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Adipose development is consistent across hunter–gatherers and diverges from western references

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Despite agreement that humans have evolved to be unusually fat primates, adipose patterning among hunter–gatherers has received little empirical consideration. Here we consider the development of adiposity among four contemporary groups of hunter–gatherers, the Aka, Savanna Pumé, Ju'/Hoansi and Agta using multi-level generalized additive mixed modelling to characterize the growth of tricep skinfolds from early childhood through adolescence. In contrast to references, hunter–gatherers show several consistent patterns: (i) children are lean with little fat accumulation; (ii) no adiposity rebound at 5 years is evident; (iii) girls on average have built 90% of their body size, and reach menarche when adiposity is at its maximum velocity; and (iv) a metabolic trade-off is evident in young, but not older children, such that both boys and girls prioritize skeletal growth during middle childhood, a trade-off that diminishes during adolescence when height velocity increases in pace with fat accumulation. Consistent results across hunter–gatherers living in diverse environments suggest that these patterns reflect a general forager pattern of development. The findings provide a valuable baseline for adipose development not apparent from reference populations. We emphasize both generalized trends among hunter–gatherers, and that inter-population differences point to the plasticity with which humans organize growth and development.

1. Introduction

Building adipose tissue is a critical somatic demand that both consumes energy to store for the future and spends down energy to buffer against fluctuations in food availability [1]. Among primates, humans are particularly proficient at accumulating energy reserves and are unusually sexually dimorphic [2]. Adult females have on average nearly twice the fat mass as males, a trait probably linked to our evolved life history of short birth intervals and rapid reproductive pace, and consequent sex differences in reproductive biology [3]. The general human capacity to build adipose stores, as well as sex-specific differences, emerge during ontogeny, yet we know surprisingly little about how adipose development varies across human populations [4,5]. The vast majority of scholarly work on adipose development has been restricted to industrialized populations, which represent a very recent energetic environment [6]. Constructing growth models of adiposity under non-industrialized energetic conditions provides important insights into the derived human pattern of fat development, how that pattern varies across populations and is changing today with food abundance.

During development, the human body manages the competing demands of funding growth, immune function and reproductive maturation [7,8]. Adipose stores subsidize several costly events, including early brain growth [9], building the immune system [10,11], skeletal growth spurts [12] and reproductive capacity in girls [13–15]. Human infants, who are born relatively fat, continue to gain adiposity during the first six months [16] after which they lose fat (% of mass) until the age of at least 2 years [17]. After infancy, childhood is characterized by a uniquely human suite of slow skeletal growth [18,19], paired with continued intense caloric demands for brain growth [9] and sensitivity to infection [20]. These multiple demands constrain a child's body's ability to build fat stores, evidenced in their remaining stable or declining slightly from the age of 2 to 5 years.

For girls, an increase in fat stores initiates the path to reproductive maturity [21,22]. Marked sex differences emerge during puberty, which is characterized by a skeletal growth spurt and, for girls the development of an energetically costly reproductive system [14]. For boys, the costs of the reproductive system itself are relatively minor [23], and the evidence for an association between adiposity and pubertal onset is mixed. Some studies find a positive association [22] and others a negative or no association [24]. Thus, adiposity has a complex role in several developmental steps that combine to build adults that have greater adiposity than other closely related primates.

If an elevated capacity to store adipose tissue is among the suite of human adaptive phenotypic traits, the best lens on its development is in populations not exposed to factors that disproportionately affect weight and fat gain. For example, the adiposity rebound, an increase in fat stores that occurs after the completion of brain growth, is evident in industrialized populations [25–27], but not among hunter–gatherers [4,5]. Energy-rich environments, or settings where the nutrition transition (the displacement of traditional foods by diets high in saturated fats, sugar and refined foods accompanied by a change in physical activity levels [28]) is underway, probably affect adipose development during childhood and puberty in novel ways. Here, we use data on adipose development in four hunter–gatherer populations since their diet and lifestyle lack these features [18,29,30].

Our interest lies in understanding fat tissue development in the absence of a reliance on agricultural or market foods. Subsistence-based hunter–gatherers offer valuable insights into the adaptive range of maturational trajectories in environments characterized by natural fertility, mortality schedules that are unabated by medical intervention, habitual activity, limited overconsumption of food and seasonal fluctuation in caloric availability [29,31,32]. Such conditions stand in contrast to the recent shifts towards low mortality, low fertility and abundant caloric availability associated with the demographic and nutrition transitions in the developed and developing world.

Although forager lifestyles are diverse [33–37], their subsistence base is generally distinguished by dependence on collected and hunted foods, rather than food produced through animal husbandry or agriculture. Reliance on wild resources in a wide range of ecologies means that hunter–gatherer diets vary considerably in composition, relative inputs of plant versus animal foods and sources of macro-nutrients. Furthermore, foraging strategies express a continuum between immediate and delayed returns to subsistence activities. Immediate-return foraging strategies tend to be associated with equatorial environments, limited food storage and food consumption within a few days of procurement [38].

Accounts of hunter–gatherer diets describe them as diverse, incorporating many fallback foods, often high in protein and high-fibre carbohydrates, having few simple carbohydrates and few if any refined sugars or highly processed carbohydrates [39,40]. With respect to fat tissue development, adiposity is sensitive to food intake and is particularly responsive to simple low-fibre carbohydrates and refined sugars [41], which are limited in hunter–gatherer diets, but common in agricultural and industrial diets, respectively [40].

In addition to dietary composition, periodic exposure to food shortages may play a role in adipose development. For example, cycles of feast and famine are hypothesized to have shaped key features of human metabolism, by favouring metabolic phenotypes that are efficient at storing fat during seasons of plenty [42]. However, these adaptations appear derived in populations with an ancestry of food production and may not reflect developmental traits prior to agriculture [43,44]. Recent evidence shows that foragers experienced less food famine than other subsistence modes [45,46], and that behavioural strategies and plasticity buffer against genetic selection by famine [3,47]. Although famine and starvation are not common features of hunter–gatherer subsistence, seasonal resource fluctuations, which alongside energy constraints, high pathogen loads and the cost of immune system functioning, can also draw energy from somatic development [10,11,48].

It is important to recognize that hunter–gatherers today inhabit a limited range of ecologies compared to even a hundred years ago, and that they vary broadly in being buffered from or exposed to contemporary and historic colonial, market and geopolitical forces [37]. In many cases, they have been marginalized into challenging environments [49], and in others, globalizing factors may influence physical development [37,50]. Despite these varied experiences throughout the Holocene, including contemporary hunter–gatherers in growth and development analyses expands the known variation of human development that would otherwise be under-represented, and helps to unravel the sources and drivers of variability.

Compared to industrial growth references, currently available data from two foraging populations indicate that adipose development in hunter–gatherers is distinct in several ways. First, adiposity decreases across early and middle childhood with an increase only prior to the onset of puberty. Second, the adiposity rebound, which has been thought to be a universal feature of development, is muted or not evident in those hunter–gatherers observed to date [4,5]. Third, for hunter–gatherer children, adipose gains at puberty are more pronounced for girls than boys compared to growth references developed for industrialized populations. For example, Savanna Pumé and Ju//Hoansi girls continue to gain adiposity through adolescence and young adulthood, while boys' adiposity fluctuates and stays at low levels following puberty [4,5]. Likewise, among the Hadza (sub-Saharan foragers), tricep skinfolds decline during early and middle childhood and increase around 9–10 years with the subsequent development of a pronounced sex difference [29].

While adiposity has a key role in complex interactions with other growth processes, much of the research on physical development has focused on height and weight ([31], but see [51,52]). To produce new knowledge about adiposity and its

underlying effect on variation in growth rates, body size and the timing of sexual maturation, first, we generate a baseline by fitting age- and sex-specific growth and velocity curves for skinfold measures for four forager populations. This baseline represents the best estimate of how human bodies store and use fat for development across these populations. Second, to assess the consistency of this baseline, we qualitatively explore the variance across populations in the parameters that describe adipose gains and velocity curves. By doing so, we highlight areas of similarity and difference in adipose development across the four groups, with particular attention to variance in absolute values of fat, velocity of fat deposition and key age-specific shifts in velocity. These parameters are both an assay for total available energy stores throughout development and represent significant milestones in ontogeny. Third, age-specific velocity estimates for adiposity are compared to height to find when during development trade-offs may occur between competing body composition expenditures. These potential, but critical trade-offs, may be masked in growth references constructed from energy-rich populations, where children's bodies can afford to invest in linear growth while simultaneously building fat stores. Under leaner more adaptively representative conditions, children may stagger and prioritize different investments as strategies to make the most of energy constraints [5]. Finally, we discuss evidence for a generalized growth pattern that describes adipose development among four hunter-gatherer populations and offer potential explanations for between-population variation in terms of ecological determinants of mortality, disease and diet. The generalized pattern generates a model from which to explore variation in other hunter-gatherer or foraging populations.

2. Material and methods

The data include tricep skinfolds and height from four foraging populations: the Savanna Pumé (Venezuela), the Ju'/Hoansi (Nambia), Agta (Philippines) and the Aka (Congo) (table 1). The four populations differ in terms of ecology and population history. The Agta and the Aka are both short-statured tropical forest foragers. The Savanna Pumé live in a hyper-seasonal flooded savannah, and Ju'/Hoansi live in a semi-arid and tree-scrub savannah (see the electronic supplementary material for more ethnographic detail). In the hunter-gatherer groups included here, children are breastfed until weaning between 2 and 3 years old, have physically active childhoods, largely traditional foraging diets, with some exposure to market foods in some populations, and grow up in relatively unsanitized epidemiological environments [53]. Few datasets exist that have detailed measures of adiposity alongside anthropometrics, particularly for children and adolescents.

(a) Adiposity measures

Skinfolds and height were obtained using conventional anthropometric techniques. Tricep skinfolds are a non-invasive measure and a reliable indicator of children's nutritional status and overall fat reserves [54,55]. Skinfolds are widely reported in the cross-cultural literature, and the standard for measuring adiposity in remote areas without electricity or medical facilities. In addition to tricep skinfolds, three of the four foraging populations have subscapular skinfold measures, which is an additional measure of adiposity. These data are cross-sectional, though the Savanna Pumé children and some Ju'/Hoansi children have multiple measures at different ages. Individuals from birth to the age of 25 years are included in the analysis. Data and analysis scripts are available at <https://doi.org/10.5061/dryad.f7m0cfz53>.

(b) Statistical analysis

The raw data are used to model sex-specific growth curves for tricep skinfolds, using a generalized additive mixed-effects modelling (GAMM), which captures the nonlinear trends in tricep skinfolds with age, while accounting for the variability of different populations [56]. This modelling approach differs from a conventional use of loess smoothing to derive growth curves among cross-sectional growth data from small-scale populations [31]. While both approaches can be useful for analysing growth data from different populations, GAMM offers the additional advantages of flexibility, incorporating random effects, statistical inference and automatic smoothness selection and has been used in modelling anthropometric growth [57,58].

The procedure incorporates smooth functions for age and population effects, which produces a model that estimates both a baseline—a model average curve—incorporating all populations, and population-specific curves. The model's hierarchical nature allows the population-specific curves to 'borrow' information from the overall model to adjust parameters. Thus, this model's key feature is that the smooth functions are allowed to vary across populations, while still drawing on information from the sample as a whole. The model is estimated by maximizing the likelihood of observing the data given their structure and parameters and generates a predicted growth curve for each population using predicted tricep values at quarter-year increments (every three months).

From these skinfold growth curves, we estimate velocity curves to extract the age at take-off, the maximum velocity and the age at maximum velocity. Age at take-off is determined by selecting the point on the curve where the velocity in tricep growth was closest to 0 prior to increasing. For girls, velocity at menarcheal age is also estimated. We compare these parameters to the same velocity parameters taken from height curves. For height, a simple loess smoothing function is employed to produce the growth and velocity curves. We chose a loess smoothing function for height rather than the more complicated GAMM modelling because height increases monotonically with age during childhood and adolescence, whereas adiposity both increases and decreases during the same age periods. A sensitivity analysis for height using the GAMM models is included in the electronic supplementary material and shows qualitatively similar results to those reported below.

Table 1. Sample descriptives.

population	<i>n</i> individuals			<i>n</i> observations		
	observations	repeated	individual	tricep	scapula	height
females						
Agta	113	0	113	113	113	113
Aka	120	0	120	107	107	119
Ju/Hoansi	568	340	228	342	332	330
Pumé	103	40	63	92	0	100
males						
Agta	134	0	134	134	134	133
Aka	106	0	106	98	98	106
Ju/Hoansi	504	281	223	316	306	280
Pumé	88	34	54	79	0	86

Finally, the estimated skinfold curves are plotted against published reference curves derived from multiple data sources in the United States [59]. These reference curves were constructed using five nationally represented surveys (two waves of National Health Examination Survey and three waves of the National Health and Nutrition Examination Survey) in the United States and are the same sample as those used to create the Center for Disease Control and Prevention 2000 Growth Charts (hereafter referred to as the reference).

3. Results

(a) Generalized hunter–gatherer adipose growth

The *generalized hunter–gatherer curve* shows low levels of adiposity for both boys and girls compared to the reference (figures 1*b* and 2*b*). Girls in the sample consistently have thinner tricep skinfolds than the reference. Their tricep reaches its maximum at 10.95 mm at approximately the age of 20 years. At the same age, the reference median was 18.73 mm, with no indication of levelling off [59]. In addition, the reference shows an adiposity rebound of around 6.5 years. By contrast, forager girls' adiposity continues to decline until the age of 8 years where it stays between 6.6 and 6.7 mm before beginning to increase again at 10 years. For girls, this take-off point is very similar across the hunter–gatherer groups, occurring at a mean age of 9.25 years, with populations ranging from 8.5 to 10 years (table 2), which is 2–3.5 years later than the reference.

The boys in the sample have notably lower adiposity levels compared to the reference. In the reference, the boys' tricep declines from 9.74 mm at 1.5 years to 8.17 mm at 6.5 years before increasing to 9.73 mm at the age of 11.5 years and dropping again to 8.18 mm by the age of 16 years. Thus, United States boys' median tricep thickness fluctuates between approximately 8.0 and 9.75 mm throughout development. By contrast, the generalized hunter–gatherer curve, tricep skinfolds decline from approximately 8 mm at six months to 5.75 mm by 6.5 years. Then between the ages of 6.5 and 20, the curve fluctuates between 5.75 and 5.25 mm. That is, boys stay close to approximately 5 mm throughout adolescence and into adulthood and are consistently approximately 3 to 4.5 mm leaner than the United States reference. Additionally, there is little difference in the amount of fat between take-off and maximum velocity (table 2). Finally, boys take-off at similar ages across populations (at the age of 11.3–13 years), apart from the Aka (8.08 years), though given the low levels of fat and fluctuations throughout childhood and adolescence, it is unclear how biologically meaningful this take-off is.

(b) Differences in adipose growth between hunter–gatherer populations

The population-specific curves are consistent across the hunter–gatherer groups in the overall levels of fat and timing of take-off, strengthening the interpretation that the generalized hunter–gatherer curve reflects a meaningful estimate of adiposity across the four populations. For the girls, the timing of take-off (at approx. age 9 years) and level of adiposity (at approx. 6.5 mm) are very similar across populations. Nonetheless, several population differences are evident. The Aka have the highest tricep skinfolds (13.09 mm) and continue to deposit fat well into adulthood, peaking in their late 20s (electronic supplementary material, figure S3), whereas the Agta have the lowest levels by the end of adolescence (8.67 mm). In addition to variation in absolute levels of fat, the rate of fat deposition differs among girls. The Savanna Pumé show the highest levels of velocity (1.25 mm per four months during peak), double that of the Ju/Hoansi (0.61) and nearly triple the Agta (0.43) maximum velocities. In addition to a higher maximum velocity, the Savanna Pumé reach maximum velocity earlier than the other populations. From take-off, at 8.5 years old, the Savanna Pumé reach peak velocity at the age of 12.25 years, in 3.75 years. In other populations, it takes 6–8.5 years from take-off to reach peak velocity.

Notably, fewer population differences in adiposity are observed for boys compared to girls, suggesting greater canalization in boys' than girls' adipose development. Minimum levels of boys' tricep curves range from 4.76 to 5.81 mm with the Agta

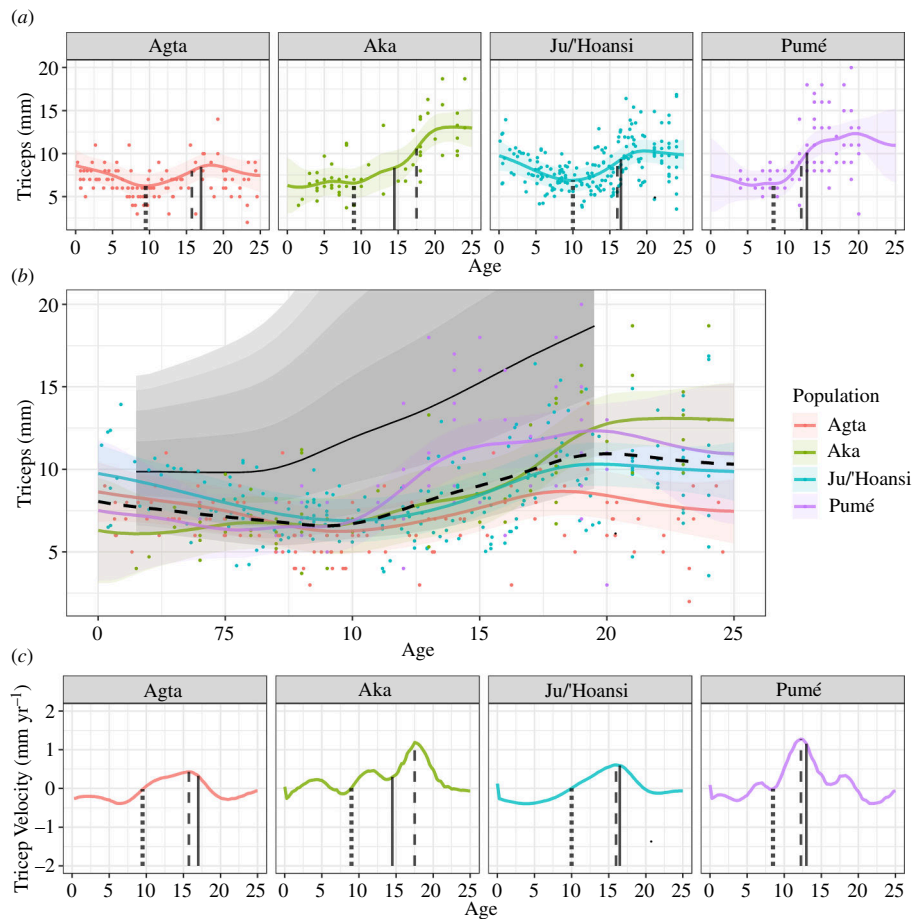


Figure 1. Girls' triceps gains and velocity curves predicted from the GAMM. (a) plots the estimated, population-specific curves with the raw data from each population. (b) plots all curves, including the model-specific generalized hunter–gatherer curve (black dashed line). The solid black line reflects the median of the United States reference curve [59] with the grey shaded areas denoting the 50th, 75th, 90th, 95th and 97th percentiles of the reference curve. (c) plots the velocity curves. The solid vertical lines show the age at menarche, the dashed vertical line shows the age at maximum velocity and the dotted line shows the estimated age at take-off.

lowest and the Ju/'Hoansi highest. Similar to girls, the Savanna Pumé and the Aka show slightly higher maximum adiposity velocity during adolescence than the Agta and Ju/'Hoansi (table 2). However, the overall low levels of adiposity make it difficult to assess how biologically significant these fluctuations are.

(c) The timing of and trade-off between skeletal growth and adipose deposition

For both boys and girls, peak fat velocity and peak height velocity (table 3; electronic supplementary material, figure S2) occur at different ages, suggesting a shifting prioritization in body composition through development where height gains are prioritized before fat gains. For girls, age for peak height velocity ranged from 9 (Savanna Pumé) to 14 years (Ju/'Hoansi). At peak velocity, height gains vary from 4.4 (Ju/'Hoansi) to 7.5 cm per year (Savanna Pumé). Across the four groups, peak skeletal growth occurs between 2 and 3.25 years prior to peak triceps velocity, with the exception of the Aka where peak skeletal growth is nearly 8 years earlier, reflecting their extended period of adipose deposition.

For boys, peak height velocity occurs across a wider age range than girls, from 10.75 (Aka) to 17 years (Ju/'Hoansi). At peak velocity, height gains varied from 4.59 (Ju/'Hoansi) to 8.21 cm yr⁻¹ (Aka). Similar to the girls, in most populations, peak triceps velocity follows peak height velocity by 0.5–3.75 years, with the exception of the slow-growing Ju/'Hoansi where the pattern is reversed, and triceps velocity peaks 3.75 years prior to peak skeletal growth.

To better understand the prioritization of fat versus skeletal growth during development, height velocity is plotted against triceps skinfold velocity (figure 3), which points to potential trade-offs in energy allocation. The figure stratifies childhood (<9 years) and adolescence (≥9 years), and each panel is divided into quadrants. In the upper right quadrant, both fat and skeletal velocities are positive, suggesting lack of a trade-off. By contrast, in the lower right quadrant skeletal velocity is positive, but fat velocity is negative pointing to a potential trade-off. Most data points, however, fall in the lower right quadrant, indicating that children of ages 3–9 years make gains in skeletal growth (velocity is positive) with little to no fat deposition (adiposity is flat or negative). This pattern is more pronounced for boys than girls.

The trade-off between an increase in height velocity and declining triceps velocity observed in younger children reverses in older children. After the age of 9 years, the relationship between height and adipose velocity clearly changes. For girls, most data points fall in the upper right quadrant, indicating that both skeletal growth and fat deposits are positive. Furthermore, three of the four populations show a positive correlation, indicating that as skeletal growth increases, fat deposition does as well. The Aka are an exception, consistent with their selection for shorter stature and reduced skeletal growth [60]. For boys,

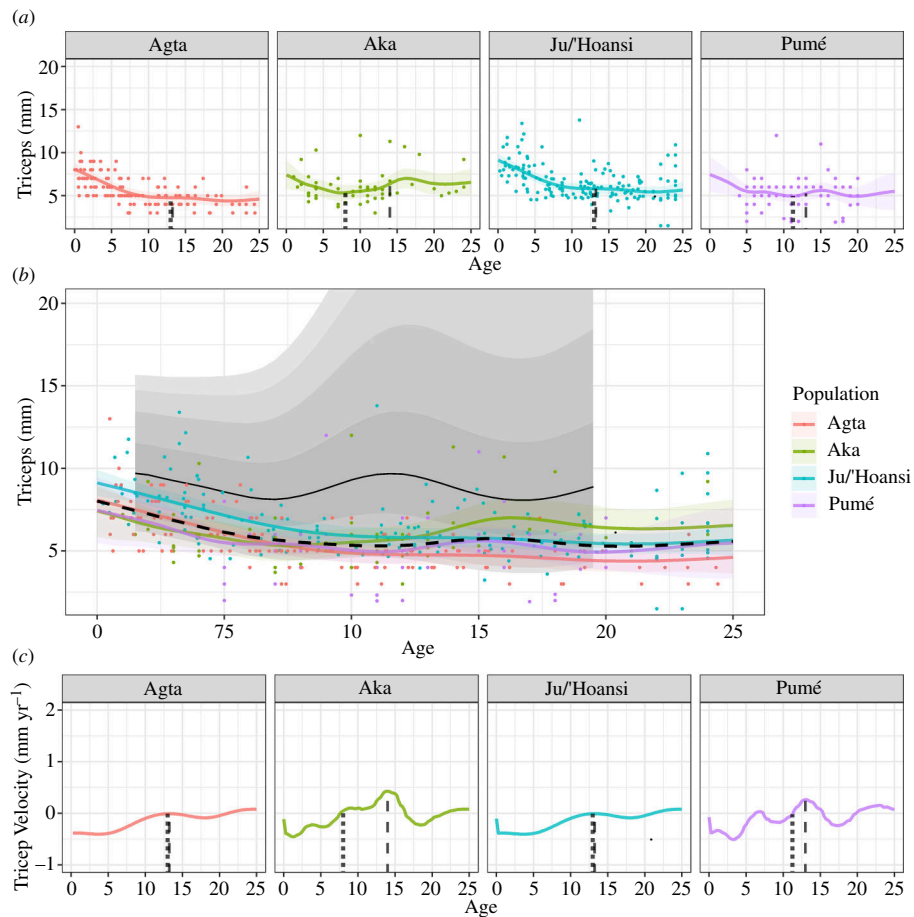


Figure 2. Boys tricep growth and velocity curves predicted from the GAMM. (a) plots the estimated, population-specific curves with the raw data from each population. (b) plots all curves, including the model-specific generalized hunter–gatherer curve (black dashed line). The solid black line reflects the median of the United States reference curve [59] with the grey shaded areas denoting the 50th, 75th, 90th 95th and 97th percentiles of the reference curve. (c) plots the velocity curves. The dashed vertical line shows the age at maximum velocity and the dotted line shows the estimated age at take-off.

Table 2. Timing (age) of growth and velocity of triceps skinfolds for boys and girls.

population	max tricep	age at max tricep	min tricep	age at min tricep	max tricep velocity	age at max tricep velocity	menarche	tricep at menarche	tricep velocity at menarche	% of max tricep at menarche	% of max tricep velocity at menarche
females											
Agta	8.67	18.25	6.24	9.5	0.43	15.75	17	8.47	0.33	98%	76%
Aka	13.09	22.25	6.58	9	1.19	17.5	14.5	8.36	0.3	64%	25%
Ju/Hoansi	10.32	19.75	6.9	10	0.61	16	16.5	9.34	0.6	91%	98%
Pumé	12.34	19.5	6.53	8.5	1.28	12.25	13	10.11	1.16	82%	91%
males											
Agta	5.12	8.25	4.76	13	−0.01	13.25					
Aka	7.01	16.25	5.34	8	0.43	14					
Ju/Hoansi	6.17	8.25	5.81	13	−0.01	13.25					
Pumé	5.62	15.25	4.94	11.25	0.27	13					

the pattern is similar yet muted given their low levels of adiposity. That is, during adolescence as skeletal velocity increases for boys, fat velocity also increases. In summary, during adolescence, skeletal growth does not appear to trade off with fat deposition, as it appears to do prior to puberty.

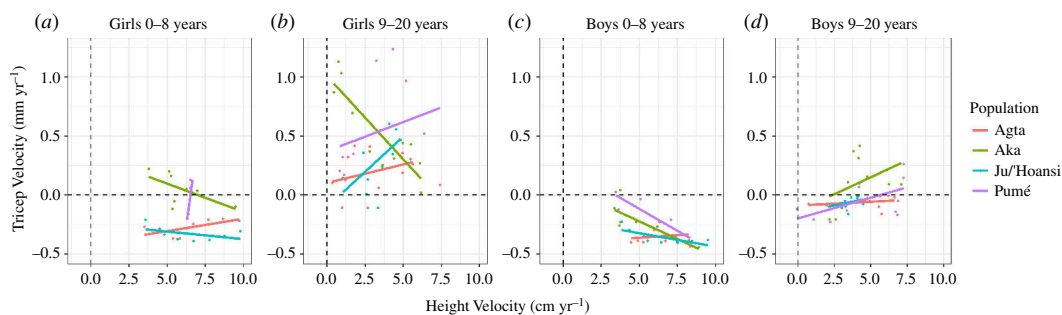


Figure 3. Height velocity plotted against tricep velocity for girls, age 0–8 years (a) and age 9–20 years (b), and boys, age 0–8 years (c) and age 9–20 years (d) with dashed lines indicating 0 velocity. Data points reflect age-specific averages of both velocity measures, rounded to the nearest whole year. Coloured line segments are simple Ordinary Least Squares regression lines. All data points are right of the centre line, reflecting positive skeletal growth throughout development. Data points below the horizontal dashed line show negative velocity, or fat stores shrinking from one year to the next (as in (a) and (c)). Data points above the dashed horizontal line show an increase in fat stores from year to year. The generally positive association during adolescence (9–20 years old) indicates no evidence for a trade-off between skeletal growth and fat deposition.

Table 3. Height velocity and timing (age) for males and females.

population	height max velocity	age at max height velocity	max height	age at max height	age at max tricep velocity	age at menarche	height at menarche	height velocity at menarche	% of max height velocity at menarche	% of max height at menarche
females										
Agta	6.02	13.5	148.55	24.5	15.75	17	142.07	1.38	23%	96%
Aka	6.23	9.5	146.16	20.25	17.5	14.5	139.87	3.24	52%	96%
Ju/Hoansi	4.94	14	151.42	20.5	16	16.5	144.34	3.81	77%	95%
Pumé	7.46	9	150.88	20	12.25	13	141.11	3.28	44%	94%
males										
Agta	6.91	12.25	154.11	19.5	13.25					
Aka	8.21	10.75	149.77	20	14					
Ju/Hoansi	4.59	17	156.41	20	13.25					
Pumé	8.09	12.5	164.35	18.75	13					

(d) Adipose development and menarche

Average age at menarche varies from age 13 to 17 years across the four populations, and patterns with adipose and height velocity. Girls reached menarche 0.5 and 1.25 years after peak adipose velocity (figure 1), after achieving 82–98% of adult adiposity. The exception is Aka girls, who reach menarche at 64% of maximum tricep measures, reflecting a period of adipose deposition that extends well into adulthood. In contrast to fat, and consistent with known associations between skeletal growth and menarche [15], girls reached menarche very close to adult height (approx. 94–96% of adult height) in all the populations.

4. Discussion

(a) Establishing a hunter–gatherer baseline for adiposity development

Several consistent patterns of adipose gains are evident among the four hunter–gatherer populations: (i) compared to the United States reference, hunter–gatherer children, as sampled here, are lean across all ages, particularly boys, with modelled and observed levels of fat well below the reference; (ii) consistent with previous findings for two of the groups [4,5], an adiposity rebound at 5–6 years is not evident for either boys or girls. Similar to the reference, the adiposity of hunter–gatherer children declines in early childhood, which is probably owing to the canalized energy demands of brain growth [61,62]. Indeed, energy used by the brain peaks at two-thirds of resting metabolic rate, when children are close to 5 years old, and decreases until achieving adult levels at around 10 years [9]; and (iii) in contrast to the reference, children in our sample do not put on adipose tissue during middle childhood. Rather, the period between the completion of brain size, between the ages of 5 and 6 years, and the onset of puberty, between the ages of 9 and 11 years, is characterized by low adiposity and low or negative fat velocity. That is, children from these four foraging populations do not prioritize fat deposition during middle childhood, as

they do in energy-rich reference populations evidenced by the adiposity rebound [63]. These results and contrasts imply two important points. First, the occurrence of the adiposity rebound in energy-rich populations after peak brain growth suggests that additional energy availability does not lead to additional brain growth, nor does it hasten skeletal growth. Rather, it goes directly to fat stores [64]. Second, under the age of nine, hunter–gatherer children face a metabolic trade-off between investing in height and fat, as evidenced in their putting on height while losing fat reserves.

(b) Interpreting low adiposity of forager children

The foragers examined here are lean and have among the smallest skinfold thickness recorded in contemporary human populations, which raises an open and debated question of interpretation. Is hunter–gatherer leanness reflective of current conditions of marginalization, exacerbated social and political stress, undernutrition, and pathological insult; or is leanness an ancestral trait to which hunter–gatherers are adapted [50,65]? In other words, does forager leanness observed here reflect the range of human developmental plasticity, or a pathological accommodation [66,67]?

For example, studies among the Ju/Hoansi have found mixed evidence for malnutrition prior to the 1970s [68], with conflicting interpretations of body size and composition as an indication of nutritional stress. More recent studies found an increase in weight among the Ju/Hoansi over time alongside concurrent changes in diet [69]; however, it is not clear how much of this increase is owing to changes in diet composition or overall caloric increases. On average between 1969 and 1987, adult males gained only 1.4 kg while adult females gained 1.9 kg, despite a marked increase in nutritional status [70]. This would seem a small change if the population were chronically undernourished in 1969. Different interpretations in part reflect whether one is addressing an evolutionary question or seeking a public health solution to human impoverishment. The appropriate use of anthropometrics across diverse populations to indicate evidence of suffering or pathology has been subject to debate in the last two decades [71–73]. What is clear is the need for quantitative data that can speak to the causal links between anthropometric measures, such as tricep skinfolds, and cognitive development, morbidity and mortality, to substantiate both their statistical and their biological significance [74].

(c) Timing of skeletal growth and adiposity among hunter–gatherers

In this sample of hunter–gatherers, the metabolic trade-off observed during middle childhood attenuates during adolescence, when children aged 9–18 years make gains in both height and adiposity. The positive association between height and fat velocity is evident for boys and girls but is most prominent for girls. The lack of an apparent trade-off during puberty raises a question about where the energy comes from to make substantial gains in skeletal growth as well as to grow or maintain fat reserves. One candidate explanation is the reduction in the energetic demands of the brain through childhood and into adolescence. Based on results from a United States sample, energy demands of the brain reach a peak at 5 years and drop to adult levels at about the age of 10 years [9]. More specifically, for boys and girls, the brain accounts for approximately 66% of glucose consumed at rest at the age of 5 years, declining to 40% at the age of 10 years. By 10 years of age, a quarter of the glucose used at rest can be reallocated to skeletal growth and/or increased adipose deposition. In energy-rich populations, starting at the age of 5 years, the decline in energy dedicated to brain growth leads directly to increased allocation to adipose tissue well before the onset of puberty. Among forager children facing more stringent caloric availability, the prioritization of fat tissue development may only occur after the metabolic demands of brain growth have been reduced, typically after the age of 10 years.

This internal reallocation of metabolic resources may also result in staggering peak growth in different somatic domains. For example, we previously found evidence that peak velocity in Savanna Pumé girls' height, weight and adiposity is distributed over a 5-year period, while in industrialized populations, reference girls experience all three peak gains over a 2-year period [5]. Thus, distributing the timing of peak growth spurts may be an important developmental strategy in food-limited environments. In addition to metabolic strategies, adolescents can behaviourally manage investments in both height and fat by either increasing caloric intake or downwardly adjusting energy expenditure. In some ethnographic cases, pubertal girls, for example, are preferentially fed [75] while in others, as among the Savanna Pumé, pubertal girls have lower activity loads, which avails more energy to fund somatic investments in skeletal growth and adipose stores [76,77].

Our results further find that adipose deposition is not in competition with skeletal growth among the girls, which adds clarity and nuance to the long-standing argument about whether pelvic diameter or adipose stores are the more robust predictor of age at menarche [13,15]. Secular trends in industrialized populations show links between increasing body mass index and puberty development [78], with longitudinal evidence showing that the timing of menarche is first associated with bone age and then with per cent body fat [21]. Our results likewise support this association (the Aka are an exception). Girls reach menarche at between 94 and 96% of adult height, compared to 64–98% of maximum adiposity. At menarche, height velocity is slowing down as adult skeletal size is nearly complete, and fat is being deposited rapidly.

(d) Plasticity in hunter–gatherer adipose development

Between-population comparisons highlight the consistency of adipose development among the sampled hunter–gatherers, particularly during middle childhood. In three of the four populations, boys' age at take-off is at least 2.5 years later (13, 13 and 11.25 years) than girls. This is consistent with the later initiation of puberty in boys than girls observed in energy-rich populations [79,80], which may be increased under conditions of energy restriction. The Aka are an exception, with boys

reaching take-off sooner than girls (8 versus 8.5 years). As calories needed to grow the brain are reduced, the newly available energy may be differentially reallocated by males and females [81]. For girls, skeletal growth may take priority in adolescence to achieve reproductive maturity. By contrast, males may benefit from delayed skeletal growth or by prioritizing lean mass through adolescence, a pattern observed among industrial populations [2].

After adipose take-off, the timing and rate of adiposity deposition are more variable between the hunter–gatherer populations. Both the Savanna Pumé and Aka girls have more rapid fat deposition and are associated with earlier ages at menarche. By contrast, Ju/Hoansi and Agta girls deposit fat more slowly and have later ages at menarche [61,82]. Variations in diet, mortality and pathogen burdens are key explanatory candidates for the observed population differences in adipose development, and its association with skeletal growth and reproductive ontogeny. With respect to dietary differences, evidence from energy-rich populations suggests that along with caloric intake, specific dietary components, and protein in particular have a demonstrated impact on advancing the timing of maturation (see [82] for a review). A recent meta-analysis across multiple countries, including almost 11 000 girls, found that early menarche is associated with higher intakes of protein, iron and polyunsaturated fats [83]. Similarly, a large United Kingdom sample (10 000 children followed from *in utero* to 8 or 9 years) from the Avon Longitudinal Study of Parents and Children found that girls who have higher total caloric intake and higher protein intake at the age of 6 years had earlier ages at breast stage 2, peak height velocity and menarche. The pubertal timing of boys in the study, however, was associated with total energy intake only [84]. Given these findings, a dietary explanation for between-population differences in adiposity and timing of reproductive development would focus on both average total caloric consumption as well as macronutrient composition of children and adolescents. Reliable data on macronutrient intake, however, are available for very few subsistence populations (see [85] for a discussion of Amazonian horticulturalists).

Life-history theory posits that high juvenile or subadult mortality may lead to faster growth and development [86,87]. Variations in extrinsic mortality may influence population differences in life histories including growth rates, age at menarche and the onset of reproduction [31,88–92]. Extrinsic mortality may be signalled by detectable cues to harsh environmental conditions, which are known to influence ontogeny in nonhumans [93]. However the relationship between mortality and growth is complex. For example, among the Savanna Pumé, the early reproductive maturation and the relatively fast deposition of fat during puberty may result from their relatively high mortality [90]. Another study analysing genetic variation among African rainforest hunter–gatherers suggests a reversal of the causal direction, such that age at reproduction is a pleiotropic effect of genes related to height [94].

Immune response likewise may influence variation in adolescent growth among the four hunter–gatherer groups, as pathogen burdens and mounting an immune response have been shown to compete with energy available to grow and to impact growth rates [10]. Thus, populations living in contexts with higher pathogen loads, all else being equal, are expected to have smaller bodies or slower growth owing to costly investments in the immune system at the cost of the skeleton [10,48]. Alternatively, if pathogen stress constitutes a central mortality risk, then pathogen load may be associated with increased growth rates and earlier reproduction. However, it is unknown whether predictions that focus on skeletal growth rates and body size would apply to adiposity. For instance, current evidence finds that across populations, higher pathogen loads are associated with lower central but not peripheral fat deposits [95]. Signatures of selection in response to pathogen stress have been documented among Amazonian populations [96,97] and among the Aka [60]. Additionally, ecological differences in pathogen burden and reduced selection for genes related to immune function are reported among the Ju/Hoansi compared to the neighbouring Khomeini [98]. This difference is interpreted to be the result of less exposure to outside groups among the more isolated Ju/Hoansi.

(e) Caveats, limitations and future directions

Estimating growth curves using cross-sectional data from populations rather than longitudinal data from individuals within the population comes with notable limitations [19]. Cross-sectional data provide a single temporal snapshot that can mask individual differences in growth patterns owing to averaging effects. They also cannot capture dynamic changes that occur over time. In addition, cross-sectional results cannot account for confounding factors that may impact growth trajectories. Thus, misinterpretations of trends can arise from cohort effects and selection biases in sample composition. Among hard-to-reach hunter–gatherers, collecting longitudinal data is logistically challenging, particularly if they are mobile foragers with flexible camp membership as is the case with the groups studied here. Additionally, long-term and longitudinal follow-up studies require institutional funding commitments that may not be incentivized. However, cross-sectional data provide valuable insights into growth trends and patterns, offering a starting point for understanding development within these unique and evolutionary appropriate contexts. Our results point to future work that incorporates data from the other few studies of foraging populations that have recorded tricep skinfolds, or other measures of adiposity [32,52]. Of particular interest would be data from South American groups that might corroborate the differences between the Savanna Pumé and the African and southeast Asian populations. Results from the Inuit would also be of specific interest given their role as ancestors to extant Amazonian populations [99].

5. Conclusion

Our results have important implications for understanding human adipose development. Several generalized patterns are observed across foraging societies despite differences in ecological settings. Patterns of adiposity for girls and boys across our sample suggest that a decline in adiposity during middle childhood with a pre-pubertal increase reflects different

developmental patterns compared to post-industrial reference. In addition, the trade-off in adiposity and skeletal growth during middle childhood provides important empirical evidence for the understanding that brain growth has priority during development, and how reduced energy consumption by the brain may lead to flexibility in energy allocation across the sexes during puberty. Three of the four populations show very similar patterns of adiposity and skeletal growth, especially among girls. Whether this consistency, observed among tropical foragers, reflects a general pattern of adipose development requires analyses of growth in a wider breadth of foraging ecologies and lifestyles. Expanding the analyses of body fat development to more diverse hunter–gatherer populations, as well as other small-scale subsistence populations, will clarify the extent to which our results reflect a forager baseline and provide insights into the range of variation in adipose development in non-industrial populations.

Ethics. Ethical approval was provided by the UCL Ethics Committee (UCL Ethics code 3086/003) and carried out with permission from local government and tribal leaders in Palanan. Informed consent was obtained from all participants, and parents signed the informed consents for their children (after group and individual consultation and explanation of the research objectives in the Agta language. Informed consent for the Pume research was obtained in accordance with Venezuelan local legislation and national guidelines. Protocols were approved by IRB ethics committees at Harvard and Stony Brook Universities.

Data accessibility. Data and analysis scripts are submitted to the Dryad Digital Repository [100].

Supplementary material is available online [101].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. J.V.H.: conceptualization, data curation, formal analysis, visualization, writing—original draft, writing—review and editing; B.C.C.: conceptualization, data curation, visualization, writing—original draft, writing—review and editing; B.H.: data curation, writing—original draft; A.E.P.: data curation, writing—review and editing; K.L.K.: conceptualization, data curation, writing—original draft, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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