

Childhood Daily Energy Expenditure Does Not Decrease with Market Integration and Is Not Related to Adiposity in Amazonia

Samuel S Urlacher,^{1,2} J Josh Snodgrass,^{3,4} Lara R Dugas,⁵ Felicia C Madimenos,⁶ Lawrence S Sugiyama,³ Melissa A Liebert,⁷ Cara J Joyce,⁵ Enrique Terán,⁸ and Herman Pontzer^{9,10}

¹Department of Anthropology, Baylor University, Waco, TX, USA; ²Child and Brain Development Program, CIFAR, Toronto, Ontario, Canada; ³Department of Anthropology, University of Oregon, Eugene, OR, USA; ⁴Center for Global Health, University of Oregon, Eugene, OR, USA; ⁵Department of Public Health Sciences, Loyola University Chicago, Chicago, IL, USA; ⁶Department of Anthropology, Queens College, Queens, NY, USA; ⁷Department of Anthropology, Northern Arizona University, Flagstaff, AZ, USA; ⁸College of Health Sciences, Universidad San Francisco de Quito, Quito, Ecuador; ⁹Department of Evolutionary Anthropology, Duke University, Durham, NC, USA; and ¹⁰Duke Global Health Institute, Duke University, Durham, NC, USA

ABSTRACT

Background: Childhood overweight and obesity (OW/OB) is increasingly centered in low- and middle-income countries (LMICs) as rural populations experience market integration and lifeway change. Most explanatory studies have relied on imprecise estimates of children's energy expenditure, restricting understanding of the relative effects of changes in diet and energy expenditure on the development of OW/OB in transitioning contexts.

Objectives: This study used gold-standard measurements of children's energy expenditure to investigate the changes that underlie OW/OB and the nutrition/epidemiologic transition.

Methods: Cross-sectional data were collected from "rural" ($n = 43$) Shuar forager-horticulturalist children and their "peri-urban" ($n = 34$) Shuar counterparts (age 4–12 y) in Amazonian Ecuador. Doubly labeled water measurements of total energy expenditure (TEE; kcal/d), respirometry measurements of resting energy expenditure (REE; kcal/d), and measures of diet, physical activity, immune activity, and market integration were analyzed primarily using regression models.

Results: Peri-urban children had higher body fat percentage (+8.1%, $P < 0.001$), greater consumption of market-acquired foods (multiple $P < 0.001$), lower concentrations of immune activity biomarkers (multiple $P < 0.05$), and lower REE (−108 kcal/d, $P = 0.002$) than rural children. Despite these differences, peri-urban children's TEE was indistinguishable from that of rural children ($P = 0.499$). Moreover, although sample-wide IgG concentrations and household incomes predicted REE (both $P < 0.05$), no examined household, immune activity, or physical activity measures were related to children's overall TEE (all $P > 0.09$). Diet and energy expenditure associations with adiposity demonstrate that only reported consumption of market-acquired "protein" and "carbohydrate" foods predicted children's body fat levels (multiple $P < 0.05$).

Conclusions: Despite underlying patterns in REE, Shuar children's TEE is not reliably related to market integration and—unlike dietary measures—does not predict adiposity. These findings suggest a leading role of changing dietary intake in transitions to OW/OB in LMICs. *J Nutr* 2021;151:695–704.

Keywords: obesity, nutrition transition, economic development, doubly labeled water, Ecuador

Introduction

The epidemic of overweight and obesity (OW/OB) is increasingly affecting children. In 2016, it was estimated that 18% of all school-age children and adolescents globally were OW/OB, up from only 4% in 1975, and with prevalence reaching 65% in some countries (1). Troublingly, children who are OW/OB are likely to remain OW/OB into adulthood and present greater long-term risk of developing noncommunicable diseases,

such as type 2 diabetes and heart disease (2). These findings demonstrate the importance of preventing childhood OW/OB for promoting lifelong health and well-being.

Childhood OW/OB is no longer limited to wealthy populations. The most rapid rise is now in low- and middle-income countries (LMICs), those with populations experiencing increasing engagement with market-based economies (i.e., "market integration") and associated lifeway changes (3, 4). Like models for the adult nutrition and epidemiologic

transition (5, 6), models for childhood OW/OB typically identify diet and physical activity as the primary ecological factors moderating risk (7, 8). These models are inherently energetic in nature, implying that increasingly sedentary lifestyles—lowering daily total energy expenditure (TEE; kcal/d)—and greater dependency on high-calorie, market-acquired diets—increasing daily energy intake—act in tandem to promote positive energy imbalance and body fat accrual in LMICs. Combined with technological and infrastructure advancements that reduce pathogen burden and immune activity (e.g., access to clean water), these energetic changes are thought to ultimately drive the epidemiologic transition from infectious to noncommunicable diseases (5, 9).

Problematically, the relative importance of changes in diet, physical activity, and immune activity on the development of OW/OB and noncommunicable diseases in LMICs remains contested. Subsistence-based rural populations are typically far more physically (10, 11) and immunologically (12) active than urban and industrialized populations. However, recent measurements of free-living TEE suggest that adults living in these populations do not expend more calories each day than their more market-integrated counterparts (13, 14). Similar measurements of energy expenditure among children in LMICs have been overwhelmingly restricted to urban contexts (15), limiting understanding of the energetics of childhood OW/OB during the critical early transition from a rural, subsistence-based to a market-based lifestyle.

We recently reported measurements of children's energy expenditure among Shuar forager-horticulturalists of Amazonian Ecuador that challenged the standard model for the transition to childhood OW/OB (16). Despite having a heavy burden of infectious disease and significantly greater physical activity than children living in industrialized populations, rural Shuar children's TEE, measured using the gold-standard doubly labeled water (DLW) method, was indistinguishable from that of more overweight children in the United States and United Kingdom. This finding suggests that changes in diet, not reduced energy expenditure, may best explain the transition to positive energy imbalance and OW/OB in LMICs. Although suggestive, this initial study was limited by its comparison of genetically, culturally, and geographically dissimilar populations on the far ends of the economic development spectrum, preventing examination of within-population energetic changes during market integration and epidemiologic transition. The study was also limited by an inability to investigate relationships between specific aspects of market integration, energy expenditure, and children's adiposity.

Here, we build on previous work among the Shuar to provide the first within-population investigation of measured children's energy expenditure during early market integration and transition to OW/OB. We capitalize on a peri-urban/rural data set that includes DLW-based measurements of TEE and

respirometry-based measurements of resting energy expenditure (REE; kcal/d) to test common energetic assumptions for children's nutrition and epidemiologic transition. We have 3 main objectives: 1) to examine peri-urban/rural differences in children's market integration, diet, energy expenditure, and body fat levels; 2) to determine how variation in market integration, physical activity, and immune activity predict children's energy expenditure; and 3) to investigate the relative effects of variation in energy expenditure and the consumption of market-acquired foods on children's adiposity.

Methods

Study communities and participants

The Shuar are an Indigenous population from Amazonian Ecuador and Peru. Like many other Amazonian populations, Shuar are currently experiencing varying degrees of economic development and integration into the wider regional/global market economy (17–19). This study was performed under the Shuar Health and Life History Project (<https://www.shuarproject.org/>), established in Ecuador in 2005. Data were collected from 1 “rural” and 1 “peri-urban” community during the annual dry seasons in 2016 and 2017, respectively. The rural Shuar community and sample have previously been described (16). The community is composed of ~300 individuals and is located in the remote cross-Cutucú geographic region. It is accessible only by canoe or trail and has no running water or health clinic. Integration into the market economy is limited, and community members continue to rely heavily on subsistence horticulture, hunting, fishing, and foraging. Parasitic infectious disease rates among children are high (20, 21). In contrast, the peri-urban Shuar community is within a rapidly growing regional market center of ~11,000 individuals, with both Shuar and non-Shuar residents. It is connected by roadways to major cities and has central electricity and plumbing, a hospital, restaurants, and numerous other market amenities.

All prepubertal children aged 4–12 y residing in the rural community were invited with their parents to participate in this study. Recruitment in the peri-urban community was done at a bilingual Shuar primary school, with all parent-identifying Shuar prepubertal children aged 4–12 y invited to participate. The overall participation rate was ~95%, with a final recruited sample of 44 rural and 34 peri-urban children. Participation was voluntary, and parental written informed consent with child informed assent was obtained from all participants. Study methods and procedures were approved and conducted in accordance with guidelines set by community and school leaders, the *Federación Interprovincial de Centros Shuar*, and the Committee on the Use of Human Subjects Institutional Review Boards of the University of Oregon and the City University of New York.

Data collection

Data collection protocols were identical for the 2 community-based samples and involved a 14-d study period. Measures collected at multiple time points on study days 0, 7, and 14 (see below) were averaged to provide a uniform cross-sectional data set. A short medical review was taken from parents, and participants were found to be generally healthy (i.e., no known medical conditions) and nonmedicating. Participants' current health status was monitored over the duration of the study period by weekly investigator-initiated observations and body temperature assessment using a tympanic thermometer (Welch Allyn Thermoscan Pro 6000; mean \pm SD = 37.0 \pm 0.3°C, range = 36.6–37.7°C). No cases of acute illness were detected.

Market integration.

Household market integration data were collected via structured interviews with parents as previously described (17, 18). Total number of household residents was recorded. Household income (US\$/mo) was calculated as the total reported monthly cash earnings for all members of a household from any activity (e.g., wage labor or produce sales), averaged across the previous year. Additional basic household

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Supplemental Tables 1–8 and Supplemental Figures 1 and 2 are available from the “Supplementary data” link in the online posting of the article and from the same link in the online table of contents at <https://academic.oup.com/ijn>.

Address correspondence to SSU (e-mail: samuel_urlacher@baylor.edu).

Abbreviations used: AEE, activity energy expenditure; BF%, body fat percentage; CRP, C-reactive protein; DBS, dried blood spot; DLW, doubly labeled water; FFM, fat-free mass; FM, fat mass; FQ, food quotient; LMIC, low- and middle-income country; MVPA, moderate-vigorous physical activity; OB, obese/obesity; OW, overweight; PAL, physical activity level; REE, resting energy expenditure; SedPA, sedentary physical activity; TEE, total energy expenditure.

information was collected, including report of having a dirt floor (yes/no), running water (yes/no), and access to a latrine/toilet (yes/no).

Diet—market-acquired item consumption.

Diet was assessed at the household level with parents using a 30-item FFQ developed specifically for the Shuar (18). Reported consumption frequency of all market-acquired food items (i.e., those requiring purchase) was summed. Following previous analysis among the Shuar (17) and other developing Amazonian populations (22), market-acquired item consumption was also divided into specific food groups relating to market “carbohydrates” (i.e., rice, pasta, and bread), market “proteins” (i.e., beef, pork, and milk), and market “fats/sugars” (i.e., soda, potato chips, butter, oil, and cookies and sweets).

Anthropometry and daily physical activity.

Height (Seca 214) and weight (Tanita BF-689) were measured at enrollment, and BMI (in kg/m^2) was subsequently calculated. Physical activity was assessed for a random subsample of children ($n = 25$ peri-urban, $n = 30$ rural, assigned with a randomizer) over the complete 14-d study period using waterproof Actical triaxial accelerometers (Phillips Respironics) worn continuously at the right hip. Valid accelerometer days were defined by wear time ≥ 10 h/d, as determined using a common macro program (11). All children had ≥ 3 valid days of data (mean \pm SD = 12.8 ± 3.3 d), reflecting ≥ 12.8 h/d wear time (mean \pm SD = 15.7 ± 2.1 h/d). Time spent in moderate-vigorous physical activity (MVPA) and sedentary physical activity (SedPA) were determined using child-specific activity count cutoffs with 1-min bins (23).

TEE and body composition.

Free-living TEE and body composition were measured using the DLW method (24), as previously described for the rural sample (16). Briefly, oral doses of DLW (6% $^2\text{H}_2\text{O}$, 10% H_2^{18}O , tailored to body weight) were given to children on day 0. Associated urine samples were collected before dosing, ~ 6 h postdose, and on \sim days 3, 7, and 11. Once collected, samples were stored at -20°C and then shipped to the United States for the measurement of ^2H and ^{18}O isotope enrichment using cavity ring-down spectroscopy (Picarro L2120i) in the Human Evolution and Energetics Lab at Hunter College. Isotope depletion rates and dilution spaces were calculated using the slope-intercept method, with rate of carbon dioxide production determined using a 2-pool approach (24). Production of carbon dioxide was converted to TEE using a food quotient (FQ) of 0.93 for the rural sample (16), equivalent to the mean FQ estimated for subsistence-based Amazonian populations (25) and conservative for the present analysis. Similarly, a conservative FQ of 0.89 was used for the peri-urban sample, reflecting the value reported for moderately market-integrated Mosenen indigenous Amazonians (26). Fat-free mass (FFM) was calculated using a hydration constant of 0.73 (16), with fat mass (FM) and body fat percentage (BF%) subsequently determined from total body mass. As reported previously (16), the reliability of 6 TEE and body composition measurements was confirmed against duplicate isotope ratio MS measurements at an external DLW lab (between assay $\text{CV}_{\text{TEE}} = 2.0\%$, $\text{CV}_{\text{FFM}} = 0.3\%$).

REE.

Children's REE was measured using a QuarkRMR respirometry system (COSMED) on 3 separate occasions (days 0, 7, and 14) and results were averaged to provide a final REE measurement (16). Eight children (5 rural and 3 peri-urban) were measured only twice. Measurements were made in a quiet room and in the supine position using a canopy hood, with parents nearby. All measurements were made under careful observation in the morning (mean time \pm SD = $06:28 \pm 0:40$), after an overnight fast for ≥ 8 h, and before strenuous physical activity. Device calibration was performed before each measurement using a manufacturer-provided standard gas mixture and volume syringe. Children's oxygen consumption and carbon dioxide production were recorded for ≥ 30 min, with the initial 10 min of data discarded and the remaining steady-state period averaged to facilitate calculation of REE using the modified Weir equation (24).

Immune activity.

Immune activity was assessed using minimally invasive finger-prick dried blood spot (DBS) samples, as previously described for Shuar children (16, 27, 28). Samples were collected on days 0, 7, and 14 following standard procedures (29) and were stored at -20°C until shipment to the United States for -30°C storage and analysis in the Global Health Biomarker Laboratory at the University of Oregon. Concentration of C-reactive protein (CRP)—a measure of nonspecific inflammation (30)—was determined using a modified high-sensitivity DBS ELISA protocol (31). Concentrations of total IgG—the dominant class of circulating antibody in humans (30)—and total IgE—the class of antibody produced predominantly in response to microparasite infection (30)—were determined using commercial ELISA kits (Bethyl Laboratories) validated for use with DBS. Samples were measured in duplicate with multilevel controls and met performance standards (Supplemental Table 1). Final IgG and IgE values were the mean of children's weekly measures. Owing to its highly acute nature among Shuar children (27), serum-equivalent CRP concentration was treated as a binary variable indicating either presence ($\text{CRP} \geq 1$ mg/L) or absence ($\text{CRP} < 1$ mg/L) of acute inflammatory response (27, 32) on any 1 of a child's 3 repeated weekly measurements.

Data analysis

Child activity energy expenditure (AEE; kcal/d) was calculated as $\text{TEE} - (\text{REE} + 0.1\text{TEE})$, with 0.1TEE representing the generally stable thermic effect of food (33). Child physical activity level (PAL—a measure of physical activity energy allocation) was calculated as AEE/TEE (33). Age- and sex-specific z scores were calculated for height (height- z), weight (weight- z), and BMI (BMI- z) using WHO growth standards (34) and for BF% (BF%- z) using available NHANES references (35). The normality of all data was assessed by numerical and graphical methods. When necessary, nonnormal data were log transformed or analyzed as tertiles. One rural child was removed from the analysis owing to outlying body fat level (BF%- $z = -6.47$), providing a final sample size of 43 rural and 34 peri-urban children. This removal was conservative and had no impact on the overall results of the analysis. There were no missing data.

Peri-urban/rural differences in study measures (Objective 1) were examined using t tests and chi-square tests (for unadjusted measures) or linear regression and logistic regression models (for measures adjusted for confounding effects). Chi-square tests with zero-value cells were simulated 2000 times. Predictors of energy expenditure (Objective 2) and adiposity (Objective 3) across the complete data set were examined using linear regression models (for models with individual-level predictors only) and multilevel linear mixed-effects models (for models that included household-level predictors). Post hoc diagnostics indicated acceptable degrees of linearity, heteroscedasticity, and multicollinearity for all final models. Model fit was assessed using residual sum of squares and, in the case of multilevel models, conditional r^2 values (36). Analyses were performed in R (cran.us.r-project.org/), with results considered significant at $P < 0.05$.

Results

Peri-urban children were more market-integrated, consumed more market-acquired foods, and had greater adiposity and prevalence of overweight than rural children

Peri-urban households had fewer residents [$t(27.78) = 3.18$, $P = 0.004$] (Table 1), were less likely to have a dirt floor [$\chi^2(1, n = 39) = 5.2$, $P = 0.038$], were more likely to have running water [$\chi^2(1, n = 39) = 23.255$, $P < 0.001$], and reported nearly 3 times the monthly income of rural households [$t(32.92) = -3.38$, $P = 0.002$]. This greater level of economic development and market integration was associated with 311% greater reported consumption of market-acquired food items [$t(34.72) = -7.30$, $P < 0.001$], reflecting greater consumption of all 3 examined market dietary categories

TABLE 1 Measures of interest for rural and peri-urban children¹

| | Rural children (<i>n</i> = 43) | Peri-urban children (<i>n</i> = 34) | Peri-urban/rural difference ² |
|--|------------------------------------|---|---|
| Participant characteristics | | | |
| Sex, female | 51 | 50 | ns |
| Age, y | 8.1 ± 2.1 | 8.1 ± 2.3 | ns |
| Anthropometry ³ | | | |
| Stature, cm | 119.5 (117.9, 121.1) | 120.5 (118.6, 122.3) | ns |
| Body mass, kg | 23.9 (22.7, 25.2) | 25.8 (24.4, 27.2) | ns |
| BMI, kg/m ² | 16.6 (16.1, 17.1) | 17.2 (16.7, 17.7) | ns |
| Fat-free mass, ⁴ kg | 20.4 (19.7, 21.1) | 19.2 (18.5, 20.0) | −1.2* |
| Fat mass, ⁴ kg | 2.9 (2.7, 3.2) | 5.0 (4.5, 5.6) | +2.1*** |
| Body fat percentage, ⁴ % | 12.5 (11.6, 13.4) | 20.6 (18.9, 22.3) | +8.1*** |
| Growth and nutritional status | | | |
| Height <i>z</i> score | −1.32 ± 0.90 | −1.23 ± 0.94 | ns |
| Weight <i>z</i> score | −0.36 ± 0.69 | −0.16 ± 1.02 | ns |
| BMI <i>z</i> score | 0.38 ± 0.64 | 0.56 ± 0.78 | ns |
| Body fat percentage <i>z</i> score | −0.95 ± 0.90 | 0.56 ± 0.67 | +1.51*** |
| Household | | | |
| Income, \$/mo | 92 ± 161 | 253 ± 132 | +161** |
| Residents, <i>n</i> individuals | 7.4 ± 2.4 | 5.4 ± 1.5 | −2.1** |
| Dirt floor, yes | 22 | 0 | −4.1 OR* |
| Running water, yes | 0 | 76 | +82.2 OR*** |
| Latrine/toilet, yes | 33 | 62 | ns |
| Diet—market-acquired food consumption | | | |
| Total items, <i>n</i> /d | 0.9 ± 0.9 | 3.7 ± 1.4 | +2.8*** |
| “Carbohydrate” items, <i>n</i> /d | 0.3 ± 0.5 | 1.9 ± 0.6 | +1.6*** |
| “Protein” items, <i>n</i> /d | 0.2 ± 0.3 | 0.7 ± 0.4 | +0.5*** |
| “Fat and sugar” items, <i>n</i> /d | 0.4 ± 0.5 | 1.1 ± 0.8 | +0.7** |
| Immune activity ³ | | | |
| C-reactive protein ≥1 mg/L, yes | 37.2 | 32.4 | ns |
| IgG, ⁴ g/L | 7.5 (7.1, 8.0) | 6.7 (6.3, 7.2) | −0.8* |
| IgE, ⁴ ng/mL | 8958 (6703, 11,971) | 4706 (3396, 6519) | −4252** |
| Physical activity ⁵ | | | |
| Accelerometer wear time, h/d | 16.4 (15.7, 17.1) | 14.8 (14.0, 15.5) | −1.6** |
| Activity counts, ⁴ counts/min | 446 (413, 481) | 436 (400, 474) | ns |
| Moderate-vigorous activity, ⁴ min/d | 78 (71, 87) | 80 (71, 89) | ns |
| Sedentary activity, min/d | 232 (221, 243) | 239 (227, 251) | ns |
| Energy expenditure and allocation ⁶ | | | |
| Total energy expenditure, kcal/d | 1824 (1768, 1880) | 1789 (1724, 1855) | ns |
| Resting energy expenditure, kcal/d | 1252 (1215, 1288) | 1143 (1100, 1187) | −108** |
| Activity energy expenditure, kcal/d | 391 (338, 444) | 466 (403, 528) | ns |
| Physical activity level | 1.45 (1.40, 1.50) | 1.56 (1.50, 1.63) | +0.11* |

¹Values are percentages, mean ± SD, or mean (95% CI) unless indicated otherwise.

²Group-level differences in 2-tailed *t* tests, chi-square tests, or regression models. ns, nonsignificant (*P* > 0.05).

³Values are adjusted for child age and sex.

⁴Values are back-converted from analysis of log-transformed measures.

⁵Values are for an accelerometry subsample of *n* = 25 peri-urban and *n* = 30 rural children, with activity values adjusted for child age, sex, and accelerometer wear time.

⁶Values are adjusted for child age, sex, fat mass, and fat-free mass. Values for REE, AEE, and PAL are also adjusted for REE measurement time.

****Significant difference: **P* < 0.05, ***P* < 0.01, ****P* < 0.001.

(“carbohydrates,” “proteins,” and “fats/sugars”; all *P* < 0.01) (Table 1).

Accompanying these differences, peri-urban children had greater adiposity as assessed by BF%-*z* [*t*(77) = 8.41, *P* < 0.001] and raw body fat measures (Table 1). Models adjusting for age and sex demonstrated that peri-urban children had 8.1-units greater BF% ($\beta = 0.50$, SE = 0.06, *P* < 0.001), reflecting a 65% relative increase in mean body fat. Whereas all rural children had normal adiposity, more than one-third (36%) of peri-urban children were “overweight” (i.e., BF% ≥ NHANES 85th

percentile). No children were “obese” (i.e., BF% ≥ NHANES 95th percentile). No differences were detected in overall body size and growth, with both groups of children having similar height-*z*, weight-*z*, and BMI-*z* measures (all *P* > 0.2) (Table 1).

Peri-urban children had lower REE than rural children but had similar TEE

Peri-urban children had 108-kcal/d or 9% lower REE after adjusting for age, sex, FFM, FM, and REE measurement time ($\beta = -108$, SE = 34, *P* = 0.002) (Figure 1, Table 1, Supplemental

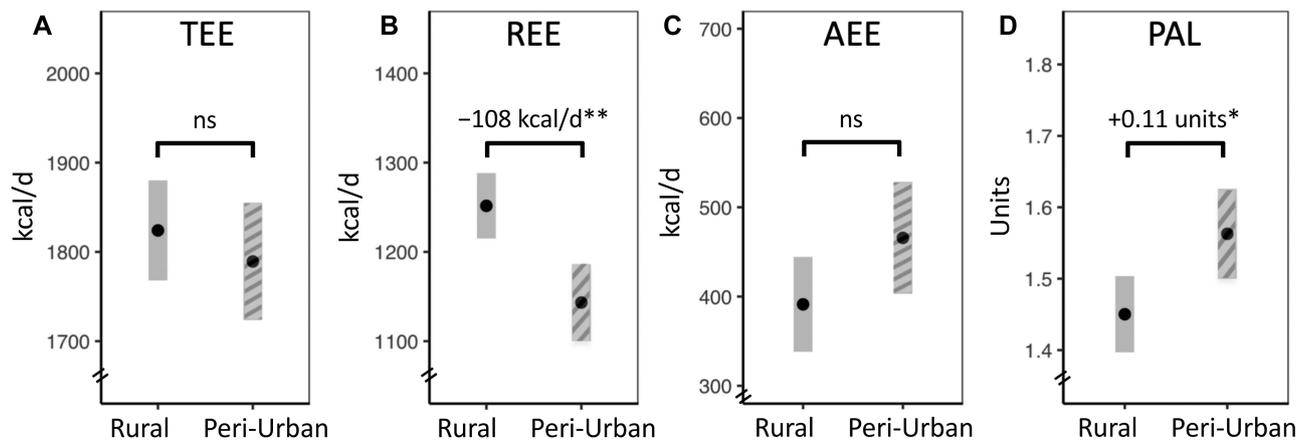


FIGURE 1 Energy expenditure (A–C) and allocation (D) measures for rural ($n = 43$) and peri-urban ($n = 34$) children. Group estimated marginal means, with shaded 95% CIs, from linear regression models adjusting for age, sex, fat-free mass, and fat mass. Models for REE, AEE, and PAL also adjusted for REE measurement time. Peri-urban children’s TEE was indistinguishable from that of rural children, despite significantly lower measured REE. See text for alternative models with similar results. **, Significant difference between groups: * $P < 0.05$, ** $P < 0.01$. AEE, activity energy expenditure; ns, nonsignificant ($P > 0.05$); PAL, physical activity level; REE, resting energy expenditure; TEE, total energy expenditure.

Table 2). However, there was no TEE difference between the peri-urban and rural cohorts when similarly adjusting for age, sex, FFM, and FM ($\beta = -35$, SE = 51, $P = 0.499$) (Figure 1, Table 1, Supplemental Table 2). These results were consistent in alternative models using variable FQs in TEE calculations (Supplemental Table 3). They were also consistent in alternative 3-group models that included published data for US/UK children (37, 38) that were previously used for comparison with Shuar (16). Notably, in 3-group comparisons, peri-urban children had REE values that were intermediate between rural and industrialized children, yet TEE remained indistinguishable between the 3 cohorts (Figure 2, Supplemental Table 4).

Peri-urban children had lower immune activity than rural children but had similar levels of physical activity

Peri-urban children had 16% lower concentrations of IgG ($\beta = -0.11$, SE = 0.05, $P = 0.023$) (Table 1) and 47% lower concentrations of IgE ($\beta = -0.64$, SE = 0.22, $P = 0.004$) (Table 1) in models adjusting for age and sex. There was no group difference in likelihood of CRP elevation ($\beta = -0.21$, SE = 0.49, $P = 0.666$) (Table 1).

In contrast to general immune activity differences, peri-urban and rural children had similar levels of accelerometer-measured physical activity. There was no detected group difference in counts per minute ($\beta = -0.02$, SE = 0.06, $P = 0.707$), MVPA ($\beta = 0.02$, SE = 0.08, $P = 0.828$), or SedPA ($\beta = 7.34$, SE = 8.44, $P = 0.389$) in models adjusting for age, sex, and accelerometer wear time (Table 1). Likewise, no group difference was found for peri-urban (17 of 25) and rural (27 of 30) children’s likelihood to meet WHO guidelines (39) for 60 min MVPA/d ($\beta = -1.25$, SE = 0.91, $P = 0.169$). Accelerometry-based measures of physical activity were consistent with calculated AEE indexes, such that no peri-urban/rural difference was detected in AEE ($\beta = 74$, SE = 49, $P = 0.136$) (Figure 1, Table 1, Supplemental Table 2). However, as a result of lower measured REE yet similar measured TEE, peri-urban children’s PAL was 0.11 units greater than that of rural children ($\beta = 0.11$, SE = 0.05, $P = 0.026$) (Figure 1, Table 1, Supplemental Table 2).

Children’s REE was related to IgG concentration and household income, but overall TEE was not predicted by household, immune activity, or physical activity measures

Across the sample, REE was negatively related to household income, such that children living in households in the top income tertile had 85-kcal/d lower REE than those in the bottom tertile ($\beta = -85$, SE = 36, $P = 0.023$) (Table 2, Supplemental Figure 1, Supplemental Table 5). Children’s REE was also positively related to immune activity, such that a 1-SD increase in log IgG was related to a 32-kcal/d increase in REE ($\beta = 147$, SE = 56, $P = 0.010$) (Table 2, Supplemental Figure 1, Supplemental Table 5).

Despite these findings for REE, no examined household, immune activity, or physical activity measures were related to children’s overall TEE (all $P > 0.09$) (Table 2, Supplemental Figure 2, Supplemental Table 5). Physical activity measures were similarly not related to AEE or PAL (all $P > 0.4$) (Table 2, Supplemental Table 5), although a positive effect of income on calculated AEE and PAL was detected (Table 2, Supplemental Table 5). These findings were consistent in alternative models including peri-urban/rural group as an additional covariate (Supplemental Table 6).

Children’s adiposity was related to reported market-acquired food consumption but not to TEE or PAL

Dietary factors predicted children’s adiposity across the entire sample (Table 3, Supplemental Table 7). Reported overall consumption of market-acquired diet items was not related to children’s BF%-z in models adjusting for peri-urban/rural group ($\beta = 0.06$, SE = 0.09, $P = 0.512$). However, analysis of specific categories of market-acquired items revealed significant underlying relationships. Reported market-acquired “protein” item consumption was positively related to measures of adiposity, such that children from households in the middle and upper tertiles of reported consumption had BF%-z scores that were 0.88 (SE = 0.25, $P = 0.001$) and 0.96 (SE = 0.31, $P = 0.005$) units greater, respectively, than that of children in the lower tertile (Figure 3A). In contrast, reported market-acquired “carbohydrate” item consumption was negatively related to

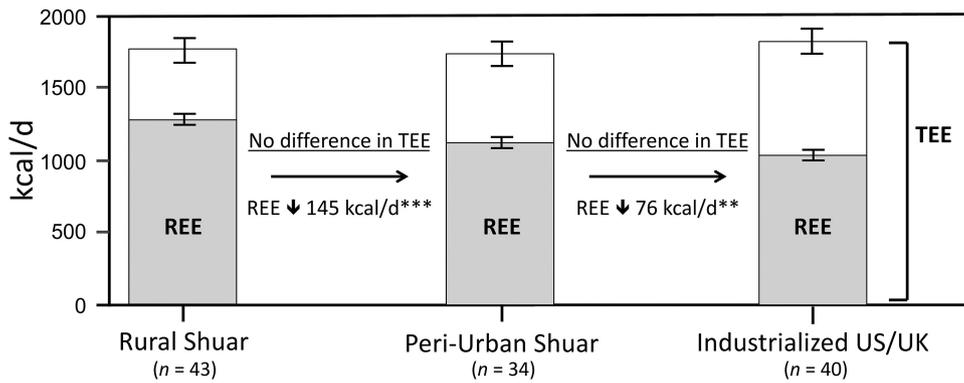


FIGURE 2 Energy expenditure profiles for rural, peri-urban, and comparative industrialized children. Group estimated marginal means, with bracketed 95% CIs, from 3-group linear regression models adjusting for age, sex, fat-free mass, and fat mass. No group differences were found in TEE ($P > 0.05$). However, peri-urban children's REE was intermediate between those of rural and industrialized children. See text for alternative models with similar results. ***,***Significant difference between groups: ** $P < 0.01$, *** $P < 0.001$. REE, resting energy expenditure; TEE, total energy expenditure.

measures of adiposity, such that children from households in the middle and upper tertiles of consumption had BF%-z scores that were 0.63 ($\beta = -0.63$, $SE = 0.26$, $P = 0.026$) and 0.80 ($\beta = -0.80$, $SE = 0.38$, $P = 0.049$) units lower, respectively, than that of children in the lower tertile (Figure 3B). These findings were consistent in models that included additional household-level covariates, such as income and number of residents (Supplemental Table 8).

In contrast to market dietary factors, children's energy expenditure and allocation measures were not significantly related to adiposity in any examined model (Figure 3C, D, Table 3, Supplemental Table 7). This null finding was consistent in models predicting children's BF%-z using both TEE ($\beta = -0.0002$, $SE = 0.0004$, $P = 0.680$) and PAL (although the relationship approached significance: $\beta = -1.14$, $SE = 0.63$,

$P = 0.073$). It was also consistent in alternative models that included household income and number of residents as additional covariates (Supplemental Table 8).

Discussion

This study found that relatively market-integrated, peri-urban Shuar children do not expend fewer calories each day than their leaner rural counterparts. It also found that reported consumption of market-acquired foods, but not traditional energy expenditure and allocation risk factors for OW/OB (i.e., TEE and PAL, respectively), is reliably related to children's adiposity. Together, these results provide evidence supporting the view that changing dietary intake, rather than reduced daily

TABLE 2 Predictors of children's energy expenditure and allocation measures¹

| | REE, kcal/d | TEE, kcal/d | AEE, kcal/d | PAL |
|--|-------------|-------------|--------------|---------------|
| Household model | | | | |
| Income, \$/mo | | | | |
| Tertile 2 | -60 ± 37 | 68 ± 58 | 126 ± 49* | 0.14 ± 0.05** |
| Tertile 3 | -85 ± 36* | -4 ± 56 | 86 ± 48 | 0.11 ± 0.05* |
| Residents, <i>n</i> individuals | 2 ± 9 | 11 ± 15 | 9 ± 13 | 0.00 ± 0.01 |
| Dirt floor, yes | -42 ± 45 | -42 ± 71 | 7 ± 59 | 0.07 ± 0.06 |
| Running water, yes | -40 ± 46 | 28 ± 71 | 70 ± 62 | 0.01 ± 0.04 |
| Latrine, yes | -19 ± 32 | -28 ± 50 | -9 ± 43 | 0.03 ± 0.04 |
| Model conditional <i>r</i> ² | 0.829 | 0.884 | 0.714 | 0.611 |
| Immune activity model ² | | | | |
| C-reactive protein ≥1 mg/L, yes | 1 ± 24 | -23 ± 35 | — | — |
| Log IgG, g/L | 147 ± 56** | 82 ± 80 | — | — |
| Log IgE, ng/mL | 2 ± 13 | 33 ± 19 | — | — |
| Model adj. <i>r</i> ² | 0.737 | 0.842 | — | — |
| Physical activity (accelerometry) model ³ | | | | |
| Log moderate-vigorous PA, min/d | — | -8 ± 86 | -56 ± 77 | -0.01 ± 0.07 |
| Sedentary PA, min/d | — | 0.62 ± 0.80 | -0.02 ± 0.71 | -0.00 ± 0.00 |
| Model adj. <i>r</i> ² | — | 0.860 | 0.634 | 0.448 |

¹ $n = 77$. Values are $\beta \pm SE$ from multilevel and multivariate linear regression models adjusted for age, sex, fat-free mass, and fat mass. Models for REE, AEE, and PAL also adjusted for REE measurement time. Models for PA also adjusted for device wear time. See text for alternative models with similar results. AEE, activity energy expenditure; PA, physical activity; PAL, physical activity level; REE, resting energy expenditure; TEE, total energy expenditure.

² Immune markers measured in finger-prick whole blood.

³ Accelerometry subsample of $n = 25$ peri-urban and $n = 30$ rural children.

***Significant difference: * $P < 0.05$, ** $P < 0.01$.

TABLE 3 Diet and energy expenditure and allocation predictors of children's body fat percentage z score¹

| | Summary diet model | Detailed diet model | Diet and TEE model | Diet and PAL model |
|---|--------------------|---------------------|--------------------|--------------------|
| Diet—market-acquired food consumption | | | | |
| Total items, <i>n</i> /d | 0.06 ± 0.09 | — | — | — |
| "Carbohydrate" items, <i>n</i> /d | | | | |
| Tertile 2 | — | -0.63 ± 0.26* | -0.63 ± 0.27* | -0.57 ± 0.27* |
| Tertile 3 | — | -0.80 ± 0.38* | -0.81 ± 0.39 | -0.78 ± 0.40 |
| "Protein" items, <i>n</i> /d | | | | |
| Tertile 2 | — | 0.88 ± 0.25** | 0.86 ± 0.25** | 0.74 ± 0.26** |
| Tertile 3 | — | 0.96 ± 0.31** | 0.97 ± 0.32** | 0.84 ± 0.32* |
| "Fat and sugar" items, <i>n</i> /d | | | | |
| Tertile 2 | — | -0.38 ± 0.26 | -0.35 ± 0.27 | -0.32 ± 0.27 |
| Tertile 3 | — | -0.13 ± 0.26 | -0.12 ± 0.27 | -0.11 ± 0.27 |
| Energy expenditure and allocation | | | | |
| TEE, kcal/d | — | — | -0.0002 ± 0.0004 | — |
| PAL | — | — | — | -1.14 ± 0.63 |
| Model conditional <i>r</i> ² | 0.605 | 0.615 | 0.604 | 0.624 |

¹*n* = 77. Values are $\beta \pm$ SE from multilevel models adjusted for peri-urban/rural group. The model for TEE also adjusted for age and sex. The model for PAL also adjusted for age, sex, and resting energy expenditure measurement time. See text for alternative models with similar results. PAL, physical activity level; TEE, total energy expenditure. ***Significant difference: **P* < 0.05, ***P* < 0.01.

energy expenditure, is likely often the dominant factor driving the early epidemiologic transition and the rise in childhood OW/OB in LMICs.

Compared with their rural peers, peri-urban Shuar children had greater adiposity and prevalence of OW, lived in more market-integrated households, consumed more market-acquired diet items, and had reduced immune activity and lower measured REE. However, despite these wide-ranging differences, measured TEE was indistinguishable between the

2 cohorts. This relative stability in children's daily energy expenditure across market integration was confirmed in 3-level analyses including industrialized cohorts, as well as in more robust individual-level models. Moreover, although IgG antibody concentration and household income were significant predictors of REE, no examined household, immune activity, or physical activity measures were related to children's overall TEE. Models directly investigating the impacts of diet and energy expenditure measures on adiposity demonstrated that

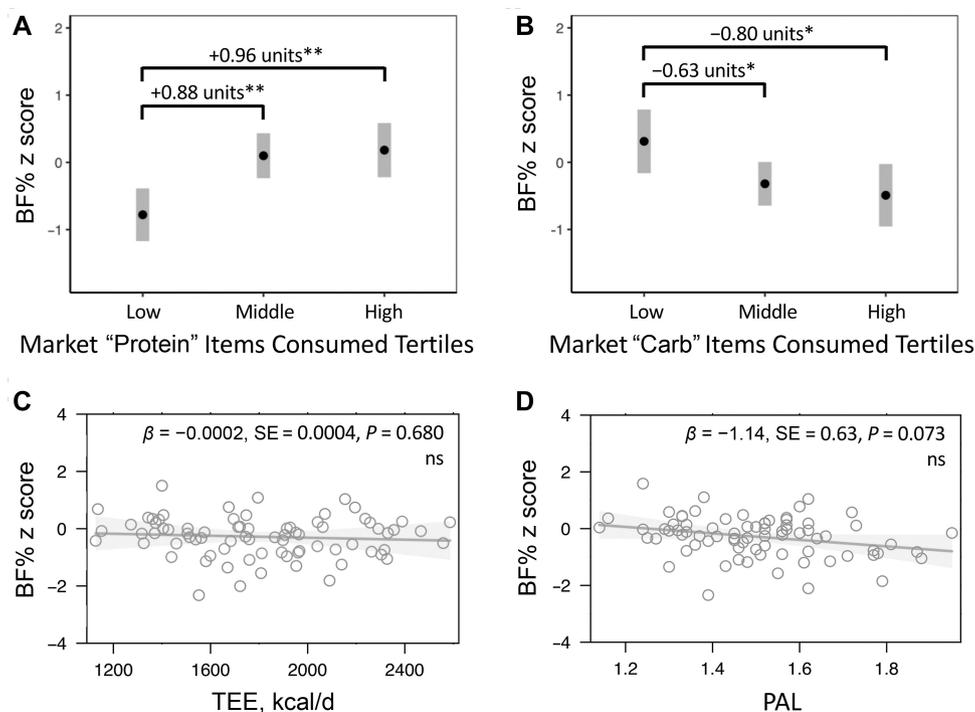


FIGURE 3 Relationships between reported market-acquired food item consumption and children's (*n* = 77) BF% z score (A, B), with a lack of similar detected significant relationships involving energy expenditure and allocation measures (C, D). Group estimated marginal means with shaded 95% CIs (diet measures) and partial regressions with shaded 95% CIs (energy expenditure measures) from multilevel models adjusting for urban/rural group. Models for TEE and PAL also adjusted for age and sex. The model for PAL also adjusted for REE measurement time. Significant effects on adiposity were detected for dietary measures but not for energy expenditure. See text for alternative models with similar results. ***Significant difference between groups: **P* < 0.05, ***P* < 0.01. BF%, body fat percentage; ns, nonsignificant (*P* > 0.05); PAL, physical activity level; REE, resting energy expenditure; TEE, total energy expenditure.

the reported consumption of market-acquired diet items, but not measured TEE or PAL, reliably predicted BF%-z.

The negligible effect of market integration on children's measured TEE shown here is consistent with previous DLW studies among adults (13, 14) and infants (40) that reported similar TEE between subsistence-based and industrialized populations. It is also consistent with previous analysis of the present rural sample, which found no difference in measured TEE between rural children and US/UK cohorts (16). It is widely assumed that differences in habitual physical activity translate into differences in TEE across market integration (5, 39), including among children (8, 15, 41). However, the results of the present study demonstrate no TEE differences between rural, peri-urban, and industrialized children with widely differing lifestyles. More directly, accelerometry-based measures of physical activity had no detectable impact on Shuar children's TEE. This finding is in keeping with the observation that physical activity assessed objectively by accelerometry is often a poor predictor of free-living TEE in both adults and children (42).

Immune activity is a metabolically costly but commonly overlooked component of habitual energy expenditure (43, 44). Given that the rise in obesity occurs alongside a reduced burden of infectious disease during the epidemiologic transition (6, 9), it is notable that the possible role of decreased immune activity-related energy expenditure in driving trends in energy balance has not been, to our knowledge, systematically investigated. Shuar children's total IgG and IgE concentrations were significantly lower in the peri-urban sample, and IgG was positively related to REE, suggesting decreasing metabolic costs of chronic, asymptomatic immune activity (no children presented a fever or were otherwise overtly ill during this study) with market integration. Yet, like findings for physical activity, these measures of chronic immune activity had no detectable impact on children's overall TEE. Together, these findings indicate TEE constraint and underlying energy allocation trade-offs during childhood (see below).

The general consistency in childhood TEE shown here suggests that, contrary to the predominant model of the nutrition transition (5), daily energy expenditure changes may play a relatively modest role in the epidemic of childhood OW/OB in LMICs. Peri-urban Shuar children spent the same total number of calories each day as their rural counterparts, yet they were significantly fatter (20.6% compared with 12.5% mean BF%) and more OW (36% compared with 0% incidence). Similar to findings from DLW studies among industrialized children (45, 46), TEE and PAL were not related to children's adiposity (the relation with PAL did approach significance but, importantly, PAL is a measure of energy allocation, not daily energy expenditure). These findings support the position put forth by several others that differences in habitual energy intake, as opposed to daily energy expenditure, may best explain secular trends in obesity (47–50). The importance of physical activity for child and adult health—including for weight management via appetite regulation (51)—is firmly established and indisputable (39). However, the present findings suggest a likely primary direct role of dietary change in children's transition to OW/OB during market integration.

Differences in diet were large in the present sample, with peri-urban children and their parents reporting >4 times greater consumption of all market-acquired dietary items. Although self-reported dietary data have known limitations (52), these findings are consistent with the rapid shift to purchased, energy-dense foods documented elsewhere among the Shuar

(17, 18) and observed broadly among children in Ecuador (53) and other LMICs (54). The general positive impact of market-acquired foods on adiposity in market-integrating populations has been previously documented (55, 56). The positive relationship between the consumption of market-acquired “protein” items and Shuar children's adiposity is consistent with these findings. Interestingly, the consumption of market-acquired “carbohydrate” items was negatively related to children's adiposity. Future analyses should investigate this finding, which may be related to the relatively low energy density of the market “carbohydrate” items (predominantly rice) that are currently being consumed by the Shuar. Future research on this topic should also investigate micronutrient-related obesogenic effects of changes in children's dietary composition (57), preferably using individual-level dietary data that can account for possible variation in food consumption patterns within households (17).

For basic understanding of childhood energy expenditure patterns, the findings of this study provide additional support for a model of energetic constraint and trade-offs. The constraint and trade-offs model has been previously described in detail for both adults (58, 59) and children (16). It proposes that humans, like many organisms, have evolved to maintain TEE within a conservative and relatively narrow species-specific habitual range by balancing underlying energy allocation to competing metabolic tasks via trade-offs. Applied to the nutrition transition, this framework can explain why dramatic changes in individual components of energy expenditure—such as decreased immune activity and the suggested drop in childhood REE documented here—have little resulting impact on overall TEE. Because this model predicts a relatively consistent relationship between body size (particularly FFM) and TEE, physical growth is critical in shaping lifetime energy requirements and should be sensitive to trade-offs involving signals of future energy demands (16, 27). Chronic childhood immune activity may, for example, suppress growth, even in contexts of current energy abundance, a hypothesis that is supported by nutrition supplementation studies and other evidence from populations suffering from heavy burdens of infectious disease (40, 60, 61). In this manner, the constraint and trade-offs model can generate novel predictions for understanding the etiology of the dual burden of child growth stunting and adult obesity in LMICs (62).

This study has several limitations. Foremost, it utilizes a cross-sectional observational design that restricts the interpretation of causal relationships. It cannot be stated with certainty using these data that market integration has no impact on TEE as children experience market changes during their own lifetime. Nor can it be stated that TEE is unrelated to future adiposity. We note, however, that a number of studies among children in industrialized countries provide prospective evidence for a lack of relationship between TEE and body fat change (45, 46). The relevance of this study's findings for the nutrition transition in populations undergoing their own unique experience of market integration and in currently industrialized populations also must be determined. Shuar children are not malnourished, potentially limiting the relevance of these findings for populations experiencing high rates of insufficient dietary intake and wasting. It is also possible that childhood TEE in industrialized countries is more responsive than documented here. This seems unlikely, however, as nationally representative DLW data similarly show no impact of environmental and lifestyle proxies on TEE among children in the United Kingdom (63).

Like many global health challenges, childhood OW/OB is a complex problem. The findings presented here provide evidence for a possible primary role of dietary change in the nutrition transition and the rise of childhood OW/OB in LMICs. However, numerous additional factors, including larger macrolevel climatic, environmental, economic, and socio-political phenomena, are clearly involved in this process (4, 7, 8, 64). A successful approach for reducing the global burden of childhood OW/OB must consider all these factors and their interactions. It must also account for the often overlooked yet critical early phase of market integration and the initial presentation of OW/OB in rural communities (65, 66). Analyses utilizing objective measures of energy expenditure can serve an important role for accurately modeling the energetic pathways underlying the epidemiologic transition and the pandemic of childhood OW/OB.

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Data availability

Data described in the article, as well as the code book, and analytic code will be made available upon request pending agreement to data use and participant privacy policy.

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