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Original Research Article

Catch-Up Reproductive Maturation in Rural Tonga Girls, Zambia?

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ABSTRACT To compare the timing of reproductive maturation among urban and rural Tonga girls in Zambia, anthropometric measures and Tanner stages of breast development were obtained. Subjects were 774 (282 rural, 492 urban) girls ages 6–18. Results indicate that rural girls are shorter and have smaller triceps and subscapular skinfolds than their urban counterparts. Median age at menarche for the entire sample, as estimated by probit analysis, was 14.8 years (95% CL = 14.34–15.40). Onset of breast development among urban girls was significantly younger than for the rural girls: 11.47 (95% CL 11.22–11.71) years vs. 13.15 (95% CL 12.40–14.15) years. In contrast, the two groups did not differ in timing of pubertal completion as assessed by median age for Tanner Breast Stage 5: 17.01 (95% CL 16.30–18.33) vs. 16.96 (95% CL 16.37–17.56) years. Predictors of pubertal onset, based on multivariate logistic regression, included dental maturation, height, and triceps skinfold. Triceps skinfold was the only significant predictor of pubertal completion. These results suggest that rural girls progress through puberty more rapidly than the urban girls despite their later start. This finding of maturational catch-up contrasts with earlier urban/rural comparisons of girls as well as previous results among Gwembe boys, for which later pubertal onset is associated with longer duration of pubertal maturation. While the mechanism remains unclear, biocultural explanations suggest preferential feeding during adolescence as a source for rural girl's maturational catch-up. Am. J. Hum. Biol. 16:658–669, 2004. © 2004 Wiley-Liss, Inc.

Population variation in age at menarche is extensively documented (see Eveleth and Tanner, 1976; Wood, 1994, for summaries). Although a variety of factors are known to influence age at menarche, including nutritional status, sports activity, genetics, and size at birth (Adair, 2001; Berkey et al., 2000; Merzenich et al., 1993; Ekele et al., 1996), differences in energy balance (Thomas et al., 2001), and hence the time required to attain sufficient frame size for successful birth, remains the most prominent explanation for variation across populations (Ellison, 2001). The recent finding that the onset of puberty is related to a characteristic amount of fat (Vizmanos and Marti-Henneberg, 2000) provides additional support for the argument that the timing of reproductive maturation is a function of childhood nutritional status.

Compared to age at menarche, much less is known about variation in the onset or duration of reproductive maturation among girls and its underlying causes. Earlier pubertal maturation has been associated with longer duration of maturation within a well-fed population of Spanish girls (Marti-Henneberg and Vizmanos, 1997). On the other hand, later pubertal onset between populations that vary in nutritional status has been associated with longer duration of pubertal maturation (Worthman, 1993; Cameron et al., 1993). For instance, girls from rural Vaalwater in Northern Transvaal (R.S.A.) started puberty roughly 1.5 years later than their better-off urban counterparts in Soweto, but completed puberty roughly 3 years later (Cameron et al., 1993). Thus, it is clear that poor nutrition not only delays the onset of puberty, but also lengthens its duration.

The Gwembe Tonga of southern Zambia provide an opportunity for a closer examination

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of ecological effects on urban/rural differences in the timing of pubertal maturation among girls and its relationship to growth measures. The studies above have compared the timing of pubertal maturation across different ethnic populations; thus, the results may confound ecological and genetic differences across the groups. The genetic similarity of the urban and rural Tonga subpopulations means that differences in the timing of reproductive maturation between the two groups can be attributed more to ecological differences, including nutrition and disease burdens (Campbell et al., 2004). Previous results show that the urban Tonga children have better somatic growth throughout childhood compared to their rural counterparts (Gillett-Netting, 2004). Furthermore, compared to the urban population, rural boys demonstrate onset of testicular growth 1.2 years later and take 0.6 years longer to progress through puberty (Campbell et al., 2004), a difference that is associated with markers of poorer nutritional status.

As with the boys, we hypothesize that rural Tonga girls will show delayed pubertal maturation compared to the urban girls. In fact, because adipose stores are generally considered more important to female reproductive function (Ellison, 2001), we expect that urban/rural differences in reproductive maturation among the girls will be more dramatic than those exhibited by the boys. However, because rural Tonga girls have been observed receiving preferential feeding around the age of 12 or 13 (Gillett-Netting, 2004), and we know that rural girls do not fall behind their urban counterparts in nutritional status to the same extent as the boys (Gillett, 1995), we expect girls to show less of a difference in the rate of progression through puberty compared to that exhibited by the boys. That is to say, while we expect a delay in the onset of the maturational process among rural Tonga girls, we do not anticipate the duration of the process itself to be extended.

To test these hypotheses, we compare the timing of Tanner Breast Stage 2, a marker of pubertal onset, Tanner Breast Stage 5, a measure of pubertal completion, as well as age at menarche between the urban and rural subpopulations. In addition, to investigate the role of nutritional status in the timing of pubertal maturation among the girls, we use multivariate analyses to compare measures of somatic growth, including height, arm muscle and skinfolds, as well as dental maturation, as predictors of pubertal timing between the two subpopulations.

SUBJECTS AND METHODS

Gwembe Tonga Growth Project

The longitudinal Gwembe Tonga Research Project (GTRP) was initiated in the late 1950s to assess the effects of forced resettlement on the Gwembe Tonga of southern Zambia. The Tonga were forced to move entire villages from the Zambezi river valley to surrounding uplands as a result of inundation caused by the construction of the Kariba Hydroelectric Dam on the middle Zambezi River (Scudder and Colson, 2002). Data analyzed here were collected in 1993 as part of Gillett-Netting's larger Gwembe Tonga Growth Project (GTGP) (Gillett, 1995; Gillett-Netting, 2004). The GTGP is the human biology component of the GTRP, designed to assess the effects of the forced resettlement on the health and physical status of the Gwembe Tonga. The project includes village-based samples from rural Gwembe Valley Tonga, rural Plateau Tonga, and urban Tonga school children. The protocol and procedures employed were reviewed and approved by the University of Zambia's Institute of Economic and Social Research (formerly the Institute for African Studies) and the Indiana University Human Subjects Committee.

The urban component includes individuals attending a fee-paying nursery school (5- and 6-year-olds) and a Basic school (ages 6–19) in Choma, Zambia. At the time of data collection, Choma was an area with a population of about 33,000. School attendance at this Choma school required some fees, uniforms, with admittance requiring time on a waiting list. The two rural village areas included in this analysis are located within the Gwembe Valley. There is limited transportation up the escarpment (80 km) to the plateau above and little remaining infrastructure, making the valley remote, with little economic opportunity for the inhabitants (Gillett, 1995).

The parents and guardians of children attending the urban sample schools are employed in the formal sector, with many also participating in informal sector wage opportunities. The living conditions for rural Gwembe Tonga subsistence farmers are basic, with no electricity, unreliable clean water sources, and minimal use of pit latrines. Looking back over the twentieth century, this is a region that experiences drought approximately three of every five years, as well as annual hunger seasons (Scudder, 1993). Since many rural Tonga children do not attend school regularly, the rural sample was defined by villages and not restricted to school children. A higher relative socioeconomic status is represented by the urban school children than that found in the rural populations. Urban and rural children have suboptimal nutritional status (Gillett, 1995). Using WHO (1986) recommendations for classifying chronic (stunted growth, underweight for age) protein energy malnutrition (PEM) in these populations we find 11.6% of urban girls are stunted and more than 7.8% are underweight for their age, both of these measures are indicative of chronic mild to moderate malnutrition. The situation for rural Tonga is more compromised, with 34.2% of the girls stunted and 27.3% underweight for age or exhibiting chronic PEM among girls in the rural villages (Gillett-Netting, 2004). The present sample consists of 492 urban and 282 rural (n = 774) girls, ages 6–18.

Measures

Age. For urban girls, age is based on school records which were cross-verified with birth certificates, and under-5 years clinic cards. In the rural sample, school records are not reliable; however, approximately half of the individuals are included in the GTRP demographic database and we therefore have ages accurate within a month and usually within a couple of days. For individuals under 12 years whose age is not verifiable in the database or by other means, an age is assigned using the Choma (Tonga) tooth emergence standard (Gillett, 1998), by which an age is assigned to the individual based on the number of permanent teeth present/emerged through the gums. This population-specific method of age assignment was developed using Choma schoolchildren of known age and tested on urban and rural Tonga children of documented age (Gillett, 1997).

Growth. Anthropometric measurements were taken by Gillett-Netting and a trained research assistant during the cold season of 1993 using standardized methods (Lohman et al., 1988) and equipment. Measures include height (cm), weight (kg), midarm circumference (cm), as well as triceps and subscapular skinfolds (mm). All measurements were taken with the subject wearing light school clothing. Reliability and replicability measures fall within acceptable parameters (Gillett, 1995). In addition, upper arm muscle area was calculated following the methods of Frisancho (1981).

Reproductive maturation. Reproductive maturation was assessed with three markers: Tanner Breast Stage 2, Tanner Breast Stage 5, and menarcheal status. The development of Tanner Breast Stage 2 is defined by the raising of breast and papilla as a small mound with some enlargement of the areolar area, referred to as the breast bud, and is one of the first events of pubertal development in girls, occurring in about two-thirds of girls before the onset of pubic hair. Tanner Breast Stage 5 is defined by only the nipple projecting above the breast, the areola having receded to the general level of the breast, and is considered the last stage of pubertal maturation for girls. Menarche or first menstrual bleeding is the most visible marker of reproductive cycling and occurs soon after peak height velocity, or roughly about two-thirds of the way through the process of pubertal maturation (Tanner, 1978, pp. 65–67). All observations of breast development were made by one observer (R.G-N.). Menarcheal status was assessed using status quo sampling. This sampling strategy requests a "yes" or "no" answer to an inquiry as to whether or not the individual has begun menstruating.

Dental maturation. In addition to anthropometric and maturational indicators, dental emergence was recorded. Any tooth which has begun to emerge through the gum is classified as emerged for the application of the Choma aging standard. The variable of dental maturation is based on the number of 2nd molars emerged (in the case of Breast Stage 2) or the number of 3rd molars emerged (in the case of Breast Stage 5).

Although some environmental effects such as earlier eruption following early deciduous tooth loss are known, dental emergence is under fairly high genetic control. There is less effect from endocrine, metabolic, and nutritional disorders on dental development than there is with other aspects of growth (Garn et al., 1965). Teeth seem to mature independently of other systems (Ryman et al., 1975; Bailey and Garn, 1986). Second molars emerge around 10.5–11.0 years among the Tonga girls, about average for African populations (Gillett, 1998). Emergence of the 2nd molar seems to occur within a couple-year range across populations; however, the timing of the emergence of 3rd molars shows great variability both within and across populations (15–24 years) (Levesque et al., 1981).

Statistical analyses

Probit analysis was used to determine the onset and completion of puberty. Probit analysis gives an estimate of the age at which 50% of the sample meets or exceeds the selected criteria, in this case Tanner Breast Stage 2 for pubertal onset or Tanner Breast Stage 5 for pubertal completion (Tanner, 1976). Median age at menarche was also estimated using probit analysis.

Because the growth and development measures are all interrelated, multivariate logistic regression was used to determine which ones are independent predictors of the onset of puberty, as defined by breast development. In these models, Tanner Breast Stage 2 or Breast Stage 5 are the outcome variables and residence (rural, urban), age (in years), dental maturation (number of third molars emerged), height (cm), upper arm muscle area, and triceps skinfolds (mm) the predictive variables.

The anthropometric variables were added according to the following rationale. First, a single model with residence and age is run, then dental maturation is added because it is only weakly related to somatic growth (Anderson et al., 1975; Demirjian et al., 1985). Height is added next as a cumulative measure of growth representing long-term energy balance (Waterlow, 1972). Next, upper arm muscle area is added because it represents shorter-term energy balance, and finally triceps skinfolds as a measure of energy stores and current energy balance (Frisancho, 1981) is added to the model.

RESULTS

Figure 1 shows the mean height, upper arm muscle area, triceps skinfolds, and subscapular skinfolds of girls in the rural vs. urban population by 1-year age intervals from age 6–18. All measures increase significantly with age, as expected. When controlled for age, the urban girls are taller than their rural counterparts (beta = 0.159; $P < 0.001$). For upper arm muscle area, multiple regression shows an increase with age, and large values for the rural population (Overall $r^2 = 0.64$ age beta = 0.79; $P < 0.001$; urban residence beta = 0.09; $P < 0.001$). A significant age*residence interaction term (beta = –0.362; $P < 0.001$) indicates a greater increase in upper arm muscle area among the rural population.

For triceps skinfolds, multiple regression results include a significant and positive residence*age interaction term (beta = 0.647; $P = 0.001$). When this term is included in the model, the sign for urban residence turns negative. Similar results are obtained for subscapular skinfolds (overall $r^2 = 0.385$. age beta = 0.483; $P < 0.001$; beta residence = –0.359; $P = 0.001$; residence*age beta = 0.483; $P < 0.001$). Together, these results can be interpreted to indicate that urban girls start out with lower skinfolds than do their rural counterparts, but gain more fat with age than do the rural girls.

Table 1 shows the timing of pubertal maturation in the two groups. Probit analysis of attaining Breast Stage 2 shows that rural girls (median age = 13.15 years; 95% CI = 12.40–14.15) lag behind urban girls (11.47 years; 95% CI = 11.22–11.71) in the onset of puberty by nearly 2 years. This difference is statistically significant, as indicated by the lack of overlap between the 95% confidence limits. In contrast, the two groups do not differ substantially in the completion of sexual maturation (rural girls median age at Breast Stage 5 = 16.73 years; 95% CL 16.15–17.64 vs. 17.01 years; 95% CL 16.30–18.33 for the urban girls). Comparison of age at menarche for the two groups shows that rural girls lag behind the urban girls by almost a year (15.34 years vs. 14.53 years), but that this difference does not quite reach statistical significance as indicated by the very slight overlap in confidence intervals (95% CL = 14.68–16.22 vs. 14.29–14.81).

Table 2 shows the relationship between predictors of pubertal maturation, including height, triceps skinfolds, subscapular skinfolds, upper arm muscle area, dental maturation, Tanner Breast Stage, and age at menarche. As expected, all of the measures are positively related, with the tightest

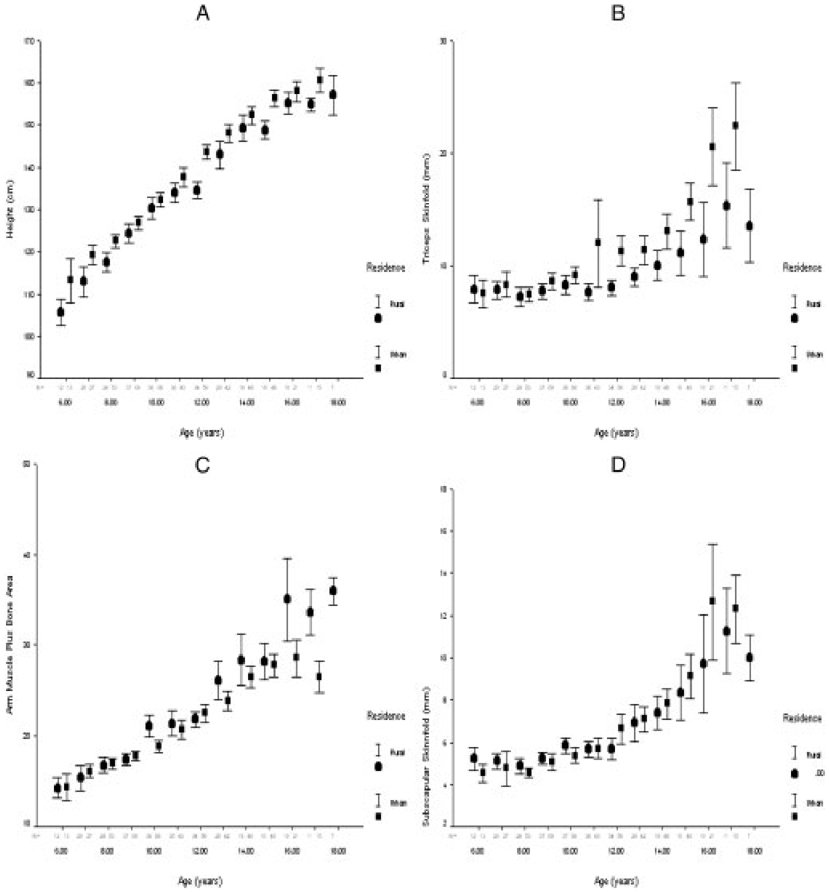

Fig. 1. Comparison of anthropometric measures among urban and rural Tonga girls. **A**: Height. Multiple regression indicates that height increases with age and is significantly greater in the urban sample throughout the entire age range. Overall $r^2 = 0.803$; urban residence beta = 0.159; $P < 0.001$; age beta = 0.879; $P < 0.001$. **B**: Triceps skinfolds. Multiple regression indicates that triceps skinfolds increases with age and is greater overall among the urban subpopulation. (Overall $r^2 = 0.258$. urban residence beta = 0.196; $P = < 0.001$; age beta = 0.467; $P < 0.001$.) In addition, a significant residence*age interaction term (beta = 0.647; $P = 0.001$) indicates that triceps skinfolds are smaller among urban girls at the beginning of the age range, but increase more quickly with age. **C**: Upper arm muscle area. Multiple regression shows an increase in arm muscle plus bone area with age, and significantly higher values among the rural subpopulation. (Overall $r^2 = 0.694$ age beta = 0.191; $P < 0.001$; urban residence beta = –0.815; $P < 0.001$.) In addition, a significant residence*age interaction (beta = –0.972; $P < 0.001$) indicates a greater increase with age among the rural population. **D**: Subscapular skinfolds. Multiple regression shows that subscapular skinfolds increase with age, are smaller at the outset among urban girls, but grower fast as indicated by a positive (and significant) residence*age interaction. (Overall $r^2 = 0.385$; age beta = 0.483; $P < 0.001$; beta residence = –0.359; $P = 0.001$; residence*age beta = 0.483; $P < 0.001$.)

correlations between height and number of 2nd molars emerged ($r = 0.788$) and Tanner Breast Stage ($r = 0.766$). The loosest correlations are exhibited by upper arm muscle area and triceps ($r = 0.151$) and subscapular skinfolds ($r = 0.199$). All of the correlations are significant, as might be expected given the relatively large sample size.

Table 3 shows the results of logistic regression for the predictors of pubertal onset. In the original model both age and urban residence are significant predictors of Tanner Breast Stage 2. Dental maturation is also a significant predictor when added to the model, while age and residence remain significant. With the addition of height, all variables in the model are significant predictors. Upper arm muscle area is not a significant predictor when added to the model. When triceps skinfolds is added in the final

TABLE 1. Estimates of pubertal timing

Pubertal stage	Urban n = 492	Rural n = 282	Overall n = 774
Onset of puberty (yrs)	11.47 (11.22–11.71)	13.15 (12.40–14.15)	12.10 (10.17–14.85)
Menarche (yrs)	14.53 (14.29–14.81)	15.34 (14.68–16.22)	14.80 (14.34–15.40)
Completion of puberty (yrs)	17.01 (16.30–18.33)	16.96 (16.15–17.64)	16.85 (16.37–17.56)

Estimates based on probit analysis. Parentheses represent 95% confidence limits. Onset of puberty defines as Tanner Breast Stage 2 or greater. Complete of puberty defined as Tanner Breast Stage 5.

TABLE 2. Correlation of anthropometric measures, dental maturation, and age at menarche

Variable	Triceps skinfolds	Subscapular skinfolds	Upper arm muscle area	2^{nd} molars	3^{rd} molars	Breast development	Menarche
Height	0.463	0.600	0.334	0.788	0.329	0.766	0.593
Triceps skinfolds		0.714	0.151	0.397	0.333	0.546	0.472
Subscapular skinfolds			0.199	0.505	0.442	0.699	0.588
Muscle plus bone area				0.258	0.200	0.267	0.226
2^{nd} molars					0.247	0.684	0.464
3^{rd} molars						0.420	0.396
Breast development							0.738

Correlations shown are partial correlations controlling for residence. All P values <0.000.

TABLE 3. Determinants of pubertal onset

Overall model					
X^2	597.7	620.0	666.7	668.3	676.9
n	774	766	766	765	765
Variable	Beta	Beta	Beta	Beta	Beta
Residence	1.60***	1.80***	1.20***	1.33**	1.27***
Age	1.10***	0.81***	0.36**	0.33***	0.30**
Dental maturation		0.49***	0.35***	0.34***	0.34**
Height			0.142***	0.13***	0.11***
UMA			0.07	0.09*	
Triceps skinfolds					0.09*

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. Pubertal onset defined as achieving Tanner breast stage 2. Dental maturation is based on the number of 2^{nd} molars emerged. UMA = upper arm muscle area.

model, it is a significant predictor, along with age, urban residence, and height.

Thus, dental maturation, long-term growth, and current energy balance all contribute independently to variation in the timing of reproductive maturation. Similar results are obtained if triceps skinfolds is replaced with subscapular fat, reinforcing the interpretation of skinfolds as measures of adipose tissue and current energetic status.

Table 4 shows the result of a logistic regression for the completion of breast development. Here the findings are quite different from those obtained for the onset of puberty. For the first three models, only age is a significant predictor; none of the anthropometric measures reach $P < 0.05$. However, in the final model both triceps skinfolds and upper arm muscle area achieve significance along with age. As with pubertal onset, similar results are obtained when triceps skinfolds is replaced with subscapular skinfolds (not shown), reinforcing the interpretation that triceps skinfolds represent the effects of adipose tissue. An interaction between triceps skinfolds and urban residence was tested and not found significant.

DISCUSSION

Our results indicate that rural Tonga girls begin puberty 20 months later than their urban counterparts, but show no difference in the timing of pubertal completion; i.e., the duration of puberty for the rural girls is almost 24 months less than it is for the

TABLE 4. Determinants of pubertal completion

Overall model					
X^2	151.3	153.5	156.5	158.1	169.6
n	766	766	765	765	765
Variable	Beta	Beta	Beta	Beta	Beta
Residence	0.15	0.16	−0.17	0.12	−0.31
Age	0.98***	0.90***	0.74**	0.70***	0.58***
Dental maturation		$0.29^{\dagger}$	0.27	0.27	0.15
Height			$0.06^{\dagger}$	0.05	0.04
UMA				0.05	0.10*
Triceps skinfolds					0.10***

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; $^{\dagger}P < 0.1$. Pubertal completion defined as achieving Tanner breast stage 5. Dental maturation is number of 3rd molars emerged. MPBA is muscle plus bone area.

urban girls. In fact, although the rural Tonga girls exhibit a delay in menarche of 10 months compared to the urban sample, this difference is only marginally significant. Thus, the rural girls appear to have caught up to their urban counterparts by this important marker of reproductive maturation.

These results contrast with previous findings that girls in populations with later onset of puberty also progress through puberty more slowly (Cameron et al., 1993; Worthman, 1993), as well as earlier findings that rural Tonga boys take longer to progress through puberty than their urban counterparts (Campbell et al., 2004). As such, our findings suggest that preferential feeding experienced by the rural girls (Gillett-Netting, 1995) does in fact hasten the process of reproductive maturation, although the mechanism and its potential impact on fecundity remains uncertain.

Relationship of reproductive maturation to growth and maturation measures

The onset of breast development among the Tonga girls was related to dental maturation, height, and triceps skinfolds. In others words, taller, fatter girls with more advanced dental development for their age are more likely to have begun pubertal development. These results are consistent with previous findings for height (Vizmanos et al., 2001), measures of subcutaneous fat, including upper arm fat mass (Vizmanos and Marti-Henneberg, 2000), and dental maturation (So, 1995), and support the general expectation that faster attainment of frame size will be associated with earlier reproductive maturation (Ellison, 2001).

In comparison, the predictors of pubertal completion, triceps skinfolds, and upper arm muscle area suggest that energetic status, rather than linear growth, is important to the continuation of pubertal maturation once sufficient frame size is achieved. Lack of an association between puberty completion and height is consistent with the finding that age at pubertal onset is not related to final attained height (Vizmanos et al., 2001). That completion of breast development is associated with greater triceps skinfolds may be taken to represent increasing levels of estrogen, which in turn promote both breast development and adipose tissue deposition (deRidder et al., 1990).

Comparison of anthropometric predictors of pubertal timing reported here with those previously reported for Tonga boys (Campbell et al., 2004) adds additional support to the importance of energetic status in the pubertal maturation of Tonga girls. Unlike for the girls, triceps skinfolds in Tonga boys was not related to the onset of puberty, although the completion of puberty was predicted by an interaction between urban/rural residence and triceps skinfolds. Together, these results suggest, as expected, that adipose tissue is closely related to both the onset and progress of reproductive maturation for females in both populations. On the other hand, energetics appear to be particularly important to pubertal progression among boys in the more energetically constrained rural population.

Population comparisons in age at menarche

The median age of menarche of 14.80 years for the entire sample of Tonga girls is some 2.5 years later than the 12.16 years for African-American girls in the U.S. reported by Herman-Giddens et al. (1997). It is also

TABLE 5. Variation in age at menarche among selected African populations

Community	N	Menarche	Source
America			(Herman-Giddens et al., 1997)
African-American	1,639	12.16 + 1.21	
White	15,438	12.88 + 1.20	
Mahe, Seychelles	1,122	12.84 + 1.08	(Grainger, 1980)
Nigeria (Hausa)			(Rehan, 1994)
Urban	2,088	12.97 + 1.39	
Rural	3,516	13.53 + 1.31	
Johannesburg			(Chaning-Pearce and Solomon, 1987)
White	355	13.1 + 1.4	
Black	362	13.9 + 1.7	
Somalia (Urban)	397	13.1 + 0.18	(Gallo and Mastriner, 1980)
Cameroon			(Pasquet et al., 1999)
Urban (Yaounde)	156	13.18 + 1.08	
Suburban (Mfou)	466	13.98 + 1.55	
Rural (Campo)	195	14.27 + 1.65	
South Africa			(Cameron et al., 1993)
Soweto	148	13.2	
Vaalwater	175	14.57	
Mozambique	753	13.2 + 1.18	(Padez, 2003)
centre		12.96 + 1.1	
slums		13.68 + 0.98	
Jos, Nigeria (high altitude)	331	13.21 + 1.01	(Ekele et al., 1996)
Khartoum, Sudan			(Attallah, 1983)
Well-off girls	335	13.35 + 1.32	
Middle Class girls	636	13.85 + 1.36	
Poor girls	401	14.06 + 1.38	
Uganda (Kampala)	168	13.4 + 0.165	(Burgess, 1964)
Ilorin, Nigeria	162	13.6 + 0.97	(Fakeye, 1985)
Nigeria			(Oduntan et al., 1976)
Urban (Ibadan)	2,029	13.7 + 1.35	
Rural (Igbo-Ora)	251	14.5 + 1.43	
Marrakesh, Morocco	239	13.75 + 0.17	(Loukid et al., 1996)
So. West. Nigeria (Urban)	352	13.94 + 1.31	(Abioye-Kuteyi et al., 1997)
Ile-Ife, Nigeria	1,054	13.98 + 1.30	(Dare et al., 1992)
Ghana (Kumasi District)	2,087	13.98 + 1.42	(Adadevoh et al., 1989)
Copperbelt & Lusaka, Zambia	525	14.2 + 1.4	(Pillai, 1995)
Kenya	458	14.4 + 2.45	(Rogo et al., 1987)
Segou Region, Mali (West Africa)	1,056	14.4 + 0.42	(Pawloski, 2002)
Urban		14.1 + 0.61	
Rural		14.7 + 0.59	
GWEMBE TONGA			current study
URBAN	492	14.44	
RURAL	282	15.33	
Gondar, North Western Ethiopia	362	14.5 + 0.89	(Haile and Roth, 1984)
Kenya (Kipsigis-Rural)	33	14.9	(Borgerhoff-Mulder, 1989)
Tanzania (Nyakyusa)	392	14.93 + 0.26	(Hautvast, 1971)
Zaire (Bunia)	950	15.67 + 0.08	(Ekisawa et al., 1986)
Senegal (rural)	343	16.0 + 2.0	(Simondon et al., 1997)

toward the high end of the range of results obtained from other African populations shown in Table 5. These results range from 12.9 years for girls from the Seychelles (Grainger, 1980) to 16.0 years for a sample of rural Senegalese girls (Simondon et al., 1997).

Looking more carefully at urban/rural comparisons, Padez (2003) reports median age at menarche based on probit analysis of 12.96 and 13.68 for girls in the urban center and slums of Maputo, Mozambique. Pasquet et al. (1999) report age at menarche based on probit analysis of 13.18, 13.98, and 14.27 years in urban, suburban, and rural Cameroon, respectively. Cameron et al. (1993) report a median age at menarche of 13.2 for girls from urban Soweto compared to 14.57 for rural Vaalwater. Thus, while median age at menarche of 15.35 years for the rural Tonga population is delayed compared to other rural African populations, the median age of 14.53 years for the urban girls represents a more substantial delay compared to other urban populations. The greater delay in Tonga urban girls may represent the fact that the urban sample here is based in a town, rather than a truly urban setting, and might be better compared with age at menarche among the suburban setting of Cameroon.

Comparison of pubertal onset and completion

Cameron et al. (1993) report that girls from rural Vaalwater began puberty at 11.6 years, 0.7 years later than those from urban Soweto. Furthermore, the rural sample completed puberty at 16.61 years compared to 13.58 years for the urban girls, a duration of 5 years, compared to 3.5 years for the urban girls. Thus, not only does the rural population start puberty later, but it also takes longer to progress through puberty. These results are in direct contrast to our findings that rural Tonga girls start puberty 1.7 years later than the urban girls, yet reach Breast Stage 5 at the same time.

Findings that the timing of pubertal onset and age at menarche are inversely related (Vizmanos and Marti-Henneberg, 1997) suggest that the later-maturing rural girls in our sample might catch up to the urban girls even in the absence of food supplementation. However, Vizmanos and Marti-Henneberg's (1997) sample represents a well-fed population in which variation in pubertal timing may be linked more to genetic variation than nutritional status, as in our sample. Furthermore, Cameron et al. (1993) also note that delayed maturation due to nutritional status is particularly evident in Tanner Breast Stages 4 and 5, in direct contrast to our findings.

Although the Vaalwater and Soweto populations studied by Cameron et al. (1993) differ in environmental conditions, including nutritional status, they also have different ethnic backgrounds, making it difficult to rule out the possibility that genetic differences may play a role in the observed patterns of pubertal timing. The genetic similarity of the two subpopulations of Tonga girls strengthens the assumption that any urban/rural differences in the timing of pubertal maturation are primarily related to social and ecological factors.

Beginning around age 12 or 13, when girls look like they are developmentally close to puberty, girls in the rural population experience an increase in household level workload. At the same time they have been observed receiving 50–100 extra calories per day over their male counterparts in the same households (Gillett-Netting, unpubl. commun.). This is a behavior that has not been studied among urban Tonga girls. This degree of calorie supplementation is not sufficient to allow the rural girls to catch up in terms of adipose stores as judged by subscapular skinfolds, but it does allow them to experience catch-up growth: an acceleration in linear growth (height) and an increase in mass (weight and upper arm muscle mass). Our results suggest that the supplementation is sufficient to not only retard the slowing of pubertal development expected on the basis of delayed pubertal onset, but it actually enables the rural girls to go through puberty more quickly.

Although the mechanism remains unclear (see below), the conclusion that preferential feeding underlies the catch-up in reproductive maturation among the rural girls is strengthened by previous findings that rural Tonga boys, who do not receive additional feeding during adolescence (Gillett-Netting, unpubl. commun.), not only start puberty later than urban boys, but also take longer to complete puberty (Campbell et al., 2004). Thus, although the rural population exhibits poorer childhood nutritional status than the urban population, the nutritional gap between the rural and urban girls is reduced with preferential feeding during puberty, resulting in catch-up maturation.

Possible mechanisms relating nutritional status to pubertal maturation

While the hormonal mechanisms that trigger the onset of puberty remain largely unresolved (Ellison, 2001), once puberty is under way breast development is related to estrogen stimulation (Drife, 1986; Laurence et al., 1991). Estrogen is produced both by the ovary and the conversion of androgens to estrogen by aromatase within the breast itself (Labrie et al., 2001). Thus, the increased rate of breast development in rural girls might, on the face of it, represent either increased ovarian production of estrogen and/or the conversion of androgens to estrogen within breast tissue.

The potential effects of additional calories during puberty on ovarian production of estrogen are hard to judge from our current results. Estrogen production by the developing follicle is a function of both follicle stimulating hormone (FSH) stimulation and aromatase action within the granulose cells in converting androgens produced by the thecal cells into estrogens (Erikson, 1987). Aromatase activity within the ovary is promoted by both FSH and insulin (la Marca et al., 2002) and basal insulin levels have been positively correlated with body mass index in menarcheal girls (van Hooff et al., 2000). Thus, increased caloric intake could result in elevated aromatase levels within the ovary, and thus increased levels of estrogen stimulation and increased follicular development (van Dessel et al., 1996).

In turn, higher circulating levels of estrogen are associated with greater deposition of fat (deRidder et al., 1990), and earlier cessation of bone growth (Culter, 1997; Klein et al., 1996). Because cessation of long bone growth is related to estrogen levels, the fact that rural girls do not fully catch up in height to the urban girls is consistent with an accelerated increase in estrogen levels. On the other hand, because fat deposition is related to energy balance as well as estrogen levels, the fact that the rural girls catch up in breast development but not in skinfold measures is consistent with increased estrogen exposure and/or production, but poorer overall energy balance.

However, the fact that the rural girls still exhibit a year delay in age at menarche compared to their urban counterparts suggests that, unlike for breast development, rural girls may not exhibit catch-up in menstrual cycling. Within populations, later-maturing girls show slower increases in ovulatory cycles even when age of menarche is taken into account (Apter and Vihko, 1983); the same may be true of the difference between rural and urban girls here.

Thus, local conversion of androgens into estrogen within the breast (Labrie et al., 2001) may be a more likely explanation than ovarian estrogen production for the more rapid breast development in the rural girls. Changes in insulin levels associated with poorer prenatal nutrition (Ibanez et al., 1999) have been related to the timing of reproductive maturation. Small for gestational age girls show advanced adrenarche (Francois and Zegher, 1997; Ibanez et al., 1998, 1999) and elevated DHEAS levels can be converted into estrogen within the breast (Labrie et al., 2001), hastening breast maturation. Thus, lower birth weights among the rural girls, coupled with increased caloric intake starting prior to puberty, might lead to increased DHEAS levels and faster breast maturation once pubertal maturation starts. Unfortunately, our data do not allow us to speak to this important question directly.

Biocultural implications

In parts of the Gwembe Valley puberty seclusion still occurs, with the goal being a healthy, plump young woman who can now enter the marriage process. Preferential feeding of girls at puberty among the Gwembe Tonga may be related to cultural concerns about fertility and marriage. Bridewealth payments for a daughter are an important source of income for the young women's father (to a lesser extent, the household) and as they are extended over decades they serve as a source of financial and resource insurance that he can draw on both financially and through obligation (Gillett-Netting, 2004). Bridewealth payments essentially pay for the transfer of reproductive capabilities from one generation to the next. In fact, reproductive capability has been cited as one of the factors that determines the asked bridewealth in many societies (Borgerhoff-Mulder, 1988). Among the Kipsigis of Kenya, the earlier a girl reaches menarche, the more she is worth in bridewealth. Additionally, a plump Kipsigis girl is worth more bridewealth than a skinnier Kipsigis girl (Borgerhoff Mulder, 1988). Among the Annang of Nigeria, girls are put through fattening rituals right before they are married, and infertility is among the ailments for which a woman will be prescribed the fattening ritual as treatment (Brink, 1995). If the goal of rural Tonga mothers and fathers is to speed their daughters' sexual development, they succeed, as the rural Tonga girls finish pubertal development at the same time as urban girls despite starting almost 1.5 years later. In addition to the catch-up maturation is the added benefit of these young women entering their first pregnancy healthier and with essential fat stores. Whether this same cultural practice also enhances their daughter's fecundity, and hence her fertility as a result, remains an object for further study.

CONCLUSION

Despite starting the maturational process almost 2 years later, rural Gwembe Tonga girls go through pubertal development at a faster rate than their urban counterparts, catching up by the end of puberty as defined by Tanner Breast Stage 5. This pattern contrasts with results from earlier findings demonstrating that girls in rural populations start puberty later and progress more slowly. It also contrasts with earlier results from boys in this same population who show both later onset and slower progression through puberty compared to their urban counterparts. Thus, the unusual trajectory of pubertal development seen in the rural Gwembe Tonga girls may be attributed to the preferential feeding they receive preceding and during puberty. Whether such preferential feeding also leads to increased fecundity and is related to marriagibility or bridewealth requires additional study.

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