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Adolescence is characterized by more sedentary behaviour and less physical activity even among highly active forager-farmers

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Over 80% of adolescents worldwide are insufficiently active, posing massive public health and economic challenges. Declining physical activity (PA) and sex differences in PA consistently accompany transitions from childhood to adulthood in post-industrialized populations and are attributed to psychosocial and environmental factors. An overarching evolutionary theoretical framework and data from pre-industrialized populations are lacking. This cross-sectional study tests hypotheses from life history theory, that adolescent PA is inversely related to age, but this association is mediated by Tanner stage, reflecting higher and sex-specific energetic demands for growth and reproductive maturation. Detailed measures of PA and pubertal maturation are assessed among Tsimane forager-farmers (age: 7–22 years; 50% female, $n = 110$). Most Tsimane sampled (71%) meet World Health Organization PA guidelines (greater than or equal to 60 min/day of moderate-to-vigorous PA). Like post-industrialized populations, sex differences and inverse age-activity associations were observed. Tanner stage significantly mediated age-activity associations. Adolescence presents difficulties to PA engagement that warrant further consideration in PA intervention approaches to improve public health.

1. Introduction

Inadequate physical activity (PA) is one of the leading causes of global chronic disease burden, responsible for billions of dollars in healthcare costs and lost productivity each year [1]. Recent population-based surveys of self-reported PA found 28% of adults worldwide are insufficiently active, defined as less than 150 min week^{-1} of moderate intensity PA or 75 min week^{-1} of vigorous PA [2]. Additional concern stems from the recognition that a staggering 80% of adolescents (11–17) worldwide are insufficiently active, defined as less than 60 min d^{-1} of moderate-to-vigorous PA [3]. True prevalence of inadequate PA is likely even higher because self-reports typically overestimate PA relative to wearable devices [4–6]. In the USA, just 5% of adults and 8% of adolescents meet PA guidelines when measured via actigraphy [5].

Two of the most consistent findings in epidemiological studies are that PA declines with age and that males are more active than females [7,8]. The steepest age-related declines in PA are observed during adolescence and occur at earlier ages for girls than boys in several post-industrialized countries [5,7,9–14]. A pooled analysis of 26 longitudinal studies of primarily self-reported PA in adolescents aged 10–19 estimates a 7% decline in PA per year [9]. Long-term longitudinal studies of adolescents in the UK and Canada found that low PA levels following these precipitous declines largely persist into adulthood [13,14], a pattern also supported by cross-sectional epidemiological research in the USA [5]. It is critical to understand factors underlying these consistently observed sex differences and decreases in PA in adolescence to inform the development of more targeted and effective PA interventions.

Although epidemiological patterns of PA in adolescence are consistent across most post-industrialized populations studied to date, we have a limited understanding of factors influencing PA during adolescence in settings more reminiscent of our pre-industrial past. While no single population represents the mosaic of environments in which humans evolved, populations living a subsistence-based lifestyle that necessitates high levels of obligatory PA, with little to no access to social media, television or video games offer interesting contrasts to post-industrialized populations in urbanized settings. Research on PA in adolescents in these populations is needed to help disentangle the influence of post-industrialized environments and lifestyle versus developmental constraints on PA during the transition from childhood to adulthood.

A growing body of epidemiological research shows that PA during adolescence is not only associated with age, but also timing of biological maturation. Sex differences in the pace of PA decline are attenuated when using an estimate of maturation-relative age (i.e. biological age), rather than chronological age [7,14–21]. When included in the same statistical model, maturation-relative age more strongly predicts PA than chronological age [7]. A range of measures have been used to estimate biological age in these studies including predictive equations to estimate proportion of adult height reached [17] or age from peak height velocity based on population-based averages [7,19], while a few studies have measured peak height velocity [14,22] and/or used self-reported measures of Tanner stage of reproductive maturation [14,21]. Notably, biological age is often considered a factor that 'confounds' the understanding of sex differences and age-related declines in PA [15,17,19].

One hypothesis to explain the association between biological maturation and PA is that the psychosocial stress of puberty leads adolescents to adopt 'health risk' behaviours (e.g. tobacco, alcohol and drug use, and unprotected sex) [13,15]. Physical inactivity is considered a health risk behaviour in post-industrialized settings, where the leading causes of death are non-communicable diseases (e.g. heart disease, stroke, type 2 diabetes), inactivity is pervasive, and PA occurs primarily through leisure time exercise rather than through obligatory subsistence labour or transportation. To further test predictions based on this and other hypotheses, studies are needed that include objective measures of PA, more accurate measures of biological maturation and are conducted in populations where physical inactivity is not necessarily a health risk behaviour.

Life history theory provides an alternative framework to derive hypotheses for examining the relationships between age, biological maturation and PA/inactivity, positing that because energy and time are finite, organisms face trade-offs in how to allocate time and energy during their lifespans between competing demands of growth, reproduction and maintenance (i.e. immune system and somatic repair) [23,24]. The optimal way to allocate limited time and energy between these competing demands has been shaped by natural selection in ways that reliably promoted survival and reproductive success over large evolutionary time scales. Traditional life-history models have been expanded to integrate how energy intake and expenditure, including PA, influence and are influenced by life-history trade-offs [25].

Hormones are key regulators coordinating the strategic allocation of energy between somatic functions in ways that are age, sex and environment specific. Adolescence is a life stage characterized by distinct endocrinological, anatomical and cognitive changes that likely require substantial energetic resources, though the energetic costs of these hormones and related physiological sequelae have not been fully quantified [26]. Puberty is associated with higher resting and total energy expenditure, partly due to increases in body size and fat-free mass; but skeletal growth, pubertal hormones and neurocognitive changes are also assumed to play a role [26]. During periods of greater energetic demands for growth and development (i.e. adolescence, pregnancy, lactation), PA may be reduced and sedentary time increased to help conserve energy for meeting these demands. Among Hiwi and Ache hunter–gatherers, for example, nursing mothers spend less time foraging and acquire less food than do non-nursing women [27].

A large body of research has demonstrated that high levels of PA, or low food intake, can also delay puberty, or suppress the female reproductive axis—adaptively shifting energy toward survival and away from reproduction when food availability is low or physical demands are high [28–36]. Sex differences in PA and sedentary time may, therefore, emerge regardless of environmental context during the transition from childhood to adulthood because sexually dimorphic changes prior to and during pubertal maturation increase the relative energetic costs of engaging in PA for females (e.g. smaller lung volume and capacity, lower cardiorespiratory fitness, lower anaerobic energy production and power, more body fat relative to fat-free mass) [37], while female reproductive maturation and fecundity can benefit from conserving energy and accumulating adipose tissue needed for pregnancy and lactation [25,38]. By contrast, PA facilitates accumulation of muscle mass and strength, which is particularly beneficial for males in preparation for future adult reproductive and economic roles in pre-industrialized environments.

The goal of this study is to help clarify the roles biology and environment play in influencing sex differences in PA, and the relationships between age, biological maturation and PA through in-depth measurement of PA and maturation in a pre-industrialized environment more reminiscent of our evolutionary past. This cross-sectional study among Tsimane children and adolescents includes measures of PA and sedentary time and intensity using Actigraph wGT3X+ accelerometers, contextualized with concurrent 24-hour PA recall interviews, and Tanner stage assessments validated with hormonal and somatic measures of growth and maturation: dehydroepiandrosterone (DHEA), testosterone, height velocity, body fat and grip strength. The Tsimane are an indigenous population of forager-horticulturalists residing in the Amazon basin in lowland Bolivia. They have little to no access to electricity or running water, show high levels of habitual PA [39], minimal hypertension (3.9%) [40] and the lowest recorded prevalence of coronary artery disease [41]. The vast majority of calories in the diet are produced through slash-and-burn horticulture, hunting and fishing; less than 10% of calories are derived from store-bought goods (e.g. cooking oil, refined sugar and salt) although market items are becoming increasingly prevalent [42].

The overarching hypothesis is that the energetic needs for growth, reproductive maturation and reproduction are heightened during adolescence and pose fundamental constraints on the energy available for PA across all environments. A negative association between age and PA is consistently observed during the transition from childhood to adulthood because these energetic demands trade-off against energy available for PA. Thus, we predict that age-activity associations would be observed among Tsimane adolescents, even though high levels of PA are necessary for daily life, and physical inactivity is not a health risk behaviour in this population (P1). We also predict that Tsimane males would have higher levels of PA, similar to the sex differences observed in post-industrialized countries, because changes prior to and during reproductive maturation also change the costs and benefits of PA, favouring higher levels of PA in males (P2). Lastly, we predict that the association between age and PA is mediated by Tanner stage of reproductive maturation, supporting the hypothesis that the wide range of anatomical and neuroendocrine changes encompassed within Tanner stages explain the associations between age and PA, rather than confound them (P3).

2. Results

(a) Sedentary time and physical activity

Tsimane children and adolescents spent 356 ± 80 min of daytime hours in sedentary time, 327 ± 76 min d^{-1} in light intensity PA, 92 ± 49 min d^{-1} in moderate-to-vigorous PA (MVPA) and accumulated 13 334 ± 4026 steps d^{-1} on average (table 1). The majority (71%) meet professional guidelines of greater than or equal to 60 min of MVPA d^{-1} for PA in children and adolescents [3].

Self-reported activities from 24-hour recall interviews are presented in electronic supplementary material, table S2. Device-based measures of PA and sedentary were minimally impacted by attending school, as the majority of participants (60%) spent no time in school during study participation, while 24% spent one 4-hour day and 16% spent two 4-hour days in school, with no sex differences and younger children more likely to have spent time in school than older children. In the full sample, recalled wake-time was divided accordingly: sedentary leisure activities (33%); sedentary habitual/obligatory activities (22%); light intensity habitual/obligatory activities (11%); moderate-to-high intensity transportation (11%), habitual/obligatory activities (10%) and leisure activities (8%); followed by light intensity leisure activities (4%) and transportation (1%) with sedentary transportation (less than 1%) making up the smallest proportion of recalled wake-time.

(b) Device-measured sedentary and PA behaviour by sex and age (P1 and P2)

Consistent with P1, age was positively associated with sedentary time, and negatively associated with light PA and steps/day (*p*'s < 0.001), and MVPA (*p* = 0.05, table 2*a*), adjusting for sex. Each year increase in age was associated with 4% more sedentary time (15 min d^{-1}, s.e. = 1.81), 6% less light intensity PA, 4% less MVPA and 426 fewer steps d^{-1} (4%). Consistent with P2, males had 14% less sedentary time than females (330 ± 84 versus 382 ± 69 min d^{-1}), 91% more MVPA min/day (122 ± 45 versus 64 ± 33 min d^{-1}) and accumulated 33% more steps d^{-1} (mean ± s.d.: 15 278 ± 3954 versus 11 524 ± 3819 steps d^{-1}), while light PA was not significantly different in males and females (table 2). Sex differences remained significant after controlling for age (*p*'s < 0.001, table 2*a*). Sex × age interactions were not significant for any PA outcome, so were not included in the reported models.

(c) Mediation through Tanner stage (P3)

Standardized estimates from structural equation models (SEM) testing the mediating effect of Tanner stage on the associations between age and sedentary/PA outcomes are presented in table 3 and figure 1. The indirect effect of Tanner stage significantly mediates the associations between age and all four outcomes: sedentary min d^{-1} ($z = 3.97$, $p < 0.001$), light intensity PA min d^{-1} ($z = -2.05$, $p = 0.04$), MVPA ($z = -2.68$, $p = 0.005$) and steps d^{-1} ($z = -2.81$, $p = 0.005$). The direct effects between age and sedentary/PA outcomes are no longer significant when accounting for the indirect effect through Tanner stage except in the MVPA model ($z = 2.27$, $p = 0.02$). The correlation matrix for SEM variables is presented in electronic supplementary material, table S3.

The indirect effect of age on sedentary time through Tanner stage indicates that each year increase in age is associated with an increase of 23 sedentary min/day (7%). The indirect effect of age on light intensity PA through Tanner stage suggests that each year increase in age is associated with a decrease of 12 min of light intensity PA d^{-1} (4%). The direct effect of age on MVPA suggests that each year increase in age is associated with an increase of 9 min of MVPA d^{-1} (10%), whereas the indirect effect of age through Tanner stage suggests that each year increase in age is associated with a *decrease* of 11 min of MVPA d^{-1} (12%). The indirect effect of age on steps/day through Tanner stage indicated that each year increase in age is associated with a decrease of 1014 steps d^{-1} (8%). Figure 2*a* displays PA time and intensity within sex by Tanner stage, representing the direct effects observed in the SEM.

(d) Self-reported activity type and intensity by sex and Tanner stage

Figure 2*b* displays the proportions of recalled wake-time spent in each activity type/intensity by Tanner stage and within sex. Both males and females in later Tanner stages reported smaller proportions of time in leisure time MVPA (e.g. playing chase, playing with others, playing soccer) in a linear pattern, which started and ended higher in males (males: 20% in Tanner 1 to 8% in Tanner 5 versus females: 8% in Tanner 1 to less than 1% in Tanner 5). Inverse linear patterns across Tanner stages were observed for habitual/obligatory activities (e.g. labour to produce/process food): females in later Tanner stages reported larger proportions of time in light intensity habitual/obligatory activities like food processing and washing clothes (6% in Tanner 1 and 30% in Tanner 5), whereas males in later Tanner stages

Table 1. Participant characteristics, Actigraph estimates and measures of somatic growth and maturation. Values are provided for the full sample, separately by sex and within sex by Tanner stage. Means and (standard deviations) and significant sex differences presented below. Abbreviations: T, Tanner stage; MVPA, moderate-to-vigorous physical activity; DHEA, dehydroepiandrosterone.

	females						males						
	all females	T1	T2	T3	T4	T5	all males	T1	T2	T3	T4	T5	full sample
N	55	10	9	10	10	16	55	14	10	10	9	12	110
age	13.7 (3.1)	10.1 (1.0)	11.2 (1.9)	13.1 (1.1)	14.3 (1.1)	17.5 (1.8)	13.7 (3.3)	9.9 (1.2)	12.4 (1.0)	13.4 (0.8)	15.0 (1.1)	18.3 (1.9)	13.7 (3.2)
anthropometry													
weight (kg)	41.8 (10.1)	27.7 (2.1)	33.0 (3.4)	44.5 (4.7)	46.8 (4.2)	50.7 (6.7)	43.5 (15.7)	26.7 (3.0)	37.5 (8.3)	40.1 (4.7)	51.0 (4.9)	65.6 (11.0)	42.7 (13.1)
height (cm)	143.6 (9.2)	129.2 (4.4)	137.5 (6.3)	147.6 (5.3)	148.7 (3.3)	150.3 (3.2)	146.4 (15.0)	126.6 (4.6)	140.4 (6.4)	147.5 (5.5)	158.6 (3.2)	164.4 (2.7)	145.0 (12.4)
body fat (%)	19.2[a] (2.8)	16.1 (1.9)	17.8 (1.4)	20.0 (2.9)	21.6 (1.8)	20.1 (2.1)	6.6 (3.1)	4.9 (2.2)	6.2 (1.7)	5.9 (1.7)	7.3 (1.2)	9.1 (5.0)	13.0 (7.0)
actigraph													
sedentary (min d^{-1})	381.6[b] (69.1)	294.6 (49.9)	334.9 (35.1)	386.7 (36.6)	432.9 (60.0)	430.0 (37.2)	330.2 (83.5)	247.1 (56.3)	318.9 (55.7)	331.8 (72.3)	411.6 (77.4)	380.4 (47.0)	356.4 (80.4)
light intensity PA (min d^{-1})	320.7 (71.7)	395.4 (26.8)	380.6 (36.9)	307.7 (37.5)	280.1 (77.9)	268.1 (55.1)	333.7 (79.4)	390.4 (76.0)	355.8 (50.6)	363.2 (67.1)	279.1 (58.6)	267.1 (50.7)	327.1 (75.5)
MVPA (min d^{-1})	63.7[a] (32.7)	87.2 (45.7)	65.5 (13.4)	67.4 (35.8)	59.3 (30.1)	47.0 (21.6)	121.9 (45.1)	133.6 (42.1)	119.1 (27.3)	104.3 (36.1)	113.9 (73.7)	128.7 (42.0)	92.3 (48.8)
steps d^{-1}	11 464.2[a] (3130.4)	13 371.3 (3091.5)	12 494.1 (2989.0)	11 976.6 (3368.2)	10 876.8 (2421.4)	9585.6 (2652.6)	15 277.6 (3954.4)	17 443.8 (4123.0)	15 671.8 (3497.8)	14 692.8 (2881.7)	13 745.2 (4762.9)	13 947.9 (3567.2)	13 334.2 (4025.9)
growth and maturation													
height velocity (cm yr^{-1})	3.7 (2.9)	5.5 (1.0)	6.4 (1.0)	6.0 (1.8)	2.7 (1.6)	0.2 (0.9)	4.5 (2.2)	4.7 (0.8)	5.5 (1.3)	6.4 (1.6)	4.8 (2.7)	1.7 (1.5)	4.1 (2.6)
grip strength	19.9[b] (5.6)	14.7 (2.3)	15.8 (3.5)	20.8 (4.8)	21.5 (3.5)	23.9 (5.9)	24.9 (11.4)	13.9 (1.8)	18.0 (3.5)	21.7 (4.6)	31.6 (7.2)	41.1 (6.4)	22.4 (9.3)
DHEA (pg/ml)	44 270.2 (46 196.7)	15 250.2 (9754.3)	24 705.9 (21 180.3)	29 397.1 (27 349.5)	61 064.0 (25 795.2)	73 068.7 (69 579.8)	37 524.7 (37 387.3)	11 951.8 (8322.3)	22 533.5 (17 132.5)	27 898.4 (12 966.0)	64 248.7 (47 504.8)	68 348.4 (44 441.5)	40 864.7 (41 911.0)
testosterone (pg/ml)	26 203.1 (20 068.1)	14 908.6 (12 498.2)	20 448.1 (21 137.2)	23 001.0 (16 943.4)	25 187.3 (7910.1)	39 031.3 (25 125.7)	27 530.2 (23 392.0)	9136.0 (5185.4)	17 755.8 (14 505.4)	27 842.3 (23 765.7)	38 008.3 (22 350.7)	48 437.6 (24 047.4)	26 860.2 (21 680.3)

[a]Significant sex differences, $p < 0.001$.

[b]Significant sex difference, $p < 0.01$.

Table 2. Linear regression models of age- and sex-related differences in sedentary time and physical activity. Abbreviations: MVPA, moderate-to-vigorous physical activity. Note: sex = male served as the reference category. See electronic supplementary material, table S4 for regressions demonstrating height, these relationships are not confounded by height. Significance of bold: $p < 0.05$.

outcome	predictor	*Unstd. B*	s.e.	*p*-value	adjusted R^2
sedentary (min d^{-1})	age	15.1	1.81	**<0.001**	0.46
	sex	−50.6	11.52	**<0.001**	
light intensity PA (min d^{-1})	age	−15.1	1.78	**<0.001**	0.41
	sex	12.5	11.36	0.27	
MVPA (min d^{-1})	age	−2.3	1.18	0.05	0.37
	sex	58.2	7.6	**<0.001**	
steps d^{-1}	age	−426	101	**<0.001**	0.33
	sex	3800	646	**<0.001**	

Table 3. Direct and indirect effects testing Tanner stage as a mediator of the relationships between age and activity variables. Abbreviation: MVPA, moderate-to-vigorous physical activity. Significance of bold: $p < 0.05$.

outcome variables	exploratory variables	standardized estimate	s.e.	*p*-value
sedentary minutes	direct effect - age	−0.32	0.07	0.16
	indirect effect - Tanner	**0.92**	**0.23**	**<0.001**
light minutes	direct effect - age	−0.08	0.27	0.78
	indirect effect - Tanner	**−0.56**	**0.27**	**0.04**
MVPA minutes	direct effect - age	**0.64**	**0.28**	**0.02**
	indirect effect - Tanner	**−0.79**	**0.28**	**0.005**
steps per day	direct effect - age	0.49	0.30	0.10
	indirect effect - Tanner	**−0.83**	**0.3**	**0.005**

reported a larger proportion of time spent in moderate-to-high intensity habitual/obligatory activities like chopping trees and accompanying others to get materials from the forest (6% in Tanner 1 to 14% in Tanner 5).

Females in Tanners 1–4 reported similar proportions of time in moderate-to-high habitual/obligatory activities (approx. 10%), and Tanner 5 females reported a similar proportion of time as males (14%). Males reported negligible light intensity habitual/obligatory activities. Three categories were fairly consistent across Tanner stages and sexes: moderate-to-high intensity transportation (approx. 10%), sedentary habitual/obligatory (approx. 20%) and sedentary leisure (approx. 30%). See electronic supplementary material, figure S1 for social and non-social leisure activities.

3. Discussion

Given the high prevalence of insufficient PA in adolescents worldwide and the increasing prevalence of childhood obesity and lifetime chronic diseases associated with inactivity, this study sought to help clarify the underlying biological and environmental factors that influence PA and sedentary time at this critical life stage. In line with our predictions, we found a significant positive association between age and sedentary time, and negative associations between age and steps/day and time spent in light intensity PA and MVPA among Tsimane children and adolescents despite their rural, pre-industrialized, subsistence lifestyle. The age-activity associations did not vary by sex, and males and females had similar levels of light intensity PA. Males spent significantly less time being sedentary, almost twice as much time in MVPA, and accumulated more steps/day than females.

These findings provide an important comparison to help disentangle the effects of the environment and biology on PA during adolescence. The strikingly similar patterns observed in the Tsimane, and a large body of epidemiological research conducted in post-industrialized populations, suggests that the age-activity associations and sex differences in PA/sedentary time in the transition from childhood to adulthood may be based on universal energetic trade-offs during the pubertal transition, and hence an innate feature of the human lifespan. Tsimane children and adolescents live in an environment that is more reminiscent of those faced by our ancestors for most of human history than in post-industrialized settings. During the period of study, they did not have access to computers, video games, tablets or smartphones; they spent very little time in formal schooling; and they are maturing into a subsistence-based economy that relies on high levels of PA to produce food through foraging and small-scale horticulture. Despite these environmental differences, older adolescents spent more time being sedentary, less time in light intensity PA and MVPA, and accumulate fewer steps/day than children.

By contrast, absolute levels of PA were much higher, and the prevalence of insufficient PA is much lower in the

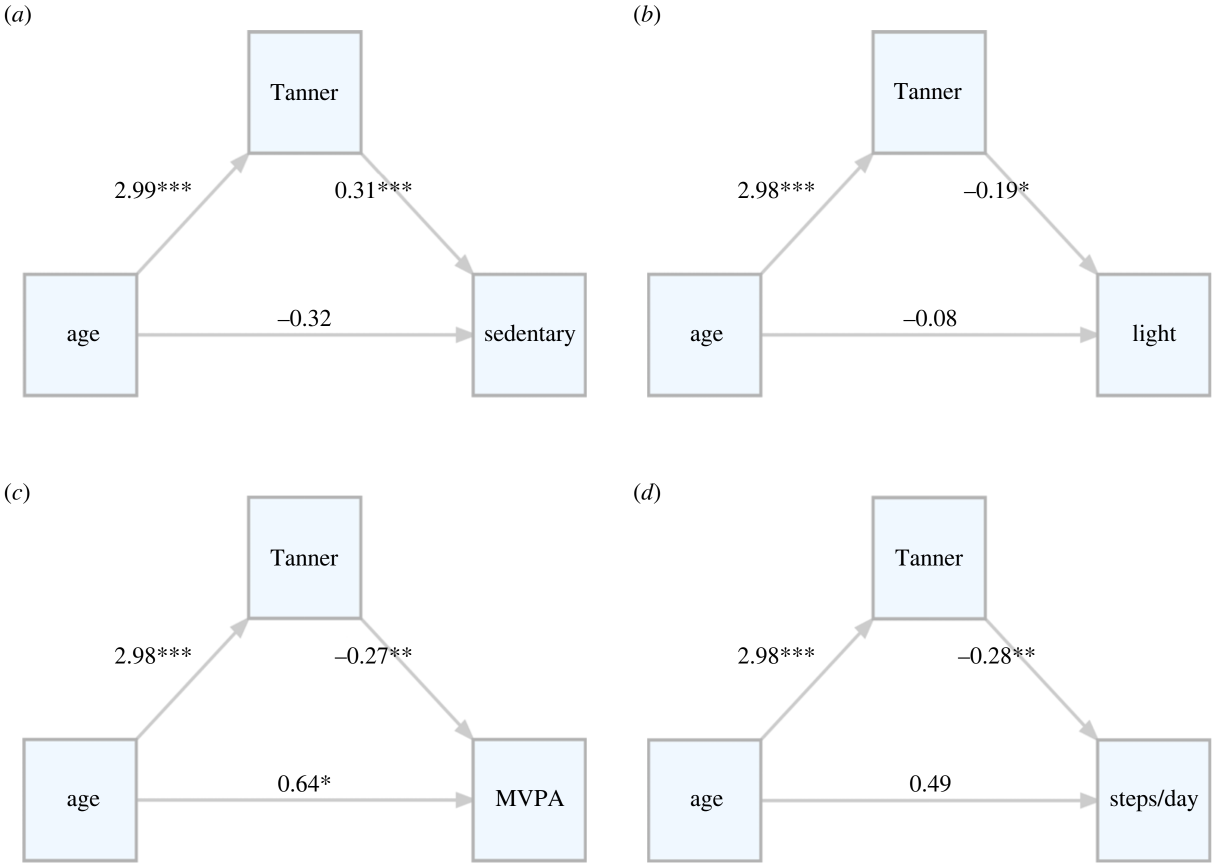

Figure 1. Structural equation models testing Tanner stage as a mediator of the age-activity relationships. Standardized estimates for each path testing Tanner stage as a mediator of the relationships between age and PA outcomes ((*a*) sedentary time, (*b*) light intensity PA, (*c*) MVPA, (*d*) steps d^{-1}) in the full sample. Abbreviation: MVPA, moderate-to-vigorous physical activity. Statistical significance for each direct path are noted as follows: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

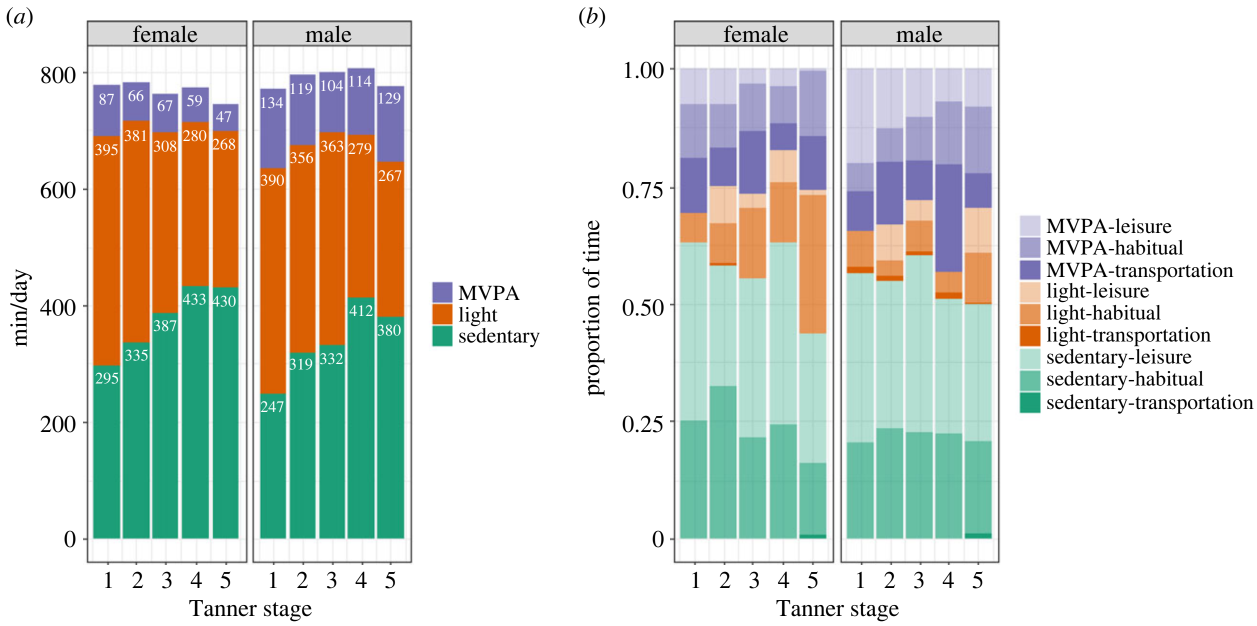

Figure 2. Device-measured (*a*) and self-reported (*b*) physical activity and sedentary time within sex by Tanner stage. Abbreviation: MVPA, moderate-to-vigorous physical activity.

Tsimane compared with most populations studied to date, even when comparing device-measured PA in the Tsimane to self-reported survey data that tends to *overestimate* PA. Just 29% of our sample, which had a broader age range, do not meet PA guidelines, whereas 80% of adolescents (aged 10–17 years) worldwide do not meet PA guidelines based on a recent pooled analysis of survey data [3]. Even though MVPA levels were high, Tsimane in our sample still self-reported spending most of their time in sedentary leisure and habitual activities, as well as light intensity habitual/obligatory activities, consistent with observations in Tsimane adults [39], and other indigenous populations with highly active lifestyles [43], demonstrating that sedentary behaviours are common in people of all ages, and leisure time

PA is not the primary contributor to high levels of PA observed in adults in pre-industrialized populations.

This study also helps clarify why biological maturation, rather than age alone, is a stronger predictor of PA during adolescence. We tested predictions derived from a life-history framework, that associations between age and activity are explained by a wide range of anatomical and neuroendocrine changes encompassed within Tanner stages by testing mediational path models in SEM with indirect paths between age and activity through Tanner stage. Our mediational results demonstrate that Tanner stage explains the relationships between age and sedentary time, MVPA min d^{-1}, steps d^{-1}, and to a lesser degree, light intensity PA. In all models but MVPA, the inclusion of a mediational path through Tanner stage eliminated the significant relationship between age and PA.

The current findings do not support the hypothesis that adolescents become more sedentary as a form of increasing health risk behaviours in response to the psychosocial stress of puberty because physical inactivity is not a health risk behaviour for the Tsimane. Instead, our findings support our primary hypothesis that the energetic needs for growth, maturation and reproduction are heightened during adolescence, and so trade-off against the energy available for PA, regardless of the environmental context. Another study of device-measured PA in adolescent Yucatec Maya agriculturalists also supports the hypothesis that energy for growth competes with energy available for PA [44]. In that study, observational PA measures and anthropometry were measured over a 20-year span during which a school and mechanized technologies were introduced to a rural community, but diet (energy availability) was minimally changed. PA level declined substantially, while height, weight and body fat increased. It could also be that the importance of building embodied social capital through communication-based social activities becomes increasingly important during reproductive maturation [45]. The self-report data revealed that lower intensity social leisure activities were more prevalent in Tanner stages 2–5 than Tanner 1, while moderate-to-vigorous social activities were more prevalent in Tanner 1 than Tanner 2–5. Time spent in non-social leisure activities were similar across individuals in all Tanner stages. Obligatory and work-related activities were also reported more frequently in more mature Tanner stages.

Of note, older Tsimane males in our sample, classified as Tanner 4 and 5, had higher mean MVPA min/day than those in Tanner stages 2 and 3, but lower than Tanner 1 (table 1), which coincides with the stages where mean height velocity was the highest. This contrasts with long-term longitudinal studies in the UK using device-measured PA and Canada using self-reported PA which found that PA in adulthood remained lower after the adolescent decrease in activity [13,14]. Although the direction of this effect is opposite in terms of the association between age/Tanner stage and PA in older adolescents in different contexts, it also highlights a similarity in the importance of economic productivity for influencing PA in older adolescents. In pre-industrialized contexts, food and economic production require high levels of PA; whereas in post-industrialized contexts, food production requires minimal physical effort and future economic productivity can benefit from more sedentary behaviours (i.e. more schooling). Indeed, Tsimane males in later Tanner stages reported doing more moderate-to-high intensity activities like chopping trees, clearing foliage, getting materials from the forest, than those in earlier Tanner stages, and less higher intensity leisure activities, like playing soccer or playing chase. Similarly, Tanner 5 females reported spending less than 1% of time in higher intensity leisure activities, but a larger proportion of time in light *and* moderate-to-high intensity habitual/obligatory activities, like tending children, washing clothes, removing rice from the hull and retrieving firewood. In line with a study of Hadza children and juveniles [46], sexual division of labour appears in middle-childhood and can be seen even in those classified as Tanner 1, with habitual/obligatory activities classified as being lighter intensity reported more among females, whereas moderate-to-high intensity obligatory activities were reported more frequently among males.

In the current study, Tanner stage serves as a proxy for a variety of endocrine and somatic changes that characterize the transition from childhood to adulthood. Tanner stage was significantly associated with DHEA, testosterone, height velocity, strength and body fat in males and females in ways that are consistent with the existing literature conducted in post-industrialized populations (electronic supplementary material, table S2) [47,48]. Notably, sex differences in body fat are evident in Tanner 1, and body fat was still more strongly associated with Tanner and all hormonal and somatic measures of growth and maturation in females. By contrast, grip strength was more strongly associated with Tanner stage in males compared with females. The association between Tanner and height velocity in males was relatively weak. This is likely driven by correlations only testing the linear relationship between variables, whereas the means of height velocity by Tanner stage suggest that there is a quadratic relationship between height velocity and Tanner stage that is particularly evident in males because of the later timing of maximum height velocity in Tanner 3 rather than Tanner 2 in females (table 1).

Given the Tsimane are a food-limited population with high pathogen burden, natural fertility and earlier age of first birth [42,49,50], the energetic trade-offs between growth/maturation/reproduction and energy available for PA may be more intense than for those in energy-rich, post-industrialized populations where food availability is much higher and the immune system burden is much lower. However, this straightforward prediction is complicated by the fact that subsistence lifestyles require high levels of PA. Direct comparisons between our data and the existing literature are difficult, as most studies use self-report PA [9], or a different measure of biological age or metric for device-measured PA by Tanner stage [14,21]. A larger, longitudinal study among Tsimane with a broader range of energetic condition and access to food can help clarify if this energetic condition moderates the effects of Tanner stage on PA.

There is some evidence that Tsimane adolescents exhibit steeper trade-offs between growth/maturation/reproduction and activity. The highest mean height velocity in our sample was the same for males and females (6.4 cm yr^{-1}), which is lower than values observed in the USA which also vary by sex (females: 9 cm yr^{-1}, males: 10 cm yr^{-1}) [37]. Notably, in the global study of self-report PA [3], the prevalence of insufficient PA was higher among adolescents in low-income countries compared with those in middle- to high-income countries, whereas this pattern is reversed in adults [2]. Overall, adolescents in post-industrialized countries exhibit low PA levels, despite more access to food and lower immune system burden. In terms of the underlying biology, this pattern suggests that additional energy availability in post-industrialized environments is prioritized for skeletal growth, energy storage and higher levels of reproductive hormones over increased motivation to expend energy in PA.

Trade-offs between reproductive efforts and energy for PA may be more severe for Tsimane females compared with post-industrialized populations. Tsimane males in our sample accumulated 33% more steps/day than females; whereas a study in Australian males reported only 19% more steps than females measured by pedometer, although their age range was smaller, 8–12 [51]. Tsimane males in the current study also have 91% more MVPA min/day than females, whereas compared with females, males in the USA between the ages of 6 and 19 had 72% more MVPA min d^{-1} [5], Portuguese males between 13 and 14 have 39% more MVPA min d^{-1}, 13-year-old Canadian males have 31% more MVPA [19] and approximately 12-year-old males in the UK have 56% higher MVPA min d^{-1} [21].

The primary limitation of this study is that it was cross-sectional. A longitudinal design would provide a clearer picture of the associations between growth and maturation on PA/inactivity. In addition, our sample size within each Tanner stage was small, and all data were collected in one season when school was not in session, so we cannot generalize the PA levels we found to those experienced year-round, or while school is in session. However, an advantage of this design is that our PA estimates were not affected by seasonality and were therefore not confounded by school-age children attending school and older adolescents not attending school, nor by vigorous horticultural activities that occur in specific seasons that could have skewed the data if collected for some participants during seasons where those activities take place. In addition, Tanner stage captures a constellation of changes that occur during the transition from childhood to adulthood. Several changes are co-occurring at this life stage, and likely affect each other, as well as behaviour. Future work aiming to tease apart the differential effects would benefit from including additional measures, particularly hormones related to growth, (e.g. insulin-like growth factor 1 (IGF-1)) and energetic condition (e.g. leptin, ghrelin, C-peptide). A complete life-history model would also include measures of diet, energetic condition, as well as immune markers, to capture the roles that these factors play in shaping the energy available for PA in children and adolescents. However, this analysis is meant to represent an important first step toward clarifying the relationships between age, maturation and PA in adolescence, and these limitations are balanced with several other strengths. This study was conducted in a unique population living a vastly different lifestyle in a vastly different environment than populations typically studied in the epidemiology or kinesiology literature. In addition, we used device-measured estimates of PA time and intensity, as well as self-reports to capture the types of activities Tsimane children and adolescents engage in. We also included Tanner stage assessments and validated them with hormone levels and markers of somatic growth and maturation and included a wide age range of participants to provide a better picture of PA across the transition from childhood to adulthood.

Taken together with the existing literature, our findings raise important considerations for improving public health in energy-rich, post-industrialized environments that are mismatched to environments faced by humans for the vast majority of our evolutionary past. Adolescence has emerged as a critical window to intervene on exercise and PA engagement, but our findings, and those of several others in post-industrialized settings, suggest that the limited time and resources for public health interventions may be more effective if targeting increasing PA in early to mid-childhood. Interventions in adolescents may be more effective if they focus on breaking up sedentary time, and limiting reductions in PA, rather than increasing PA participation. Adolescents may be drawn to lower intensity activities that provide opportunities for social engagement. Sex-specific interventions may also be needed once adrenarche and puberty lead to sexual dimorphism in the absolute and relative costs and benefits of PA. The most effective intervention may require modifying our environments to incorporate more PA in habitual/obligatory activities, providing safe opportunities for active transportation, rather than relying exclusively on exercise and sports participation to reach PA guidelines. Negative associations between reproductive maturation and PA also highlight additional consequences for energy-rich populations where maturation is occurring at earlier ages. Shorter childhood means fewer years spent where the costs of PA participation are low.

Life history theory provides a useful framework for understanding the complex set of factors that influence PA in adolescence and across the lifespan. Absolute levels of PA are strongly influenced by the obligatory PA necessary in a given environment. Cross-cultural consistencies in PA patterns observed in Tsimane adolescents and those from post-industrialized countries suggests that a coordinated system has evolved that responds to intensifying energetic needs for growth and maturation during adolescence by prioritizing energetic effort toward growth and maturation over leisure-time PA, irrespective of energy stores or cues of energy abundance in the environment. Maturation and cognitive development may also include an increased interest in building social relationships through low-intensity social activities, and a decreased interest in higher intensity, play-based social activities. The constellation of life-history shifts simultaneously occurring: increased stature, muscle and fat deposition, and social skill development each impact PA. Growth, reproductive maturation and reproduction place fundamental constraints on the energy, time and motivation for PA that warrant consideration in future PA research and intervention development.

4. Material and methods

(a) Experimental design

Data for this study were collected among Tsimane children and adolescents from four adjacent villages located along the Maniqui River in the summer of 2014 in collaboration with the Tsimane Health and Life History Project [49]. To encompass the transition from childhood to adulthood, a wide age range of participants (ages 7–22) were recruited, in line with a broader conceptualization of adolescence that extends the upper limit to align more closely with brain development [52]. The average age of menarche in the Tsimane is 13.9 years [53]. Tsimane children and younger adolescents play with others in neighbouring families, assist in caring for younger siblings and food production, and spend limited time in formal schooling compared with children in post-industrialized populations. Older Tsimane adolescents in this age range are typically married with children, and produce food, but typically reside in family clusters and are still reliant on their parents and grandparents for additional food production and allocare [54].

Participants were recruited during their annual medical exam with the THLHP medical team by A.C. and P.H. All individuals between the ages of 7 and 22 who attended their medical exam were invited to participate ($n = 126$, 37% of individuals in this age range resident in these communities in 2014).

Participation lasted 3–4 days allowing inclusion of all eligible participants from each community during the medical team visit (1 to 3 weeks). On day 1 participants and parents provided informed consent/assent, completed a structured interview, and had anthropometric and strength measurements taken (detailed below). Participants wore ActiGraph wGT3X + accelerometers on their hip for the duration of study participation. On days 2 and 3, participants provided first void urine samples to measure urinary hormones (detailed below). On days 2, 3 and 4 (where possible) participants completed 24-hour PA recall interviews while concurrently examining Actigraph data on a computer screen to validate wear-time and aid in recall. Small gifts were provided to remunerate participants for each day of study participation including pens and notebooks, backpacks, soccer jerseys, sardines and oil.

All study methods were approved by the Institutional Review Board (IRB) at the University of New Mexico (HRRC # 07-157). Informed consent was established at three levels: (1) the Tsimane governing council, (2) village leadership and (3) study participants. Informed assent was established with parents/guardians of minors.

(b) Participant characteristics

A total of 110 Tsimane children and adolescents (mean ± s.d. age = 13.7 ± 3.2 years, 50% female) were sampled from four villages (electronic supplementary material, figure S2). Table 1 summarizes sample characteristics for all variables of interest in the full sample, separately by sex and within sex by Tanner stage. Males and females were similar with respect to mean age, weight, height, DHEA, testosterone and distribution across Tanner stages, $X^2(4,\ n = 110) = 1.34$, $p = 0.85$. Males have significantly higher grip strength, non-significantly (*ns*) higher mean height velocity (4.5 ± 2.2 versus 3.7 ± 2.9 cm yr^{-1}, $p = 0.09$); while females had significantly higher mean body fat. The highest mean height velocity across Tanner stages was the same in males and females (6.4 cm yr^{-1}) and was observed in Tanner 2 females and Tanner 3 males.

(c) Measures

(i) Age and anthropometry

Age was obtained from census data collected by the Tsimane Health and Life History Project (THLHP) over the past 20 years. Height was measured to the nearest mm with a portable stadiometer (Seca 213) and weight with a digital scale (Tanita BC-1500). Body fat was estimated using the Jackson & Pollack 3-measurement skinfolds taken in triplicate using FatTrackII Digital Body Fat Calipers (AccuFitness). Grip strength was measured taking the average of three measurements [55] using a hydraulic dynamometer (Baseline, TN).

(ii) Free-living PA and sedentary time

ActiGraph wGT3X+ accelerometers were used to estimate PA/sedentary time and intensity. Actigraphs were initialized with a 30 hz sampling rate. Participants were fitted with the device on the hip, instructed on the proper positioning and to only remove the device when submerging themselves in water. Daily 24-hour activity recall interviews were completed to assess activity types among participants who lived within a reasonable distance from the mobile medical camp and could return daily. To aid participants' recall of the previous day and validate Actigraph wear-time in real-time, investigators and participants viewed Actigraph data together on a laptop screen while completing the interview. Completed files were downloaded using Actilife software with the normal filter into 60 s epochs and converted to csv tables. Data were processed in R (v4.1). Wear-time was additionally assessed using a criterion of 60 consecutive minutes of zero-counts with an allowance of 1–2 min of counts to 100 [5]. Epochs were delineated into periods of sedentary, light and MVPA activity levels with an algorithm developed in Brazilian adolescents using vector magnitude counts [56]. Sixty-second activity data were summed into person-day summaries including separating the 12-hour periods from 7.00 to 19.00 and 19.00 to 7.00. Person-day summaries were averaged into individual daily estimates of activity. Participants were included in analysis if there was at least 10 h of valid wear-time between 7.00 and 19.00. Reported daily estimates for light intensity, MVPA and steps/day were based on a 24-hour day from 7.00 until the following morning at 7.00; while sedentary activity was based on a 12-hour period from 7.00 to 19.00 to separate daytime sedentary behaviour from sleep. For daytime sedentary behaviour, person-day level data were included if there were at least 9 hour of valid wear-time between 7.00 and 19.00. Of the initial 110 enrolled in the accelerometry protocol, four did not meet the criteria of at least one valid day daytime sedentary behaviour and an additional two participants did not meet the valid wear-time criteria for PA (figure 4). The remaining participants provided 1.9 days (s.d. = 0.4) of data. Previous work indicates that 1–3 days of accelerometer wear-time is sufficient to capture reliable estimates of habitual PA [21,57–59]. We examined the reliability of our estimates using a larger unpublished dataset of wrist-worn Actigraph estimates of steps/day for 1986 person-days among $n = 299$ Tsimane (age 7–22) with greater than or equal to four valid days of PA data (collected 2019–2022). The correlation of steps/day estimated using all valid days with steps/day estimated with a random selection of only 2 days was strong ($r = 0.76$, $p < 0.001$) with good reliability (ICC = 0.74, $p < 0.001$), suggesting 2 valid days of accelerometer data is sufficient to estimate habitual PA.

Daily 24-hour activity recall interviews were completed among $n = 99$ participants, covering an average of 3.8 days (s.d. = 0.06), 15.6 h per day (s.d. = 3.0) and 3601 min per participant (s.d. = 962). In total, 62 activities were recorded with mean = 37 activities (s.d. = 9.1) recorded/participant. The 62 activities were coded using previously used Troject time allocation codes [60]. Activities were grouped into nine bins along two dimensions: intensity (sedentary, light, moderate-to-high) and type (transportation, habitual/obligatory and leisure) by A.C. and H.D. and modified until consensus was reached among all authors who have completed fieldwork with the Tsimane (electronic supplementary material, table S2). Sleep was not included in the results and accounted for 43.3% of total recall time. Time periods when participants could not recall what they were doing for a given time period, and activities involving medical exams or interaction with anthropologists were also excluded, accounting for 8.9% of time captured by the interviews.

(iii) Tanner stage

Tanner staging is considered the gold standard for tracking the development and sequence of secondary sex characteristics throughout puberty. It is typically evaluated on a scale from 1 to 5 by a physician through clinical examination of secondary sex characteristics such as pubic hair growth and breast/genital development [61]. However, it is challenging to perform in field settings because of the sensitivity of the assessment and the need for privacy—particularly in anthropology field settings where direct examinations, interviews or pictorial representations of breasts and genitals are not culturally appropriate. Thus, Tanner stage

1–5 was assessed by two authors (A.E.C. and P.L.H.) independently based on secondary sexual characteristics visible through clothing, including breast development and underarm hair, as well as menarche, lactation status and reproductive history obtained from THLHP medical records. Facial/underarm hair, muscular development, jaw shape and voice change served as additional maturation cues in males. Inter-rater reliability was high, with discrepancies reflecting only ±1 stage difference that were resolved through discussion between researchers. Tanner stage assessments were validated with measures of growth and reproductive maturation.

(iv) Urinary hormone assays

First morning void urine specimens were collected by participants on two consecutive days, and frozen in liquid nitrogen within several hours of specimen collection. They were stored for up to 1 month in liquid nitrogen, before being transferred on dry ice to the USA where they were stored at −80°C for 2 years before analyses. After arrival, specimens were thawed, specific gravity was measured with a refractometer (Atago Inc), and urine specimens were analysed in duplicate via enzyme immunoassay for DHEA (Enzo Life Sciences, ADI-901-093) and testosterone (R156/7 [62]). All specimens were run on the first freeze–thaw, and results were specific-gravity corrected [63]. See electronic supplementary material for a detailed description of DHEA and testosterone during maturation.

(v) Height velocity

Height velocity in 2014 was computed using height measurements collected 1–4 years prior to 2014, with the majority (70%) taken 2 years prior to the study. Height velocity was calculated as:

$$\text{height velocity}\left(\frac{\text{cm}}{\text{year}}\right) = \frac{\text{Height}_{\text{Current}} - \text{Height}_{\text{Previous}}}{\text{Years since Height}_{\text{previous}}\text{ measure}}.$$

(d) Statistical analysis

Analyses were performed in R version 4.1. Sex differences in participant characteristics were assessed using independent sample *t*-tests for continuous variables and χ^2-tests for distribution across Tanner stages. Spearman correlations were tested to validate Tanner stage with log-transformed hormone levels (DHEA and testosterone which were both skewed) and measures of somatic growth and maturation (height velocity, grip strength and body fat). Non-parametric tests were used because Tanner stage is ordinal, and body fat in males violated normality assumptions [64]. To test P1 and P2, separate linear regression models were run for each activity outcome (sedentary time, light intensity PA, MVPA, steps/day) with age, sex and the age × sex interaction included as independent variables. To test the mediating role of Tanner stage on age-sedentary/PA associations (P3), structural equation models (SEM) were fit in the lavaan package version 0.6-11 using listwise deletion for participants missing sedentary ($n = 4$) or PA outcome data ($n = 6$). Diagonally weighted least-squares estimation was used to account for Tanner stage being ordinal as opposed to continuous. Age and outcome variables were standardized to facilitate model convergence given the vastly different scales of the variables. Categorization and visual representation of self-reported PA was performed in R 2022.02.0 using the ggplot2 and lmer packages.

(e) Validity of Tanner stage with hormone levels and somatic maturation markers

Estimates of the within-sex Spearman correlations between Tanner stage assessment and DHEA, testosterone, height velocity, grip strength and body fat are presented in electronic supplementary material, table S1. Tanner stage assessments were significantly correlated with all these variables in both sexes (p's < 0.01), with coefficients in females ranging from $r = 0.46$ for testosterone to $r = -0.79$ for height velocity and in males from $r = -0.38$ for height velocity to $r = 0.92$ for grip strength.

Ethics. All study methods were approved by the Institutional Review Board (IRB) at the University of New Mexico (HRRC # 07-157). Informed consent was established at three levels: (1) the Tsimane governing council, (2) village leadership and (3) study participants. Informed assent was established with parents/guardians of minors.

Data accessibility. All relevant computer code, variable definitions and statistical analysis will be downloadable from the following repository: https://doi.org/10.5061/dryad.4j0zpc8js [65]. Individual-level data are stored in the Tsimane Health and Life History Project (THLHP) Data Repository, and are available through restricted access for ethical reasons. THLHP's highest priority is the safeguarding of human subjects and minimization of risk to study participants. The THLHP adheres to the CARE Principles for Indigenous Data Governance, which assure that the Tsimane: (1) have sovereignty over how data are shared, (2) are the primary gatekeepers determining ethical use, (3) are actively engaged in the data generation, and (4) derive benefit from data generated and shared use whenever possible. The THLHP is also committed to the FAIR Principles to facilitate data use. Requests for individual-level data should take the form of an application that minimally details the exact uses of the data and the research questions to be addressed, procedures that will be employed for data security and individual privacy, potential benefits to the study communities, and procedures for assessing and minimizing stigmatizing interpretations of the research results (see the following webpage for links to the data sharing policy and data request forms: https://tsimane.anth.ucsb.edu/data.html). Requests for individual-level data will require institutional IRB approval (even if exempt) and will be reviewed by an Advisory Council composed of tribal leaders, tribal community members, Bolivian scientists and the THLHP leadership. The study authors and the Tsimane leadership are committed to open science and are available to assist interested investigators in preparing data access requests.

Supplementary material is available online [66].

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

Authors' contributions. A.E.C.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, visualization, writing—original draft, writing—review and editing; D.K.C.: data curation, formal analysis, visualization, writing—review and editing; P.L.H.: conceptualization, investigation, methodology, project administration, resources, software, writing—review and editing; B.C.T.: data curation, methodology, writing—review and editing; M.D.G.: funding acquisition, methodology, writing—review and editing; J.S.: conceptualization, methodology, writing—review and editing; H.E.D.: data curation, methodology, writing—review and editing; H.K.: funding acquisition, methodology, resources, supervision, 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 have no competing interests to disclose.

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References

1. Ding D, Lawson KD, Kolbe-Alexander TL, Finkelstein EA, Katzmarzyk PT, van Mechelen W, Pratt M. 2016 The economic burden of physical inactivity: a global analysis of major non-communicable diseases. *Lancet* **388**, 1311–1324. (doi:10.1016/S0140-6736(16)30383-X)
2. Guthold R, Stevens GA, Riley LM, Bull FC. 2018 Worldwide trends in insufficient physical activity from 2001 to 2016: a pooled analysis of 358 population-based surveys with 1.9 million participants. *Lancet Glob. Heal.* **6**, e1077–e1086. (doi:10.1016/S2214-109X(18)30357-7)
3. Guthold R, Stevens GA, Riley LM, Bull FC. 2020 Global trends in insufficient physical activity among adolescents: a pooled analysis of 298 population-based surveys with 1.6 million participants. *Lancet Child Adolesc. Heal.* **4**, 23–35. (doi:10.1016/S2352-4642(19)30323-2)
4. Sallis JF, Saelens BE. 2000 Assessment of physical activity by self-report: status, limitations, and future directions. *Res. Q Exerc. Sport* **71**, S1–S14.
5. Troiano RP, Berrigan D, Dodd KW, Mâsse LC, Tilert T, Mcdowell M. 2008 Physical activity in the United States measured by accelerometer. *Med. Sci. Sports Exerc.* **40**, 181–188. (doi:10.1249/mss.0b013e31815a51b3)
6. Prince SA, Adamo KB, Hamel ME, Hardt J, Connor Gorber S, Tremblay M. 2008 A comparison of direct versus self-report measures for assessing physical activity in adults: a systematic review. *Int. J. Behav. Nutr. Phys. Act.* **5**, 56. (doi:10.1186/1479-5868-5-56)
7. Cairney J, Veldhuizen S, Kwan M, Hay J, Faught BE. 2014 Biological age and sex-related declines in physical activity during adolescence. *Med. Sci. Sports Exerc.* **46**, 730–735. (doi:10.1249/MSS.0000000000000168)
8. Sallis JF. 2000 Age-related decline in physical activity: a synthesis of human and animal studies. *Med. Sci. Sports Exerc.* **32**, 1598–1600. (doi:10.1097/00005768-200009000-00012)
9. Dumith SC, Gigante DP, Domingues MR, Kohl HW. 2011 Physical activity change during adolescence: a systematic review and a pooled analysis. *Int. J. Epidemiol.* **40**, 685–698. (doi:10.1093/ije/dyq272)
10. Riddoch CJ, Andersen LB, Wedderkopp N, Harro M, Klasson-Heggebø L, Sardinha LB, Cooper AR, Ekelund U. 2004 Physical activity levels and patterns of 9- and 15-yr-old European children. *Med. Sci. Sports Exerc.* **36**, 86–92. (doi:10.1249/01.MSS.0000106174.43932.92)
11. Lopes VP, Vasques CMS, Maia JAR, Ferreira JCV. 2007 Habitual physical activity levels in childhood and adolescence assessed with accelerometry. *J. Sports Med. Phys. Fitness* **47**, 217–222.
12. Caspersen CJ, Pereira MA, Curran KM. 2000 Changes in physical activity patterns in the United States, by sex and cross-sectional age. *Med. Sci. Sports Exerc.* **32**, 1601–1609. (doi:10.1097/00005768-200009000-00013)
13. Kwan MY, Cairney J, Faulkner GE, Pullenayegum EE. 2012 Physical activity and other health-risk behaviors during the transition into early adulthood: a longitudinal cohort study. *Am. J. Prev. Med.* **42**, 14–20. (doi:10.1016/j.amepre.2011.08.026)
14. Metcalf BS, Hosking J, Jeffery AN, Henley WE, Wilkin TJ. 2015 Exploring the adolescent fall in physical activity: a 10-yr cohort study (EarlyBird 41). *Med. Sci. Sports Exerc.* **47**, 2084–2092. (doi:10.1249/MSS.0000000000000644)
15. Sherar LB, Cumming SP, Eisenmann JC, Baxter-Jones ADG, Malina RM. 2010 Adolescent biological maturity and physical activity: biology meets behavior. *Pediatr. Exerc. Sci.* **22**, 332–349. (doi:10.1123/pes.22.3.332)
16. Machado Rodrigues AM, Coelho E Silva MJ, Mota J, Cumming SP, Sherar LB, Neville H, Malina RM. 2010 Confounding effect of biologic maturation on sex differences in physical activity and sedentary behavior in adolescents. *Pediatr. Exerc. Sci.* **22**, 442–453. (doi:10.1123/pes.22.3.442)
17. Cumming SP, Standage M, Gillison F, Malina RM. 2008 Sex differences in exercise behavior during adolescence: is biological maturation a confounding factor? *J. Adolesc. Heal.* **42**, 480–485. (doi:10.1016/j.jadohealth.2007.10.005)
18. Thompson AM, Baxter-Jones ADG, Mirwald RL, Bailey DA. 2003 Comparison of physical activity in male and female children: does maturation matter? *Med. Sci. Sports Exerc.* **35**, 1684–1690. (doi:10.1249/01.MSS.0000089244.44914.1F)
19. Sherar LB, Esliger DW, Baxter-Jones ADG, Tremblay MS. 2007 Age and gender differences in youth physical activity: does physical maturity matter? *Med. Sci. Sports Exerc.* **39**, 830–835. (doi:10.1249/mss.0b013e3180335c3c)
20. Baker BL, Birch LL, Trost SG, Davison KK. 2007 Advanced pubertal status at age 11 and lower physical activity in adolescent girls. *J. Pediatr.* **151**, 488–493. (doi:10.1016/j.jpeds.2007.04.017)
21. Riddoch CJ, Mattocks C, Deere K, Sounders J, Kirkby J, Tilling K, Leary SD, Blair SN, Ness AR. 2007 Objective measurement of levels and patterns of physical activity. *Arch. Dis. Child.* **92**, 963–969. (doi:10.1136/adc.2006.112136)
22. Thompson AM, Baxter-Jones AD, Mirwald RL, Bailey DA. 2003 Comparison of physical activity in male and female children: does maturation matter? *Med. Sci. Sport. Exerc.* **35**, 1684–1690.
23. Stearns SC. 1989 Trade-offs in life history evolution. *Funct. Ecol.* **3**, 259–268.
24. Charnov EL. 1993 Oxford Series in Ecology and Evolution: Life history invariants: some explorations of symmetry in evolutionary ecology. New York, NY: Oxford University Press.
25. Ellison PT. 2017 Endocrinology, energetics, and human life history: a synthetic model. *Horm. Behav.* **91**, 97–106. (doi:10.1016/j.yhbeh.2016.09.006)
26. Cheng HL, Amatoury M, Steinbeck K. 2016 Energy expenditure and intake during puberty in healthy nonobese adolescents: a systematic review. *Am. J. Clin. Nutr.* **104**, 1061–1074. (doi:10.3945/ajcn.115.129205)
27. Hurtado AM, Hill K, Hurtado I, Kaplan H. 1992 Trade-offs between female food acquisition and child care among hiwi and ache foragers. *Hum. Nat.* **3**, 185–216. (doi:10.1007/BF02692239)
28. Schneider JE. 2004 Energy balance and reproduction. *Physiol. Behav.* **81**, 289–317. (doi:10.1016/j.physbeh.2004.02.007)
29. De Souza MJ, Miller BE, Loucks AB, Luciano AA, Pescatello LS, Campbell CG, Lasley BL. 1998 High frequency of luteal phase deficiency and anovulation in recreational women runners: blunted elevation in follicle-stimulating hormone observed during luteal-follicular transition. *J. Clin. Endocrinol. Metab.* **83**, 4220–4232. (doi:10.1210/jcem.83.12.5334)
30. Loucks AB, Heath EM, Law T, Verdun M, Watts JR. 1994 Dietary restriction reduces luteinizing hormone (LH) pulse frequency during waking hours and increases LH pulse amplitude during sleep in young menstruating women. *J. Clin. Endocrinol. Metab.* **78**, 910–915. (doi:10.1210/jcem.78.4.8157720)
31. Loucks A, Verdun M, Heath EM. 1998 Low energy availability, not stress of exercise, alters LH pulsatility in exercising women. *J. Appl. Physiol.* **84**, 37–46.
32. Loucks AB. 2003 Energy availability, not body fatness, regulates reproductive function in women. *Exerc. Sport Sci. Rev.* **31**, 144–148. (doi:10.1097/00003677-200307000-00008)
33. Williams NI, Leidy HJ, Hill BR, Lieberman JL, Legro RS, De Souza MJ. 2015 Magnitude of daily energy deficit predicts frequency but not severity of menstrual disturbances associated with exercise and caloric restriction. *Am. J. Physiol. Endocrinol. Metab.* **308**, E29–E39. (doi:10.1152/ajpendo.00386.2013)
34. Ellison PT. 2008 Energetics, reproductive ecology, and human evolution. *PaleoAnthropology* **2008**, 172–200.
35. Jasienska G. 2011 Why energy expenditure causes reproductive suppression in women: an evolutionary and bioenergetic perspective. In *Reproductive ecology and human evolution* (ed. PT Ellison), pp. 59–84. New York, NY: Aldine de Gruyter.
36. Ellison PT. 2001 *On fertile ground*. Cambridge, MA: Harvard Press.
37. Keller BA. 2008 State of the art reviews: development of fitness in children: the influence of gender and physical activity. *Am. J. Lifestyle Med.* **2**, 58–74. (doi:10.1177/1559827607308802)
38. O'Sullivan AJ. 2009 Does oestrogen allow women to store fat more efficiently? A biological advantage for fertility and gestation. *Etiol. Pathophysiol. Obes.*

Rev. **10**, 168–177. (doi:10.1111/j.1467-789X.2008.00539.x)

39. Gurven M, Jaeggi AV, Kaplan H, Cummings D. 2013 Physical activity and modernization among Bolivian Amerindians. *PLoS ONE* **8**, e55679. (doi:10.1371/journal.pone.0055679)
40. Gurven M, Blackwell AD, Rodríguez DE, Stieglitz J, Kaplan H. 2012 Does blood pressure inevitably rise with age?: Longitudinal evidence among forager-horticulturalists. *Hypertension* **60**, 25–33. (doi:10.1161/HYPERTENSIONAHA.111.189100)
41. Kaplan H *et al.* 2017 Coronary atherosclerosis in indigenous South American Tsimane: a cross-sectional cohort study. *Lancet* **389**, 1730–1739. (doi:10.1016/S0140-6736(17)30752-3)
42. Kraft TS, Stieglitz J, Trumble BC, Martin M, Kaplan H, Gurven M. 2018 Nutrition transition in 2 lowland Bolivian subsistence populations. *Am. J. Clin. Nutr.* **108**, 1183–1195. (doi:10.1093/ajcn/nqy250)
43. Raichlen DA, Pontzer H, Zderic TW, Harris JA, Mabulla AZP, Hamilton MT, Wood BM. 2020 Sitting, squatting, and the evolutionary biology of human inactivity. *Proc. Natl Acad. Sci. USA* **117**, 7115–7121. (doi:10.1073/pnas.1911868117)
44. Urlacher SS, Kramer KL. 2018 Evidence for energetic tradeoffs between physical activity and childhood growth across the nutritional transition. *Sci. Rep.* **8**, 369. (doi:10.1038/s41598-017-18738-4)
45. Kaplan H, Gurven M, Winking J. 2009 An evolutionary theory of human life span: embodied capital and the human adaptive complex. In *Handbook of theories of aging* (eds VL Bengston, D Gans, N Pulney, M Silverstein), pp. 39–60. Berlin, Germany: Springer Publishing Company.
46. Froehle AW, Wells GK, Pollom TR, Mabulla AZP, Lew-Levy S, Crittenden AN. 2019 Physical activity and time budgets of Hadza forager children: implications for self-provisioning and the ontogeny of the sexual division of labor. *Am. J. Hum. Biol.* **31**, e23209. (doi:10.1002/ajhb.23209)
47. Dorn LD, Dahl RE, Woodward HR, Biro F. 2006 Defining the boundaries of early adolescence: a user's guide to assessing pubertal status and pubertal timing in research with adolescents. *Appl. Dev. Sci.* **10**, 30–56. (doi:10.1207/s1532480xads1001_3)
48. Chavarro JE *et al.* 2017 Validity of self-assessed sexual maturation against physician assessments and hormone levels. *J. Pediatr.* **186**, 172–178. (doi:10.1016/j.jpeds.2017.03.050)
49. Gurven M, Stieglitz J, Trumble B, Blackwell AD, Beheim B, Davis H, Hooper P, Kaplan H. 2017 The Tsimane Health and Life History Project: integrating anthropology and biomedicine. *Evol. Anthropol.* **26**, 54–73. (doi:10.1002/evan.21515)
50. Blackwell AD, Trumble BC, Maldonado Suarez I, Stieglitz J, Beheim B, Snodgrass JJ, Kaplan H, Gurven M. 2016 Immune function in Amazonian horticulturalists. *Ann. Hum. Biol.* **43**, 382–396. (doi:10.1080/03014460.2016.1189963)
51. Telford RM, Telford RD, Olive LS, Cochrane T, Davey R. 2016 Why are girls less physically active than boys? Findings from the LOOK longitudinal study. *PLoS ONE* **11**, e0150041. (doi:10.1371/journal.pone.0150041)
52. Sawyer SM, Azzopardi PS, Wickremarathne D, Patton GC. 2018 The age of adolescence. *Lancet Child Adolesc. Heal.* **2**, 223–228. (doi:10.1016/S2352-4642(18)30022-1)
53. Walker R *et al.* 2006 Growth rates and life histories in twenty-two small-scale societies. *Am. J. Hum. Biol.* **18**, 295–311. (doi:10.1002/ajhb.20510)
54. Hooper PL, Gurven M, Winking J, Kaplan HS. 2015 Inclusive fitness and differential productivity across the life course determine intergenerational transfers in a small-scale human society. *Proc. R. Soc. B* **282**, 20142808. (doi:10.1098/rspb.2014.2808)
55. Mathiowetz V, Kashman N, Volland G, Weber K, Dowe M, Rogers S. 1985 Grip and pinch strength: normative data for adults. *Arch. Phys. Med. Rehabil.* **66**, 69–74.
56. Romanzini M, Petroski EL, Ohara D, Dourado AC, Reichert FF. 2014 Calibration of ActiGraph GT3X, Actical and RT3 accelerometers in adolescents. *Eur. J. Sport Sci.* **14**, 91–99. (doi:10.1080/17461391.2012.732614)
57. Matthews CE, Chen KY, Freedson PS, Buchowski MS, Beech BM, Pate RR, Troiano RP. 2008 Amount of time spent in sedentary behaviors in the United States, 2003-2004. *Am. J. Epidemiol.* **167**, 875–881. (doi:10.1093/aje/kwm390)
58. Kocherginsky M, Huisingh-Scheetz M, Dale W, Lauderdale DS, Waite L. 2017 Measuring physical activity with hip accelerometry among U.S. older adults: how many days are enough? *PLoS ONE* **12**, e0170082. (doi:10.1371/journal.pone.0170082)
59. Trost SG, Pate RR, Freedson PS, Sallis JF, Taylor WC. 2000 Using objective physical activity measures with youth: how many days of monitoring are needed? *Med. Sci. Sports Exerc.* **32**, 426. (doi:10.1097/00005768-200002000-00025)
60. Gurven M, Winking J, Kaplan H, von Rueden C, McAllister L. 2009 A bioeconomic approach to marriage and the sexual division of labor. *Hum. Nat.* **20**, 151–183. (doi:10.1007/s12110-009-9062-8)
61. Tanner JM. 1962 *Growth at adolescence*, 2nd edn. Thomas: Springfield, Ill.
62. Trumble BC, Brindle E, Kupsik M, O'Connor KA. 2010 Responsiveness of the reproductive axis to a single missed evening meal in young adult males. *Am. J. Hum. Biol.* **22**, 775–781. (doi:10.1002/ajhb.21079)
63. Miller RC, Brindle E, Holman DJ, Shofer J, Klein NA, Soules MR, O'Connor KA. 2004 Comparison of specific gravity and creatinine for normalizing urinary reproductive hormone concentrations. *Clin. Chem.* **50**, 924–932. (doi:10.1373/clinchem.2004.032292)
64. West SG, Finch JF, Curran PJ. 1995 Structural equation models with non-normal variables: problems and remedies. In *Structural equation modeling: concepts, issues, and applications* (ed. RH Hoyle), pp. 56–75. Sage Publications, Inc.
65. Caldwell AE, Cummings DK, Hooper PL, Trumble BC, Gurven M, Stieglitz J, Davis HE, Kaplan H. 2023 Data from Adolescence is characterized by more sedentary behaviour and less physical activity even among highly active forager-farmers. Dryad Digital Repository. (doi:10.5061/dryad.4j0zpc8js)
66. Caldwell AE, Cummings DK, Hooper PL, Trumble BC, Gurven M, Stieglitz J, Davis HE, Kaplan H. 2023 Adolescence is characterized by more sedentary behaviour and less physical activity even among highly active forager-farmers. Figshare. (doi:10.6084/m9.figshare.c.6887622)