Analysis of the growth and development of the Daasanach from Ileret, Kenya in relation to ecology and subsistence strategy

By

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To my mom,
family, friends, mentors, and professors
who have nurtured my growth and development,
cultivated an environment of optimal conditions,
and allowed me to far exceed my own expectations.

"You have to do your own growing no matter how tall your grandfather was."
--*Abraham Lincoln*

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ABSTRACT

Body size is highly variable among modern human populations, as it is influenced by the interactions between genetic information and external nutritional and environmental variables during growth. Across traditional societies a relationship between life history strategy, relative adult body size, and extrinsic variables (e.g. ecology, subsistence strategies) has been documented to inform the theoretical foundation that explains observed variability. However, individual populations, such as east African pastoralists, are known to deviate from expectations. Cross-sectional data on height and weight were taken from an ontogenetic sample of Daasanach individuals (n=223, ages 2-55) from Ileret, Kenya to test the null hypothesis that the Daasanach conform to the expected growth timings and adult body size parameters for traditional populations of similar ecologies and subsistence strategies. From the collected data critical growth checkpoints and growth velocity values were obtained to compare the timing of Daasanach growth and development with previously studied comparative populations. The results show that while Daasanach adult height is consistent with predictions based on comparative samples, their growth trajectory deviates from them. Daasanach grow slowly during childhood and experience an early adolescent growth spurt over a relatively short duration of time. These results suggest that Daasanach growth velocities during the adolescent growth spurt may be absolutely higher than expected. However, it is important to note the subset of the Daasanach population sampled from Ileret, Kenya may not be representative of the larger Daasanach tribe considering the plastic and responsive nature of growth trajectories.

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INTRODUCTION

Health and economic status is correlated with adult body size and rates of subadult growth and development among modern human populations. Research examining US and European populations since 1950 found a strong relationship between adult height and external factors such as income per capita and infant mortality (Bozzoli *et al.* 2007). Intuitively, this association follows the logic that final adult height is representative of the available energy during growth and development, where energy is the net nutrients in the body. Increased economic status provides a steadier and greater quantity of higher quality foods. Additionally, better health (correlated with better economy) reduces loss of nutrients needed to fighting disease (Bozzoli *et al.* 2007). In fact, growth is the best assessment of nutrition and health for children, and is an indirect qualifier for the quality of life of a population or individual (de Onis *et al.* 1993). However, these statements are built from studies of industrialized populations. Human variation in adult body size does not necessarily correlate to health and nutrition outside of the industrialized west (US and Western Europe).

Deaton (2007) uses data obtained from the “Monitoring and Evaluation to Assess and Use Results Demographic and Health Surveys (MEASURE DHS)” project, subsequently referred to as the DHS funded by the US Agency for International Development (USAID) to investigate the relationship between economics and health with adult height across non- Western populations. While the trend loosely persists, when compared to the rest of the world, African populations fail to adhere to the trend of adult height being positively predicted by income or lack of disease. Across broad global geographical regions (Africa, Europe, Asia, North America, South America), Africa represents the tallest stature of the non- Western regions though Africa is generally the poorest and most disease afflicted of the regions (Deaton 2007). Furthermore, a World Health Organization (WHO) study looking at 5-year-olds across 79 developing countries found that while Latin America shows a low prevalence of both stunting (low height-for-age) and wasting (low weight-for-height), and Asia shows high/ very high prevalence for both stunting and wasting, Africa generally shows high/very high wasting combined with low/moderate stunting (de Onis *et al.* 1993).

The African deviation from this otherwise global trend and the similar deviation of populations with recent African ancestry outside of Africa point to a strong genetic influence on stature. However, genetic similarities in the other non-Western regions are not maintained in emigration. Asian and Latin American immigrants to the US or Europe reach higher statures closer to the “Western” height norms within a few generations. Additionally, those of African ancestry in the US or Europe conform to the local trends in adult size (Deaton 2007). Variations within lower income regions may relate to the cultural level and may be indicative of different subsistence strategies and nutritional availabilities independent of economy (Deaton 2007).

The variations in growth trajectory and body size across modern human populations beg investigation into the relative effects of the numerous extrinsic factors that affect growth and development towards final adult heights. Variability is most interesting in traditional, non- Western populations. In traditional societies, numerous environmental conditions are influential in a population's growth trajectory due to adaptation through strong selection pressures (Deaton 2007, Walker *et al.* 2006).

In this thesis, the pastoralist Daasanach tribe from the desert/ dry savanna of Ileret, Kenya on the northeast coast of Lake Turkana is chosen to observe and help understand variation in growth and development in non- Western societies. Height and weight data obtained from this population is analyzed to extrapolate growth timing and trajectories. The growth patterns derived will then be considered in respect to their external factors, particularly local ecology and subsistence strategies, which drive human variation in relation to growth and body size. In order to consider any extrinsic factor's influence, first a comprehension of the processes and mechanisms that drive human growth and development must be obtained from both theoretical models and empirical population level studies. These other populations will serve as a comparative sample by which to analyze the Daasanach. Through such comparison, questions about the relative influence of certain variables, such as ecology, on growth and development, the nature and degree of variation within traditional societies, and the Daasanach specific patterns of growth can be explored.

For this study, generalized ecology will be a factor predominantly considered in answering some of these questions. A better understanding of the relationship between a population's ecology and growth can inform several scientific, political, economic, and humanitarian inquiries. In the human fossil record only skeletal and dental materials remain to inform on somatic processes in the past. Investigations into the external conditions that affect the body, especially during subadult growth and development may inform interpretations of life history changes throughout hominin evolution. Among early modern humans, a better understanding of the relationship body size has to ecology and subsistence strategy may aid interpretations of bioarchaeological remains. Additionally, discovering patterns in extant human populations contributes to policy decisions regarding economic programs and humanitarian relief for people living in non-industrialized settings.

BACKGROUND

Human Growth and Development

To begin to assess a population’s growth and development, specifically the population’s unique eccentricities that represent localized adaptations, the processes and mechanisms must first be understood. Humans follow a consistent sequence of growth events from birth through early adulthood. While the sequence of developmental events is concrete, the nature of these events such as timing, duration, and magnitude, are subject to variation from genetic and environmental factors (Kramer and Greaves 2011). Both the static sequence and causes of variation will be explored in this section.

Bogin (1988) describes that the normal human growth velocity curve has height velocity (cm/yr) sharply decline post-natal and throughout infancy, remain low throughout early childhood and slowly increase showing a mid- growth spurt at the end of childhood, declining again through juvenility until a sharp inflection marking the adolescent growth spurt. Throughout all subadult stages there is overall skeletal growth resulting in increases in stature. However, these developmental stages are uniquely defined by somatic changes and development.

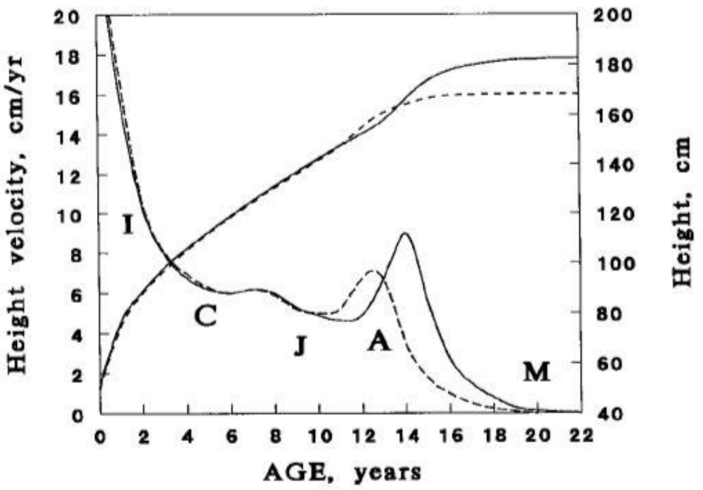

Fig. 1. Idealized mean velocity and distance curves of growth in height for healthy girls (dashed lines) and boys (solid lines) showing the postnatal stages of the pattern of human growth. Note the spurts in growth rate at mid-childhood and adolescence for both girls and boys. The stages of postnatal are abbreviated as follows: I, infancy; C, childhood; J, juvenility; A, adolescence; M, mature adult. Data used to construct the curves come from Prader (1984) and Bock and Thissen (1980).

Figure 1. From Bogin (1997:64), idealized representation of growth and growth velocity.

Infancy occurs from birth until weaning (Bogin 1988). During infancy the child is completely dependent on the mother for nutrients, typically provided through breast milk. Across highly social mammals, including wolves/dogs, elephants, lions, and primates, there is a juvenile period between infancy and adulthood (Bogin 1997). The juvenile developmental period begins at weaning and ends at sexual maturity (Kramer and Greaves 2011). Pereira and Altmann (1985) describe the juvenile period as prepubescent yet independent of the parents, or others, for survival.

However, humans have incorporated an additional developmental stage between infancy and juvenility. The hominin lineage has expanded the juvenile stage, hypothesized to be a means for children to accumulate more complex culture through an elongated learning period known as “childhood” (Bogin 1997, Klein 2009). However, research has shown that the processes that regulate the endocine, biochemical, and morphological changes that define the human “childhood” may be genetically rooted early in primate evolution (Bernstein *et al.* 2012). Regardless, the human juvenile period is segmented into childhood and adolescence before full sexual maturity marking adulthood (Kramer and Greaves 2011).

Immediately after weaning begins the uniquely human developmental stage of childhood (Bogin 1988, 1997). From a worldwide survey, the median age at termination of weaning is 36 months (Dettwyler 1995). This age will be used henceforth, and discussion of childhood will be assuming a start age of 3 years old. This stage has conflicting biological and behavioral definitions. Overall, childhood in humans is marked by rapid brain growth and the development of the digestive tract (Kramer and Greaves 2011). Biologically across primates, childhood ends with the eruption of the first permanent molar and the ability for the child to eat adult foods, this usually occurs in humans between ages 3- 7 (Kramer and Greaves 2011). In traditional societies, childhood is when the children begin to obtain some resources on their own, initiating a trend towards economic and nutritional independence, however there is still some dependence on others for a portion of their needs (Kramer and Greaves 2011). The maintained reliance on parents, or other, older group members to completely provide for or at least supplement the child is the distinction between childhood in humans and a juvenile period in other mammals (Bogin 1997). Though, it is important to note that some refer to the biological period between the eruption of the first permanent molar and the initiation of the adolescent growth spurt as a human juvenile period. Nonetheless, childhood functionally occurs in humans from about age 3 until about the age of 10, regardless of the biological marker of the eruption of the first permanent molar. Following childhood there is a brief stage resembling the mammalian juvenile period where individuals are capable of resource independence but have not yet entered the next developmental stage of adolescence marked by the onset of rapid growth (adolescent growth spurt) concurrent with hormonal changes beginning puberty (Hochberg 2009, Kramer and Greaves 2011).

The insertion of the childhood stage then has interesting implications for the general patterns of human growth relative to other mammals and primates. While human growth during gestation is rapid and in line with a general primate model, there is a long period of slow growth between birth and the adolescent growth spurt, however, later in development they align with expectations (Leigh 2001). Leigh (2001) also finds that chimpanzees and bonobos (genus *Pan*), the sister genus to *Homo*, also exhibit an elongation of pre-adolescent growth, though not as pronounced as humans. Leigh (2001) represents primate growth in a series of “periods” with the first period defined as birth until the onset of the subadult (adolescent) growth spurt, the second period is from the onset of the spurt until the peak velocity, and the third period is from the peak velocity until the spurt ends. Relative to other primates, humans have a later second growth period (adolescent growth spurt), with females exhibiting a more abbreviated growth phase than males, however, males and females enter into the third period at the same time (Leigh 2001). These generalized patterns allow for the comparison of different populations to uncover the natural variation. Variation among human populations and across primate taxa shows that growth patterns can easily respond to selection pressures for a delay in the subadult growth spurt, and the variation in the growth spurt acts independently of body size (Leigh 2001). Species maximize survival and reproductive success through optimal life history strategies, though flexibility in life history to react to environmental signals is important for successful adaptation (Konner 2010).

Factors that Shape Growth Patterns

Within a population, individuals will vary in their growth trajectory towards their final adult height. Tanner and colleagues (1966) note that among British children, during childhood when growth is more gradual, an individual's centile relative to other members of the population of the same age will likely be the same centile that individual falls within as an adult. However, during adolescence an individual who matures early will rise in centile temporarily, but will eventually reach adult stature and return to their relative childhood centile, just as a late maturer will drop in centile rank until their adolescent growth spurt returns them to their pre-adolescent centile (Tanner *et al.* 1966). Environmental factors impact height-for-age more during childhood, and that impact decreases towards adolescence (Beunen et al. 2000; Kramer and Greaves 2011)

Between populations of differing adult heights, variations in growth trajectories are more indicative of the population's adaptation. While external factors such as nutrition and environment may manipulate an individual's growth, genetics influence variation between populations in relation to stature, especially when discussing the extremely tall and short populations (Kuzawa and Bragg 2012). However, across recent human evolution (within the last 30,000 years) changes in stature and body mass have fluctuated, following environmental and behavioral changes. The fact that humans have lived in highly variable environments implies that evolution has selected for variable, responsive abilities that are retained today (Leslie and Little 2003). While these may be genetically determined, the secular trend in growth trajectories over the last 150 years due to the Industrial Revolution cannot be attributed to genetic changes (Hochberg and Albertsson-Wikland 2008). Even if genetic differences compete with secular trends, for each genotype there are variable phenotypes to be expressed across a range of different environments (Crespi and Denver 2005). These phenotypes are collectively referred to as reaction norms, where reaction norms are results of a compromise between cost and benefits for trait variations (Walker *et al.* 2006). Konner (2010) simplifies reaction norms as predictable relationships between the environment and a life course, either in an individual, population, or species. Konner's (2010) use of reactions norms, like Walker and colleagues (2006), seeks to explain the optimal trajectory.

Phenotypic plasticity is advantageous in fluctuating conditions; however, in a stable environment selection favors less plastic growth trajectories (Walker *et al.* 2006). The standard model of a slow juvenile growth rate exploding into an adolescent growth spurt to quickly reach adult stature has been formed using data from industrialized populations in consistently healthy and nutritious conditions (Kramer and Greaves 2011). However, more hazardous conditions have yielded alternative growth trajectories as reactions to different environmental pressures. Therefore, while adaptations have occurred to environmental conditions such as latitude, altitude, and generalized ecology over many generations, and these conditions generally change slowly, there is additional plasticity to changing nutritional conditions that can fluctuate rapidly, and both predictably and unpredictably (Hochberg 2009).

The relative influence an external factor has on the growth trajectory and final adult size is determined in part by the developmental stage that influence occurs in. Conditions during early childhood, specifically at the age of weaning, contribute to determining an individual's adult height. Much of the current variation in adult height reflects nutrition during childhood, where shortfalls in growth by age 2 or 3 represents deficits relative to healthy values in final adult stature (Kuzawa and Bragg 2012). Hochberg and Albertsson-Wikland (2008) have similar findings, where each month's delay in the transition from infancy to childhood, a response to so called "crises" in energy availability, relates to a deficit of 0.4cm in boys and 0.5cm in girls at age 5 years. This deficit follows through to adulthood since these delayed individuals continue normal growth patterns and trajectories, but effectively start childhood smaller (Hochberg and Albertsson-Wikland 2008).

However, later nutritional deficits during the late juvenile, early adolescent period are less informative on final adult height, though such deficits could slow the rate of maturation (Kuzawa and Bragg 2012). At the onset of puberty, individuals with abundant fat stores who are better nourished throughout childhood will enter puberty earlier, with a shorter but more intense adolescent growth spurt, and reach maturity earlier. As nutritional quality deteriorates, the beginning of puberty is delayed, with the characteristic growth spurt becoming more gradual over a longer period of time (Kuzawa and Bragg 2012).

Life History Theoretical Models

While Walker and Hamilton (2008) do not dispute that growth and development are influenced by nutritional constraints, they argue that a life history analysis is more comprehensive in explaining human variation. From observations of both humans and other primates life history theories have been formulated to relate the different life events of growth and development to external pressures such as nutrition, extrinsic mortality risk, and other environmental factors. Life history theory provides a framework for researchers to assess different observed growth trajectories by fitness costs and benefits as well as by energetic constraints (Walker *et al*. 2006). Human variation in life history, allowed by phenotypic plasticity to environmental conditions, impacts growth rate, body size, reproduction, and life span (Kuzawa and Bragg 2012). The focus of life history analysis is reiterated by Migliano *et al.* (2007) who observe that extremely small stature in pygmy populations cannot exclusively be explained by poor nutrition, as Rift Valley pastoralists, among the tallest populations in the world, experience similar nutritional deficiency. Furthermore, Walker *et al.* (2006) and Walker and Hamilton (2008) propose to explain small body size through variable life history adaptations where their model predicts that pygmy populations are the result of a fast life history strategy from high mortality rates, while a slow life history strategy is characterized by the resource limited Gainj and Ju/'hoansi (Kung!) with better survival probabilities.

Understanding the evolution of human body size under a life history model requires a comprehensive model accounting for both energetic constraints and the effect of subadult mortality as a selection pressure (Walker and Hamilton 2008). As has been previously shown, an individual's adult height is influenced by the conditions during childhood. Across populations, childhood growth (growth velocity between ages 3-10) is one of the best measures to compare populations since growth rates appear to be stable and linear in this stage (Walker *et al.* 2006).

In populations with a high risk of extrinsic juvenile mortality, life histories are accelerated to allow for earlier reproduction (Migliano *et al.* 2007, Walker *et al.* 2006, Walker and Hamilton 2008). One cause of extrinsic mortality, especially in traditional societies, is disease. In environments of low sanitation and high epidemiological risks it would be assumed that more energy would be allocated towards an immune response (Walker *et al.* 2006). The energetic constraints ultimately come from a population's nutritional availability. Assessments of nutrition are incorporated into life history analysis through the consideration of metabolic risk aversion models, which have been applied to account for some of the variation across primates in residual growth rates (Leigh 2001, Jansen and van Schaik 1993). This model suggests that in periods of low metabolic risks there is more rapid growth, where higher risk scenarios yield lower growth rates (Jansen and van Schaik 1993). However, larger body size at younger ages is important for a strong immune response against parasites and infectious diseases (Walker *et al.* 2006). These assessments seem contradictory, though Walker and colleagues (2006) have interpreted these results by considering that high mortality yields fewer siblings so that the surviving children have more energetic support from the parents with decreased competition, allowing for simultaneously increased immune power and faster growth. Such an interpretation, then, supports Migliano *et al.* (2007), and other empirical studies that show accelerated life history in costly situations.

In optimal conditions of western populations there is a relationship between adult size and growth trajectory. Females in well-nourished populations grow faster, reaching sexual maturity earlier, yet also achieve a larger adult body size compared to those from poorer nutritional conditions (Hill 1993). There is a selection among females for relatively earlier sexual maturity and attainment of adult body size compared to males to increase fertility (Leigh 2001). Studies of small scale societies have shown a positive correlation between larger body size and increased fertility (Walker *et al.* 2006). Each year an individual waits to reach maturity they are able to allocate energy towards growth that may increase body size and reproductive value; however, each year the probability the individual will survive decreases as well (Hill and Hurtado 1996). The additional energetic costs for a larger body and the loss of reproductive opportunity with an elongated growth period makes a larger body extremely costly in populations with less available nutrition (Walker & Hamilton 2008). This is confirmed by the empirical data in Hochberg and Albertsson-Wikland (2008) where individuals adapt to avoid nutritional crises by decreasing body size.

In poor nutritional and environmental conditions the costly trade off of growth to immune response should result in slower growth. However, some empirical data (Deaton 2007, Kramer and Greaves 2011, Walker *et al.* 2006) shows faster growth than would be expected given poor conditions. Energetics and extrinsic risks then alone do not explain variations in life history strategy. Reznick and colleagues (2002) faced similar disparities between theoretical predictions and empirical realities in their study of guppy life histories in relation to various external factors. In order to understand the origins and selective influences of human growth patterns, additional factors must also be considered. Kramer and Greaves (2011) relate observational data of time allocations and activity levels for Pumé juvenile females and conclude, for that population, high subsidy by older members of the community and relatively low activity levels allow for more energetic allocation to greater than normal growth during the juvenile period. This finding adds habitual cultural and behavioral reactions to certain environments as components to growth patterns.

Additionally, nutrition and relative life history strategies do not immediately correlate to variation in adult size. Migliano *et al.* (2007) observes that east African pastoralists share with the Aeta and Biaka (pygmy populations of the Philippines and west Africa respectively) the nutritional constrains that lead to early developmental deficits in growth rates until approximately age 12, however there is between a 25-35cm difference in adult body heights between east African pastoralists and pygmy populations. Never the less, observations of Rift Valley pastoralists indicate that they are incurring the costs of longer growth periods and larger bodies contrary to theoretical predictions (Little *et al.* 1983).

A generalized theoretical life history model emerges from the above articles relating the influences of the various internal and external factors on subadult growth and development. This model links the dependent variables of relative mean adult stature and life history strategy (relative speed of maturation) in relation to the independent variables of mortality risk, disease, and nutritional quality to explain the patterns of varied human growth trajectories across environmental and ecological conditions. This model is generally applied to explain a range of patterns observed across traditional societies as opposing selective pressures shape growth and development. In high extrinsic risk environments energetic allocations shift from future to current offspring investment where large body size at earlier ages is advantageous in combating factors such as disease and violence that are more likely in smaller individuals (Migliano *et al.* 2007, Walker *et al.* 2006). However, strengthened immunity or higher maintenance costs compete with somatic growth for energetic resources (Hochberg 2009, Walker and Hamilton 2008, Walker *et al*. 2006).

Therefore, even in populations that adopt a fast life history strategy to combat high extrinsic risk, nutritional availability is the ultimate determining factor for growth potential. When malnutrition is a greater risk than other extrinsic factors, populations will adopt a slower growth trajectory (Walker *et al.* 2006). This may account for the continued slow growth of east African pastoralists for 3-4 years after cessation of growth by pygmies at age 12 (Migliano *et al*. 2007). However, the tall mean stature for Rift Valley pastoralist populations may have a partial genetic explanation (Kuzawa and Bragg 2012) which prolongs a slow growth trajectory limited by caloric availability over a longer period of time. Even though pygmies are characterized by a fast life history strategy, the smaller caloric budget from poorer nutritional conditions has the Aeta and Biaka growing at a slower rate than the average western (US and Europe) population (Migliano *et al.* 2007). Considering the geographical relationship between the two populations, the Aeta in the Philippines and the Biaka in western Africa, genetic influences can be discounted for the growth trajectory and body size of these populations. Furthermore, the Pumé have also adopted an accelerated life history in a foraging subsistence strategy yet have mean adult heights at or above other traditional societies (Kramer and Greaves 2011). These population specific examples begin to unravel the life history theories that propose to explain human growth and size variation.

Population Based Studies

Considering the generalized stages and processes of human growth, the factors that impact the timing, duration, and magnitude of those processes, and the life history models that attempt to integrate these factors into predictable patterns, detailed investigation of east African pastoralists can be laid down to generate hypotheses about Daasanach growth and development to be tested with the collected data. East African pastoralist is a broad term linking diverse populations from the Sudan, Ethiopia, Kenya, Uganda, and Tanzania (Little 2002). The subsistence strategies are just as broad, where some populations are sedentary, incorporating cultivation with herding, and others maintain nomadic or semi-nomadic practices relying heavily on their livestock for subsistence (Little 2002). The Turkana subset studied by Little (1983, 1987, 2002) is one of the last remaining nomadic east African pastoralist populations, though some members of the Daasanach have also retained these practices.

The Daasanach are a generally nomadic/ semi-nomadic pastoralist tribe that range from the northeast coast of Lake Turkana, throughout north central and north eastern Kenya, and into southeastern Ethiopia and southwestern Sudan (Fig. 2). Daasanach share an ecology and subsistence strategy similar to other Turkana basin and east African Rift Valley tribes, as well as a presumed close genetic relatedness. Their ecology is a semi-arid savanna/desert with highly seasonal rainfall and high temperatures yearlong (28º- 38º C); these conditions are similar to those described in Little *et al.* (1983), Little and Johnson (1987), and Little (1989) for the Ngisonyoka Turkana located southwest of Lake Turkana (Fig. 2). Some Daasanach families have either permanently or seasonally settled in the town of Ileret, Kenya, located along the northeast shore of Lake Turkana where data collection occurred.

While previous studies have investigated growth in populations from the Turkana basin, no studies of yet have particularly used the Daasanach tribe. Discussion of studies from other Turkana basin tribes will follow, noting that it is possible Daasanach individuals could be included under a generalized "Turkana" heading. Little and colleagues (1983) discuss difficulties in studying pastoralists groups, including nomadic lifestyles, independence from national infrastructures, geographical isolation, and warlike tendencies. These conditions make longitudinal studies difficult and have restricted the available data.

When Little and colleagues (1983) conducted a cross-sectional study of Ngisonyoka males they found a lag of 1 to 2 years in height when the Ngisonyoka males were compared to U.S. African American values throughout the teen years (age 12- 18), though by age 20-23 the Ngisonyoka reached equivalent stature. Ngisonyoka females similarly fell behind U.S. values after childhood, and their lag began earlier than males at about 8-9 years of age (Little *et al.* 1983). From the cross-sectional study it was found that Ngisonyoka also lack a defined adolescent growth spurt, and instead experience continuously gradual growth for an elongated period to reach their adult height (Little *et al.* 1983).

In order to confirm their results and to catch unpredictable growth fluctuations due to changing food availability, Little and Johnson (1987) resampled some members of the Ngisonyoka tribe, with variation in the time lapse between measurements across individuals. In the longitudinal study, a growth velocity peak was found for males (at age 15.5), but undetected in females (Little and Johnson 1987). When the longitudinal height distance curve is compared to the cross-sectional curve, there is congruency until age 8, where the longitudinal increases in height are greater than those shown in the cross-sectional curves, showing that the individuals selected for the longitudinal study are growing normally, or faster than normal for the population (Little and Johnson 1987).

Recently, environmental and economic factors have forced many of the east African pastoralists to settle in areas of trade, work, or cultivation (Little 1989, 2002, Little and Gray 1990). Little and Gray (1990) compared growth of settled schoolchildren and nomadic children, both of the Ngisonyoka (ages 4-9), and found significant differences in height between the two groups at all ages, with the absolute differences increasing with age. Additionally, settled children tended to weigh more than nomadic children of the same age, and this difference was significant at most ages between the sexes, but weight-for-height was about equal between the two groups (Little and Gray 1990).

However, even though there are significant differences between these two populations, when compared to the National Center for Health Statistics (NCHS) percentiles for U. S. children, the nomadic Ngisonyoka males reach the 20th centile for height, settled males reach the 35th centile, nomadic females reach the 30th centile, and settled females reach the 50th centile (Little and Gray 1990). When weight data is compared to NCHS, all sex/age groups fall below the 5th centile, and weight-for-height is similarly below the 5th centile over the age of 5 (Little and Gray 1990). These results by Little and Gray (1990) conform to the generalized and unique African patterns discusses by Deaton (2007) and de Onis *et al.* (1993) where height achievement is not sacrificed in poorer nutritional conditions.

Interpretation based on this data set alone is problematic. It is unknown if the inferred nutritional differences between the two groups began in infancy (due perhaps to higher socio-economic status (SES)) or when the children entered nursery school and started to receive the school's meals. If the differences are linked to SES then the nomadic deficits in growth seen in this childhood sample will maintain throughout development into adulthood (Hochberg and Albertsson-Wikland 2008, Kuzawa and Bragg 2012). However, if the differences begin once the settled children begin school then the nomadic group may only be experiencing a temporary lag that will be reduced later in growth and development (Kuzawa and Bragg 2012). Little *et al.* (1983)'s findings that nomadic Ngisonyoka fall behind U.S. estimates in childhood but catch up in adulthood suggests that the discrepancies between settled and nomadic may only persist in childhood.

There has been an implied question of how African, particularly east African individuals reach abnormally tall stature in light of the numerous problematic nutritional, health, and environmental conditions. Little and colleagues (1983, 1987, 1989, 2002) attribute the protein rich diet from numerous animal sources (blood, milk, meat) of east African pastoralists as a contributing factor to their growth and body size. Fratkin *et al.* (1999) report similar findings where pastoralists get sufficient protein, iron, fat, and calcium from animal products; though their diets have a caloric deficiency. If true, these patterns would be highly conserved from early members of the genus *Homo* living in the east African Rift Valley for almost the last 2 million years. A widely accepted hypothesis for the increase in brain and body size for early *Homo erectus/ ergaster* is a shift to more hunting and scavenging, incorporating more animal proteins into the hominin diet (reviews of these hypotheses in Klein 2009, Stanford and Bunn 1999).

Assumptions have been made, then, that shifts from strict nomadic pastoralism to more sedentary lifestyles provide caloric supplements through agriculture or trade. However, studies into the effects of sedentarization of pastoralist groups show variable effects on health and growth. Reasons for settlement across traditionally nomadic pastoralists groups include government pressures, economic pressures, ecological changes, and increased access to healthcare and education (Fratkin *et al*. 1999, Fratkin *et al.* 2004, Little 1989). The nature and location of the settlements determine the relative positive or negative effect sedentarization has on childhood growth and health. Fratkin *et al.* (1999) looked at nomadic and sedentary populations in the Marsabit District of northern Kenya. In poorer or more isolated communities, trade of nutritious animals for cheaper and nutritionally poorer food items has a negative impact on childhood growth, though larger and richer

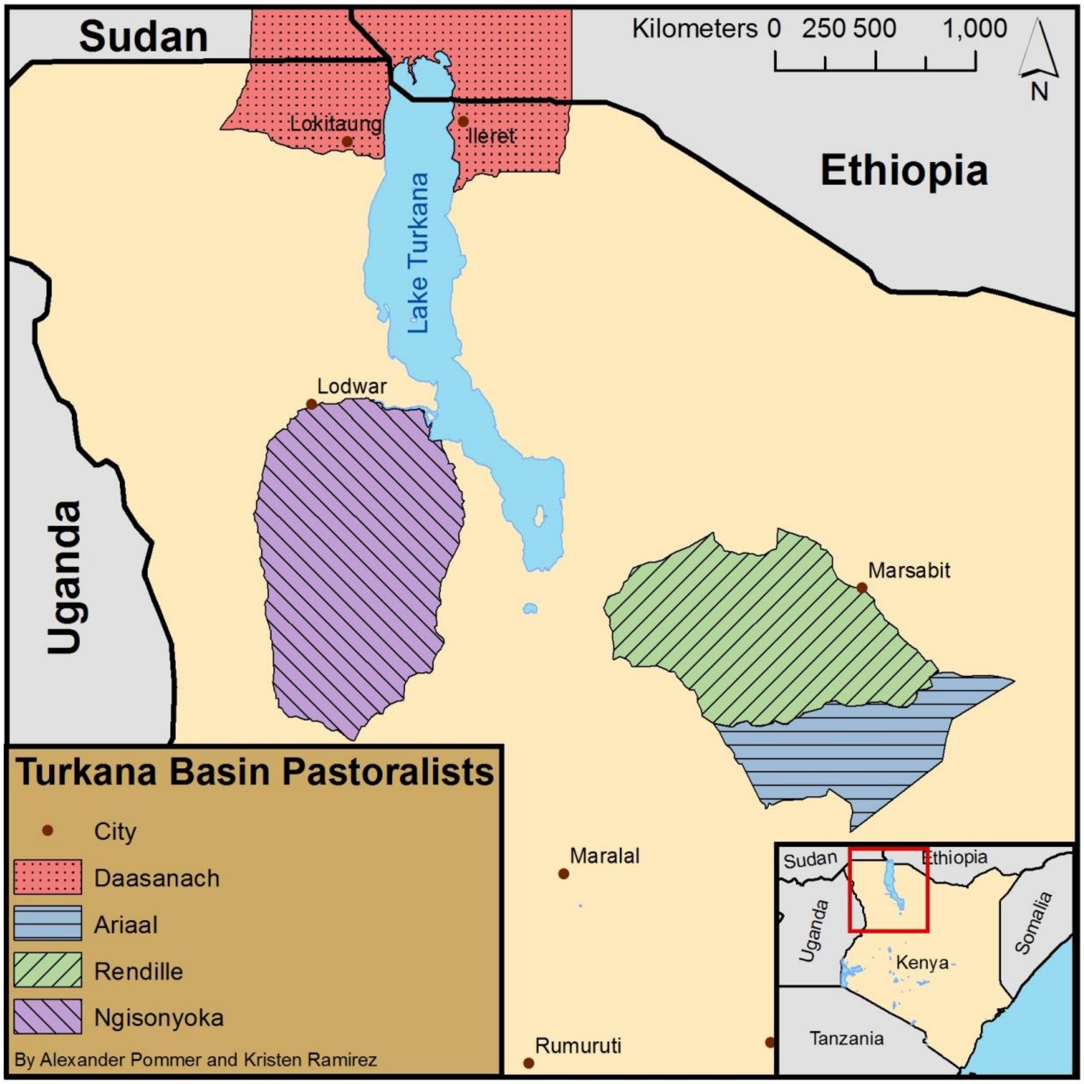

Figure 2. Map of Studied Turkana Basin Pastoralists. Ariaal from Fratkin *et al.* 1999, Rendille from Fratkin *et al.* 1999 and Fratkin *et al.* 2004, Ngisonyoka from Little *et al.* 1983, Little and Johnson 1987, Little and Gray 1990. Pastoralist boarders approximated from descriptions using political and natural barriers and maps from published sources, Daasanach boarder approximated from interviews by Ramirez. Map generated using ArcGIS by Pommer and Ramirez.

communities that engage in commercial and subsistence agriculture show an improvement in childhood health and growth (Fratkin *et al.* 1999).

Furthermore, nomadic pastoralists have been shown to be better at withstanding extreme environmental conditions such as drought. Nathan *et al.* (1996)

and Fratkin *et al.* (1999) show following an intense drought in 1992 the sedentary populations exhibited more malnutrition and growth deficits than the nomadic pastoralist group of the same region. The pastoralist continued access to milk from their herds, providing children with adequate protein to continue satisfactory growth, where sedentary children experienced nutritional shortfalls (Fratkin *et al.* 1999).

The Turkana studies from two geographically and ecologically similar populations, sharing a subsistence strategy and similar conditions of settlement show the variation in adaptive changes of a traditionally pastoralist group to a sedentary lifestyle. Though the intra-regional variation is present and rooted in nutritional factors, there is a global relationship between generalized ecological type and body size (Walker *et al.* 2006). While habitual behaviors may slightly influence selection and available nutrition impacts individuals, an organism's ecology is the ultimate source of selection pressures, as it defines the natures of the adaptations.

Into adulthood, the hunter- gatherer !Kung of the Kalahari Desert in southern Africa exhibit a short and thin body size that Howell (2010) does not see as a direct effect of life history and nutritional factors theoretically discussed above. One prediction by Howell (2010) is that the hot temperatures of the Kalahari may have selected smaller individuals who are better able to thermoregulate. Another is that the high energy expenditure in food acquisition: foraging, carrying food back, processing prior to consumption, paired with the bitter and difficult to process foods that primarily make up the !Kung diet are unlikely to be over-consumed, especially by younger individuals who crave sweeter foods similar to their mother's milk, and that these factors may have !Kung individuals consuming the minimal amount for survival (Howell 2010).

Unlike pygmies (Migliano *et al.* 2007) the !Kung do not exhibit an accelerated life history strategy and continue growing to a later age than pygmies with a relatively late adolescent growth spurt (Howell 2010). !Kung childhood growth is slow, especially between the ages of 7-12 where the children are the thinnest members of the population exhibiting stunted height and weight by international standards (Howell 2010). When compared to U.S. standards compiled by the Center for Disease Control, the median stature-for-age of !Kung children correlates to the lower 3rd centile of U.S. children, the value used to determine normal and undernourished U.S. individuals, though the !Kung are reported to be a healthy population (Howell 2010).

The Pumé, a savanna hunter- gatherer population from west-central Venezuela, also show mosaic effects on life history and growth from the various external factors surrounding their subadult condition. Kramer and Greaves (2011) describe the food supply to fluctuate according to seasonal and annual environmental changes. Pumé mothers begin to introduce supplementary foods as early as six months, as lactation in the poorer wet season is costly and detrimental to mother's health (Kramer 2008). A Pumé mother will lose up to 8% of her body weight during the wet season, exposing her infant to stress accounting for the high infant mortality rates seen in the population (Kramer 2008). This results in Pumé children growing up in poor health conditions with high stress and risk of disease (Kramer and Greaves 2011).

According to predictions by Kuzawa and Bragg (2012), this should impact final adult height. Contrary to this prediction, compared to other populations of similar subsistence strategies (foraging and horticulture) Pumé females are in the higher ranges for height variation (Kramer and Greaves 2011). Additionally, when compared to published Center for Disease Control data, Pumé girls are relatively taller, when adult size is considered, during their juvenile period and therefore may not be experiencing a distinct adolescent growth spurt (Kramer and Greaves 2011). While during the developmental periods Pumé female growth deviates from normative expectations, their adult stature is within normal ranges compared to other indigenous South American populations (Kramer and Greaves 2011).

From a life history perspective relative to extrinsic mortality, the Pumé conform to accelerated life history like that seen in pygmies (Migliano *et al.* 2007). The Pumé infant mortality rate has been consistently high (34.6% recorded in 2000-2005) for decades of observations and is closer to the mortality rate of pygmy populations than other hunter- gatherers such as the !Kung (Kramer 2008). Pumé females achieve early skeletal growth, reaching 88% of their population's mean adult stature by age 10, described by Kramer and Greaves (2011) to be the end of the mid juvenile period. The accelerated growth is consistent with life history theory prediction that high mortality risks will result in earlier reproduction (Kramer 2008, Kramer and Greaves 2011, Migliano *et al.* 2007). The unique Pumé juvenile growth curve is also seen in the slightly shorter and unrelated Hiwi population of foragers located approximately 50 km north- west in a similar savanna environment (Kramer and Greaves 2011).

In light of the ecological impact on adult height discussed by Walker *et al.* (2006), this study tests the null hypothesis that the Daasanach will conform to the growth trajectory of ecologically similar populations. Deviations from the patterns outlined by the comparative populations will be considered given the known influences on life history and growth and development timings and durations to assess the relative influence of the various external factors on different components of subadult growth.

MATERIALS

Data were collected on a cross- sectional ontogenetic sample (n=223; males: n=177, females: n=46) of Daasanach in Ileret, Kenya in the field during the summer of 2012 over 5 days of active data collection in early July.

Table 1. Age Frequency by Sex

Subadult

Age	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Male	4	11	8	6	3	7	11
Female	2	7	5	2	3	2	2

Age	**9**	**10**	**11**	**12**	**13**	**14**	**15**
Male	6	19	5	24	17	13	13
Female	4	1	-	3	4	2	1

Age	**16**	**17**	**18**	**19**	**20**	**21**	**22**
Male	8	3	5	2	5	-	1
Female	-	-	-	1	-	-	1

Age	**23**	**24**	**25**	Total Subadult
Male	-	-	-	171
Female	1	1	-	42
				213

Adult

Age	**26-29**	**30-39**	**40-49**	**50-59**	Total Adult
Male	-	2	1	3	6
Female	-	-	2	2	4
					10

Subadult subjects were recruited from the Ileret Primary School because the students at the school, or the administrators, had the most accurate knowledge of the subject's age compared to other Daasanach children who did not attend school. Additionally, the school provides a daily lunch at 12 noon of maize and peas to all students according to interviews with the headmaster. Nursery aged children (age 2-5) also receive porridge at 10:00 am. Only using subadult subjects from the school is believed to help control for confounding factors such as socio- economic status and nutritional quality.

It must be noted that the settled Daasanach who attend the school may have different growth trajectories from nomadic or lower SES individuals. Differences in growth between sedentary and nomadic pastoralist groups are discussed above (Fratkin *et al.* 1999, Fratkin *et al.* 2004, Little and Gray 1990, Nathan *et al.* 1996), though these studies show that the directionality and magnitude of the probable differences between the settled Daasanach sampled and more nomadic Daasanach cannot be known without additional information.

For analytical purposes, adults are assumed to have completed growth, so the distinction between subadult and adult is made at age 25 to capture growth that may be extended beyond the teenage years. In Little *et al.* (1983)'s cross- sectional Turkana childhood growth study, their age cutoff was 25 years as well. This is done because of predictions that east African pastoralists extend their adolescent growth trajectories to later ages (Migliano *et al.* 2007, Walker *et al.* 2006). Subadult subjects (age<25; n= 213; males: n=171, females: n=42) were predominately obtained from the Ileret Primary School. Any subject <18 of age was a student at the school, though

15 subjects (males: n=11, females: n=4) ages 18-25 were not school students. These subjects were recruited as the adult subjects (25<age<55; n=10, males: n=6, females: n=4) were through an announcement made by Father Florian von Bayern at the Ileret Catholic Mission asking for volunteers. Adult subject affiliation with the school is unknown as well as the reliability of their self-reported age. However, error in reported ages for individuals over age 25 will not skew the analysis of the subadult growth curve since only data for the subadult subjects was used to derive the velocity curve. Adults were sampled to determine the average adult measurements of height and weight by which to compare the Daasanach to other populations, and to assess the progress of the Daasanach subadults at various ages towards their presumed final adult height.

METHODS

Each measurement for each Daasanach individual was take once by co-PI Ramirez. The numerical value for the measurement was visually assessed by Ramirez and a student from the Koobi Fora Field School acting an assistant, where the recorded value was agreed upon by both Ramirez and the assistant. Stature was recorded to the closest 0.1cm using a rigid metric tape measure oriented perpendicular to the ground. The subject was placed in front of the tape measure and asked to stand up straight, feet together, back erect, head level with the ground facing forward. Weight was obtained from a dial scale set in kilograms to the closest 0.5 kg.

Other anthropometric measurements were taken with a soft tailor’s measuring tape in centimeters. These measurements were: functional arm length (greater tubercle of the humerus to tip of the middle finger), functional leg length (greater trochanter of the femur to floor), shoulder circumference, hip circumference, foot length, and foot width at metatarsal heads.

Measurements Taken

Figure 3. Measurements taken of Daasanach subjects. a- height, b- weight, c- arm length, d- leg length, e- shoulder circumference, f- hip circumference, g- foot width, f- foot length.

For the purposes of this investigation only height and weight data will be used. Male and female height and weights are reported for each subject; however, only male data is used to generate growth velocities and to compare the Daasanach to other populations. Female data is insufficient or missing for many critical ages and therefore growth curves derived would not be accurate. LOESS curvilinear fit in SYSTAT13 smoothed the height and weight values per age. Smoothed values are less influenced by outliers than the alternative of averaging the values. The difference in either height or weight data between consecutive ages becomes the velocity value of cm/yr or kg/ yr. Velocity curves are plotted in PAST using a LOESS Smoothing Model. Age-at-take-off (ATO) and age-at-peak (APV) velocity visually assessed using the velocity curve. Age-at-return-to-take-off (ARTO) velocity is the first age (x value) of the same take-off velocity value (y value) as ATO. Childhood velocity calculated as the difference between either height or weight at age 3 and age 10, divided by 7 as reported in Walker *et al.* (2006). Adult values for height and weight calculated as the average of all adult (age>25) subjects.

These analyses were chosen to be able to compare Daasanach data to published data from other traditional populations summarized in Walker *et al.* (2006) to test the hypothesis that Daasanach growth trajectory and life history strategy is strongly influenced by the local ecology. Using the data in Table 1 of Walker *et al.* (2006:298) where each population's country, ecology, and economy (subsistence strategy) is reported, populations were separated into groups by these factors. T- tests were performed between the groups' adult male height. The geographical groups (New World, Africa, and Eurasia) and economic groups (farming/ farming-foraging, forager, mixed) showed no statistical difference between adult male statures. The ecological grouping of neotropical forest, tropical forest, coastal, highlander, forest against desert, savanna/woodland, dry forest yielded two statistically significant groups with male adult height ($p<0.001$). This is consistent with a conclusion by Walker *et al.* (2006) that ecology is related to body size variation in traditional societies. The ecological influence on growth trajectory towards final height will be identified by the degree to which Daasanach conform to growth trends seen in these ecologically similar groups.

The Daasanach data already shows affinities with the ecologically similar populations. Daasanach fall within the range of ecologically similar (desert, savanna/woodland, dry forest) populations ($z=1.46$, $p=0.0721$), and outside the range of ecologically dissimilar populations ($z=4.044$, $p<0.0001$). Then, to test the hypothesis that the Daasanach growth patterns are similar to ecologically similar populations the distinction between generalized ecological groups discussed above will be made for the comparative analyses below. PAST was used to plot relationships between growth variables across populations using both OLS and RMA regression.

RESULTS

Height

The shape of the growth curve from the height data for the Daasanach subjects is on par with expectations from across human populations. Daasanach males and females in early childhood are the same height (Fig. 4). Females begin to surpass their male counterparts later in childhood indicating they are beginning their adolescent growth spurt earlier than males. However later in adolescence males ultimately become taller, and reach their growth plateau later in life compared to the female subjects.

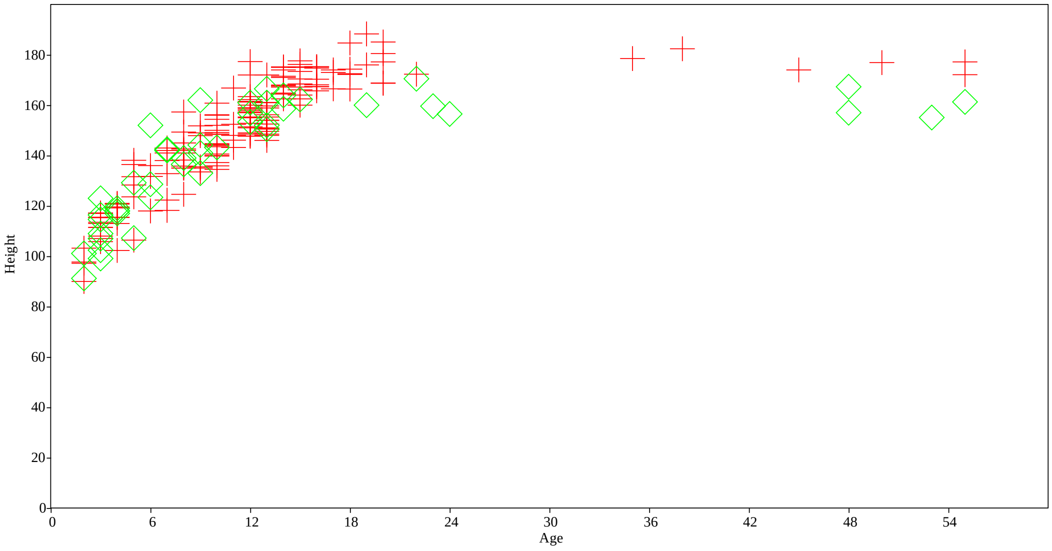

Figure 4. Daasanach height by age for all subjects. Females marked by green diamonds and males marked by red crosses.

For the Daasanach male height growth velocity curve, the generalized human shape described by Bogin (1997) is expressed (Fig. 1). The adolescent growth spurt is shown through the velocity curve as it is marked in time as beginning at the age of take-off velocity (ATO), and ends when the growth velocity returns to take-off velocity (ARTO). It is also interesting to note the peak growth velocity point (APV) as Leigh (2001) uses the peak velocity as a critical point in his view of primate growth as a series of periods. The end of the adolescent growth spurt at ARTO does not end adolescence nor does it signal the achievement of final adult height. Humans will continue to gradually grow for as many as ten years following the growth spurt. For the Daasanach males, the age at take-off velocity is 11.5 years, age at peak velocity is 13 years, and the age at the return to take-off velocity is 14.5 years (Fig. 5).

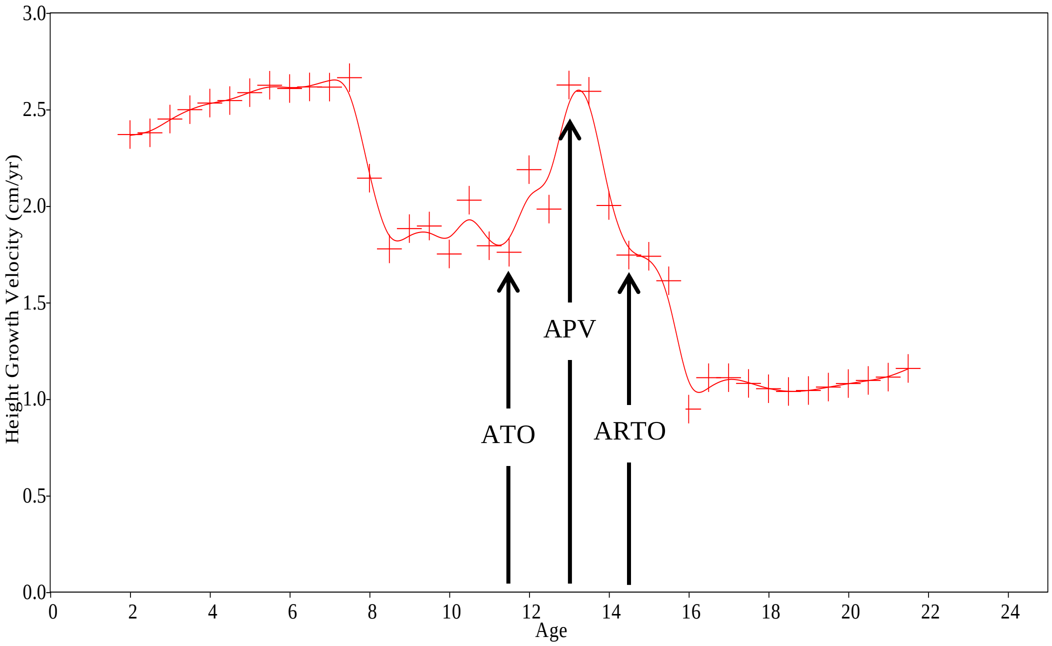

Figure 5. Male Daasanach height growth velocity (cm/yr) at each year produced by LOESS smoothing of Daasanach male height data. Age at take-off velocity (ATO), age at peak velocity (APV), and age at return to take-off velocity (ARTO) marked.

Walker *et al.* (2006) show a positive correlation between childhood height growth velocity (age 3-10) and a population's adult body height with a reported y=0.04x-1.51 and R²=0.3698 for males (Fig. 3b.:303). However, when the Daasanach data is compared to Walker *et al.* (2006)'s populations, they fall below the expected childhood growth velocity for their adult height (Fig. 6).

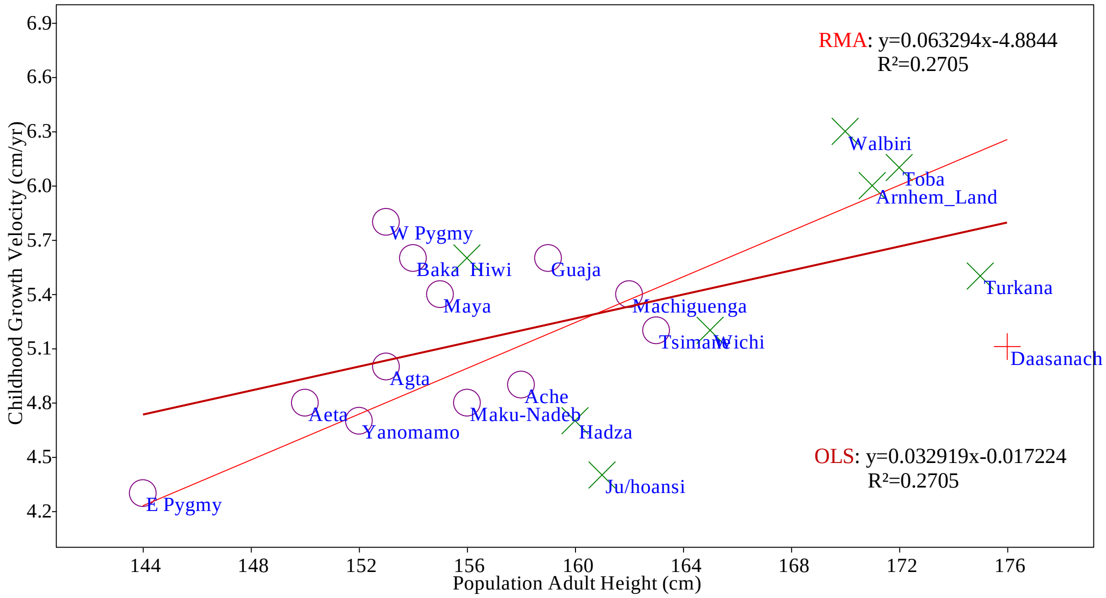

Figure 6. Relationship between childhood (ages 3-10) height growth velocity (cm/yr) and population adult male height. Daasanach marked as a red cross, ecologically similar groups marked as green x, and ecologically dissimilar groups marked with purple circle. Both RMA and OLS regression plotted.

The childhood growth velocity is calculated from age 3 to age 10. Kuzawa and Bragg (2012) discuss that nutritional deficits affect final adult height more when insufficiencies occur before the age of 2 or 3, where nutritional constraints later in childhood into the juvenile period are less influential in describing final adult height but may slow the rate of maturation. Then, considering the slow childhood growth rate a delayed and gradual adolescence would be expected. However, the Daasanach are shown to reach the critical velocity points (take-off, peak, and return to take-off) at early ages when compared to Walker *et al.* (2006)'s populations of which this data is available (Fig. 7).

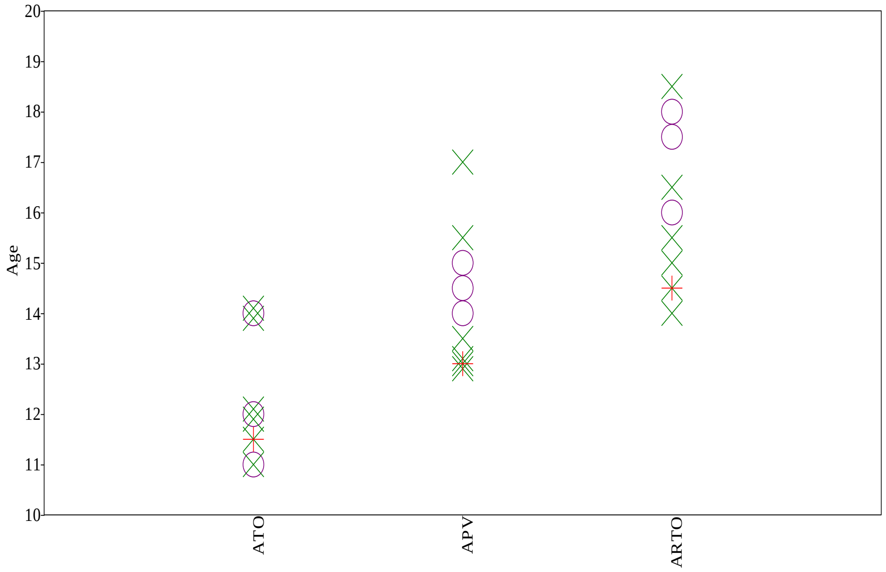

Figure 7. Comparison of ages at critical velocity points from the height growth velocity curve across comparative populations. Daasanach marked as red cross, ecologically similar populations marked as green x, and ecologically dissimilar populations marked as purple circle.

When considering the distribution of ages at the critical growth velocity points it is important to note that ecology does not group traditional populations as it did when considering final adult height. There is also much variation across ecological types and final adult heights when considering the duration of the adolescent growth spurt, in years between ATO and ARTO.

A weak, though statistically significant ($\alpha=0.01$, RMA: $p=2.2717E-07$; OLS: $p=8.5683E-07$) negative relationship between growth spurt duration and final adult height is observed in Walker *et al.*'s populations. Daasanach males loosely conform to this trend, though among other tall- bodied populations they exhibit a short growth spurt duration (Fig. 8).

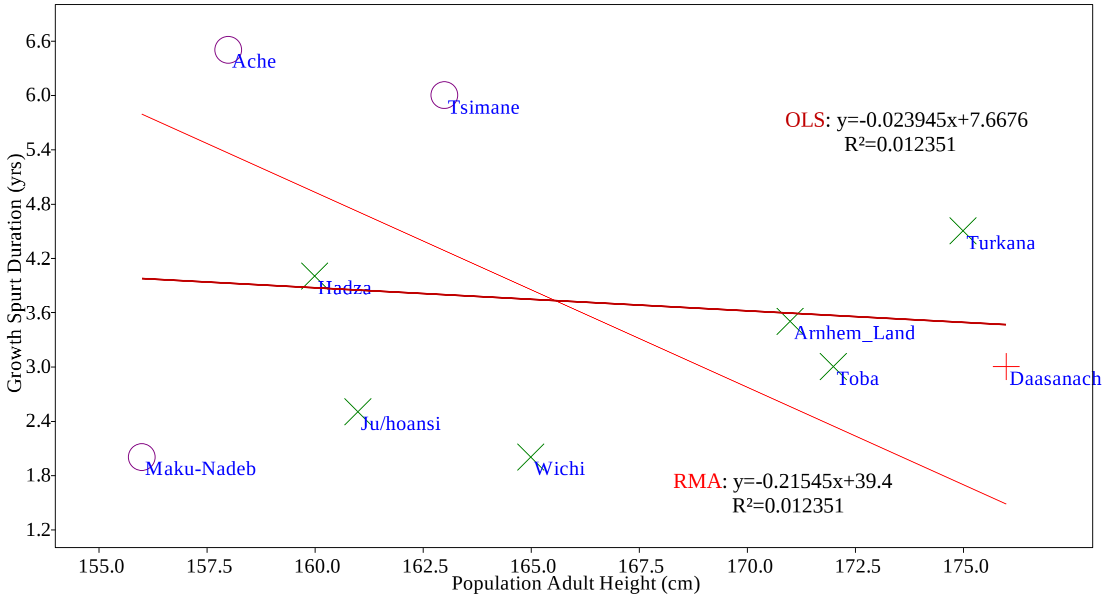

Figure 8. Relationship between adolescent height growth spurt duration (ARTO-ATO) and adult height across populations. Daasanach are marked by a red cross, ecologically similar populations marked by a green x, and ecologically dissimilar populations marked by a purple circle.

Weight

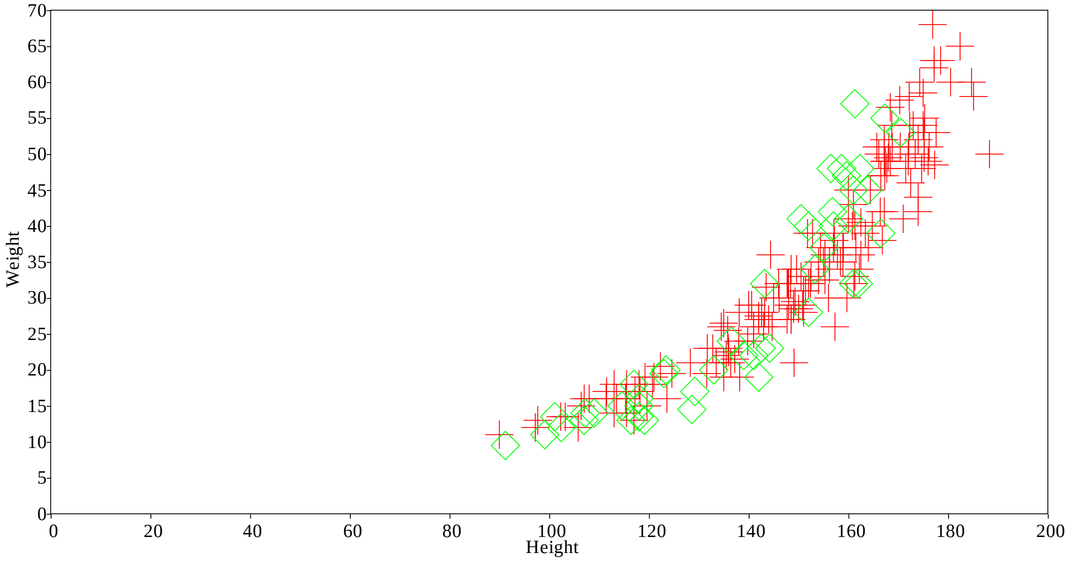

Figure 9. Weight for height of all Daasanach subjects. Daasanach males marked by red cross, females marked by green diamond.

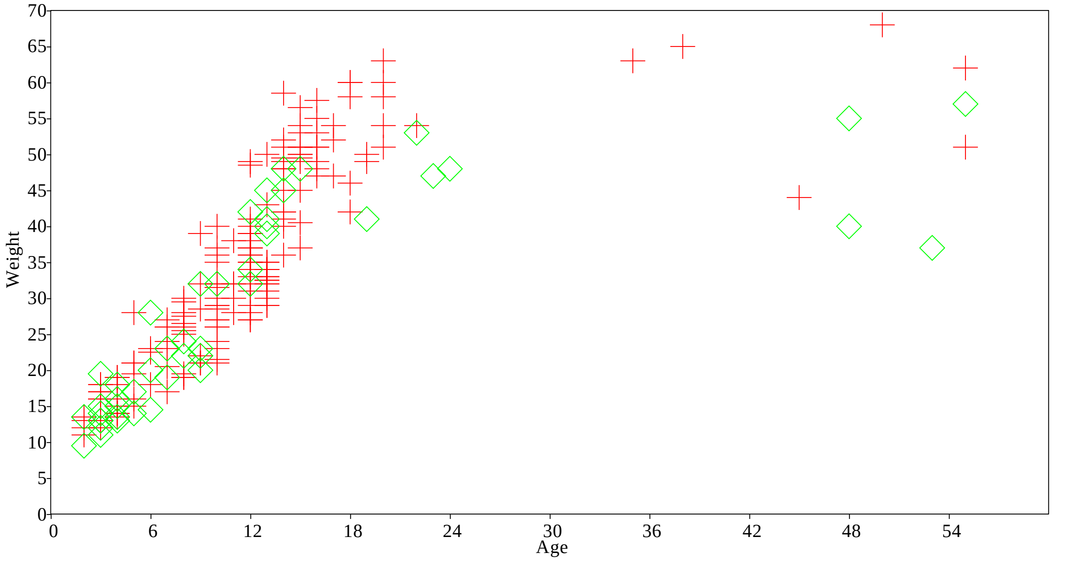

Figure 10. Daasanach weight by age for all subjects. Females marked by green diamonds and males marked by red crosses.

Similar to the height velocity curve, growth velocity can also be extrapolated from the Daasanach male data. When compared to the height data, the Daasanach take-off velocity age for both height and weight is the same at 11.5 years. However, the Daasanach extend the growth spurt in relation to weight by reaching peak velocity at 13.5 years (age 13 for height), and returning to take-off velocity at 16 years (14.5 for height) (Fig. 11, Table 2).

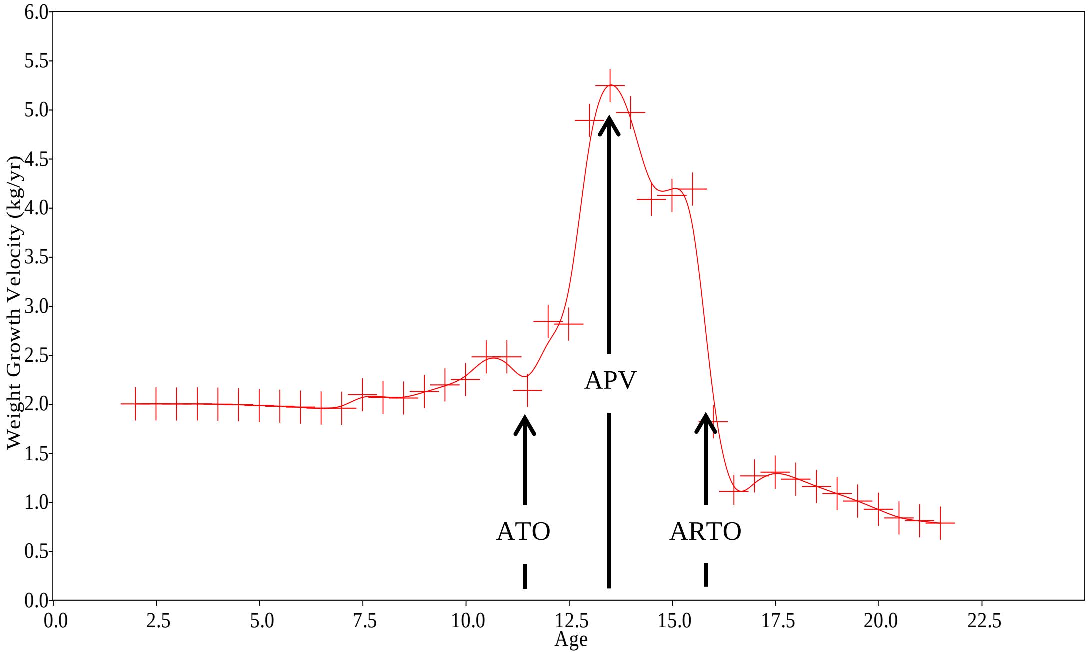

Figure 11. Male Daasanach weight growth velocity (kg/yr) at each year obtained from LOESS smoothing of Daasanach male height data. Age at take-off velocity (ATO), age at peak velocity (APV), and age at return to take-off velocity (ARTO) marked.

Table 2. Daasanach Critical Velocity Ages for Height and Weight

	ATO	APV	ARTO	Duration (ARTO-ATO)
Height	11.5	13	14.5	3
Weight	11.5	13.5	16	4.5

Early in childhood the Daasanach males experience consistent, but relatively low increases in kilograms each year. Though low relative to the velocity during adolescence, the Daasanach have a relatively high childhood weight growth velocity for their final adult weight compared to the other traditional populations (Fig. 12).

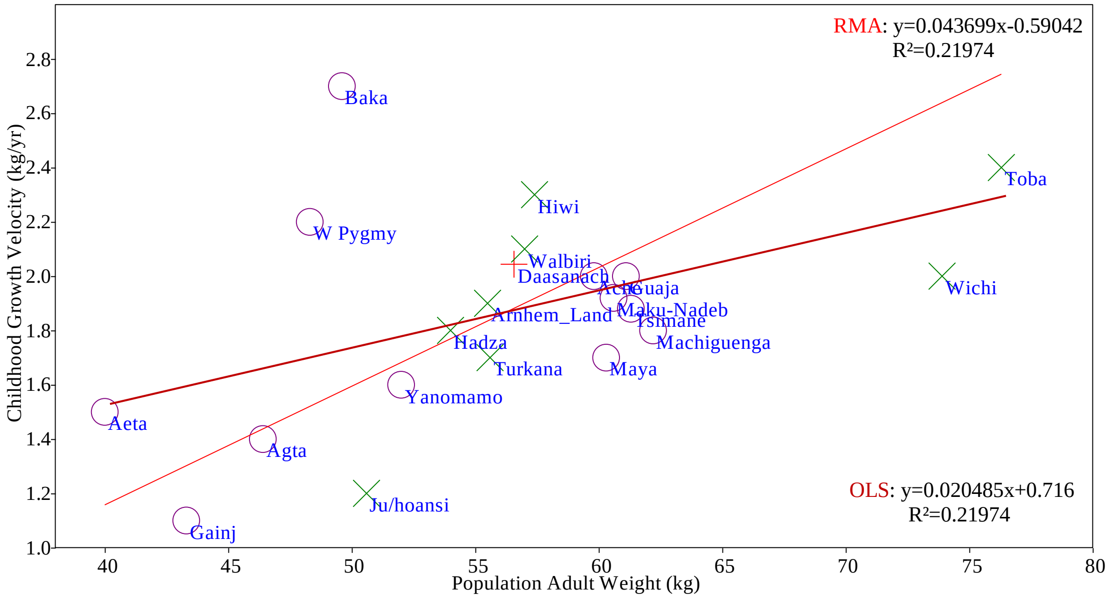

Figure 12. Relationship between childhood (ages 3-10) weight growth velocity (kg/yr) and population adult male weight. Daasanach marked as a red cross, ecologically similar groups marked as green x, and ecologically dissimilar groups marked with purple circle.

For the subsequent adolescent weight growth spurt, when the ages at these critical weight growth velocity points are compared to the Walker *et al.* (2006) samples, the Daasanach continue to be entering into the adolescent growth spurt early, however, the cessation of the growth spurt is happening closer to the median age for the traditional populations than the Daasanach height ARTO (Fig. 13).

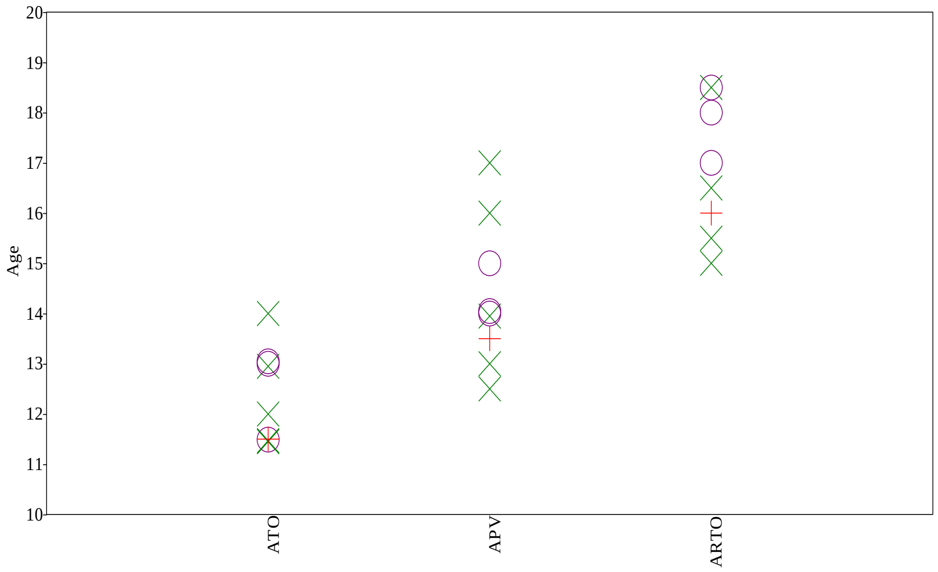

Figure 13. Comparison of ages at critical velocity points for the weight growth curve across comparative populations. Daasanach marked as red cross, ecologically similar populations marked as green x, and ecologically dissimilar populations marked as purple circle.

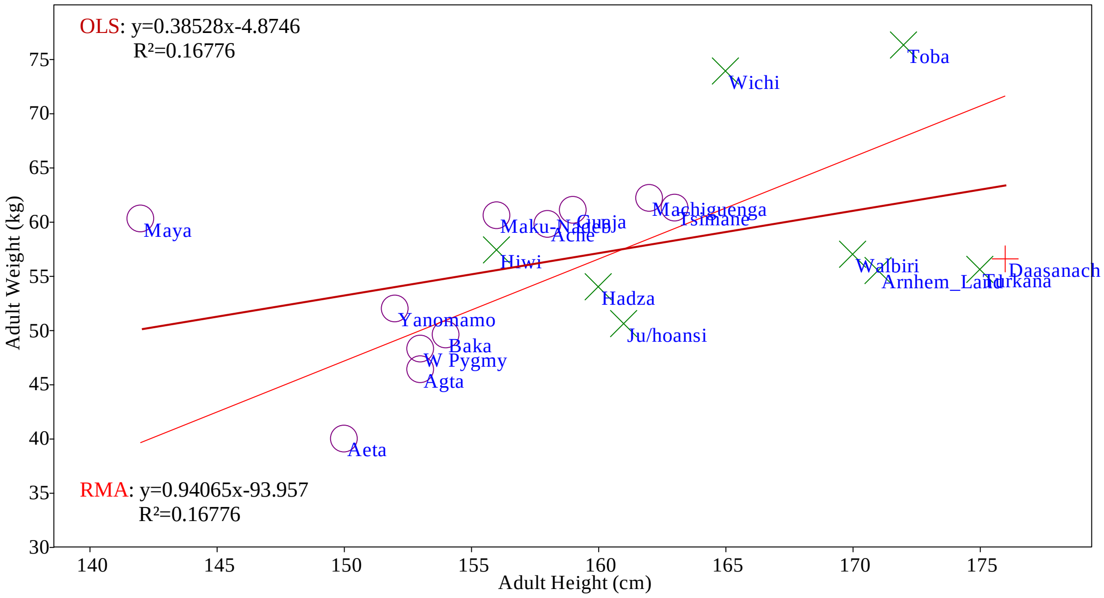

Figure 14. Relationship between weight (kg) and adult height (cm) across the comparative traditional populations. Daasanach marked by a red cross, ecologically similar populations marked with a green x, and ecologically dissimilar populations marked with a purple circle.

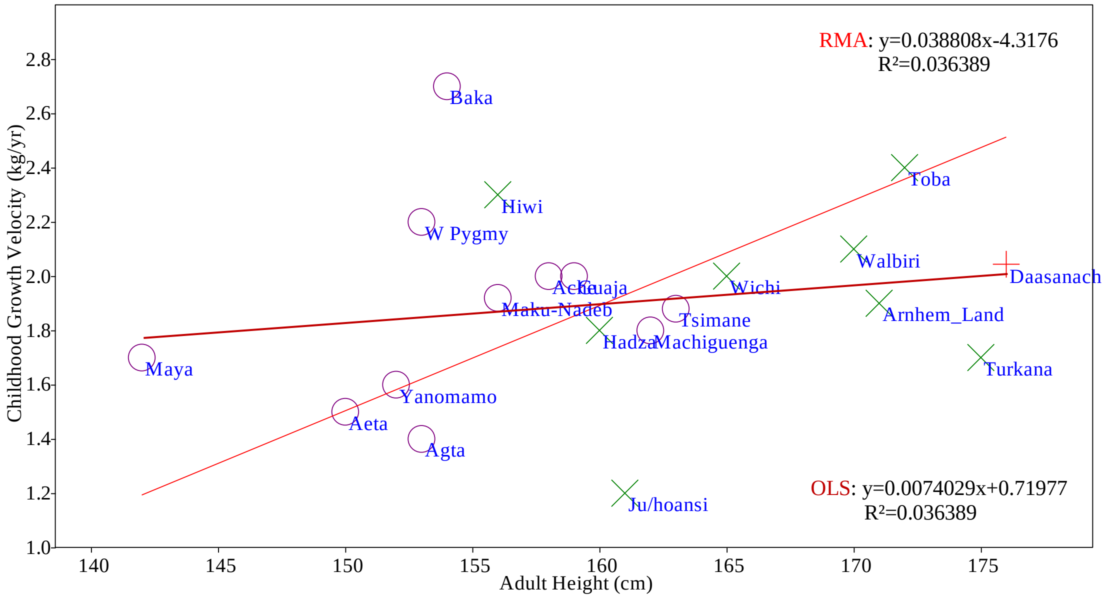

Figure 15. Relationship between childhood weight growth velocity (kg/yr) and adult height across the comparative traditional populations. Daasanach marked by a red cross, ecologically similar populations marked with a green x, and ecologically dissimilar populations marked with a purple circle.

DISCUSSION

Overall, the results show that settled Daasanach in Ileret, Kenya who attend the primary school experience a distinct and marked adolescent growth spurt (Fig. 5). This is important to note because some traditional populations (e.g. the Ngisonyoka from Little *et al.* 1983) go through gradual and elongated subadult growth that does not exhibit the phases discussed by Bogin (1988, 1997) and illustrated in Figure 1. The growth spurt present in the data may be caused by sedentary lifestyle of the subjects and the supplementary meals provided at the school daily. Little and Gray (1990) showed settled Ngisonyoka experienced a growth spurt when nomadic members of the same tribe did not (Little *et al.* 1983, Little and Johnson 1987). While the growth spurt is characteristic of industrialized, Western populations (Bogin 1988, Bogin 1997, Tanner *et al.* 1996), many other traditional societies also experience a distinct growth spurt (Walker *et al.* 2006), and these results then cannot be immediately dismissed as not representing adaptations to a traditional lifestyle in a given ecology. However, for the remainder of this analysis, statements about the Daasanach will extend only to the subjects, and members of the same immediate community as the subjects in Ileret, Kenya since the degree and directionality of the effect of sedentarization (if present) cannot be known (Fratkin *et al.* 1999, Fratkin *et al.* 2004).

Regardless of the possible discrepancies between settled and nomadic populations in regard to the growth spurt, Daasanach have incongruent growth timings and durations relative to the patterns seen in Walker *et al.* (2006) in both height and weight growth trajectory. This may be a factor of the incongruent relative height and weight rankings for the Daasanach compared with these other populations. While the Daasanach are the tallest males among the traditional societies, the Daasanach are in the lower half by their weight (Fig. 14). However, the Daasanach do fall closer to the comparative pattern when childhood weight growth velocity is related to adult height (Fig. 15).

In relation to Daasanach growth in overall stature, the Daasanach deviate from the trends seen in ecologically similar groups. Through childhood the males experience a slower growth rate (Fig. 6) preceding a relatively early and short growth spurt (Fig. 7 and Fig. 8). This contradicts the patterns of the comparative ecologically similar populations from Walker *et al.* (2006) as well as deviates from the theoretical trajectory predicted by Bogin (1988), Leigh (2001), and Kuzawa and Bragg (2012). Intuitively, these Daasanach childhood and adolescent patterns contradict each other. Towards being the tallest in the population in the comparative sample, Daasanach are not growing quickly in childhood, and this height deficit precedes an early and short adolescent growth spurt. It is then concluded that Daasanach males must have an absolutely higher magnitude of growth velocity during the growth spurt.

Numerous explanations for such a pattern have been previously explored above, though each is problematic when applied to the Daasanach data. One hypothesis is that increased juvenile risk will result in faster growth trajectories

(Migliano *et al.* 2007, Walker *et al.* 2006, Walker and Hamilton 2008). One globally prevalent risk is disease. Fratkin *et al.* (2004) and Nathan *et al.* (1996) show that sedentarization increases communicable diseases in the Rendille compared to their nomadic counterparts. However, if extrinsic juvenile mortality was a driving factor, the Daasanach should have a faster, not slower than expected childhood growth velocity (cm/yr) (Fig. 6). Though the faster childhood weight growth velocity could be indicative of this hypothesis (Fig. 12), there is no direct evidence for increased disease in Ileret compared to the nomadic Daasanach. Furthermore, the clinic in Ileret would help alleviate any increased health stress due to settlement.

On the other end of the spectrum, Hill (1993) and others (Bogin 1988, Walker and Hamilton 2008) propose that better nutritional conditions leads to an increase in body size and accelerated growth, where in hazardous nutritional conditions large body size is costly. This has been proposed to explain the overall greater body sizes in industrialized populations over those in developing countries (Bozzoli *et al.* 2007, Kramer and Greaves 2011). However, regional analyses of developing nations show that Africans generally deviate from the prediction that body size results from nutritional availability (Deaton 2007, de Onis *et al.* 1993). This being the case, Daasanach results cannot only be ascribed to be changes in the nutritional condition between the observed subjects and the unknown nomadic members of the population.

An intermediate hypothesis is the metabolic risk aversion model proposed by Jansen and van Schaik (1993), where decreased metabolic risk will increase the growth rate. This would assume that Daasanach have reduced disease morbidity and energy expenditure so that more energy can be allocated towards growth.

Additionally, this model does not necessarily assume an increase in nutritional quality, though such an effect is possible. It is likely that the sedentarization of Daasanach reduce disease morbidity and mortality through access to healthcare at the community clinic and decrease energy expenditure throughout life by abstaining from extended movements characteristic of nomadic members of the population. Furthermore, in the Rendille observed by Fratkin *et al.* (2004) and Nathan *et al.* (1996), there may not be a concrete increase in nutritional quality among settled pastoralists compared their nomadic counterparts.

Regardless of life history models, increased fat stores at the onset of the adolescent growth spurt will result in an earlier and faster maturation (Kuzawa and Bragg 2012). Considering the early and rapid height growth spurt, the Daasanach cross sectional weight data may explain the deviations observed in height trajectory. The Daasanach exhibit a delayed increase in weight relative to height with weight gain accelerating as height increases (Fig. 9). This is reiterated in the weight velocity curve where the growth spurt coincides with the height growth spurt, and is a dramatic change from the stable weight gain in childhood (Fig. 11). Additionally, the extension of the weight growth spurt through and beyond the height spurt (Tbl. 2) may be fueling the stature gains. Transversely, the opposite pattern is typically seen across populations where energy intake during growth periods is more allocated to increasing size than gaining weight through fat storage (Kuzawa and Bragg 2012). When Daasanach weight is considered by age there is a steady increase during growth (Fig. 10), and the increase in weight accelerates as height increases (Fig. 9).

Even in childhood Daasanach are gaining mass at a faster rate than expected given their final adult weight (Fig. 12). But Daasanach are still lighter than expected given their adult height when compared to other traditional societies (Fig. 14).

CONCLUSIONS

The derived growth velocity curve for the Daasanach follows the generalized pattern of human growth outlined by Bogin (1988, 1997) and Leigh (2001). However, the relative timings, durations, and magnitudes do not conform to those seen in ecologically similar populations reported in Walker *et al.* (2006). Therefore, we must reject the null hypothesis that the Daasanach will conform to a growth trajectory similar to ecologically similar traditional populations.

Viewing the results of the Daasanach male subadult growth velocity curve in a comparative lens shows the Daasanach exhibit an uncharacteristic height growth trajectory for the population’s adult stature. As the tallest population in the comparative sample, the Daasanach grow slowly during childhood (Fig. 6). Furthermore the Daasanach reach critical velocities (take off, peak, and return to take off) that describe the adolescent growth spurt at earlier ages (Fig. 7). Interestingly, to achieve such a large adult stature with slow childhood growth and an early adolescent growth spurt, the duration of this growth spurt is also relatively short (Fig. 8). Though the critical velocities are not known for the comparative populations, these results suggest that the Daasanach have a much more intense height growth spurt. Higher growth velocities during the adolescent growth spurt could explain how the

Daasanach can surpass most other populations in stature though they obtain less of their growth during childhood and experience short growth spurt duration.

The causes of this deviation from the expected pattern are not yet clear. Kuzawa and Bragg show some relationships between nutrition at different times during growth, and growth trajectory (2012). The Daasanach may be following the prediction that an early and intense growth spurt occurring under conditions of increased fat storage during childhood. This is consistent with the observation that while during childhood height growth rate is relatively slow (Fig. 6) while mass growth rate is relatively fast (Fig. 12). The stature growth is uncharacteristically early and fast relative to final height following an uncharacteristically high weight growth velocity in childhood relative to final adult weight. Furthermore, Leigh (2001) observes that variation in growth, specifically the adolescent growth spurt can act independently of a population’s body size and is subject to external selective pressures.

While subadult nutritional conditions may influence growth trajectories, the relationship is not directly found with the population’s ecology. Further work into the nutritional availability throughout developmental stages and across traditional populations is needed to better understand the observed variations in human growth and development.

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