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RESEARCH ARTICLE

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# Growth references for Tsimane forager-horticulturalists of the Bolivian Amazon

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## Abstract

**Objectives:** Growth standards and references currently used to assess population and individual health are derived primarily from urban populations, including few individuals from indigenous or subsistence groups. Given environmental and genetic differences, growth may vary in these populations. Thus, there is a need to assess whether international standards are appropriate for all populations, and to produce population specific references if growth differs. Here we present and assess growth references for the Tsimane, an indigenous population of Bolivian forager-horticulturalists.

**Methods:** Mixed cross-sectional/longitudinal anthropometrics (9,614 individuals; 30,118 observations; ages 0–29 years) were used to generate centile curves and Lambda-Mu-Sigma (LMS) tables for height-for-age, weight-for-age, body mass index (BMI)-for-age, and weight-for-height (WFH) using Generalized Additive Models for Location Shape and Scale (*GAMLSS*). Velocity curves were generated using SuperImposition by Translation and Rotation (*SITAR*). Tsimane $\leq$5 years were compared to World Health Organization (WHO) standards while those $>$5 years were compared to WHO school age references. All ages were compared to published references for Shuar forager-horticulturalists of the Ecuadorian Amazon.

**Results:** Tsimane growth differs from WHO values in height and weight, but is similar for BMI and WFH. Tsimane growth is characterized by slow height velocity in childhood and early adolescent peak height velocity at 11.3 and 13.2 years for girls and boys. Tsimane growth patterns are similar to Shuar, suggesting shared features of growth among indigenous South Americans.

**Conclusions:** International references for BMI-for-age and WFH are likely appropriate for Tsimane, but differences in height-for-age and weight-for-age suggest Tsimane specific references may be useful for these measures.

KEYWORDS
growth, height, weight, BMI, growth velocity, Tsimane, Amazonians, indigenous South Americans, GAMLSS

Abbreviations: BCCG, Box-Cox Cole and Green; BMI, body mass index; CDC, centers for disease control and prevention; GAIC, Generalized Akaike information criterion; *GAMLSS*, generalized additive models for location shape and scale; LMS, Lambda-Mu-Sigma; *SITAR*, superimposition by translation and rotation; WFH, weight-for-height; WHO, World Health Organization.

## 1 | INTRODUCTION

When evaluating the growth of children, much of the world currently uses growth standards or references from the World Health Organization (WHO) (de Onis, Onyango, Borghi, Siyam, Nishida, & Siekman,

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2007b) or the United States (US) Centers for Disease Control and Prevention (CDC) (Kuczmarski, Ogden, Guo, Grummer-Strawn, Flegal, Mei, ... Johnson, 2002). International growth standards, designed to reflect the growth of children under non-limiting conditions, have been created by the WHO for infants and young children (age 0–5 years). However, similar standards for the growth of older children and adolescents have not been created (de Onis et al., 2007b) and so, in lieu of international standards, WHO and CDC growth references derived from US samples are frequently used to assess growth patterns in older children and adolescents across a range of populations. However, recent analyses suggest that WHO and CDC references for childhood and adolescent growth may not be appropriate for assessing growth in many populations, particularly those of non-Western descent (Guedes, De Matos, Lopes, Ferreirinha, & Silva, 2010; Hasan, Batieha, Jadou, Khawaldeh, & Ajlouni, 2001; Hakeem, Shaikh, & Asar, 2004; Mushtaq, Gull, Mushtaq, Abdullah, Khurshid, Shahid, ... Akram, 2012; Neyzi, Furman, Bundak, Gunoz, Darendeliler, & Bas, 2006; Urlacher, Blackwell, Liebert, Madimenos, Cepon-Robins, Gildner, ... Sugiyama, 2016a). Environmental differences in climate, energy availability, foraging ecology, and mortality risk have selected for genetic variation across human populations in both growth and the reaction norms regulating how growth responds to environmental influences (Becker, Verdu, Froment, Le Bomin, Pagezy, Bahuchet, & Heyer, 2011; Eveleth, & Tanner, 1990; Lunde, Melve, Gjessing, Skjaerven, & Irgens, 2007; Hadley and Hruschka, 2014; Migliano, Vinicius, & Lahr, 2007; Perry and Verdu, in press; Urlacher et al., 2016a). These differences may be particularly salient for indigenous populations, many of whom have remained genetically and culturally isolated from national populations, and thus represent a significant portion of human genetic diversity (Henn, Gignoux, Jobin, Granka, Macpherson, Kidd, ... Feldman, 2011; Karafet, Osipova, Gubina, Posukh, Zegura, & Hammer, 2002; Wang, Lewis, Jakobsson, Ramachandran, Ray, Bedoya, ... Ruiz-Linares, 2007). The scant data available from these groups suggest growth patterns can differ across many features, including those relating to juvenile growth rates, the timing and magnitude of adolescent growth, degree of sexual dimorphism, and relative trade-offs between height growth and weight growth (Eveleth and Tanner, 1990; Walker, Gurven, Hill, Migliano, Chagnon, De Souza, ... Yamauchi, 2006; Ulijaszek, 1994; Urlacher et al., 2016a). While these differences are most apparent at later ages, some differences may emerge as early as infancy (Hadley and Hruschka, 2014).

Although published growth data from indigenous populations exist (Draper and Howell, 2005; Foster, Byron, Reyes-García, Huanca, Vadez, Apaza, ... Leonard, 2005; Rozzi, Koudou, Froment, Le Bouc, & Botton, 2015; Walker et al., 2006; Urlacher et al., 2016a,b) detailed descriptions from large samples with accurate ages are rare and few growth references derived specifically for indigenous populations are available. Given the high degree of individual variability in growth, conclusions about growth based on small samples are often problematic or inconclusive. Thus, growth references based on large, representative samples are needed to thoroughly answer questions about universal and variable features of human growth, and to investigate the links between growth, health, and nutritional status. Moreover, large samples are needed to thoroughly assess whether international references are appropriate for all individuals, or whether population specific references might sometimes be beneficial.

To address the need for detailed descriptions of growth, and to assess the appropriateness of international references for evaluating Tsimane, we generate and describe growth references for Tsimane forager-horticulturalists of the Bolivian Amazon using mixed cross-sectional and longitudinal data on 9,614 individuals under age 30 from 88 communities ($n = 30{,}118$ observations). We first generate centile references and Lambda-Mu-Sigma (*LMS*) curves (Cole and Green, 1992) for Tsimane height-for-age, weight-for-age, body mass index (BMI)-for-age, and weight-for-height (WFH), providing an extensive description of growth patterns in a subsistence-level population. We then produce velocity curves both from cross-sectional data and from individual longitudinal changes using the SuperImposition by Translation and Rotation (SITAR) method (Cole, Donaldson, & Ben-Shlomo, 2010; Cole, Pan, & Butler, 2014). Finally, we assess the extent to which Tsimane growth is similar to or different from growth as described by WHO standards and WHO and CDC references, as well as growth references for Shuar forager-horticulturalists of Amazonian Ecuador, one of the only other Amazonian populations to have comparable references based on a large sample (Urlacher et al., 2016a). These comparisons aim to determine whether Tsimane growth differs sufficiently from international references to justify the use of Tsimane specific growth references. Finally, we discuss the features of Tsimane growth in reference to human life history evolution.

## 1.1 | The Tsimane

Tsimane are a rapidly expanding [3.6% annual growth rate (Gurven, von Rueden, Stieglitz, Kaplan, & Rodriguez, 2014)] population of ∼15,000 individuals, that live in over 90 villages along the Maniqui River and surrounding areas in lowland Beni, Bolivia. Although Tsimane growth data have been used frequently in research (Foster et al., 2005; Godoy, Nyberg, Eisenberg, Magvanjav, Shinnar, Leonard, ... Tanner, 2010; Gurven, Stieglitz, Hooper, Gomes, & Kaplan, 2012; McDade, Reyes-Garcia, Tanner, Huanca, & Leonard, 2008; Reyes-García, McDade, Molina, Leonard, Tanner, Huanca, & Godoy, 2008; Veile, Winking, Gurven, Greaves, & Kramer, 2012) as both an outcome and predictor, detailed patterns of growth describing all ages, individual variation by age, and growth velocities have not been fully characterized.

Tsimane subsist by hunting, fishing, and cultivating plantains, rice, corn and manioc. Adult diets consists of 74% plant products and 26% animal products, with <10% of calories coming from purchased foods (Martin, Lassek, Gaulin, Evans, Woo, Geraghty, ... Gurven, 2012). In general Tsimane children are short and lean, but have low rates of wasting and arm muscularity similar to US children, suggesting adequate protein (Foster et al., 2005). However, stunting is prevalent (Gurven, 2012), and low bone mineral density suggests the possibility of micronutrient deficiencies (Stieglitz, Beheim, Trumble, Madimenos, Kaplan, & Gurven, 2015; Stieglitz, Madimenos, Kaplan, & Gurven, 2016). Tsimane are a natural fertility population, with a total fertility

**TABLE 1** Prevalence of stunting, wasting, low weight, and low BMI in the full sample, as determined by WHO standards

| | | Height | | | Weight | | | BMI | | | WFH | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Age Range (Years) | | % $Z \leq -2$ | Median $Z$ | Obs | % $Z \leq -2$ | Median $Z$ | Obs | % $Z \leq -2$ | Median $Z$ | Obs | % $Z \leq -2$ | Median $Z$ | Obs |
| Girls | (0,0.5] | 19.8 | −0.33 | 455 | 11.6 | −0.08 | 458 | 13.2 | 0.21 | 446 | 14.1 | 0.37 | 448 |
| | (0.5,1] | 20.6 | −0.87 | 442 | 13.5 | −0.53 | 444 | 12.4 | 0.02 | 435 | 12.3 | 0.06 | 438 |
| | (1,2] | 51.0 | −2.04 | 906 | 17.4 | −0.83 | 917 | 6.4 | 0.50 | 889 | 7.8 | 0.22 | 898 |
| | (2,5] | 54.6 | −2.11 | 2,613 | 14.2 | −1.00 | 2,622 | 2.2 | 0.47 | 2,563 | 2.4 | 0.47 | 2,592 |
| | (5,10] | 38.7 | −1.73 | 3,735 | 12.0 | −0.93 | 3,744 | 0.6 | 0.21 | 3,676 | 1.4 | 0.34 | 2,943 |
| | (10,15] | 35.6 | −1.63 | 2,757 | 13.4[a] | −0.70[a] | 2,755 | 0.6 | 0.19 | 2,729 | 0.0 | 0.43 | 112 |
| | (15,20] | 38.9 | −1.84 | 1,822 | 7.4[a] | −0.50[a] | 1,828 | 0.2 | 0.49 | 1,820 | – | – | 0 |
| Boys | (0,0.5] | 25.1 | −0.64 | 427 | 16.4 | −0.37 | 438 | 15.6 | 0.05 | 424 | 16.3 | 0.30 | 417 |
| | (0.5,1] | 33.9 | −1.35 | 484 | 20.5 | −0.90 | 487 | 15.4 | −0.08 | 474 | 15.1 | −0.08 | 476 |
| | (1,2] | 58.9 | −2.32 | 907 | 23.4 | −1.14 | 913 | 8.7 | 0.38 | 884 | 10.8 | −0.03 | 893 |
| | (2,5] | 55.7 | −2.16 | 2,669 | 14.1 | −0.99 | 2,679 | 2.0 | 0.62 | 2,613 | 2.6 | 0.52 | 2,650 |
| | (5,10] | 42.5 | −1.81 | 3,860 | 13.6 | −0.93 | 3,866 | 0.6 | 0.36 | 3,792 | 0.9 | 0.61 | 2,977 |
| | (10,15] | 40.9 | −1.79 | 2,697 | 18.9[a] | −1.14[a] | 2,684 | 1.1 | 0.02 | 2,636 | 0.9 | 0.76 | 108 |
| | (15,20] | 34.9 | −1.75 | 1,322 | 10.2[a] | −0.85[a] | 1,318 | 0.6 | 0.18 | 1,308 | – | – | 0 |

Values include the full sample, prior to excluding outliers for growth curve construction.
[a]For weight over age 10, WHO standards are not available, so CDC references were used. WFH standards extend to 121 cm, and few children over age 10 were below this height.

rate of 9.1 births per woman (Blackwell, Tamayo, Beheim, Trumble, Stieglitz et al., 2015; Gurven, Kaplan, & Supa, 2007; McAllister, Gurven, Kaplan, & Stieglitz, 2012); women breastfeed their infants on-demand, weaning at 19 months on average (Veile et al., 2014).

Tsimane are exposed to a wide array of pathogens and parasites which likely influence growth patterns, including hookworm (50% prevalence), giardia (37%), and roundworm (15%) (Blackwell, Martin, Kaplan, & Gurven, 2013; Martin, Blackwell, Gurven, & Kaplan, 2013). Other common afflictions include upper and lower respiratory infection, gastrointestinal problems, skin infections, urinary tract infections, and traumatic injuries (Blackwell, Trumble, Maldonado Suarez, Stieglitz, Beheim et al., 2016; Gurven et al., 2012). Overall, infectious disease accounts for roughly half of all deaths, including pre-adult deaths (Gurven et al., 2007).

## 2 | METHODS

### 2.1 | Data collection

Data for this study come from the Tsimane Health and Life History Project (THLHP, http://www.unm.edu/~tsimane), which has worked continuously with the Tsimane since 2002 (Gurven, Kaplan, Stieglitz, Trumble, Blackwell, Beheim, & Hooper, in press). For the present study we utilize data on height and weight collected by the THLHP between 2002 and 2015. Data were collected during medical examinations by THLHP physicians, who visited Tsimane villages as part of a larger mobile medical team approximately once per year. Patients seen by THLHP physicians were given routine physical exams including assessment of medical history, symptom investigation and clinical diagnosis, collection of vital signs (e.g., blood pressure, temperature), and anthropometrics. Following on-site analysis of blood and fecal samples for indicators of infection, physicians administered vitamins and medications as warranted. Standing and sitting height were measured without shoes to the nearest millimeter with a portable Seca 213 stadiometer. Weight was measured with a Tanita BF-572 scale in light clothing without shoes. Growth data used for this study is provided in Supporting Information File S1 and summarized relative to CDC references in Table 1.

### 2.2 | Ethics approval

The study was reviewed and approved by the Gran Consejo Tsimane, the governing body overseeing Tsimane affairs and research projects, and by the IRBs of the University of California-Santa Barbara (UCSB) and the University of New Mexico. Informed consent was obtained at two levels. During a community meeting open to all residents, communities decided collectively whether they would participate in the THLHP. To date, all communities that have been approached have agreed to participate in the THLHP. Study participants gave informed consent before each medical visit. For minors, both parental consent and child assent were obtained.

### 2.3 | Centile curve modeling

We constructed centile curves for height-for-age, weight-for-age, BMI-for-age, and WFH following procedures very similar to those previously

**TABLE 2** Sample sizes for longitudinal and cross-sectional growth curve analyses

| | | | | Age Range (years) | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | [0,2] | (2,5] | (5,10] | (10,15] | (15,20] | (20,25] | (25,30] |
| Males | Height | Cross | *n* | 1,400 | 1,659 | 1,879 | 1,386 | 806 | 650 | 576 |
| | | | obs | 1,808 | 2,663 | 3,850 | 2,687 | 1,321 | 1,141 | 1,046 |
| | | Long | *n* | 572 | 903 | 862 | 920 | 499 | 288 | – |
| | | | obs | 807 | 1,732 | 2,430 | 2,049 | 936 | 666 | – |
| | Weight | Cross | *n* | 1,415 | 1,659 | 1,879 | 1,379 | 805 | 652 | 572 |
| | | | obs | 1,831 | 2,672 | 3,858 | 2,671 | 1,318 | 1,143 | 1,042 |
| | | Long | *n* | 612 | 925 | 858 | 916 | 492 | 284 | – |
| | | | obs | 891 | 1,784 | 2,452 | 2,035 | 929 | 652 | – |
| | BMI | Cross | *n* | 1,380 | 1,643 | 1,864 | 1,372 | 798 | 646 | 569 |
| | | | obs | 1,771 | 2,622 | 3,787 | 2,638 | 1,307 | 1,135 | 1,035 |
| | | Long | *n* | 519 | 874 | 841 | 909 | 495 | 281 | – |
| | | | obs | 728 | 1,670 | 2,352 | 2,009 | 924 | 638 | – |
| Females | Height | Cross | *n* | 1,380 | 1,608 | 1,799 | 1,330 | 947 | 789 | 652 |
| | | | obs | 1,796 | 2,603 | 3,726 | 2,737 | 1,818 | 1,567 | 1,303 |
| | | Long | *n* | 485 | 609 | 811 | 946 | 621 | 269 | – |
| | | | obs | 747 | 1,309 | 2,308 | 2,187 | 1,404 | 382 | – |
| | Weight | Cross | *n* | 1,389 | 1,612 | 1,795 | 1,335 | 950 | 788 | 651 |
| | | | obs | 1,813 | 2,618 | 3,729 | 2,744 | 1,826 | 1,557 | 1,296 |
| | | Long | *n* | 582 | 905 | 816 | 948 | 610 | 257 | – |
| | | | obs | 880 | 1,764 | 2,375 | 2,197 | 1,354 | 350 | – |
| | BMI | Cross | *n* | 1,363 | 1,593 | 1,780 | 1,328 | 945 | 787 | 649 |
| | | | obs | 1,771 | 2,567 | 3,677 | 2,718 | 1,813 | 1,547 | 1,291 |
| | | Long | *n* | 504 | 862 | 800 | 941 | 606 | 254 | – |
| | | | obs | 699 | 1,660 | 2,302 | 2,181 | 1,347 | 350 | – |

*n* = number of unique individuals, obs = number of measurements. Note that due to the longitudinal nature of the data, the same individual may appear in more than one age group.

used to construct growth references for Shuar (Urlacher et al., 2016a), and replicating, to the extent possible, the curve fitting procedures of the WHO (Borghi, de Onis, Garza, Van den Broeck, Frongillo et al., 2006; de Onis et al., 2007b). Centile curves were constructed for each sex between the ages of 0–29 years using Generalized Additive Models for Location Scale and Shape (*GAMLSS*)(Rigby and Stasinopoulos, 2005). For height, weight and BMI, ages up to 29 were included to anchor curves and avoid edge effects (Indrayan, 2014). For WFH, ages up to 20 were included, and dummy cases with values below the lowest height measurement were added to WFH models to reduce edge effects. Models were fit using the R-package gamlss (http://www.gamlss.org/) in R 3.2.4 (http://cran.us.r-project.org/). Smoothing degrees of freedom were determined as follows:

1. Models were first fit with a Box-Cox Power Exponential distribution as *BCPE*[$x$=age$^{\lambda}$, df ($\mu$)=14, df ($\sigma$)=3, $\nu$=1, $\tau$=2] with values of the age-transformation power $\lambda$ ranging from 0.05 to 1.0. The $\lambda$ parameter from the model with the smallest global deviance was selected.
2. Using the selected $\lambda$ model, outliers with predicted *z*-scores $>3.5$ or $<-3.5$ were removed, since most of these outliers likely represented errors in data entry. This led to the exclusion of 0.3% of height and BMI observations and 0.3% of weight observations.
3. Generalized Akaike information criterion (GAIC) was used to determine the appropriate degrees of freedom for $\mu$, $\sigma$, $\nu$, and $\tau$. Degrees of freedom for $\mu$ and $\sigma$ were selected by comparing all models with df ($\mu$) ranging from 1 to 22 and df ($\sigma$) ranging from 1 to 20. Models with $\nu = 1$ or df ($\nu$) ranging from 1 to 14 were then compared. To allow the production of LMS parameters we fixed $\tau = 2$ in all models, resulting in the reduction of distribution

**TABLE 3** Tsimane total sample sizes and BCPE smoothing parameters for GAIC best-fit *GAMLSS* models

| | | $N_{individuals}$ | $n_{observations}$ | Age power transformation | df ($\mu$) | df ($\sigma$) | df ($\nu$)[a] |
|---|---|---|---|---|---|---|---|
| Height | Males | 4,852 | 14,516 | 0.65 | 14 | 12 | 10 |
| | Females | 4,757 | 15,550 | 0.65 | 15 | 11 | 9 |
| Weight | Males | 4,852 | 14,535 | 0.60 | 15 | 14 | 10 |
| | Females | 4,762 | 15,583 | 0.70 | 14 | 10 | 12 |
| BMI | Males | 4,826 | 14,295 | 0.40[b] | 12 | 10 | 6 |
| | Females | 4,746 | 15,384 | 0.40[b] | 13 | 11 | 9 |
| WFH | Males | 4,111 | 12,121 | 1.90 | 14 | 14 | 3 |
| | Females | 4,051 | 12,536 | 1.90 | 13 | 9 | 14 |

[a]Referred to as $\lambda$ when using LMS notation.
[b]For BMI the power transformation was fixed to improve fitting of ages $<$ 2 years.

functions to the simpler 3-parameter Box-Cox Cole and Green (BCCG) distribution (Cole and Green, 1992).

4. Goodness of fit for all final models was assessed using grid tests to compare observed and expected proportions of observations above and below specific centiles (Borghi et al., 2006; Healy, Rasbash, & Yang, 1988).

Final *GAMLSS* model parameters were used to produce centile tables and LMS curves for each sex and anthropometric measure of interest. Final model parameters and sample sizes are given in Tables 2 and 3. Complete R code for growth curve modeling is given in Supporting Information File S2. The L, M, and S parameters from growth models are given in Supporting Information Files S4–S7. Centile references are given in Supporting Information Files S8–S15.

## 2.4 | Velocity curve modeling

Velocity curves were generated in two ways. First, we generated pseudo-velocity curves from the first derivative of the median ($\mu$) curves obtained from *GAMLSS* models. We utilize median curves since these are available for all reference populations and allow direct comparisons with comparable methods. However, median curves may smooth growth spurts and misrepresent the shape of velocity curves. We therefore also used the *SITAR* method to generate velocity curves from longitudinal data (Cole et al., 2010, 2014). SITAR fits a non-linear mixed model with a cubic spline representing the average growth curve and uses three random effects terms to model each individual longitudinal growth trajectory, scaling the growth curve in terms of size, tempo, and velocity to fit each individual trajectory. Detailed descriptions of this scaling can be found elsewhere (Johnson, Llewellyn, van Jaarsveld, Cole, & Wardle, 2011). Since SITAR fits individual growth curves, smoothing of spurts is minimized as the random effects account for spurts occurring at different ages in different individuals. Prior to fitting SITAR models, we excluded individuals with fewer than three longitudinal measurements and used the *velout* function in the SITAR package to eliminate outliers with unusual velocities. Curves were fit separately by sex and in two age groups, 0–7 years and 5–25 years. Separate age groups were used to simplify model convergence, and since we reasoned that curve translation and rotation in infancy might not necessarily be linked to similar transformations in adolescence. Complete R code for cleaning and velocity curve modeling is given in Supporting Information File S3.

## 2.5 | Growth reference data

### 2.5.1 | WHO multicenter standards for children under age five

These standards were developed to represent the growth of children under "ideal" conditions, who were breastfed, relatively affluent, and unburdened by major disease, food insecurity, or smoking (World Health Organization, 2006). In replacing older references, the WHO multicenter standards increased international representation by including children from Brazil, Ghana, India, Norway, Oman, and the United States, and also avoided penalizing breastfed infants by treating them as the standard, as opposed to formula-fed infants who grow more slowly in the first two months but more rapidly thereafter (de Onis and Onyango, 2003; de Onis, Garza, Onyango, & Borghi, 2007a). Standards were produced by fitting BCPE distributions to data with *GAMLSS*.

### 2.5.2 | WHO references for school-age children and adolescents

These references were developed once it was decided that constructing multicenter standards for children and adolescents would be infeasible due to the difficulty of identifying and maintaining ideal circumstances for older ages across such a range of countries (de Onis et al., 2007b). Instead these references represent a reanalysis of the 1977 NCHS/WHO growth reference data from the US, using *GAMLSS* methods.

### 2.5.3 | WHO longitudinal velocity standards for infants

These standards provide *z*-scores for height and weight velocities for ages up to two years (World Health Organization, 2009). They were developed with a subsample of 882 infants studied during development of the WHO multicenter standards. Data came from all six international sites. Standards were produced by fitting BCPE distributions to data with *GAMLSS*.

#### 2.5.4 | US CDC growth charts

The 2000 CDC references were developed primarily using data from five National Center for Health Statistics (NCHS) cross-sectional surveys of the US, conducted between 1963 and 1994, and birth weight data from birth certificates (Kuczmarski et al., 2002). The nationally representative data included a mix of breast and formula fed infants. In constructing their references for weight-for-age, the CDC excluded data from the most recent survey, since they included a higher proportion of overweight children.

#### 2.5.5 | Shuar growth references for ages 0–25

Shuar are an Amazonian population from lowland Eastern Ecuador, roughly 1,800 km from Tsimane territory. The language groups to which Shuar and Tsimane belong are separate linguistic isolates (Clement, Denevan, Heckenberger, Junqueira, Neves, Teixeira, & Woods, 2015; Harner, 1984; Karsten, 1935; Sakel, 2011), and there is no close genetic relation between the two populations (Bert, Corella, Gene, Perez-Perez, & Turbon, 2015; Corella, Bert, Pérez-Pérez, Gené, & Turbón, 2007). Urlacher et al. (2016a) produced Shuar references using 4,878 mixed cross-sectional/longitudinal observations on 2,463 Shuar. Curve fitting methods were very similar to those used here. Median velocity curves were produced from the first derivative of the median growth centile curve.

## 3 | RESULTS

### 3.1 | Tsimane stunting, wasting, low weight-for-age, and low BMI-for-age

Table 1 gives the prevalences of stunting (height-for-age *z*-score $\leq -2$), low weight (weight-for-age *z*-score $\leq -2$), low BMI (BMI-for-age *z*-score $\leq -2$), and wasting (WFH *z*-score $\leq -2$) as determined relative to WHO standards or references for the Tsimane sample up to age 20, prior to excluding outliers for curve fitting purposes. In general, Tsimane have high prevalences of stunting at all ages, and moderately high prevalences of low weight-for-age. Wasting and low BMI-for-age have moderate prevalences under age two, but are very uncommon over age five.

### 3.2 | Centile and LMS curve fits

Final sample sizes for the mixed cross-sectional and longitudinal samples are given in Tables 2 and 3. Given large sample sizes, coverage across all ages was excellent, allowing for the production of detailed centile curves (Figures 1–5). Centile curves in Figures 1 and 2 are largely for illustration purposes. More detailed centiles and LMS tables are given in Supporting Information Files S4-S15. Detailed growth charts suitable for tracking growth are given in both English and Spanish in Supporting Information Files S16 and S17.

### 3.3 | Velocity curve modeling

Velocity curves were generated both as pseudo-velocity curves by taking the slope of the 50$^{th}$ centile line, and by fitting individual growth curves as random effects terms with SITAR (Figures 4 and 5). Velocity curves from both methods were similar, except under ~6 months of age, where SITAR curves for male height and weight suggested lower velocities than median curves, and SITAR curves for BMI suggested little change in BMI under age 6 (olive lines, Figure 6). These differences likely reflect the fact that longitudinal measurements were taken an average of 1.2 years apart, and may not capture the rapidly changing velocities in the first 6 months of age. At older ages curves were very similar, but SITAR velocity curves resulted in less blunting of adolescent height and weight growth spurts. Interestingly, SITAR curves also suggested negative BMI velocities after age 20 for women, which were not reflected in median curves.

### 3.4 | Growth from birth to 24 months

Under age five, we compare Tsimane growth to WHO standards (Figures 3 and 5; Tables 4–6), and velocities to WHO longitudinal velocity standards. Our data does not include direct measures of birth weight, since most Tsimane give birth at home, but does include measures taken within the first few weeks of life. At 1 week of age, median Tsimane weight and length are 3.41 kg/49.9 cm for boys and 3.33 kg/50.1 cm for girls. Median values at 1 week from WHO standards are 3.49 kg/51.1 cm for males and 3.34 kg/50.3 cm for females. These suggest that even at 1 week Tsimane boys may be small, though they are still heavier than Tsimane girls. In contrast, values for Tsimane girls are quite close to median values from the WHO.

Tsimane median growth curves roughly follow WHO growth curves for the first few months, though with boys remaining small relative to WHO standards (though still bigger than girls). At six months, Tsimane median length, weight, and BMI were equivalent to the WHO 13$^{th}$, 23$^{rd}$, and 39$^{th}$ centiles for boys and 27$^{th}$, 37$^{th}$, and 51$^{th}$ centiles for girls. After six months, median growth curves for length, and to some extent weight, diverge more dramatically from WHO standards. By age two, Tsimane curves are distinguished by low length/height and weight, but high BMI: at age 2, Tsimane median length/height, weight, and BMI fall at the 1$^{st}$, 14$^{th}$, and 75$^{th}$ WHO centiles for boys and the 1$^{st}$, 18$^{th}$, and 75$^{th}$ centiles for girls. Tsimane references have moderately higher $\sigma$ parameters than WHO standards across all ages under two years, indicating moderately wider distributions, while $\lambda$ parameters suggest some positive skew in male infant length for Tsimane, but relatively little skew for both Tsimane and WHO on other measures.

Mean velocity curves tell a similar story (Figure 6). In cross-sectional height curves (orange lines, Figure 6), a dip in velocity is apparent for both boys and girls between 6 months and 1 year of age, possibly suggestive of growth faltering during the transition from exclusive breast-feeding. However, when examined more closely, velocities are also low at 3 months. For boys, median height velocities are at the 17$^{th}$, 37$^{th}$, 17$^{th}$, and 33$^{rd}$ WHO percentiles at 3 months, 6 months, 1 year, and 2 years, respectively. For girls, velocities are at the 20$^{th}$, 33$^{th}$,

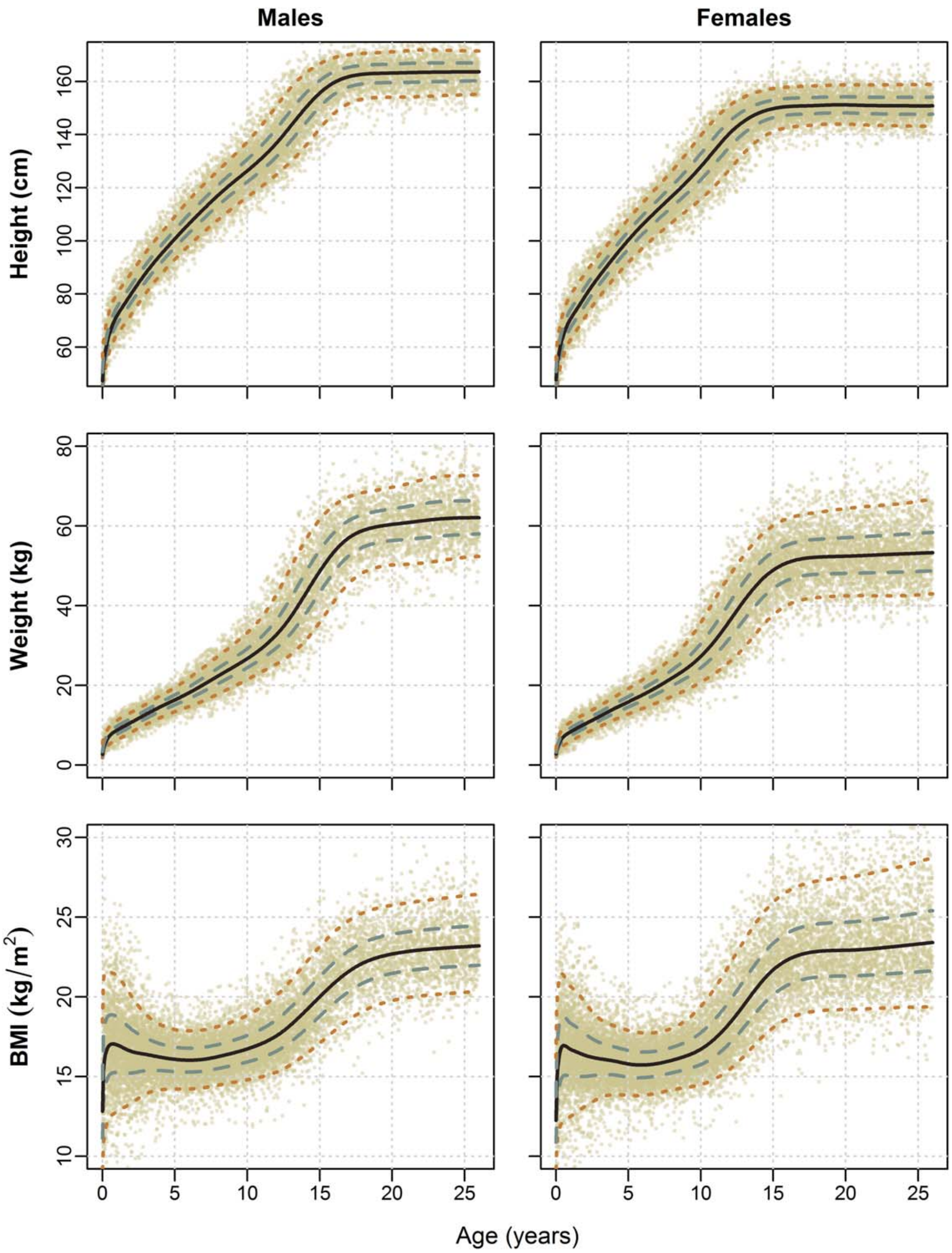


**FIGURE 1** Centile curves for Tsimane height, weight, and BMI from age 0 to 25 years. Solid black lines = 50th centile; Dashed slate blue lines = 25th and 75th centiles; Dotted brown lines = 5th and 95th centiles. Complete centile values and accompanying LMS parameters are provided in online Supporting Information Files S4-S6 and S8-S13

13th, and 32nd percentiles at these same ages. Weight velocities follow WHO standards more closely. Percentiles on WHO velocity standards at the median velocity at ages 3 months, 6 months, 1 year, and 2 years were 22nd, 37th, 36th and 44th for boys, and 32nd, 31st, 37th, and 43rd for girls, respectively.

BMI velocity curves for both WHO and Tsimane decline toward zero between 6 months and 1 year of age. Interestingly, WHO BMI velocities fall below zero between 6 months and 2.5 years of age, while Tsimane curves show only very slight negative BMI velocities during this period. This lack of decline in BMI is also evident in velocity curves from SITAR models.

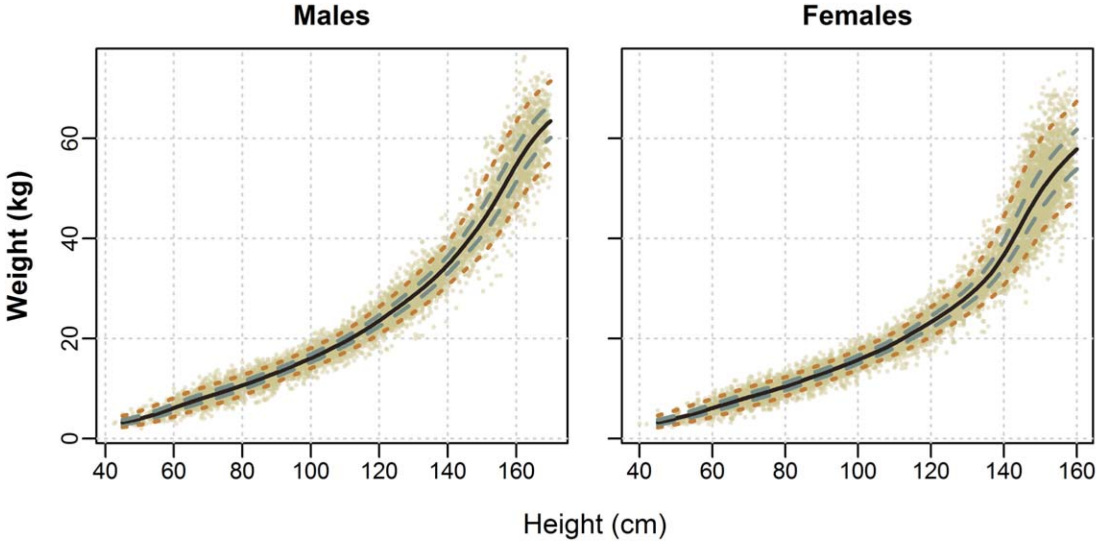


**FIGURE 2** Centile curves for Tsimane WFH from age 0 to 25 years. Solid black lines = 50th centile; Dashed slate blue lines = 25th and 75th centiles; Dotted brown lines = 5th and 95th centiles. Complete centile values and accompanying LMS parameters are provided in online Supporting Information Files S7 and S14-S15

### 3.5 | Growth from 2 to 10 years

From ages 2 to 5 we compare Tsimane to the WHO standards, and over age five to the WHO school age references (Figure 4; Tables 4–6). Median height for both boys and girls tracks between the 2$^{rd}$ and 4$^{th}$ percentiles for ages 2–10 years (Table 4). Median weight tracks between the 14$^{th}$ and 18$^{th}$ percentiles (Table 5), and median BMI values fall between the 52$^{nd}$ and 68$^{th}$ percentiles (Table 6). For ages 2–10 height has a range of variation similar to WHO values, but somewhat lower variation in weight and BMI (Figure 4; $\sigma$ values). For these ages, Tsimane show little consistent evidence of skew in distributions, while WHO standards have slight evidence of positive skew in weight and BMI as indicated by negative $\lambda$ curves.

Between ages 2 and 10, Tsimane pseudo-velocity and mean velocity curves follow the shape of WHO pseudo-velocity curves fairly closely, though both height and weight velocities are somewhat lower (Figure 7). The differences between WHO and Tsimane velocity curves increase around age six, when WHO curves begin to show increases in velocity leading up to adolescent growth, while Tsimane height velocity continues to decline until after age ten for males, and until age 8 or 9 for girls. Weight velocity remains relatively constant until after age ten for both sexes.

### 3.6 | Growth from 10 to 25 years

Over age ten and under age 19, we compare Tsimane height and BMI to WHO references, and weight to CDC references since WHO references are not available past age 10 for weight (Figure 7). Over age ten median Tsimane height for both sexes is at or below the 5$^{th}$ centile (Table 4). Weight falls between the 14$^{th}$ and 19$^{th}$ centiles for boys and the 26$^{th}$ and 32$^{nd}$ centiles for girls (Table 5). BMI is relatively high, with median values between the 52$^{th}$ and 69$^{th}$ centiles (Table 6). Over age 10, Tsimane weight and BMI show far less variation than WHO references. Tsimane $\lambda$ parameters are characterized by negative skew ($\lambda > 1$) in both males and females during the adolescent growth spurts. This may suggest delayed growth spurts for some Tsimane. From SITAR models, we estimate an average peak height velocity of 8.8 cm/year at 13.2 years for males and 8.2 cm/year at 11.3 years for females. Weight velocity is estimated to peak at 6.5 kg/year at 12.0 years for females, and 6.9 kg/year at 13.7 years for males.

### 3.7 | Weight-for-height references

As with BMI-for-age references, Tsimane WFH distributions show considerable overlap with WHO weight-for-height standards (Figure 5). Median Tsimane WFH falls between the 54$^{th}$ and 89$^{th}$ WHO percentiles (Table 7). At statures under 80 cm, Tsimane distributions tend to be more variable than WHO distributions, with higher $\sigma$ parameters. As a consequence, despite high median WFH values, 8–11% of Tsimane would be expected to have evidence of wasting (WFH $z$-scores $\leq -2$) according to WHO references (Table 7). Empirical values on raw data show similar median WFH $z$-scores at or well above the WHO median, but moderate rates of wasting in younger age groups (Table 1). Above 85 cm or above age five, wasting is very uncommon, afflicting 1% or less of children (Tables 1 and 7).

### 3.8 | Comparison with other amazonian populations

In Figures 8–10, we compare Tsimane growth references with previously described references for the Shuar (Urlacher et al., 2016a). Shuar and Tsimane have strikingly similar growth patterns. When overlaid, Shuar and Tsimane growth in height, weight, and BMI resemble each other closely, both in terms of median values and distributions (Figure 8, left column), as well as in pseudo-velocity curves (Figure 8, middle column). Both groups have slowed height growth through childhood and delayed weight growth, though Tsimane are slightly shorter than

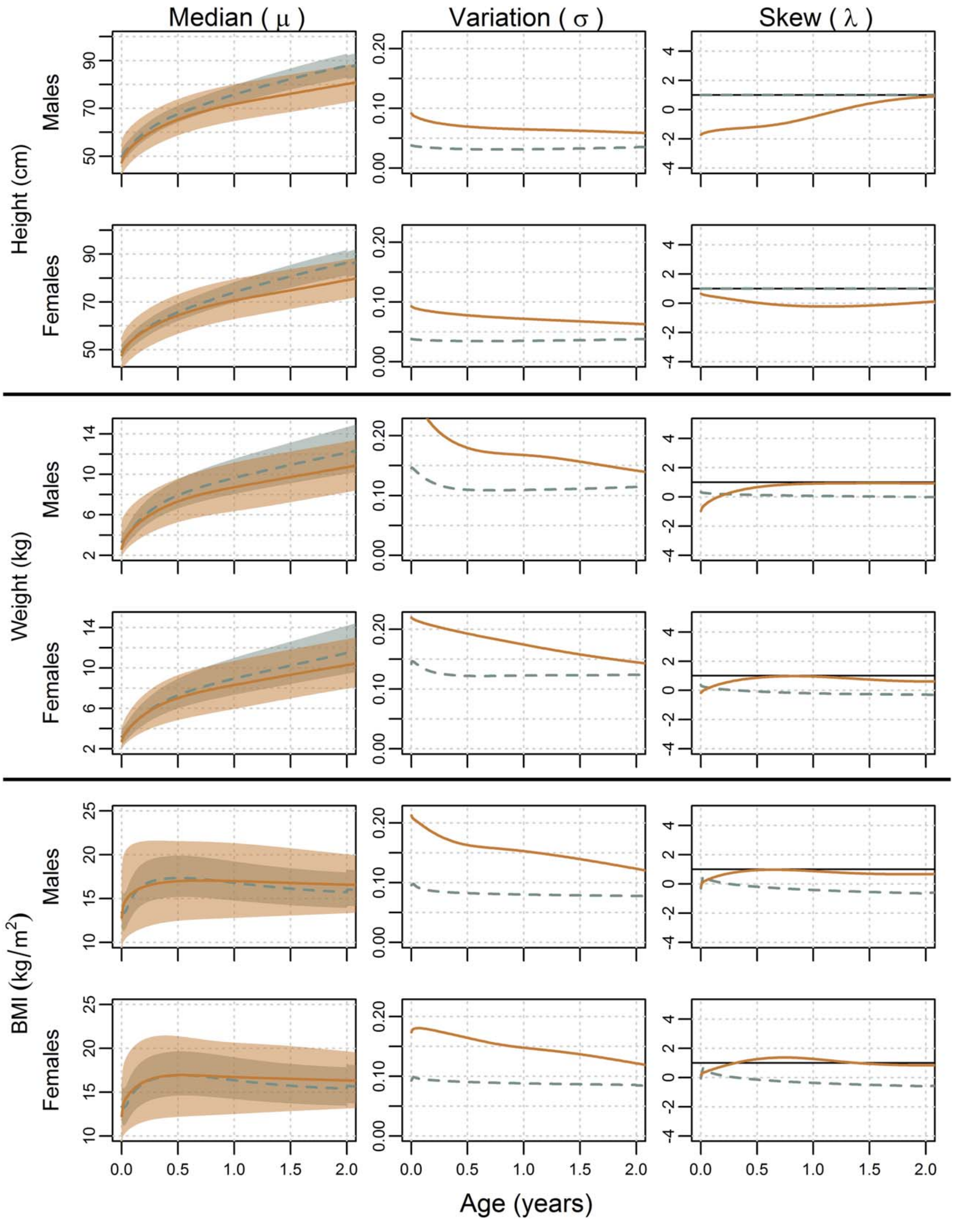


**FIGURE 3** Tsimane LMS parameters in the first two years of life, relative to WHO standards. Lines indicate parameter values for Tsimane (solid, brown) and WHO (dashed, slate blue). Shading on median graphs indicates the range between the 5th and 95th percentiles. $\mu$ = median parameter, i.e. the 50th percentile. $\sigma$ = sigma parameter, indicative of variation in the distribution. $\lambda$ = lambda parameter, indicative of skew in the distribution; values >1 indicate negative skew and <1 indicate positive skew

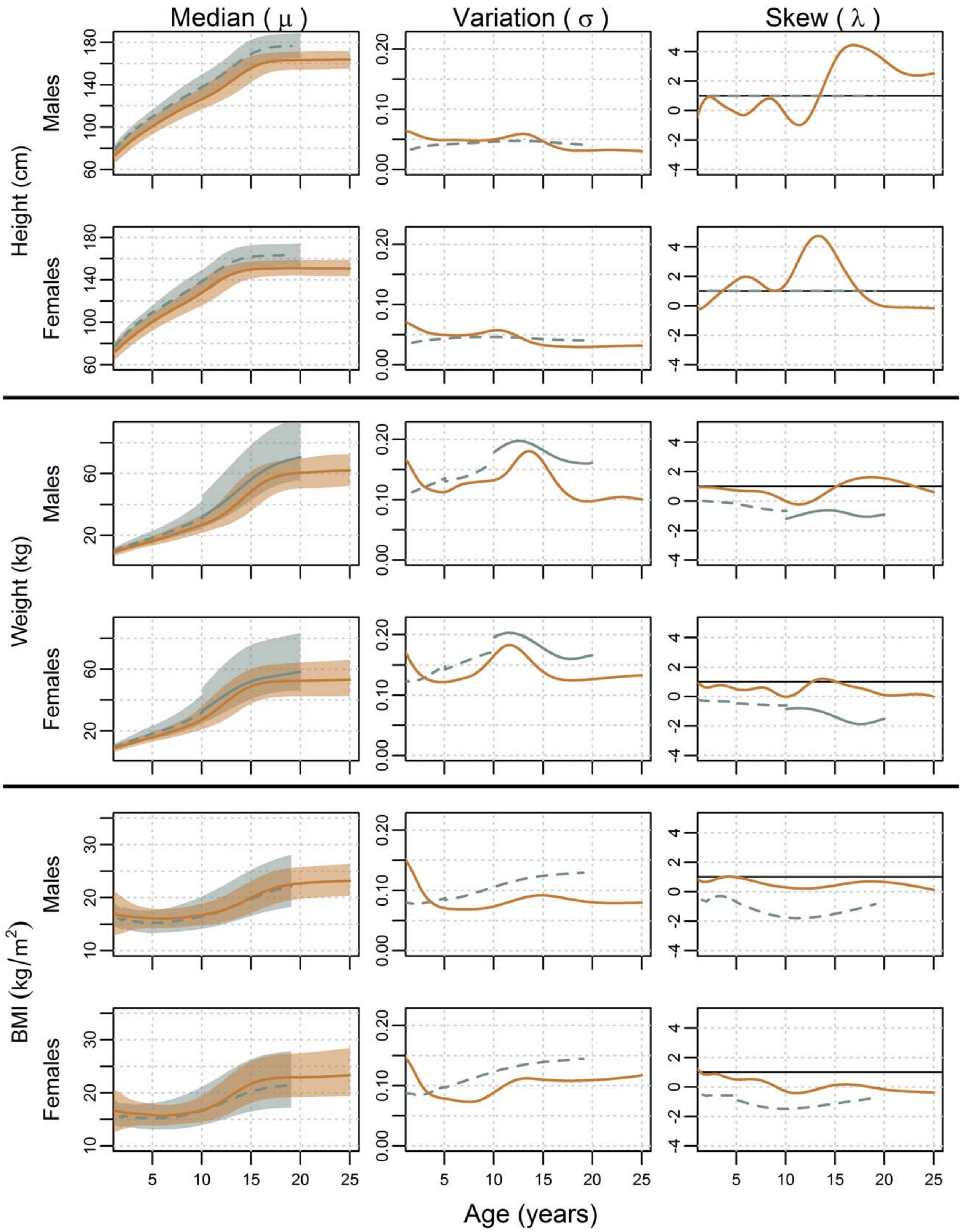


**FIGURE 4** Tsimane LMS parameters from 2 to 25 years of age, relative to WHO standards (under age 5) and WHO references (over age 5). CDC references are used for weight-for-age over age 10, since the WHO does not provide WFH references for these ages. Lines indicate parameter values for Tsimane (solid, brown), WHO (dashed, slate blue), and CDC (solid, slate blue),. Shading on median graphs indicates the range between the 5th and 95th percentiles. μ = median parameter, i.e. the 50th percentile. $\sigma$ = sigma parameter, indicative of variation in the distribution. λ = lambda parameter, indicative of skew in the distribution; values >1 indicate negative skew and < 1 indicate positive skew

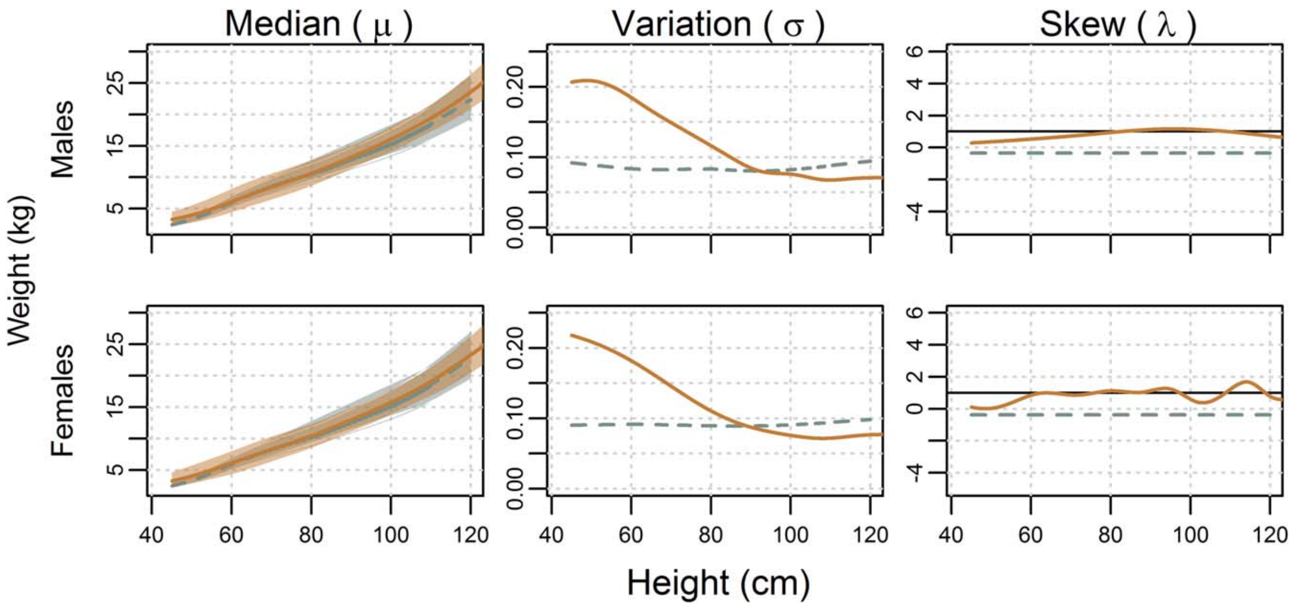


**FIGURE 5** Tsimane LMS parameters for WFH relative to WHO standards. Lines indicate parameter values for Tsimane (solid, brown) and WHO (dashed, slate blue). Shading on median graphs indicates the range between the 5th and 95th percentiles. $\mu$ = median parameter, i.e. the 50th percentile. $\sigma$ = sigma parameter, indicative of variation in the distribution. $\lambda$ = lambda parameter, indicative of skew in the distribution; values $>1$ indicate negative skew and $<1$ indicate positive skew

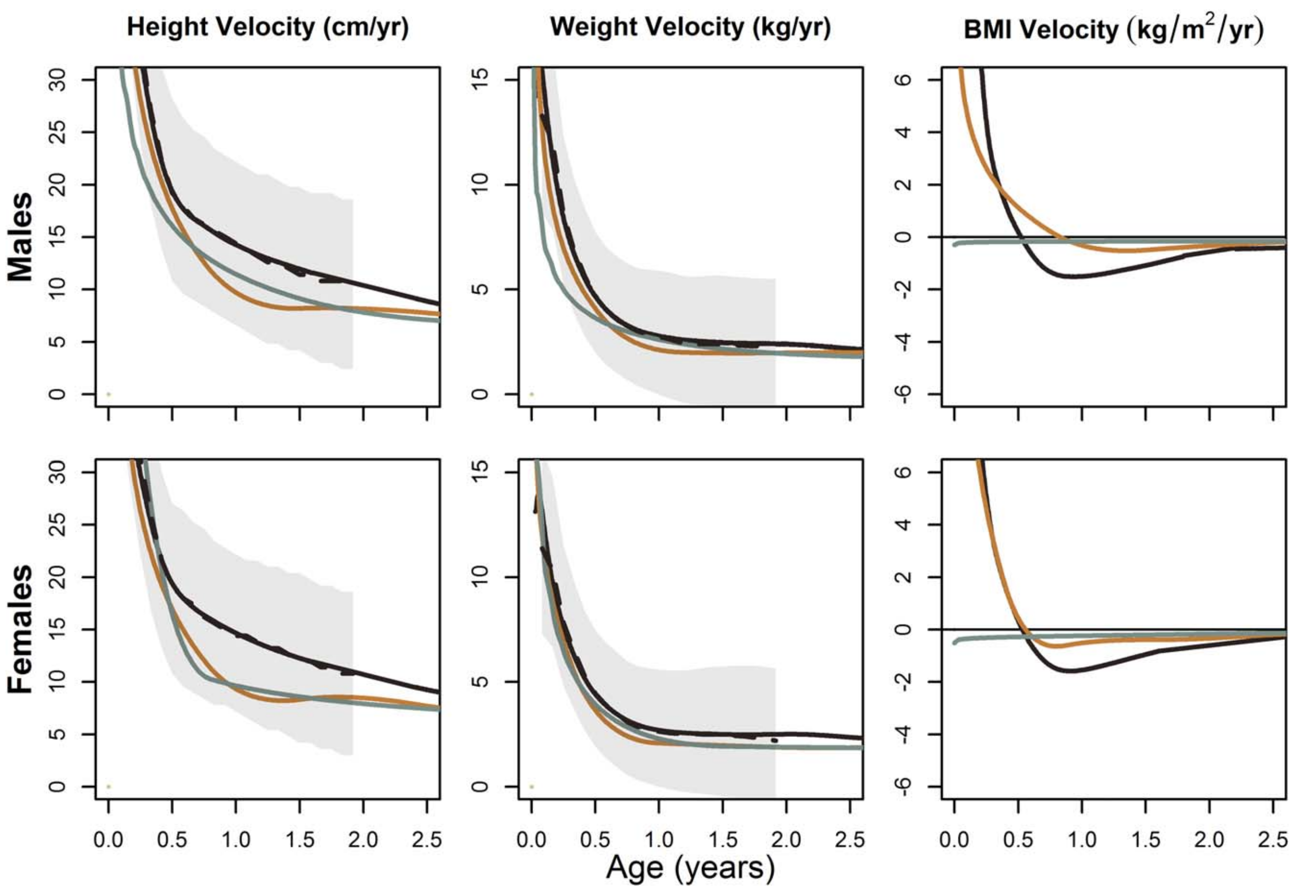


**FIGURE 6** Tsimane velocity curves for the first 2.5 years of life. Tsimane curves derived from cross-sectional GAMLSS (brown) and SITAR (slate blue line) analyses are shown, relative to WHO curves derived from the median of the cross-sectional (dashed black line) or longitudinal velocity standards (solid black line). Shading shows the 5th to 95th percentiles for the WHO growth velocity standards

**TABLE 4** Equivalent height centiles from WHO and Shuar references for Tsimane centile values

| Age range (Years) | | Relative to WHO standards/references 5th | 50th | 95th | % $Z \leq -2$ | Relative to Shuar references 5th | 50th | 95th | % $Z \leq -2$ |
|---|---|---|---|---|---|---|---|---|---|
| Girls | (0,2] | 0.00 | 9.8 | 98.4 | 37.3 | 0.1 | 40.4 | 99.8 | 15.2 |
| | (2,5] | 0.00 | 1.9 | 47.4 | 52.4 | 1.1 | 35.2 | 94.1 | 8.1 |
| | (5,10] | 0.03 | 4.3 | 48.2 | 39.3 | 4.0 | 52.1 | 96.3 | 3.1 |
| | (10,15] | 0.04 | 5.2 | 42.6 | 35.1 | 8.8 | 67.6 | 97.4 | 1.6 |
| | (15,20] | 0.17 | 3.6 | 24.6 | 38.8 | 17.6 | 71.8 | 98.1 | 0.3 |
| Boys | (0,2] | 0.00 | 4.9 | 96.7 | 43.8 | 0.6 | 41.8 | 99.3 | 9.4 |
| | (2,5] | 0.00 | 1.6 | 46.5 | 54.1 | 2.0 | 40.1 | 94.8 | 4.8 |
| | (5,10] | 0.03 | 3.3 | 45.7 | 43.4 | 4.9 | 54.9 | 97.8 | 2.4 |
| | (10,15] | 0.03 | 4.1 | 52.7 | 40.5 | 12.7 | 74.7 | 99.5 | 0.7 |
| | (15,20] | 0.09 | 3.8 | 25.9 | 38.3 | 17.7 | 83.3 | 99.5 | 0.7 |

Values show the mean centile value for the Tsimane 5$^{th}$, 50$^{th}$, and 95$^{th}$ centile lines when compared against WHO standards ($\leq$5 years) or references (>5 years) or Shuar references, as well as the expected proportion of Tsimane falling $\leq -2$ *z*-scores on the respective reference.

Shuar in childhood and slightly taller after early adolescence. In terms of centiles, Shuar references perform well when applied to Tsimane values, and Tsimane values perform well when applied to Shuar, in that each produces centile estimates roughly in line with the other (Figure 8, right column; Figures 9 and 10; Tables 4–6).

## 3.9 | Impact of secular trends on growth references

Since data for this study were collected over 13 years, we investigated whether secular trends might affect the validity of growth references. We controlled for age and for repeated measures and community with random effects, and fit linear mixed models with time predicting Tsimane specific *z*-scores for all Tsimane $\leq$ 25 years. Overall, secular trends in height-for-age were small and identical for boys and girls, with *z*-scores increasing by 0.08 *z*-scores per decade ($p < .001$), equivalent to 0.6 cm per decade in adult height. Secular trends in weight-for-age were larger, but only for girls; weight-for-age *z*-scores increased by 0.19 *z*-scores per decade ($p < .01$) for girls, equivalent to 1.4 kg in adult weight, and by 0.07 *z*-scores per decade ($p = .004$) for boys, or 0.5 kg for adults. *Z*-scores for BMI similarly increased by 0.20 *z*-scores per decade for girls ($p < .001$) and 0.09 *z*-scores per decade for boys ($p = .003$), equivalent to 0.56 kg/m$^2$ and 0.16 kg/m$^2$ for adults, respectively.

**TABLE 5** Equivalent weight centiles from WHO/CDC and Shuar references for Tsimane centile values

| Age range (Years) | | Relative to WHO/CDC standards/references 5th | 50th | 95th | % $Z \leq -2$ | Relative to Shuar references 5th | 50th | 95th | % $Z \leq -2$ |
|---|---|---|---|---|---|---|---|---|---|
| Girls | (0,2] | 0.1 | 29.8 | 94.1 | 17.2 | 4.7 | 72.3 | 99.5 | 3.1 |
| | (2,5] | 0.2 | 16.2 | 68.9 | 16.8 | 5.2 | 58.5 | 97.6 | 2.4 |
| | (5,10] | 0.4 | 17.8 | 67.3 | 13.8 | 4.8 | 49.9 | 95.8 | 2.3 |
| | (10,15] | 0.3 | 25.6 | 73.7 | 12.2 | 5.5 | 60.9 | 98.4 | 2.3 |
| | (15,20] | 0.9 | 31.5 | 75.0 | 8.2 | 5.4 | 62.3 | 99.2 | 2.3 |
| Boys | (0,2] | 0.0 | 19.9 | 93.2 | 23.3 | 5.4 | 61.3 | 99.9 | 1.2 |
| | (2,5] | 0.3 | 16.6 | 69.5 | 15.6 | 7.0 | 59.7 | 96.2 | 1.7 |
| | (5,10] | 0.4 | 17.5 | 67.9 | 14.4 | 5.3 | 49.8 | 96.1 | 2.0 |
| | (10,15] | 0.2 | 14.0 | 63.8 | 19.2 | 7.8 | 66.3 | 99.7 | 1.1 |
| | (15,20] | 0.5 | 18.7 | 57.0 | 11.8 | 9.2 | 65.8 | 98.1 | 1.2 |

Values show the mean centile value for the Tsimane 5$^{th}$, 50$^{th}$, and 95$^{th}$ centile lines when compared against WHO standards ($\leq$5 years), WHO references (5–10 years), CDC references ($\geq$ 10 years) or Shuar references, as well as the expected proportion of Tsimane falling $\leq -2$ *z*-scores on the respective reference.

**TABLE 6** Equivalent BMI centiles from WHO and Shuar references for Tsimane centile values

| Age range (Years) | | Relative to WHO standards/references 5th | 50th | 95th | % $Z \leq -2$ | Relative to Shuar references 5th | 50th | 95th | % $Z \leq -2$ |
|---|---|---|---|---|---|---|---|---|---|
| Girls | (0,2] | 0.2 | 62.8 | 99.6 | 11.0 | 8.0 | 79.8 | 99.5 | 2.2 |
| | (2,5] | 9.7 | 68.4 | 97.0 | 1.1 | 10.3 | 62.7 | 96.7 | 0.8 |
| | (5,10] | 16.1 | 57.9 | 88.3 | 0.2 | 6.4 | 46.9 | 92.9 | 1.4 |
| | (10,15] | 12.8 | 58.9 | 91.4 | 0.5 | 3.1 | 46.0 | 97.5 | 3.7 |
| | (15,20] | 21.3 | 68.8 | 94.2 | 0.2 | 2.3 | 46.6 | 97.3 | 5.0 |
| Boys | (0,2] | 0.0 | 57.8 | 99.8 | 13.9 | 2.3 | 58.6 | 99.6 | 4.9 |
| | (2,5] | 9.3 | 73.1 | 98.7 | 1.3 | 6.6 | 49.0 | 95.0 | 1.1 |
| | (5,10] | 17.3 | 64.8 | 92.5 | 0.3 | 7.0 | 40.6 | 89.0 | 0.7 |
| | (10,15] | 9.4 | 51.9 | 86.1 | 1.0 | 3.8 | 44.9 | 96.6 | 2.8 |
| | (15,20] | 13.5 | 55.5 | 86.6 | 0.4 | 1.6 | 39.2 | 95.2 | 6.5 |

Values show the mean centile value for the Tsimane 5$^{th}$, 50$^{th}$, and 95$^{th}$ centile lines when compared against WHO standards ($\leq$5 years) or references (>5 years) or Shuar references, as well as the expected proportion of Tsimane falling $\leq -2$ $z$-scores on the respective reference.

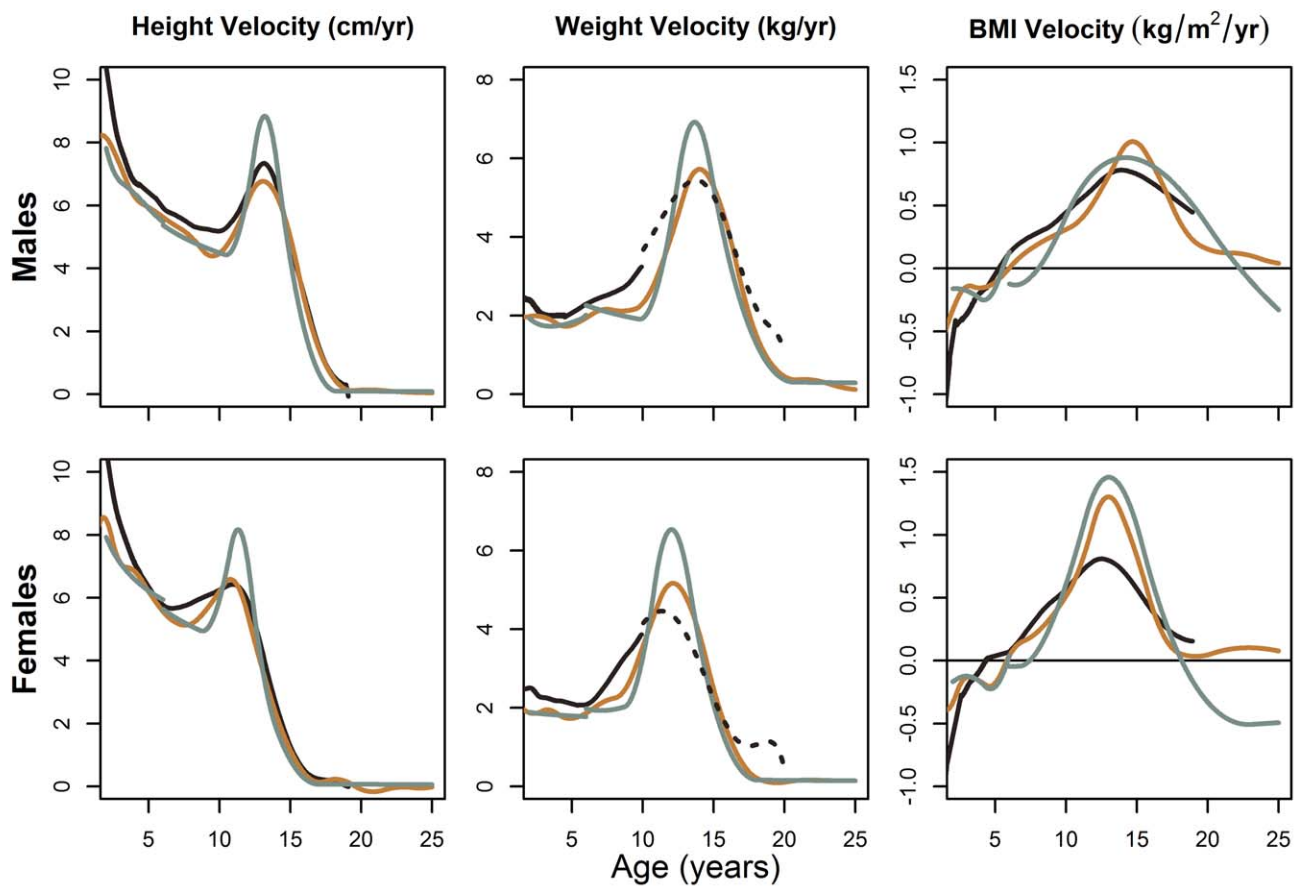


**FIGURE 7** Tsimane velocity curves 2 to 25 years of age. Tsimane curves derived from cross-sectional GAMLSS (orange) and SITAR (slate blue line) analyses are shown, relative to WHO (solid black line) standards (under age 5) and references (over age 5) and CDC references (dashed black line)

**TABLE 7** Equivalent WFH centiles from WHO standards for Tsimane centile values

| | | Relative to WHO standards | | | |
|---|---|---|---|---|---|
| | Height | 5th | 50th | 95th | % $Z \leq -2$ |
| Girls | (45,65] | 0.4 | 88.5 | 100.0 | 8.1 |
| | (65,85] | 0.6 | 59.8 | 98.9 | 7.6 |
| | (85,105] | 12.5 | 68.4 | 96.7 | 0.7 |
| | (105,120] | 13.8 | 61.9 | 92.7 | 0.5 |
| Boys | (45,65] | 0.2 | 87.7 | 100.0 | 9.7 |
| | (65,85] | 0.2 | 53.9 | 99.3 | 11.2 |
| | (85,105] | 11.3 | 71.6 | 97.9 | 1.1 |
| | (105,120] | 22.3 | 71.9 | 95.9 | 0.2 |

Values show the mean centile value for the Tsimane 5$^{th}$, 50$^{th}$, and 95$^{th}$ centile lines when compared against WHO standards, as well as the expected proportion of Tsimane falling $\leq -2$ $z$-scores on the WHO standards.

## 4 | DISCUSSION

We present growth references for the Tsimane of lowland Bolivia, from a sample of 30,118 observations collected over 13 years. This sample size is considerably larger than those previously used to examine growth in small-scale populations (Draper and Howell, 2005; Hurtado, 1996; Orr, Dufour, & Patton, 2001; Stinson, 1989; Walker et al., 2006). For comparison, our sample includes roughly the same number of observations used to construct the WHO multicenter growth standards, and (excluding birth records) about half the number of observations used to construct the CDC references (Kuczmarski et al., 2002). Given that this represents only a single, relatively homogenous population, we have a high degree of confidence that our data accurately represent Tsimane growth, and given modest secular trends, that these data accurately represent Tsimane growth patterns over longer time spans. Moreover, we have chosen modeling procedures that mirror the methods used by the WHO to make our results directly comparable (de Onis et al., 2007b).

Our results show that Tsimane growth differs modestly from WHO references in the first few months of life, particularly for girls. However, after approximately 6 months growth diverges more considerably. Pseudo-velocity curves suggest that between 6 and 24 months Tsimane height velocities for both boys and girls dip below WHO values. The timing of this divergence may coincide with the introduction of complementary foods, which may be a vector for disease and may affect nutritional availability (Martin, Garcia, Kaplan, & Gurven, 2016; Veile et al., 2014). Divergence after 6 months is primarily in height, with Tsimane infants maintaining higher median BMIs and mean BMI velocities than infants in WHO references. Median WFH $z$-scores similarly suggest that median weight is relatively high, although in younger ages Tsimane also show more variance in WFH, with 12% of Tsimane under age two having evidence of wasting.

The pattern of slow height growth persists through early and midchildhood. Median Tsimane height growth remains at or below the fifth WHO centile for both sexes at all ages past infancy, with approximately 40% of individuals considered stunted ($z$-score $\leq -2$) across all ages (Table 4).

Tsimane weight diverges from references less than height, but median Tsimane weight still remains below the WHO 25$^{th}$ centile for most ages (Table 5). About 20% of Tsimane have weight $z$-scores $\leq -2$ in younger age groups, declining to about 9% by adulthood (Table 5). However, weight is generally appropriate for height, and median Tsimane BMI remains approximately between the WHO 50$^{th}$ and 70$^{th}$ centiles for all ages (Table 6). After age two, very few Tsimane have low BMI-for age or low WFH (Table 1). The distribution of Tsimane growth for weight is generally narrower than that observed in reference populations, and shows less evidence of positive skew.

In contrast to differences between Tsimane and WHO standards or references, Tsimane growth closely mirrors the growth of Shuar forager-horticulturalists of Ecuador. Some of these similarities reflect trends that others have noted. Amazonians, in general, are characterized by high rates of child stunting but low rates of underweight and wasting when compared to international standards or references (Orr et al., 2001; Piperata, Spence, Da-Gloria, & Hubbe, 2011; Stinson, 1990; Victora, 1992). The similarities between Shuar and Tsimane growth distributions suggest that Amazonian growth patterns, overall, follow similar trajectories and likely respond similarly to shared environmental factors. These similarities also suggest that Tsimane and Shuar references might be useful for other populations, and that in the future a common growth reference might be constructed that would be applicable to many South American populations.

At 11.3 and 13.2 years for girls and boys, the ages of peak height velocity we report for Tsimane are slightly earlier than those reported for other populations. For example 12.1 and 14.1 for British adolescents (Tanner, Whitehouse, & Takaishi, 1966), 11.8 and 13.4 for Canadian Caucasians (Iuliano-Burns, Mirwald, & Bailey, 2001), 13.3 and 16.1 in Gambian adolescents (Prentice, Dibba, Sawo, & Cole, 2012), and 12.1 and 14.3 for black South African adolescents (Cameron, Gordonlarsen, & Wrchota, 1994). Interestingly one population reporting early peak height velocity is the Shuar, with estimates of 10.2 and 13.6 years based on pseudo-velocity curves from median LMS values (Urlacher et al., 2016a). Pseudo-velocity curves likely result in earlier estimates than SITAR models. This may be particularly true for girls, where less dramatic growth spurts are more easily smoothed by averaging. For the Tsimane pseudo-velocity curves estimate peak height velocities at 10.7 and 13.1. These early height velocities again suggest that Shuar and Tsimane may show similarities in growth patterns.

### 4.1 | Application and need for population specific growth references

From a clinical standpoint, international growth standards are useful for assessing possible differences in health and nutritional status between populations (Eveleth and Tanner, 1990). However, for individual assessment a more interpretable comparison is sometimes how a child's growth compares to that of others in local communities. The danger of using such local references is that they may socially

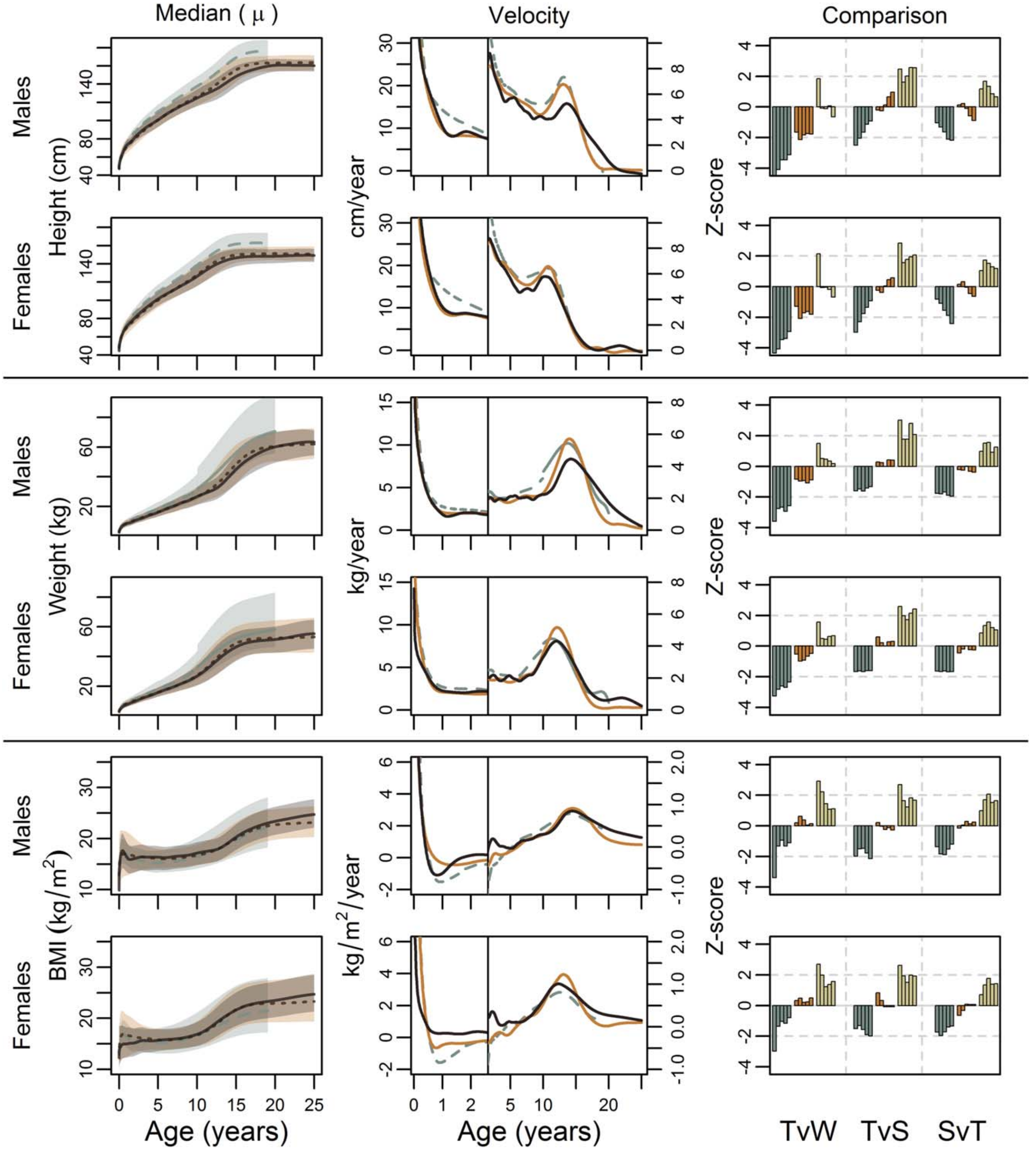


**FIGURE 8** Comparison of Tsimane and Shuar (Urlacher et al., 2016) growth references. Left, overlay of Shuar (black solid line, grey shading), Tsimane (dotted black line, tan shading), and WHO standards/references (dashed blue line, blue shading) or CDC references for weight over age 10 (solid line, blue shading). Middle, comparison of Shuar (solid black), Tsimane (solid tan), and WHO (dashed blue) or CDC (solid blue, weight only) pseudo-velocity curves. Right, comparison of *Z*-scores obtained for Tsimane using WHO standards/references (TvW), Tsimane using Shuar references (TvS) and Shuar using Tsimane references (SvT) at the values corresponding to −2 (blue), 0 (orange), or +2 (yellow) *Z*-scores on the original reference. Bars within each grouping represent age groups of 0–2, 2–5, 5–10, 10–15, and 15–20 years in increasing order. Note TvW for weight over age 10 also uses CDC references instead of WHO standards/references

normalize growth that could be indicative of or associated with poor health or social outcomes (Messer, 1986). Thus, a primary goal of this paper has been to compare Tsimane specific references to WHO references, to help determine under which contexts each reference should be used. Our results suggest that Tsimane references are similar to WHO standards in terms of BMI-for-age and WFH (Figure 10). The

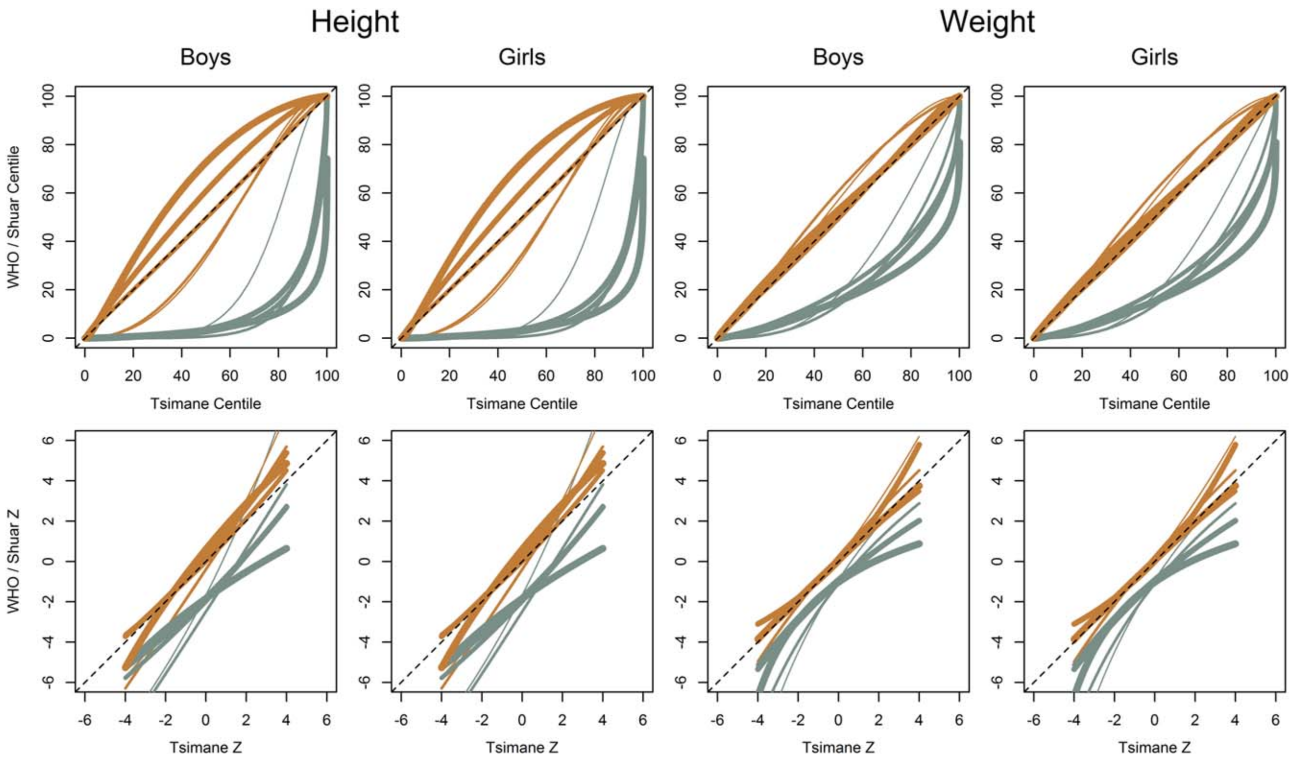


**FIGURE 9** WHO (slate blue) or Shuar (orange) centile or *z*-score values for equivalent Tsimane values for height or weight. Lines, from thinnest to thickest, represent values at 1, 2, 5, 10, and 20 years of age, respectively. For weight over age 10, CDC references are used instead of WHO

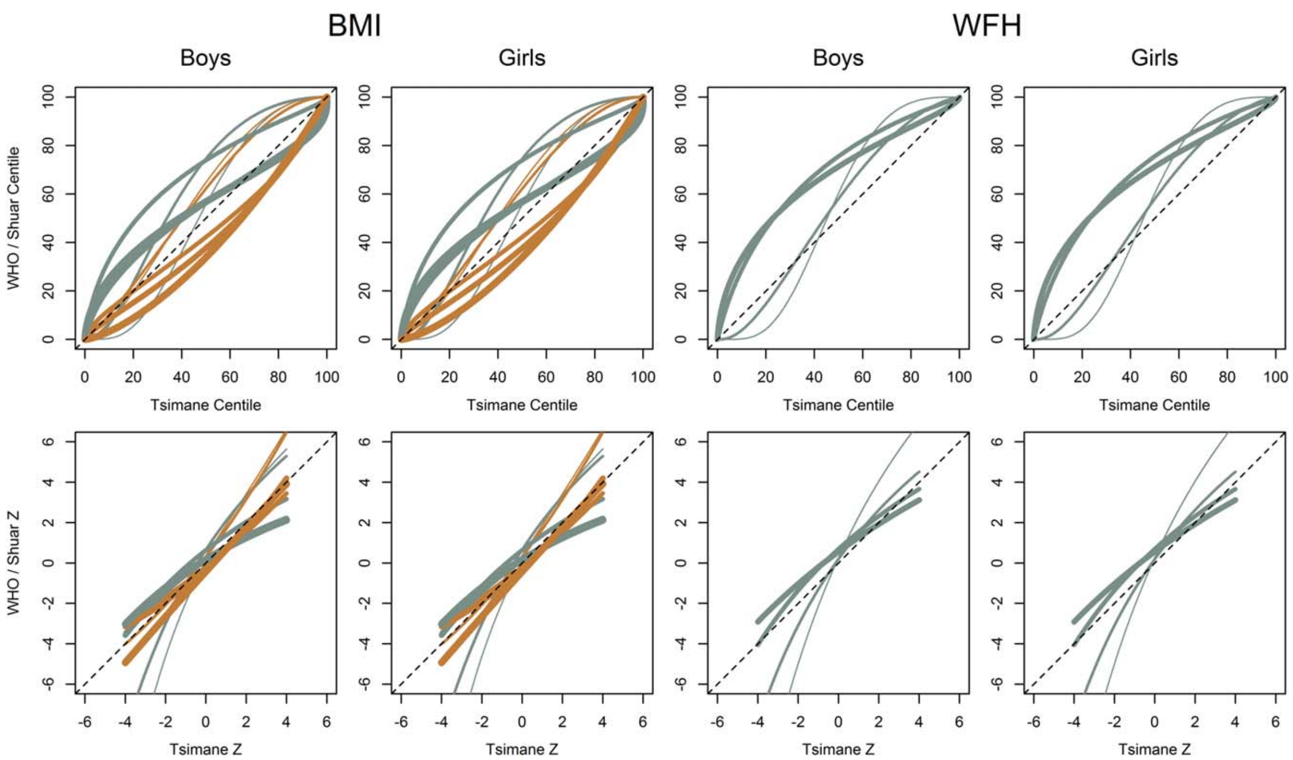


**FIGURE 10** WHO (slate blue) or Shuar (orange) centile or *z*-score values for equivalent Tsimane values for height or weight. For BMI, lines, from thinnest to thickest, represent values at 1, 2, 5, 10, and 20 years of age, respectively. For WFH, lines represent 60, 80, 100, and 120 cm, respectively

primary difference is that Tsimane show more variation in these two measures of weight relative to height at younger ages. Since the Tsimane sample is not restricted to only children known to be healthy, as is the WHO sample, it would be reasonable to assume that this variation might represent early growth disturbances; i.e. by WHO standards, 12% of Tsimane under age 2 can be considered to have evidence of wasting, despite overall high population medians for WFH. This suggests that for the assessment of BMI and WFH as clinical indicators, at least at younger ages, WHO standards might be more appropriate.

Where Tsimane differ most from WHO references is in height, and as a consequence of height differences, in weight. These differences are consistent across all ages, and represent the entire population, as the entire distribution is shifted and there is little evidence of excessive skew. There is little doubt that Tsimane suffer from high burdens of infection and disease (Blackwell et al., 2016; Gurven, 2012). It is likely that this high pathogen burden contributes to the growth patterns we observe. Length/height growth, in particular, appears to be sensitive to infectious disease; inflammation is associated with poorer growth in infant length (Kosek, Haque, Lima, Babji, Shrestha et al., 2013; Prendergast, Rukobo, Chasekwa, Mutasa, Ntozini et al., 2014), and in studies previously completed with the Shuar and Tsimane, higher levels of immune biomarkers are associated with poorer growth in children (McDade et al., 2008), and shorter height in adults (Blackwell, Snodgrass, Madimenos, & Sugiyama, 2010). It remains an open question exactly how genetics and environment interact to produce these outcomes. Genetic pleiotropies may affect both growth and immunity, leading to variation across individuals. Individual growth outcomes are also likely the result of reaction norms governing how growth and other life-history demands trade-off, by regulating relative investment into growth in response to environmental exposures (Blackwell et al., 2010; Mangel and Stamps, 2001; McDade et al., 2008). Similarities between Shuar and Tsimane suggest either similar reaction norms expressed in similar environments, or possibly less plastic shared genetic potentials.

With regard to growth references, then, one relevant question may be how much of Tsimane growth is determined by reaction norms, and might be expected to change if pathogen loads were lower or nutritional status improved. One way to approach this question is by examining the stability of Tsimane growth patterns over the study period of 13 years, during which time access to markets and health care has increased. Overall, secular trends during this period have been small, relative to the differences between WHO references and Tsimane values. We observe increases in height for both sexes approximately equivalent to an increase of 0.6 cm in adult height per decade. At this rate it would take ~200 years of constant increase for Tsimane median height to reach WHO median height. In contrast, women have gained ~1.4 kg per decade and men ~0.5 kg per decade, meaning weight has increased more rapidly. Similar changes have been reported for the Shuar (Blackwell, Pryor, Pozo, Tiwia, Sugiyama, & Pryor, 2009; Urlacher et al., 2016b) and previously reported for the Tsimane with a retrospective sample born between 1920 and 1980 (Godoy, Leonard, Reyes-Garc??A, Goodman, McDade, Huanca et al., 2006).

These trends suggest that changes in pathogen load and nutrition are likely to have effects on Tsimane growth, but also that these changes may not be sufficient to make Tsimane growth look exactly like the growth patterns described by WHO references. Indeed, changes in weight largely represent increases in overweight and obesity, meaning that the current references which have been developed on the Tsimane during a period when overweight is rare may prove particularly useful for defining healthy weight in the future as overweight becomes more common. A similar outcome resulted in the CDC excluding more recent measures in the development of US growth references. In terms of height, references might be updated at some future date, but with current rates of secular change Tsimane are unlikely to reach heights equivalent to international references. For this reason, Tsimane specific height references might be useful in many contexts, in particular for comparisons between Tsimane children, such as in identifying the Tsimane children most at need and in assessing the causes of growth outcomes.

## 4.2 | Growth as an adaptation

The idea that smaller stature might in some cases be "adaptive" remains controversial, despite decades of research and debate (Schell and Magnus, 2007). On the one hand, a clinical model might argue that any growth deficit relative to standards is evidence of suffering, and a failure of a child to "adapt" to disease. On the other, an adaptationist perspective might suggest that small stature can be adaptive due to reduced energy demands, improved thermoregulation, or faster maturation (Migliano et al., 2007; Stinson, 1990; Walker et al., 2006), or that overall smaller stature in Amazonians may represent an adaptation to high pathogen load, and the need to prioritize energy for immune defenses (Blackwell et al., 2016; Gurven et al., 2016; Stieglitz et al., 2016; Urlacher et al., 2016a).

The failure of these two perspectives to reconcile may stem in part from different uses of the word "adaptive." From a clinical perspective, the word "adapt" is used to suggest overcoming of hardship or deprivation, i.e., growing at full potential even in the face of hardship. This perspective rightly acknowledges that this is impossible or at least difficult. From this perspective, adaptiveness is assessed as a comparison between growing to full potential and not growing to full potential, and the conclusion is reached that growing to full potential is better.

However, in an evolutionary sense a trait can be adaptive even if it does not result in the ideal outcome. What is required is that a trait result in higher fitness relative to whatever the actual alternative is. In the case of resource deprivation, the alternative to growing to a shorter stature is to put as many resources as possible into growth, at the detriment of other processes such as immune function or reproduction. When such trade-offs must be made, the result is always going to be "making the best of a bad deal", since the outcome will never be as ideal as having unlimited resources. Moreover, there is no guarantee that the adaptive response will not result in suffering or unhappiness, only that it will result in higher fitness compared to the alternative.

At a fundamental level, growth can be viewed as the outcome of processes by which nutrients and energy are converted into cell divisions. Natural selection can act on at least two elements of these processes: (1) the rate at which cell divisions occur when energy is sufficient for all needs, and (2) the priority given to cell divisions in tissues such as bone and muscle relative to divisions or processes in other cells, when energy and other resources are limited. Note that this priority need not be static, but can be regulated dynamically in response to need, i.e., in the case of infection the division of short lived neutrophils might be critical for survival and so be given a higher priority than other cell divisions.

The first process can be thought of as what is frequently called the "genetic potential" for growth, though the concept of genetic potential is itself problematic, as it implies a ceiling to growth, and that reaching this ceiling means achieving full potential. This may not be the best way to think about growth, as growing larger than is optimal may also be possible, particularly in evolutionarily novel contexts of resource over-abundance. This is clear for weight growth, but might also be possible for height. The second set of processes are the physical processes underlying plasticity in growth and other traits, i.e., reaction norms.

In considering adaptation, researchers may be inexact in specifying the level at which a trait was selected for or is adaptive (Schell and Magnus, 2007). The factors which select for lower growth potential in a population may be different from those that select for changes in reaction norms determining individual plasticity. Thus, the tradition of treating height as the trait under selection, rather than the actual traits regulating growth, leads to confusion about what the selective forces are and exactly what they are acting upon.

Is small stature in Amazonians adaptive? We can ask this question in two ways. First, have there been sufficient costs associated with large size in Amazonians to select for lower potential height growth, even when resources are abundant? Small body size among African rainforest populations is influenced by multiple genes with evidence of selection, and has evolved multiple times (Perry and Verdu, in press). The Americas have been inhabited for much less time and migrations into and out of rainforest environments may have been more frequent. Thus, there are reasons to both hypothesize that Amazonians will differ in genetic potentials for height, and to suspect that such differences might be less than is observed in some African populations. The good news is that even if we cannot answer this question with direct genetic evidence, a natural experiment is currently underway which will answer this question within a few decades; Tsimane and other Amazonian populations are rapidly market integrating and gaining access to market goods and health care (Blackwell et al., 2009; Gurven et al., 2015; Urlacher et al., 2016b). While it may take a few generations to have a definitive answer, if Tsimane do differ genetically from other populations we should see relatively modest secular changes in height, regardless of economic development. Advances in genetic research may further tell us whether these differences are due to selection or more neutral processes like drift.

Second, are reductions in growth in response to resource shortages representative of adaptive reaction norms, or does reduced growth represent the failure of adaptations? First of all, both can be true. In the face of resource shortages organisms no doubt have mechanisms for first trying to make up shortages by becoming more efficient at energy usage or improving resource acquisition. Moreover, individuals will vary in these capacities, making some individuals more resilient in the face of adversity than others. In a sense, it is when these mechanisms fail that reaction norms regulating trade-offs in the face of shortages must come into play. Showing that these mechanisms make ideal allocations or would have made ideal allocation under some past environmental conditions is difficult. However, showing that mechanisms exist which prioritize resources is trivial. If they did not exist then deprivation would affect all physiological systems equally, including the growth of the brain and other organs, and the maintenance of the immune system. This does not appear to be the case, as growth must be severely compromised before deficiencies in other systems, such as cognition, become apparent (Mendez and Adair, 1999).

All of this aside, questions about adaptation are secondary to the more pressing question of whether short stature in Amazonians is indicative of suffering and a need for public health intervention. Whether a trait is adaptive says nothing about whether it is desirable or good, to assume so is to commit the naturalistic fallacy. Are short Tsimane statures indicative of poor growth? Likely they are, however since they also likely indicate population differences, interpreting them as only indicative of poor growth is problematic. Further, analyses have suggested that shorter stature in Tsimane is not necessarily associated with reduced health or well-being (Godoy et al., 2010), and that even with more subtle social outcomes, such as status, other traits such as strength are just as important as height (von Rueden, Gurven, & Kaplan, 2008; von Rueden, Gurven, Kaplan, & Stieglitz, 2014).

Tsimane specific growth curves are not informative with regard to how Tsimane health compares to the health of other populations. However, WHO standards and references are also likely imperfect for assessing the Tsimane, and likely to overestimate the prevalence of problematic poor growth, especially with regard to height. Thus, we would suggest that both measures should be used in combination, and interpreted carefully. An individual who is stunted on both measures is likely at much higher risk than one stunted by WHO references, but in the 50$^{th}$ percentile relative to other Tsimane. Moreover, height may not be the best indicator of nutritional status for Amazonians, as their relatively shorter stature may be partially due to genetic differences. Other indicators, like the prevalence of wasting in Tsimane children under age two are likely better measures. Even better, numerous other studies document the specific health and disease burdens Tsimane face.

## 5 | CONCLUSION

The detailed growth references given here illustrate key differences between the Tsimane and the growth patterns outlined by international standards. Very few small-scale indigenous populations have been described at this level of detail, as most reports are limited to small, often cross-sectional samples. The growth references given here are provided in a variety of formats, including LMS files (S4-S7), centile tables (Supporting Information files S8-S15), and growth charts in English and Spanish (S16-S17). Our hope is that these references may be useful for both research and in the individual assessment of growth amongst the Tsimane and other South American populations.

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## AUTHOR CONTRIBUTIONS

A.D.B. and S.S.U. conceptualized and wrote the paper; A.D.B. conducted all analyses; B.B., C.v.R., A.J., J.S., and B.C.T. organized and compiled project data and oversaw data quality control; A.D.B., B.B., J.S., B.C.T., M.G., and H.K. obtained funding; M.G. and H.K. directed medical teams and project staff; All authors provided editorial contributions to the manuscript.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.