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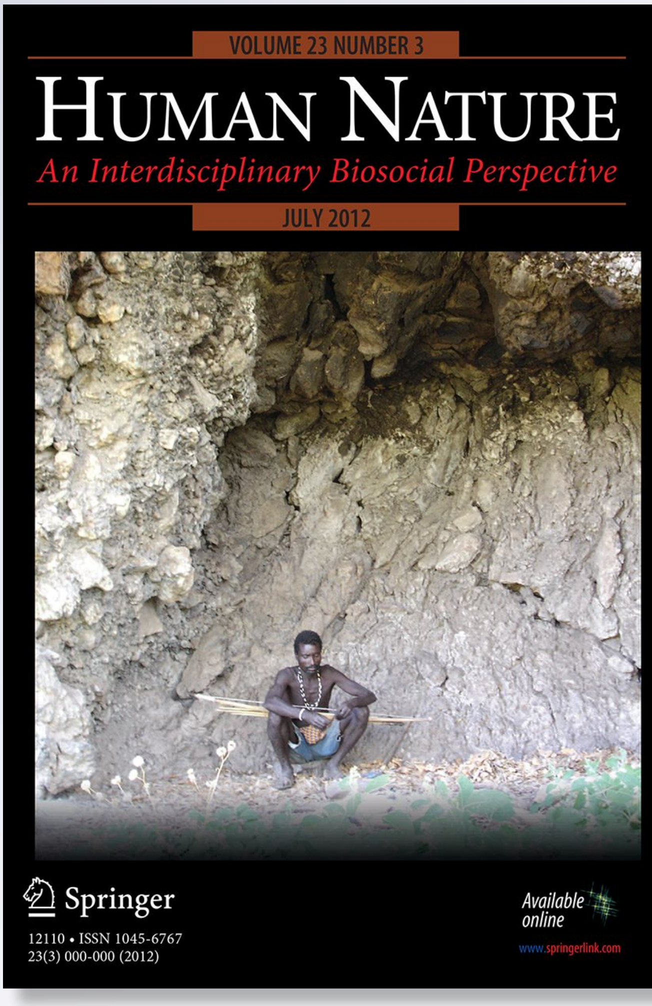
Human Nature
An Interdisciplinary Biosocial Perspective

ISSN 1045-6767
Volume 23
Number 3

Hum Nat (2012) 23:270-282
DOI 10.1007/s12110-012-9145-9



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Sex Differences in Hadza Dental Wear Patterns

A Preliminary Report

J. Colette Berbesque · Frank W. Marlowe · Ian Pawn · Peter Thompson · Guy Johnson · Audax Mabulla

Published online: 30 June 2012

Abstract Among hunter-gatherers, the sharing of male and female foods is often assumed to result in virtually the same diet for males and females. Although food sharing is widespread among the hunting and gathering Hadza of Tanzania, women were observed eating significantly more tubers than men. This study investigates the relationship between patterns of dental wear, diet, and extramasticatory use of teeth among the Hadza. Casts of the upper dentitions were made from molds taken from 126 adults and scored according to the Murphy dental attrition scoring system. Females had significantly greater anterior occlusal wear than males when we controlled for age. Males exhibited greater asymmetry in wear, with greater wear on the left side in canines, first premolars, and first molars. We suggest that these sex differences in wear patterns reflect the differences seen in the diet, as well as in the use of teeth as tools.

The paper on which this manuscript is based received the Best Paper by a New Investigator award from the Evolutionary Anthropology Section of the American Anthropological Association at the annual meeting in 2010.

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Keywords Dental wear · Hadza · Hunter-gatherers · Paleo-diet · Sexual division of labor

Dental wear can be used to reconstruct diet, local ecology, health, and cultural practices both within and across populations. Much of the work on tooth wear has been focused on tracking differences across subsistence patterns, and in particular the timing and consequences of transitions to agriculture in various populations (McKee and 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 and Turner 1988). Dental attrition is also used to establish age at death for individuals in archaeological contexts (Arnold et al. 2007; Hillson 1996; 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 of sex differences in the Hadza diet (Berbesque et al. 2011) as well as sex differences observed in their use of teeth as tools (or as a "third hand").

Tooth wear can result from physical abrasion or chemical erosion. Physical abrasion can result from consumption of particular abrasive foods, food processing (e.g., from grinding or pounding with stone), tooth-on-tooth contact, and using the dentition for purposes other than eating (as tools, or extramasticatory use; Molnar 1971a). Chemical erosion most typically results from the consumption of acidic foods (Jarvinen et al. 1991). Another factor affecting dental wear is the developmental timing of eruption. Age of eruption is different for each tooth class, and this factor is critical in the relative degree of wear between tooth classes (even within one individual) (Molnar 1971b). Teeth that erupt earlier tend to show greater wear because they have been used longer. Although tooth wear, antemortem tooth loss, dental eruption patterns, and caries rates are all known to covary, we only report on tooth wear in this paper. Future research with a larger sample size will study other aspects of Hadza oral health indicators.

Studies on wear patterns among skeletal collections of hunter-gatherers and agriculturalists often report greater wear in hunter-gatherer dentition, particularly in the anterior teeth (Deter 2009; Hinton 1981). Variation in both the severity and the patterns of wear have been documented across different foraging populations, and often these differences are attributed to ecological conditions leading to differences in diets (Richards 1984b; Walker 1978). Gender and status are two major factors that often affect within-population variation. Since the Hadza are egalitarian (and have very little differential access to resources), we should not expect status differences (Woodburn 1979). On the other hand, among foragers the division of labor typically reflects gender roles in the context of obtaining and processing food. We therefore focus on sex differences in dental wear among the Hadza because they may provide insight into the bioarchaeological signals of the sexual division of foraging labor.

Studies of other human populations (with various subsistence strategies) present varied findings with regard to sex differences in attrition rates. Some studies find no sex differences in attrition (Deter 2009; Kieser and Groeneveld 1985; Lovejoy 1985), while others find greater rates of attrition in males (e.g., Greenland natives and modern Igaloolik Eskimos; Davies and Pederson 1955; Tomenchuk and Mayhall 1979). Others still report higher rates of attrition in females (e.g., prehistoric American Indians and Australian Aborigines: Molnar 1971b; Richards 1984a).

Only a few studies of the dental attrition of contemporary foragers have been reported (van Reenen 1992; Walker and Hewlett 1990). Walker and Hewlett (1990) found that both Aka (Central African Republic) and Mbuti (Congo) men showed 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.

A previous study of the Hadza (Berbesque et al. 2011) found sex differences in the in-camp eating frequencies of different food types. Hadza women eat far more tubers than Hadza men. Hadza men eat more meat as a proportion of their diet. Tubers are very fibrous and tough (Dominy et al. 2008), and they are perhaps the most abrasive food that the Hadza eat. Therefore, we would expect that Hadza females should exhibit 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 are hunter-gatherers who number approximately 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 (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 (see description of Hadza foods below). They mainly take meat and honey, as well as some baobab, back to camp. They may eat a lot of the honey they find, but they generally 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 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).

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 preferred food for the Hadza (Berbesque and 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, but the Hadza do eat most of the animal (including tendons, ligaments, etc.). They also gnaw on the larger bones and chew 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 their 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 (Schoeninger 2001). The seeds are only eaten when baobab is taken back to camp to pound into flour. The process of pounding baobab seeds may result in the inclusions of rock particles, especially because Hadza use big, open rock surfaces as anvils. This 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 the tubers have high fiber content; 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 1 shows the in-camp diet considered as a whole. The in-camp diet is defined here as 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 the composition of the male and female diet can be compared, despite the fact that females more frequently eat (and are more often present) in camp. Even in camp, men eat more meat than women, and women eat more tubers. Women

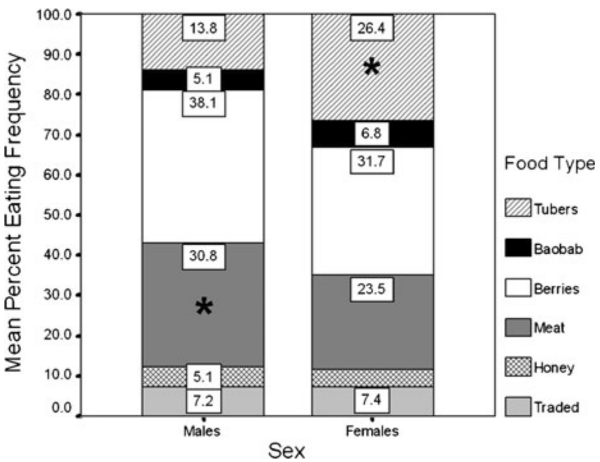

Fig. 1 Hadza mean eating frequencies by sex and food type. * indicates the sex with higher mean eating frequency of a food type (significant at $p < 0.05$)

also eat tubers outside of camp (whereas men do not), so overall women eat tubers far more frequently than men (Berbesque et al. 2011).

The Hadza frequently use their teeth as tools. Men use their teeth to work arrows (Fig. 2), tighten bow strings, and strip bark from branches to make twine. Women use their teeth to cut beading string, and they chew leather hides and bow strings to make them supple. Hadza men and women use their teeth to puncture tuber "skin" and then to peel the tuber before eating it. Both men and women occasionally use small sticks as toothpicks, and they occasionally chew on a particular type of twig (species unknown) to clean their teeth.

Methods

Molds of Hadza maxillary dentition made using President Jet molding material were 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. Impressions of second molars were captured in some cases (most commonly when the individual had lost some of his or her other teeth) but were dropped from analyses because of the small sample size for this tooth class. Each tooth in the casts was then scored for attrition based on the Murphy (1959) scoring system (as modified by Smith 1984) for incisors, canines, and premolars. In this system the scores range from one to eight based on level of destruction of the tooth's crown and dentine exposure. Similar methods developed by Scott (1979) and summarized by Buikstra and Ubelaker (1994) were used for molars. For molars, the wear scores range from one to ten, and each quadrant of the molars is scored separately. From these quadrant wear scores we calculated a mean wear score for the entire tooth.

Fig. 2 Hadza woman and man using their teeth as tools. Left panel shows Hadza woman stripping the peel from a tuber with her teeth (photo by Colette Berbesque). Right panel shows a Hadza man straightening an arrow with his teeth (photo by Frank W. Marlowe)

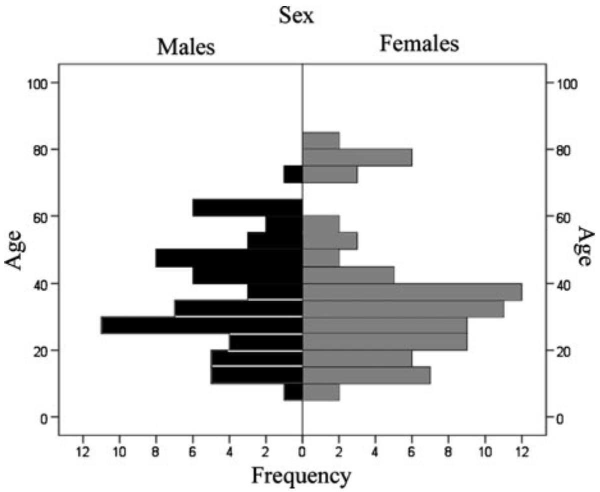

Fig. 3 Distribution of sample by age and sex

We used linear regressions to look at sex differences in wear because we do not have a large enough sample size in each 10-year age cohort to perform nonparametric statistics (but see Appendix Table 3 for a table of results of Mann-Whitney U tests by tooth class and age cohort). We have a rare opportunity in that we know the nearly exact ages of our subjects rather than the more common situation with skeletal populations of needing to use age estimates. Analyzing traits by 10-year age cohorts makes sense when individuals are aged by estimates which typically span plus or minus 5 to 10 years.

Interobserver error was measured by scoring the wear in each tooth type present in the maxillary arcades of 24 individuals (see Appendix Table 4 for results by tooth type). The ages of most Hadza are 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. The mean age of males in the sample was 37.9 years old and the mean age of females was 38.6 years old. Figure 3 shows the sample distribution by age and sex.

To gauge overall wear by tooth class, we analyzed left dentition in each tooth class, substituting the right for that tooth class when the left was not present. Mean wear by tooth class is shown in Fig. 4.

First molars showed the greatest degree of wear in the population, followed by first incisors. The timing of eruption likely explains this pattern, since first molars are usually the first tooth class from the permanent dentition to erupt (at approximately 6 years of age), followed by central incisors at approximately 7 years of age. 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 (“wisdom teeth”; 17–21 years) (Buikstra and Ubelaker 1994),

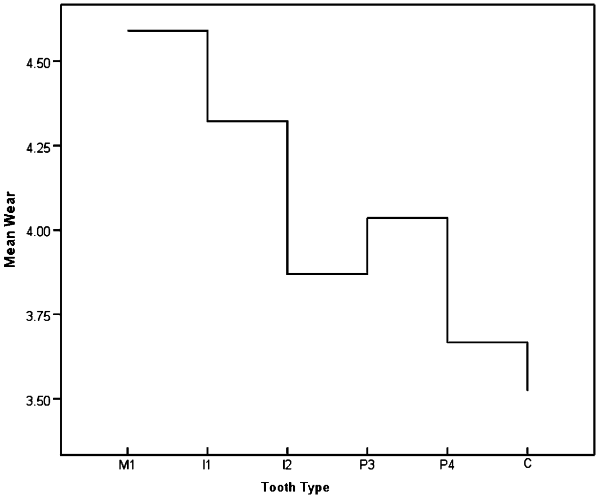

Fig. 4 Mean wear by tooth class (in order of eruption)

but see Tompkins (1996) for potential causes of variability in eruption timing across populations.

Table 1 shows the mean score of attrition and sample sizes in each tooth class for the 10-year age cohorts. Figure 5 shows the trends for each tooth class over time. Note that central incisors (I1) are already more heavily worn than other tooth classes by the teen years.

In a linear regression controlling for age, females had greater (left) central incisor (I1) wear than males (B=0. 214, p=0.013, df=87). Females also had greater wear in the (left) lateral incisor, but this was just shy of significance in a two-tailed test (B= 0.146, p=0.058, df=86). There were no significant sex differences in other tooth classes.

Though the convention for skeletal populations is to analyze only the left dentition to avoid "double counting" individuals when there are fragmentary remains, we analyzed both sides of dentition when possible. Comparing left versus right side wear patterns on a single individual enabled us to examine asymmetry in wear patterns. Males had greater asymmetry in tooth wear than females (Fig. 6). Males had greater wear on the left side in first molars (t=−2.837, df=30, p=0.008) as well

Table 1 Mean wear score by tooth class and age cohort (males and females combined)

Age of Cohort	I1 (*n*)	I2 (*n*)	C (*n*)	P3 (*n*)	P4 (*n*)	M1 (*n*)
15–19	2.95 (9)	2.13 (8)	1.78(9)	2.44 (9)	2.56 (9)	2.91 (8)
20–29	3.74 (27)	3.08 (26)	2.57(28)	2.91 (28)	2.73 (28)	3.60 (27)
30–39	4.30 (22)	3.91 (23)	3.72(23)	4.02 (25)	3.52 (25)	4.83 (23)
40–49	4.36 (18)	4.44 (17)	4.61 (18)	4.24 (17)	4.06 (18)	5.58 (16)
50–59	4.60 (10)	4.60 (10)	4.70(10)	5.05 (10)	5.00 (10)	6.45 (11)
60+	6.75 (4)	6.00 (5)	6.00(7)	6.00 (6)	5.88 (8)	7.69 (7)

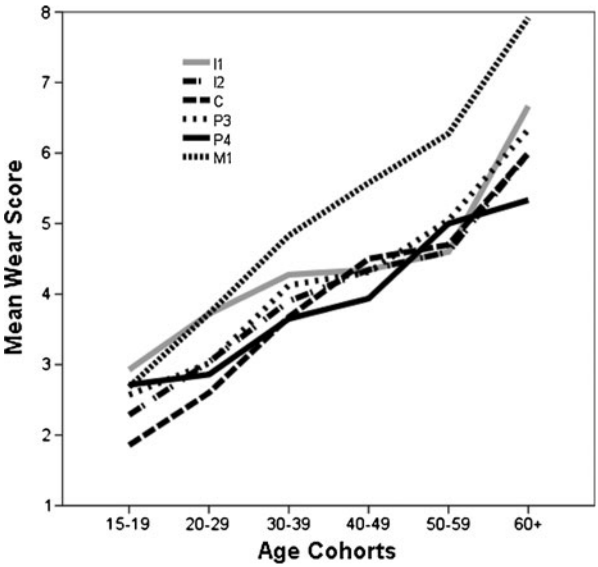

Fig. 5 Mean wear by tooth class and age cohort (males and females combined)

as first premolars (t=−1.706, df=41, p=0.096) with one-tailed tests. Females only had significant asymmetry in wear in canines (t=3.346, df=40, p=0.002).

Using data from the right side only (and controlling for age), we found that females had significantly more wear on P3s than males did (B=0.188, p=0.020, 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

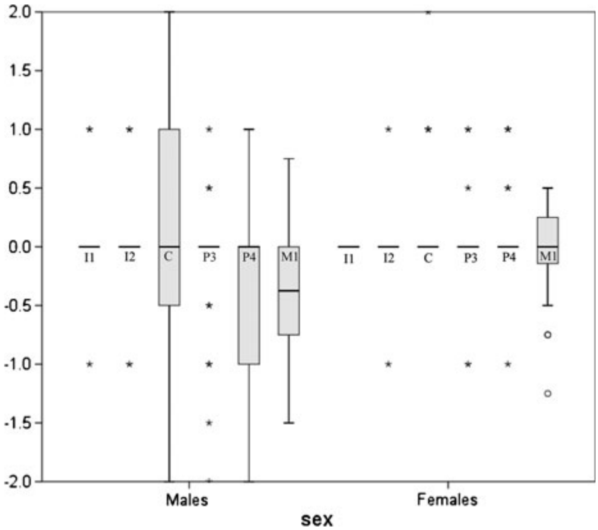

Fig. 6 Right side wear minus left side wear by tooth class and sex. Midlines indicate medians, boxes indicate first to third quartiles, whiskers indicate maximum excluding outliers (shown as *circles*) and extremes (*asterisks*)

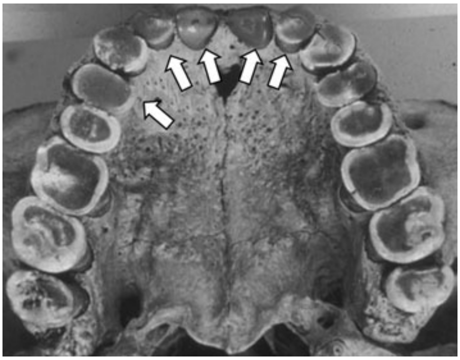

Fig. 7 Maxillary dental arcade of prehistoric hunter-gatherer (arrows indicate the teeth for which Hadza exhibit sex differences in wear). Photograph of specimen from the Windover (8BR246) site in Florida (8,120–6,980 ^{14}C years BP) courtesy of Glen Doran

first premolars. Figure 7 shows the maxillary dental arcade of a skeletal population, with the teeth that are significantly more worn in Hadza females indicated by arrows.

Table 2 shows the inter-item covariances and correlations for 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.

Discussion

Overall, the Hadza fit the pattern commonly described for hunter-gatherers—they exhibit a great deal of wear compared with most agricultural populations, particularly in the anterior dentition (Deter 2009; Hinton 1981). Females had more heavily worn anterior dentition than males. We propose two explanations: women were more frequently observed eating tubers than men, and they use their anterior teeth as tools. The Hadza (particularly women) demonstrate a wear pattern on their anterior dentition that is also seen in prehistoric forager skeletal samples (Comuzzie and Steele 1988; Irish and Turner 1987; Turner and Machado 1983) as well as historic Senegalese skeletal populations (Irish and Turner 1997). This lingual surface attrition of the maxillary anterior teeth (LSAMAT) is interpreted as the result of pulling or holding abrasive material between the tongue and the lingual surface (the side facing the

Table 2 Left dental arcade covariances and correlations across tooth types by sex

	Mean	Variance	*N* of Items
Male inter-item covariances	1.290	0.150	6
Female inter-item covariances	1.837	0.082	6
Male inter-item correlations	0.678	0.015	6
Female inter-item correlations	0.786	0.006	6

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 from tubers. Men also do this, but far less frequently than women—both because they eat tubers less frequently and because men often carry knives. Women carry knives less often and therefore more often rely on their teeth.

Males demonstrated significantly greater asymmetry in wear, with the left side of the dental arcade showing heavier wear than the right. Females had significantly asymmetrical wear in canines only. The greater asymmetry in males is interesting particularly because a study controlling for age found that Hadza females actually have greater fluctuating asymmetry than Hadza males (Gray and Marlowe 2002). The sex-specific asymmetry in wear might not be seen in conventional analyses, in which only the left side of each tooth class is analyzed. Several authors have indicated that this asymmetrical wear, along with particular directional wear patterns, is associated with working sinew for bows, nets, ropes, etc. (Lozano et al. 2008; Scott and Turner 1988). Males also exhibited greater variance and lower correlation across tooth types in tooth wear even in 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 therefore interpret the male pattern of asymmetrical wear as partly due to use of the dentition as tools—working arrows and tightening bow strings. The pattern of greater wear on the left side may be consistent with stabilizing the object with the left dentition (P4, M1, and perhaps M2) and pulling away from the face on the right. In 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 degree of wear seen in the posterior dentition. A larger sample size along with behavioral data on use of teeth as tools is necessary to determine whether the sex differences in Hadza wear patterns are predominantly caused by use of teeth as tools or by differences in the diet.

Acknowledgments We thank the Hadza for their enduring tolerance and hospitality. Thanks to Johannes and Lena Kleppe for providing us with a base camp in Tanzania and Daudi and Truda Peterson for assistance and innumerable favors, and Costech for permission to conduct research. We would like to thank P. S. Berbesque and three anonymous reviewers for their comments. This research was supported by NSF grant number 0544751 to FWM and a University of Roehampton grant to JCB.

Appendix

Our methods do impose some limitations. In skeletal populations, dentine exposure is more clearly distinguished owing to the changes in the relief of the occlusal plane and the color of the dentine (brown) in contrast to the (white) enamel. Because our dental casts are monochromatic, each researcher can only identify dentine exposure from the relief pattern of the crown surface. Although the dental casts enable the collection of 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.

Table 3 Mann-Whitney U results of dental wear by sex and tooth class in 10-year age cohorts. Shaded cells indicate age classes within each tooth type with a sample size of less than 10 for either sex

	LXI1	LXI2	LXC	LXP3	LXP4	LXM1	RXI1	RXI2	RXC	RXP3	RXP4	RM1
Ages 10–19	$N_1=2$	$N_1=2$	$N_1=2$	$N_1=2$	$N_1=2$	$N_1=1$	$N_1=2$	$N_1=2$	$N_1=2$	$N_1=2$	$N_1=2$	$N_1=0$
	$N_2=4$	$N_2=4$	$N_2=4$	$N_2=4$	$N_2=4$	$N_2=3$	$N_2=4$	$N_2=4$	$N_2=3$	$N_2=3$	$N_2=3$	$N_2=2$
	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Ages 20–29	$N_1=13$	$N_1=12$	$N_1=12$	$N_1=12$	$N_1=13$	$N_1=11$	$N_1=13$	$N_1=13$	$N_1=13$	$N_1=13$	$N_1=13$	$N_1=10$
	$N_2=19$	$N_2=17$	$N_2=18$	$N_2=21$	$N_2=21$	$N_2=21$	$N_2=20$	$N_2=19$	$N_2=20$	$N_2=20$	$N_2=20$	$N_2=16$
	0.305	0.777	0.851	0.868	0.675	1.0	0.434	0.472	0.928	0.281	0.744	0.586
Ages 30–39	$N_1=10$	$N_1=9$	$N_1=9$	$N_1=11$	$N_1=11$	$N_1=9$	$N_1=10$	$N_1=10$	$N_1=11$	$N_1=11$	$N_1=11$	$N_1=10$
	$N_2=11$	$N_2=11$	$N_2=11$	$N_2=12$	$N_2=11$	$N_2=9$	$N_2=11$	$N_2=11$	$N_2=11$	$N_2=11$	$N_2=11$	$N_2=9$
	0.197	0.095	0.067	0.118	0.478	0.297	0.099	.020[a]	.005[b]	.016[a]	0.151	0.133
Ages 40–49	$N_1=10$	$N_1=9$	$N_1=10$	$N_1=9$	$N_1=10$	$N_1=8$	$N_1=9$	$N_1=9$	$N_1=10$	$N_1=10$	$N_1=10$	$N_1=9$
	$N_2=6$	$N_2=7$	$N_2=5$	$N_2=6$	$N_2=5$	$N_2=5$	$N_2=6$	$N_2=5$	$N_2=7$	$N_2=6$	$N_2=8$	$N_2=7$
	0.263	0.837	.040[a]	0.529	0.594	0.524	0.529	0.518	0.962	0.562	1.000	0.606
Ages 50–59	$N_1=7$	$N_1=7$	$N_1=7$	$N_1=7$	$N_1=6$	$N_1=7$	$N_1=7$	$N_1=7$	$N_1=5$	$N_1=6$	$N_1=7$	$N_1=6$
	$N_2=3$	$N_2=2$	$N_2=3$	$N_2=3$	$N_2=3$	$N_2=3$	$N_2=3$	$N_2=3$	$N_2=3$	$N_2=3$	$N_2=3$	$N_2=3$
	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Ages 60–69	$N_1=0$	$N_1=1$	$N_1=2$	$N_1=2$	$N_1=2$	$N_1=2$	$N_1=0$	$N_1=0$	$N_1=0$	$N_1=2$	$N_1=1$	$N_1=1$
	$N_2=3$	$N_2=3$	$N_2=5$	$N_2=4$	$N_2=6$	$N_2=5$	$N_2=4$	$N_2=5$	$N_2=4$	$N_2=3$	$N_2=4$	$N_2=4$
	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

[a] Females had greater wear ($p<0.05$)

[b] Females had greater wear ($p<0.01$—males never had significantly more wear)

NA=Sample size<5 in either group (sex); statistics not performed

Table 4 Interobserver error as measured by Cronbach's alpha

Tooth type (maxillary)	Cronbach's alpha*	*N*
Left central incisor	0.763	24
Left lateral incisor	0.839	20
Left canine	0.913	20
Left third premolar	0.892	24
Left fourth premolar	0.869	25
Left first molar	0.950	6
Right central incisor	0.809	23
Right lateral incisor	0.815	23
Right canine	0.746	20
Right third premolar	0.774	22
Right fourth premolar	0.784	22
Right first molar	0.875	13

* All are significant at $p<0.01$

References

Arnold, W. H., Naumova, E. A., Koloda, V. V., & Gaengler, P. (2007). Tooth wear in two ancient populations of the Khazar Kaganat region in the Ukraine. *International Journal of Osteoarchaeology, 17*, 52–62.

Berbesque, J. C., Crittenden, A. N., & Marlowe, F. W. (2011). Sex differences in Hadza eating frequency by food type. *American Journal of Human Biology, 23*, 339–345.

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

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.

Buikstra, J. E., and D. H. Ubelaker (eds.) (1994). *Standards for Data Collection from Human Skeletal Remains*. *Arkansas Archaeological Survey Research Series No. 44*.

Comuzzie, A. G., & Steele, D. G. (1988). Maxillary lingual anterior tooth wear in prehistoric hunter-gathers from the Texas Coast. *American Journal of Physical Anthropology, 75*, 197–198.

Davies, T. G. H., & Pederson, P. O. (1955). The degree of attrition of the deciduous teeth and first molars of primitive and urbanized Greenland natives. *British Dentistry Journal, 99*, 35–43.

Deter, C. A. (2009). Gradients of Occlusal Wear in Hunter-Gatherers and Agriculturalists. *American Journal of Physical Anthropology, 138*, 247–254.

Dominy, N. J., Vogel, E. R., Yeakel, J. D., Constantino, P., & Lucas, P. W. (2008). Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. *Evolutionary Biology, 35*, 159–175.

Gray, P., & Marlowe, F. W. (2002). Fluctuating asymmetry of a foraging population: The Hadza of Tanzania. *Annals of Human Biology, 29*, 495–501.

Hillson, S. (1996). *Dental Anthropology.* Cambridge: Cambridge University Press.

Hinton, R. J. (1981). Form and patterning of anterior tooth wear among aboriginal human groups. *American Journal of Physical Anthropology, 54*, 555–564.

Irish, J. D., & Turner, C. G., II. (1997). First evidence of LSAMAT in non-Native Americans: Historic Senegalese from West Africa. *American Journal of Physical Anthropology, 102*, 141–146.

Irish, J. D., & Turner, C. G., II. (1987). More lingual surface attrition of the maxillary anterior teeth in American Indians: prehistoric Panamanians. *American Journal of Physical Anthropology, 73*, 209–213.

Jarvinen, V. K., Rytomaa, I. I., & Heinonen, O. P. (1991). Risk factors in dental erosion. *Journal of Dental Research, 70*, 942–947.

Kieser, J. A., & Groeneveld, H. T. (1985). Patterns of dental wear in the Lengua Indians of Paraguay. *American Journal of Physical Anthropology, 66*, 21–29.

Lovejoy, C. O. (1985). Dental wear in the Libben population: its functional pattern and role in the determination of adult skeletal age at death. *American Journal of Physical Anthropology, 68*, 47–56.

Lozano, M., de Castro, J. M. B., Carbonell, E., & Arsuaga, J. L. (2008). Non-masticatory uses of anterior teeth of Sima de los Huesos individuals (Sierra de Atapuerca, Spain). *Journal of Human Evolution, 55*, 713–728.

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

Mays, S. (2002). The relationship between molar wear and age in an early 19th century AD archaeological human skeletal series of documented age at death. *Journal of Archaeological Science, 29*, 861–871.

McKee, J. K., & Molnar, S. (1988). Measurements of tooth wear among Australian Aborigines, II: Intrapopulational variation in patterns of dental attrition. *American Journal of Physical Anthropology, 76*, 125–136.

Molnar, S. (1971a). Human tooth wear, tooth function and cultural variability. *American Journal of Physical Anthropology, 34*, 175–189.

Molnar, S. (1971b). Sex, age, and tooth position as factors in production of tooth wear. *American Antiquity, 36*, 182–188.

Murphy, T. R. (1959). Gradients of dentine exposure in human tooth attrition. *American Journal of Physical Anthropology, 17*, 179–185.

Richards, L. C. (1984). Principal axis analysis of dental attrition data from 2 Australian Aboriginal populations. *American Journal of Physical Anthropology, 65*, 5–13.

Schoeninger, M. J. (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.
Sciulli, P. W. (1997). Dental evolution in prehistoric Native Americans of the Ohio Valley area, part 1, Wear and pathology. *International Journal of Osteoarchaeology, 7*, 507–524.
Scott, G. R., & Turner, C. G., II. (1988). Dental anthropology. *Annual Review of Anthropology, 17*, 99–126.
Scott, E. C. (1979). Dental wear scoring technique. *American Journal of Physical Anthropology, 51*, 213–218.
Smith, B. H. (1984). Patterns of molar wear in hunter-gatherers and agriculturalists. *American Journal of Physical Anthropology, 63*, 39–56.
Tomenchuk, J., & Mayhall, J. T. (1979). A correlation of tooth wear and age among modern Igaloolik Eskimos. *American Journal of Physical Anthropology, 51*, 67–78.
Tompkins, R. L. (1996). Human population variability in relative dental development. *American Journal of Physical Anthropology, 99*, 79–102.
Turner, C. G., II, & Machado, L. M. C. (1983). A new dental wear pattern and evidence for high carbohydrate consumption in a Brazilian archaic skeletal population. *American Journal of Physical Anthropology, 61*, 125–130.
van Reenen, J. R. (1992). Dental wear in San (Bushmen). In J. R. Lukacs (Ed.), *Culture, Ecology and Dental Anthropology* (pp. 201–213). Delhi: Kamla-Raj Enterprises.
Walker, P. L. (1978). A quantitative analysis of dental attrition rates in the Santa Barbara Channel area. *American Journal of Physical Anthropology, 48*, 101–106.
Walker, P. L., & Hewlett, B. S. (1990). Dental-health diet and social status among Central African Foragers and Farmers. *American Anthropologist, 92*, 383–398.
Woodburn, J. (1979). Minimal politics: The political organization of the Hadza of North Tanzania. In W. A. Shack & P. S. Cohen (Eds.), *Politics in Leadership* (pp. 244–266). Oxford: Clarendon.

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