Hadza Hunter-Gatherer Men do not Have More Masculine Digit Ratios (2D:4D)

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ABSTRACT

Objectives: The ratio between the length of the second and the length of the fourth digit (2D:4D) is sexually dimorphic such that males of many species possess a lower ratio than females, particularly in the right hand. Still, men and women often exhibit overlapping 2D:4D ranges and the ratio is highly variable between populations. In order to further explore populational variability, we chose to analyze 2D:4D in the Hadza, a population of hunter-gatherers living in Tanzania.

Materials and Methods: Data were collected separately by two researchers over the course of three years (1998, 2001, 2006) from 152 adult participants (male: $n = 76$, female: $n = 76$). Independent samples t-tests were used to explore sex differences, paired samples t-tests were used to explore directional effects within each sex, and linear regression and one-way ANOVA were used to test possible age effects.

Results: In none of the years, or pooled ($n = 152$), did we find evidence that adult men have a lower 2D:4D than adult women. If anything, the data suggest that women in this population have a significantly lower right hand 2D:4D than men ($P < 0.001$, $d = 0.57$). In contrast, left hand 2D:4D did not exhibit a sex difference ($P = 0.862$, $d = 0.03$).

Discussion: These findings challenge the current view that lower 2D:4D in men is a uniform characteristic of our species. Cross-populational variance in 2D:4D may be related to known patterns of hormonal variation resulting from both genetic and environmental mechanisms, though this relationship merits further investigation. Am J Phys Anthropol 000:000–000, 2015.   © 2015 Wiley Periodicals, Inc.

The ratio between the length of the second digit and the length of the fourth digit (2D:4D) reportedly exhibits a longitudinally stable sex difference (Garn et al., 1975; McIntyre et al., 2005; Trivers et al., 2006), resulting from prenatal exposure to androgens in the uterine environment (Lutchmaya et al., 2004; Hönekopp et al., 2007). While present in both hands, this effect appears to be strongest in the right hand (c.f. Hönekopp and Watson, 2010 for a recent meta-analysis), and manifests as early as 14 weeks in utero (Robinson and Manning, 2000; Malas et al., 2006; but see Knickmeyer et al., 2011). A number of lines of evidence suggest that this sex difference is a consequence of differences in androgen exposure between male and female fetuses during development (cf. McIntyre, 2006 for review). While the mechanism still remains unclear, it has been argued that circulating androgens during perinatal development influence the expression of homeobox (Hox) genes (Manning, 2002), which underlie the morphological development of both the fingers and the genitals (Mortlock and Innis, 1997; Kondo et al., 1997).

Experiments with rodents have causally linked fetal androgen exposure to 2D:4D development. Testosterone administration in a small sample of pregnant rats resulted in decreased 2D:4D in pups relative to control mothers (Talarovičová et al., 2009), and bisphenol A (BPA), an antiandrogenic compound, administration similarly resulted in a more feminized 2D:4D ratio in male rat offspring (Auger et al., 2013; see Lilley et al., 2010 for a discussion of the role of corticosterone). Likewise,

an association between high testosterone in the uterine environment during routine amniocentesis and lower 2D:4D has been uncovered in human toddlers relative to toddlers gestated in lower testosterone uterine environments (Lutchmaya et al., 2004). However, it remains unclear to what extent prenatal exposure to androgens and estrogen interweave to produce populational variance in 2D:4D.

2D:4D reportedly varies greatly by population; indeed, between-population variance is typically reported to be much higher than within-population variance (e.g., Manning et al., 2000, 2003). Furthermore, though a sex difference in 2D:4D has been reliably documented in numerous studies in humans (e.g., Manning et al., 1998, 2000; Peters et al., 2002; Putz et al., 2004) and non-humans (e.g., Peters et al., 2002; McFadden and Bracht, 2005;

Leoni et al., 2005; McIntyre et al., 2009), the size of the difference varies greatly across human populations. Manning (2002) hypothesizes a global average difference of approximately 0.02 between the mean values of male and female 2D:4D ratios (e.g., average 2D:4D was 0.93 and 0.95 for men and women respectively in a Finnish sample from Manning et al., 2000), yet this sex difference is often weakly significant and some populations reportedly exhibit no difference between males and females in 2D:4D in either or both hands (e.g., a Zulu population in South Africa from Manning et al., 2000; English populations from Manning et al., 2000 and Brosnan, 2008; a Dutch population from Rammsayer and Troche, 2007; a Jamaican population from Manning et al., 2002). In fact, the sex differences in digit ratios are smaller than the differences between human ethnic groups, and ranges of expected male and female 2D:4D greatly overlap in most populations (Manning et al., 2000, 2003; Manning, 2002). Furthermore, increased gender equality putatively correlates with decreased sex differences in 2D:4D in a recent analysis from multiple countries (Manning et al., 2014).

While intrauterine environment appears to play a role in the formation of 2D:4D, twin studies have indicated a significant additive genetic and non-shared environmental influence on digit ratios (Rubolini et al., 2006; Gobrogge et al., 2008). For instance, some have implicated variants in the LIN28B gene (Medland et al., 2010), while others argue for the impact of repeat polymorphisms in the androgen receptor (AR) gene (Manning et al., 2003b; but see Hönekopp, 2013; Voracek, 2014). Genetic disorders may similarly influence digit ratios. It has been demonstrated that both male and female individuals with congenital adrenal hyperplasia (CAH) exhibit decreased 2D:4D relative to control individuals (e.g., Brown et al., 2002; Ciumas et al., 2009; Rivas et al., 2014; see Hönekopp and Watson, 2010 for a recent meta-analysis). Indeed, 2D:4D ratios of these women are similar to control males (Rivas et al., 2014), or in some cases even lower than control males (Okten et al., 2002). Similarly, females with polycystic ovary syndrome (PCOS), a heritable condition associated with hyperandrogenism and high androgen exposure in utero (see Ehrmann, 2005 for review), reportedly also exhibit lower 2D:4D relative to control females (Cattrall et al., 2005), though others have failed to replicate this finding (Lujan et al., 2010a,b; Manning et al., 1999). Interestingly, high androgen females experience higher fecundity and reportedly give birth to more sons in resource poor environments (Manning et al., 2000; see Cashdan, 2008 for discussion), consistent with the finding that more masculine characteristics in potential partners are preferred by both sexes in resource poor environments (DeBruine et al., 2010). Moreover, sexual preferences both between (Marlowe et al., 2005; Little et al., 2007) and within (Sorokowski and Sorokowska, 2012) populations are malleable and have been shown to vary with exposure to industrialized and non-industrialized environments.

Sex hormone concentrations are known to vary worldwide in women and men as a consequence of both genetic mechanisms and behavioral ecological characteristics including energetics (Ellison, 2003; Jasienska et al., 2006), mating systems (Burnham et al., 2003), and levels of parental investment (Gray et al., 2002). These hormonal variations are known to directly affect fertility in females (e.g., Valeggia and Ellison, 2001, 2009; Jasienska et al., 2006) and may alter muscular content in males (e.g., Bribiescas, 1996, 2001), reducing metabolic expenditures in both sexes. Populational variation in 2D:4D simi-

larly accords with, and may be a consequence of, this high degree of hormonal variability.

Due to ease of measurement and its putative association with androgenic programming, 2D:4D has been frequently studied in a variety of behavioral domains in both sexes. Correlates of 2D:4D include: athletic ability (e.g., Bailey et al., 2005; Longman et al., 2011, 2015; cf. Hönekopp and Schuster, 2010); sexuality (e.g., Robinson and Manning, 2000; Williams et al., 2000; Lippa, 2003; Gobrogge et al., 2008); and aggression and dominance (e.g., Bailey et al., 2005; McIntyre et al., 2007; cf. Hönekopp and Watson, 2011). However, the overwhelming majority of 2D:4D research has been conducted on Western populations in highly controlled laboratory environments. Given the variation in both sex hormones and 2D:4D ratios worldwide in response to energetic and environmental correlates of differing environments, 2D:4D among non-industrialized populations is rendered of particular interest.

The Hadza hunter-gatherers of Northern Tanzania are remote, characterized by an extreme departure from modern life, and present an interesting population for 2D:4D research. While it is estimated that about 1,000 individuals identify as Hadza, only 300 to 400 still subsist primarily by means of hunting and gathering. Prior research on 2D:4D among the Hadza has focused on this larger population of Hadza whose lives have, more or less, diverged from a hunting and gathering subsistence. Specifically, such research began in 2007 and has concentrated on those living in and around Mangola (e.g., Butovskaya et al., 2010, 2012, 2015, personal communication), a comparatively modernized village on the edge of Hadzaland frequently visited by Western tourists. The Hadza in these studies have shown the characteristic sex difference observed in other populations wherein men display lower digit ratios than women (Table 1). Yet while there has been a small amount of tourism in Mangola for decades, it has become 10 to 20 times more frequent since 1995 (Marlowe, 2010). Through this tourist influence, Mangola area Hadza today are more sedentary, use monetary currency, participate in market transactions and rely less on hunting and gathering for food (Marlowe, 2010; Apicella et al., 2014). In addition, alcohol-related dependencies, abuses, and deaths are more frequent in this area (Marlowe, 2010). The present research largely relies on older data, collected between 1998 and 2006, and focuses on the smaller subpopulation of Hadza living deeper in the bush who, at the time of collection, were practicing many of their characteristic traditions.

Given the association between 2D:4D and a number of sexually-mediated traits in both men and women and its proposed significance in evolution, hunting and gathering, the Hadza may offer unique insights into 2D:4D sexual dimorphism in subsistence environments similar to those prior to the advent of agriculture. For these reasons we chose to examine 2D:4D in this evolutionarily relevant sub-population of hunter-gatherers.

METHODS

Participants

The Hadza live in the Lake Eyasi region of Tanzania and are characterized by a highly fluid pattern of mobility—they freely move between residence camps of approximately 25 people, and camps physically shift location every 4 to 6 weeks (Marlowe, 2010). There is sexual division of labor, in which men primarily collect honey and hunt for game with bow and arrow, and

*TABLE 1. Mean 2D:4D ratios among the Hadza from all available studies*

Sample size	Age range		Right hand 2D:4D, Mean (SD)		Left hand 2D:4D, Mean (SD)		Effect size, Cohen's d		Significantly lower in men?	Citation
	Male	Female	Male	Female	Male	Female	Right	Left		
N = 152 (male: n = 76, female: n = 76)	18–78	18–71	0.989 (0.04)	0.967 (0.04)	0.984 (0.04)	0.983 (0.04)	0.57	0.03	No	Current study (all years)
N = 55 (male: n = 29, female: n = 26)	18–78	19–70	0.994 (0.04)	0.980 (.06)	0.997 (.05)	1.01 (0.04)	0.28	−0.29	No	Current study (1998)
N = 35 (male: n = 18, female: n = 17)	21–60	21–71	0.988 (.05)	0.970 (0.04)	0.973 (.05)	0.965 (.05)	0.40	0.16	No	Current study (2001)
N = 87 (male: n = 45, female: n = 42)	19–66	18–48	0.982 (.03)	0.965 (0.04)	0.977 (.03)	0.977 (.03)	0.43	0	No	Current study (2006)
N = 249 (male: n = 116, female: n = 133)	7–86	6–78	0.984 (0.04)	0.975 (0.04)	0.983 (0.04)	0.988 (.05)	0.23	−0.11	No	Current study (all years, relaxed inclusion criteria)
N = 123 (male: n = 61, female: n = 62)	7–20	7–20	0.95 (.004)	0.98 (.004)	0.95 (.005)	0.97 (.004)	−7.50	−5.7	Yes	Butovskaya et al. (2010)
N = 142 (male: n = 142, female: n = 0)	16–70		0.972 (0.04)		0.979 (0.04)		–	–	Yes	Butovskaya et al. (2012)
N = 380 (male: n = 209, female: n = 171)	Unspecified		0.97 (0.04)	0.98 (0.04)	0.98 (0.04)	0.99 (0.04)	−0.25	−0.25	Yes	Butovskaya et al. (2015)

women primarily gather tubers, water, and other food-stuffs. When medium to large game is brought into camp, it is shared across households (Marlowe, 2003). Though not undernourished, the Hadza are often hungry, as food is rarely abundant (Marlowe, 2010). In fact, 25% of the women in our sample for whom body fat percentage was obtained had below 14% body fat ($M = 17.68$, SD = 7.65). Similarly, average age of menarche among Hadza girls is 17, which is about 5 years later than girls in industrialized countries (Marlowe et al., 2005). However, despite the potential mitigating role of nutritional stress on ovarian function (Ellison, 2003; Jasienska et al., 2006), Hadza women are very fertile. Average age at first marriage is 17 years (Marlowe et al., 2005), median age at first birth is 19 (Marlowe, 2010), and mean number of children over the course of a lifetime is 6.2 (Blurton-Jones et al., 1992). Additionally, the Hadza are generally egalitarian, perhaps a corollary of the food stress they frequently experience (Woodburn, 1982). Aside from the sexual division of labor, they exhibit almost no role differentiation; women have a considerable amount of autonomy, self-expression, and freedom (Marlowe, 2010). The subpopulation of 300 to 400 Hadza who subsist primarily by hunting and gathering is the focus of our study. Two-hundred and eighty-five individuals from 18 different Hadza camps around the Eastern and Northern parts of Lake Eyasi participated in the current study (female: $n = 150$, male: $n = 135$) over three field seasons from 1998 to 2006.

In order to obtain the most accurate ratios possible, we established a set of a priori rules that would merit exclusion from analyses. Individuals were excluded if only one measurement was obtained for each finger, rather than repeated measures for which intraclass correlation coefficients (ICC) could be calculated ($n = 83$), or if any trauma was reported for the fingers, hands, or wrists ($n = 12$). Additionally, though 2D:4D remains largely longitudinally stable (McIntyre et al., 2005), juvenile individuals (age < 18 years, $n = 14$) were excluded from analyses; similarly, individuals for whom no birth year was available were excluded ($n = 24$)[1]. In total, 152 adult individuals (female: $n = 76$, male: $n = 76$) were included in the final sample. Of these participants, approximately 30% of the men and 32% of the women were measured three times. However, due to participant fatigue, the remaining participants were measured twice. Within the final sample, the Hadza men ranged from 18 to 78 years old, with a mean age of 37.48 ± 13.71 at the time of collection. The Hadza women ranged from 18 to 71 years old, with a mean age of 36.17 ± 15.24 at the time of collection (Table 1). 2D:4D data for 20 individuals in this final sample was collected in two field seasons[2].

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[1]Participants were cross-referenced with a directory collected over more than 30 years by Blurton-Jones and Marlowe. The Hadza do not measure age in years; however, they accurately report birth order of group members, and so relative age of multiple individuals can be deduced. Furthermore, for younger individuals, age estimates are even more accurate, as researchers are often present either for their mother's pregnancy or the birth itself.

[2]As additional exploratory analyses, we subsequently investigated 2D:4D in a larger sample ($n = 249$), including both juveniles and individuals for whom only one measurement was obtained. Individuals with recorded pathologies and those without known year of birth were still excluded. Results for these two analyses were similar and are reported separately for comparison.
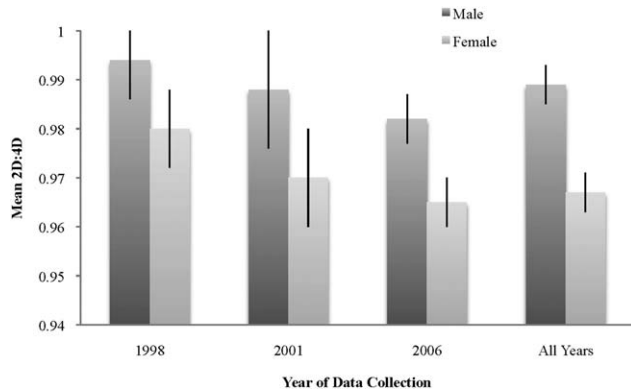
Fig. 1. Mean right hand 2D:4D ratios for each year of collection, differentiated by sex, are presented here with bars representing ±1 standard error.

Procedure

Digit length measurements were first obtained in order to assess 2D:4D for each individual. In all years (1998, 2001, and 2006) second and fourth digit lengths were measured directly from the hands of each participant using an absolute digital caliper (Mitutoyo Ltd., Model CD-6) accurate to 0.01 mm. Each digit was measured from tip to basal crease, alternating left and right hand. All measurements were averaged to obtain an final finger length from which 2D:4D ratios were calculated. 2D:4D was calculated by dividing the average of all second finger lengths by the average of all fourth finger lengths. D_{R-L} was also calculated as the difference between right and left 2D:4D, following prior study (e.g., Manning and Peters, 2009). Data were independently collected by both CLA (one field season, 2006) and FWM (two field seasons, 1998 and 2001) and later aggregated and used to calculate 2D:4D ratios for the purposes of the present analyses. For the 20 individuals for whom 2D:4D was collected across two years, the 2D:4D ratios from both years were averaged; data for 15 of these individuals were collected by both FWM and CLA, allowing for interobserver comparison.

Reliability

Though 2D:4D may be more reliably collected through other means, such as computer-assisted software (e.g., Kemper and Schwerdtfedger, 2009; Allaway et al., 2009), calipers were utilized in this study for their ease of use in a field environment. Calipers are routinely used for 2D:4D research for this ease of use and prior study has shown high reliability estimates, which we confirm here (e.g., Manning et al., 2003; Butovskaya et al., 2015).

The intraclass correlation coefficients (ICC) between all repeated measurements were high within observers in the left digits (CLA: 2D $r = 0.993$, $P < 0.001$, 4D $r = 0.993$, $P < 0.001$, FWM: 2D $r = 0.988$, $P < 0.001$, 4D: $r = 0.989$, $P < 0.001$) and right digits (CLA: 2D $r = 0.994$, $P < 0.001$, 4D $r = 0.993$, $P < 0.001$, FWM: 2D $r = 0.976$, $P < 0.001$, 4D $r = 0.984$, $P < 0.001$). Additionally, the ICC between all repeated measures were high between observers, as calculated from 15 individuals for whom data were collected by both CLA and FWM, in both the left digits (2D $r = 0.811–0.977$, $P < 0.001–0.068$, 4D: $r = 0.957–0.977$, $P < 0.001–0.005$) and right digits (2D $r = 0.897–0.962$, $P < 0.001–0.024$, 4D $r = 0.839–0.972$, $P < 0.002–0.006$).

Analysis

In line with standard protocol, independent sample t-tests were used to compare the differences between male 2D:4D and female 2D:4D in each hand, a composite measure of both hands, and in D_{R-L}. Paired sample t-tests were used to compare the differences between mean 2D:4D in the left and right hand in both males and females. Nonparametric tests were used for comparison and the results were qualitatively similar. Longitudinal 2D:4D analyses have not been previously performed in any Hadza group. Possible age related changes in 2D:4D were examined here by 1) investigating the relationship between year of birth and 2D:4D using linear regression and 2) comparing 2D:4D in age quartiles using a one-way ANOVA.

Ethics statement

Institutional approvals were obtained prior to conducting this study from the Committee on the Use of Human Subjects at Harvard University and the Tanzanian Commission for Science and Technology (COSTECH). Verbal informed consent was obtained from all participants due to low literacy rates.

RESULTS

Descriptive statistics are reported in Table 1. There was no significant sex difference between male and female 2D:4D in the left hand ($t = 0.174$, $P = 0.862$, CI [−0.012 to 0.015], $n = 152$, $d = 0.03$). However, there was a highly significant sex difference between male and female 2D:4D in the right hand—contrary to what is observed in other populations, Hadza women exhibited a significantly lower 2D:4D than men ($t = 3.47$, $P < 0.001$, CI [0.009 to 0.034], $n = 152$, $d = 0.57$). Furthermore, the difference between 2D:4D in the right hand of Hadza males and females is so pronounced that the average 2D:4D in both hands is significantly different between males and females ($t = 2.536$, $P < 0.013$, CI [0.005 to 00.040], $n = 152$, $d = 0.41$). A lower mean 2D:4D value in females is observed in the right hand in all three years (Table 1), although this difference is only significant in one year (2006: $t = 2.42$, $P < 0.03$, CI [0.002 to 0.032], $n = 87$, $d = 0.487$); notably, this year also had the largest sample size (Fig. 1).

Mean right 2D:4D was significantly lower than left mean 2D:4D among Hadza women ($t = −4.171$, $P < 0.001$, CI [−0.024 to −0.008], $n = 76$, $d = −0.409$), a difference not observed between the left and right hands of Hadza men ($t = 1.107$, $P = 0.272$, CI [−0.004 to 0.013], $n = 76$, $d = 0.109$). Accordingly, sex differences in D_{r-l} were also highly significant ($t = 3.678$, $P < 0.001$, CI [−0.009 to 0.032], $n = 152$, $d = 0.600$).

Consistent with expected patterns of sexual dimorphism, mean digit lengths among men and women indicate that men have higher absolute finger lengths; however, the right index fingers of women are shorter than their left index fingers, whereas ring finger lengths remain approximately the same in both sexes (Table 2). Thus, a lower digit ratio among women in the right hand may result from alterations in index finger length, although this relationship is obscure. Consistent with prior study (e.g., McIntyre et al., 2005), no age effects were reported in this sample ($F = 0.457$, $P = 0.713$), an effect that remained when examining women ($F = 0.467$, $P = 0.706$) and men ($F = 0.493$, $P = 0.688$) separately.

TABLE 2. Mean finger lengths (mm)

	R 2D Length, mean (SD)	R 4D Length, mean (SD)	L 2D Length, mean (SD)	L 4D Length, mean (SD)
Male (n = 76)	66.01 (4.41)	66.87 (4.52)	66.96 (4.72)	68.06 (4.32)
Female (n = 76)	60.82 (4.89)	62.97 (5.09)	62.00 (5.03)	63.15 (5.02)

DISCUSSION

The Hadza hunter-gathering lifestyle presents one of the most extreme departures from modern life, in part illustrating how some human groups may have cooperated, acquired food and resources, and chosen mates for much of human history prior to the advent of agriculture (Apicella et al., 2012). Here we report that sex differences in 2D:4D ratios among Hadza hunter-gatherers do not conform to sex differences exhibited in many other human populations. These findings challenge the view that lower 2D:4D in men is a uniform characteristic of our species and accord with prior reports of hormonal variability cross-populationally (Ellison, 2003).

We find no sex difference in 2D:4D in the left hand in Hadza hunter-gatherers. Unexpectedly, we also find that Hadza women have a significantly lower right 2D:4D than men, a reversal of the direction of the usual sex difference. Our findings are from 152 adult individuals and are replicated in mean values across three years of sampling from multiple Hadza camps. Sex differences in D_{r-l} were also highly significant in both samples, and exhibited an effect size of Cohen's $d = 0.600$ and Cohen's $d = 0.343$, respectively. The similarity in findings between the smaller and larger samples indicates that these data reflect real sex differences, or lack thereof, in 2D:4D digit ratios among the Hadza.

Our findings contrast with prior studies yielding sex differences in 2D:4D ratios among mostly settled Hadza in the Mangola region (Butovskaya et al., 2012, 2015). As shown in Table 1, Butovskaya and colleagues have reported significant sex differences in 2D:4D between Hadza men and women (2015) and boys and girls (2010), with males exhibiting lower ratios on average from 142 men from an earlier study (Butovskaya et al., 2012), indicating that overlapping samples may in part drive the replication of these significant sex differences. It should be noted that multiple, and varying, mean values of 2D:4D for male and female Hadza have been published by this same group of researchers. For instance, a strikingly lower 2D:4D was reported for Hadza boys than men in both hands (Butovskaya et al., 2010; Table 1), though the ratio is thought to be stable throughout the lifespan. Similar differences in mean 2D:4D exist when comparing their samples of Hadza females. Also, the sex difference reported in these prior studies range from small (Cohen's $d = 0.25$) to unusually large (Cohen's $d = 7.5$) effect sizes. Reported effect sizes across a number of populations are generally small (Cohen's $d = 0.20$) to medium (Cohen's $d = 0.50$), rendering a Cohen's d of 7.5 much higher than is typical (Manning, 2002). Though not as sizable, inconsistent results in 2D:4D have been reported for other populations. For instance, some studies report a modest sex difference in 2D:4D among the Zulu (Manning et al., 2003), while others report no sex difference among the Zulu (Manning et al., 2000). Thus, the results of this study and the lack of conformity to prior studies of the same population are not atypical, and merely confirm the finding that 2D:4D exhibits a high degree of variability both within and between populations.

There are a number of reasons we may have failed to replicate the results reported by Butovskaya et al. For instance, results may not replicate across studies due to insufficient statistical power. However, we combined 3 years of data, independently collected by two researchers, to achieve an adequately large sample for detecting small to medium effects with over 90% power. Indeed, we detected a significant sex difference in the opposite direction. Also, when the years were examined separately, none of the point estimates suggested that men have a lower right 2D:4D.

Sampling variation may also contribute to the difference in findings between the Hadza studies. The greatest sex difference in 2D:4D recorded among the Hadza was reported for Hadza children (Butovskaya et al., 2010). However, these children were attending a boarding school in Mangola, a comparatively Westernized town on the edge of Hadzaland, and may represent a more sedentary subset of the Hadza population. Likewise, 2D:4D was more recently reported from a large sample of Hadza adults (Table 1; Butovskaya et al., 2015), the majority of whom lived in Mangola (Butovskaya, personal communication). Yet, the adult Hadza in our study were still largely subsisting by means of hunting and gathering. Therefore, this discrepancy in results between Hadza adults in our study and the Hadza adults and children in other studies may be due, in part, to divergences in lifestyle from nomadic to settled life, which could impact prenatal environments. If this is the case, our lack of conformity with these results for more settled Hadza should not be surprising, although the appearance of this effect would be generational—the differing mean 2D:4D values between Hadza boys and men may offer some preliminary credence to the hypotheses. However, this association is speculative and merits testing as a fruitful next step for research.

Although right hand 2D:4D is generally considered a more sensitive marker of prenatal environments than left hand 2D:4D (Hönekopp and Watson, 2010), several studies have previously found no sex difference in the right hand digit ratio (e.g., an Estonian population from Manning et al., 2002; a Zulu population from Manning et al., 2003). Though the lack of sex difference in left hand 2D:4D ratios and reverse sexual dimorphism found in the right hand among Hadza men and women appear at first pass to be unusual, further examination instead indicates that this population may simply represent one point on a continuum of possible diversity in 2D:4D that is mediated by a multitude of both environmental and genetic factors. Indeed, while the average 2D:4D of Hadza men is higher than some other populations and the average 2D:4D of Hadza women is lower than some other populations, neither are outliers (see Table 2 in Hönekopp and Watson, 2010 for a meta-analysis).

Extreme variability in 2D:4D ratio between populations and overlapping ranges between male and female 2D:4D ratios have previously been observed (Manning, 2000).

Okten et al. (2002) report a right hand 2D:4D ratio of 1.00 for a population of Turkish women, whereas Lippa (2003) reports a right hand 2D:4D ratio of 0.949 among American women. Likewise, Manning et al. (2002) report a right hand 2D:4D ratio of 0.99 for a population of Estonian men, whereas Voracek et al. (2007) report a right hand 2D:4D ratio of 0.924 for a population of Lithuanian men. Similarly, others have suggested there may be a weak curvilinear relationship between 2D:4D and latitude of a given population, such that lower ratios are observed at the extremes (Manning, 2000). Individuals of European and Middle Eastern descent for example, display higher average 2D:4D ratios compared to people of African descent (Manning et al., 2000, 2007). Though 2D:4D is generally correlated with fetal androgen exposure rather than adult circulating androgens (e.g., Malas et al., 2006; Klimek et al., 2015; but see Klimek et al., 2014), this is potentially consistent with reports that ethnic groups of African descent have 13 to 15% higher adult circulating testosterone than counterparts of European descent, after controlling for socioeconomic status and sex (Ellis and Nyborg, 1992). Others have similarly demonstrated that hormonal profiles vary globally as a result of environmental and energetic influences, and that these alterations in turn can have very real consequences for fertility and fecundity (Ellison et al., 2002; Ellison, 2003; Jasienska et al., 2006).

Since low 2D:4D in men is associated both with traits deemed attractive by women and others thought to confer a competitive edge in direct male-male competitions, it has been suggested that the phenotype associated with low 2D:4D was sexually selected (Manning and Taylor, 2001). Indeed, 2D:4D in men has previously demonstrated an inverse relationship with fecundity (Manning et al., 2000, 2003; Klimek et al., 2014), contrary to findings in women positively linking 2D:4D with fecundity (Manning et al., 2000; but see Manning et al., 2003 for a negative association between 2D:4D and fecundity in South African women). However, there is reason to suspect that the phenotype associated with low 2D:4D among females could also be a product of specific ecological contexts, following known correlations between resource scarcity and alterations in sex hormones and sexual preferences. The lower digit ratios of Hadza women may be due, in part, to variations in sex hormones. Increased androgens in women have been hypothesized to be favored under conditions where women's work is physically demanding and requires increased strength and stamina (Cashdan, 2008). Unsurprisingly, foraging is strenuous work. Hadza women contribute approximately 58% of the calories in their camps (Marlowe, 2010), a product of working about 6.5 h daily and traveling to and from food acquisition sites, digging tubers, and collecting and carrying food, water and firewood (Hawkes et al., 1997). These energetic demands are clearly higher than those of the normal American woman, who engages in little manual labor and walks an average of only 2.18 km per day (Frank et al., 2004). As Hadza women typically bring more daily calories into camp than men and men bring in calories that are more widely shared among families, a woman's fitness may highly depend on her own ability to acquire resources (Marlowe, 2001). Due to the strenuous nature of women's work, men consider it very important that a wife be able to forage well (Marlowe et al., 2005; Little et al., 2007; Cashdan, 2008).

Energetic constraints are also known to alter ovarian function—hormonal modifications suppressing female sex hormones alter the estrogen to androgen ratio, affecting conception, gestation, and the duration of lactational amenorrhea (Valeggia and Ellison, 2001, 2009). Thus it is plausible that the phenotype associated with low 2D:4D may increase female fecundity in an energetically stressed, physically demanding environment like that of Hadza hunter-gatherers (Manning et al., 1999; Cashdan, 2008). Though the relationship between 2D:4D and reproductive success in the Hadza was not directly tested in this study, this would be a rich area for future study. Others have suggested that early anatomically modern humans (Qafzeh 9) and Neanderthals (Kebara 2, La Ferrassie I, and Shanidar 4) may have exhibited lower 2D:4D ratios than modern humans (Nelson et al., 2011), potentially consistent with the hypothesis that more demanding environments correspond with lower 2D:4D than what might be observed in more physically relaxed environments, though this relationship is clearly slight.

Higher digit ratios in Hadza men may similarly be associated with alterations in hormonal profiles resulting from various factors. It has been suggested that suppression of testosterone might be advantageous in energetically stressed populations, reducing muscle composition and the metabolic requirements of its maintenance (Bribiescas, 1996), as has been demonstrated in reduced testosterone levels among fasting individuals (cf. Bribiescas, 2001 for review). However, importantly, these associations are observed among adult males only and any mechanisms underlying alterations in prenatal environments are as yet unclear. More direct associations may be observed, however, in noting that Hadza men, who typically live monogamously and invest in a high amount of paternal care, are characterized by decreased levels of testosterone relative to Datoga pastoralists, who frequently live polygynously and exhibit a lower investment in paternal care (Muller et al., 2009). A number of studies document that both committed pair-bonding (e.g., Burnham et al., 2003; Gray et al., 2007) and fatherhood (e.g., Gray et al., 2002) are associated with lower testosterone in males. Across camps, Hadza fathers are responsible for a mean of 7.1% of the time a child is held (Crittenden and Marlowe, 2008). Further, fathers with young children frequently forage relatively more and hunt relatively less, favoring a stable resource over the unpredictability of hunting returns when provisioning small children (Marlowe, 2010). This is similarly consistent with the finding that Hadza men are characterized by higher 2D:4D ratios than Datoga men (Butovskaya et al., 2015). Thus, a higher 2D:4D in Hadza males relative to other populations nearby may also be a consequence of differences in hormone levels associated with the typical patterns of investment in parenting, sexual relationships, and potentially energetic status between the groups.

No published studies have directly examined reproductive hormones among Hadza women, and only a single study has examined testosterone among Hadza men (Muller et al., 2009). The results uncovered in this study are both surprising and intriguing, but potential explanatory efforts are stymied by a dearth of relevant endocrinological information for this unique population of hunter-gatherers. However, there is some indirect evidence that suggests women may exhibit altered hormonal profiles relative to women from industrialized societies. Both the waist-to-hip ratio (WHR) (Marlowe et al., 2005) and face shape (Little et al., 2007) of Hadza women are, on average, more masculine compared to women from industrialized populations. Both these features are sexually dimorphic

and are thought to exhibit a dose-dependent response to hormone exposure. For example, higher WHRs are linked to lower estrogen-to-androgen ratios in women (Jasienska et al., 2004), and facial masculinity increases in boys following puberty through the effects of testosterone on bone growth (Vanderschueren and Bouillon, 1995). Furthermore, both facial masculinity in males (Neave et al., 2003; Burriss et al., 2007; Meindl et al., 2012) and WHR in females (Manning et al., 1999; Fink et al., 2003, 2006) have demonstrated inverse correlations with 2D:4D in other populations.

Future study that analyzes hormonal data from the Hadza is warranted, especially in conjunction with further investigation of 2D:4D and other measures (like facial masculinity, WHR, and reproductive success) that are associated with sex hormones. Similarly, future study that directly examines the uterine environment of a chronically energy stressed population would be useful. Perhaps sex hormone alterations in energetically stressed mothers depress both estrogen and testosterone in the uterine environment, creating a more masculine digit profile for women and a more feminine one for men. Previous study has demonstrated that female infants born in the highest weight/height (ponderal) index classes had 37% higher levels of estradiol than female infants born in the lowest classes (Jasienska et al., 2006). Similarly, low infant birth weight has been associated with low testosterone (Cicognani et al., 2002). Birth weight among the Hadza is largely unknown, but body fat percentages among pregnant mothers in other populations are known to affect infant birth weight—generally, higher maternal body fat is also associated with higher infant body fat (Sewell et al., 2006; Hull et al., 2008). Thus, low body fat percentages among Hadza women likely result in leaner infants, and may plastically alter their hormonal profiles as a corollary. Importantly, the possible influence of diverse patterns of hormonal plasticity posited here may also not be mutually exclusive—clinical study has demonstrated that elevated maternal androgen levels are associated with a lower infant birth weight (Carlsen et al., 2006). Maternal androgen levels can directly increase from genetic factors, like PCOS, or indirectly from environmental factors, like energetic stress, by altering the estrogen to androgen ratio in females, thus reducing fecundity but potentially conferring a competitive advantage in the physically rigorous demands of women's daily work in hunter-gatherer society (Cashdan, 2008).

Multiple, interweaving patterns of hormonal plasticity resulting from environmental influences may thus primarily underlie the development of the unusual patterns of sexual dimorphism uncovered by the present study. However, genetic effects also influence hormonal variation across species—indeed, a reverse sexual dimorphism in which females exhibit a lower 2D:4D ratio than males, though unusual, has also been previously documented among some strains of inbred mice (Bailey et al., 2005). Reduced digit ratios in both sexes have been documented in reports of other strains inbred mice, yielding no significant sex differences (Bailey et al., 2005; Yan et al., 2009). Though studies among human populations are sparse, reduced digit ratios have also been noted in Turkish children born from the marriage of first cousins (Ozener et al., 2014). Both genetic studies (Tishkoff et al., 2012; Lachance et al., 2009) and ethnographic accounts (Woodburn, 1988; Blurton-Jones, unpublished data) suggest that the Hadza infrequently intermarry with outgroup members, and as such are characterized by a high degree of genetic homozygosity. Lower 2D:4D ratios and unusual sex differences in this population may also be partially attributable to such patterns of homozygosity, but this relationship is tenuous and should be investigated with further study.

Our main finding that men do not have more masculine digit ratios than women is surprising and merits further examination in other traditional populations. Future work should explore whether 2D:4D varies across societies in a way that would predicted based on the energetic demands of their labor, in accord with known variations in adult sex hormones resulting from energetic constraints (Ellison, 2003; Valeggia and Ellison, 2001). Although the sexual dimorphism in digit ratios has been consistently reported in previous studies, our finding that men and women possess comparable 2D:4D digit ratios could be a reflection of the unique nature of the population studied. Women in labor intensive environments, like the Hadza, may benefit from having higher levels of androgens in utero and thus a more masculine behavioral profile, potentially leading to lower 2D:4D digit ratios (Cashdan, 2008). Similarly, Hadza men live monogamously and invest highly in paternal care, traits which have both been associated with decreased testosterone (Gray et al., 2002, 2003), and Hadza men reportedly exhibit higher 2D:4D ratios than nearby populations that more frequently practice polygyny (Butovskaya et al., 2015). Energetic stress in both adult men and women results in lower sex-typical hormone levels (Bribiescas, 2001; Ellison, 2003), and infants born to these mothers tend to be marked by the same (Cicognani et al., 2002; Jasienska et al., 2006). The Hadza also experience a relatively high degree of genetic homozygosity resulting from low levels of admixture with neighboring groups, and genetic homozygosity has also been correlated with reduced or perhaps reversed sexual dimorphism in 2D:4D in rodent studies (Bailey et al., 2005; Yan et al., 2009).

In summary, we find no evidence that Hadza men have lower digit ratios than Hadza women. These findings accord with known patterns of hormonal variance across populations and lifestyles, and challenge the current view that lower ratios in men is a uniform characteristic of our species.

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