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Who reaps the rewards and who pays the costs of precocious investment in reproduction?: Adolescent reproduction in the Bolivian amazon.

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Short Abstract: Age at first reproduction (AFR) negatively correlates with adult body size. It is generally assumed cessation of growth determines AFR. We investigate the AFR-growth relationship among the Tsimane, Bolivian forager-farmers (women's mean AFR=18.25±2.60, n=1335, 13% reproduce before 16). We find: (1) faster growth before age 13 predicts earlier AFR (b*= -0.25, p=0.03) and menarche (b*= -0.24, p<0.01), and greater adult height (b*= 0.30, p<0.01); (2) early AFR predicts shorter adult height despite post-partum growth (b*= 0.27, p=0.05); (3) women with AFR ≤15 have more children, despite lower infant survivorship (adjusted total fertility rate by AFR: ≤15=9.67, 16-19=8.86, ≥20=7.04); and their first-born sons, but not daughters, are small-for-age (F(2,559)=5.23, p<0.005). Our results suggest rapid early growth enables early AFR and that early AFR limits growth rather than an earlier growth asymptote. Furthermore, in a preindustrial population, and likely during our evolutionary past, the benefits of early reproduction may outweigh the costs.

Introduction: Observed variation in women's AFR within and among populations suggests alternate life history strategies; and that women's AFR may be adaptive beyond conditions that discount the future or focus on offspring quality[1–7]. Across species, age at first reproduction negatively correlates with adult body size [8]. It is generally assumed cessation of growth determines AFR. Most studies in humans on adolescent reproduction, maternal growth and reproductive success have looked across populations, focused on developed or developing urban populations with better health and nutritional stability than found in our ancestral environments, and/or had relatively low sample sizes that do not allow for within population comparisons of different life history strategies. We investigate the effects of pre-pubescent condition on AFR and the consequences of early AFR on maternal growth and reproductive success among the Tsimane, a culturally homogenous population of Bolvian forager-farmers with relatively uniform high infant and adult mortality, and low variation in socioeconomic inequality and health[9,10]. Here we present a longitudinal study showing Tsimane women investing in two divergent life history strategies: (1) Fast – pre-pubescent investment in skeletal growth; and (2) Slow – continual low velocity prolonged investment in skeletal growth. These distinct life history strategies, in addition to differing pre-pubescent investment in body size (height and weight-for-height), vary in AFR, age at last birth and fertility. This demonstrates that within a relatively homogenous human population small pre-pubescent differences in health and nutrition can have large effects on women's reproductive success. We introduce a path model assessing the relationship between precocious investment in growth and the onset of menarche and AFR, and adult height (a proxy for investment in growth). We assess the reproductive success of each strategy by comparing fertility, child survivorship and first-born condition among women.

Data and Methods: Height and reproductive data were collected amongst the Tsimane by the Tsimane Health and Life History Project (THLHP). The heights and weights of 1663 women aged 10 to 45 years were measured using a portable stadiometer and Tanita weight scale between 2002 to 2012. The mean ±SD for repeat measures of these women was 3.51 ±2.74. Only the heights of women not pregnant at time of measurement were included. The demographic interviews and methods used to collect reproductive data and ascribe ages are described in Gurven et al (2007). Reproductive data has been systematically updated through bi-annual censuses and medical checkups by THLHP doctors.

Study Population: The Tsimane are lowland Amerinidian forager-farmers living in the Beni Department of Bolivia. Two thirds of their diet is from swidden horticulture that is supplemented with hunting, fishing and gathering. The Tsimane are relatively culturally homogenous. Variation in education, Spanish fluency, distance to the nearest town (San Borja, population ~24,000), and contact with non-Tsimane are minimal and associated with variation in individual levels of market integration and participation, and access to modern healthcare. Market participation, especially wage labor, is dominated by men; for most women non-traditional life-ways -- options beyond motherhood and household labor -- are unavailable. Tsimane have high fertility (total fertility rate = 9) and infant mortality (13%) [9], both of which co-vary with distance to town.

In our sample women are divided in to three groups by their AFR: early (AFR $\leq$ 15 years); norm (AFR 16-19 years); and late reproducers (AFR $\geq$ 20 years). These divisions have both a cultural and biological basis. Age at first reproduction $\leq$ 15 years is not taboo among the Tsimane but it is considered young (unpublished data) and only 13% of women give birth at $\leq$ 15 years; it is also approximately one standard deviation from the population mean AFR (mean=18.25 ±SD2.60). Furthermore, reproduction at or before 15 years is associated with

higher infant and maternal mortality in other populations (CITE). Similarly, AFR ≥ 20 years is associated, in other populations with lower infant and maternal mortality, but is considered old for first birth among the Tsimane (unpublished data).

Preliminary Findings: Table 1 shows the general and AFR specific reproductive environments. AFR ≤15 women make up 13% of this subpopulation, AFR 16-19 59% and AFR ≥20 28% (Figure 1). Multiparity by 20 years is more common in AFR ≤15 women (78% multiparous by 20) than AFR 16-19 women (42% multiparous by 20). The TFR of AFR ≤15 women is 11.11, 1.20 more than AFR 16-19 women (TFR = 9.91) and 3.11 more than AFR ≥20 women (TFR = 8.00). The larger TFR of AFR ≤15 women is likely a factor of more years of reproduction due to both earlier onset and later termination (Figure 2), rather than shorter inter-birth intervals.

Table 1. Reproductive characteristics of Tsimane women born 1952 -1992 by AFR group.

	Women's Year Born		Age at Menarche (yrs)		Age First Married (yrs)		Age at First Reproduction (yrs)		Pregnancies-for-age		Interbirth Interval Previous Infant Lives (months)	
	n	Mean ±SD	*n*	Mean ±SD	*n*	Mean ±SD	*n*	Mean ±SD	*n*	Mean ±SD	*n*	Mean ±SD
12-15	170	1978.75 ±9.63	86	12.90 ±1.07	20	14.60 ±1.27	170	14.35 ±0.91	170	0.42 ±1.08	161	29.44 ±10.62
16-19	784	1979.32 ±9.06	418	13.07 ±0.98	147	15.54 ±1.40	784	17.52 ±1.09	784	0.05 ±0.95	522	29.54 ±10.03
20-25	381	1976.05 ±8.69	187	12.99 ±0.95	88	17.09 ±2.38	381	21.51 ±1.54	381	-0.29 ±0.99	172	30.13 ±10.17
All (12-25 years)	1335	1978.32 ±9.14	691	13.03 ±0.99	255	16.00 ±1.97	1335	18.25 ±2.60	1335	-0.00 ±1.00	683	29.64 ±10.16

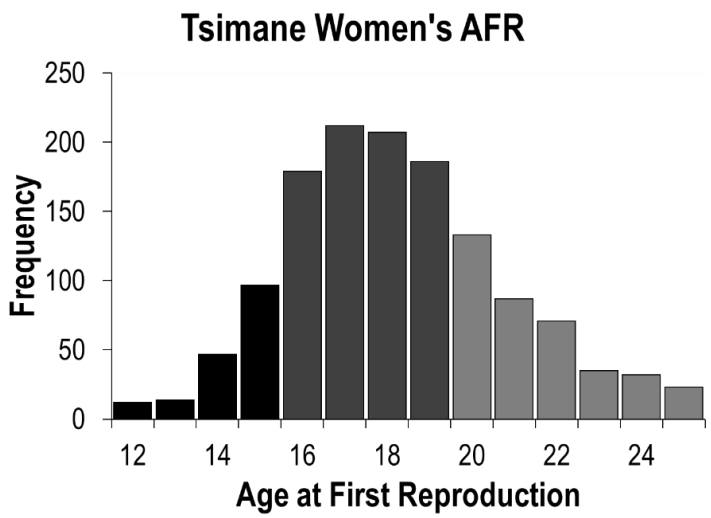

Fig.1. Distribution of age at first reproduction of the Tsimane women included in this study (*n* = 1335).

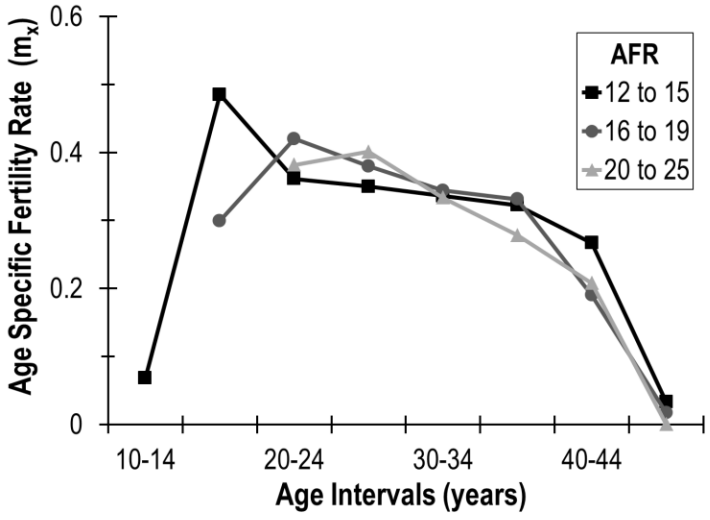

Fig. 2. Age specific fertility rate within each five year period of a Tsimane woman's reproductive life.

Early reproduction compromises but does not terminate growth in stature. AFR ≤15 women ((*n* = 148), mean ±SE = 150.65 ±0.34 cm) are 1.44 ± 0.38 cm shorter as adults than AFR 16-19 women ($p < 0.001$) and 1.35 ±0.41 cm shorter than AFR ≥20 women ($p = 0.003$; $F(2,1332) = 7.379$, $p = 0.001$) (Figure 3). Catch up growth can occur post-reproduction but does not fully recover the height deficit caused by early investment in reproduction; 79% of women with AFR 12-15 gained ≥2.5cm in height post-birth (paired t-test ($t = 6.776$, $df = 33$, $p < 0.001$)).

Women who reproduce at ≤15 years are usually tall-for-age before birth -- suggesting a faster life history trajectory with/or better health and nutrition enabling earlier reproduction – but short-for-age post-reproduction – supporting compromised growth during mid-to-late adolescence in early reproducers (Figure 4). AFR ≥16 women experience greater and more sustained growth in stature and are taller by 19 years.

Fig. 3. Mean adult height of Tsimane women (n = 1335) by age at first reproduction. One standard error is shown.

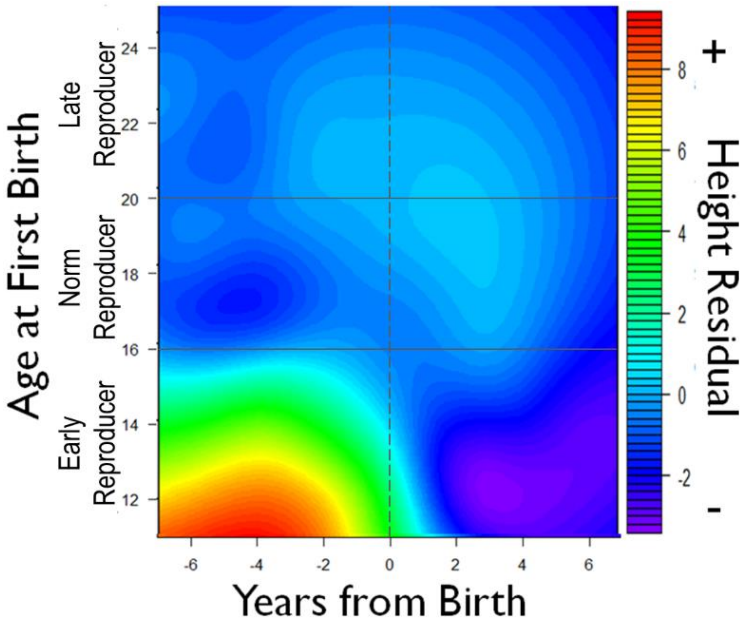

Fig. 4. Shows height-for-age for a subset of Tsimane women with multiple height measurements recorded during childhood and adolescence (n = 313). The solid horizontal lines divide the graph by AFR (AFR ≤ 15 years (n = 76), AFR 16-19 years (n = 204), and AFR ≥ 20 years (n = 33). The vertical dashed line indicates first birth. The heat scale is shown to the right of the graph. Women that reproduce at ≤15 years are tall-for-age before birth but short-for-age post-AFR compared to women that reproduce later.

Women who experience early growth (tall-for-age between 10-12 years) have earlier ages at menarche and AFR (Figure 5). However, early menarche is not associated with earlier AFR or adult height. Early growth is associated with greater adult height if AFR is delayed, suggesting that AFR – the timing of which is under both cultural and biological control – is the limiting factor for women's adult height, and not a fast life history trajectory with early cessation of growth followed by early reproduction.

Looking across all Tsimane women with known reproductive histories, regardless of whether their anthropometrics are known, shows that early reproducers have greater reproductive success (Table 2); suggesting a strong payoff to precocious investment in reproduction and low

costs. Women who reproduce at ≤15 years have more infant deaths over their reproductive lives than AFR 16-19 women; however, it is not sufficient to bring their reproductive success below that of women with later AFR. However, their first-born sons ($F(2,559) = 5.23$, $p<0.01$), but not daughters, are small-for-age (Figure 6). This suggests a trade-off between early reproduction and investment in maternal and offspring quality, and maternal reproductive success. In preindustrial societies where children provide valuable labor and support in old age, large kin networks are valued for their sociopolitical power, fertility positively correlates with status, and women are restricted to a mothering role early AFR and high fertility are beneficial.

Table 2. Infant mortality rates (death at ≤1 year) of Tsimane women born 1943-1990 by mother's age at infant's birth. Women are separated by AFR. Number of births at risk of infant death by AFR: ≤15 = 331, 16-19 = 1350, ≥20 = 463.

Mother's Age at Infant's Birth (years)	Infant Deaths at ≤ 1 years per 1000 Births			
	AFR ≤ 15	AFR 16 - 19	AFR 20 - 25	All Women
10 - 14	83.33	NA	NA	83.33
15 - 19	164.95	95.24	NA	109.47
20 - 24	98.36	120.99	150.60	126.58
25 - 29	80.00	106.72	135.71	112.87
30 - 34	159.09	92.59	102.27	105.44
35 - 39	76.92	127.27	106.38	112.24
40 - 44	166.67	78.95	90.91	107.14
45 - 50	500.00	0.00	NA	250.00
All Ages	129.91	106.67	129.59	115.21
Predicted Total Children Surviving to ≥ 1 Year	***9.67***	***8.86***	***7.04***	***8.46***

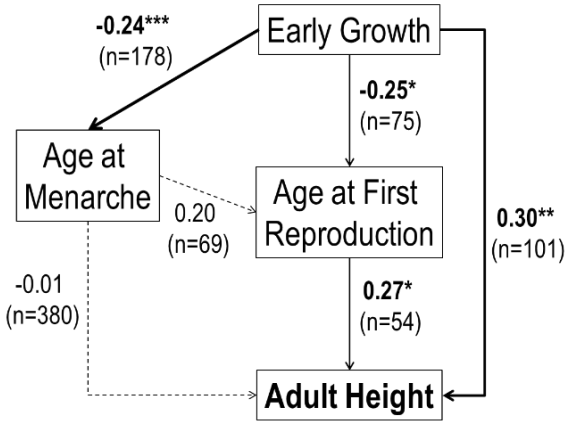

Fig. 5. Path model showing early growth (tall-for-age at 10-12 years) is associated with earlier menarche and AFR, and greater adult height if AFR delayed. Menarche not linked with AFR or adult height. Standardized betas, sample size and p-values shown; n=380, with 54 women in all steps of the model. Bolded standardized betas have significant p-values (*<0.05, **<0.01, ***<0.001).

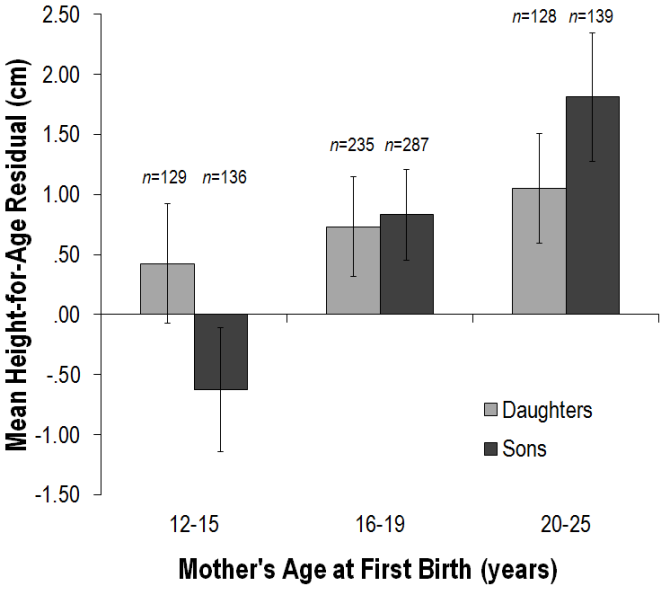

Fig. 6. Mean height-for-age of women's first born children by women's AFR and child sex. One standard deviation is shown.

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