AMERICAN JOURNAL OF HUMAN BIOLOGY 00:00–00 (2011)

Original Research Article

Sex Differences in Hadza Eating Frequency by Food Type

J. COLETTE BERBESQUE,[1*] FRANK W. MARLOWE,[2] AND ALYSSA N. CRITTENDEN[3]
[1]*Centre for Research in Evolutionary Anthropology (CREA), Department of Life Sciences, Roehampton University, Holybourne Avenue, London SW15 4JD, United Kingdom*
[2]*Department of Anthropology, Durham University, Durham, DH1 3LE, United Kingdom*
[3]*Center for Academic Research and Training in Anthropogeny (CARTA), University of California, San Diego 9500 Gilman Drive, La Jolla, California 92093-0060*

Objectives: We investigate sex differences in frequencies of adults eating in a foraging population—the Hadza of Tanzania.

Methods: We use eating frequency data from instantaneous scan observations of the Hadza, 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.

Results: 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.

Conclusions: At least in the case of the Hadza, we see pronounced sex differences in the in-camp diet. 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. 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. Am. J. Hum. Biol. 00:00–00, 2011.

Among most hunter-gatherers, men and women acquire and eat different types of foods while foraging. 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 (Marlowe, 2007). 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 (Hawkes et al., 1995; Jones et al., 1997; 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 (Jones et al., 1997; Marlowe and Berbesque, 2009). Some reports of consumption in other foragers are also calculated as a per capita measure (with perfect sharing assumed), (Hurtado and Hill, 1990; Kaplan et al., 2000; Lee, 1979). Some have reported on the portions of foods given to the household of the producer versus other households (Hawkes et al., 2001; Kaplan et al., 1984; Wood and Marlowe, ND). These studies are informative for investigating the producer's control of food (and inform the debate about who hunts and why) (Bird and Bird, 2008; Gurven and Hill, 2009). Other descriptive ethnographies of human foragers comment anecdotally on consumption, and indicate sex-differences (Hewlett et al., 1985; Walker and Hewlett, 1990). Hames and McCabe (2007) used instantaneous scan data 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 pronounced sexual dimorphism in size as well as body composition (particularly in muscle and fat) (Pond, 1992; Power and Schulkin, 2008). Hadza women have 9% higher body fat on average than Hadza men, and Hadza men are on average 13% heavier (Marlowe and Berbesque, 2009). The energetic cost of both foraging and reproduction in human natural fertility populations (such as the Hadza) is poorly understood. Until these energetic demands are documented, non-human primates may provide some general insight into the nature of sexual dimorphism as it relates to dietary differences. Dimorphic traits such as size are associated with slight to pronounced separation in the diet of the sexes in some primates (Bean, 1999; Kamilar and Pokempner, 2008). The cost of reproduction in some female primates is large enough to require energy levels equivalent to that of males 30–50% larger in body size (Dufour and Sauther, 2002; Key and Ross, 1999). 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

Contract grant sponsor: NSF; Contract grant number: 0544751; Contract grant number: 0242455; Contract grant number: 0650574.

*Correspondence to: J. Colette Berbesque, Centre for Evolutionary Anthropology (CREA), Department of Life Sciences, Roehampton University, Holybourne Avenue, London SW15 4JD, United Kingdom.
E-mail: Colette.Berbesque@roehampton.ac.uk

Received 19 February 2010; Revision received 31 August 2010; Accepted 25 October 2010

DOI 10.1002/ajhb.21139

Published online in Wiley Online Library (wileyonlinelibrary. com).

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 ~1,000. They live in a savanna-woodland habitat that encompasses about 4,000 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 an out of camps (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 fruit, 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 three to eight adults plus nurslings and often some older children. They mainly collect baobab, gather berries, and dig tubers of several species. They will also 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 (300–600 mm) 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 and 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 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 it is such a major food 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 and 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 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 1. Numbers of species by type of food in Hadza diet

	Frequency	Percent
Domestics	7	0.8
Berries	26	3.0
Fruits	8	0.9
Mammals	56	6.4
Tubers	18	2.1
Honeys	7	0.8
Birds	741	84.4
Reptiles	2	0.2
Invertebrates	1	0.1
berry or fruit	2	0.2
fruit/nut	3	0.3
Greens	1	0.1
Insects	1	0.1
Vegetables	2	0.2
Eggs	1	0.1
Roots (other)	2	0.2
Total	878	100.0

Diet by numbers of species in each category.

Data collection

Hourly instantaneous scan observations of all individuals in camp were recorded throughout the day with a maximum of 13 scans per day from 7 AM (sunrise) to 7 PM (sunset). During each observation the behavior of all people present was recorded. Eating was one of the behaviors recorded. The type of food eaten was also 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. 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.

Scan data are not ideal for measuring exact amounts of food consumed. They do however have the benefit of being a perfectly random sample of all activities of all individu-

TABLE 2. Composition of Hadza foods

	Fat	Protein	Carbs (starch)	Sugars	Kcal
Honey	<8.0[1]	<4.0[1]	Trace[1]	**87.7**[1]**–96.0**[1]	403–439[1]
Meat	1.3–9.0[4]	**57.3–68.2**[4]	Trace[5]	Trace[5]	216[6]–609[7]
Tuber	0.6[3]–3.4[3]	2.3[2]–10.4[3]	**19.4**[2]**–61.3**[3]	6.2[2]–48.3[2]	73–85[8], 146–298[2], 177–279[3]
Berries	<2.0[1]	7.1[1]–15.2[1]	Trace	61.1–72.7[1]	108–145[8], 318–342[1]
Baobab[a]	**15.0**[1]	19.4[1]	5.5[1]	23.4[1]	328.5[1]

Note:- Bold numbers indicate which food has the highest value for each macronutrient.
[1](Murray et al., 2001).
[2](Schoeninger et al., 2001).
[3](Vincent, 1985).
[4](Van Zyl and Ferreira, 2004).
[5](Cordain et al., 2002).
[6](Weiner, 1973).
[7](McCullough and Ullrey, 1983).
[8](Galvin et al., ND).
All values based on grams per 100 grams dry weight. All values are averages, foods vary by species, location, and season. Meat macronutrient values are based on springbok, blesbok, and impala samples. Meat kilocalories are based on deer species.
[a]Baobab composition is based on a ratio of 50% pulp and 50% seed by weight of a pod.

TABLE 3. Correlations of daily individual eating observations with food acquisition

	Honey	Meat	Baobab	Berries	Tubers
Females	NA	$\rho = -0.411$, $P = 0.272$, $n^1 = 81$, $n^2 = 9$	$\rho = 0.219$, $P = 0.495$, $n^1 = 249$, $n^2 = 12$	$\rho = 0.092$, $P = 0.551$, $n^1 = 358$, $n^2 = 44$	$\rho = 0.216$, $P = 0.005$, $n^1 = 580$, $n^2 = 168$
Males	NA	$\rho = 0.120$, $P = 0.594$, $n^1 = 134$, $n^2 = 22$	NA	NA	$\rho = 0.707$, $P = 0.182$, $n^1 = 18$, $n^2 = 5$

n^1 = person-day observations of eating, n^2 = person-day acquisition.

als in camp across the day. Focal individual follows are better for estimating the exact amount eaten by an individual throughout some time period. Following one human all day long is very taxing for the focal individual. On the other hand, the hourly scans give us a complete picture of what occurs in camp each and every day before the people in a camp move to another location. This means scans are ideal for analyzing just how frequently all individuals eat each type of food while in camp.

There are some limitations since scans do 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, we are investigating sex differences and there is no a priori reason why this should affect one sex more than the other.

We tested whether individual production or the common pool of the entire camp's production better predicts the patterns of observed eating in camp across all camps. For the individual production test, we ran correlations of each individual's daily acquisition of foods that are taken back to camp (by weight) against eating observations of those foods by that same individual on those days in that camp. We ran paired t tests for the entire camp production of foods 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 that camp. All analyses (other than the camp wide t tests above) were done on an individual level, first as: (a) raw counts of eating, then: (b) controlled for number of observations of that person, then: (c) controlled as a percentage of all eating frequencies of that person.

Our data come from a total of 69,294 person-scans that were collected over a period of 11 non-sequential years (1995–2006 in 12 different camps) (see Appendix A). People in fewer than 20 scans were dropped from the analyses. This was done to avoid overestimation due to few observations of particular individuals (for example, a visitor appearing in only one scan might 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 (SD = 5.4, range = 0–41) for males and 10.0 (SD = 8.6, range = 0–44) for females.

An individual's daily acquisition of each food type did not correlate with their eating frequencies of those foods (see Table 3), except in the case of tubers (see Appendix E). Meat was negatively correlated with acquisition for females because they bring in very little but eat quite a lot. Some correlations did not have a large enough sample size to be analyzed statistically because although all foods are eaten by both sexes, some foods are only rarely acquired by one sex (they are mostly acquired by the other sex).

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 4), giving us confidence that the scan data are reliable (even with smaller package items such as honey).

Females were observed eating far more frequently than males ($t = -6.101$, $P < 0.0005$, df = 323.126, $n^1 = 152$, $n^2 = 190$). However, due to females' greater time spent in camp, this is not entirely surprising. Figure 1 below demonstrates that females were eating more frequently ($t = -7.040$, $P = 0.003$, df = 339.679, $n^1 = 152$, $n^2 = 190$) even when time in camp was controlled for by dividing observa-

TABLE 4. Sex differences in Hadza eating frequency (raw counts) by food type

	T	df	sig (two-tailed)	n^1	n^2
Honey	−2.210	335.671	0.028	152	190
Meat	−2.329	335.911	0.020	152	190
Berries	−2.106	332.279	0.036	152	190
Baobab	−2.176	297.368	0.030	152	190
Tuber	−2.176	288.246.	0.000	152	190

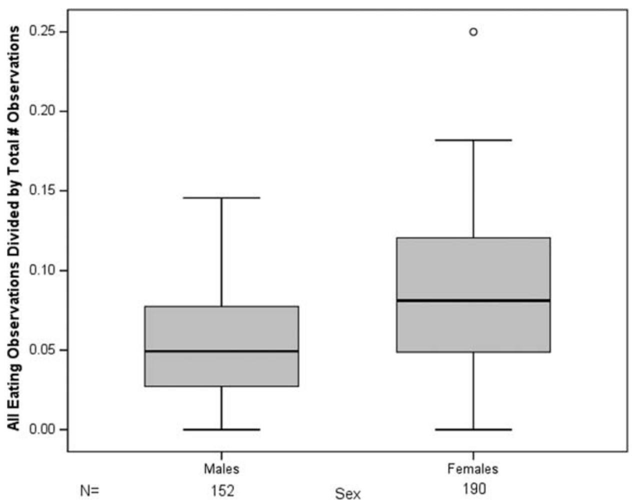

Fig. 1. Hadza eating frequencies controlled for presence in camp. Midlines indicate medians, bars indicate first to third quartiles, whiskers indicate maximum excluding outliers, which are shown as circles and extremes as stars.

tions of a person seen eating by total observations of that person seen in camp.

In terms of absolute eating frequencies (not controlled for time in camp), females were eating significantly more of every food category than were males (see Table 5). This trend is more pronounced with tuber consumption than any other food category. Figure 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). Controlling for number of observations, females were observed eating every food category more frequently than males were, but only significantly more tubers ($t = -5.288$, $P < 0.0005$, df $= 325.933$, $n^1 = 152$, $n^2 = 190$).

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* of all eating events by males? Are these frequencies different from those of females? Figure 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 ($t = -2.733$, $P = 0.007$, df $= 318$, $n^1 = 152$, $n^2 =$ 190).

TABLE 5. Summary of Hadza eating frequency results by food type

Meat	Raw #	women > men	$P = 0.020$
	Divided by observations	women = men	NS
	As % of diet	**men > women**	$P = 0.024$
Tuber	Raw #	women > men	$P < 0.0005$
	Divided by observations	women > men	$P < 0.0005$
	As % of diet	women > men	$P = 0.007$
Berries	Raw #	women > men	$P = 0.036$
	Divided by observations	women = men	NS
	As % of diet	women = men	NS
Baobab	Raw #	women > men	$P = 0.030$
	Divided by observations	women > men	NS
	As % of diet	women = men	NS
Honey	Raw #	women > men	$P = 0.028$
	Divided by observations	women = men	NS
	As % of diet	women = men	NS
Total	Raw #	women > men	$P < 0.0005$
	Divided by observations	women > men	$P = 0.003$
	As % of diet	NA	NA

NS—not significant.The only analysis in which males are eating significantly more than females is in bold.

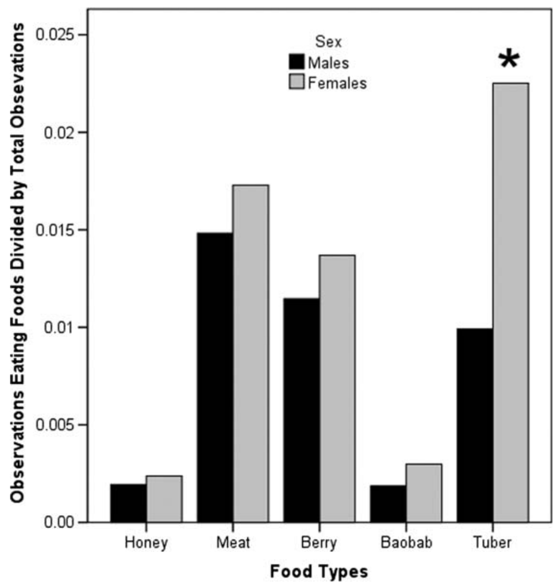

Fig. 2. Observations of Hadza eating frequencies by sex and food type.

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 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 ~95% of the diet by weight (Marlowe and Berbesque, 2009).

To find out which sex is more frequently eating the foods acquired by the other sex 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 0.36 of all baobab eating instances to "male acquired foods" and 0.64 of baobab eating instances to "female acquired foods" so the production of each sex was represented. The other food categories were dominantly

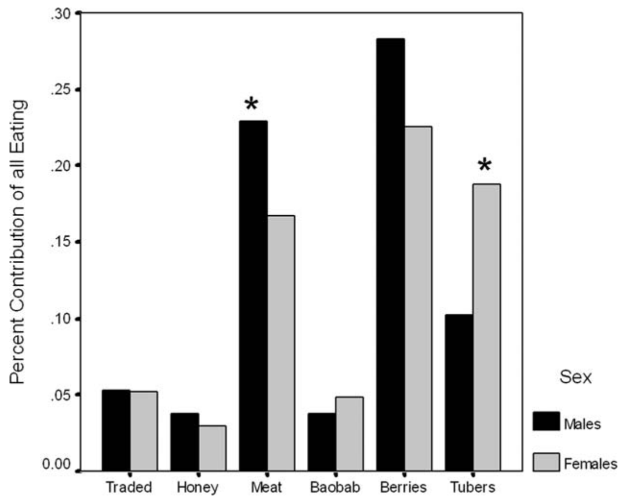

Fig. 3. Hadza eating observations by food type divided by total eating observations.

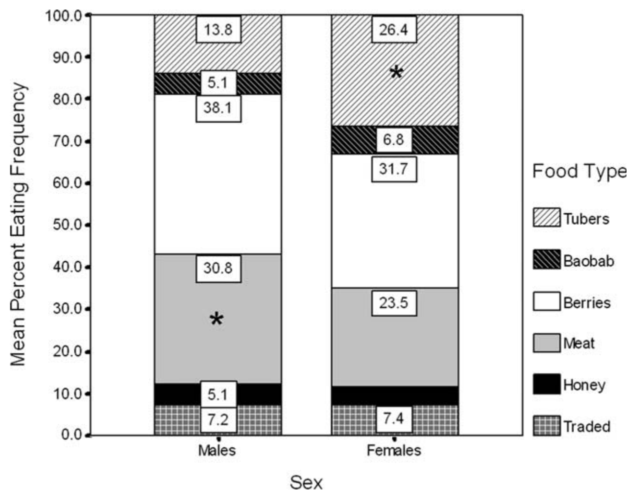

Fig. 4. Hadza mean eating frequencies by sex.

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 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 in Figure 5.

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 ($t = 2.387, P = 0.018$, $\text{df} = 264.449, n^1 = 138, n^2 = 184$). Females are not eating significantly more of their own foods.

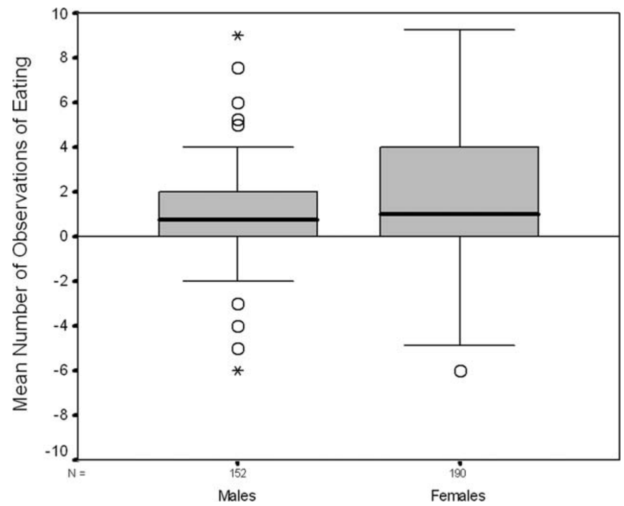

Fig. 5. Mean number of observations of males and females eating female acquired foods minus mean number of observations of males and females eating male acquired foods. Midlines indicate medians, bars indicate first to third quartiles, whiskers indicate maximum excluding outliers, which are shown as circles and extremes as stars.

Females are eating more frequently overall in camp. Because of this, it is not surprising without correcting for the number of all observations (i.e., presence in camp), females are eating significantly more of both male acquired foods ($t = -2.951, P = 0.003, n^1 = 152, n^2 = 190$) and female acquired foods ($t = -4.836, P < 0.0005, n^1 = 152, n^2 = 190$).

Table 6 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, and (3) frequencies of eating as a percentage of the total diet for each sex.

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 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 also 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. 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 are eating high quality foods (such as meat and honey) both in and out of camp. While women 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 and Marlowe (2007) reported on the nutritional homogeneity among the Hadza as measured by percent body fat (%BF) and body mass index (BMI). However, 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, but women's did. 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.

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 (Marlowe and Berbesque, 2009).

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 h a day for women versus 6.1 h a day for men). Similar observations have been made anecdotally about "snacking" by Aka pygmy women (Walker and Hewlett, 1990). Maintaining adequate body fat and a positive energy balance are important factors for female fertility (Ziomkiewicz et al., 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, 1970). However, if female fertility is significantly enhanced from regular caloric intake (even at the expense of overall health) female foragers may maximize their reproductive success 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 (see Fig. 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 (see Fig. 4). In the future we will analyze the total diet (including consumption while foraging as well as in-camp consumption). This will likely demonstrate sex-differences that are more pronounced than those presented in this analysis, which may have important consequences for female fertility.

ACKNOWLEDGMENTS

The authors thank Johannes and Lene Kleppe for providing a base camp in Tanzania and Audax Mabulla for help with research permission and logistics. They thank Daudi Peterson for assistance and innumerable favors, and Costech for permission to conduct research. They thank the Hadza for their enduring tolerance and hospitality. They thank Brian Wood and two anonymous reviewers for their comments.

LITERATURE CITED

Bean A. 1999. Ecology of sex differences in great ape foraging. In: Lee PC, editor. Comparative primate socioecology. Cambridge: Cambridge University Press. p 339–362.

Berbesque JC, Marlowe FW. 2009. Sex differences in food preferences of Hadza hunter-gatherers. Evol Psychol 7:601–616.

Bird RB, Bird DW. 2008. Why women hunt risk and contemporary foraging in a western desert aboriginal community. Curr Anthropol 49:655–693.

Brown JK. 1970. A note on division of labor by sex 72:1073–1078.

Clutton-Brock TH. 1977. Some aspects of intraspecific variation in feeding and ranging behavior in primates. In: Clutton-Brock TH, editor. Primate ecology: Studies of feeding and ranging behavior in lemurs, monkeys and apes. London: Academic Press. p 539–556.

Cordain L, Eaton SB, Miller JB, Mann N, Hill K. 2002. The paradoxical nature of hunter-gatherer diets: meat based, yet non-atherogenic. Eur J Clin Nutr 56:S42–S52.

Dufour DL, Sauther ML. 2002. Comparative and evolutionary dimensions of the energetics of human pregnancy and lactation. Am J Hum Biol 14:584–602.

Galvin K, Hawkes K, Maga JA, O'Connell JF, Blurton-Jones N. ND. The composition of some wild plant foods used by East African hunter-gatherers.

Gurven M, Hill K. 2009. Why do men hunt? A reevaluation of "man the hunter" and the sexual division of labor. Curr Anthropol 50:51–74.

Hames R, McCabe C. 2007. Meal sharing among the Ye'kwana. Hum Nat 18:1–21.

Hawkes K, Blurton Jones NG, O'Connell JF. 1995. Hadza children's foraging: juvenile dependency, social arrangements, and mobility among hunter-gatherers. Curr Anthropol 36:688–700.

Hawkes K, O'Connell JF, Jones NGB. 2001. Hunting and nuclear families. Curr Anthropol 42:681–709.
Hewlett BS, Koppel JMHvd, Koppel Mvd. 1986. Causes of death among Aka Pygmies of the Central African Republic. In: Cavalli-Sforza LL, editor. African Pygmies. New York: Academic Press. pp 95–101.
Hurtado AM, Hill KR. 1990. Seasonality in a foraging society: Variation in diet, work effort, fertility, and sexual division of labor among the Hiwi of Venezuela. J Anthropol Res 46:293–346.
Jones NGB, Hawkes K, O'Connell JF. 1997. Why do Hadza children forage? In: Segal NL, Weisfeld GE, Weisfield CC, editors. Uniting psychology and biology: integrative perspectives on human development. New York: American Psychological Association. p 297–331.
Jones NGB, Hawkes K, O'Connell JF. 2005. Older Hadza men and women as helpers: residence data. In: Hewlett BS, Lamb ME, editors. Hunter-gatherer childhoods: evolutionary, developmental and cultural perspectives. New Brunswick: Transaction. p 214–236.
Kamilar JM, Pokempner AA. 2008. Does body mass dimorphism increase male-female dietary niche separation? A comparative study of primates. Behavior 145:1211.
Kaplan H, Hill K, Hawkes K, Hurtado A. 1984. Food sharing among ache hunter-gatherers of Eastern Paraguay. Curr Anthropol 25:113–115.
Kaplan H, Hill K, Lancaster J, Hurtado AM. 2000. A theory of human life history evolution: diet, intelligence, and longevity. Evol Anthropol 9:156–185.
Key C, Ross C. 1999. Sex differences in energy expenditure in non-human primates. R Proc Biol Sci 266:2479–2485.
Lambert PM. 2009. Health versus fitness competing themes in the origins and spread of agriculture? Curr Anthropol 50:603–608.
Lee RB. 1979. The !Kung San: men, women, and work in a foraging society. Cambridge: Cambridge University Press. p 260–271.
Lukacs JR. 2008. Fertility and agriculture accentuate sex differences in dental caries rates. Curr Anthropol 49:901–914.
Marlowe FW. 2003. A critical period for provisioning by Hadza men: implications for pair bonding. Evol Hum Behav 24:217–229.
Marlowe FW. 2006. Central place provisioning: the Hadza as an example. In: Hohmann G, Robbins M, Boesch C, editors. Feeding ecology in apes and other primates. Cambridge: Cambridge University Press. p 357–375.
Marlowe FW. 2007. Hunting and gathering—the human sexual division of foraging labor. Cross Cultural Res 41:170–195.
Marlowe FW. 2010. The Hadza: hunter-gatherers of Tanzania (origins of human behavior and culture). Berkley: University of California Press. 400 p.
Marlowe FW, Berbesque JC. 2009. The impact of seasonality and fallback foods on Hadza hunter-gatherers. Am J Phys Anthropol 140:751–758.
McCullough DR, Ullrey DE. 1983. Proximate mineral and gross energy composition of white-tailed deer. J Wildlife Manage 47:430–441.
Murray SS, Schoeninger MJ, Bunn HT, Pickering TR, Marlett JA. 2001. Nutritional composition of some wild plant foods and honey used by Hadza foragers of Tanzania. J Food Compos Anal 14:3–13.
Pond CM. 1992. An evolutionary and functional view of mammalian adipose tissue. Proc Nutr Soc 51:367–377.
Power ML, Schulkin J. 2008. Sex differences in fat storage, fat metabolism, and the health risks from obesity: possible evolutionary origins. Br J Nutr 99:931–940.
Schoeninger MJ, Bunn HT, Murray SS, Marlett JA. 2001. Composition of tubers used by Hadza foragers of Tanzania. J Food Compos Anal 14:15–25.
Sherry DS, Marlowe FW. 2007. Anthropometric data indicate nutritional homogeneity in Hadza Foragers of Tanzania. Am J Hum Biol 19:107–118.
Smith CC. 1977. Feeding behaviour and social organization in howling monkeys. In: Clutton-Brock TH, editor. Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes. London: Academic Press. p 97–126.
Tarnaud L. 2006. Feeding behavior of lactating brown lemur females (*Eulemur fulvus*) in mayotte: influence of infant age and plant phenology. Am J Primatol 68:966–977.
Van Zyl L, Ferreira AV. 2004. Physical and chemical carcass composition of springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus dorcas phillipsi*), and impala (*Aepyceros melampus*). Small Ruminant Res 53:103–109.
Vincent AS. 1985. Plant foods in savanna environments, a preliminary report of tubers eaten by the Hadza of Northern Tanzania. World Archaeol 17:131–148.
Walker PL, Hewlett BS. 1990. Dental health diet and social status among Central African foragers and farmers. Am Anthropol 92:383–398.
Weiner J. 1973. Dressing percentage, gross body composition and caloric value of the roe deer Acta Theriol 18:209–222.
Wood BM, Marlowe FW. 2010. Where do men's foods go? The sharing and eating of male acquired foods among the Hadza. American Journal of Physical Anthropology; Suppl. 50. pp. 247–247.
Ziomkiewicz A, Ellison PT, Lipson SF, Thune I, Jasienska G. 2008. Body fat, energy balance and estradiol levels: a study based on hormonal profiles from complete menstrual cycles. Hum Reprod 23:2555–2563.

APPENDIX A

Person-scans conducted by region

Region	Total Person-scans	Percent of total
Mangola	3,403	4.9
Dunduiya	8,049	11.6
Tli' ika	40,579	58.6
Sipunga	17,262	24.9
Total	69,293	100.0

Person-scans conducted by season

Season	Total Person-scans	Percent of total
Early wet	13,842	20.0
Late wet	22,791	32.9
Early dry	26,211	37.8
Late dry	6,449	9.3
Total	69,293	100.0

APPENDIX B

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 ($t = -1.172$, $P = 0.242$, $n^1 = 137$, $n^2 = 183$). There were few instances of other food types eaten (e.g., figs, eggs, leaves, etc.). These are labeled "other."

APPENDIX C

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).

APPENDIX D

We broke the day into three 4-h blocks (7 am–10 am, 11 am–3 pm, 4 pm–7 pm). Hourly scans begin at 7 am (approximately sunrise) and end at 7 pm (approximately sunset) year-round because there is little difference in light across seasons so close to the equator. Both men ($\chi^2 = 35.914$, df = 2, $P < 0.0005$) and women ($\chi^2 = 104.966$, df = 2, $P < 0.0005$) were eating significantly more frequently in the mid-day time block (11 am–3 pm) than in the other two time blocks. However, females are eating significantly more frequently than men in all three time blocks (which should not be surprising based on the far greater frequency of female eating reported in our paper).

APPENDIX E

Tubers were the only food category that an individual's acquisition was correlated with their consumption. Women dig for tubers together, so they all acquire many of the same types of tubers. There is little reason for them to share with other women because of this. They typically eat some tubers out of camp, and take the rest back to eat later on.