

Ontogenetic Allometry of Body Height and Body Mass of Girl in Baduy, Indonesia

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ARTICLE INFO

Article history:
Received May 1, 2018
Received in revised form June 15, 2018
Accepted July 1, 2018

KEYWORDS: ontogenetic allometry, growth, menarche, body fat, body size, Baduy

ABSTRACT

Several small-scale populations exhibited phenotypic plasticity whereby growth spurt of body height occurred much earlier than age at menarche and this was not followed by same early spurt of body weight. This leads to question whether growth trajectory of stature follow the same growth trajectory of body mass and whether the trajectory itself is associated to sexual maturity. We evaluated developmental plasticity observed in Baduy girl, a traditional population in Indonesia, in facing strenuous environmental and biocultural conditions. We measured stature and body mass cross-sectionally. We determined age at menarche as population average of age of girls that had already got their first menstruation. Growths of body fat and weight followed a same mode and timing and their spurts pivoted on the age at menarche. In contrast, growth spurt of body height occurred four years earlier than menarche and velocity curve of body linearity progressed in opposite direction to that of body ponderality. The prevailing poor nutrition and high physical activity elicited principle of ontogenetic allometry to synchronize the acceleration and deceleration of growths in body linearity and ponderality whereby growth in body height functions to reach the body size target and to provide skeletal framework for development of body mass. The biocultural conditions lead to slow bodily growth rate with low spurt resulting in the characteristics of Baduy girl that was small in size and late in both sexual maturity and full-grown ages.

1. Introduction

Growth trajectory of body size charts the health and nutritional statuses of a population (Eveleth and Tanners 1990; Bogin 1999; Rogol et al. 2000; Walker et al. 2006; Migliano et al. 2007; Kramer and Greaves 2010; Urlacher et al. 2016). Healthy environment and better nutrition provide children with resources to grow faster and taller compare to children living in poor condition (Eveleth and Tanners 1990; Bogin 1999; Adair 2001; Walker et al. 2006). In this optimum bioculture, the timing of female sexual maturity is matched to and provides a pivot for adolescent growth spurts in body mass and stature. In 2-compartment biomass model consisting of fat and lean masses, a threshold of body fat proportion relates to the endocrinal hypothalamic-pituitary-gonadal (HPG) axis and also involves in the regulation of the hypothalamic-pituitary-adrenal (HPA) axis feedback mechanism in triggering menarche (Frisch and Revelle 1969, 1970, 1971a, b; Frisch et al. 1973; Frisch and McArthur 1974; Frisch 1975; Malina et al. 2004; Ebling 2005; Kaplowitz 2007). Menarche is also closely

* Corresponding Author. E-mail Address: suryobroto@ipb.ac.id related to skeletal development via adrenocortical secretion of anabolic androgens in HPA axis. Skeletal segments add up to body height and several growth studies found that age at peak growth velocity (APV) of this linear feature of body is reached close to the timing of menarche (Frisch and Revelle 1969; Ellison 1981, 1982; Chang et al. 2000; Malina et al. 2004).

In contrast, poor living condition modulates stages and rates of body development to restrict the adult size (Walker et al. 2006; Migliano et al. 2007; Kramer and Greaves 2010; Kawulur et al. 2012, 2013). For instance, girls living in populations that have low energy availability and environmental constraints grow slowly with low spurt leading to late menarche, delay growth cessation, and small adult size (Frisch 1975; Eveleth and Tanners 1990; Bogin 1999; Gurven and Walker 2006; Walker et al. 2006). Furthermore, small-scale populations exhibited phenotypic plasticity whereby APV of body height was reached much earlier than age at menarche and this was not followed by same early APV of body weight (Walker et al. 2006; Kramer and Greaves 2010). This leads to question whether growth trajectory of stature follow the same growth trajectory of body mass and whether the trajectory itself is associated to sexual maturity. The base of this question pertains to the ontogenetic allometrical principle that governs differential agerelated changes in components that make up the total size of organism (Gould 1966).

There were few reports that specifically employ allometric perspective on age-related changes of stature and body mass and its covariation to menarche. This is understandable given nutritional improvement in well-developed societies diminished ethnic differences in growth of body height and weight and leads to stereotypical generalization in interpreting life history data. We should therefore seek the answer to the above question to populations that are local and less or not involved in the network of social services, economics, and politics. Here we report developmental plasticity observed in Baduy, a traditional population in Indonesia (Wessing and Barendregt 2005), in facing strenuous environmental and biocultural conditions (Ichwandi and Shinohara 2007).

Baduy people inhabit isolated area (around 5100 ha) of mountainous rainforest in Kanekes Village, Lebak Regency, Indonesia. Main topography of their area is hilly with an average slope 49.1%, average annual rainfall 4000 mm, and soil type clay latosol (Iskandar and Ellen 1999; Ichwandi and Shinohara 2007). The tradition stipulates strict socio-cultural conducts and daily obligatory duties to protect the sustainability of swidden farming in the mineral-poor and erosion-risk terrain. Their agricultural practice restricts mechanical tool merely to digging sticks and chopping- and finger-knives. In complement to prohibition to any modern farming technologies, the religious beliefs preclude external influences and ban the formal education (Ichwandi and Shinohara 2007; Erwinantu 2012; Hasman and Reis 2012). The socio-cultural isolation and endogamous marriage system make their life history unique, so in recording their growth trajectory we expect to get insight into principles that govern their adaptation.

We found that in Baduy girl the growths of body mass components, i.e. body fat and weight, followed a same mode and timing and their APVs pivoted on the age at menarche. In contrast, APV of body height occurred four years earlier than menarche and velocity growth curve of body linearity progressed in opposite direction to that of body ponderality. These phenomena reveal the principle of ontogenetic allometry in synchronizing the acceleration and deceleration of the growths of stature and body mass.

2. Materials and Methods

2.1. Subject

Cross-sectional interview and measurements were conducted in July to November 2011 and January to November 2014. Subjects were girls from 37 out of 61 hamlets totaling 312 individuals with age ranged from 4 to 26 years. Each subject or parent was explained about the purpose of this study, and if they agree to participate, they signed or thumb printed the informed

consent form. The interview and measurement protocols were approved by Office of National Unity, Politics and Public Protection of Lebak Regency and the research followed the regulation attached on the permit letter (No.300/246-Kesbang Pol and Linmas/VI/2013). This research abode by the Baduy customs outlined by Head of Kanekes Village.

2.2. Birth Date

Age was calculated as the number of days since birth date to the date of interview. We set age class in a one-year interval and determined each age class to the nearest birth date of the relevant year. However, most subjects do not have birth date record. For girls with unknown birthdate, we used the procedure outlined in Rohmatullayaly *et al.* (2017).

2.3. Sexual Maturation

Subjects for sexual maturation analysis were 151 girls; they were subset of the total sample. We determined age at sexual maturity as population average of age of girls that had already got their first menstruation. Given an age class, the menarcheal statuses of girls were identified. The menarche/non-menarche events across the pre- to post-pubertal age classes follow yes/no binomial distribution and we used Generalized Linear Models (GLM) using probit link (Venables and Ripley 1999) to calculate the median age.

2.4. Growth Velocity of Body Size

There are accumulating evidences that indicate animals measure dimensions rather than cell number when they grow (Sprent 1972; Day and Lawrence 2000; Lecuit and Le Goff 2007). In measuring total size of organisms, the readily observed components are their length and mass. Present human biology research used stature (body height, BH) as body length; it was measured with accuracy 1 mm. Body mass was measured by weight (BW) with accuracy 100 g. BW consists of two chemically distinct compartments: fat and lean masses (Frisch et al. 1973; Frisch 1975; Malina et al. 2004). Adipose cells produce leptin that directly affects the onset of puberty (Matkovic et al. 1997; Fechner 2002; Karapanou and Papadimitriou 2010). Therefore, in addition to BW, we also measured body fat to see how it developed in relation to sexual maturity. The body fat component was approached by measuring skinfold thickness at triceps (TS) and subscapular (SbS) points with accuracy 0.1 mm to reveal subcutaneous fat (Malina et al. 2004). Percentage of body fat (PBF) from total BW was estimated as PBF = $1.33 (TS+SbS) - 0.013(TS+SbS)^2 -$ 2.5 (Slaughter et al. 1988).

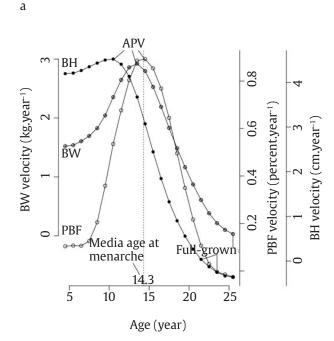
In allometric perspective, length is considered a linear whereas mass a cubic dimension (Gould 1966). We derived body linearity index (BLI) by scaling BH (in cm) to cube root of BW (in kg) and ponderal index (PI) by scaling BW (in kg) to cubed BH (in m).

Each growth trajectory of BH, BW, PBF, BLI, and PI was estimated from 50th percentile values of yearly cohort in the cross-sectional data. We used Generalized Additive Models for Location, Scale and Shape (GAMLSS) (Stasinopoulos and Rigby 2007) to predict the percentile. Annual velocities were calculated as increments between consecutive years and velocity curve was charted by linking midyear points. We identified two landmarks on each velocity curves. The first is APV that represents the growth spurt. The second is age at speed equaled zero when the girls got full growth; we consider this age as the adult age of each trajectory. In considering the sampling bias and secular effect, we approached the growth cessation at the nearest midpoints to the zero speed. All procedures were run on R software version 3.3.2 for Mac (R Development Core Team 2016).

3. Results

Half of Baduy girls reached sexual maturity at age 14.3 year (2.5-97.5% range 11.5-17.2 year; Figure 1a and b). The median age at menarche coincided with APVs of body fat and weight (Figure 1a). Before reaching APV 14.5 year, juvenile PBF followed an increasing growth path for ten years. At the spurt the PBF amounted to 20.5% of the total body weight. The growth rate then decreased reaching zero at age 23.5 year to get full-grown PBF 24.9%. Prepubertal growth rate of BW also increased to attain maximum growth speed at 13.5 year (32.1 kg), one year before menarche; given the temporal resolution of one year in determining birth date and the positing of annual velocity point at midyear, the difference between APV of BW and age at menarche may be considered as non-significant. After that, the rate decreased to zero at 25.5 year reaching grown-up BW at 47.7 kg. The increasingdecreasing path of growth velocities of PBF and BW shows that these two measurements of body mass followed a same mode and timing and their spurts were reflected on the age at menarche. Furthermore, the allometrically scaled body mass PI (Figure 1b) went after the same increasing-decreasing growth trend of PBF and BW though its maximum speed was reached a little bit later than age at menarche.

In contrast, Baduy girls got peak of BH growth velocity (10.5 year, 124.6 cm; Figure 1a) four years earlier than menarche, that is, well before APVs of PBF and BW (Figure 1a). Comparing to ten years interval of increasing growth rate of body mass, BH experienced the increase for only six years prior to decreasing for 11 years passing menarche landmark (at 139.0 cm) until fully developed (at 149.4 cm) at 21.5 year. As well as growth spurt, the age at growth completion of BH was earlier than that of PBF (23.5 year) and BW (25.5 year). The gap between the courses of stature and body mass was further accentuated by differing growth path of body linearity BLI. While ponderal index increased at prepubertal age, growth speed of



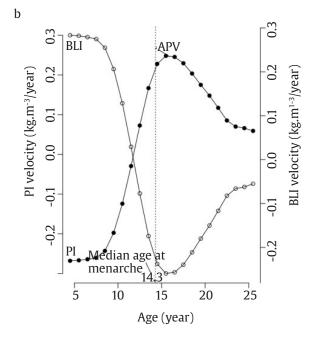


Figure 1. Median age at menarche and growth velocity of body size. (a) Growth speeds of body masses (fat and weight) firstly increased, reaching APVs at menarche before decreasing to zero at fullgrown. In contrast, BH reached APV four year in advance of menarche before continuing to decrease in following different pathway. (b) The allometrically scaled body mass PI went after the same increasing-decreasing growth trend of PBF and BW though its maximum speed was reached a little bit later than age at menarche. In contrast, growth speed of body linearity was decreasing before reversed around puberty so, instead of APV, growth of BLI had nadir of velocity at about one year after menarche before bounced back and plateau after 23.5 year. APV age at peak velocity, BH body height, BLI body linearity index, BW body weight, PBF percentage of body fat to total body weight, PI ponderal index

body linearity was decreasing before reversed around puberty (Figure 1b). Instead of APV, growth of BLI had nadir of velocity at about one year after menarche before bounced back and plateau after 23.5 year. The increasing growth speed of BLI offset the decreasing growth rate of BH. As it is expected, the allometrically scaled PI and BLI had growth rate routes that mirror image one another. These results shows that growth trajectory of BH was clearly dissociated from that of body mass.

4. Discussion

The dissociation and opposition in growth trends of body linearity and body ponderality reveals the synchronization of acceleration and deceleration between different growth rates of length and mass that make up the total size of organism. In light of this concept, the observed gap between the two growth trends would be meaningful if we interpret the growth of BH functions as to reach body size target and to provide skeletal framework for development of body mass. With this interpretation we think that metabolic costs of growth are divided into skeletal completion in advance of metabolic commitments to body weight and to reproductive maturation (Frisch 1972; Frisch and McArthur 1974; Kramer and Greaves 2010). Present results show that the target of total

body size was determined by BH when completing to grow at 21.5 year, earlier than PBF and BW that continued to develop before reaching zero speed at 23.5 and 25.5 year, respectively. The parsing of metabolic cost can also be seen at puberty. Compared to other populations (Walker et al. 2006; Figure 2), APV of BH was reached early while reproductive maturity of Baduy girl can be considered as late. The early spurt of BH might be interpreted as to prepare skeletal build and the late APVs of PBF and BW represent the time needed for fat to grow to its critical proportion in triggering sexual maturation. The longer time to reach critical proportion for initiation of menarche was caused by slow growth rate and low growth spurt (Rohmatullayaly et al. 2017).

The mechanics of ontogenetic allometry leads to the characteristics of Baduy girl that was small in body size and late in both sexual maturity and full-grown age (Rohmatullayaly *et al.* 2017). This phenotype is apparent in comparison to Bogor and American girls (Figure 2). Bogor is urban population of Sundanese (Suhartini 2007) that is the main tribe of Baduy, while American data is from Frisch and Revelle (Frisch and Revelle 1969, 1971a,b; Frisch 1975) who provided the original hypothesis on the relationship between fat and sexual maturity. The age-related changes in proportion of PBF, BW, and BH to their adult magnitudes were used to avoid differences in

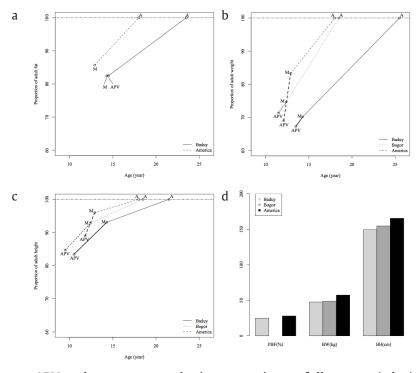


Figure 2. Body sizes at APV and age at menarche in proportion to full-grown. (a,b,c). Growth trajectory of Baduy girl is distinct from that of America and Bogor girls, while both of the later overlap. Compare to the two populations, Baduy girl is smaller in adult body size with later ages at spurt, menarche and full-grown. (d) Body size at full-grown. A age at growth velocity equals zero, APV age at peak velocity, BH body height, BW body weight, PBF percentage of body fat to total body weight, M age at menarche. Sources: Bogor, Suhartini (2007); America, Frisch and Revelle (1969; 1971a,b; 1975).

methods to measure the magnitudes (Figure 2a-c). Adult sizes of PBF, BW, and BH of Baduy girls were smaller (Figure 2d) and at APV and age at menarche the bodily proportions were also lower (Figure 2ac) than the two populations. It should be noted that the long time it took to complete the growth was accomplished by slow rate with low spurt. This life history efficiently economizes body growth and maintenance in facing low caloric and/or protein availability (Frisch and Revelle 1971b; Frisch 1975; Walker et al. 2006; Urlacher et al. 2016). Beside poor nutrition, several studies showed that high physical activity (Walker et al. 2006; Ajita and Jiwanjot 2014) also influenced the bodily growth. Baduy people work their swidden farm for eight months in a year (Ichwandi and Shinohara 2007) and their children start to learn farming at age 10 year (Erwinatu 2012). The condition of hilly terrain with average slope of 49.1% (Ichwandi and Shinohara 2007) and working with only manual tools require intense physical exercise. However, the demandingly high activity was not met by adequate nutrition. A measurement in 1983 found that average energy intake of an adult Baduy male at 2517 kcal was lower than energy he expended at 2935 kcal per day (Hestiwati 1983). There is no data on female energy requirement; however, the general condition of caloric depletion in male may also be the same for female. Moreover, juveniles below-five-yearold boys and girls were reported to get energy and protein intakes about 1125 kcal and 21 g per capita per day, which were lower than recommended dietary allowances (Sukandar and Mudjajanto 2009).

In summary, poor nutrition and high physical activity elicited principle of ontogenetic allometry to synchronize the acceleration and deceleration of growths in body linearity and body ponderality whereby growth in body height functioned to reach the body size target and to provide skeletal framework for development of body mass. The biocultural conditions lead to slow bodily growth rate with low spurt resulting in the characteristics of Baduy girl that was small in size and late in both sexual maturity and full-grown ages.

Acknowledgements

We thank to Mr. Jaro Dainah (former head of Kanekes village) for guiding our research. We also thank to Mr. Saidam and his family, Mr. Marsadi (deceased) and his family, Ms. Eros, and all subjects for help during data sampling. A part of this research was funded by LPDP 2013 (Ministry of Finance, Indonesia) for E.N.R dissertation fund. The first author benefited from Beasiswa Unggulan 2012 (Ministry of Education and Culture, Indonesia) for PhD scholarship.

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