

Original Research Article

Energy Expenditure and Activity Among Hadza Hunter-Gatherers

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Objectives: Studies of total energy expenditure, (TEE; kcal/day) among traditional populations have challenged current models relating habitual physical activity to daily energy requirements. Here, we examine the relationship between physical activity and TEE among traditional Hadza hunter-gatherers living in northern Tanzania.

Methods: Hadza adults were studied at two camps, with minimal intervention so as to monitor energy expenditure and activity during normal daily life. We measured daily walking distance and walking speed using wearable GPS units for 41 adults. For a subset of 30 adults, we measured TEE using doubly labeled water, three indices of work load (foraging return rate, maternal status, and number of dependent children), and urinary biomarkers of metabolic activity and stress (8-hydroxydeoxyguanosine, cortisol, and testosterone).

Results: Fat-free mass was the single strongest predictor of TEE among Hadza adults ($r^2 = 0.66$, $P < 0.001$). Hadza men used greater daily walking distances and faster walking speeds compared with that of Hadza women, but neither sex nor any measure of physical activity or work load were correlated with TEE in analyses controlling for fat-free mass. Compared with developed, industrial populations, Hadza adults had similar TEE but elevated levels of metabolic stress as measured by 8-hydroxydeoxyguanosine.

Conclusion: Our results indicate that daily physical activity may not predict TEE within traditional hunter-gatherer populations like the Hadza. Instead, adults with high levels of habitual physical activity may adapt by reducing energy allocation to other physiological activity. *Am. J. Hum. Biol.* 27:628–637, 2015. © 2015 Wiley Periodicals, Inc.

Over the past three decades, the doubly labeled water (DLW) method has been used in many studies to measure daily energy expenditures across a wide range of populations, lifestyles, and living conditions (Black et al., 1996; Dugas et al., 2011; Kashiwazaki et al., 1995; Pontzer et al., 2012; Snodgrass et al., 2006; Stein et al., 1988). These studies paint a complex picture of the interactions between activity level and metabolic energy expenditure. In principle, total energy expenditure (TEE) might be expected to correspond directly to variation in physical activity level (PAL). Indeed, widely used “factorial” models apply this additive approach in estimating TEE from activity budgets (FAO/WHO/UNU, 2001). In practice, although extreme differences in physical activity (e.g., confined to bed versus engaged in military training) and experimentally imposed exercise regimes have been shown to affect TEE (Black et al., 1996; Cooper et al., 2011; Westerterp et al., 1992), comparisons across diverse lifestyles and populations have often shown little or no difference in TEE despite substantial differences in habitual levels of activity (Dugas et al., 2011; Luke et al., 2002; Pontzer et al., 2012).

Our recent measurements of TEE among Hadza hunter-gatherers (Pontzer et al., 2012) provide an opportunity to examine the relationship between activity level and daily energy expenditure within a traditional, habitually active population. The Hadza are a population of approximately 1,200 living in semi-arid Savannah woodland in the Lake Eyasi region of northern Tanzania. Approximately 400 continue to follow a traditional hunting and gathering lifestyle (Marlowe, 2010). Traditional

Hadza live in simple grass huts, in camps of ~10–30 individuals (about two to 10 families), and have no agriculture, livestock, machinery, or other modern tools. Traditional Hadza occasionally trade with neighboring pastoralist and farming groups for maize or other goods, but more than 90% of their diet comes from wild foods that they forage themselves. For a thorough review of Hadza lifestyle and ecology, see Marlowe 2010.

Several factors are expected to affect variation in energy expenditure or allocation among Hadza adults. Both men and women walk several kilometers each day, over hilly and rocky terrain, to forage for food, collect water, firewood, and other resources, and to visit neighboring camps (Marlowe, 2010). Digging for tubers (done mostly by women) and climbing and chopping into trees to extract honey (done mostly by men) also incur energy costs. Reproduction and child care can also be expected to affect daily energy requirements. Pregnant and nursing mothers incur substantial energy costs that have been shown to increase TEE in other populations (Butte and

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King, 2005; Dufour and Sauter, 2002). Hadza fathers with young, nursing infants also produce more food (and presumably work harder to do so) in order to compensate for the lower food returns of the mother (Marlowe, 2005).

Energy expenditures among hunter-gatherer populations such as the Hadza are of particular interest because of their relevance to overweight and obesity prevalence in developed countries. Many in public health, including the World Health Organization 2011, suggest that unhealthy weight gain among industrialized populations stems in part from a decrease in physical activity and energy expenditure relative to the hunting and gathering lifestyle to which our bodies are adapted. Our initial report on Hadza TEE found no difference in daily energy expenditure between them and a large comparative sample of US and European adults, despite the Hadza's greater activity levels (Pontzer et al., 2012). The similarity in TEE among Hadza hunter-gatherers and Westerners suggests that daily energy expenditure may be less labile and responsive to differences in habitual activity levels than sometimes thought. This view is consistent with the similarity in TEE reported in a global comparison of diverse populations that vary in their level of economic development (Dugas et al., 2011; see Pontzer H. Constrained total energy expenditure and the evolutionary biology of energy balance. *Exerc Sport Sci Rev*, manuscript in press).

In this article, we investigate variation in TEE and daily physical activity among Hadza adults in order to compare two competing models for metabolic adaptation to physical activity: an additive TEE model, which predicts a dose-dependent relationship between physical activity and TEE (FAO/WHO/UNU, 2001), and a constrained TEE model, in which the body adapts dynamically to variation in physical activity to maintain TEE within some physiological range (Pontzer et al., 2012; see Pontzer H. Constrained total energy expenditure and the evolutionary biology of energy balance. *Exerc Sport Sci Rev*, manuscript in press). First, we examine the effects of body mass, fat-free mass (FFM), sex, and age on TEE. Second, we examine the relationships between physical activity, workload, and family structure on TEE. Third, we examine whether TEE and physical activity predict urinary biomarkers of metabolic stress (cortisol and oxidative stress products) and anabolic metabolism (testosterone) within the Hadza, and whether the Hadza experience elevated metabolic stress compared with Western populations. Our objective was to develop a model integrating physical activity and daily energy requirements for traditional hunter-gatherer populations like the Hadza.

SUBJECTS AND METHODS

Subjects

We recruited 41 Hadza adults (26 women and 15 men; age range, 18–80 years) residing at several camps located east of the Lake Eyasi, to take part in this study. To be eligible, subjects needed to be 18 years or older and residing in camps practicing a traditional hunting and gathering lifestyle, where 90% or more of the food eaten was foraged from the wild. We enrolled as many eligible participants as possible, given the limited number of GPS units and DLW doses. Data were collected during several periods of field work between August 2009 and July 2011. Human subjects permissions were obtained from all cognizant US

institutions (Washington University in St. Louis) and Tanzanian authorities (The Commission for Science and Technology [COSTECH], National Institute for Medical Research [NIMR], and local governments) prior to data collection, and all subjects provided informed verbal consent (explicitly approved in our protocols) prior to participation. All discussions were conducted in Kiswahili, the Swahili language, in which the Hadza are fluent.

Height (measured via stadiometer), weight (digital scale), and estimated age were recorded for each subject. FFM was measured via deuterium dilution (IAEA, 2009) for subjects in our DLW sample (see later). The Hadza are attuned to the lunar cycle and to seasonal changes, but they do not adhere to a calendar and are generally uncertain of their age. However, the birth dates of most young adults (<30 years) are known to within a 6-month window from previous field research campaigns, which have collected censuses every 1–3 years since 1985. The ages of older adults have been estimated by Nicholas Blurton Jones using physical indicators, reproductive histories, and an age-ranking procedure calibrated to historical events and a few partial censuses carried out before 1985 (Blurton Jones, personal communication). Point age estimates for the oldest individuals (70+ years) are likely to be more error prone, but we believe they are accurate to within a window of ~5 years.

Daily walking distance and median walking speed

The Hadza travel solely on foot; they have no vehicles, livestock, or other means of conveyance. To measure the distances and speeds walked each day, all 41 subjects were fitted with wearable GPS devices (Forerunner 301; Garmin International; Olathe, KS) that they wore during daylight hours for 6 or more days. A GPS recording was included in the analysis if it captured a minimum of 9 continuous hours of activity. GPS units recorded latitude and longitude automatically every ~10 s. Note that epoch duration for these GPS units is variable during autonomous recording, but this setting provided better spatiotemporal resolution than the shortest fixed-epoch setting available (30 s) on this unit. Our approach resulted in approximately 1,000–3,500 recorded epochs per day per subject.

GPS recordings were analyzed using custom-written routines in R (R Foundation for Statistical Computing, Vienna, Austria; available at: <http://www.R-project.org>). Latitude and longitude data were analyzed to calculate the straight-line distance traveled between each recorded location. These segment distances were then divided by elapsed time to calculate the mean travel speed between each epoch. GPS recordings were then filtered to remove any epochs with biologically unrealistic speeds (<0 or >8 m/s). This filtering removes incorrect location data from the GPS recording, eliminating one source of error. Segment distances were then summed to calculate daily travel distance (km/day). Elevation data were found to be very noisy and, thus, were not included in analysis of daily travel.

The energy cost of walking, both in terms of kcal/km and kcal/min, increases at faster walking speeds (Margaria, 1968) and could also affect TEE. To calculate average walking speed, we first needed to remove all epochs in which the subject was at rest during some or all of the epoch. Given the limit of precision for wearable GPS units, small errors (~2 m) in location between epochs can

TABLE 1. Key characteristics and measurements for Hadza adults in this study

Date	Camp	Subject	Spouse	Sex	Age (yr)	Height (cm)	Mass (kg)	BMI	Body fat (%)	Fat-free mass (kg)	TEE (kcal/day)	Estimated BMR	Estimated PAL
May 2010	Setako	HZ1		F	18	154.3	49.0	20.6	20	39.1	2,108	1,177	1.79
May 2010	Setako	HZ2	HZ19	F	18	144.5	42.2	20.2	17	35.1	1,655	1,046	1.58
June 2010	Sengeli	HZ3	HZ22	F	18	145.1	41.8	19.9	26	31.1	1,522	1,045	1.46
Sept 2009	Setako	HZ4	HZ20	F	20	164.5	49.4	18.3	20	39.6	1,976	1,243	1.59
June 2010	Sengeli	HZ5		F	25	142.7	40.4	19.8	23	30.9	1,459	1,016	1.44
Sept 2009	Setako	HZ6	HZ25	F	29	148.5	49.0	22.2	27	36.0	1,679	1,141	1.47
May 2010	Setako	HZ7	HZ24	F	30	140.5	37.6	19.0	14	32.5	2,460	1,001	2.46
June 2010	Sengeli	HZ8	HZ26	F	30	164.1	55.0	20.4	20	44.0	2,223	1,262	1.76
June 2010	Sengeli	HZ9	HZ27	F	38	150.7	50.6	22.3	28	36.6	2,596	1,159	2.24
May 2010	Setako	HZ10		F	42	137.4	37.6	19.9	17	31.1	1,594	986	1.62
May 2010	Setako	HZ11		F	45	141.3	34.0	17.0	12	29.8	1,554	976	1.59
May 2010	Setako	HZ12	HZ28	F	45	149.0	53.0	23.9	22	41.2	2,314	1,170	1.98
June 2010	Sengeli	HZ13	HZ29	F	45	138.3	41.2	21.5	20	33.0	1,946	1,020	1.91
Sept 2009	Setako	HZ14	HZ30	F	59	153.2	45.2	19.3	24	34.2	2,097	1,127	1.86
May 2010	Setako	HZ14	HZ30	F	60	153.2	43.2	18.4	19	35.1	1,919	1,024	1.87
May 2010	Setako	HZ15		F	70	142.2	37.2	18.4	–	37.2	1,815	926	1.96
May 2010	Setako	HZ16		F	72	142.8	37.6	18.4	19	30.3	1,459	932	1.57
June 2010	Sengeli	HZ17		F	75	134.9	37.8	20.8	28	27.4	1,539	901	1.71
				Female mean	40.0	146.7	43.4	20.1	21	34.7	1,877	1,063	1.76
				st. dev.	19.4	8.5	6.4	1.7	5	4.5	364	111	0.28
May 2010	Setako	HZ18		M	18	170.5	55.8	19.2	12	48.9	3,078	1,450	2.12
May 2010	Setako	HZ19	HZ2	M	18	154.4	46.8	19.6	–	46.8	2,853	1,270	2.25
Sept 2009	Setako	HZ20	HZ4	M	20	162.2	52.8	20.1	14	45.3	2,704	1,381	1.96
June 2010	Sengeli	HZ21		M	25	149.5	43.6	19.5	7	40.4	2,912	1,209	2.41
June 2010	Sengeli	HZ22	HZ3	M	25	158.3	52.4	20.9	12	45.9	3,363	1,363	2.47
May 2010	Setako	HZ23		M	30	154.3	47.6	20.0	13	41.6	2,008	1,240	1.62
May 2010	Setako	HZ24	HZ7	M	30	144.5	41.6	19.9	–	41.6	2,654	1,119	2.37
June 2010	Sengeli	HZ24		M	30	144.5	43.4	20.8	13	37.7	2,374	1,140	2.08
Sept 2009	Setako	HZ25	HZ6	M	31	161.6	50.6	19.4	15	42.8	2,248	1,314	1.71
June 2010	Sengeli	HZ26	HZ8	M	32	157.7	58.2	23.4	23	44.8	2,309	1,380	1.67
June 2010	Sengeli	HZ27	HZ9	M	37	165.1	54.6	20.0	18	44.7	3,054	1,379	2.22
May 2010	Setako	HZ28	HZ12	M	42	167.4	54.0	19.3	8	49.6	2,449	1,384	1.77
June 2010	Sengeli	HZ29	HZ13	M	58	161.0	57.8	22.3	14	49.7	2,685	1,393	1.93
Sept 2009	Setako	HZ30	HZ14	M	64	152.5	44.7	19.2	11	39.7	2,165	1,079	2.01
May 2010	Setako	HZ30	HZ14	M	65	152.5	44.2	19.0	10	39.8	2,352	1,073	2.19
				Male mean	33.1	158.4	50.9	20.2	13	44.6	2,649	1,305	2.04
				st. dev.	14.4	7.3	5.4	1.3	4	3.6	395	113	0.28

Note there were two measurements for Subjects 14, 24, and 30; the mean of these two measurements was used for analyses, including female and male means shown here.

give the impression of slow movement even when the subject is still. Similarly, an epoch in which the subject is moving for only a portion of the elapsed time will provide an inaccurately low estimate of walking speed. Therefore, we first removed all epochs with speeds below 0.5 m/s (an uncomfortably slow walking speed, which we never observed among Hadza adults), and then calculated median speed from the remaining epochs. Note that running is very rare among Hadza adults, accounting for less than 2% of men's travel and less than 1% of women's travel in a recent analysis of GPS data (Pontzer et al., 2014b).

Total energy expenditure

A subset of 30 subjects (17 women and 13 men; age range, 18–75 years; Table 1), residing at two camps (Setako and Sengeli) located east of the Lake Eyasi, took part in DLW measurement of TEE (IAEA, 2009). All data were collected during the dry season, in August–September 2009 (Setako) and May–June 2010. TEE was measured using established methods described in detail elsewhere (IAEA, 2009). Subjects drank 110 ml of water containing approximately 6% APE $^2\text{H}_2\text{O}$ and 10% APE H_2^{18}O , sufficient to achieve enrichment for a 2-week study. Urine samples were collected prior to dosing, 6 h post-dose, and then 3, 7, and 11 days post-dose. Urine samples were stored in liquid nitrogen in the field and then transferred to a -5°C freezer for storage prior to analysis. Samples were analyzed for ^2H and ^{18}O isotopic enrich-

ment via gas isotope ratio mass spectrometry by Dr. William Wong at Baylor College of Medicine. Isotope depletion curves were used to calculate the rate of CO_2 production (moles/day) for each subject using the slope–intercept method. The rate of CO_2 production was used to calculate TEE assuming a food quotient of 0.85 (IAEA, 2009).

Estimated physical activity level, activity energy expenditure, and physical activity index

Following previous studies (Black et al., 1996), we calculated three common indices of activity for all TEE subjects ($n = 30$), using measured TEE and estimates of basal metabolic rate (BMR). Estimated BMR was computed from age, height, sex, and body mass following predictive equations in Henry 2005. PAL was calculated as $\text{PAL} = \text{TEE} / \text{estimated BMR}$; activity energy expenditure (AEE) was calculated as $\text{AEE} = \text{TEE} - \text{estimated BMR}$; and physical activity index (PAI) was calculated as $\text{PAI} = 0.9 \times \text{TEE} - \text{estimated BMR}$. AEE provides an estimate of the energy available for dietary thermogenesis (i.e., digestion) and physical activity, whereas PAI provides an estimate of the energy available for physical activity, assuming thermogenic energy expenditure is equivalent to 10% of TEE.

Biomarkers of metabolic stress

A subset of duplicate urine samples from the TEE subjects was kept in liquid nitrogen throughout the study

and shipped via a liquid nitrogen dry shipper to the University of Arizona, where they were stored at -80°C . These samples were then shipped on dry ice to the Hominoïd Reproductive Ecology Laboratory at the University of New Mexico for analysis of cortisol, testosterone, and 8-hydroxydeoxyguanosine (8-OHdG) via enzyme-immunoassay. Urinary measurements have the advantage of being less invasive, and, for steroid hormones that experience rapid serum fluctuations, urinary levels provide an integrated estimate of production over several hours time.

Cortisol is a steroid product of the hypothalamic–adrenal–pituitary axis that increases the bioavailability of glucose to facilitate responses to a wide variety of environmental and psychosocial stressors (Sapolsky, 1992). Serum cortisol levels increase in response to intense or prolonged physical activity, particularly when energy availability is already low (Emery Thompson et al., 2010; Few, 1974; Sapolsky, 1992; Tabata et al., 1984; VanBruggen et al., 2011). We assessed cortisol in urine using materials created, validated, and provided by the Clinical Endocrinology Laboratory at the University of California, Davis (antibody R4866, sensitivity ~ 16 pg/ml; see Emery Thompson et al., 2010). The interassay coefficient of variation (CV) was 5.9% for a low control and 11.0% for a high control. Intra-assay CV, determined by the average CV of duplicate determinations, was 6.2%.

Testosterone is reported to increase transiently in response to intense exercise (Daly et al., 2005; Webb et al., 1984), though prolonged physical activity leads to low testosterone (Cumming et al., 1989). Populations with more physically active lifestyles tend to have lower testosterone, at least during early adulthood (Ellison et al., 2002). Prior to analysis, samples were deconjugated via hydrolysis with beta-glucuronidase (*Helix pomatia*, Calbiochem, $<2\%$ aryl-sulfatase activity) to recover the primary urinary metabolite of testosterone (Muller and Wrangham, 2004). Testosterone assays were also performed with protocols and reagents supplied by University of California, Davis (antibody R156/7, ref. 29). Interassay CVs were 14.1% for low sample and 8.4% for high sample. Intra-assay CVs averaged 6.2%.

Reactive oxygen species are produced during skeletal muscle contraction, and high or persistent levels of oxidative damage can lead to muscle fatigue and other long-term degenerative effects (Powers and Jackson, 2008). To estimate oxidative stress, we quantified urinary 8-OHdG, a measure of DNA oxidation (Wu et al., 2004). We used the 8-OHdG Check kit developed by the Japan Institute for the Control of Aging (sensitivity ~ 0.5 ng/ml, Cat. KOG-200SE, Genox, Baltimore, MD). Interassay CVs were 5.6% and 13.3% for low and high samples, respectively. Intra-assay CVs averaged 12.4% for 8-OHdG.

One hundred samples from 26 individuals (one to eight samples per individual) were analyzed for cortisol. A subset of 80 samples was analyzed for 8-OHdG. The 45 samples obtained from 11 male subjects were analyzed for testosterone. All samples were standardized to creatinine (Cr) (Tausky, 1954). It was not possible to compare absolute levels of steroid hormones to published literature because of differences in assays. We did, however, compare Hadza 8-OHdG levels with that of published findings, which we restricted to studies using urine, the same kit, a Cr correction, and a similar distribution of ages.

Foraging return, dependent demand, and maternal status

In order to assess mean daily work load among the adults in our sample, we calculated a foraging return and dependent demand score for each individual. Foraging return was designed to capture the amount of physical work, in addition to walking, done to acquire food. All of the food brought back to camp each day by each subject was weighed on a spring scale and recorded. Mean food returns (kg/day) were then calculated for each subject for each of the six food categories: berries, tubers, baobab pods, meat, honey, and traded foods. The foraging return score for each subject was calculated by summing the mean return per day (kg/day) for all six categories. We also examined return rates for tubers and honey independently, as these foods require substantial work to extract.

Dependent demand was designed to measure the magnitude of demand from dependent children on each adult. These demands are inherently difficult to quantify, and will vary with the number and age of children as well as with each child's particular needs. We collected genealogical and household-level demographic data and, thus, determined for each adult in our sample the number and ages of their co-residing children. Hadza children typically sleep in a nuclear-family household until adolescence, whereupon they begin sleeping in a nearby house with age-mates or perhaps with an older relative. Even with such a shift in residence, children continue to eat most of their morning and evening meals with their parents and siblings before marriage. Many Hadza camps include three generations of a family, including adult siblings and their children. Much giving of care is organized along these lines of kinship (Crittenden and Marlowe, 2008; Marlowe, 2003; 2010; Wood and Marlowe, 2013), but the full network of care and support in a Hadza camp is much larger, more or less linking together all camp residents. The Hadza regularly share parenting duties among relatives, and thus the number of co-residing dependent children of a particular parent is not necessarily a complete measure of one's social obligations or effective dependents. Further, all Hadza adults share food with others upon returning to camp; it is both a cultural norm and a social imperative among the Hadza to share (Marlowe, 2010; Wood and Marlowe, 2013). In a society as cooperative and dynamic as the Hadza, it remains an open question how the number of one's own children influences activity patterns. With these caveats in mind, we developed four categories of dependent demand, defined as follows: 0, no dependent children co-residing in camp; 1, only older children (6–12 years old) co-residing; 2, at least one young child (1–5 years); and 3, at least one infant (<1 year) co-residing. For subjects with children in more than one category, the higher rank was assigned.

We also analyzed whether pregnancy or lactation affected energy expenditure or foraging effort. For these analyses, maternal status categories were assigned as follows: 0, not pregnant, not nursing; 1, pregnant; and 2, nursing. It should be noted that women early in a pregnancy could have been incorrectly designated as (0) not pregnant not nursing; we did not perform hormone-based pregnancy tests. However, energy demands in the first trimester are relatively low (Butte and King, 2005).

Data analysis

Statistical analyses were performed in R, with a significance level set at $P < 0.05$. Multivariate regression was



Fig. 1. Energy expenditure plotted against age for Hadza and Westerners. Comparative data redrawn from Black et al. 1996. Hadza AEE and PAL values were calculated using estimated BMR.

used to analyze the effects of body mass, FFM, age, sex, and other factors on TEE, following Tschöp et al. 2011. TEE, mass, and FFM were log-transformed for these analyses due to the power-law relationship between body size and metabolic rate. We also used multivariate regression to examine the relationships among travel distance, travel speed, and TEE. A similar analytical approach was used for biomarker data. We used general linear models to test for effects of age, sex, TEE, and PAL on each of the log-transformed biomarkers. Similarly, differences among dependency demand and maternal status categories were analyzed using analysis of variance (ANOVA).

RESULTS

Body size, sex, and age

TEE was positively correlated with body size among Hadza adults (Table 1). Total body mass was significantly correlated with TEE ($r^2 = 0.43$). The model improves to $r^2 = 0.60$ when sex is added, with lower TEE for females ($P = 0.001$). However, this sex difference in TEE is solely

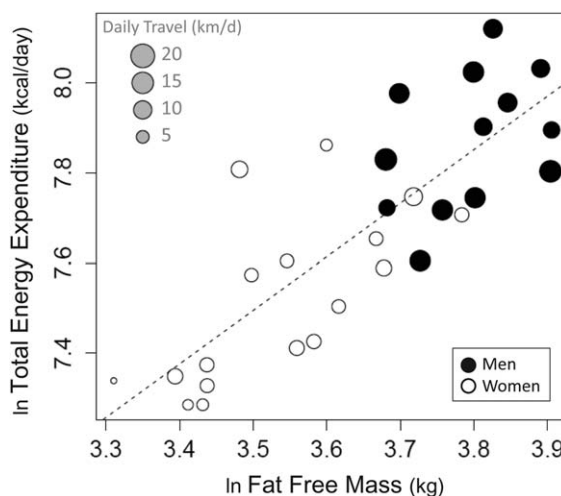


Fig. 2. TEE plotted against fat-free mass for Hadza adults. Closed symbols: men and open symbols: women. Symbol diameter indicates each subject's mean daily travel distance. Dashed line indicates ordinary least squares regression ($y = 1.19x + 3.33$, $r^2 = 0.66$, $P < 0.001$).

due to differences in body fat percentage. FFM was strongly correlated with TEE ($r^2 = 0.66$, Fig. 1), and there were no significant effects of sex ($t(27) = 1.38$, $P = 0.18$) or interactions between FFM and sex ($t(26) = -0.42$, $P = 0.68$) in multivariate analyses of FFM and TEE. Among husband-wife pairs ($n = 9$), there was no correlation between spouses' residual TEE (controlling for FFM; $P = 0.82$), nor were there sex differences (i.e., husband and wife residual TEEs were similar). Age had no effect on TEE in this sample after controlling for FFM ($t(27) = -0.35$, $P = 0.73$), although we noted that the distribution of TEE with age is similar to that reported for a much larger sample by Black et al. (1996; Fig. 2).

As we discussed in our initial report from this study (Pontzer et al., 2012), energy expenditure among the Hadza was similar to that for Western (US and European) adults (Fig. 2). Using data for body mass and TEE from socioeconomically developed populations (Human Development Index = 2) reported by Dugas et al. 2011, we calculated the least squares linear regressions for male ($n = 53$) and female ($n = 79$) cohorts, and used these regressions to calculate the predicted TEE for Hadza men and women given their body mass. Observed TEE for Hadza men ($2,649 \pm 395$ kcal/day; Table 1) and women ($1,877 \pm 364$ kcal/day) was near the predicted values and well within the prediction intervals (men: 2,421 kcal/day; range, 1,568–3,277 kcal/day; women: 1,864 kcal/day; range, 1,314–2,417 kcal/day) for developed populations.

Activity and energy expenditure

GPS data were recorded for a mean of 12.4 days per subject (range, 6–26 days). Mean daily travel distances calculated for each subject in the sample ($n = 41$) revealed effects of sex and age. Men had greater daily travel distances (12.2 ± 2.7 km/day) than that of women (6.2 ± 1.7 km/day, $n = 26$, $P < 0.001$, t -test), and age was negatively correlated with mean daily travel distance ($t(33) = -2.1$, $P = 0.04$) in multivariate analysis including sex. The effect of age, although statistically significant, was modest: mean daily travel distance decreased at a

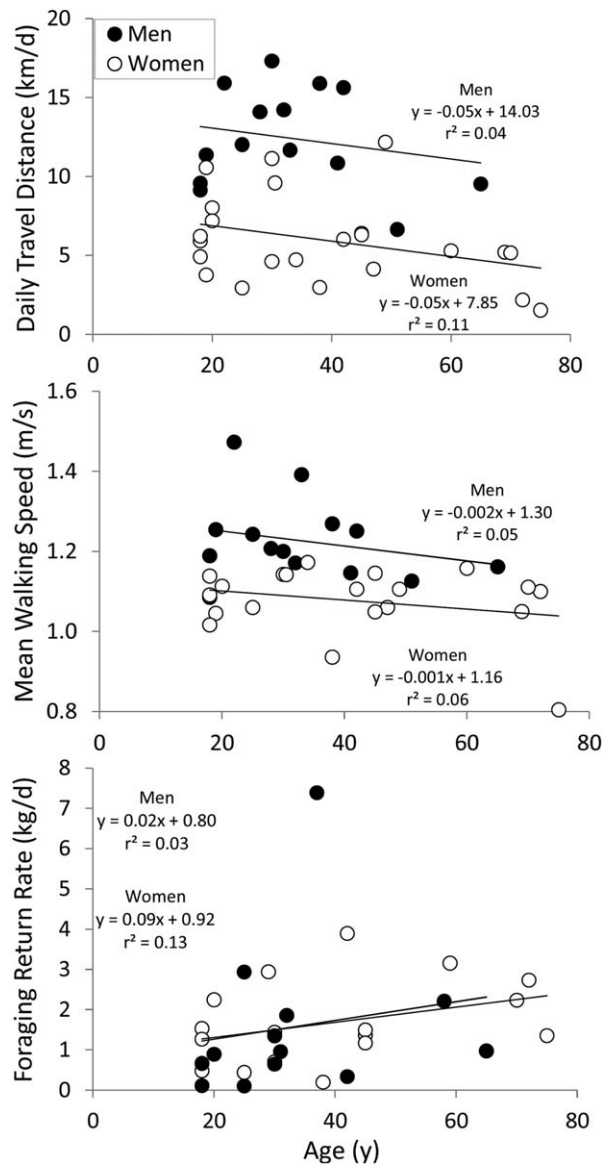


Fig. 3. Mean daily walking distance, walking speed, and foraging return rate plotted against age for Hadza men and women.

rate of 0.04 km per year in both men and women (Fig. 3). At 65 years of age, Hadza men and women have predicted mean daily travel distances of 10.8 km/day and 4.7 km/day, respectively. Median walking speeds also differed by sex (men: 1.22 ± 1.18 m/s and women: 1.05 ± 0.09 m/s, $P < 0.001$, t -test), but the effect of age only approached significance ($t(33) = -1.5$, $P = 0.13$) when controlling for sex. Sex differences in daily walking distance and speed were unrelated to differences in body size. Neither height nor body mass were correlated with daily travel distance or median speed in analyses controlling for sex ($P = 0.34$ or greater, all comparisons).

Mean daily walking distance (Table 2) was greater for men in the TEE subsample (11.6 ± 2.5 km/day, $n = 13$) than for women (5.8 ± 1.7 , $n = 17$, $P < 0.001$, t -test). However, daily travel distance was not correlated with TEE ($t(27) = 1.11$, $P = 0.28$) in multivariate analyses including

sex and FFM, nor was median walking speed ($t(27) = -0.44$, $P = 0.66$). These results did not change when we examined the product of walking distance and body mass. Similarly, residual TEE (controlling for FFM) did not differ among dependent demand or maternal status categories (Figs. 4 and 5), and residual TEE was not correlated with foraging return score ($t(28) = 0.23$, $P = 0.82$), even when men and women were examined separately. Foraging return score was likewise unrelated to body mass ($t(28) = 0.39$, $P = 0.71$). We ran additional analyses to determine whether residual TEE was related to the foraging return rate of tubers (women) or honey (men), because these foods require substantial effort to obtain: tubers must be dug from deep within the soil using a wooden digging stick, and honey is generally acquired only after several minutes of chopping into a tree limb with a small axe to expose the hive (tree climbing is often involved as well). However, residual TEE was unrelated to the return rate of tubers (women) or honey (men).

We found a similar lack of correspondence between behavioral activity measures and estimated PAL, AEE, and PAI. As noted in our initial report (Pontzer et al., 2012), Hadza men had greater PAL than that of women (men: 2.04 ± 0.28 , women: 1.76 ± 0.28 , $P = 0.02$, t -test). Note that the mean PAL values here are lower than that we initially reported, particularly for men (Pontzer et al., 2012), because of improved age estimates for two men and one woman in our sample and the correction of an arithmetic error in the estimation of BMR for five men in our initial analysis. Nonetheless, as discussed in our initial analysis (Pontzer et al., 2012), compared with PAL values for socioeconomically developed populations (Human Development Index = 2) reported by Dugas et al. 2011, Hadza men had greater estimated PAL than male cohorts in developed populations (1.78 ± 0.19), whereas estimated PAL for Hadza women was near the mean for female cohorts in developed populations (1.72 ± 0.14). Hadza men and women did not differ in estimated PAI or AEE in multivariate analyses controlling for FFM. PAL, which differed between sexes (see earlier), was not correlated with daily travel distance ($t(27) = -0.08$, $P = 0.94$) in multivariate analysis controlling for sex. PAI and AEE, which are correlated with FFM, were not correlated with daily travel distance ($P > 0.45$ both comparisons) when controlling for FFM. Similarly, foraging return score was not correlated with estimated PAL, PAI, or AEE when controlling for sex or FFM ($P > 0.80$ all comparisons).

Biomarkers of energetic stress

Cortisol levels in the Hadza did not differ by sex ($t(24) = 0.60$, $P = 0.56$), nor did they increase with age ($r^2 = 0.01$, $P = 0.75$). Cortisol was not predicted by TEE ($r^2 = 0.04$, $P = 0.35$). Testosterone levels did not change with age ($r^2(10) = 0.16$, $P = 0.23$) and were not correlated with TEE ($r^2 = 0.04$, $P = 0.56$) in the small ($n = 11$) male sample.

Oxidative stress (8-OHdG) in the Hadza did not differ by sex ($t(24) = -0.72$, $P = 0.48$) and exhibited a nonsignificant increase with age ($r^2 = 0.11$, $P = 0.10$). 8-OHdG was not predicted by TEE alone ($r^2 = 0.01$, $P = 0.57$), but adding age into the model revealed a significant interaction between age and TEE (TEE: $t = -1.44$, $P = 0.16$; age: $t = -2.11$, $P < 0.05$; and TEE \times age: $t = 2.18$, $P = 0.04$). 8-OHdG increased with TEE among older Hadza adults,

TABLE 2. Activity data, dependent demand, and maternal status

Date	Subject	Sex	Daily travel distance (km/day)	Median walking speed (m/s)	Dependent demand	Maternal status	Food returns (kg/day)					
							Tubers	Berries	Baobab	Meat	Honey	Trade foods
May 2010	HZ1	F	5.66	1.08	3	2	1.14	0.39	0.00	0.00	0.00	0.00
May 2010	HZ2	F	6.58	1.07	0	1	0.82	0.45	0.00	0.00	0.00	0.00
June 2010	HZ3	F	5.79	0.94	0	0	0.23	0.00	0.25	0.00	0.00	0.00
Sept 2009	HZ4	F	7.19	1.16	0	0	1.23	0.28	0.00	0.00	0.00	0.73
June 2010	HZ5	F	4.41	1.03	3	2	0.23	0.00	0.21	0.00	0.00	0.00
Sept 2009	HZ6	F	6.07	1.06	3	2	2.25	0.69	0.00	0.00	0.00	0.00
May 2010	HZ7	F	8.05	1.03	2	2	1.11	0.28	0.00	0.00	0.05	0.00
June 2010	HZ8	F	5.99	1.00	3	2	0.32	0.00	0.00	0.00	0.39	0.00
June 2010	HZ9	F	4.45	0.98	2	0	0.20	0.00	0.00	0.00	0.00	0.00
May 2010	HZ10	F	5.96	1.09	3	2	3.23	0.49	0.00	0.00	0.00	0.18
May 2010	HZ11	F	6.99	1.12	2	0	0.97	0.40	0.00	0.00	0.00	0.00
May 2010	HZ12	F	9.48	1.07	1	0	1.35	0.15	0.00	0.00	0.00	0.00
June 2010	HZ13	F	5.45	0.90	3	2	1.17	0.00	0.00	0.00	0.00	0.00
Sept 2009	HZ14	F	6.23	1.05	0	0	2.92	1.41	0.00	0.00	0.00	0.00
May 2010	HZ14	F	4.50	1.11	0	0	1.53	0.35	0.00	0.00	0.07	0.03
May 2010	HZ15	F	5.54	1.01	0	0	1.09	1.15	0.00	0.00	0.00	0.00
May 2010	HZ16	F	3.74	1.08	0	0	1.98	0.76	0.00	0.00	0.00	0.00
June 2010	HZ17	F	2.12	0.79	0	0	1.35	0.00	0.00	0.00	0.00	0.00
	Female mean		5.81	1.03	1.47	0.88	1.23	0.35	0.03	0.00	0.03	0.05
	st. dev.		1.67	0.09	1.37	0.99	0.82	0.36	0.08	0.00	0.09	0.18
May 2010	HZ18	M	9.66	1.04	0	–	0.00	0.06	0.00	0.58	0.03	0.00
May 2010	HZ19	M	10.67	1.05	0	–	0.00	0.04	0.00	0.00	0.08	0.00
Sept 2009	HZ20	M	9.27	1.27	0	–	0.00	0.00	0.00	0.84	0.05	0.00
June 2010	HZ21	M	12.05	1.25	3	–	0.00	0.00	0.00	0.10	0.00	0.00
June 2010	HZ22	M	10.69	1.24	0	–	0.00	0.00	2.50	0.00	0.44	0.00
May 2010	HZ23	M	13.06	1.20	1	–	0.00	0.05	0.00	1.30	0.00	0.00
May 2010	HZ24	M	12.25	1.05	2	–	–	–	–	–	–	–
June 2010	HZ24	M	18.46	1.14	2	–	0.00	0.00	0.05	0.00	0.59	0.00
Sept 2009	HZ25	M	13.06	1.72	3	–	0.00	0.00	0.00	0.68	0.28	0.00
June 2010	HZ26	M	12.99	1.10	3	–	0.00	0.00	1.30	0.28	0.28	0.00
June 2010	HZ27	M	13.25	1.11	2	–	0.00	0.00	0.30	7.09	0.00	0.00
May 2010	HZ28	M	15.54	1.21	1	–	0.00	0.00	0.02	0.27	0.04	0.00
June 2010	HZ29	M	8.04	1.05	3	–	0.00	0.00	0.41	0.89	0.91	0.00
Sept 2009	HZ30	M	9.20	1.21	0	–	0.59	0.00	0.00	0.06	0.51	0.00
May 2010	HZ30	M	6.41	1.04	0	–	0.00	0.00	0.00	0.00	0.26	0.53
	Male mean		11.65	1.19	1.38	–	0.02	0.01	0.35	0.93	0.24	0.02
	st. dev.		2.53	0.18	1.33	–	0.08	0.02	0.74	1.90	0.28	0.07

See text for details. Note there are two measurements for Subjects 14, 24, and 30; the mean of these two measurements was used for analyses, including mean female and male values here.

but not among younger individuals. Estimated PAL was also not a significant predictor of 8-OHdG on its own ($r^2 = 0.01$, $P = 0.70$), but its interaction with age mirrored the relationship observed with TEE. Among older Hadza, higher estimated PAL was associated with higher oxidative stress (PAL: $t = -1.75$, $P = 0.09$; age: $t = -1.72$, $P = 0.10$; and age \times PAL: $t = 2.12$, $P < 0.05$).

8-OHdG levels in the Hadza averaged 15.04 ± 3.56 (standard deviation) ng/mg-Cr for 15 women and 18.91 ± 10.85 ng/mg-Cr for 10 men. These levels indicate greater oxidative stress than comparable estimates from nonsubsistence populations. For example, American women breast cancer survivors aged 18–70 years had levels of 9.14 ± 8.90 ng/mg-Cr; more than 1 standard deviation below the Hadza women (Thomson et al., 2005). American men boilermakers aged 18–59 years with chronic workplace toxin exposures had urinary 8-OHdG levels averaging 13.3 ± 1.04 ng/mg-Cr at baseline and 15.22 ± 0.99 after an acute exposure to ash and fumes (Kim et al., 2004). Even Tanzania city-dwellers had lower levels of 8-OHdG in the absence of disease: healthy men and women aged 46–58 years averaged 10.1 ± 5.2 ng/mg-Cr, whereas the mean of individuals with hypertension (17.4 ± 14.8) was closer to the Hadza value (Negishi et al., 2000).

DISCUSSION

Hadza living in traditional foraging camps lack domesticated plants and animals, mechanized tools, firearms, and vehicles, and have limited means of storing excess food for long-term use (Marlowe, 2010). Accordingly, adults set out on foot each day for food, water, wood for fuel, and for various other errands, including social visits among camps. Our measurements of daily walking distance, walking speed, and foraging return (Table 2; Fig. 3) indicate that Hadza adults maintain high levels of physical activity and productivity well into their 60s and 70s, which is consistent with previous reports of healthy aging in the Hadza (Hawkes et al., 1997) and other traditional populations (Gurven et al., 2012).

Apart from the sexual division of foraging effort (i.e., hunting versus gathering), Hadza adults all engage in a similar set of daily activities; no one has a different or specialized job. Thus, although our measures of physical activity are not exhaustive, it would be difficult for a Hadza adult to work harder without walking farther, or faster, or bringing in more food. Indeed, the distance walked per day, assessed by pedometer, is typically associated quite strongly with other measures of physical activity such as accelerometry (Tudor-Locke et al., 2002). As

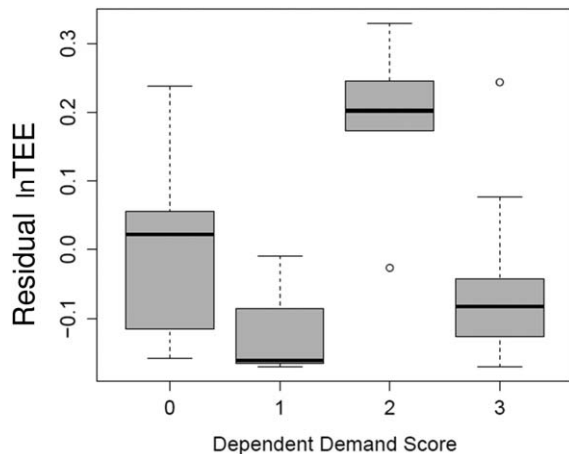


Fig. 4. Residual ln TEE (controlling for FFM, see Fig. 1) across dependent demand categories: 0, no dependent children co-residing ($n = 12$); 1, only older children (6–12-years old) co-residing ($n = 3$); 2, at least one young child (1–5 years) co-residing ($n = 5$); and 3, at least one infant (<1 year) co-residing ($n = 10$). For subjects with children in more than one category, the higher rank was assigned. No difference among groups (ANOVA $P = 0.95$, $F = 0.004$).

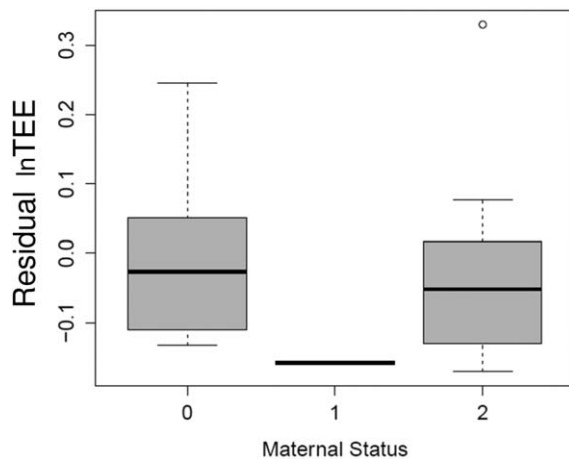


Fig. 5. Residual ln TEE (controlling for FFM, see Fig. 1) across maternal status categories. 0, not pregnant, not nursing ($n = 9$); 1, pregnant ($n = 1$); and 2, nursing ($n = 7$). No difference among groups (ANOVA $P = 0.96$, $F = 0.002$).

such, the lack of correspondence between our behavioral measures of physical activity and TEE is somewhat surprising, and challenges additive TEE models that assume a simple, positive relationship between physical activity and TEE (FAO/WHO/UNU, 2001).

Figure 6 depicts the model of energy expenditure and physical activity among Hadza hunter-gatherers that emerges from our results. FFM and its determinants, sex and body mass, have strong relationships with TEE and some measures of activity (median walking speed and daily walking distance). Maternal status and dependent demand are unrelated to energy or activity measures, and foraging return is similarly orphaned in our analysis. Notably, behavioral measures of physical activity (daily travel distance, median walking speed, and foraging return rate) were not correlated with TEE (Fig. 6) or with

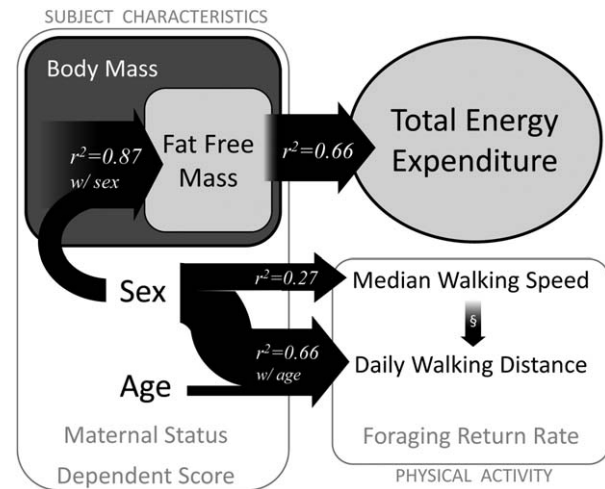


Fig. 6. A model of energy expenditure and activity for Hadza hunter-gatherers. Black arrows depict significant ($P < 0.05$) relationships as determined from multivariate analyses (see text); arrow width reflects the statistical strength of the relationship. Physical activity measures were not correlated with TEE, nor were they correlated with indices PAL, AEE, or PAI. [§]Median walking speed was positively correlated with daily walking distance in analyses including sex and age (model adjusted $r^2 = 0.71$).

common indices of physical activity (estimated PAL, PAI, and AEE).

Given the size of our TEE sample ($n = 30$), we lack sufficient statistical power to rule out small or moderate effects of age, social factors (e.g., dependents), or physical activity on daily energy requirements; effects of $r = 0.5$ or greater on residual TEE (controlling for FFM) would be necessary for detection with power = 0.80. Nonetheless, it is evident that our measures of physical activity do not have a strong effect on TEE. For example, daily walking activity varied considerably among Hadza adults in our sample (CV: 0.42), ranging from 2.1 km/day (~45 min/day) to 18.5 km/day (~4.5 h/day, see distances and walking speeds in Table 2), but had no discernible effect on average TEE over a 2-week period. In contrast, Ravussin et al. (1982) reported significant effects of limited daily activity on TEE among subjects confined to a calorimetry chamber, and Westerterp et al. (1992) reported significant increases in TEE with only four weekly 10–30 min bouts of imposed exercise. Indeed, a recent review by Westerterp (2013) found significant (if sometimes modest) effects of activity on TEE and PAL across a broad range of studies.

The lack of relationship between physical activity measures and TEE is consistent with a constrained TEE model for energy expenditure (Pontzer H. Constrained total energy expenditure and the evolutionary biology of energy balance. *Exerc Sport Sci Rev*, manuscript in press) and suggests that Hadza adults may be compensating either behaviorally or physiologically to keep total daily energy requirements in check. One possibility is that individuals modulate their behavior to keep total physical activity relatively constant, as proposed in the “activity-stat” hypothesis first put forth by Rowland (1998). Individuals with larger daily travel distances might compensate by reducing activity in other areas, for example by lying down instead of standing, or resting instead of doing domestic chores, consequently maintaining similar total activity

levels to individuals who walk less. Multiday accelerometry studies are needed to test this hypothesis among the Hadza.

Physiological changes in energy allocation among tasks could also reduce variation in daily energy requirements and obscure the relationship between a given activity, such as walking, and TEE. Reduction in metabolic activity in other tasks (e.g., immune response, somatic repair, reproductive investment, and fat or muscle deposition) in response to increased physical activity should be evident in BMR. Although we lack measurements of BMR for the subjects in this study, humans and other species have been shown to reduce BMR when activity demands are increased (e.g., Heini et al., 1991; Westerterp et al., 1992; reviewed in Pontzer H. Constrained total energy expenditure and the evolutionary biology of energy balance. *Exerc Sport Sci Rev*, manuscript in press). For example, Westerterp et al. (1992) reported decreased sleeping metabolic rates in men and women enrolled in a 40-week exercise program, and in both humans and mice, increased exercise has been shown to result in decreased ovarian activity (Ellison and Lager, 1986; Perrigo, 1987).

Changes in energy allocation may be particularly important for Hadza women during pregnancy and lactation. Women in some traditional populations have been shown to reduce BMR during pregnancy, diminishing the increase in TEE typically observed in pregnant women in developed countries (Dufour and Sauter, 2002; Heini et al., 1991). More work will be needed to test for similar compensation among Hadza women; we found no effect of maternal status on TEE, but we lack BMR measures from pregnant Hadza women, and our sample of pregnant and nursing mothers was very small. However, we did not find evidence of reduced physical activity among pregnant and nursing women. Maternal status had no effect on daily travel distance ($F(13) = 0.14$, $P = 0.71$) or foraging return ($F(13) = 0.02$, $P = 0.96$ for all foods and $F(13) = 0.15$, $P = 0.70$ for tubers), albeit with small samples. Larger samples, and biomarker measures of activity among different physiological tasks (e.g., reproduction, immune response, and somatic maintenance), may enable us to investigate physiological trade-offs in future work.

The increase in oxidative stress, as measured by heightened 8-OHdG levels, with TEE in older adults may reflect an age-related shift in energy allocation away from maintenance, or may simply reflect the accumulation of oxidative stress (which appears to be quite high among the Hadza) with age. The accumulation of oxidative stress has been implicated in some models of aging in humans and other animals (Pontzer et al., 2014a; Speakman, 2005). Improving our understanding of the determinants of TEE may also shed light on the downstream effects of variance in energy throughput.

Population comparisons of TEE

At a broader scale, population differences in energy allocation strategies may explain why Hadza TEE is similar to less-active Western populations (Pontzer et al., 2012), and why PAL and TEE are so similar across widely divergent lifestyles (Dugas et al., 2011; Luke et al., 2002; Pontzer et al., 2012; 2104; see Fig. 1). This hypothesis is consistent with the limited comparative endocrine data available. For example, Ellison et al. (2002) reported lower levels of testosterone (an anabolic hormone) among

men in traditional foraging and subsistence agriculture populations compared with men in the United States.

Population differences in energy resource allocation might also help to explain the high 8-OHdG levels evident among Hadza adults: their greater levels of physical activity may decrease the energy available for physiological activities that reduce oxidative damage. Alternatively, the Hadza lifestyle, with heavy sun exposure, common tobacco use, exposure to smoke from cooking fires, and vigorous physical activity may incur greater oxidative stress than is typical for Western populations. The sources of the unexpectedly high levels of oxidative stress among Hadza adults in this sample warrant further investigation.

Daily energy requirements and physical activity measures among Hadza adults challenge current factorial models for TEE. Despite their high levels of physical activity, the Hadza show no evidence of elevated TEE relative to less-active populations (Pontzer et al., 2012), nor do they show strong relationships between daily activity and TEE (Fig. 6). Further work is needed to investigate whether this disconnection between physical activity and TEE is common among other traditional populations. Although consistent correlations between physical activity and TEE have been reported among developed populations (Westerterp, 2013), individuals in energy-limited environments may adapt to increased workloads to keep daily energy requirements in check (Pontzer H. Constrained total energy expenditure and the evolutionary biology of energy balance. *Exerc Sport Sci Rev*, manuscript in press). Such physiological adaptation would imply that models for estimating TEE in traditional populations should be based on body size and composition, with less emphasis on activity level.

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