and premolars. In this system the scores range from one to eight based upon increasing destruction of the tooth’s crown and dentine exposure. Similar methods developed by Scott (1979) were used for molars as summarized by Buikstra and Ubelaker (1994). The only differences in this system are that the wear scores range from one to ten, and each quadrant of the molars are scored separately. From these quadrant wear scores, we calculated a mean wear score for the entire tooth.
Inter-observer was measured by scoring the wear in each tooth type in the left dental arcade of 24 individuals. The mean intraclass-coefficient for all teeth scored was .822 (df=13, p=<.0005). The ages of most Hadza are fairly well known (from long-term demographic data). We analyzed attrition rates by age as well as by sex.

**Results**

We used a sample of 126 adults (15 years old and over). The sample consisted of 55 males and 71 females. Mean age of males in the sample was 37.9 years old and the mean age of females was 38.6 years old. Figure 4.3 shows the sample distribution by age and sex.

![Distribution of sample by age and sex](image)

Figure 4.3. Distribution of sample by age and sex

To gauge overall wear by tooth class, we analyzed left dentition in each tooth class, using the right for that tooth class when the left was not present. Mean wear by tooth class is shown in Figure 4.4.
First molars had the greatest degree of wear in the population, followed by first incisors. The timing of eruption explains this pattern, since first molars are usually the first tooth class from the permanent dentition to erupt (at approximately 6 years old), followed by central incisors at approximately 7 years old. The next tooth classes to erupt are: lateral incisors (8 years), first premolars (10-11 years), second premolars (10-12 years), second molars (10-12 years), canines (11-12 years), and finally third molars (17-21 years) (wisdom teeth) (Buikstra and Ubelaker 1994).

Table 4.1 shows the mean score of attrition and sample sizes in each tooth class by 10 year age cohorts. For median scores see Appendix C2. Figure 4.5 shows the same data as a trend for each tooth class over time. Attrition scores for the total dental arcade by age cohort and sex are shown in Appendix
C3. It is noteworthy that central incisors (I1) are already more heavily worn than other tooth classes by the teen years.

Table 4.1. Mean Wear Score by Tooth Class and Age Cohort (Males and Females Combined)

<table>
<thead>
<tr>
<th>Cohort</th>
<th>I1 (n)</th>
<th>I2 (n)</th>
<th>C (n)</th>
<th>P1 (n)</th>
<th>P2 (n)</th>
<th>M1 (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>15-19</td>
<td>2.95 (9)</td>
<td>2.13 (8)</td>
<td>1.78 (9)</td>
<td>2.44 (9)</td>
<td>2.56 (9)</td>
<td>2.91 (8)</td>
</tr>
<tr>
<td>20-29</td>
<td>3.74 (27)</td>
<td>3.08 (26)</td>
<td>2.57 (28)</td>
<td>2.91 (28)</td>
<td>2.73 (28)</td>
<td>3.60 (27)</td>
</tr>
<tr>
<td>30-39</td>
<td>4.30 (22)</td>
<td>3.91 (23)</td>
<td>3.72 (23)</td>
<td>4.02 (25)</td>
<td>3.52 (25)</td>
<td>4.83 (23)</td>
</tr>
<tr>
<td>40-49</td>
<td>4.36 (18)</td>
<td>4.44 (17)</td>
<td>4.61 (18)</td>
<td>4.24 (17)</td>
<td>4.06 (18)</td>
<td>5.58 (16)</td>
</tr>
<tr>
<td>50-59</td>
<td>4.60 (10)</td>
<td>4.60 (10)</td>
<td>4.70 (10)</td>
<td>5.05 (10)</td>
<td>5.00 (10)</td>
<td>6.45 (11)</td>
</tr>
<tr>
<td>60+</td>
<td>6.75 (4)</td>
<td>6.00 (5)</td>
<td>6.00 (7)</td>
<td>6.00 (6)</td>
<td>5.88 (8)</td>
<td>7.69 (7)</td>
</tr>
</tbody>
</table>
In a linear regression controlling for age and using the left side of each tooth class, females had greater central incisor (I1) wear than males (B=.214, p=.013, df=87). Females also had greater wear in the lateral incisor, significant in a one-tailed test (B =.146, p=.058, df=86). There were no significant sex-differences in other tooth classes using the left side of each tooth class.

Males, however, had greater asymmetry in tooth wear than females (Figure 4.6). Males had greater wear on the left side than the right side of their arcade in two tooth classes. Male left side wear was significantly greater than right side wear in first molars (t= -2.837, df=30, p=.008), as well as first premolars (t=-1.706, df=41, p=.096) with one-tailed tests. Females only had significant asymmetry in canines (t=3.346, df=40, p=.002).
Figure 4.6. Right Side Wear Minus Left Side Wear by Tooth Class and Sex
Midlines indicate medians, bars indicate first to third quartiles, whiskers indicate maximum excluding outliers, which are shown as circles and extremes as stars.

Using the right side only (rather than the convention of using the left side), females had significantly more wear on P1’s than males did, controlled for age (B=.188, p=.020, df=87). There were no other significant sex differences by tooth class. In summary, females had significantly greater attrition in central and lateral incisors as well as right first premolars. Figure 4.7 shows the maxillary dental arcade of a skeletal population, with the teeth that are significantly more worn in Hadza females highlighted in red.
Figure 4.7. Maxillary dental arcade of prehistoric hunter-gather population (teeth with sex-differences in wear in the Hadza highlighted in red)
Photograph of Windover (8BR246) courtesy of Glen Doran.

Table 4.2 shows the inter-item covariances and correlations of each tooth class by sex. Because males showed significant asymmetry in the right and left sides of their dentition, we used left sides only in this analysis. Hadza females had less variance in dental wear by tooth type than males. Female dental wear was also more highly correlated across each tooth type than in males.

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
<th>Variance</th>
<th>N of Items</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male Inter-Item Covariances</td>
<td>1.290</td>
<td>.150</td>
<td>6</td>
</tr>
<tr>
<td>Female Inter-Item Covariances</td>
<td>1.837</td>
<td>.082</td>
<td>6</td>
</tr>
<tr>
<td>Male Inter-Item Correlations</td>
<td>.678</td>
<td>.015</td>
<td>6</td>
</tr>
<tr>
<td>Female Inter-Item Correlations</td>
<td>.786</td>
<td>.006</td>
<td>6</td>
</tr>
</tbody>
</table>
Discussion

Overall, the Hadza fit the pattern commonly described for hunter-gatherers—they have a great deal of wear compared to most agricultural populations, particularly in the anterior dentition. The anterior dentition was more heavily worn in females than in males. We propose two possible explanations for this. The first is that women were more frequently observed eating tubers than men. The second is that women are using their anterior teeth as tools. The Hadza (particularly women) demonstrate a wear pattern on their anterior dentition that is also seen in prehistoric skeletal samples (Comuzzie & Steele, 1988; Irish & Turner, 1987; Turner & Machado, 1983) as well as historic Senegalese skeletal populations (Irish & Turner, 1997). This is lingual surface attrition of the maxillary anterior teeth (LSAMAT). LSAMAT is interpreted as the result of pulling or holding abrasive material between the tongue and the lingual surface (side facing the tongue) of the upper anterior teeth, causing wear on the lingual surface of the anterior teeth rather than just the occlusal plane (the plane where upper and lower teeth meet). An example given by Scott and Turner (1988) is the pulling of manioc root. Hadza women often use their teeth to peel the tough skin off of tubers. Men also do this, but far less frequently than women both because they eat tubers less frequently and because men often carry knives that they can use to peel tubers. Women less often carry knives, and so more often rely on their teeth.

Males demonstrated greater significant asymmetry in wear, with left side of the dental arcade showing heavier wear than the right. Females had significantly asymmetrical wear in canines only. The sex-specific asymmetry in wear might not be seen in conventional analyses, wherein only the left side of each tooth class is analyzed (unless missing, when the right is then used). This convention was established primarily to avoid double counting individuals when isolated teeth were found. We measured both sides of the dental arcade and found asymmetry in males. We would not have found this if we had followed the standard method of using the left side preferentially unless the asymmetry was so pronounced that it was obvious before data collection. Asymmetry may be related to use of the dentition as tools. Several authors have indicated that this, along with particular directional wear patterns have been associated with working sinew for bows, nets, ropes, etc. (Lozano, de Castro, Carbonell, & Arsuaga, 2008; Scott & Turner, 1988). Males also demonstrated greater variance and lower correlation in tooth wear even within the left side of the dental arcade. This too is consistent with the use of teeth as tools and preferentially using a dominant side.
We think the male pattern of asymmetrical wear is due to use of the dentition as tools—working arrows, and tightening bow strings. It may be that the greater left side wear pattern is consistent with stabilizing with the left dentition (P2, M1 and perhaps M2) and pulling away from the face on the right. Within the left side of the arcade, the lower correlation of wear across tooth types is also consistent with the use of particular areas of the arcade for tool making. Further analyses will investigate directionality of molar wear (mesio-distal or bucco-lingual) to distinguish wear stemming from eating versus using the teeth as tools. Asymmetrical wear may be obscuring sex differences in the posterior dentition. A larger sample size is necessary to investigate these patterns across age and sex.
CHAPTER # 5
DISCUSSION

The importance of the diet in understanding behavior cannot be overstated. Diet affects the morphology, ranging patterns, social organization, and mating behavior of animals. Therefore, dietary information on hunter-gatherers is a critical piece of information when reconstructing the past.

Food Preferences

There may or may not be cultural prescriptions or proscriptions involved in stated food preferences. If preferences are wired into the brain such that quality can be recognized independent of cost (Symons, 1979), we might expect that females’ stated preferences would be the same as men’s. Constraints on the acquisition of a particular food due to pregnancy, lactation, or childcare should (at least in theory) not affect preferences for that food. Cost-free food preferences have been studied in other species (Hayward, O’Brien, Hofmeyr, & Kerley, 2007b; Wobber et al., 2008). Many researchers interested in the evolution of the hominin diet have presented cost/benefit models of food choices (Griffith, Long, & Sept, 2010; Mithen, 1989), but there are no cost-free studies of human forager food preferences. The costs of acquiring foods must surely vary by age, sex, and reproductive status. Different currencies may be maximized by males versus females. Because we can ask humans about their food preferences we have a unique opportunity to see how taste maps onto nutritional properties of foods—or their perceived benefits, something that could only be accomplished in other species by presenting them with different foods.

My findings have implications for the theory that big-game hunting by males is primarily motivated and pursued to signal mate quality to females as opposed to provisioning the hunter’s household. If men are signaling their quality by acquiring meat in pursuit of mating opportunities, then we might expect females to prefer meat over everything else. In fact, women raked meat 4rth out of 5 foods.
Hadza food preferences also have implications for the constraint hypothesis of why females in many foraging societies do not hunt. Females prefer meat less than males, which may indicate that all constraints aside meat may not be as nutritionally beneficial for females as it is for males. This may be due to a variety of factors. One possibility is that females need less protein than males. Another possibility is that the optimal diet for females is far more dependent on eating frequency than males. If this is the case, lower variance foods might be more preferred, and the concordance in ranking might be less strong in females. It is possible that females have benefited from being more equally interested in whatever food is easy to obtain, whereas males may benefit from seeking out the highest quality foods.

**Eating Frequency by Food Type**

Hadza men and women target different foods while out of camp. Each sex eats some of their food before returning to camp. This is why we would expect to see far less difference in in-camp consumption than in out-of-camp consumption. Nevertheless, the sex-differences seen in in-camp eating frequencies by food type are striking given that the majority of food-sharing happens in camp. Women are eating every food at far higher frequencies than men for type if raw frequencies are used. Whether examined as raw frequencies, frequencies controlled for by presence in camp, or frequencies as a percentage of overall eating, females are eating more tubers. Men are eating significantly more meat than women but only as a percentage of their in-camp diet (not in absolute terms). In light of this meat sharing looks fairly equitable, at least when brought back to camp. Because men eat some of their meat out of camp, if we added out of camp consumption to this data we may find that men are eating as much or more meat in absolute terms. In addition, men eat particular portions of large game in private that are taboo for women to eat.

Why would females be eating every food type more frequently than males? Females may be pursuing a dietary strategy that minimizes the variance in daily caloric intake, perhaps at the expense of targeting more high quality foods. This strategy might be better for maintaining fecundity as well as for childcare. Several researchers have hypothesized that there was increased fertility with the beginning of agriculture due to an increase in sedentism and more regular caloric intake (of relatively low quality foods). It is possible that forager women pursue a somewhat similar strategy. Forager women also tend to spend less time out of camp foraging than men do. Perhaps a lower energy throughput along with
very regular caloric intake is beneficial for female fertility (Ziomkiewicz et al., 2008). This strategy seems very compatible with childcare. It is easier to obtain a surplus of these low variance foods to provision children, and children cannot go long periods of time without food. Feeding a child a very high calorie meal every third day simply will not work as well as feeding them a lower calorie meals several times a day (even if the average daily kilocalories are equal).

**Attrition**

The Hadza have a great deal of wear compared to most agricultural populations, particularly in the anterior dentition. The anterior dentition was more heavily worn in females than in males. There are two possible explanations for this. The first is that women were observed eating more frequently than men. Women’s tuber eating frequency was much higher, and tubers are very fibrous and tough. It is surprising that the posterior dentition is not significantly more worn in females than in males in light of the sex differences in tuber consumption. The second explanation for greater wear in the anterior dentition is that women are using their anterior teeth as tools.

Males had significantly greater asymmetry in wear, with left side of the dental arcade showing heavier wear than the right. Females did not have significantly asymmetrical wear. The male pattern of asymmetrical wear is likely due to use of the dentition as tools—working arrows, and tightening bow strings. Working an arrow, for instance, a Hadza man might bite down more with one side of his dental arcade more so than the other. It is less likely that pulling, or stripping materials with the anterior dentition would produce right to left side asymmetry. The greater lingual wear on the Hadza dentition likely indicates that this wear pattern is not the result of chewing food alone.

The use of teeth as tools makes interpretation of sex differences in dental wear patterns more difficult. A greater sample size may be necessary to estimate the effects of particular wear patterns on the overall attrition of each tooth type by sex. Future work will investigate the directionality of wear patterns macroscopically as well as microwear patterns to better document tool use as a factor in the dental wear of the Hadza.

Teeth provide information on more than just the diet of an individual during its life-time. They also provide information on the dietary niche and selective pressures facing the animal. Recent research suggests that the morphology of the dentition may be heavily influenced by periods of food shortages.
(Constantino, Lucas, Lee, & Lawn, 2009; Ungar, 2009). Natural selection should favor exploitation of any foods that would help minimize wasting and starvation during the season with fewer preferred foods. These foods are called “fallback foods”, and are defined as foods that are taken when more preferred foods are not available (Altmann, 2000; Malenky & Wrangham, 1994). The fallback food for the Hadza is clearly tubers—the least preferred food for both sexes (Berbesque & Marlowe, 2009; Marlowe & Berbesque, 2009).

It is noteworthy that Hadza women provide nearly all of the tubers eaten, and therefore all of the fallback food for the Hadza. Hadza women’s body mass index and percent body fat (but not men’s) decline in times when more tubers are taken. This might mean that women are suffering during times of more tubers, or it might be that at other times women are buffering themselves by adding more fat, which they then lose in the lean season (Marlowe & Berbesque, 2009). In either case, Hadza women are relying far more heavily on fallback foods than Hadza men.

In the future I will investigate other aspects of the dentition such as eruption, microwear, and stable isotope analyses. Once we have sufficient data on out of camp consumption, we will add that data to the in camp data presented here. Finally, I will continue to investigate whether there are sex differences in nutritional requirements, and if so, how they relate to sexual division of foraging labor.
A1. 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 below). 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 2\textsuperscript{nd} for meat and 4\textsuperscript{th} for berries. Females were tested for concordance in ranking berries 2\textsuperscript{nd} and meat 4\textsuperscript{th}. Male concordance in rank was high across all food categories except baobab. Female concordance was significant only for honey, berries, and tubers (Table 4). It appears that females really do prefer berries over meat because more females ranked berries at 2\textsuperscript{nd} than expected from the null assumption. On the other hand, the ranking of baobab as the 3\textsuperscript{rd} most preferred food by both sexes appears to result from ranking other foods higher or lower than chance.

<table>
<thead>
<tr>
<th></th>
<th>Honey</th>
<th>Meat</th>
<th>Baobab</th>
<th>Berries</th>
<th>Tubers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males observed (n = 45)</td>
<td>.688**</td>
<td>.311*</td>
<td>.222</td>
<td>.311*</td>
<td>.444**</td>
</tr>
<tr>
<td>Females observed (n = 49)</td>
<td>.449**</td>
<td>.244</td>
<td>.184</td>
<td>.306*</td>
<td>.449**</td>
</tr>
<tr>
<td>Total observed (n = 94)</td>
<td>.564**</td>
<td>.213</td>
<td>.202</td>
<td>.245</td>
<td>.447**</td>
</tr>
</tbody>
</table>

**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% 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.

A2. 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.
APPENDIX B
EATING FREQUENCY

B1. Eating was coded whether food type could be ascertained or not. Food type was also coded 73.2% of the time. There appeared to be no systematic bias in food type coding by sex ($t=-1.172$, $p=.242$, $n^1=137$, $n^2=183$). There were few instances of other food types eaten (e.g. figs, eggs, leaves, etc.). These are labeled ‘other’.

B2. 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).
C1. There are some limitations imposed by these methods—in skeletal populations dentine exposure is more clearly distinguished because of both the changes in the relief of the occlusal plane and the brown color of the dentine in contrast to the white enamel. Our dental casts are monochromatic, so each researcher must identify dentine exposure from the relief pattern of the crown surface only. While the dental casts of the Hadza allow for collecting more detailed data, and independent assessment of scoring (calculation of interobserver error), dentine exposure in the casts is more difficult to discern than in actual dentition.
**C2. Mean Wear Score by Tooth Class and Age Cohort (Males and Females Combined)**

<table>
<thead>
<tr>
<th>Cohort</th>
<th>Age</th>
<th>I1 (n)</th>
<th>I2 (n)</th>
<th>C (n)</th>
<th>P1 (n)</th>
<th>P2 (n)</th>
<th>M1 (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>15-19</td>
<td>Mean (n)</td>
<td>17.55</td>
<td>2.95 (9)</td>
<td>2.13 (8)</td>
<td>1.78 (9)</td>
<td>2.44 (9)</td>
<td>2.56 (9)</td>
</tr>
<tr>
<td></td>
<td>Median</td>
<td>18.00</td>
<td>2.83</td>
<td>2.00</td>
<td>1.71</td>
<td>2.33</td>
<td>2.50</td>
</tr>
<tr>
<td>20-29</td>
<td>Mean (n)</td>
<td>25.10</td>
<td>3.74 (27)</td>
<td>3.08 (26)</td>
<td>2.57 (28)</td>
<td>2.91 (28)</td>
<td>2.73 (28)</td>
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<td></td>
<td>Median</td>
<td>25.22</td>
<td>3.46</td>
<td>2.96</td>
<td>2.46</td>
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<tr>
<td>30-39</td>
<td>Mean (n)</td>
<td>34.18</td>
<td>4.30 (22)</td>
<td>3.91 (23)</td>
<td>3.72 (23)</td>
<td>4.02 (25)</td>
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<tr>
<td></td>
<td>Median</td>
<td>34.29</td>
<td>4.55</td>
<td>4.19</td>
<td>3.83</td>
<td>4.11</td>
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<tr>
<td>40-49</td>
<td>Mean (n)</td>
<td>44.35</td>
<td>4.36 (18)</td>
<td>4.44 (17)</td>
<td>4.61 (18)</td>
<td>4.24 (17)</td>
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<td>Mean (n)</td>
<td>53.68</td>
<td>4.60 (10)</td>
<td>4.60 (10)</td>
<td>4.70 (10)</td>
<td>5.05 (10)</td>
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<td>Median</td>
<td>53.50</td>
<td>4.71</td>
<td>4.56</td>
<td>4.79</td>
<td>5.13</td>
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<tr>
<td>60+</td>
<td>Mean (n)</td>
<td>71.03</td>
<td>6.75 (4)</td>
<td>6.00 (5)</td>
<td>6.00 (7)</td>
<td>6.00 (6)</td>
<td>5.88 (8)</td>
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<tr>
<td></td>
<td>Median</td>
<td>72.00</td>
<td>7.00</td>
<td>6.00</td>
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</tbody>
</table>
C3. Mean Wear Score of Total Dental Arcade by Age Cohort and Sex
LIST OF REFERENCES


BIOGRAPHICAL SKETCH

Curriculum Vitae

J. Colette Berbesque

Education:

August 2010  Expected date of Ph.D. completion

A.B.D. 2007  Florida State University Department of Anthropology
Dissertation Title- Sex differences in food preferences, consumption, and dental attrition: implications from the Hadza
Advisor- Frank W. Marlowe

M.S. 2005  Anthropology, F.S.U.
Thesis Title- Enamel Hypoplasia and Patterns of Developmental Insult in Early North American Hunter-Gatherers
Advisor: Glen Doran

B.A. 1998  Major: Anthropology, Bryn Mawr College

Employment:

2009-present  Visiting Assistant Faculty in Research, FSU

2004-2009  Departmental Assistant, FSU
Assisted various faculty in teaching and research.

2005-2007  Research Assistant. FSU.
Casted skeletal material and endocasts in various materials for Professor Dean Falk, Department of Anthropology.

2004-2005  Curation Technician. South East Archaeological Center, Tallahassee, FL
Identified, organized, and catalogued various artifacts and objects ranging from Archaic bone to historic metals.

2004-2005  Research Assistant. Tallahassee, FL (funded by U.S. Army Corps of Engineers, Galveston) Photographed, identified, and catalogued skeletal material from Buckeye
Knoll Collection for the purposes of further research and documentation. Consulted on methods of cataloguing and analysis of digital images.

2002-2006 **Sleep Technician.** Tallahassee Sleep Disorder Center
Conducted inservice training for technicians on polysomnograph scoring. Administered polysomnograph testing on various populations for both clinical and research purposes. (Board certified R.P.S.G.T. 2004)

2000-2002 **Sleep Technician.** University of Pennsylvania Center for Sleep
Administered and scored polysomnograph testing on various populations for both clinical and research purposes. Maintained databases and prescribed data management protocols.

2000 **Neurorehab Specialist.** Center for Neuro Skills-Encino, CA
Assisted in the development of rehab programs tailored to meet specific needs of traumatic brain injury patients. Coordinated with Physical Therapists, Occupational Therapists, Speech Therapists and Counselors.

1998-1999 **Research Assistant.** Thomas Jefferson Hospital, Department of Neurology Philadelphia, PA
Administered neuropsychological and cognitive testing for surgery candidates, assisted with development of research protocols, maintained research databases, performed preliminary statistical analysis, and was responsible for background research for publication projects.

**Publications:**

(in prep) **Berbesque, J.C.** and Marlowe, F.W. Sex differences in Hadza hunter-gatherer dental attrition.


**2007**  
*Berbesque, J. C.* Archaic stress: a tale of two cemeteries. [Chapter for Army Corps of Engineers site report on Buckeye Knoll, Victoria county, Texas (41vt98)]

**1999**  

**Conference Presentations:**

**2010**  

**2009**  

**2008**  
Berbesque, J. C., and Marlowe, F. W. Sex differences in Hadza food preferences, acquisition, and consumption. Talk given by JCB in session: Evolutionary Perspectives on Health and Nutrition at the Evolutionary Anthropology Society section of the AAA conference. San Francisco, CA

**2008**  
Berbesque, J. C., Marlowe, F. W. Food preferences of Hadza hunter-gatherers. Human Behavior and Evolution Society. Talk given by JCB. Kyoto, Japan

**2008**  
Marlowe, F. W., Berbesque, J. C., From Rousseau to Hobbes: More ‘altruistic’ punishment in larger societies. Human Behavior and Evolution Society. Talk given by FWM. Kyoto, Japan

**2008**  

**2008**  

**2007**  


Field Experience:

Summers 07, 08, 09- Fieldwork was funded by an NSF award to F. W. Marlowe for the project “Foraging, Food-Sharing, and Family Formation among the Hadza: Part 2”. I collected data on food preferences, food acquisition, and various anthropometric data such as height, weight, and body fat. I conducted focal individual follows of both men and women while foraging. I also made casts of Hadza dentition for the analysis of dental wear (attrition), and gathered visual inspection data on other dental health indicators such as linear enamel hypoplasias, caries, antemortem tooth loss, and dental eruption (in juveniles).

Teaching Experience:

2007 Fall ANT 4525- Human Osteology (instructor)

2007 Summer ANT 2511- Introduction to Human Evolution and Prehistory (instructor)

2007 Spring ANT2100- Introduction to Archaeological Science Laboratory

(instructor for 2 lab sections)

2006 Fall ANT 2511- Introduction to Human Evolution and Prehistory Laboratory (instructor for 2 lab sections)

Awards and Fellowships:
2008 Conference presentation grant—Congress of Graduate Students (F.S.U.)
2007 Conference presentation grant—Congress of Graduate Students (F.S.U.)
2004-2009 Departmental Assistantships

**Professional Organizations:**
American Anthropological Association
Evolutionary Anthropology Society of the AAA
Human Behavior and Evolution Society
American Association of Physical Anthropologists