ARTICLE IN PRESS

Evolution and Human Behavior xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org

Original Article

Eat first, share later: Hadza hunter–gatherer men consume more while foraging than in central places

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ARTICLE INFO

Article history:
Initial receipt 17 March 2015
19 January 2016
Final revision received 24 January 2016
Available online xxxx

Keywords:
Central place foraging
Energetics
Foraging
Hadza
Hunter–Gatherers
Paleodiet
Provisioning

ABSTRACT

The foraging and food sharing of hunter–gatherers have provided the backdrop to several different evolutionary hypotheses about human life history. Men's foraging has often been characterized as primarily targeting animals, with high variance and high rates of failure. To the best of our knowledge, however, there are as yet no quantitative studies reporting the amounts of food that men eat while foraging, before returning to their households either empty-handed or with foods. Here, we document this under-reported part of forager's diets—men's eating while out of camp on foray. Our dataset consists of 146 person/day follows (921 hours total) collected over a period of 12 years (from 2001–2013, including 12 camps). Hadza men consumed a substantial amount of food while out of camp foraging. Men did more than just snack while out of camp foraging, they consumed a mean of 2,405 kilocalories per foray, or approximately 90% of what is estimated to be their mean daily total energy expenditure (TEE). The characterization of men's foraging strategies as "risky", in terms of calorie acquisition, may be exaggerated. Returning to camp empty-handed did not necessarily mean the forager had failed to acquire food, only that he failed to produce enough surplus to share. Surprisingly, the vast majority of the kilocalories eaten while out of camp came from honey (85%). These observations are relevant to evolutionary theories concerning the role of male provisioning. Understanding primary production and consumption is critical for understanding the nature of sharing and the extent to which sharing and provisioning supports reproduction in hunter–gatherers.

1. Introduction

Knowledge of food sharing and the sexual division of labor in hunter–gatherers is mostly based on the distribution of foods at central places (e.g. Bahuchet, 1990; Kitanishi, 1998; Ziker, 2007), or in mixed-sex or single sex groups (e.g. Kaplan, Hill, Hawkes, & Hurtado, 1984; Ziker, 2002). In groups that split apart (fission) to forage as individuals or in smaller groups and then bring foods back to camp to share (e.g. central place provisioners) (Marlowe, 2006), it is logistically difficult for researchers to record the behavior of those in camp and those foraging out of camp at the same time. It is probably largely due to these logistical problems that studies of food sharing in central places are so much more common than studying out of camp behavior (e.g. Bahuchet, 1990; Bird & Bird, 1997; Gurven, 2004; Kaplan, Hurtado, & Hill, 1990; Speth, 1990; but see Crittenden (2013) as a noteworthy exception). In fact, these studies are so common that students of anthropology often have the impression that all foods acquired are brought back to the residential group to be shared with others. This impression is easy to understand in light of statements like those of Marshall (1998:71,77) who, despite documenting out of camp eating by the Nye Nye !Kung, goes on to write "!Kung are quite conscious of the value of meat-sharing and they talk about it. The idea of sharing is deeply implanted and very successfully imposes its restraints…. The idea of eating alone is shocking to the !Kung. It makes them shriek with an uneasy laughter. Lions could do that, they say, not men."

Nevertheless, many ethnographers report hunters eating spoils before returning to camp, including the Ache, Aka, Batek, G/Wi, Lengua, Mbuti, Nukak, and !Kung (Endicott 1988; Grubb, 1911:190; Lee, 1979; Marshall, 1976; Politis, 2009; Silberbauer, 1981; Walker & Hewlett, 1990). However, analyses of producer generosity and patterns of sharing, to date, have not systematically taken this out of camp eating into account. The difficulties of systematically capturing these data are sometimes lamented (e.g. Politis, 2009; Speth, 1990). In other cases, ethnographers document total quantities of foods acquired but do not mention whether any of the foods were consumed before foragers returned to camp (Endicott, 1988; Hart, 1978).

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http://dx.doi.org/10.1016/j.evolhumbehav.2016.01.003
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Patterns of eating while out of camp may lead to small or even large corrections to estimates of the total diet of hunter–gatherers. These data also inform studies of food sharing practices in camp. Decisions to share foods, or to request foods from others, are necessarily affected by how hungry or satiated individuals are when they return to camp. Thus, studies that are based solely on in-camp behavior can provide only part of the larger picture of the diet and food sharing practices of central place provisioners. For example, Hadza men have been documented eating on average only 8% (median 0%) of the total caloric value of foods they brought back to camp (Wood & Marlowe, 2013). In the absence of information on out of camp eating, this paints an unrealistic picture of food distribution and overall diet. Men eating while out of camp sheds light upon their patterns of sharing when in camp. Not considering data on out of camp eating would lead to overestimations of both the failure rate of men's foraging decisions, and the degree to which their energetic budgets are subsidized by others. These data call attention to the fact that characterizing patterns of diet by sex, age, marital status, or other factors should involve careful considerations of how individual diets vary across space, relative to where researchers make their observations. Our analysis indirectly bears on previous interpretations of data on patterns of food distribution in hunter–gatherers, and has consequences for our understanding of the evolution of hunting.

2. Materials and Methods

2.1. Subject Population

The Hadza are a group of traditional, central-place hunter–gatherers who number approximately 1,000, however only approximately 250 individuals still acquire the majority of their diet by foraging. 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, averaging 30 individuals per camp (Marlowe, 2006). Camp membership often changes as people move in and out of camps (Blurton Jones, Hawkes, & O'Connell, 2005). Hadza camps move about every 6 weeks, on average (Marlowe, 2010).

While foraging, Hadza men typically search for animals, honey, and sometimes fruit. Hadza men rarely dig for tubers, which is a task that women and sometimes children specialize in. They typically go on walkabout every day, and they usually go alone. They hunt birds and mammals using only bow and arrows. In large game kills poison arrows are used, whereas with small game poison is not used. They always have their bow and arrows with them, even when they carry an ax to access honey (Marlowe, 2010).

The Hadza diet can be conveniently categorized into six main food types: honey, meat, berries, baobab (*Adanosia digitata*), and tubers, and in one region only, marula nuts (*Sclerocarya birrea*). The berries that the Hadza eat consist mostly of seed encased in a small amount of high-sugar pulp. Baobab fruit is common across much of Africa, and it is a major food in terms of kilocalories and kilograms in the Hadza diet. Many tubers are continuously available throughout the year, and are a source of carbohydrates and an important 'fallback food' for the Hadza (Marlowe & Berbesque, 2009).

2.2. Procedure

Men were followed on walkabout, their behaviors were continuously recorded from the time they departed camp to the time they returned to camp. Men usually begin their day of foraging early, between 6 and 7 am. Hadza men forage opportunistically and even if they have a particular goal in mind, such as looking for bee nests in a particular stand of trees, they are generally alert for other foraging opportunities. The researcher followed approximately 5–10 meters behind the focal individual(s), recording a variety of behavioral data, including every instance in which they ate foods. While observing the Hadza, the researcher walked as silently as possible, attempting to minimize observer effects, and providing no direction whatsoever to the Hadza about where or how to forage or behave during any of the observations.

Focal individuals selected using simple random sampling without replacement, with the goal of following all males in residence in each camp at least one time, regardless of whether the focal individual was alone or in a group. In contrast to some other ethnographically documented hunters (e.g. Alvard, 2002; Hill, 2002), Hadza men very often forage alone (Marlowe, 2010). A total of 118 follows were conducted, most of which were of men foraging alone, though in 13 cases (11% of follows), more than one person was present (group foray) and data were also collected on non-focal individuals. Data on non-focal individuals in a group follow were only analyzed when all group members were present and observed throughout the foray. Due to group follows, these 118 follows constitute our focal sample of 146 person/follows. The mean number of men present in group focal follows (as opposed to follows of a single individual was 4.6 (mode = 3, maximum = 8). Our focal follow data consists of totals 146 person/day follows (921 hours total) collected over a period of 12 years from 2001 to 2013, with follows in every region of Hadzaland and in every season (see Table 1 for a breakdown of follows by region and season). The average duration of follows was 6.3 hours per foray, with a range of 30 minutes for the shortest foray to 770 minutes (or 12.8 hours) for the longest foray. On average, each of the 75 men followed was observed 1.95 times (median = 1 and mode = 1), with a range of 1–9 observation days per man. However, only 8 (11%) of the 75 men were followed on more than three person days, and many of these repeat follows of the same individual happened in different years. The men followed ranged in age from 16 to 59 years old, with a mean age of 35 years (median = 34 years, mode = 41 years). Most forays (90%) lasted 2 hours or longer.

Amounts (kilograms) of foods eaten on focal follows were estimated using methods similar to those outlined by Rothman, Chapman, and Van Soest (2012). This entails visual estimation of units of foods consumed (e.g. three handfuls of berries) and the collection of corresponding data that allows one to estimate the weight of such units (e.g. the

Table 1
Person/Follows by Region and Season.

Year	Region	Season	Camp	Follows
2001	Dunduyia	Early dry	Sungu	2
2002	Tli'ika	Early wet	Bashana	3
2002	Tli'ika	Early dry	Gibanola	2
2003	Siponga	Early wet	Sedaiko	4
2003	Tli'ika	Early dry	Sangeli	3
2004	Siponga	Early wet	Sedaiko	13
2004	Tli'ika	Early dry	Kisanakwipi	8
2004	Tli'ika	Late dry	Sanola	1
2005	Dunduiya	Early dry	Mayai	13
2005	Dunduiya	Late dry	Wamkwimba	3
2005	Mangola	Early dry	Gola	6
2005	Mangola	Late dry	Gola	1
2005	Siponga	Early wet	Tuwa	1
2005	Siponga	Early wet	Siponga	1
2005	Siponga	Late wet	goandeka	1
2005	Siponga	Late dry	Tuwa	22
2005	Tli'ika	Early dry	Gangidape	4
2005	Tli'ika	Early dry	Bashana	4
2006	Mangola	Late wet	Gola	4
2006	Mangola	Early dry	Gola	10
2006	Tli'ika	Early wet	Kisanakwipi	7
2006	Tli'ika	Late wet	Lelangidako	9
2006	Tli'ika	Late dry	Hukumako	12
2009	Han!abe	Late dry	Setako	4
2010	Tli'ika	Late wet	Sangeli	1
2010	Tli'ika	Early dry	Sangeli	4
2011	Tli'ika	Early wet	Sangeli	1
2012	Tli'ika	Early wet	Sangeli	1
2013	Tli'ika	Early dry	Nyalaida	1
12 Years	5 Regions	4 Seasons	29 Camps	146 Follows

In this study, we define a camp by both the geographic location and the season of researcher presence.

Please cite this article as: Berbesque, J.C., et al., Eat first, share later: Hadza hunter–gatherer men consume more while foraging than in central places, *Evolution and Human Behavior* (2016), http://dx.doi.org/10.1016/j.evolhumbehav.2016.01.003

number of berries in an average hand full). Honey acquisition was estimated using units of volume that were intuitive for the purposes of visual estimation (e.g. teaspoons, tablespoons, and golf-ball sized bites of honey), following Wood and Marlowe (2014). Kilocalories of Hadza foods were calculated using formulae including the percentage of water in each food and the caloric values per 100 grams (dry weights) of each food.

Nutritional values for honey, berries, and baobab were based on previous studies of Hadza foods (Murray, Schoeninger, Bunn, Pickering, & Marlett, 2001; Schoeninger, Bunn, Murray, & Marlett, 2001). Large game animals have more body fat than small game (Cordain et al., 2000), thus two caloric estimates of kcal/weight for animal carcasses were used. To estimate the caloric value of small animal carcasses (used for all animals under 32 kilograms), the kcal/kg values from studies of New Zealand White rabbits *Octolagus cuniculus* (Daszkiewicz, Gugołek, Janiszewski, Kubiak, & Czoik, 2012) were used, and in the case of large game, >32 kilograms, estimates based on white tailed deer carcasses *Odocoileus virginianus* were used (Weiner, 1973).

Neither data on duration of foray nor the sum of kilocalories eaten per foray were normally distributed variables, so we used non-parametric tests, except when analyzing repeated measures, when we used log transformations of non-normal variables in GLM models. We used SPSS version 21 for all analyses.

3. Results

There was a great deal of variation in kilocalories eaten while on walkabout, with a range from 0 to 22,007 kilocalories consumed by a single individual on a single foray. The median number of kilocalories consumed per foray was 910, with a mean of 2,405, and standard deviation of 3,637 kilocalories. The data were highly positively skewed (see Fig. 1), with a skewness of 2.693 (S.E. = .201). The interquartile range of kilocalories acquired per person/day was 37–3047. Men consumed 1,000 kilocalories or more in 55% of forays observed, less than 500 kilocalories in 45%, and zero kilocalories in only 20% of forays (see Fig. 1).

Amounts of foods, as well as types of foods eaten out of camp varied by season (see Fig. 2 and Table 2), with more honey and small game eaten in the wet seasons and more large game eaten in the dry seasons. In terms of overall contribution of calories throughout the year, honey was by far the food type most frequently eaten by men out of camp, whether analyzed in number of observations or in kilocalories (see Table 2). Of all forays where any foods were acquired, honey was eaten in 58% of those follows, and contributed 85% of the total kilocalories eaten out of camp.

The number (and percentage) of person/days out of camp where a particular food type was eaten, the range of kilocalories eaten, the mean amount of kilocalories eaten by food type, and the mean hourly consumption rates by food type are presented in Table 3 (but see Appendix 1 available on the journal's website at www.ehbonline.org for unusual eating events not listed in Table 3). More than a single food type was eaten on many forays, although in some forays no food was acquired. Thus, the total (166 events of food acquisition) is more than the number of person/follows (n = 146).

For each food type, we examined the ratio of what was consumed on the spot relative to the total amount acquired (consumed / consumed + brought back to camp). Although honey was frequently encountered (and eaten) while out of camp, the foods with the highest percentage of kilocalories consumed on the spot rather than taken back to camp were berries (99%), followed by honey (84%), and finally baobab (63%). The average percentage of meat from complete animal carcasses that was immediately consumed by individuals while out of camp differed greatly by the carcass size of the animal (small game = 55% versus large game < 1%) (see Figs. 3 and Appendix 2 available on the journal's website at www.ehbonline.org).

Forays in which small game animals were acquired were most commonly individual forays (mean = 1.9 individuals, median = 1). In contrast, the majority of forays during which large game animal meat was eaten were forays that were intended to retrieve a large game animal carcass killed in a previous foray (which are much more often solo). All five forays in which meat from large game animal carcasses was eaten were collaborative group forays (range = 2–7 people, mean = 4.2, median = 4), with several Hadza sharing portions of the carcass.

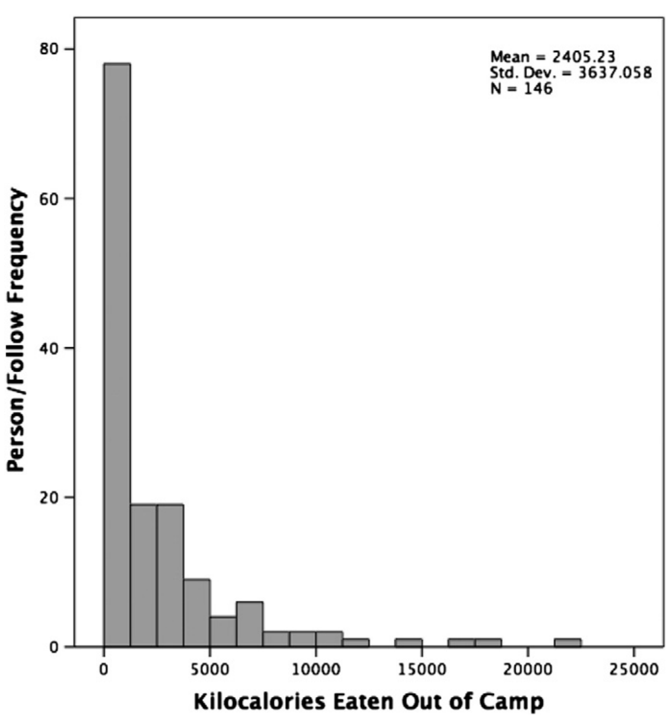

Fig. 1. Histogram of kilocalories consumed per foray.

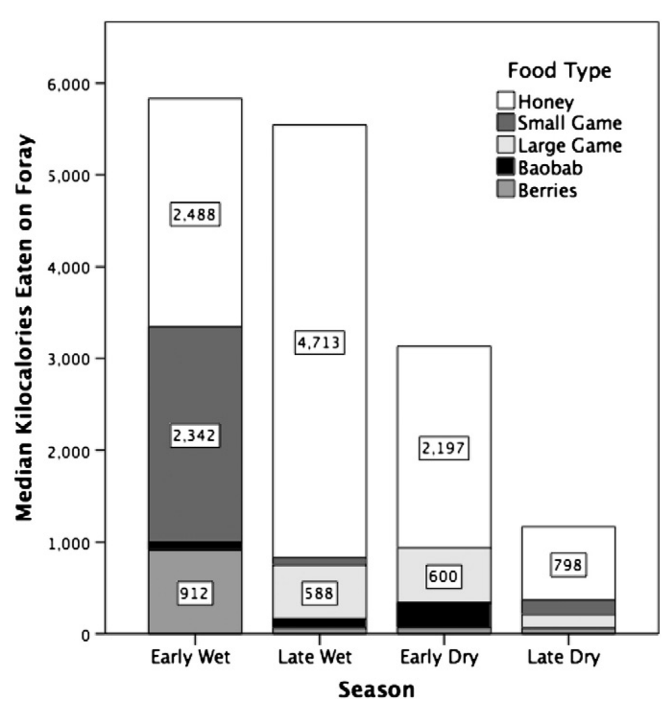

Fig. 2. Median kilocalories eaten on foray by season.

Table 2
Descriptive Statistics of Food Types Eaten by Season.

Season	Food type	Median	Mean	SD	range	IQR	Skewness	S.E. skewness	N
Early wet	Honey	2488	3933	4380	194–17117	194–5874	1.655	0.501	21
	Small game	2342	2068	587	748–2342	2056–2342	−1.92	0.687	10
	Large game	NA	NA	NA	NA	NA	NA	NA	0
	Baobab	89	89	NA	NA	NA	NA	NA	1
	Berries	912	830	603	190–912	NA	−0.601	1.225	3
Late wet	Honey	4713	6015	6008	97–20777	1114–8969	1.4	0.564	16
	Small game	165	554	820	0–1496	NA	NA	NA	3
	Large game	588	588	NA	NA	NA	NA	NA	1
	Baobab	99	99	NA	0–198	NA	NA	NA	2
	Berries	63	197	356	2–1231	31–257	2.903	0.661	11
Early dry	Honey	2197	3087	3131	194–14039	748–4098	1.792	0.388	37
	Small game	0	0	NA	NA	NA	NA	NA	1
	Large game	600	524	482	75–1236	75–935	0.68	0.913	5
	Baobab	272	272	NA	247–297	NA	NA	NA	2
	Berries	65	73	67	5–216	29–65	1.658	0.637	12
Late dry	Honey	798	992	894	0–3178	397–1339	1.772	0.687	10
	Small game	157	1073	2067	0–7590	0–1289	2.797	0.597	14
	Large game	150	150	NA	NA	NA	NA	NA	1
	Baobab	0	60	103	0–179	NA	NA	NA	3
	Berries	60	80	82	10–288	15–109	1.637	0.637	12

Foods with a minimum of zero are foods that were acquired, however they were not eaten. Foods not acquired are not shown.

Very small amounts of meat from large game were shared by the ‘recovery team’, which helps to carry most of the meat back to camp. When stalking is involved, the ‘recovery team’ most commonly only involves men; however, when the carcass location is known, this group can consist of men, women and children old enough to help.

There were a total of 24 animal acquisitions. Nineteen out of the 24 (or 79%) of the game animals acquired in our sample were small game animals. In a Spearman's correlation, more kilocalories of meat acquired (larger carcass size) was associated with a smaller percentage of the animal eaten before bringing the remainder back to camp to share ($\rho = -.334$, *n = 35 people eating animal carcasses*, $p = .050$) (note: this includes multiple individuals eating on group foray acquisitions). Additionally, in absolute terms, there was no clear association between kilocalories of meat acquired and the amount of kilocalories immediately eaten per person present ($\rho = .216$, *n = 35 instances of meat eating*, $p = .214$). However, when analyzing large and small game categories separately, more kilocalories were eaten in small game animals when these animals were larger ($\rho = .473$, *n = 27 instances of people eating small game*, $p = .013$). However, within the category of large game animals (weighing over 32 kilograms) there was no association between the number of kilocalories acquired (the mass of the animal) and the number of kilocalories immediately eaten ($\rho = -.077$, *n = 8 instances of people eating large game*, $p = .857$).

Similarly, smaller percentages of honey were eaten when more honey was acquired ($\rho = -.572$, *n = 84 cases of people acquiring honey*, $p < .001$). In contrast with how large game is consumed, however, the more absolute kilocalories of honey that were acquired, the more kilocalories of honey were immediately eaten ($\rho = .904$, *n = 84 cases of people acquiring honey*, $p < .0001$).

In a Spearman's rank correlation, longer forays were not significantly associated with more kilocalories being eaten out of camp, whether or not we included forays in which no foods were eaten ($\rho = .000$, *n of forays where foods were eaten* $= 116$, $p = .998$; $\rho = -.067$, *n of person forays* $= 146$, $p = .421$). Longer forays were also not associated with a higher percentage of kilocalories eaten on the spot versus taken back to camp ($\rho = .062$, *n of forays where foods were eaten* $= 116$, $p = .509$). In univariate GLM models controlling for repeated focal individual observations, we found no association between the age of males and the amount of kilocalories eaten (log transformed to correct for heteroscedasticity) while out of camp per foray ($F = 1.013$, $df = 85$, $p = .503$) (see Fig. 3). There was also no significant association found between the age of the males and the percent of kilocalories eaten immediately on the foray versus returned to camp by ($F = 1.034$, $df = 85$, $p = .475$), or in the duration of forays by age ($F = 1.303$, $df = 100$, $p = .161$).

4. Discussion

Most Hadza men consumed a substantial amount of kilocalories while foraging. The mean number of kilocalories consumed by males per foray was 2,404. The mean daily total energy expenditure (TEE) for Hadza men has been measured to be 2,649 ± 395 (range

Table 3
Acquisition and Consumption Rates on Foray by Food Type.

Food type	Mean/Median kcal acquired	Mean/Median kcal eaten/foray	SD kcal acquired/eaten	Mean kcal eaten/hour	Range† kcals eaten/foray	IQR kcals acquired	IQR kcals eaten	N person forays acquired/% person forays	Mean foray duration (minutes)
Honey	6822/2515	3582/2398	10371/4191	614	97*–20776	726–6393	559–4784	84/58%	350
Meat (total)	26364/2342	1164/628	90481/1486	205	75–7590	299–5236	75–2342	35/24%	341
Small game	10211/2342	1335/942	31130/1610	206	90*–7590	355–2536	22–2342	28/19%	389
Large game*	90974/1236†	480/588	90974/420	196	75–1236	75†–64627	75–633	7/5%	147†
Berries	181/64	171/64	323/314	21	2–1388	29–172	29–172	38/26%	483
Baobab	655/220	126/134	1271/120	15	89*–297	181–284	0–234	8/5%	491

* For categories indicated, range does not include values of zero. In the other categories (not indicated) instances of individuals acquiring a food type without eating any of it are included in this analysis, but we have chosen to report the minimum (non-zero) value eaten on foray.

† The large game category includes eating of large game as gifts of meat from others, in which cases the amount acquired will be substantially less than the body size of the animal. We analyze percent of carcasses eaten later in this manuscript.

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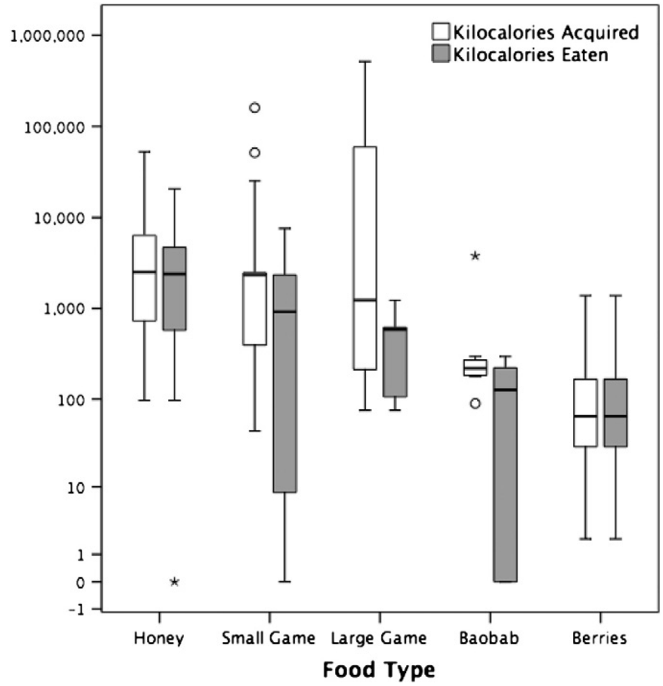

Fig. 3. Boxplot of kilocalories acquired versus eaten.

2,008–3,363) kilocalories per day (Pontzer et al., 2012). Using the average values for men's consumption/foray and TEE/day, we estimate that men are consuming approximately 90% of their TEE on average while foraging out of camp. Of course, there is significant variation in these values across forays, with only 20% of forays where no food was acquired. Also, bear in mind that upon returning to camp, Hadza men eat foods brought by other men as well as women—so much so that researchers have represented Hadza men's diets using only in-camp data to this point. Patterns of out of camp consumption are rarely (if ever) reported in other central place provisioning groups, yet these values for Hadza men show that out of camp eating constitutes a significant percent of their average TEE.

Hadza men's high rate of eating while out of camp complements recent research that examined Hadza men's sharing of foods in camp (Wood & Marlowe, 2013), which showed that men consumed little of the food they brought back to camp themselves, but instead shared the foods with their wives, children, and co-resident kin. This sharing in camp is less costly to men when they have already fed themselves while foraging out of camp.

Hadza men's diet while foraging is strikingly different from their diet in camp. Honey contributes the most kilocalories to the out of camp diet of men, followed by meat. For example, only 14% of kilocalories brought into camp are from honey (Marlowe, Berbesque, Wood, Crittenden, & Porter, 2014), while honey contributes 85% of the kilocalories consumed out of camp by men. Honey has recently gained attention as a potentially important source of energy in human evolution (Crittenden, 2011; Marlowe et al., 2014; McGrew, 2001; Wood, Pontzer, Raichlen, & Marlowe, 2014; Wrangham, 2011), and it is the most preferred food of the Hadza (Berbesque & Marlowe, 2009). A recent study using a large cross-cultural database showed that most hunter–gatherers in warm climates exploit honey (Marlowe et al., 2014). Given this ubiquity of honey consumption, and the possibility that honey consumption in these populations may be under-reported due to it being consumed out of camp, the importance of honey as an energy source may be underestimated generally for hunter–gatherers.

Hadza men have been documented eating meat in camp significantly more frequently than are women (Berbesque, Marlowe, & Crittenden, 2011), and meat constitutes 11% of men's out of camp diet—whereas women rarely eat meat out of camp. Given the amount of both meat and honey eaten on foray by Hadza men, it is likely they are eating a far more energy-dense diet than are Hadza women. Substantial sex differences in the Hadza diet have recently been documented in in-camp eating frequencies (Berbesque et al., 2011), resulting in sex differences that have been documented in Hadza dental wear patterns (Berbesque et al., 2012), as well as in the gut microbiome (Schnorr et al., 2014). The sex-difference in foraging patterns and return rates can even be seen in Hadza childhood (Crittenden, Conklin-Brittain, Zes, Schoeninger, & Marlowe, 2013). Sex differences in many hunter–gatherer diets may be greater than previously appreciated, as most reports on hunter–gatherer diets are from the in camp portion of diet only—which is the portion of the diet that is taken back to camp and is more likely to be shared or used for provisioning. It is important to note that major cross-cultural studies of the diets of hunter–gatherers (e.g. Cordain, Eaton, Miller, Mann, & Hill, 2002), do not report out of camp eating, nor do they discriminate between the diets of men and women. These are almost always based on per capita estimates of foods arriving in camp, and assume perfect sharing among all adults—which, in the case of the Hadza, is grossly inaccurate.

Some researchers have described Hadza men as targeting large game animals to the exclusion of small game or other foods in order to signal their phenotypic quality to potential mates (Bunn & Gurtov, 2014; Hawkes, O'Connell, Blurton Jones, Oftedal, & Blumenschine, 1991; Hawkes, O'Connell, & Jones, 2001). However, in our analysis, 79% of the kills made by adult men (ages 16 years and older) were small game animals (weighing less than 32 kg). This is consistent with data from Wood and Marlowe (2013, 2014), which show that 79% of the animals that men brought back to seven different camps weighed less than 10 kg. Thus Hadza men should not exclusively be considered large game specialists.

Understanding men's provisioning and sharing with others are important components of understanding foraging decisions and family structures, but choices related to prey selection are also influenced by the goal of eating—which has not been well-documented to this point. Hadza men's foraging is driven by the goals of getting enough calories to eat and potentially to provision their families. In the Hadza ecology, hunting is not an exclusive activity that entails a high rate of foraging failure, requiring men to be fed by others upon returning to camp empty handed. More accurately, hunting is scheduled in a way that also permits high levels of energetic self-sufficiency. Men take advantage of a suite of high-quality foods – especially honey – and this strategy allows them to both feed themselves and pursue riskier food types that have higher chances of failure upon pursuit.

An adjustment of the characterization of the riskiness of men's foraging strategies may be in order—since coming back to camp empty-handed does not always mean that their strategy to acquire food failed, only that it failed to produce enough surplus to return to camp to share.

5. Conclusions

Descriptions of contemporary hunter–gatherers have played a central role in models of past human forager societies, and their evolution. Our understanding of the evolution of human life history partly depends on knowing possible sources of bias in data on contemporary hunter–gatherer populations. There are several aspects of this study that bring to light possible biases in our understanding of men's production. First, if small game is more likely to be eaten on the spot rather than brought back to camp to be shared (and thus documented), perhaps the characterization of men as large-game hunters to the exclusion of small game is exaggerated in the archaeological record. Second, if our study population is comparable to other warm climate populations, honey consumption is undoubtedly under-reported in ethnographies, and owing to preservation bias, is also practically invisible to the archaeologist or paleontologist studying fossilized materials. Third, Hadza men (and perhaps any solitary foragers) bring the spoils of their foraging

Please cite this article as: Berbesque, J.C., et al., Eat first, share later: Hadza hunter–gatherer men consume more while foraging than in central places, *Evolution and Human Behavior* (2016), http://dx.doi.org/10.1016/j.evolhumbehav.2016.01.003

back to camp, whether to provision others or to signal, only after they have already eaten most (if not all), of what they need. As these data show, out of camp food consumption has real consequences for our understanding of hunter–gatherer diets and the dynamics of food sharing systems.

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2016.01.003.

Acknowledgements

We would like to thank the Leakey Foundation, (to CB and BW), Wenner Gren (to BW), and NSF (1062879 to BW) and (0544751, 0242455, and 0650574 to FWM). We would also like to thank the John Templeton Foundation for their support for CB. The opinions expressed in this publication are those of the authors and do not necessarily reflect the views of the John Templeton Foundation. We thank Costech for permission to conduct research. We would also like to thank Andrea Migliano, and an anonymous reviewer for their helpful suggestions. We would like to thank Daudi and Trude Peterson and Carla Wood Mallol for all of their help and support, and Todd C. Rae and Peggy Berbesque for their comments on drafts. Finally, we thank the Hadza for their enduring tolerance and hospitality.

References

Alvard, Michael S. (2002). Carcass ownership and meat distribution by big-game cooperative hunters. *Research in Economic Anthropology*, *21*, 99–132.

Bahuchet, S. (1990). Food sharing among the pygmies of Central Africa. *African Study Monographs*, *11*, 27–53.

Berbesque, J. C., & Marlowe, F. W. (2009). Sex differences in food preferences of the Hadza hunter-gatherers. *Evolutionary Psychology*, *7*, 601–616.

Berbesque, J. C., Marlowe, F. W., & Crittenden, A. N. (2011). Sex differences in Hadza eating frequency by food type. *American Journal of Human Biology*, *23*, 339–345. http://dx.doi.org/10.1002/ajhb.21139.

Berbesque, J. C., Marlowe, F. W., Pawn, I., Thompson, P., Johnson, G., & Mabulla, A. (2012). Sex differences in Hadza dental wear patterns. *Human Nature*, *23*, 270–282.

Bird, R. L. B., & Bird, D. W. (1997). Delayed reciprocity and tolerated theft - The behavioral ecology of food-sharing strategies. *Current Anthropology*, *38*, 49–78.

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

Bunn, H. T., & Gurtov, A. N. (2014). Prey mortality profiles indicate that Early Pleistocene Homo at Olduvai was an ambush predator. *Quaternary International*, *322*, 44–53.

Cordain, L., Eaton, S. B., Miller, J. B., Mann, N., & Hill, K. (2002). Fatty acid analysis of wild ruminant tissues: Evolutionary implications for reducing diet-related chronic disease. *European Journal of Clinical Nutrition*, *56*, 181–191.

Cordain, L., Miller, J. B., Eaton, S. B., Mann, N., Holt, S. H., & Speth, J. D. (2000). Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets. *The American Journal of Clinical Nutrition*, *71*, 682–692.

Crittenden, A. N. (2011). The importance of honey consumption in human evolution. *Food Foodways*, *19*, 257–273.

Crittenden, A. N., Conklin-Brittain, N. L., Zes, D. A., Schoeninger, M. J., & Marlowe, F. W. (2013). Juvenile foraging among the Hadza: Implications for human life history. *Evolution and Human Behavior*, *34*, 299–304.

Daszkiewicz, T., Gugołek, A., Janiszewski, P., Kubiak, D., & Czoik, M. (2012). The effect of intensive and extensive production systems on carcass quality in New Zealand white rabbits. *World Rabbit Science*, *20*, 25–32.

Endicott, K. (1988). Property, power and conflict among the Batek of Malaysia. Hunters and gatherers 2, 110–127. In T. Ingold, D. Riches, & J. Woodburn (Eds.), *Hunter-gatherers. Property, power and ideology*, *vol. II*, . Berg Berg.

Grubb, W. B. (1911). *An unknown people in an unknown land.* London: Seeley.

Gurven, M. (2004). Reciprocal altruism and food sharing decisions among Hiwi and Ache hunter–gatherers. *Behavioral Ecology and Sociobiology*, *56*, 366–380.

Hart, J. A. (1978). From subsistence to market: A case study of the Mbuti net hunters. *Human Ecology*, *6*, 325–353.

Hawkes, K., O'connell, J. F., Blurton Jones, N. G., Oftedal, O. T., & Blumenschine, R. J. (1991). Hunting income patterns among the Hadza: big game, common goods, foraging goals and the evolution of the human diet [and discussion].". *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *334*, 243–251.

Hawkes, K., O'Connell, J. F., & Jones, N. B. (2001). Hadza meat sharing. *Evolution and Human Behavior*, *22*, 113–142.

Hill, K. (2002). Altruistic cooperation during foraging by the Ache, and the evolved human predisposition to cooperate. *Human Nature*, *13*(1), 105–128.

Kaplan, H., Hill, K., Hawkes, K., & Hurtado, A. (1984). Food sharing among Ache hunter-gatherers of eastern Paraguay. *Current Anthropology*, *25*, 113–115.

Kaplan, H., Hurtado, A. M., & Hill, K. (1990). Risk, foraging and food sharing among the Ache. In E. Cashdan (Ed.), *Risk and Uncertainty in Tribal and Peasant Economies* (pp. 107–143). Boulder: West-view Press.

Kitanishi, K. (1998). Food sharing among the Aka hunter-gatherers in northeastern Congo. *African Study Monographs*, *25*, 3–32.

Lee, R. B. (1979). *Men, women, and work.* Cambridge: Cambridge University Press.

Marlowe, F. W. (2006). Central place provisioning: The Hadza as an example. In M. Robbins, C. Boesch, & G. Hohmann (Eds.), *Feeding ecology in apes and other primates* (pp. 359–377). Cambridge: Cambridge University Press.

Marlowe, F. W. (2010). *The Hadza: Hunter-Gatherers of Tanzania.* Berkeley: University of California Press.

Marlowe, F. W., & Berbesque, J. C. (2009). Tubers as fallback foods and their impact on Hadza hunter-gatherers. *American Journal of Physical Anthropology*, *140*, 751–758. http://dx.doi.org/10.1002/ajpa.21040.

Marlowe, F. W., Berbesque, J. C., Wood, B., Crittenden, A. N., & Porter, C. (2014). Honey, hunter-gatherers, Hadza, and human evolution. *Journal of Human Evolution*, *71*, 119–128. http://dx.doi.org/10.1016/j.jhevol.2014.03.006.

Marshall, L. (1976). *The !Kung of Nyae Nyae.* Cambridge: Harvard University Press.

Marshall, L. (1998). Sharing, talking, and giving: Relief of social tensions among the !Kung. In J. M. Gowdy (Ed.), *Limited wants, unlimited means: A reader on hunter-gatherer economics and the environment,* (pp. 65–85). Washington D. C.: Island Press.

McGrew, W. (2001). The other faunivory. In C. B. Stanford, & H. T. Bunn (Eds.), *Meat-eating and human evolution.* Oxford: Oxford University Press.

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

Politis, G. (2009). *Nukak: Ethnoarchaeology of an Amazonian people.* Walnut Creek, CA: Left Coast Press.

Pontzer, H., Raichlen, D. A., Wood, B. M., Mabulla, A. Z. P., Racette, S. B., & Marlowe, F. W. (2012). Hunter-Gatherer energetics and human obesity. *PloS One*, *7*, e40503.

Rothman, J. M., Chapman, C. A., & Van Soest, P. J. (2012). Methods in primate nutritional ecology: A user's guide. *International Journal of Primatology*, *33*, 542–566.

Schnorr, S. L., Candela, M., Rampelli, S., Centanni, M., Consolandi, C., Basaglia, G., ... Crittenden, A. N. (2014). Gut microbiome of the Hadza hunter-gatherers. *Nature Communications*, *5*.

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

Silberbauer, G. (1981). Hunter/gatherers of the Central Kalahari. In R. Harding, & G. Teleki (Eds.), *Omnivorous primates*. Columbia University Press.

Speth, J. D. (1990). Seasonality, resource stress, and food sharing in so-called "egalitarian" foraging societies. *Journal of Anthropological Archaeology*, *9*, 148–188.

Walker, P. L., & Hewlett, B. S. (1990). Dental health, diet, and social status among Central African foragers and farmers. *American Anthropologist*, *92*, 383–398.

Weiner, J. (1973). Dressing percentage, gross body composition and caloric value of the roe deer. *Acta Theriologica*, *18*, 209–222.

Wood, B., & Marlowe, F. (2013). Household and kin provisioning by Hadza men. *Human Nature*, *24*, 280–317.

Wood, B., & Marlowe, F. (2014). Toward a reality-based understanding of Hadza men's work: A response to Hawkes et al. *Human Nature*, *25*, 620–630.

Wood, B. M., Pontzer, H., Raichlen, D. A., & Marlowe, F. W. (2014). Mutualism and manipulation in Hadza–honeyguide interactions. *Evolution and Human Behavior*, *35*, 540–546.

Wrangham, R. W. (2011). Honey and fire in human evolution. In D. Pilbeam, J. Sept, & C. Vogel (Eds.), *Casting the Net Wide: Papers in Honor of Glynn Isaac and His Approach to Human Origins Research* (pp. 149–167). Oxford: Oxbow Books.

Ziker, J. (2002). Raw and cooked in Arctic Siberia: Diet and consumption strategies in socio-ecological perspective. *Nutritional Anthropology*, *25*, 20–33.

Ziker, J. P. (2007). Subsistence and food sharing in Northern Siberia: Social and nutritional ecology of the Dolgan and the Nganasan. *Ecology of Food and Nutrition*, *46*, 445–467.