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High energy requirements and water throughput of adult Shuar forager-horticulturalists of Amazonian Ecuador

Lauren Christopher[1] | Felicia C. Madimenos[2,3] | Richard G. Bribiescas[4] | Samuel S. Urlacher[5] | James J. Snodgrass[6] | Lawrence S. Sugiyama[6] | Herman Pontzer[5]

[1] Department of Human Evolutionary Biology, Harvard University, Cambridge, Massachusetts
[2] Department of Anthropology, Queens College (CUNY), Flushing, New York
[3] New York Consortium on Evolutionary Primatology (NYCEP), New York, New York
[4] Department of Anthropology, Yale University, New Haven, Connecticut
[5] Department of Evolutionary Anthropology, Duke University, Durham, North Carolina
[6] Department of Anthropology, University of Oregon, Eugene, Oregon

Correspondence
Herman Pontzer, Duke University, Evolutionary Anthropology, 104 Biological Sciences Building, Campus Box 90383, Durham, NC 27708-9976.
Email: pontzer@gmail.com

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Abstract

Objectives: We measured total energy expenditure (TEE; kcal/d) and water throughput (L/d) among Shuar forager-horticulturalists from Amazonian Ecuador to compare their daily energy and water demands to adults in other small-scale and industrialized populations.

Methods: TEE and water throughput were measured using the doubly labeled water method among 15 Shuar adults (eight women, seven men; age range 18-60 years) living in a relatively remote village. We used multiple regression to assess the effects of anthropometric variables (body size, fat free mass, age, and sex) on TEE and water throughput. We also compared Shuar TEE and water throughput to those of other small-scale and industrialized societies.

Results: TEE among Shuar adults (men: 4141 ± 645 kcal/d, women: 2536 ± 281 kcal/d) was most strongly correlated with fat free mass. Estimated physical activity levels (PAL) calculated as (TEE/estimated BMR), were greater for men (2.34 ± 0.29) than women (1.83 ± 0.14, $P < 0.001$). Water throughput was also greater among Shuar men (9.37 ± 2.34 L/d) than women (4.76 ± 0.36 L/d, $P < 0.001$). Shuar TEE and water throughput were elevated compared to adults in industrialized populations.

Discussion: TEE and PAL of Shuar men are among the highest recorded during normal daily life, and likely reflect both high levels of physical activity and cultural dietary practices. Drinking large amounts of chicha, a traditional carbohydrate-rich drink made from manioc, likely contributes to the high levels of water throughput among Shuar men, and may contribute to elevated TEE.

1 | INTRODUCTION

An individual's total energy expenditure, TEE (kcal/d), reflects the summed cost of physical activity, somatic maintenance (eg, tissue repair, immune system activity), and investment in growth and reproduction. Researchers in human ecology and public health have long used estimates of TEE derived from activity budgets and body size to investigate variation in food requirements, activity workload, and health outcomes (Dufour, Reina, & Spurr, 1999; Dufour & Piperata, 2008; Piperata & Dufour, 2005, 2007; FAO/WHO/UNU, 2001). These studies often measure TEE as a straightforward function of physical activity costs and basal metabolic rate, BMR (kcal/d), itself a function of body mass (FAO/WHO/UNU, 2001; World Health Organization, 2011). Results from this activity-based approach, termed the "factorial method", have suggested that, due to higher physical activity levels, subsistence farming and foraging groups have higher TEE than more sedentary populations in developed countries (Dufour & Piperata, 2008; Popkin, Barclay, & Nielsen, 2005; Popkin & Gordon-Larsen, 2004; Prentice, 2006). However, while factorial methods can provide accurate estimates of TEE for some populations (Liu, Piao, Sun, Tian, & Yang, 2011; Morio et al., 1997), they have been shown to be poor predictors of TEE in small-scale populations and other physically active groups (Leonard, Galloway, & Ivakine, 1997; Ocobock, 2016).

More recently, research directly measuring TEE in free living populations using the doubly labeled water (DLW) method (IAEA, 2009) has shown that despite their high activity levels, subsistence farmers and other small-scale societies do not necessarily exhibit higher TEE than more sedentary populations. The DLW method measures a subject's daily rate of carbon dioxide (CO_2) production, which is directly linked to caloric expenditure. DLW is also well-validated against respirometry methods, making DLW the "gold standard" for measuring TEE in free-living populations (IAEA, 2009). In an analysis of DLW measurements from 98 global populations, Dugas et al. (2011) found that a population's Human Development Index (HDI) score, a rough indicator of daily physical activity, was unrelated to TEE or the ratio of TEE/BMR, also known as "physical activity level" (PAL). Using DLW measures, Luke and colleagues (Ebersole et al., 2008; Luke et al., 2002) showed that women in a rural Nigerian farming community had similar body size-adjusted daily energy expenditures compared to women living in urban areas in the United States. Pontzer et al. (2012, 2015) reported that TEE of physically active Hadza hunter-gatherers, measured using DLW, was similar to that of relatively sedentary individuals from the United States and Europe in analyses controlling for body size and composition. Gurven et al. (2016) recently reported marginally elevated DLW measures of TEE for Tsimane forager-horticulturalists living in the Amazon basin in Bolivia, but this elevation was largely attributable to high pathogen load and immune system activity, which substantially elevated BMR. In fact, despite their physically active lifestyle (as assessed through accelerometry, heart rate monitoring, and behavioral observation; Gurven, Jaeggi, Kaplan, & Cummings, 2013), the Tsimane had low PAL values (calculated as TEE/BMR) due to their elevated BMR (Gurven et al., 2016). In contrast, elevated TEE and PAL have been reported for Bolivian altiplano agropastoralists (Kashiwazaki et al., 2009; Kashiwazaki, Dejima, Orias-Rivera, & Coward, 1995) and Gambian farmers (Singh et al., 1989), particularly during periods of peak agricultural activity. It therefore remains unclear how activity costs and maintenance costs contribute to TEE in small-scale societies.

The DLW method also provides measures of daily water throughput (L/d), an overlooked variable in human ecology research (Rosinger, 2015; Rosinger & Tanner, 2015). Water balance, matching intake and metabolic water production to water loss, is imperative to sustain life, but determinants of water throughput in humans are not well studied. An analysis of 458 U.S. adults indicated that water throughput is only weakly correlated with age and body size (Raman et al., 2004), suggesting water throughput may be largely shaped by environmental and lifestyle factors. Hot climates and high levels of physical activity are expected to increase water throughput, as humans sweat prodigiously to thermoregulate under heat stress (Lieberman, 2015). Rosinger (2015) has reported high water throughput and high rates of dehydration among the Tsimane. Water and food intake are interdependent in humans and other species (Engell, 1988), suggesting food intake might also affect water throughput. For example, Engell (1988) found that water intake was strongly correlated with food energy intake, and that restricting subjects' drinking led to voluntary decreases in eating.

In this study, we examine TEE and water throughput among the Shuar, a forager-horticulturalist population in the Amazonian rainforest. Three aspects of the Shuar lifestyle are noteworthy with respect to their daily energy and water throughput. First, like other subsistence farmers and foragers, they are physically active (Madimenos, Snodgrass, Blackwell, Liebert, & Sugiyama, 2011), engaging in horticulture as well as hunting and gathering. Mechanized transport is rarely used in day to day life and, except for the occasional use of chainsaws, almost all daily horticultural and foraging tasks continued to be carried out by hand. PAL values determined via accelerometry for Shuar adults are lower than might be expected given their observed levels of activity (men: 1.54 ± 0.18, women: 1.42 ± 0.19; Madimenos et al., 2011). However, studies among the Tsimane (Gurven et al., 2013) have suggested that accelerometry underestimates PAL in forager-horticulturalist populations like the Shuar.

Second, the Shuar experience a high pathogen load, for example, from soil-transmitted helminths (Cepon-Robins et al., 2014), which could elevate BMR and TEE (Gurven et al., 2016). Urlacher et al. (2018) recently examined immune system activity and growth in Shuar children, showing that immune system activation was common and had energetic consequences in terms of growth. Shuar children with higher levels of immune system activity showed lower growth rates, and this effect was mitigated in children with greater body fat reserves (Urlacher et al., 2018). Chronic pathogen burden and immune response may likewise affect energy requirements and allocation among adults.

Third, Shuar adults, particularly men, commonly consume large quantities of *nijamanch* or "chicha" ("masato" in other regions of Amazonia), a fermented beverage made by women from manioc root (Colehour et al., 2014; Harner, 1984) sometimes mixed with plantain, sweet potato, or fruit. Harner (1984), using subject observation, estimated chicha consumption at 11.4-15.1 L/d for Shuar men and 3.8-7.6 L/d for Shuar women, remarkable amounts compared to measured water throughputs in other populations (eg, Raman et al., 2004).

Consuming copious amounts of a carbohydrate-rich drink like chicha may affect both TEE and water throughput.

Water consumption (whether as pure water, beverages, or in food) is the strongest single predictor of water throughput (Raman et al., 2004), and, therefore, drinking large amounts of chicha may elevate daily water throughput among the Shuar. Drinking large amounts could also affect TEE in two different ways. First, drinking 0.5 L of water has been shown in some studies to increase resting metabolic rate by as much as 30% for over an hour afterward (Boschmann et al., 2003). Results of subsequent studies have been mixed, with some showing similar effects and others no effect of drinking (Charrière, Miles-Chan, Montani, & Dulloo, 2015), but it is possible that consuming liquids at the remarkably high levels observed among the Shuar could elevate TEE. Second, following studies showing similar TEE among active and sedentary populations, Pontzer and colleagues have suggested that TEE is constrained, with the body adapting physiologically to keep TEE in line with energy availability (Pontzer, 2015, 2017; Pontzer et al., 2012, 2015, 2016). A ready source of easily digestible calories such as chicha may effectively raise energy availability among the Shuar, alleviating the constraint on TEE and permitting increased daily expenditure.

We measured TEE and water throughput among Shuar adults from the lowland neo-tropical forest region east of the Cordillera de Cutucu (Cross-Cutucu or CC region) using the DLW method, in order to examine whether high activity and high chicha consumption reported previously for the Shuar population is associated with high TEE and water throughput. We compared Shuar TEE and water throughput to similar measures from other populations in order to test whether the Shuar exhibit greater energy expenditure and greater daily water throughput than industrialized populations.

2 | METHODS

2.1 | Shuar forager horticulturalists

The Shuar are a Jivaroan-speaking Amerindian population of ~60 000-110 000 people inhabiting the Amazonian regions of Ecuador and Peru (CODENPE, 2012; Rubenstein, 2001; UNICEF, 2004). The population is increasingly heterogeneous in terms of economy and lifestyle, as Shuar participation in the market economy increases through time (Liebert et al., 2013; Urlacher et al., 2016). At the time of the study, communities in the relatively isolated CC region of Shuar territory lacked direct road access. Access to the road and small market center required approximately 1-3 or more days travel (on foot), and/or 1.5 to 12 hours travel by motor canoe. Until 2014, another 8.5-9 hours travel by dirt road was required to reach the nearest major market center of over 10 000 persons (paving of the road in 2014 shortened this trip to 5.5 hours). Upano Valley (UV) communities have closer road and market access, usually within 2 hours, and comparatively greater levels of market integration (the degree to which one produces for and consumes from the market economy) (Liebert et al., 2013). Although market integration differs somewhat between CC and UV communities, there is also significant variation within regions and communities. While some Shuar individuals live in towns with a market integrated lifestyle, the vast majority of Shuar in rural communities continue to rely on traditional cultigens of manioc and plantains for their dietary staples, augmented to varying degrees by subsistence foraging, hunting, and fishing, with minimal consumption of store-bought foods (Urlacher et al., 2016).

Since 2005, the Shuar Health and Life History Project (SHLHP) have worked with the Shuar to investigate the effects of increasing market integration on Shuar lifestyle, life history and health (http://www.bonesandbehavior.org/shuar). Data for this study were collected in the CC region of Shuar territory, characterized by neotropical riverine floodplain forest (~200 m elevation) in June and July, 2014. Participants in this study lived in a relatively remote village, where subsistence is based on slash-and-burn horticulture, fishing, foraging and hunting, with only rare consumption of market-based foods. The community was located about 1 day's walk or 3.5 hours by motor canoe from the end of the only road that entered the CC region at the time of study.

Data were collected from 15 Shuar adults (18-60 years old; 8F, 7 M) who volunteered to participate in this study. The sample was a convenience sample based on the location of the field campaign that summer. Eight men were initially enrolled, but one was subsequently excluded from analysis due to urine sample contamination. We measured body weight using a digital scale and height using standard protocol (Table 1) (Lohman, Roche, & Martorell, 1988; Urlacher, Blackwell, et al., 2016). We note that both the male and female cohort in this sample had substantially greater bodyweight than reported in previous studies of the Shuar (~30% greater for men, 18% greater for women cf. Madimenos et al., 2011). Participant ages were self-reported and were cross-checked using government issued *cedula* (identification cards) and overlapping genealogies created by the SHLHP. The local elected Shuar representative body provided authorization to conduct the research, and institutional approval was obtained from the Office for Protection of Human Subjects at the University of Oregon and Hunter College, City University of New York. Prior to data collection, village leaders and community members approved the study at an open community meeting in which everyone could ask questions and voice any concerns. All individual participants then gave informed verbal consent prior to participation at the time of each sample collection.

2.2 | Energy expenditure and water throughput

We used the DLW method to calculate each participant's TEE, water turnover, and percent body fat (IAEA, 2009). The DLW method allows the researcher to track tagged oxygen and hydrogen isotopes in order to indirectly measure

TABLE 1 Anthropometrics, depletion rates (k_D and k_O; % per day), dilution spaces (N_D and N_O; moles), TEE, and water throughput for Shuar men and women. BMR and PAL are estimated

Subject	Sex	Age	Height (cm)	Mass (kg)	FFM (kg)	Fat %	BMI	k_D	k_O	N_D	N_O	TEE (kcal)	BMR (kcal/d)	PAL	Water (L/d)
1	F	57	151.1	66.3	43.5	34.3	29.0	0.1489	0.1857	1839	1784	3008	1467	2.05	5.19
2	F	27	152.4	65.0	43.5	33.1	28.0	0.1360	0.1681	1841	1778	2596	1424	1.82	4.74
3	F	57	155.8	66.0	45.0	31.8	27.2	0.1349	0.1692	1905	1841	2915	1497	1.95	4.87
4	F	28	156.3	66.5	46.0	30.8	27.2	0.1327	0.1606	1944	1885	2343	1465	1.60	4.89
5	F	19	149.5	47.9	40.5	15.4	21.4	0.1584	0.1912	1717	1656	2422	1290	1.88	5.15
6	F	29	145.6	59.3	41.4	30.1	28.0	0.1392	0.1697	1761	1687	2320	1350	1.72	4.64
7	F	21	148.3	50.0	38.0	24.1	22.7	0.1461	0.1804	1605	1554	2415	1287	1.88	4.45
8	F	34	148.8	50.7	35.7	29.6	22.9	0.1443	0.1784	1508	1461	2268	1302	1.74	4.12
Mean		34	151.0	59.0	41.7	28.6	25.8	0.1426	0.1754	1765	1706	2536	1385	1.83	4.76
SD		*14.9*	*3.7*	*8.2*	*3.5*	*6.2*	*2.9*	*0.0086*	*0.0102*	*150*	*145*	*281*	*88*	*0.14*	*0.4*
9	M	60	168.3	82.6	58.2	29.5	29.2	0.2332	0.2749	2471	2375	4270	1835	2.33	10.92
10	M	29	165.2	84.9	71.9	15.3	31.1	0.1865	0.2233	3030	2950	4759	1846	2.58	10.71
11	M	33	171.1	84.9	64.5	24.0	29.0	0.2360	0.2732	2720	2644	4093	1851	2.21	12.17
12	M	30	172.4	79.7	66.2	16.9	26.8	0.2063	0.2473	2813	2694	4884	1832	2.67	11.00
13	M	52	163.9	77.8	55.4	28.8	29.0	0.1501	0.1837	2350	2259	3425	1761	1.94	6.69
14	M	18	155.2	60.5	51.7	14.5	25.1	0.1592	0.1927	2185	2118	3159	1555	2.03	6.59
15	M	23	164.5	66.7	56.7	15.0	24.6	0.1665	0.2079	2394	2320	4400	1667	2.64	7.55
Mean		35	165.8	76.7	60.7	20.6	27.8	0.1911	0.2290	2566	2480	4141	1764	2.34	9.37
SD		*15.3*	*5.7*	*9.5*	*7.1*	*6.7*	*2.4*	*0.0350*	*0.0371*	*297*	*292*	*645*	*113*	*0.29*	*2.3*

caloric expenditure. Participants provided a baseline urine sample at the beginning of the study. Later that same day, a dose of DLW containing ~6%^2H_2O and ~10%$H_2{}^{18}O$ was administered orally (females: 67 g; males: 73 g). The first round of urine samples was then collected at or after the 12-hour mark following dose ingestion, and then every 3-5 days over the 13-day TEE measurement period. Collection day varied for some subjects due to logistical constraints (ie, the participant was staying in the forest or distant gardens on a collection day). Upon collection, samples were immediately frozen in the field at −20°C and subsequently shipped on dry ice to the Human Evolution and Energetics Lab at Hunter College. Samples were kept frozen in a −5°C freezer until analysis with cavity ring down spectrometry (L2120i, Picarro Inc. Santa Clara, CA). We used the slope-intercept method to determine isotope dilution spaces (ie, the volume of H and O in the body) and rates of depletion (ie, the loss of ^{18}O and ^2H in % per day; Speakman, 1997). The rate of ^2H depletion was used to calculate water turnover (L/d) (IAEA, 2009; Speakman, 1997). Isotope dilution values were used to calculate total body water and thus fat free mass (FFM), under the assumption that FFM holds water whereas fat does not. We used the standard adult human hydration constant of 0.732 kg water per kg FFM (IAEA, 2009). Wang, Deurenberg, Pietrobelli, Baumbartner, and Heymsfield (1999) report the coefficient of variation in hydration constant to be 4.8% among human adults, which will have an effect of similar magnitude on our calculations of FFM. Isotope dilution approaches to measuring FFM are generally more accurate than skinfold-based approaches and other field methods for assessing body composition, and have the advantage of being applicable across populations (ie, population-specific equations are not needed) (Wells & Fretwell, 2006).

We used dilution spaces and depletion rates for ^2H and ^{18}O to calculate the mean rate of CO_2 production using eq. 4.6 I.E. (2009). We converted the rate of CO_2 production to TEE (kcal/d) using Weir's simplified equation (eq. 9 in Weir, 1949; see IAEA, 2009) and a food quotient of 0.95. Because our food frequency data does not allow estimation of the caloric contribution of current Shuar foods, we based the food quotient on the estimated caloric contribution of carbohydrates (91%), proteins (3%), and fats (6%) to the rural Shuar diet (Kroeger & Ilechkova, 1983). This dietary breakdown is conspicuously low in the contribution of fats and proteins, producing a food quotient of >0.97. Other Amazonian forager-horticulturalists (eg, Tsimane) have food quotients of ~0.93 (Gurven et al., 2016). Our use of 0.95 for the food quotient is therefore conservative, assuming that carbohydrate was likely overrepresented in the food tables by Kroeger and Ilechkova (1983).

To check for analytical error, we reanalyzed the isotope enrichment of all samples and recalculated TEE and water throughput for all subjects. Reanalyzed measures of TEE and water throughput differed from original values by 1.0 ± 7.2% and 3.4 ± 5.8%, respectively, which was not a significant difference ($P = 0.79$ and $P = 0.35$ respectively, Student's paired *t* test). We also sent samples for a subset of subjects ($n = 4$) to an isotope ratio mass spectrometry (IRMS) laboratory that specializes in DLW analyses. Measures of TEE and water throughput assessed via IRMS differed by 3.4% (range: −4.8% to 8.7%) and 1.1% (range: −3.4% to 1.2%), respectively. The results here appear to be reliable and accurate.

To estimate PAL for Shuar men and women, we calculated BMR using a regression equation reported for 204 adults in Pontzer et al. (2016), which incorporates body composition and age. The equation has similar power (adj. $r^2 = 0.55$, $SE = 178.1$) to other predictive BMR equations (eg, Henry, 2005) and has the form

$$\begin{aligned} \text{BMR} = 145.9 + 9.9\text{FFM} + 5.5\text{Fat Mass} \\ + 5.3\text{Height} + 1.42\text{Age} - 118.0\text{Sex} \end{aligned} \tag{1}$$

where FFM and fat mass are in kg, height is in cm, age is in years, and sex has a value of 1 for men and 0 for women. We divided TEE by estimated BMR to give PAL for each participant.

2.3 | Data analysis

We used Welch's t-tests to compare means by sex and general linear models to examine the effects of anthropometric variables on TEE and water throughput. ANOVA was used to assess group effects on water throughput, and when group effects were apparent Tukey's HSD was used to compare pairs of populations. All analyses were performed in R 3.3.2 (R Core Team, 2015). A $P < 0.05$ criterion was used to determine statistical significance. We confirmed that the data for male and female cohorts were normally distributed ($P > 0.05$) using both the Shapiro-Francia and Lilliefors (Kolmogorov-Smirnov) tests for normality (*nortest* package in R).

Water throughput: To test whether TEE and/or water throughput differed between Shuar and large comparative samples from other populations, we compared Shuar TEE and water throughput measurements to mean values reported for men and women in Tsimane (Rosinger & Tanner, 2015), Aymara (Kashiwazaki et al., 2009), and U.S. samples (Raman et al., 2004). Tsimane measures are estimates of water intake from dietary recall surveys (Rosinger & Tanner, 2015), and, therefore, caution is warranted when comparing results from studies, including the present analysis of the Shuar, that use isotope depletion methods. Aymara and U.S. water throughputs were both measured using deuterium depletion, as done in this study with the Shuar. For the Aymara, we used eq. 6.8 in IAEA (2009) to calculate water throughput from ^{2}H dilution space and depletion rate data reported in Table 1 in Kashiwazaki et al. (2009) for the participants 14 years and older engaged in traditional agropastoral work (8 M, 9F).

Energy expenditure: Unlike water throughput, energy expenditure is known to be strongly affected by body size and composition, and thus any comparisons among individuals or populations must account for the influence of anthropometric variables. We compared TEE measurements for Shuar individuals against similar measures from 332 adults across five global populations (Ghana, Seychelles, Jamaica, South Africa, and U.S. [Chicago]; Pontzer et al., 2016), to our knowledge the largest comparative sample of DLW-measured TEE for which the effects of FFM and other anthropometrics are reported. We calculated predicted TEE over a range of FFM values using Model 2 in Table 1 of Pontzer et al. (2016) which has the form

$$\begin{aligned} \text{TEE} = 347.7 + 42.2\text{FFM} - 2.1\text{Fat Mass} + 1.3\text{Height} \\ + 1.8\text{ Age} - 14.4\text{Sex} + \text{Population} \end{aligned} \tag{2}$$

where FFM and fat mass are in kg, height is in cm, age in years, sex has a value of 1 for males and 0 for females, and the "population" term reflects a population-specific effect on TEE (Ghana: 0, Jamaica: −374.0, South Africa: −164.0, Seychelles: 100.8, U.S.: −245.6). This model was chosen because it includes a broad set of anthropometric variables, has reasonably strong power ($df = 322$, adjusted $r^2 = 0.55$, $SE \pm 368.2$) and does not require behavioral measures (eg, accelerometry). Note that only FFM and population were significant terms in this model (Pontzer et al., 2016). When mean values for fat mass, height, age, sex, and population from the Pontzer et al. (2016) sample are imputed into Equation 2, the model simplifies to TEE = 42.2 FFM + 440.0. We used this equation ±2 standard errors to establish a 95% confidence interval (CI) for comparison with individual measures of TEE from Shuar men and women.

To compare TEE at the population level, we used Model 2 from Pontzer et al. (2016) to calculate TEE for male and female cohorts from Ghana, Seychelles, Jamaica, South Africa, and the U.S. using values for age, FFM, fat mass, height, and sex of Shuar male and female cohorts. This approach effectively gives the expected TEE for members of these comparative cohorts who were matched to the anthropometric values of the Shuar cohorts. SDs for anthropometrics-adjusted TEE for these comparative cohorts were calculated using their reported coefficients of variation (Pontzer et al., 2016). To compare the Shuar to a larger sample of populations, we compared TEE means for Shuar men and women against cohorts from a broad range of populations including Gambian farmers (Dugas et al., 2011), Aymara agropastoralists (Kashiwazaki et al., 2009), Hadza hunter-gatherers (Pontzer et al., 2012, 2015), Tsimane forager-farmers (Gurven et al., 2016), and a large global sample of industrialized populations (Dugas et al., 2011). Because FFM measures are not available for many of these populations, we compared TEE against body mass using separate trend lines for male and female cohorts to account for sex-based differences in body composition. Because Shuar TEE appears higher than that of most other populations (see below), for this analysis we used measures from Gambian and Aymara adults taken from seasons of peak physical activity and greater TEE (Heini, Minghelli, Diaz, Prentice, & Schutz, 1996; Kashiwazaki et al., 2009; Singh et al., 1989).

3 | RESULTS

Mean TEE for Shuar men (4141 ± 645 kcal/d) was significantly greater than for women (2536 ± 281, $P < 0.001$; Table 1). This was due primarily to men's larger body size, as the strongest predictor of TEE was FFM (adj. $r^2 = 0.88$, $\beta = 80.55 \pm 8.02$, $P < 0.001$, $df = 13$; Figure 1A). In separate multiple regression analyses including FFM, age, and sex, neither age ($P = 0.44$) nor sex ($P = 0.36$) were significantly correlated with TEE, nor did they improve the fit of the model. PAL values, calculated using estimated BMR, were greater for Shuar men (2.34 ± 0.29) than for women (1.83 ± 0.14, $P < 0.005$), suggesting that the difference in TEE is not entirely due to differences in size.

Shuar subjects, particularly men, consistently fell above the TEE and FFM trend lines for the comparative human sample of 332 adults (Model 2 in Pontzer et al., 2016; see above). Using residuals from the comparative trend line, Shuar women fell within the 95% confidence interval for the model but trended higher, expending 336 ± 240 kcal/d more than expected for their FFM. Shuar men mostly fell above the 95% confidence interval of the comparative sample, expending 1142 ± 441 kcal/d more than expected (Figure 1A). Compared to age- and anthropometrics-adjusted TEE values for five populations in Pontzer et al. (2016), the Shuar male cohort had much greater expenditure than others, with a mean TEE more than 2 SDs above Ghanaian men, the next highest cohort (Figure 1B). Shuar women's TEE fell within 1 SD of anthropometrically-adjusted TEE values for Ghanaian, Seychellois, and South African cohorts and within 2 SDs of all 5 comparative cohorts (Figure 1B).

When male and female Shuar cohorts are referenced against a larger, global comparative sample, Shuar adults fall above the trend lines for cohorts from industrialized societies (Figure 1C). In particular, Shuar men exhibit among the highest TEE ever recorded for men during normal daily life. Only the Gambian male farmer cohort, measured during peak agricultural season, has a greater residual from the male cohort trend line (1237 kcal/d) than the Shuar male cohort (1168 kcal/d). The residual for the Shuar female cohort (321 kcal/d) was similar to women in Gambian and Aymara farming populations (Figure 1C).

Daily water throughput was also greater for Shuar men (9.37 ± 2.34 L/day) than for women (4.76 ± 0.36 L/day; $P = 0.002$; Figure 2A). As with TEE, daily water throughput was strongly correlated with FFM (adj. $r^2 = 0.85$, $\beta = 0.23 \pm 0.03$, $P < 0.001$). In multiple regression analyses including FFM, sex, and age, neither the effect of sex ($P = 0.67$) nor age ($P = 0.64$) on water throughput was significant. In population comparisons of water throughput among the Shuar, Tsimane, Aymara, and U.S., ANOVA revealed significant differences among both female cohorts ($F[3] = 14.47$, $P < 0.001$) and male cohorts ($F[3] = 34.85$, $P < 0.001$). Among women, Shuar women had similar water throughput compared to that reported for Tsimane women ($P = 0.82$) but greater water throughput than that reported for Aymara ($P < 0.001$ both comparisons). Among men, Shuar had greater mean water throughput than Tsimane, Aymara, and U.S. men ($P < 0.001$, Figure 2B). Tsimane women also differed from Aymara and U.S. women ($P < 0.001$ both comparisons). Tsimane men had greater water throughput than U.S. men ($P = 0.01$) but only marginally elevated throughput relative to Aymara men ($P = 0.08$).

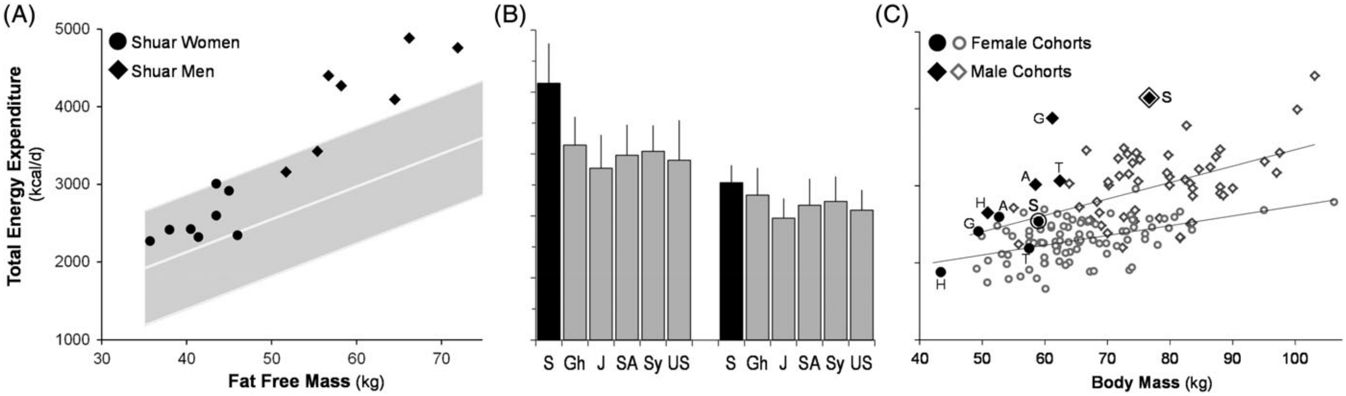

FIGURE 1 Fat free mass, FFM (kg) and total energy expenditure, TEE (kcal/d). A, Shuar women (circles) and men (diamonds). Gray region indicates ordinary least squares regression ±2 standard errors from a recent five population study (Model 2 in Pontzer et al., 2016). B, Mean (± standard deviation) TEE for male and female Shuar cohorts (black, S) compared to age- and anthropometrics-matched values for cohorts from Ghana (Gh), Jamaica (J), South Africa (SA), Seychelles (Sy) and the U.S. (US) reported in Pontzer et al. (2016). Standard deviations for non-Shuar cohorts were calculated using coefficients of variation for TEE reported for each cohort (Pontzer et al., 2016). C, Female (circles) and male (diamonds) cohort means for TEE and body mass. Subsistence populations (black closed symbols): S: Shuar (this study, outlined), A: Aymara (Kashiwazaki et al., 2009), H: Hadza hunter-gatherers (Pontzer et al., 2012), G: Gambian farmers (Heini et al., 1996; Singh et al., 1989), T: Tsimane (Gurven et al., 2016). Gray open symbols: comparative populations from industrialized societies (Dugas et al., 2011). Trend lines are ordinary least squares regressions for male (above) and female (below) cohorts from industrialized populations

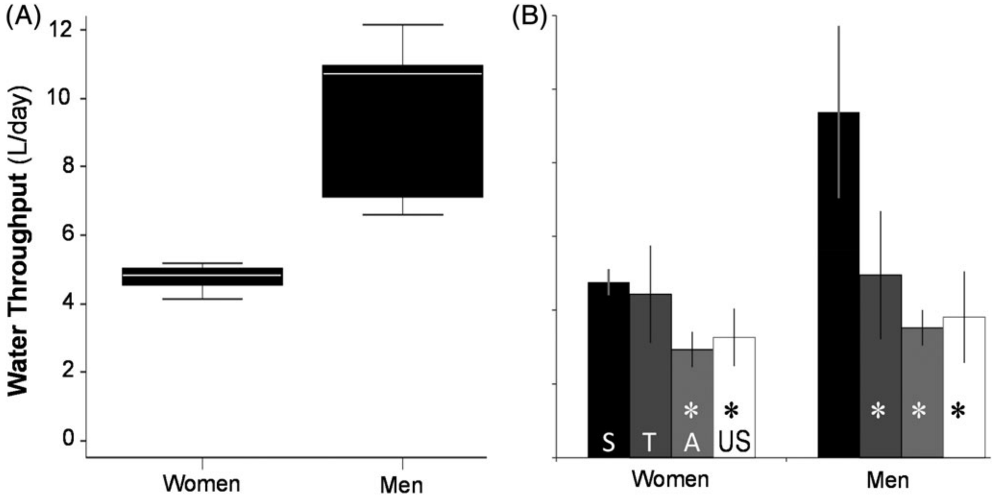

FIGURE 2 Daily water throughput (L/day). A, Boxplots (quartiles and median) of water throughput for Shuar men and women. B, Mean water throughput for Shuar adults compared Tsimane, T (Rosinger & Tanner, 2015), Aymara, A (Kashiwazaki et al., 2009), and U.S. (Raman et al., 2004) means. Asterisk (*) indicates significant difference from Shuar cohort. Error bars indicate ±1 SD. Note that Tsimane water throughput was estimated from interviews (Rosinger & Tanner, 2015)

Aymara men and women were similar in water throughput to U.S. cohorts ($P = 0.95$ and $P = 0.75$, respectively).

4 | DISCUSSION

Shuar men and women exhibited elevated TEE and water throughput compared to adults in industrialized societies. In particular, Shuar men had among the highest TEE and water throughput ever recorded outside of endurance competitions or other extreme physical events (eg, arctic trekking, cf. Cooper, Nguyen, Ruby, & Schoeller, 2011). The high TEE values of Shuar adults, particularly men, are largely attributable to their large body size and FFM (Table 1). However, even in analyses that control for size, Shuar TEE's were elevated. Only Gambian men, during the season of intensive agricultural labor, had equivalent PAL values (Heini et al., 1996). Shuar women had somewhat elevated TEE and water throughput relative to counterparts in industrialized societies, but were broadly similar to women in other subsistence populations. Together, results here are consistent with previous studies reporting elevated TEE among subsistence forager-farmers compared to those in industrialized societies (Gurven et al., 2016; Heini et al., 1996; Kashiwazaki, 1995; Kashiwazaki et al., 2009; Pontzer et al., 2012; Pontzer, 2015; Singh et al., 1989).

4.1 | Shuar activity and TEE

Elevated TEE and water throughput are most commonly thought to reflect high levels of physical activity (eg, Cooper et al., 2011; FAO/WHO/UNU, 2001; Kashiwazaki et al., 2009; Piperata & Dufour, 2005). The Shuar from the CC region in this study certainly appear to lead a physically demanding lifestyle, as judged by their TEE and PAL. Participants in this study continue to practice a mixed forager-horticulturalist subsistence strategy with some small scale agropastoral production, including the clearing of forest gardens with axes and machetes, planting and harvesting crops by hand, with a machete and digging stick, and trekking considerable distances through dense forest to hunt, fish or forage (Descola, 1994; Harner, 1984; Sugiyama, 2004).

SHLHP co-Director Sugiyama has worked annually in Shuar communities since 2005, with co-authors (Liebert, Madimenos, Urlacher, Bribiescas, Snodgrass) having worked nine field seasons among the Shuar. Among other work, this includes structured and semi-structured economic interviews from over 1000 households, direct and participant observation, households, and daily activity interviews, including in the current sample village (eg, Liebert et al., 2013; Madimenos et al. 2012; Urlacher et al., 2018), and countless hours of conversation about current Shuar life, including details of life in particular communities. First waking and afternoon salivary cortisol data collection and scheduling ($N = 298$ persons from six communities), testosterone collection ($N = 137$ men from 11 communities), and fecal samples ($N > 500$ from 13 communities) provided insight into Shuar daily activities, including observation of predawn and afternoon activities of almost 300 individuals from 6 communities, as did interviews and observations associated with fecal sample scheduling and data collection for some, including in the community reported here (eg, Cepon-Robins et al., 2014; Gildner et al., 2016; Liebert et al. (2013); Liebert et al., in prep).

Focal follows and measurement of food weights obtained and processed among closely related Shiwiar allow comparison with Shuar harvests and techniques (Sugiyama, 2004; Sugiyama & Chacon, 2000). Together, these provide a general picture of the typical Shuar workday, consistent with ethnographic reports from Shuar and closely related Achuar field studies (eg, Descola, 1994; Harner, 1984). For women, this usually includes getting up before dawn, stoking the fire, cooking, getting children ready for school if in session, and then going to their gardens. There, they dig up manioc and/or other root crops using a machete and digging stick, replant manioc stalks and weed around crops with a machete. They then carry 22-35 kg baskets of manioc and/or other products back from their gardens using a tumpline around their foreheads. Plantain bunches weigh 25-40 kg, but are more cumbersome to carry: men therefore often carry the larger bunches. Manioc is stripped of its outer skin and washed. They then cut it into chunks, boil it, then mash, and masticate it to make *nijiamanch* (*chicha*, manioc beer). In the study village, informants report that gardens are located from 0.5 to 6 hours walking distance from the community (trips to further gardens included overnight stays), with long walks to some gardens a consequence of limited arable land in the swampy region comprising this community's territory. Women sweep the house, weed and sweep the area around the house to maintain a bare earth yard. On laundry days they carry laundry to the river or spring in the afternoon, scrub the laundry by hand, whip it against a board, canoe, log or rocks if available, and then carry the wet load home to dry. When their husbands come home in the afternoon, women serve them chicha (*nijamanch*), and in the late afternoon prepare the evening meal. After they eat, they bathe if they have not done so earlier, and either go to bed or go visiting. Women's foraging for palm heart and palm grubs, and fishing is described below. If a woman has a baby, most activities are carried out while carrying the child. If the woman has a toddler, she may carry the toddler as well, particularly if any distance must be traveled.

Men typically also wake before dawn, drink chicha and often leave without eating. If they are tending one or more cows (often purchased by a wealthier *mestizo*, who splits the proceeds from the sale with the man who tends it), they are picketed in pastures up to 2 hours walk from the community. Checking on the cow involves untangling it from the picket rope if necessary, moving the animal to picket it in a new location with fresh forage, and making sure the animal has salt and water. This process is repeated in both the morning and evening. On days when men clear trees for gardens, they typically cut the large primary forest trees with an ax, while women clear the understory. When men hunt, they typically leave at dawn and walk, searching the forest for game and only stop to take a shot if game is encountered. If hunting with dogs (traditionally women ran the dogs, but men often do today) and giving chase, the hunter runs cross-country through the forest to keep the dogs within close earshot until the prey is cornered, goes to ground, or escapes. Hunting collared peccary (*Pecari tajacu*) often involves chasing them to ground, blockading entry to the burrow in which it has hidden with cut saplings, and killing the animal when it is agitated into charging or trying to escape. If monkeys are encountered (sometimes several times in a day), men will pursue them from the ground and will occasionally climb into the canopy on vines hanging from the tree to get a clear shot at them.

Men's household tasks also involve hard work. Shuar fire construction involves three logs, carried in from the garden and arranged with their ends close to touching, upon which the pot is set. Men prefer to make as few trips to haul firewood as possible, so they typically carry as heavy a load as possible that may include 3 m or longer sections of 30-40 cm diameter logs. On days when fish poison (*barbasco*) is used to fish a stream or river, both men and women may spend several hours walking or poling a canoe to the fishing location. They then dam the lower part of the run being fished, while others pound the baskets of *barbasco* root they have dug up the previous day. They then release the poison into the water upstream of the fishing run. Fishing is also done with hand lines or by stringing hooks. Both the men and women may then spend another 6-9 hours pursuing fish down the river or stream in ankle to chest high water. To acquire palm hearts or larvae (*mukindi*), men fell trees, then split the top apart to get at the heart, or split the fallen trunks to get at the palm larvae with axes. The palm tree has exceedingly hard, fibrous outer trunks (used in blowgun and lance manufacture, house post and wall material), so skill, finesse and power are necessary to fell or open the trees. Women sometimes perform this task, but it is more commonly done by men.

Our measures of TEE and estimates of PAL are consistent with the high levels of physical activity observed for Shuar adults. By contrast, estimates of physical activity (PAL) obtained via accelerometry from Shuar adults in the more market-integrated UV region are considerably lower (men: 1.54 ± 0.18, women: 1.42 ± 0.19, Madimenos et al., 2011). One possibility is that CC region Shuar are in fact much more active than their UV counterparts. However, studies of PAL among the other forager-horticulturalist Amazonians (Gurven et al., 2013) suggest that accelerometry may underestimate true PAL. While paired metabolic and accelerometry measures will be needed to resolve this issue, the metabolic measures here (TEE and PAL) certainly appear to correspond more closely to observed workload. These differences may also be explained by differences in workload and expenditure in each region. Regardless, results here highlight the potential lack of correspondence between accelerometry and energetics in ecological studies of small-scale societies.

We did not observe any sex difference in Shuar TEE in multiple regression analyses controlling for FFM. However, there is no overlap in male and female FFM, and it is possible that some of the apparent effect of FFM on TEE is due to sex differences in both measures. Consistent with this perspective, the effect of FFM (~80 kcal/kg) is approximately twice that reported in larger studies (eg, ~42 kcal/kg in Pontzer et al., 2016). Estimated PAL, which also provides a size-corrected measure of TEE, was significantly greater for

Shuar men than for women. Further, Shuar men's TEE was much greater compared to other populations, while Shuar women's TEE was only marginally elevated (Figure 1). On balance, the measures here suggest greater daily expenditure for Shuar men. This finding is consistent with that of Madimenos et al. (2011), which calculated significantly higher activity energy expenditure for UV Shuar males compared to females.

The high TEE reported for Gambian men, the only cohort measured to date with TEE and PAL similar to Shuar men, was measured during the peak period of agricultural activity (Heini et al., 1996). Similarly, Kashiwazaki et al. (2009) reported ~10-15% differences in TEE associated with the minimal seasonal changes in agricultural activity among Aymara pastoralists. It remains to be determined whether Shuar TEE shows similar seasonality. Access to fish and game does fluctuate depending on the season, but there are stable crops year round with garden clearings occurring every 3 years.

4.2 | Other potential contributors to TEE

Measurements of TEE and PAL among human populations suggest that daily energy expenditure varies little among populations despite large differences in daily physical activity (Dugas et al., 2011; Pontzer et al., 2012, 2015, 2016). From this perspective, the elevated TEE observed among Shuar men (and to a lesser extent, Shuar women) is unexpected. While high levels of physical activity likely contribute to greater TEE and PAL among the Shuar in this study, other factors should be considered as well.

Recent measurements from the Tsimane, a forager-horticulturalist population from the Amazonian rainforest in Bolivia, suggest pathogen burden may contribute to the elevated TEE observed among the Shuar in this study. Like the Tsimane and other Amazonian populations, the Shuar experience high rates of infectious and parasitic disease, with minimal access to modern healthcare (Cepon-Robins et al., 2014; Gildner et al., 2016; Jokisch & McSweeney, 2006; Urlacher et al., 2018). Among the Tsimane, pathogen burden and immune function biomarkers are positively associated with elevated BMR, which in turn largely accounts for the marginal elevation in TEE (Gurven et al., 2016). Measurements of BMR and immune activity among the Shuar are needed to determine what role immune function or other physiological activity plays in increasing TEE.

Chicha consumption could also contribute to elevated TEE, either by relaxing the constraint on TEE or through inducing thermogenesis. One hypothesis for the similarity in TEE observed among human populations is that TEE is constrained by perceived food energy availability (Pontzer, 2015, 2017). An easily digestible, readily available, and carbohydrate-rich drink like chicha may make more energy available than is typical for subsistence populations. Thermogenesis from fluid consumption could also increase TEE, accounting for some portion of the elevation in TEE observed in Shuar men in this study. However, as noted above, the thermogenic effects of fluid consumption are debated (Charrière et al., 2015), and the effect reported by Boschmann et al. (2003) might not be typical. Regardless of the mechanism, if chicha consumption does in fact contribute to TEE among the Shuar, it would help to explain the marked sex difference in TEE and PAL (Figure 1).

4.3 | Water throughput

Water throughput among Shuar men was remarkably high, well above levels observed in other populations (Figure 2). Given that water throughput is most strongly predicted by water intake (Raman et al., 2004), water throughput among Shuar men is undoubtedly related to the consumption of chicha, the only beverage that was consumed in notable amounts. Mean water throughputs for men (9.37 ± 2.34 L/day) and women (4.76 ± 0.36 L/day) in this study are consistent with Harner's (1984) estimates of men's (11.4-15.1 L/d) and women's (3.8-7.6 L/d) consumption of chicha (which is mostly water) in his ethnographic study of the Shuar. It is possible that these high levels of throughput, driven by high levels of fluid consumption, reduce the risk and prevalence of dehydration among Shuar, which has been shown to affect other Amazonian forager-horticulturalists (Rosinger, 2015). We note, however, that comparisons with Tsimane water throughput must be interpreted cautiously given the differences in methodologies between studies.

4.4 | Limitations

Limitations to this study include the small sample size, limited time frame (only one season was examined), and lack of measured activity data. The limitation imposed by small sample size is compounded by the atypically large body sizes in this sample and high-water throughputs, particularly for Shuar men. Additionally, the lack of BMR measurements prevents us from testing for elevated BMR due to pathogen burden, as shown among the Tsimane (Gurven et al., 2016). Furthermore, due to the lack of BMR measurements, we rely on estimates of PAL here. Additional work is needed to measure TEE, BMR, water throughput, and activity in other seasons and across a broader range of ages and conditions.

4.5 | Conclusion

Like some other subsistence farming populations (eg, Aymara), Shuar adults expend more energy each day than counterparts in more sedentary, industrialized societies. While strenuous physical activity likely plays a role in shaping these elevated energy expenditures, the influence of other factors (eg, immune function, water throughput, food energy availability) warrants further study. In light of the more moderate energy throughput reported for hunter-gatherers (Pontzer et al., 2012), elevated TEE among the

Shuar and other subsistence forager-horticulturalist groups is consistent with the view that the transition to agriculture may have been accompanied by greater energy availability and increased energy demand. Measurements of energy expenditure across other farming and foraging groups, in concert with additional archeological investigation of early agricultural economies, may address this hypothesis.

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CONFLICT OF INTEREST

There is no conflict of interest.

ORCID

Herman Pontzer https://orcid.org/0000-0003-2397-6543

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