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Feature Article

Growth Rates and Life Histories in Twenty-Two Small-Scale Societies

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ABSTRACT This study investigates variation in body growth (cross-sectional height and weight velocity) among a sample of 22 small-scale societies. Considerable variation in growth exists among hunter-gatherers that overlaps heavily with growth trajectories present in groups focusing more on horticulture. Intergroup variation tends to track environmental conditions, with societies under more favorable conditions displaying faster growth and earlier puberty. In addition, faster/earlier development in females is correlated with higher mortality. For example, African "Pygmies," Philippine "Negritos," and the Hiwi of Venezuela are characterized by relatively *fast* child-juvenile growth for their adult body size (used as a proxy for energetic availability). In these societies, subadult survival is low, and puberty, menarche, and first reproduction are relatively early (given their adult body size), suggesting selective pressure for accelerated development in the face of higher mortality. In sum, the origin and maintenance of different human ontogenies may require explanations invoking both environmental constraints and selective pressures. Am. J. Hum. Biol. 18:295–311, 2006. © 2006 Wiley-Liss, Inc.

Many discussions of human life history emphasize the large human brain (Dunbar, 2003; Flinn et al., 2005), long lifespan (Kaplan, 1997; Hill et al., 2001), and late age at first reproduction (Blurton Jones and Marlowe, 2002; Gurven and Kaplan, 2006). Another distinctively human characteristic is the long period of slow growth from weaning to puberty (Bogin, 1998, 1999; Leigh, 2001; Gurven and Walker, 2006). However, little is known about the causes of specific growth trajectories, especially with respect to variation in other life-history traits. Extensive variation in growth rates, growth periods, and body size among traditional populations (Eveleth and Tanner, 1990; Migliano, 2005), all without access to fast food, supermarkets, and other modern conveniences, begs evolutionary and ecological explanations.

Small size and stature in many farming and foraging populations have been interpreted as adaptations to chronic disease and malnutrition (Stini, 1969; Holmes, 1995), hot/humid rain forests (Roberts, 1953, 1978; Cavalli-Sforza, 1986), and efficient foraging (Tobias, 1964; Lee, 1979). However, "small but healthy" interpretations are complicated by abundant evidence that better nutrition and growth in both human and nonhuman animals tend to

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have positive outcomes in both fertility and survivorship (Hill and Hurtado, 1996; but see exception in Frisancho et al., 1973). Additionally, many researchers emphasized the fact that individuals from the developing world who move and grow up in developed countries invariably grow considerably larger than previous generations (Bogin, 1999). A secular trend of increasing height and weight with urbanization is well-documented (Eveleth and Tanner, 1990; Ulijaszek et al., 1998).

The primary focus of this paper is the evolution of reaction norms for optimal growth rates and growth periods in particular socioecological contexts. A reaction norm refers to the set of phenotypes that a genotype will express across a range of selectively relevant environments (Stearns, 1992). Reaction norms are molded by natural selection according to the costs and benefits of trait plasticity. Growth trajectories with potentially strong genetic components, such as growth hormone or insulin-like growth factor type 1 resistance in Pygmies (Merimee et al., 1987; Hattori et al., 1996; Jain et al., 1998), suggest that selection has acted in favor of less plastic growth under stable environmental conditions, where large adolescent growth spurts are more costly than beneficial.

The reaction norms for growth and body size may not have straightforward relationships with environmental conditions, because selective pressure and environmental constraints (i.e., limited energy availability) may be acting in opposite directions. Environmental constraints are paramount, because every unit of growth requires additional maintenance costs from the present time period until death. Environmental conditions both constrain current growth via energetic constraints and serve as indicators for a dynamic optimality problem concerning allocations to growth and maintenance (Gadgil and Bossert, 1970; McDade, 2003). To the extent that environmental conditions during fetal, infant, childhood, juvenile, and adolescent periods (sensu Bogin, 1998, 1999) are valid indicators of future nutritional regimes (Kuzawa, 2005), the prediction is that slower growth rates will accompany poorer conditions (Ellison, 2001). ("Poor environmental conditions" are defined as those where survival and/or fertility are low due to malnutrition and disease.) Poor conditions make maintenance proportionally more expensive, and increase the probability of a nutritional shortfall and starvation risk. A common result in bioanthropological studies is that better environmental conditions are associated with faster child and juvenile growth, with an earlier adolescent growth spurt resulting in larger and taller adult bodies and earlier menarche and age at first reproduction (Huss-Ashmore and Johnston, 1985; Stinson, 2000; Ellis, 2004). For example, global variation in average age at menarche ranges from around 12 years of age in affluent societies to around age 18 in disadvantaged populations (Eveleth and Tanner, 1990). The conventional bioanthropological approach considers growth and developmental rates to be mostly a function of energetic constraints.

However, some aspects of poor environmental conditions, especially high mortality risk, may prompt faster growth and earlier reproductive development. The life-history approach to growth includes both energetic constraints to growth and subsequent maintenance, and the opportunity costs of lost reproduction if sexual maturity is delayed. Life-history models predict that a delay in age at first reproduction will be costly when the probability of survival to that age is low, all else being equal (Stearns and Koella, 1986; Stearns, 1992; Charnov and Berrigan, 1993; Berrigan and Koella, 1994). Faster growth is expected under high mortality regimes (Case, 1978). This effect should be more important in socioecologies where children and juveniles who attain larger sizes at earlier ages experience higher survivorship. This scenario of size-specific mortality leading to faster growth (Sibly et al., 1985) was proposed to explain the finding that neonates in countries with a high risk of parasitic and infectious diseases have larger-than-expected birth weights (Thomas et al., 2004).

Does empirical evidence support a positive or negative association between developmental rates and environmental stress at the group level? This question can be answered by analyzing data on growth and life-history traits in small-scale societies. Previous research suggested that economizing body maintenance costs (Gurven and Walker, 2006) is the primary benefit of small size and the driving factor behind variation in growth rates. Indeed, high disease loads often co-occur with low caloric and/or protein intake (Panter-Brick et al., 2001; McDade, 2003). Thus, selection may favor metabolic phenotypes that more efficiently economize body maintenance and immune-system costs, resulting in slow growth and later development (Arendt, 1997). If true, worse conditions should correlate with negative life-history outcomes such as later menarche and age at first reproduction.

On the other hand, depending on the force of mortality and its relationship to body size, selection for earlier/faster development may be found under some conditions (Migliano, 2005). This will likely be true in high-mortality regimes where the risk of mortality from disease/violence/accidents is relatively higher than the risk of mortality from malnutrition. Multivariate analyses are used here to separate selective pressure from nutrient constraints on the evolution and maintenance of different human ontogenies. Our hypothesis is that variation in growth schedules will concurrently map onto both selective pressure and better nutrition. To separate out these two opposing effects, adult body size is used as a proxy for overall nutrient availability, and probability of survivorship to age 15 is used as a measure of the force of selection for earlier/faster development. Ideally, we would use cause-specific mortality data and per capita energy consumption in place of body size in our analyses, but unfortunately such information is lacking for most societies. Nevertheless, with the available data, we can simultaneously examine growth patterns and attempt to reconcile the life-history perspective with the more conventional nutrient-limiting view.

METHODS

Small-scale societies

Growth data were compiled for 22 groups which are characterized by mostly subsistence-based economies, which exhibit near-natural fertility, and which have low levels of access to modern healthcare. Preference was given to societies where life-history data are available. This research focuses mostly on tropical societies, to partially avoid confounding effects of climate and temperature (Katzmarzyk and Leonard, 1998). All growth data are cross-sectional. We notice no obvious cohort effect among any of the populations, but cannot rule out potential cohort effects that may alter our results. In most cases, researchers include all available individuals from birth to age 25 from one or more camps or villages. In the case of repeated measurements, the same individual is allowed to enter the sample at different ages. Table 1 provides descriptive information and sample characteristics for the study populations. Readers are encouraged to consult original sources for detailed ethnographic information and methodological issues.

Life-history data are mostly from interviews (retrospective) if available, but some studies relied on stable population models (Weiss, 1973) to estimate age-specific fertility and mortality (e.g., Hadza, Ju/'hoansi, and Yanomamo). We use demographic data that most closely match the sample from which growth data were obtained. For most groups, growth and demographic data were collected contemporaneously. However, growth data for the Agta and Yanomamo were collected about a decade after the life-history data. Demographic data from the Gainj are combined with growth data from the Asai, who are neighbors in Highland New Guinea. Available body-size data for the Gainj (Wood, 1980) suggest that they are physically similar to the Asai (Malcolm, 1970a,b). The probability of survivorship to age 15 for the Eastern Pygmies is omitted, because estimates vary widely from 0.44, based on a stable population model (Migliano, 2005), to 0.78, as calculated by Bailey and Aunger (1995).

Statistical and graphic methods

Nonparametric curve-fitting, following a protocol used to study primate growth patterns (Leigh and Shea, 1996), is conducted with the locally weighted scatterplot smoothing (LOWESS) macro in SAS (Cary, NC). The tensions of the fits vary for each sample, depending on sample dispersion and sample size. The fits are "loose" to ensure that growth spurts are not smoothed out. The smoothing parameter or "window width" controls the tension, with higher numbers representing tighter tensions. We keep the smoothing parameter low (0.05) for larger sample sizes, but allow it to tighten to 0.15 for several groups with samples sizes of less than 100 people. Growth rates can be simply estimated as the rate of change in the LOWESS fit to the distance curve (i.e., plot of weight or height by age). In the absence of raw data, we fit the LOWESS to 1-year means. These pseudovelocity curves tend to jump up and down with age because of the loose tension in distance curves, so it is common procedure to smooth the velocity curve (Bogin, 1999; Leigh, 2001). Therefore, growth rates by age are fit with another LOWESS (smoothing parameter set at 0.05) to produce relatively smooth height and weight velocity graphs. This secondary smoothing helps interpret the shape of the adolescent growth spurt, but it is not used for estimating velocities, since these are simply calculated as the rate of change in the distance curve.

Growth rates in height and weight by age illustrate several diagnostic developmental markers that are readily comparable across

TABLE 1. *General information for each population in sample*[1]

Group name	Country	Ecology	Economy	Sex	Year(s) of growth-data collection	Number of individuals < 25 years old	Average individual measures	Age accuracy
Ache	Paraguay	Neotropical forest	Farming-foraging	f	1980–2001 W/2001–2002 H	222 W/106 H	4.6 W/1 H	Day
				m		262 W/110 H	3.9 W/1 H	
Aeta	Philippines (Luzon Island)	Tropical forest	Mixed	f	2002–2003	214	1	Year
				m		151	1	
Agta	Philippines (Luzon Island)	Tropical forest	Mixed	f	2002	86	1	Day
				m		69	1	
Arnhem Land (multiple societies)	Australia	Coastal/desert	Farming-foraging	f	1940s	Large sample	1	Year+
				m		Large sample	1	
Asmat	Irian Jaya	Coastal	Forager	f				Year
Baka	Cameroon (W, Pygmy)	Tropical forest	Forager	f	1996	108 W/104 H	1	Year+
				m		109 W/108 H	1	
Batak	Philippines (Palawan Island)	Tropical forest	Mixed	f	1980, 2003	36 H	1 H	Year
				m		Too few		
Gainj and Asai	New Guinea	Highlanders	Farming	f	1960s/1970s	102	1	Year
				m		151	1	
Guaja	Brazil	Neotropical forest	Forager	f	2005	52 W/42 H	1	Day
				m		51 W/42 H	1	
Hadza	Tanzania	Savanna/woodland	Forager	f	1980s	Large sample	Multiple	Year
				m			Multiple	
Hiwi	Venezuela	Savanna/gallery forest	Forager	f	1985–1988	22	5.6 W/2.5 H	Day
				m		37	6.5 W/2.9 H	
Ju'/hoansi	Botswana/Namibia	Desert/savanna	Forager	f	1967–1969	154	5.2 W/1.5 H	Season
				m		124	4.6 W/1.4 H	
Machiguenga	Peru	Neotropical forest	Farming-foraging	f	1987–1989	31	1	Year
				m		31	1	
Maku-Nadeb	Brazil	Neotropical forest	Farming-foraging	f	2003	39	1	Year
				m		58	1	
Maya	Mexico	Forest/savanna	Mixed	f	1992–1993	93 W/81 H	1	Year
				m		89 W/80 H	1	
Pygmy (East)	Democratic Republic of Congo	Tropical forest	Forager	f	1980s–1990s	68 H	1.8 H	Half year
				m		77 H	2.0 H	
Pygmy (West)	Cameroon/Congo/ C.A.R.	Tropical forest	Forager	f	1975–1977	78 W/88 H	1+	Year+
				m		108 W/120 H	1+	
Toba	Argentina	Savanna/dry forest	Mixed	f	2003	219 W/245 H	1	Day
				m		192 W/230 H	1	
Tsimane	Bolivia	Neotropical forest	Farming-foraging	f	2002–2003	238	1	Year
				m		265	1	
Turkana	Kenya	Savanna	Pastoral	f	1981–1982	258	1	Year
				m		159	1	
Walbiri	Australia	Desert	Forager	f	1950s	41	1	Year+
				m		80	1	
Wichi	Argentina	Savanna/dry forest	Mixed	f	2005	168 W/131 H	1	Day
				m		160 W/130 H	1	
Yanomamo	Venezuela	Neotropical forest	Farming-foraging	f	1986	46	1	Year
				m		70	1	

[1] W, weight data; H, height data; if not indicated, refers to both height and weight; m, male; f, female. See Table 2 caption for sources.

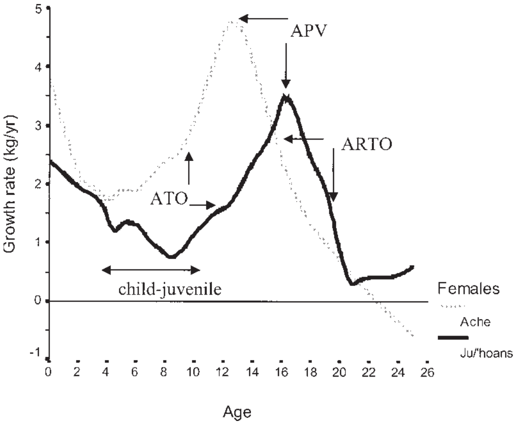

Fig. 1. Velocity curves for Ache and Ju/'hoansi females. Child-juvenile period of slow growth, age at takeoff velocity (ATO), age at peak velocity (APV), and age at return to takeoff velocity (ARTO) are marked on graph. ATO is defined as large upswing in velocity, APV is peak, and ARTO is age when velocity returns to same value as at takeoff.

different populations. These include the following: 1) average growth rate from age 3 (approximate age at weaning) to age 10; 2) age at takeoff velocity (ATO); 3) age at peak velocity (APV); and 4) age at return to takeoff velocity (ARTO). The latter three measures refer to the beginning, peak, and end of the adolescent growth spurt. Figure 1 exemplifies each of these growth characteristics in Ache and Ju/'hoansi females. These measures are useful in that they separate out the relatively stable early growth period from the adolescent growth spurt. We do not analyze the magnitude of the adolescent growth spurt, because individuals have growth spurts at a variety of ages that we cannot address with cross-sectional data. However, as long as individual growth spurts are approximately normally distributed around the mean, then the average ages at the beginning, peak, and end of the growth spurt are preserved in the analysis. Other analyses of growth in some of these small-scale societies showed that cross-sectional (e.g., Agta: De Souza, no date) and longitudinal (e.g., Hadza: Blurton Jones, no date; Ache: Walker et al., 2006) growth rates are roughly linear during the child-juvenile phase. We have more confidence in estimates of child-juvenile growth rates than we do in our adolescent growth spurt parameters because sample sizes are larger, cross-sectional data better mimic longitudinal results, and age estimates at younger ages are more accurate.

We perform regression analyses (SPSS 10.0) of growth and developmental diagnostics as functions of body size and survival. All analyses are performed separately for each sex. Given that our samples sizes in multiple regressions are dangerously small for assumptions of ordinary least-squares regression, we also calculate *P*-values for our parameter estimates using resampling with replacement or "bootstrapping" techniques (Efron, 1979) with a Pascal program. The original data distributions were resampled with replacement in 10,000 bootstrap replications for each independent variable, while holding the other variable constant. The *P*-value is then the proportion of iterations where the fitted slope to random data is absolutely larger than the slope through the observed data (Davison and Hinkley, 1997).

Data quality

For all samples where raw data are available, we calculate 95% confidence intervals for child-juvenile growth rates by fitting a linear regression through body weights and heights from ages 3–10. However, these confidence intervals assume that ages are known. Uncertainty in age estimates (see Table 1 for accuracy in age estimates for each group) are of primary concern in this paper, because systematic biases in aging can significantly alter calculations of growth rates and life-history characteristics. Eastern Pygmy data (Efe) are from R.C. Bailey, who followed cohorts for a significant amount of time. However, age estimates for the other Pygmies (including the 1996 Baka study) (Yamauchi et al., 2000), Australia, and New Guinea are the most uncertain, since they are based on tooth eruptions or "guess-timates," albeit by people of considerable experience with the study group. For child-juvenile velocity, we divide the change in size from age 3 to age 10 by 7 years. Since some of our samples have potentially a year or so error in age estimates, this results in a 14% (= 1/7) or more source of error, most worrisome if there are systematic biases (e.g., larger individuals are assumed to be older). Most studies have age estimates that are more accurate, as they are based on a combination of observed births and relative age lists tied to dated events (Ache, Hiwi, and Agta), or a combination of these with governmental or missionary birth records (Maku-Nadeb, Tsimane, Aeta, Agta, Batak, Guaja, Toba, Wichi, Maya, and Machiguenga).

RESULTS

Growth rates and developmental diagnostics vary considerably across different soci-

TABLE 2. Body growth diagnostics and life-history traits[1]

	Sex	Child-juvenile growth velocity (kg/year)	Age at takeoff velocity	Age at peak velocity	Age at return to takeoff velocity	Average adult size (kg)	Age at menarche	Age at first reproduction	Probability of survival to age 15	Life expectancy at age 15
Ache	f	2.1	10.0	12.5	16.0	53.7	14.0	17.7	0.68	50.4
	m	2.0	11.5	15.0	18.5	59.8		23.0	0.79	48.7
Aeta	f	1.6				38.0	13.8	18.7	0.33	27.3
	m	1.5				40.0		20.9	0.33	
Agta	f	1.4	10.0	12.0	15.0	40.3		19.5	0.42	33.4
	m	1.4	11.0	14.0	16.0	46.4			0.42	
Arnhem Land	f	2.1	11.0	12.5	13.5	41.3				
	m	1.9	12.0	14.0	16.5	55.5				
Asmat	f					50.0		18.5	0.50	27
Baka	f	2.9				44.4	14–15	18–19		
	m	2.7				49.6				
Batak	f					40.8	14.6	18.7	0.51	29.5
	m					46.9		22.7	0.51	
Gainj and Asai	f	1.3				38.0	18.4	25.7	0.69	29.7
	m	1.1				43.3		37.0	0.75	29.6
Guaja	f	1.8	10.0			50.4				
	m	2.0				61.1				
Hadza	f	1.9	10.0	15.0	18.0	48.0	16.0	19.0	0.58	44.0
	m	1.8	12.0		18.0	54.0			0.55	
Hiwi	f	2.6				49.7	12.6	20.5	0.45	36.3
	m	2.3				57.4			0.56	
Ju'/hoansi	f	1.1	13.5	16.0	19.5	42.2	16.6	18.8	0.60	41.5
	m	1.2	13.0	16.0	21.5	50.6			0.56	
Machiguenga	f	2.2				51.0			0.60	39.7
	m	1.8				62.2			0.60	
Maku-Nadeb	f	1.8	12.0	14.0	16.0	49.7				
	m	1.9	13.0	14.0	17.0	60.6				
Maya	f	1.2	10.0	12.0	15.0	51.3				
	m	1.7	10.0	12.0	14.0	60.3				
Pygmy (East)	f					39.4	15.5	19+		
	m					43.0				
Pygmy (West)	f	1.7	10.5			42.7	13.8		0.55	
	m	2.2	11.0			48.3			0.55	
Toba	f	2.4	10.5	12.5	14.5	64.2	12.8	17.8		
	m	2.4	11.5	12.5	15.5	76.3				
Tsimane	f	1.6	11.0	13.0	16.0	51.0	13.9	18.6	0.76	41.2
	m	1.9	13.0	14.0	18.0	61.3		23.0	0.80	
Turkana	f	1.6				48.9	16.5	22.2	0.76	46.6
	m	1.7	14.0	17.0	18.5	55.6			0.76	
Walbiri	f	1.7				45.0	14.0	17.0		
	m	2.1				57.0				
Wichi	f	2.4	10.0	11.5	13.0	62.3	12.9	16.2		
	m	2.0	11.5	13.0	15.0	73.9				
Yanomamo	f	1.5	12.0			45.4		18.4	0.48	27.0
	m	1.6				52.0			0.48	

[1] "Child-juvenile growth" column represents rate of mass growth from ages 3–10, before age at takeoff velocity or puberty. Blank cells for growth characteristics are indeterminable values usually driven by small sample sizes at critical ages, or potentially a true lack of adolescent growth spurt. Sources for growth and life-history data: Ache (Walker et al., 2006; Hill and Hurtado, 1996), Aeta (Migliano, 2005), Agta (De Souza, no date; Early and Headland, 1998), Arnmhem Land (Billington, 1948; Hamilton, 1981; Hiatt, 1965), Asmat (van Arsdale, 1978), Baka (Yamauchi et al., 2000), Batak (Migliano, 2005; Eder, 1987, 1996), Asai (Malcolm, 1970a,b), Gainj (Wood et al., 1985; Wood, 1980, 1987), Guaja (Gradimir Djurovic), Hadza (Blurton Jones et al., 1992; Blurton Jones, no date; Marlowe, 2004), Hiwi (Hurtado and Hill, 1987, unpublished data; Kaplan et al., 2000), Ju'/hoansi (Howell, 1979), Maku-Nadeb (Walker, 2004), Machiguenga (Hillard Kaplan), Maya (Karen Kramer), Eastern Pygmies (Bailey, personal communication; Dietz et al., 1989; Schebesta, 1933, 1938, 1957), Western Pygmies (van de Koppel, 1983; van de Koppel and Hewlett, 1986; Cavalli-Sforza, 1986; Bahuchet, 1979); Toba/Wichi (Valeggia and Ellison, 2004; Sánchez-Ocasio and Valeggia, 2005; Bove et al., 2002), Tsimane (Michael Gurven), Turkana (Little et al., 1983; Gray, 1994; Leslie et al., 1999); Walbiri (Abbie, 1957, 1961; Meggitt, 1965), Yanomamo (R. Hames, N. Chagnon, and W. J. Oliver; Melancon, 1982; Neel and Weiss, 1975). m, male; f, female.

eties in both weight (Table 2) and height (Table 3). Tables 2 and 3 are provided to give transparency to subsequent graphs and analyses. As we shall see, impressive variation in growth exists among groups of hunter-gatherers, despite the fact that these groups are often loosely assembled into the same macrocategory (Kelly, 1995). Many societies fit the

TABLE 3. Height growth diagnostics[1]

	Sex	Child-juvenile growth (cm/year)	Age at takeoff velocity	Age at peak velocity	Age at return to takeoff velocity	Average adult height (cm)
Ache	f	5.1	10.0	13.0	15.0	149
	m	4.9	11.0	14.5	17.5	158
Aeta	f	4.8				140
	m	4.8				150
Agta	f	5.5				143
	m	5.0				153
Arnhem Land	f	6.3	11.0	13.0	14.0	156
	m	6.0	12.0	13.5	15.5	171
Baka	f	7.1				147
	m	5.6				154
Batak	f	4.6	10.5	12.5	14.5	144
Guaja	f	6.1				144
	m	5.6				159
Hadza	f	5.2	10.0		12.0	150
	m	4.7	11.0	13.0	15.0	160
Hiwi	f	7.0				146
	m	5.6				156
Ju'/hoansi	f	4.2	13.0	15.0	16.5	150
	m	4.4	14.0	15.5	16.5	161
Machiguenga	f	6.4				149
	m	5.4				162
Maku-Nadeb	f	4.4	11.0	14.0	16.0	143
	m	4.8	14.0	15.0	16.0	156
Maya	f	4.3	10.0	12.0		142
	m	5.4	10.0	12.0		155
Pygmy (East)	f	4.6				136
	m	4.3				144
Pygmy (West)	f	5.1	10.0			145
	m	5.8				153
Toba	f	6.1				157
	m	6.1	11.5	13.0	14.5	172
Tsimane	f	4.9	10.0	12.0	13.0	149
	m	5.2	12.0	14.0	18.0	163
Turkana	f	5.4				166
	m	5.5	14.0	17.0	18.5	175
Walbiri	f	6.3				157
	m	6.3				170
Wichi	f	6.3	10.0	10.5	11.0	152
	m	5.2	12.0	13.0	14.0	165
Yanomamo	f	4.6	12.0			142
	m	4.7				152

[1] "Child-juvenile growth velocity" represents rate of height growth from ages 3–10, before age at takeoff velocity or puberty. Blank cells are indeterminable values usually driven by small sample sizes at critical ages, or potentially a true lack of adolescent growth spurt. f, female; m, male.

classic slow human developmental strategy. Growth is slow from weaning to puberty (1–2 kg/year and 4–6 cm/year), followed by a marked adolescent growth spurt. Groups with smaller adult size and stature (average for individuals aged 25–55) tend to display slower growth and later development (e.g., the Ju/'hoansi as contrasted with the Ache; Fig. 1). For example, there is a negative relationship between menarche and adult size (see regressions below). These results appear to conform to many bioanthropological studies that associated slower growth and later development with low energy availability (reviewed in Bogin, 1999; Eveleth and Tanner, 1990; Ulijaszek et al., 1998).

However, some groups like the African Pygmies, Philippine Negritos (Aeta/Batak/Agta), and Hiwi of Venezuela demonstrate a growth and developmental pattern that appears somewhat accelerated for their adult body size. This growth pattern is characterized by considerably faster (and more linear) growth across development, despite poor environmental conditions. Adolescent growth spurts tend to be diminished or absent, at least with cross-sectional data, and given the problem of aging discussed above. Growth rates during child-

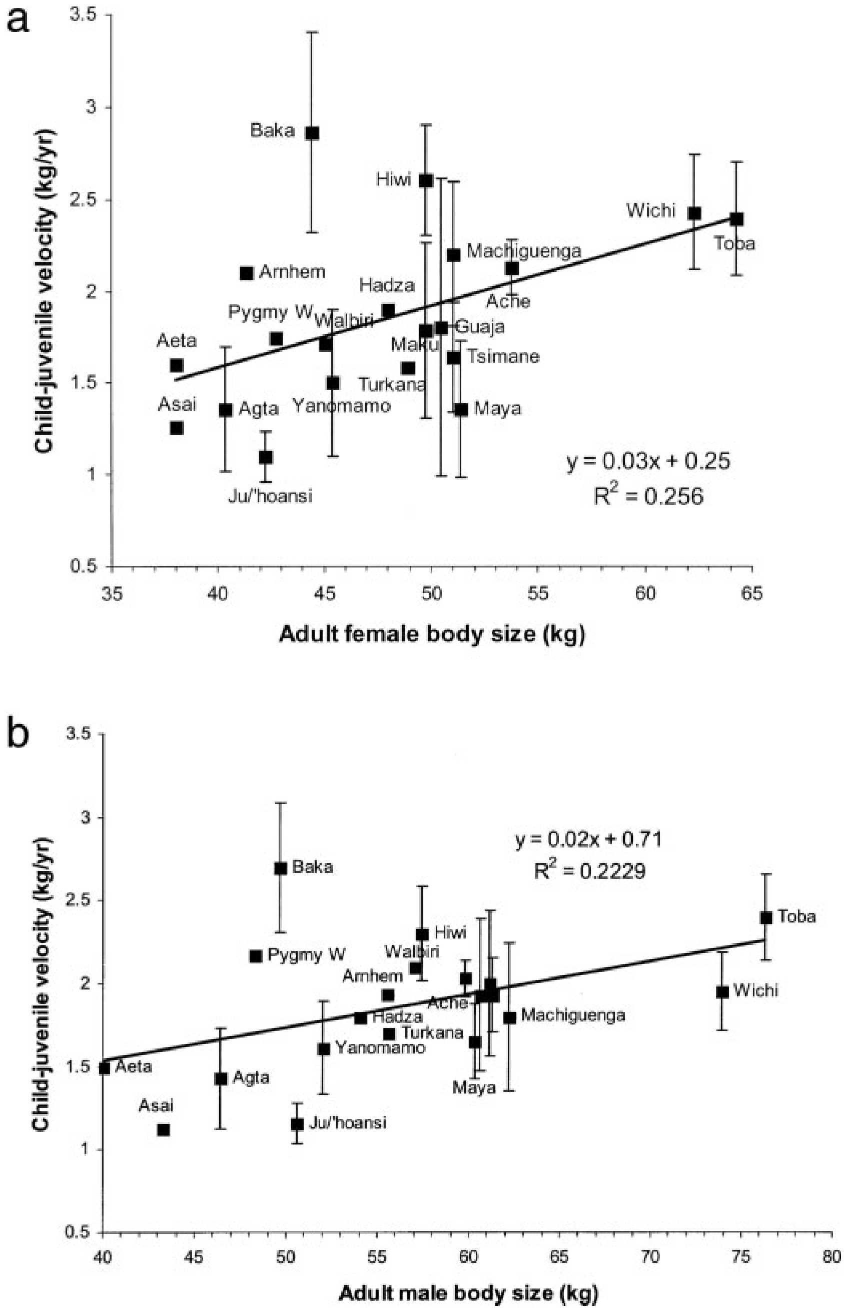

Fig. 2. Relationship between child-juvenile growth rate and adult weight for (**a**) females and (**b**) males. It should be noted that many small body-size groups are Pygmies and Negritos, which pull up left end of fit line. If one includes survival in multiple regression (see below), true body-size slope increases over what is shown here. Multiple regressions give body-size coefficient of 0.07 for females (Table 4) and 0.04 for males, which is double that shown here, illuminating the fact that Pygmies/Negritos appear to have faster-than-expected growth for their adult size, correlated with low juvenile survival rates. Error bars (95% confidence interval of slope for weights by age from ages 3–10) are provided for those societies where we have access to raw individual-level data. These error bars only capture variation in cross-sectional growth rates assuming no error in age estimates. Three unlabeled groups that clump near Ache on male graph are Tsimane, Guaja, and Maku-Nadeb.

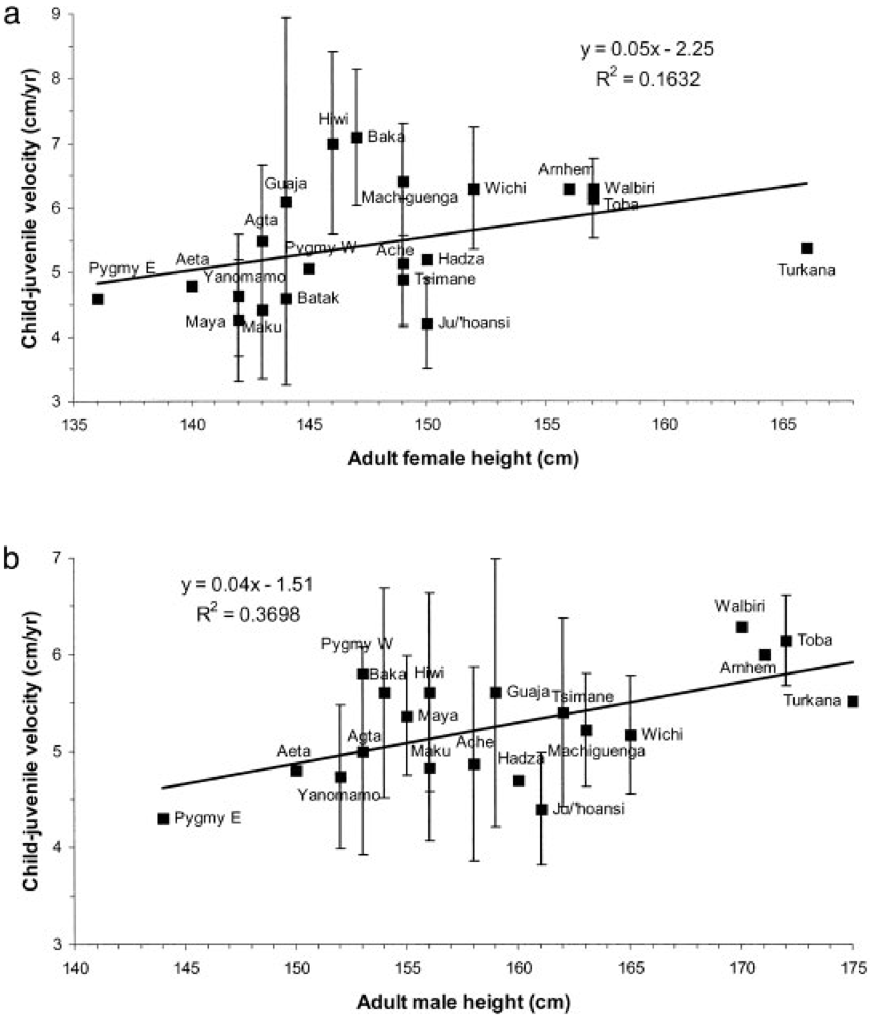

Fig. 3. Relationship between child-juvenile growth rate and adult height for (**a**) females and (**b**) males. Error bars (95% confidence interval of slope for heights by age from ages 3–10) are provided for those societies where we have access to raw individual-level data.

hood and juvenile periods (age 3–10) are surprisingly fast for some groups, especially given their small adult sizes (Figs. 2, 3). For example, child-juvenile growth for Baka girls averages 2.9 kg/year and 7.1 cm/year, and 2.6 kg/year and 7.0 cm/year for Hiwi girls. These growth rates approach or exceed those of US children and juveniles (about 3.3 kg/year and 6.5 cm/year), despite the fact that Baka and Hiwi adults are less than two thirds the weight of US adults. For the Baka and Hiwi, this translates into average size at age 10 for girls being around 70% of adult size, whereas societies like the Ju/'hoansi, Hadza, and Maya are only about 40–45% of their adult size at age 10. We believe that these large differences among groups makes it unlikely to be an artifact driven by age errors alone.

We find that average growth rate from ages 3–10, or child-juvenile velocity, is one of the best measures to compare across societies, because available longitudinal data show that growth rates appear to be mostly linear and stable during this period of slow growth (Blurton Jones, no date; Walker et al., 2006), probably because few individuals are spurting before age 10. This makes child-juvenile velocity an excellent measure when analyses are

TABLE 4. Regression models for child-juvenile growth rates, menarche, and age at first reproduction in females[1]

Model	Independent variables	Unstandardized coefficient β	SEC	Standardized coefficient (beta)	*t*-statistic	*P*-value (OLS)	*P*-value (resampling)
Child-juvenile growth in weight (kg/year) for females, n = 12, $R^2 = 0.69$							
	Constant	−0.632	0.667		−0.947	0.368	
	Body size	0.073	0.017	0.940	4.409	0.002	0.007
	Survivorship to 15	−1.724	0.658	−0.559	−2.621	0.028	0.041
Child-juvenile growth in height (cm/year) for females, n = 12, $R^2 = 0.52$							
	Constant	0.709	1.725		0.411	0.691	
	Body size	0.155	0.050	1.006	3.125	0.012	0.004
	Survivorship to 15	−4.671	1.916	−0.785	−2.439	0.037	0.020
Age at menarche (females), n = 10, $R^2 = 0.68$							
	Constant	19.545	3.078		6.349	0.000	
	Body size	−0.240	0.076	−0.763	−3.149	0.016	0.031
	Survivorship to 15	10.763	3.118	0.836	3.452	0.011	0.037
Age at menarche (females), n = 9, $R^2 = 0.62$							
	Constant	25.266	3.900		6.479	0.001	
	Body size	−0.451	0.144	−1.457	−3.134	0.020	0.003
	Life expectancy at 15	0.272	0.103	1.226	2.636	0.039	0.005
Age at first reproduction for females, n = 12, $R^2 = 0.43$							
	Constant	25.668	4.720		5.438	0.000	
	Body size	−0.255	0.115	−0.623	−2.222	0.053	0.057
	Survivorship to 15	10.002	4.521	0.621	2.213	0.054	0.068

[1] Reported *P*-values are from ordinary least-squares regression (OLS) and from a resampling technique.

desired of small sample sizes and cross-sectional data. Our smallest sample of individually reported measurements is 10 Hiwi girls between ages 3–10 who were weighed over a period of several years, for a total of 55 weights. This small sample yields a 95% confidence interval of child-juvenile velocity between 2.3–2.9 kg/year, making it significantly faster than many of the other groups. The much larger sample size for Ache girls, for example, gives a 95% confidence interval of child-juvenile velocity between 1.95–2.25 kg/year. However, this is a comparison between two groups where we have considerable confidence in age estimates.

Multivariate analyses

We attempt to separate the two opposing effects of environmental constraints vs. selective pressure on the rates and timing of development by running multiple regressions separately for males and females. Adult body size is used as a proxy for overall nutrient availability and probability of survivorship to age 15 (or *l*15) as a measure of the environmental hazards that would select for earlier/faster development. Life expectancy at age 15 (or *e*15) is also considered an alternative measure of environmental hazard level. The two survivorship measures *l*15 and *e*15 show a positive correlation of 0.59 (n = 14), but tap into different sources of mortality, i.e., juvenile vs. adult, respectively. We also tested the survivorship from ages 1–15 by removing infant mortality, and found slightly weaker effects (not shown).

Survivorship and adult body size act in opposing directions on all aspects of growth and development in this sample. Larger adult body size is associated with faster and earlier development, indexed by child-juvenile growth (weight and height), menarche, and age at first reproduction for females (Table 4). However, survivorship is associated with slower and later development, indexed by all the same variables. Growth and developmental markers are more strongly associated with *l*15 than *e*15 with the exception of menarche, which is strongly associated with both. Our results suggest that juvenile mortality risks are the main force behind faster and earlier growth (given adult body size).

From the multivariate regressions, we can calculate that age at first reproduction comes about 1 year earlier for every 4-kg increase in adult female size. Additionally, age at first reproduction comes about 1 year earlier for every 10% decline in survivorship to age 15. Similar shifts are seen in age at menarche. Not surprisingly, child-juvenile growth is faster with larger body size, at about 73 g faster per year for each additional kilogram in adult females. Additionally, a 10% decrease in survivorship is associated with an additional growth of 172 g/year in females.

It is important to note that multiple regressions show a considerably stronger relationship between body size and growth rates than is shown by the univariate regression in Figures 2 and 3, because faster/earlier development is also associated with lower survivorship. Given that most smaller body-size groups (Pygmies/Negritos) tend to have lower survival than groups with larger body size, this has the effect of increasing the body-size regression coefficient over that shown in Figure 2 (in fact, it doubles for both sexes). The result is that Pygmies and Negritos, in addition to the Hiwi, actually have faster-than-expected growth (as well as earlier menarche) for their adult body size, and these residuals are positively related to high juvenile mortality.

The sample sizes for the regressions in Table 4 are small (only 9–12 societies), but we obtain comparable (and significant) results using iterative resampling techniques that are less affected by small samples. Major-axis regressions (model II, considering that the independent variables have error) also produce significant results with strong coefficients (not shown). Finally, if we omit the two studies from the regressions in Table 4 that have the worst age estimates (Asai-Gainj and Western Pygmies), the child-juvenile growth model for females improves considerably (both P-values <0.005). However, omission of these two groups adversely affects the age at first reproduction model, already teetering at borderline levels of significance. The age at menarche remains essentially identical as reported in Table 4 with these two groups removed. We were unable to identify a clear adolescent spurt in many of the societies, disallowing multivariate analyses of ATO, APV, and ARTO. We hope that future work will compile a larger sample of all these characters, because these measures will likely further confirm our results. Finally, parameters in the regression of child-juvenile velocity for males, while in the predicted direction as found for females, are not significantly different from zero.

DISCUSSION

Our results for females support both the traditional bioanthropological and life-history perspective. Societies with larger and taller adults generally develop faster and earlier. In addition, we find that juvenile mortality is related to faster child-juvenile growth rates and earlier menarche and age at first reproduction. In fact, the relative force of nutrient constraints vs. selective pressure is approximately equal, given that the standardized regression coefficients of adult body size and survivorship tend to be about the same.

In general, male growth rates are less plastic across societies, as evidenced by a flatter slope in Figures 2 and 3 as compared to females. Male growth rates also have less spread around the regression lines in Figures 2 and 3, and this variation is not significantly associated with juvenile survival (but this could be a type II error). Male and female growth trajectories may be under different selection. Selection for early female development must be strong when survivorship is low, given that each reproductive act requires considerable time for both gestation and lactation. Males may have strong selection for a target body size for male-male competition, with fewer opportunity costs than females in terms of foregone reproduction.

Life-history theory is a powerful explanatory framework for auxology that forces researchers to delineate the fitness costs and benefits of different growth trajectories subject to energetic constraints. Traditional bioanthropological studies focused mostly on the cost side of the equation (i.e., maintenance costs) by documenting the energetic constraints imposed by malnutrition and disease. Life-history theory firmly addresses these constraints, but also considers that selection may act on different competing demands (i.e., current vs. future reproduction), and that optimal allocations are likely to change across different mortality regimes. Therefore, the conventional bioanthropological perspective is not an alternative explanation in opposition to the life-history perspective. Rather, it is probably best viewed as an emphasis on energetic constraints, and subsumed as a subset of life-history theory.

It is important to emphasize that mortality-based selection for faster/earlier development implies greater investments in current rather than future reproduction, a pattern that makes sense if future survival is less certain. Additionally, we suggest that larger body size at young ages may be important for combating parasites and infectious diseases via a more robust immune system (e.g., larger spleen/thymus) or some other form of size-dependent mortality, such as infanticide of smaller individuals. We recognize that immune function and other maintenance costs must compete with body growth for energetic resources (Panter-Brick et al., 2001; McDade, 2003), and one interpretation of our regressions is that the causal arrow points from faster growth to higher mortality, and not the other way around. However, it is difficult to understand

TABLE 5. Three-dimensional character space of juvenile survival, adult survival, and resource abundance, and their effects on human ontogenetic patterns[1]

	Low adult survival	High adult survival
High juvenile survival	High energy availability Intermediate adult size Intermediate age at first reproduction? Intermediate growth Not observed	High energy availability Large adults Intermediate menarche/puberty Intermediate age at first reproduction Intermediate growth with spurt *Ex.* Ache
	Low energy availability Small adults Late menarche Late reproduction Slow growth with small spurt *Ex.* Gainj and Asai	Low energy availability Intermediate adult size Late menarche Late reproduction Slow growth with small spurt *Ex.* Ju/’hoansi
	High energy availability Intermediate adult size Early reproduction Fast growth Not observed	High energy availability Large adults Early reproduction Fast growth Not observed
Low juvenile survival	Low energy availability Small adults Relatively early menarche Intermediate age at first reproduction Relatively fast growth, reduced spurt? *Ex.* Negritos	Low energy availability Intermediate adult size Early menarche Intermediate age at first reproduction Fast growth, reduced growth spurt? *Ex.* Hiwi

[1]“Relatively” refers to “for a given small adult body size” or “given high energetic constraints.”

why fast growers would simultaneously pay relatively higher growth and maintenance costs, only to experience higher mortality. An alternative interpretation is that higher juvenile mortality may render fewer siblings and hence less competition for parental provisions. This scenario may allow for faster child-juvenile growth and earlier reproduction. Indeed, less sibling competition may work in concert with faster development that buffers against certain mortality risks, and shortens time spent in high-mortality lifestages.

Analogous patterns of mortality-induced increases in growth and early reproduction likely evolved in other species when a developmental threshold had to be obtained quickly (Arendt, 1997). Some common themes in the literature include escaping from high predation, surviving overwintering, and achieving sexual maturation. For example, survival rates in fish are closely related to body weight and length (Lorenzen, 1996). Rapid growth may allow some species (e.g., guppies: Reznick, 1983) to reach a size refuge from heavy predation (Seed and Brown, 1978). Some snails, when exposed to a trematode parasite, appear to compensate for potential losses in future reproductive success by an increase in egg-laying soon after exposure (Minchella and Loverde, 1981). This holds true whether or not they actually become infected, but in either case, snails show a reduction in fitness, demonstrating a cost of increased early reproductive effort. Other snails were shown to grow more rapidly in the presence of crayfish, a phenomenon initiated by a water-borne cue released by crayfish feeding on conspecific snails (Crowl and Covich, 1990). Case (1978) surmised that juvenile mortality is one of the most important determinants of faster growth in homoiotherms, in order to quickly escape vulnerability in the nestling stage.

Slow and fast life histories?

The origin and maintenance of a slow human life-history strategy is easy to conceptualize. Selection for long juvenile periods in humans is likely closely tied to longer lifespans and larger brains (Harvey et al., 1987; Kaplan et al., 2000). Indeed, we show here that juvenile periods tend to be longer with higher juvenile survivorship. Human development requires extensive provisioning to unproductive offspring. Larger size may bring few benefits for pre-reproductive youngsters with underdeveloped cognitive capacities in complex foraging (Walker et al., 2002) or social settings. Selection may have acted to slow down growth rates in order for offspring to remain small and save on maintenance costs that they themselves cannot produce. With slow-growing offspring, parents can econo-

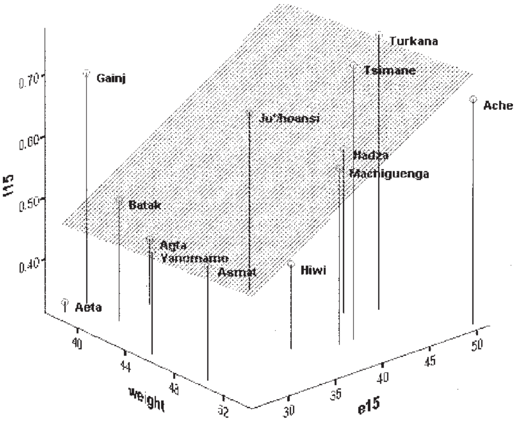

Fig. 4. Three-dimensional plot of adult female body weight (kg) on x-axis, juvenile survival (*l*15) on y-axis, and adult survival (*e*15) on z-axis, with best-fit plane. This plot emphasizes continuity or spectrum along different axes. Pygmies are not included in this plot due to lack of information for *e*15, but are likely associated near Negritos (Batak, Agta, and Aeta).

mize and better provision other dependent offspring, thereby increasing fertility (Bogin, 1999). Adult size is reached quickly via the adolescent growth spurt, which effectively saves on maintenance costs that would have accumulated during the long human child-juvenile period (Gurven and Walker, 2006).

The origin and maintenance of a faster human life-history strategy, if it exists, deserve more attention. The fast strategy appears to manifest in poor environmental conditions, yet one must ask why other groups under poor conditions, such as the Ju/'hoansi and New Guinea Highlanders (Gainj and Asai), appear to manifest slow strategies, and why the Hiwi and Baka opt to increase their cumulative maintenance costs and provisioning demands on their parents by growing fast at young ages. One interpretation is that the relative risk of death from parasites and infectious diseases prompts fast development in order to reach puberty, menarche, and first reproduction at younger ages. Faster growth must be less costly when it comes with size-related benefits that reduce mortality and morbidity (Arendt, 1997). Higher-elevation or drier environments probably reduce parasitic and infectious diseases. In these environments, the relative risk of death from starvation increases in comparison to disease. Human groups in these ecologies may do better to grow slowly and reproduce late as a maintenance-cost effective strategy. Fast growth may only be beneficial in environments where larger subadult sizes bring benefits of reduced mortality. For example, nation states with a higher prevalence of parasites and infectious disease species (PIDS) have larger-than-expected neonates, and this finding was interpreted as a mechanism to combat these PIDS (Thomas et al., 2004).

A three-dimensional character space that includes juvenile survival, adult survival, and resource abundance is useful to sort out the different conditions leading to various ontogenies (Table 5). In the upper right corner with low juvenile and adult mortality is the classic slow human life history, separated into high and low resource abundance. At the opposite end (bottom left) are the Negritos (and probably the Pygmies), characterized by high juvenile mortality that potentially drives relatively earlier development and small body size. Looking across the chart, low adult mortality correlates mainly with larger adult size, and less with developmental rates and timing, though we show a strong effect of adult mortality on earlier age at menarche (Table 4). Again, the main driver of the timing of development may be juvenile mortality, which speeds up child-juvenile growth with an early cessation of growth, and an early commencement of reproduction that potentially cuts off a robust adolescent growth spurt.

Given that we have estimates for juvenile and adult survival and adult female body size as a proxy for resource abundance, we can plot the life-history characters of each society in a three-dimensional plot (Fig. 4). Following Table 5, a plane appears with high adult and juvenile survival on the upper right, with both diminishing as one moves toward the Negritos on the lower left. The Gainj jump out as outliers from the best-fit plane. The Gainj appear to have high adult adult mortality yet excellent juvenile survival, which is perhaps related to their slow growth and development. In contrast, the Hiwi are somewhat intermediate in terms of adult body size and adult survival, but demonstrate high juvenile mortality. Indeed, the Gainj and Hiwi may represent the exceptions that prove a life-history rule of juvenile mortality selecting for developmental rates. The Asmat of Lowland New Guinea associate near the Hiwi, and we would predict fast and early growth in this society.

There is no marked adolescent growth spurt in the Hiwi, Baka, Batak, or East African Pygmies, at least with cross-sectional examination of height and weight. However, part of the in-ability to uncover the spurt is likely related to errors in age estimates (especially of the Baka) and small sample sizes at critical ages (in all these societies). The other West African Pygmies, Aeta, and Agta show some semblance of a growth spurt, but less robust than in other societies like the Ache and Ju/'hoansi in Figure 1. Under the caveat of limitations of small samples and cross-sectional data, there is the impression that faster relative growth during the child-juvenile phase is associated with a less pronounced adolescent growth spurt. A diminished adolescent growth spurt in Pygmies and Negritos is probably associated with genetic differences in the growth hormone/insulin-like growth factor type 1 axis (Merimee et al., 1981, 1987; Hattori et al., 1996; Jain et al., 1998; Clavano-Harding et al., 1999).

The Hiwi are an interesting case. Hiwi age at first reproduction (20.5 years), taken from adult women in the population, does not appear to match the very early age at menarche (12.6 years, standard deviation (SD) = 1.6, n = 11) for adolescent girls from the cohort from which growth data were obtained. While the sample size for menarche is small, the ages are determined with confidence, since the Hiwi girls undergo memorable rite-of-passage ceremonies. The average age at first birth for younger mothers under age 35 (where there is more confidence in ages) is 17.9 years. This better matches other societies, where the age difference between age at first reproduction and menarche averages 4.5 years (SD = 1.6, n = 14). Interestingly, the 14- and 15-year-old (n = 5) Hiwi girls are as large as or larger than Hiwi women in their 20s, but we have no girls in their late teens in this sample. It is unknown whether the Hiwi recently moved toward a faster developmental strategy driven by lower juvenile survival, or if this pattern is more genetic and ancient in its origin, as it may be for the Pygmies and Negritos. There is no evidence of any recent increase in nutritional status in the Hiwi (since disease load and malnutrition are commonplace; Hurtado and Hill, 1987) that would inflate recent growth in children and juveniles.

The Australian Aborigines (Walbiri and various ethnicities in Arnhem Land) in several respects also appear to have a somewhat accelerated life history. Relative child-juvenile growth rates are slightly faster than expected for their body size (Fig. 2). Reliable survivorship data are missing, so it is not possible to assess mortality-driven selection for faster development. An adolescent growth spurt is marked in the sample from Arnhem Land, and less so in the Walbiri. Nonetheless, a rather young age of menarche, first reproduction, and growth cessation, given their adult size, all support a partially advanced rate of development for these Aborigines. Unfortunately, considerable error in aging makes us uncomfortable about making more definitive statements for the Aborigines.

Growth characteristics that were promoted as distinct human universals, such as a robust adolescent growth spurt preceded by slow child-juvenile growth (Bogin, 1998, 1999; Walker et al., 2006), are not markedly visible in the "fast strategy" societies. Therefore, they may not be human universals. However, a better assessment of this idea must await more (and higher-quality) data. Despite some similarities with chimpanzee life histories, it is probably erroneous to view the "fast human life history" as the ancestral condition. If it exists, the "fast strategy" may actually be a recently derived characteristic of some human groups in response to high mortality from parasites and infectious disease, probably exacerbated by higher population densities in comparison to other hunter-gatherers.

CONCLUSIONS

It is beneficial to include growth trajectories as integral components of life histories. A complete assessment of an organism's life history requires age-specific rates of growth, survivorship, and fertility. It is unfortunate that such data are rare (and occasionally low-quality) for hunter-gatherers, given that human evolution occurred in a foraging context, and that the last century has seen a drastic global reduction in societies with this lifestyle. Detection of different developmental patterns is difficult without cross-cultural growth information, and perhaps this explains the previous lack of attention to the question of divergent human life-history strategies.

In this cross-cultural comparison, growth and life-history traits helped illuminate some differential ontogenetic strategies, and proved useful for understanding the evolutionary and ecological processes behind their existence. In sum, evidence is presented that relatively fast development may be an adaptation for some human females (e.g., Hiwi, Negritos, and Pygmies) living in several high-mortality regimes, a conclusion also reached (independently) by Migliano (2005). The commonly held assumption that worse conditions only lead to slower growth and later development has been called into question. We are not saying that energetic constraints are not important to understand delayed growth and development in these societies, but we do suggest that energy availability may only be a little over half the full story. Better or normal conditions (i.e., good survivorship and nutrition) appear to promote a slow ontogenetic strategy that is likely involved with energy conservation during long learning periods. On the other hand, more attention should be paid to high-mortality regimes that have potentially causal links to faster ontogeny and may contribute to important variation in modern human growth and development.

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