Assessment of Inter and Intra-Population Variation in Stature and Body Proportions: A Comparative Study Between Living and Bioarchaeological Populations

DISSERTATION

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By

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ABSTRACT

Variation in stature and body proportions across the globe is generally explained in terms of climatic adaptations and as resulting from overall life conditions experienced during growth. Based on growth heterochrony, different life histories should result in different adult stature and body proportions. It is nonetheless unclear to which extent such changes in growth outcomes take place at the intrapopulation level. This study explores variation in stature and body proportions at the inter and intrapopulation level by addressing four research questions in both living and archaeological populations. Specifically, this research investigates the existence of differences in growth outcomes within populations in relation to sex, severe growth retardation, and differential access to resources. Additionally, this study examines whether stature and body proportions allow us to differentiate between populations exposed to different environmental conditions. Variation in stature and segmental body proportions is examined in three living populations from South America and in two European medieval populations for a total of 2389 individuals. Anthropometric (height, sitting height, and leg length) and osteometric (skull height, long bones lengths, skeletal trunk height, and skeletal height) data are analyzed and interpreted in the context of biocultural information available for each population included in the study. The statistical methods employed to address the
research questions include the “Quick-Test” (Tsutakawa and Hewett, 1977), Monte Carlo analyses, principal component analyses, non-parametric analyses of variance and correlation analyses. Statistical significance is defined as \( p > 0.05 \). The results of this study reveal that: 1) Significant sex-related differences in body proportions are found in the majority of the populations examined, but the direction of such differences is extremely variable and appears to be due different sensitivity to environmental stress, cultural practices favoring one sex over the other, and the different selective pressures associated with female reproduction; 2) Severe growth retardation is associated with a reduction in relative leg length only in urban settings, while growth retardation appears to be accompanied by isometric changes in body size among rural Amazonians; 3) There is evidence in support of a positive relationship between differential access to resources and growth outcomes in both living and archaeological populations. However, no differences are found in one population, likely because of the inadequacy of the variable used as a proxy for resource access; 4) Significant interpopulation differences in stature and proportions are found among both living and archaeological populations, suggesting that growth outcomes reflect the unique set of life conditions experienced by each population, even within the same broad ecogeographic zone. Thanks to an innovative approach that combines the examination of biological variation in living and bioarchaeological populations in tandem, this study demonstrates that the pattern of variation in stature and body proportions across time and space is more complex than previously posited. Future research should further explore how growth outcomes are affected by specific biocultural factors such as differential offspring treatment, individual female reproductive histories, and different stressors associated with specific settlement types.
Dedicated to my parents, Margherita and Tomaso, who always fostered my curiosity and love for all life on this planet.
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Figure C.15. Scatter plot of log sitting height over log height for stunted (solid circles) and non-stunted (open circles) non-isolated female (F) Makushi. The line has a slope of 1.0 and passes through the grand mean (5.001, 4.297) of the samples. Stunted and non-stunted individuals exhibit similar distributions (p = 0.06).

Figure C.16. Scatter plot of log sitting height over log height for stunted (solid squares) and non-stunted (open squares) non-isolated male (M) Makushi. The line has a slope of 1.0 and passes through the grand mean (5.075, 4.435) of the samples. Stunted and non-stunted individuals exhibit similar distributions, suggesting that stunting among males is a rather isometric process (p = 0.084).

Figure C.17. Scatter plot of log sitting height over log height for stunted (solid circles) and non-stunted (open circles) for women from Cali, all SES groups combined. The line has a slope of 1.0 and passes through the grand mean (5.014, 4.438) of the samples. Stunted individuals tend to fall above the line, while non-stunted ones are more abundant below the line, indicating they have relatively longer legs (p = 0.0001).

Figure C.18. Scatter plot of log sitting height over log height for stunted (solid circles) and non-stunted (open circles) High SES women from Cali. The line has a slope of 1.0 and passes through the grand mean (5.025, 4.446) of the samples. Stunted individuals tend to fall above the line, while non-stunted ones are more abundant below the line, indicating they have relatively longer legs (p = 0.0004).

Figure C.19. Scatter plot of log sitting height over log height for stunted (solid circles) and non-stunted (open circles) Mid-Low SES women from Cali. The line has a slope of 1.0 and passes through the grand mean (5.010, 4.433) of the samples. Stunted individuals tend to fall above the line, while non-stunted ones are more abundant below the line, indicating they have relatively longer legs (p = 0.0001).

Figure C.20. Scatter plot of log sitting height over log height for stunted (solid circles) and non-stunted (open circles) Low SES women from Cali. The line has a slope of 1.0 and passes through the grand mean (5.010, 4.438) of the samples. Stunted individuals tend to fall above the line, while non-stunted ones are more abundant below the line, indicating they have relatively longer legs (p = 0.0001).
Figure C.21. Scatter plot of log sitting height over log height for non-isolated (solid circles) and isolated (open circles) female (F) Makushi. The line has a slope of 1.0 and passes through the grand mean (5.005, 4.307) of the samples. Isolated individuals tend to cluster above the line, while non-isolated individuals are equally distributed above and below the line (p = 0.014).

Figure C.22. Scatter plot of log sitting height over log height for non-isolated (solid squares) and isolated (open squares) male (M) Makushi. The line has a slope of 1.0 and passes through the grand mean (5.076, 4.437) of the samples. Isolated and non-isolated show similar distributions (p = 0.857).

Figure C.23. Scatter plot of log sitting height over log height for high SES (circles) and mid-low SES (diamonds) women from Cali. The line has a slope of 1.0 and passes through the grand mean (4.979, 4.412) of the samples. High SES women are more abundant above the line and mid-low SES women below it, indicating they have different body proportions (p = 0.0001).

Figure C.24. Scatter plot of log sitting height over log height for high SES (circles) and low SES (triangles) women from Cali. The line has a slope of 1.0 and passes through the grand mean (4.980, 4.419) of the samples. High SES women are more abundant above the line and low SES women below it, indicating they have different body proportions (p = 0.0001).

Figure C.25. Scatter plot of log sitting height over log height for mid-low SES (diamonds) and low SES (triangles) women from Cali. The line has a slope of 1.0 and passes through the grand mean (4.977, 4.414) of the samples. Mid-low SES women cluster above the line and mid-low status women below it, indicating they have different body proportions (p = 0.022).

Figure C.26. Scatter plot of log sitting height over log height for Makushi and Ribeirinhos females. The line has a slope of 1.0 and passes through the grand mean (4.996, 4.331) of the samples. The Ribeirinhos cluster above the line, indicating they have relatively shorter legs than the Makushi (p = 0.0001).

Figure C.27. Scatter plot of log sitting height over log height for Ribeirinhos and Cali females. The line has a slope of 1.0 and passes through the grand mean (5.013, 4.406) of the samples. The Ribeirinhos cluster below the line, indicating they have relatively longer legs than the individuals from Cali (p = 0.0001).

Figure C.28. Scatter plot of log sitting height over log height for Makushi and Cali females. The line has a slope of 1.0 and passes through the grand mean (5.023, 4.380) of the samples. The Makushi cluster below the line, indicating they have relatively longer legs than the individuals from Cali (p = 0.0001).

Figure C.29. Scatter plot of log sitting height over log height for Makushi and Ribeirinhos males. The line has a slope of 1.0 and passes through the grand mean (5.076, 4.428) of the samples. The Ribeirinhos tend to cluster below the line, indicating they have relatively longer legs than the Makushi (p = 0.001).
Figure C.30. Scatter plot of log sitting height over log height for morphotype 1 Makushi females (F - circles) and males (M - squares). The line has a slope of 1.0 and passes through the grand mean (5.038, 4.402) of the samples. The sexes cluster equally above and below the line, indicating that they exhibit similar body proportions \( (p = 0.06) \).

Figure C.31. Scatter plot of log sitting height over log height for morphotype 1 stunted (solid circles) and non-stunted (open circles) Makushi females. The line has a slope of 1.0 and passes through the grand mean (4.996, 4.3636) of the samples. Stunted individuals tend to cluster above the line while non-stunted individuals are more numerous below the line \( (p = 0.02) \).

Figure C.32. Scatter plot of log sitting height over log height for morphotype 1 stunted (solid circles) and non-stunted (open circles) isolated Makushi females. The line has a slope of 1.0 and passes through the grand mean (4.994, 4.364) of the samples. Stunted and non-stunted individuals exhibit similar distributions above and below the line \( (p = 0.416) \).

Figure C.33. Scatter plot of log sitting height over log height for morphotype 1 stunted (solid circles) and non-stunted (open circles) non-isolated Makushi females. The line has a slope of 1.0 and passes through the grand mean (4.998, 4.364) of the samples. Stunted individuals tend to cluster above the line and non-stunted individuals below it \( (p = 0.03) \).

Figure C.34. Scatter plot of log sitting height over log height for morphotype 2 stunted (solid circles) and non-stunted (open circles) Makushi females. The line has a slope of 1.0 and passes through the grand mean (5.001, 4.229) of the samples. Stunted individuals tend to cluster above the line while non-stunted individuals are more numerous below the line \( (p = 0.0001) \).

Figure C.35. Scatter plot of log sitting height over log height for morphotype 2 stunted (solid circles) and non-stunted (open circles) isolated Makushi females. The line has a slope of 1.0 and passes through the grand mean (4.997, 4.233) of the samples. Stunted individuals tend to cluster above the line while non-stunted individuals are more numerous below it \( (p = 0.0001) \).

Figure C.36. Scatter plot of log sitting height over log height for morphotype 2 stunted (solid circles) and non-stunted (open circles) non-isolated Makushi females. The line has a slope of 1.0 and passes through the grand mean (5.003, 4.227) of the samples. Stunted individuals tend to cluster above the line and non-stunted individuals below it \( (p = 0.005) \).

Figure C.37. Scatter plot of log sitting height over log height for isolated (solid circles) and non-isolated (open circles) morphotype 1 female Makushi. The line has a slope of 1.0 and passes through the grand mean (5.001, 4.368) of the samples. Isolated and non-isolated individuals show similar distributions \( (p = 0.344) \).

Figure C.38. Scatter plot of log sitting height over log height for isolated (solid circles) and non-isolated (open circles) morphotype 2 female Makushi. The line has a slope
of 1.0 and passes through the grand mean (5.010, 4.232) of the samples. Isolated and non-isolated individuals show similar distributions (p = 0.530).

Figure C.39. Scatter plot of log sitting height over log height for Ribeurinhos females (diamonds) and morphotype 2 female Makushi (triangles). The line has a slope of 1.0 and passes through the grand mean (4.994, 4.362) of the samples. Isolated and non-isolated individuals show similar distributions (p = 0.801).
CHAPTER 1: INTRODUCTION

1.1 Stature and Body Proportions in Anthropology

Biological variation in stature and body proportions has long been observed among human populations inhabiting different regions of the world. For a long time, it was a common thought that the differences in stature and body proportions between populations had mainly racial origins (Thomson, 1884; Elderton, 1912; Davenport, 1917). However, with an improved understanding of the process of evolution and particularly of natural selective pressures on human populations, such differences were subsequently considered to result from adaptation to different environments, similarly to other physiognomic traits (Walter, 1971). Variation in stature and body proportions exists even within closely related groups, likely to share the same genetic potential (Bogin et al., 2002). If that is the case, then, why does stature vary?

Extensive evidence suggests that environmental influences interact with genetic factors in determining the adult phenotype for stature. While genes set the maximum genetic potential for stature that an individual may achieve, the environment plays a major role in allowing – or rather restricting – the actual final growth outcome. Indeed, long-standing observations of human biology in both living and past populations indicate that variation in body size over time and space is generally associated with a population’s
overall environmental quality and life conditions (Boas, 1912; Lasker, 1952; Meredith, 1976; Garn, 1987; Formicola and Gianvecchini, 1999; Friedman et al., 2000; Loesch et al., 2000; Steckel, 2004; Gerhards, 2005; Maat, 2005; Gustafsson et al., 2007; Gianvecchini and Moggi-Cecchi, 2008). Specifically, human stature varies in relation to a variety of environmental factors, including climatic conditions, diet, socio-economic status, and disease (Rona and Chinn, 1991; Waterlow and Schürch, 1993; Bogin, 1999; Wadsworth et al., 2002; Bogin et al., 2002; Mascie-Taylor and Lasker, 2005). Improvements in sanitation, medical care, and access to resources in industrialized countries over the past century have provided evidence for phenotypic plasticity in height (Eveleth and Tanner, 1990; Bogin, 1999). In particular, individuals benefitting from better nutrition and overall living conditions achieve taller adult stature.

It has been observed that when stature changes in response to improved environmental conditions, body proportions change as well. Specifically, stature increase is accompanied by allometric changes in body proportions due to a greater elongation of the lower limb (Tanner et al., 1982; Bogin et al., 2002), especially in its distal segment (Holliday, 1997; Jantz and Jantz, 1999; Sylvester et al., 2008; Auerbach and Sylvester, 2011). The reasons for such a change in body shape is that human growth is a heterochronic process, meaning that different parts of the body grow at different rates during different phases of development (Huxley, 1932; Humphrey, 1998; Bass et al., 1999; Bradney et al., 2000; Nyati et al., 2006). Research on human growth has shown that during childhood the lower limb – and its distal segment in particular – grows faster than the trunk, reaching a greater percentage of its adult value prior to adolescence. On the contrary, trunk length grows more slowly, only to accelerate during adolescence to
reach adult proportions (Humphrey, 1998; Bass et al., 1999; Bradney et al., 2000). This difference in the timing and rates of skeletal growth implies that growth disruptions during different stages of the life course can affect body proportions (Karlberg, 1989). Given that childhood is characterized by fast long bone growth promoted by somatotropin (Nilsson et al., 1994), perturbations during this growth period typically have the greatest impact on long-term development and are expressed in shorter lower limb length (Karlberg, 1989; Allen, 1994). Conversely, improved conditions can promote better lower limb growth (Bogin et al., 2002).

Even though it is well accepted that differences in overall life conditions contribute to variation in height and proportions, the impact of specific factors on growth is not clearly understood. Indeed, most studies examining stature and body proportions have addressed biological variation by comparing different contemporaneous populations exposed to different environmental conditions (Stinson, 1990; Holliday, 1997; Katzmarzyk and Leonard, 1998; Weinstein, 2005) or by examining how changes in life conditions over time in the same population affect changes in growth (Zakrzewski, 2003; Temple et al., 2008). This research has shown that stature responds dynamically to overall environmental quality in relation to major population events, such as subsistence shifts, population contact, and climate change. Additionally, body proportions change predictably in relation to climatic conditions, as postulated by Bergmann’s (1847) and Allen’s (1877) ecogeographic rules. These studies have the merit of documenting skeletal growth variation between populations across space and time, but the scale of the observations is often too broad to allow an understanding of the dynamic interactions between growth and environmental selective pressures at the individual and
intrapopulation level. As a consequence, while biological variation in stature and proportions across time and space is relatively well understood, less is known of the degree and causes of variation within human populations (i.e., intrapopulation variation). Auxological and clinical growth studies have the potential to shed some light on such aspects of variation. However, their primary goal is that of identifying universal growth patterns and their pathological disruptions rather than focusing on individual differences. Additionally, these models are seldom tested in an anthropological perspective and consequently not readily applicable to geographically or temporally distant populations. Nevertheless, variation within populations does occur.

Even in genetically relatively homogeneous groups such as laboratory animals, intrapopulation variation in body size and shape arises from different occurrences, duration and timing of growth insults (Riesenfeld, 1973; Hunter and Clegg, 1973; Warren and Bedi, 1985). This evidence suggests that the analysis of stature and body proportions at the intrapopulation level may provide valuable information on specific factors and mechanisms influencing the expression of variation in growth outcomes. Furthermore, intrapopulation analyses may foster more information on individual life histories and provide more accurate and detailed information at the aggregate level. This is particularly relevant for studies of life conditions in the past, which commonly rely on stature as an indicator of environmental quality experienced by individuals during growth. Stature is undoubtedly a useful inferential tool that, combined with other lines of evidence, allows bioarchaeologists to reconstruct accounts of life in the past. Nonetheless, the relationship between early life conditions and growth in the past is often equivocal (Larsen, 1997; Klaus and Tam, 2009). This is due to the fact that stature, as the final outcome of growth,
does not necessarily capture or reflect all life history events that may interfere with
growth. In fact, human growth is a highly plastic process and, thanks to the delay of
maturation or acceleration of growth rates, individuals previously exposed to
environmental perturbations may recover from early growth retardation (Martorell et al,
1994; Cameron et al, 2005). This process, known as catch-up growth, clearly has the
potential to confound the understanding and interpretation of adult stature in relation to
life conditions. An instructive example is provided by the work of Steckel (1986, 1987),
who employed nutritional information and historical records to explain the anomalous
growth pattern of American slaves. These individuals were characterized by extremely
short stature during childhood and almost normal stature during adulthood (Steckel,
1987). Simply based on adult stature, it would be inferred that these individuals
experienced positive nutritional status throughout development, even though that was
clearly not the case (Steckel, 1986). As a consequence, adult stature can only be
informative of overall life conditions of the survivor group at the population level, but
provides no detailed insights on actual life histories. In contrast, timing and duration of
environmental stress episodes appear to have a greater, irreversible impact on body
proportions, which could therefore complement stature data to provide improved
information on individual life histories and life conditions in the past. To date, only a
small number of studies has focused on body proportions as an indicator of
environmental stress (Boldsen, 1998; Bogin et al., 2002; Bogin and Rios, 2003; Schweich
and Knüsel, 2003). Consequently, several aspects of the variation of body proportions in
relation to environmental factors within human populations remain largely unexplored.
One of the reasons for this is that the study of variation in body proportions within a population poses specific problems. First, since timing and duration of stress episodes are crucial in altering body proportions, any attempt to pinpoint the effects of specific stressors on growth would require continuous observations over an extended period of time. The scale of the observations (the entire duration of growth from birth to adulthood) clearly makes such an investigation almost impossible in practical terms. Since continuous, detailed observations of a large number of individuals are not practicable, other approaches to the problem may be sought. One such approach consists in the examination of adult body proportions (i.e., terminal growth outcomes) in relation to a variety of biocultural factors. Biocultural approaches in human biology recognize that culture is an intrinsic aspect of human nature and plays an integral role in shaping the environment in which growth and development take place (Dufour, 2006). Under this approach, biological variation, including variation in stature and body proportions, is interpreted as a response to the complex biosocial environment. Consequently, recording and measuring both biological and cultural variables is essential for improving our understanding of the causes of biological variation.

Whether they are applied to living or past populations, biocultural approaches face specific complications, primarily related to the definition and collection of relevant biocultural information. In particular, the dynamic complexity of the biological, ecological, social and cultural milieu humans are immersed in from birth makes it difficult to collect all relevant information. Specific difficulties are related to the fact that several aspects of variation may be induced by subtle, not easily recognizable social and cultural differences within a population, which would be inevitably omitted in favor of
more apparent causes for inequality. While thorough, structured research protocols may allow circumventing these obstacles in studies dealing with living populations, analogous investigations on past people are inevitably more challenging. Clearly, the reconstruction of the biocultural milieu of past populations must involve a vast number of different lines of evidence. In this sense, bioarchaeology, as the study of past populations in their entirety cannot be but a multidisciplinary endeavor (Larsen, 2006). Information from historical records and archaeological, taphonomical, geospatial, paleoecological, archaeozoological, archeobotanical, paleodemographical, paleonutritional, and paleopathological analyses must be examined concurrently to provide insights on the complex multidimensional world past people lived in. Even when all such lines of evidence are considered simultaneously and an adequate understanding of life in the past is drawn, there remain biological, social and cultural nuances that are simply beyond our reach. No matter how detailed our analyses, even our best outlook on the past is always incomplete. A possible way to overcome, at least in part, such limitations is to adopt an integrated approach (Goodman et al., 1988). Specifically, our understanding of present and past variation in stature and body proportions may be improved by examining living and bioarchaeological populations in tandem.

This dissertation is an attempt to integrate different lines of evidence and to improve our understanding of variation in stature and body proportions at the inter and intrapopulation level. To this end, I examine variation in growth outcomes directly in both living and archaeological populations in relation to known biocultural factors. Specifically, I address research questions drawn from a vast body of knowledge dealing
with the physiological processes underlying longitudinal growth and the genetic and environmental factors known to affect it.

1.2 Research Questions

In this study, I address four research questions, three regarding the causes and processes leading to intrapopulation variation in stature and body proportions, and one concerning the degree and possible causes of variation at the interpopulation level. The specific research questions addressed in this study are:

1) Do males and females within the same population exhibit different body proportions?
2) Is growth retardation associated with changes in body proportions?
3) Is differential access to resources associated with changes in stature and body proportions?
4) Do stature and body proportions allow us to differentiate between populations exposed to different environmental conditions?

1.2.1 Do Males and Females Within the Same Population Exhibit Different Body Proportions?

A review of the literature on human growth reveals that while males and females are expected to show differences in body proportions, the direction of such difference is unclear. Specifically, there are two distinct (but somewhat interrelated) lines of evidence that suggest the existence of sex-related differences in body proportions.
First, similarly to many other species (Badyaev, 2002), human males and females follow different growth trajectories. On average, females tend to enter adolescence approximately two years earlier and to have more modest pubertal growth spurts than their male peers (Gasser et al., 2000). Given the fact that leg length achieves most of its growth during pre-adolescent growth, benefitting from a longer growth period males typically are expected to have relatively longer legs than females (Leonard and Katzmarzyk, 2010).

Second, evidence indicates that males may be more sensitive to environmental perturbations (Stini, 1969; Stinson, 1985). If this is true, then all other factors being equal, males are expected to show a greater negative response to stress than females. The lower limb, especially its distal segment, is more affected by negative environmental conditions than the trunk (Bogin et al., 2002). Therefore, according to the hypothesis of greater male sensitivity, under environmental stress males are expected to have relatively shorter lower limbs – and shorter distal segments – than females.

In this study, the existence of sex differences in body proportions is tested in both living and archaeological populations. In living populations the analysis concerns the relationship between total leg length and stature; in archaeological populations the analysis includes also the relationship between proximal and distal segments of the lower limb. In order to evaluate the effects of the two competing alternate hypotheses, results are interpreted in light of available biocultural information.

1.2.2 Is Growth Retardation Associated with Changes in Body Proportions?
Assuming that the lower limb is the segment most affected by environmental perturbations, it is expected that growth retardation will result primarily in relatively shorter legs than trunks (Bogin et al., 2002). This is expected to occur similarly in the sexes. This dissertation addresses this research question in sex-specific subsamples of living populations by exploring differences in body proportions between individuals exhibiting different growth outcomes. Growth outcomes (stunted vs. non-stunted) are defined in relation to international standards.

1.2.3 Is Differential Access to Resources Associated with Changes in Stature and Body Proportions?

In most human societies, differential access to resources is often based on a multitude of different biocultural factors, including gender, age, biological ancestry, geographic proximity, wealth, hierarchy, and religion. Socio-economic status (SES) is often used to indicate groups benefitting from differential access to resources, including food, health care and education, exposure to disease, and differential workload (Bogin, 1999). The existence of clear SES groups in a variety of human populations has allowed human biologists, bioarchaeologists, economists, and historians to study biological variation in stature within closely related groups in relation to different environmental conditions over time (Bogin and McVean, 1983; Dufour et al., 1994; Johnston et al., 1985; Steckel, 1986, 1992; Larsen, 1997; Schutkowski, 2000; Bogin et al., 2002; Wadsworth et al., 2002; Godoy et al., 2005; Bassino, 2006; Mays et al., 2009). This literature shows that by altering the eco-bio-cultural milieu in which individuals grow, social inequality translates into biological inequality. Consequently, higher status
individuals are expected to exhibit greater stature and longer limbs than their lower status counterparts (Bogin, 1999).

In this study, this research question is investigated in two living populations and one archaeological sample, where SES and geographic proximity (isolation) were employed to define groups experiencing differential access to resources. Multiple lines of evidence are employed to interpret the results of the analyses.

1.2.4 Do Stature and Body Proportions Allow Us to Differentiate Between Populations Exposed to Different Environmental Conditions?

The most common approach to interpopulation variation in stature and body proportion is one that considers changes in body size and shape as due primarily to climatic adaptation (Ruff, 1994; Holliday, 1997). However, evidence of developmental plasticity and rapid morphological change under improved conditions suggests that a variety of other factors contribute to molding differences in body proportions across different populations (Bogin et al., 2002; Bogin and Rios, 2003). Even though interindividual variation indisputably exists, all members of a population share a vast majority of environmental and biocultural conditions. This implies that the unique combination of ecological, biological, social and cultural factors that make the overall life conditions to which a population is exposed should result in specific growth outcomes. At an aggregate level, therefore, inter-population differences in stature and body proportions are expected to be found between human groups growing under different environmental conditions – even in similar climatic zones or historical periods. In this study, this
research question is addressed by examining stature and body proportions’ variation in living and archaeological populations.

1.3 Organization of the Dissertation

This dissertation is divided in 9 chapters, including the present Introduction, which provides background information on the study of stature and body proportions in anthropology, and presents the research questions addressed by the present study.

Chapter 2 reviews the process of human growth and development, with particular attention to the different phases of growth and their importance for longitudinal bone growth. An important aspect presented in this chapter is the heterochrony of growth in different parts of the body, which represents the foundation for the development of adult stature and proportions. Additionally, in this chapter the endocrine controls of longitudinal bone growth are briefly reviewed, to set the bases for an understanding of how environmental stress can interfere with longitudinal growth.

Chapter 3 focuses on the developmental origins of variation in stature and body proportions. Following an introduction of important concepts such as developmental plasticity, norm of reaction and canalization, the chapter reviews the relative contributions of genetic and environmental factors to the expression of adult stature and body proportions. Lastly, I review how timing and duration of growth insults, as well as the occurrence of catch-up growth, can alter an individual’s adult growth outcomes.
Chapter 4 discusses specific aspects of the study of growth outcomes in the past, with an emphasis on the impact that the “osteological paradox” (Wood et al., 1992) has on the interpretation of the skeletal evidence. Consequently, different approaches to the issues raised by the osteological paradox in regard to stature are reviewed. Lastly, following a review of the methodological aspects of stature estimation in past populations, I review the existing literature concerned with the study of body proportions in skeletal assemblages.

Chapter 5 presents the purpose of the study and explains the rationale for undertaking such a project. Additionally, aspects of the research design, such as the adoption of biocultural approaches, sample selection criteria and methodological considerations regarding the comparison of living and archaeological populations are discussed.

Chapter 6 presents the materials and methods included in this study. This project was carried out on three different living populations from underprivileged settings in South America (Brazilian Ribeirinhos, Guyanese Makushi, and Colombian citizens of the city of Cali) and two medieval bioarchaeological populations (Trino Vercellese, Italy and Giecz, Poland). Contextual information for each sample as well as the specific methods employed to collect and analyze data are presented.

Chapter 7 presents the results of the analyses, which are organized by research question. First, the results of sex-related differences in growth outcomes are presented for Ribeirinhos, Makushi, Trino Vercellese and Giecz. Second, the results of the impact of growth retardation on body proportions are reviewed in all three living populations. Third, the results of differential access to resources on growth outcomes are presented for
Makushi, Cali and Trino Vercellese. Lastly, interpopulation variation in growth outcomes is assessed between living populations and archaeological collections.

Chapter 8 consists of the discussion of the results in light of the research questions that are tested in the study. Each research question is addressed individually for each sample analyzed and the results are reviewed in light of contextual information. Additional investigations and analyses carried out to discriminate between alternate explanations of the patterns observed are also presented when appropriate. Lastly, the results of the analyses of living and bioarchaeological populations are examined together with the goal of drawing general conclusions on the patterns of variation in human stature and body proportions.

Chapter 9 reports the conclusions of the study, summarizing the findings of the study and provides conclusive remarks.

The conclusions are followed by the list of the references cited and three appendices: A. Descriptive Statistics; B. Age Distribution Tests; C. “Quick-Test” Scatter Plots.
CHAPTER 2: AN OVERVIEW OF HUMAN GROWTH AND DEVELOPMENT

Variation in stature and body proportions results from complex interactions between genetic and environmental factors during growth. Longitudinal growth takes place over a span of several years, from conception to adulthood. Consequently, a multitude of different factors, possibly present at different times, singularly or concomitantly, may contribute to molding the growing body and influence an individual’s final growth outcome. Even though adult stature and body proportions are fixed, static variables, they are the end result of a dynamic process during which the growing organism adjusts constantly to its environmental milieu. In fact, the interest of stature and body proportions lies specifically in the fact that they allow inferences on the developmental history of individuals and human groups alike. In a way, these anthropometric variables are like a spyglass by which we explore a developmental past that is not otherwise readily accessible. They allow us to reconstruct living conditions during growth and related responses of the human body. However, the images of this developmental past that we may reconstruct thanks to this tool are not clear-cut or immutable. Rather, they are ephemeral glimpses of a process whose complexity is such that it still requires extensive interpretation. Consequently, any interpretation of the
pattern of variation in stature and body proportions within and between populations requires an understanding of the process of longitudinal growth and its variation.

In this chapter, I provide an overview of longitudinal growth, which may serve as the conceptual foundation for successive discussions regarding the origins of variation in stature and body proportions and its interpretation. First, I briefly review longitudinal bone growth at the tissue level, highlighting the endocrine controls of this finely tuned process. Subsequently, I summarize the major chronological phases of human growth, the knowledge of which is essential to understand how individual variation may arise in response to alterations of a genetically set growth pattern. Lastly, I review auxological models of human growth and their applicability to understanding individual and population variation in longitudinal growth outcomes.

2.1 Longitudinal Bone Growth

Skeletal growth is generally considered the result of two distinct processes: direct, intramembranous ossification and the formation of a cartilaginous template of bones, later replaced by endochondral ossification (ENOS). The two processes occur simultaneously in most bones, where they contribute to transversal and longitudinal growth respectively (Scheuer and Black, 2004).

Intramembranous ossification consists of the direct ossification of mesenchymal cell aggregates thanks to the formation and consequent release of hydroxyapatite crystals in extracellular, matrix vesicles (Fawcett, 1994). This process, which is evolutionary extremely well conserved, is typical of skeletal structures mainly composed of cortical bone and is the exclusive process leading to the formation of most cranial bones (Scheuer
and Black, 2004). Upon their initial deposition in the matrix, the hydroxyapatite crystals expand by epitactic nucleation (Neuman and Neuman, 1953) and form loosely organized (woven) bone. Concurrently, vascularization at the site increases dramatically, promoting further ossification around the newly formed capillary network (Hansen, 1993). As mineralization increases, more and more mesenchymal cells are recruited and differentiate in osteoblasts that promote further deposition of bone. As bone deposition progresses with further compaction of bone trabeculae, osteoblasts become trapped in the matrix and become functional osteocytes responsible for the homoestatic maintenance of bone tissue. When the growth rates slow down, primary bone is replaced by secondary bone and the mesenchyme on the surface of the bone condenses to form the periosteum, a fibrovascular structure that sheaths the entire bone and maintains osteogenic potential essential for bone maintenance and repair throughout life.

In contrast with intramembranous ossification, ENOS appeared later in time, possibly with the evolution of more complex post-cranial skeletons (Smith and Hall, 1990) and in response to specific mechanical stimuli (Carter and Beaupré, 2001). ENOS takes place in some portions of the basicranium and is primarily responsible for longitudinal growth in the postcranium in both axial and appendicular skeleton. In ENOS, embryonal mesenchimal cells condensate to form the anlage, a cartilaginous model of the bone (Figure 2.1). The anlage grows by appositional and interstitial growth, through the proliferation of chondroblasts and the production of extracellular matrix (rich in collagen II and aggrecan). The primordial diaphysis is surrounded by the perichondrium, a connective tissue sheath whose inner layer cells possess osteoprogenitor potential. These cells differentiate into osteoblasts and begin to deposit a periosteal collar of bone around
the diaphysis (at this point the perichondrium effectively becomes periosteum).

Following the deposition of the bone collar, cartilage calcification begins in the lower zone of the growth plate, that is, the cartilage layer separating diaphysis and epiphysis, leading to longitudinal bone growth.

Figure 2.1. Schematic representation of longitudinal bone growth by means of ENOS. Light-blue = cartilage; black = bone; purple = calcified cartilage; red = blood vessels. Adapted from Fawcett (1994).

In the growth plate, it is possible to recognize different cell types, reflecting different stages of cell maturation: 1) reserve precursor cells, 2) proliferative chondrocytes, and 3) hypertrophic chondrocytes. The precursor cells are found in the germinal zone of the growth plate, are small and quiescent and do not show a rigorous spatial organization. This is the only layer to receive direct vascular supply from the epiphyseal vessels. Precursor cells differentiate into proliferative chondroblasts, whose division is responsible for the longitudinal growth of the anlage. Cells in the proliferative
zone mature, increase in size and undergo mitotic division, assuming a characteristic columnar disposition, which promotes longitudinal growth (Figure 2.2).

Contextually, blood vessels and osteoblasts penetrate into the perichondrium. It has been noted that the majority of mitotic divisions occur in a transverse plane, hence
not directly contributing to longitudinal expansion of the growth plate. In fact, post-
mitotic cells undergo a reorientation as they migrate toward the lower part of the growth
plate (Serafini-Fracassini and Smith, 1974). These cells become hypertrophic, reflecting
the increased synthetic requirements associated with the production of matrix vesicles,
filled with hydroxyapatite and Vitamin D-sensitive alkaline phosphatase (Fawcett, 1994).
The release of these vesicles into the extracellular matrix and the hypertrophic
chondrocytes’ apoptosis induce the formation of calcified spicules in the matrix.

Osteoblasts start secreting osteoid (unmineralized bone matrix) on the calcified
cartilaginous spicules, leading to the formation of woven bone. This complex, known as
primary spongiosa, is later remodeled by osteoclastic and osteoblastic activity into
lamellar secondary spongiosa. Secondary spongiosa is in turn removed from the
diaphysis to form the marrow cavity, while it is preserved in the epiphyses as trabecular
bone. The histological appearance of the growth plates and the different phases of ENOS
are depicted in Figure 2.2.

2.2 Endocrine Controls of Longitudinal Growth

The hormonal regulation of the growth plate is complex, with both systemic
(endocrine) and local (paracrine) control mechanisms playing important roles. At the
systemic level, growth is complexly regulated by several hormones, including the growth
hormone (GH), insulin and sex hormones (testosterone and estrogens). The complexity of
such regulation is furthermore increased by the fact that not all hormones are present at
the same time, as a result of developmentally determined growth patterns. At the
paracrine level, numerous cytokines and growth factors mediate the action of systemic
hormones and regulate growth based on local, positional information. Insuline-like growth factors (IGF-1 and IGF-2, collectively referred to IGFs), transforming growth factors α and β (TGFs) and bone morphogenetic proteins (BMPs) are among the most important signals involved in longitudinal growth regulation. These cytokines and growth factors are synthesized locally in endothelial cells of blood vessels, stromal cells of the marrow, osteoblasts and periosteal cells, as well as in a variety of other cells localized in the bone marrow (Price et al., 1994).

The primary hormone responsible for longitudinal growth – and the only one for which dose dependence has been shown – is the growth hormone (GH). GH is produced by the pituitary gland and induces pre-chondroblast proliferation in the germinative zone. GH makes these cells susceptible to the action of insulin-like growth factors. IGFs are produced primarily by the liver (even though they have been observed also in other tissues), and their transcription is promoted directly by GH. IGFs promote clonal expansion of GH-primed cells, therefore playing a major role in cell proliferation and longitudinal growth. The importance of the interaction between GH and IGFs in regulating body size in humans and non-humans has been recently reviewed by Bernstein (2010). Even though many aspects of the regulation of the GH/IGF axis are still not entirely understood, growing evidence points out that the GH/IGF axis has a crucial role in controlling growth because it is primarily responsible for mediating the effects of the environment on the growing organisms. Specifically, the GH/IGF axis influences context-appropriate growth and metabolic responses to environmental constraints. As a result, it is likely to play “an important role in mediating life history tradeoffs” (Bernstein, 2010:57).

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While GH and IGFs influence cell proliferation at the growth plate, cell maturation and degeneration in the hypertrophic zone is regulated by thyroid hormones (T3), which arrest the proliferation induced by IGFs (Robson et al., 2000). The importance of thyroid hormones in regulating chondroblast hypertrophy was shown experimentally in mice devoid of T3 hormone receptors, whose growth plate appeared grossly unorganized. Growth retardation resulting from T3 receptor deficiency in mice affected primarily long bone length, similarly to what has been observed in children affected by hypothyroidism (Pantsiotou et al., 1991). Similarly to T3, vitamin D also plays a role in cell maturation at the growth plate and is essential for matrix ossification. Thyroid hormones and Vitamin D are not controlled (at least directly) by GH, even though indirect effects have been suggested (Nilsson et al., 1994).

Sex steroids (testosterone and estrogens) produced by the gonads also contribute to regulating longitudinal growth. Because of an early activation of the hypothalamus-pituitary-gonadal (HPG) axis, sex hormones secreted in infancy contribute to growth by promoting GH secretion and set sex-based differences in growth patterns that influence later growth (see Section 2.3.2.3). An additional role of sex hormones in promoting fast longitudinal growth independently of GH’s action is clearly visible in the adolescent growth spurt, which takes place also in individuals missing functional GH receptors (Nilsson et al., 1994). The action of sex hormones is not limited to promoting growth, but extends to controlling the timing of sexual maturation and the concomitant cessation of growth. Sex hormones, especially estrogens, have been shown to have a primary role in promoting senescence of the growth plate, therefore slowing down cell proliferation and initiating growth plate closure (Weise et al., 2001). The fusion of the growth plate occurs
when the potential for cell proliferation decreases to almost zero. At that point, all remaining chondroblasts are quickly ossified and the epiphyseal line fuses, to all effects marking the conclusion of longitudinal bone growth.

2.3 Phases of Growth and Development

Human development is characterized by several phases that show different growth rates and environmental and genetic susceptibility: prenatal (intrauterine) growth, infancy, childhood, and adolescence. All these phases are characterized by distinct metabolic and endocrine processes, whose specificity accounts for different effects of growth perturbation at different times of development.

2.3.1 Prenatal Growth

Development begins at conception with the fecundation of the oocyte, the consequent formation of a zygote, and its implantation in the endometrial wall. Intrauterine development is governed by several hormones. Insulin, insulin-like growth factors (IGF1 & IGF2) and somatomammotropin (a placental hormone similar to GH) play a major role in controlling somatic growth in utero. Prenatal development exhibits the fastest growth rates in the entire life. The increase in body size shows a peak around 32 weeks after conception and around 36 gestational weeks growth velocity slows down, due to space constraints of the maternal womb.

Prenatal growth is conventionally subdivided in three trimesters involving different developmental processes. The first trimester is characterized by rapid cell division and differentiation (embryogenesis), which through organogenesis eventually
leads to the formation of a fetus. The second trimester comprises the beginning of dental development and the maximum growth in length (measured as crown-rump length), accounting for up to 70% of total prenatal longitudinal growth (Timirias, 1972). Ponderal (i.e., body weight) increases characterize the last trimester, during which the formation of several organs is completed. These observations suggest that genetic/environmental perturbations to intrauterine development will differently affect the individual, according to the developmental stage during which they occur. The first trimester, characterized by fast cell division, is particularly sensitive to both inherited diseases and environmental factors disrupting developmental processes, such as chemicals, malnutrition and infectious diseases (Bogin, 1999). Twin and relative studies have shown higher relevance of environmental over genetic factors on somatic prenatal growth. According to these studies, the environment accounts for up to 66% of observed variation in length at birth, whereas genetic variation influences intrauterine growth for 34%, with fetal genes explaining only 10% of total variance (Robson, 1978). Indeed, differences in birth size, due to unequal intrauterine constraints, are higher between monozygotic twins than dizygotic twins (Wilson, 1979). After birth the effect of genes increases gradually, thus reducing differences between monozygotic twins and increasing those between dizygotic twins (Table 2.1).
Table 2.1. Correlation coefficients for height between monozygotic (MZ) and dizygotic (DZ) twin pairs from birth to eight years. Adapted from Wilson, 1979.

<table>
<thead>
<tr>
<th>Age</th>
<th>Total N¹</th>
<th>MZ</th>
<th>DZ - Same Sex</th>
<th>DZ - Different Sex</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birth</td>
<td>629</td>
<td>0.62</td>
<td>0.79</td>
<td>0.67</td>
</tr>
<tr>
<td>3 months</td>
<td>764</td>
<td>0.78</td>
<td>0.72</td>
<td>0.65</td>
</tr>
<tr>
<td>6 months</td>
<td>819</td>
<td>0.80</td>
<td>0.67</td>
<td>0.62</td>
</tr>
<tr>
<td>12 months</td>
<td>827</td>
<td>0.86</td>
<td>0.66</td>
<td>0.58</td>
</tr>
<tr>
<td>24 months</td>
<td>687</td>
<td>0.89</td>
<td>0.54</td>
<td>0.61</td>
</tr>
<tr>
<td>3 years</td>
<td>699</td>
<td>0.93</td>
<td>0.56</td>
<td>0.60</td>
</tr>
<tr>
<td>5 years</td>
<td>606</td>
<td>0.94</td>
<td>0.51</td>
<td>0.68</td>
</tr>
<tr>
<td>8 years</td>
<td>444</td>
<td>0.94</td>
<td>0.49</td>
<td>0.65</td>
</tr>
</tbody>
</table>

¹N = sample size.

The perturbation of prenatal growth may have dire consequences on an individual’s entire growth, depending on its severity. Intra-uterine growth retardation is conventionally diagnosed on body size values at birth falling below the third percentile of the population. Intra-uterine growth retardation may have different manifestations and long-term consequences depending on the gestational time at which a perturbation occurs (Warshaw 1992; Miller 1992; Falkner et al., 1993). Depending on the extent to which head size is affected, intra-uterine growth retardation is considered proportionate (symmetric) or disproportionate (asymmetric). Proportionate intra-uterine growth retardation is a global reduction of infant size caused by developmental perturbation during the first gestational trimester, such as genetic diseases or environmental chemicals, including maternal smoking and drug and alcohol use. Proportionate intra-uterine growth retardation is associated with poor growth rates after birth and the inability to recover, which typically result in an individual’s failure to reach his/her genetic potential for stature (Heinrich, 1992). Disproportionate intra-uterine growth
retardation generally involves reduced body size while sparing head size: it is due to environmental perturbations suffered during the second and third gestational trimesters and can be recovered during postnatal growth. The most common cause of disproportionate intra-uterine growth retardation in the developing world is maternal malnutrition. Maternal nutritional stress during pregnancy affects fetal growth by reducing fetal size and promoting an acceleration of fetal organ development. Such changes are considered adaptive because they allow the individual to be viable earlier and survive under sub-optimal extra-uterine conditions (Heinrich, 1992). It is becoming increasingly evident that maternal nutrition and well-being during pregnancy plays a crucial role in regulating fetal growth, with important long-term health consequences not limited to impaired longitudinal growth. Several authors (Barker, 1995; Cameron and Demerath 2002) have identified critical periods in human development and demonstrated high correlations between pre-natal developmental insults, the acceleration of post-natal growth and the susceptibility to aging pathologies such as cardiovascular diseases, diabetes, obesity and osteoporosis.

2.3.2 Post-natal Growth

Following birth around the 40th gestational week, human growth can be subdivided into three distinct phases characterized by different growth velocities and underlying metabolic and endocrine processes. Post-natal longitudinal growth patterns are conventionally depicted graphically with velocity curves, in which yearly increments in stature are displayed over time (Molinari and Gasser, 2004). Figure 2.3 shows an ideal individual growth velocity curve. In such a curve it is possible to observe three distinct
components that express different velocity patterns. These components correspond to different phases of growth: infancy (I), childhood (C), and adolescence (A).

Figure 2.3. Ideal human growth velocity curve. Note the fast growth associated with Infancy (I), slow and prolonged childhood (C) and the growth spurt characterizing adolescence (A).

According to the Infancy-Childhood-Puberty (ICP) model developed by Karlberg (1989) all postnatal growth phases can be expressed as distinct functions, the superimposition of which generates the growth velocity curve (Figure 2.4). In this model, infancy is best approximated by an exponential function constantly decelerating; childhood can be modeled with a second-degree polynomial; and adolescence is best represented by a logistic function.
Figure 2.4. ICP model of human growth. Each growth phase can be modeled with a mathematical function, and is associated with specific endocrine mechanisms. After Karlberg (1994), modified.

The different growth velocity patterns that characterize each phase of post-natal growth are supported by different hormonal control mechanisms and involve different parts of the body to different extents. The phenomenon that allows different body segments to grow at different growth rates during different times of development is known as heterochrony. Heterochrony is fundamental in regulating growth and allows an organism to alter its body size and proportions over time in relation to the specific needs of each life phase. In human populations, growth heterochrony, coupled with a different duration of each growth phase, contributes to determining adult body proportions. In this
regard, several authors (Eveleth and Tanner 1990; Bogin 1991; Satake et al., 1993; Bogin 1999; Piontek et al., 2001; Nyati et al., 2006) observed clear population differences in
growth velocity curves, which can, at least in part, explain the differences in body size
and shape observed among different human populations.

In order to understand more specifically how biological variation in stature and
body proportions arises from differential growth disruptions, it is important to understand
the main aspects of each post-natal growth phase, as it would take place in total absence of growth perturbations.

2.3.2.1 Infancy

Infancy is the first post-natal growth phase, which typically encompasses the first
three years of life. As the continuation of intrauterine growth, it exhibits fast growth rates
and is supported by insulin and IGFs. Infancy is responsible for fast somatic growth,
which is associated with the progressive acquisition of complex motor and cognitive
abilities. In infancy the nervous system develops faster than any other apparatus. The
activation of the hypothalamus-pituitary-gonadal (HPG) axis during infancy releases
gonadal hormones, in part responsible for fast infant growth and for establishing sex-
related differences in growth patterns. Around the second year of life the activity of the
HPG axis is suppressed, to be reactivated only at the onset of adolescence.

Due to high growth velocity, infancy is particularly sensitive to environmental
stressors such as deprivation, infection, chemicals, poor socio-economical status,
psychosocial adversity and biomechanical factors (Eveleth and Tanner, 1990; Bogin,
1999; Karlberg et al., 1994; Allen, 1994; Golding, 1994; Skuse et al., 1994). Severe
deprivation in infancy resulting in altered GH secretion can slow down growth and delay childhood onset, possibly affecting growth permanently.

2.3.2.2 Childhood

Childhood begins around three years and lasts for approximately 9-11 years. This growth phase is characterized by growth hormone (GH) secretion, which is mainly responsible for the longitudinal growth accrued during this phase. A late childhood onset is indicative of inherited pathologies (Edler, 1976; Karlberg et al., 1994; Nilsson et al., 1994) or environmental growth perturbation during infancy (Karlberg et al., 1994; Ho et al., 1998). During childhood body size increases, motor and cognitive abilities improve and deciduous teeth are substituted with permanent dentition. Childhood somatic growth is slow and prolonged for several years, requires less energy than infancy growth and allows for greater developmental plasticity (see Section 3.1). In a favorable environment childhood growth is highly predictive of adult size and individuals fully express their genetic potential for adult stature (Bogin, 1999; Humphrey, 1998). During childhood, GH stimulates longitudinal long bone growth directly and the appendicular skeleton develops faster than any other body segment, achieving about 70% of adult length before the onset of puberty (Humphrey, 1998). In contrast, growth of the axial skeleton proceeds at slower rates to increase only at the onset of adolescence. These differences in growth rates of different body segments explain the fact that the effects of growth perturbations on child growth are particularly severe on the appendicular skeleton (Bogin et al., 2002; Bass et al., 1999; Bradney et al., 2000). The prolonged duration of childhood suggests that genetic and nutritional factors delaying the onset of childhood or slowing down growth
rates will negatively affect growth, possibly permanently (Graham, 1972; Karlberg, 1994; Bogin, 1999).

Additional intrapopulation variation in growth outcomes is promoted by sexual dimorphism in childhood, expressed in terms of different somatic growth patterns and overall duration of the growth period between the sexes (Humphrey, 1998; Gasser et al., 2000). Girls are on average approximately two years ahead of boys in skeletal age. This difference is genetically determined and, allowing boys to have a more prolonged childhood, contributes to adult sexual dimorphism in stature and body proportions (see Section 3.2.1.3). Specifically, males typically have relatively longer legs than females within the same population (Leonard and Katzmarzyk, 2010).

2.3.2.3 Adolescence

Adolescence is an intense growth phase supported by both GH and sex hormones, the secretion of which is stimulated by a reactivation of hypothalamic-pituitary-gonadal axis. Typically, females have an earlier onset of adolescence (12 years) than males (14 years). Adolescent growth exhibits a sudden increase in velocity (growth spurt), reaches a peak and then progressively slows down until its complete arrest at the onset of adulthood, around 18 years of age. Adolescence is characterized by sexual maturation and somatic growth, even though body segments show different increases and age of peak velocity (Satake et al., 1993; Humphrey, 1998). In both sexes the axial skeleton shows the highest increase in velocity, whereas limb growth progressively decelerates (Bass et al., 1999; Bradney et al., 2000; Nyati et al., 2006). In spite of the fact that both sexes exhibit a general increase in body size, sex is a major factor influencing adolescent growth. On average, females enter puberty two years earlier than males, tend to have a
less intense growth spurt and muscular mass increase, and progressively accumulate fat mass. In contrast, boys generally loose fat mass and increase muscle mass. The onset of adolescence varies among individuals and populations in relation to genetic factors (Nyati et al., 2006; Sedlmeyer et al., 2002; Yap et al., 2004) and environmental conditions (Wang et al., 2005). In general, nutritional stress delays the onset of puberty, while the exposure to different environmental chemicals may delay or accelerate the onset of puberty (Wang et al., 2005). Under equal environmental conditions, differences in adolescence onset and duration, generally attributed to genotype and ethnicity (Eveleth and Tanner, 1990; Bogin, 1999), contribute to the expression of different stature and body proportions observed across human populations.

2.4 Auxological Models of Human Growth

Although different growth phases can be identified based on hormonal influences and relative growth rates, in practice human longitudinal growth is generally examined in terms of cumulative increments. The multidisciplinary science concerned with the study of growth is known as auxology. Auxology studies growth by combining lines of evidence derived from anthropology, biology, medicine, mathematics, physics, economics, history, and other related fields (Bogin, 1986). This science focuses on understanding growth at the individual and population level and has led to the definition of general growth models that are commonly employed in assessing growth within and among human populations. In this section, I review different models of human growth and their role in interpreting biological variation.
2.4.1 Classic Models of Human Growth

Human growth is generally modeled as a continuous process characterized by changes in growth velocity with age (Eveleth and Tanner, 1990; Frisancho, 1990; Bogin, 1999; Frisancho, 2008). Under this view, growth progresses in a continuous fashion and can be mathematically modeled by percentile growth curves (Figure 2.5).

In the study of human populations, these curves are used to evaluate postnatal growth and nutritional status in children and adults (Frisancho, 1990, 2008). To this end, individual anthropometric data are collected and compared to a reference or a standard. In auxology, the term reference generally indicates the growth pattern observed in the comparative sample adopted, and no judgment on the desirability of such pattern is expressed. In contrast, a standard is a growth pattern that is desirable, and deviations from it are interpreted as the results of negative environmental conditions during growth. However, quite often reference and standard are used interchangeably (Frisancho, 2008).
Figure 2.5. Growth curves for stature developed on US boys (2-20 years) by the National Center for Health Statistics (2000). Accessed online at www.cdc.gov/growthcharts.
Growth curves are developed from anthropometric measurements (ideally both cross-sectional and longitudinal) of large samples within each age category, and are statistically interpolated to provide a uniform and normally distributed baseline (Eveleth and Tanner, 1990). Raw data are not necessarily normally distributed. By assuming they are and by using them directly as references can provide misleading results. Therefore, in the development of growth curves, data are generally normalized by removing skewness through power transformations and curve smoothing (Frisancho, 2008). Data normalization is particularly helpful for inter and intrapopulation comparisons, which are typically performed employing z-scores. Z-scores\(^1\) are calculated from individual data and distribution parameters (mean and standard deviation) and provide information on the differences between an individual’s growth status and the reference in terms of standard deviation. Conventionally, the presence of growth disruptions is determined by transforming individual data into z-scores and comparing them to the standards. Negative values of z-scores indicate that growth falls behind the normal values, and scores less than or equal to -2 indicate severe growth retardation (stunting). This value represents the lower 5% of the entire reference distribution. The use of z-scores is particularly helpful, since it allows comparison of individuals of different sex and ages as well the evaluation of recovery from growth perturbations.

These growth models are used as a reference to compare growth patterns among different populations, regardless of geographic provenience, ethnicity, socioeconomic status, and dietary practices. The rationale for using these reference curves regardless of

\[
\hat{z} = \frac{x_i - \mu}{\sigma}
\]

where \(x_i\) is the individual’s measurement, \(\mu\) is the mean and \(\sigma\) the standard deviation of the reference population.
all of these biosocial factors is that these models were developed on large samples and statistically interpolated to be used in all populations (Frisancho, 2008). It has been argued that, even though some genetic differences between populations exist, most of the variation in growth is typically attributed to poor environmental quality during growth (Ulijaszek, 1994). On such basis, international references for longitudinal growth (stature, sitting height, leg length) by age based on populations with positive environmental conditions are deemed suitable to be applied universally (Ulijaszek, 1994). However, while these growth curves provide useful references and informative tools in comparing interpopulation variability in growth, their use to assess intrapopulation and individual variation poses some problems. Specifically, by assessing growth status in respect to a reference, these models may shade intrapopulation variation as the result of specific individual adaptations to suboptimal environmental conditions. Under such circumstances, the use of raw data or population-specific growth models may be more appropriate to evaluate biological variation in stature and body proportions in response to growth disruptions.

2.4.2 An Alternative Model of Human Growth: Saltation and Stasis

Classic models of human growth were initially developed as a comparative tool to assess individual progress in reference to a cohort of peers. Nonetheless, over time they have assumed a more important role as diagnostic tool, used to determine whether a child develops according to the expected model (Lampl and Thompson, 2007). In clinical practice, individual growth is routinely examined in relation to such standards and intervention policies are implemented in case a child’s growth pattern diverges from the
expected. While growth curves represent useful descriptors of growth patterns within and between populations, they have several intrinsic limitations that undermine their use as reference standards for the assessment of individual growth (Lampl and Thompson, 2007). The most important shortcoming of using these curves as growth standards is that they do not take into account inter-individual variability in growth patterns.

Lampl and colleagues (1992) provided experimental evidence that individual growth is not a linear process, but the result of alternating saltation and stasis. Figure 2.6 illustrates the saltatory nature of individual growth.

Figure 2.6. Daily length measurements in a male infant (90-218 days). Note the alternation of static and saltatory phases. Length is expressed in centimeters and age in days x 10². From Lampl et al., (1992).

In a rigorously designed study, these authors measured 31 infants on a daily, semiweekly and weekly basis, between birth and 21 months. Intra and inter-observer
errors – which due to the short time between measurements could have played a role in biasing the results – were found to be minimal and consistent with literature reports. The results of their study indicate that normal growth is a cumulative and discontinuous process, with growth phases – longitudinal and transversal – alternated by stasis phases, during which there are no significant increments in growth.

Since the formulation of the model, other authors’ findings on pulsatile growth patterns in limb length, (Hermanussen, 1998) ENOS elongation (Noonan et al., 2004) and intramembranous bone formation across species (Goldsmith et al., 2003) have further corroborated this model. Based on these considerations, what is the impact of this growth model on the validity and applicability of growth curves in the evaluation of individual growth?

A first consideration emerging from the study by Lampl and colleagues (1992) is that growth linearity as portrayed in growth curves is an artifact. This misrepresentation is the result of two factors: 1) the inadequacy of growth assessment and 2) the statistical models applied to smooth the curves. First, the evidence provided by Lampl and collaborators (Lampl et al., 1992; Lampl and Johnson, 1997) indicates that conventional growth assessment – based on weekly or even alternate day measurements – is insufficient to detect the finest increments in growth. As a consequence, the data obtained are not representative of the growth process and of limited inferential value, since they are “statistically unresolvable and either saltatory or continuous, and there is little that can be done to further identify a growth pattern that has been discretely sampled with insufficient frequency” (Lampl and Johnson, 1997:354). Second, growth linearity emerges as an artifact of the statistical interpolation of cross-sectional data. Growth
curves are a graphical display of the statistical parameters of the underlying stature/age (or weight/age, etc.) distribution in the reference sample. Even when the sample is representative of the population, its inferential value rests on this aggregate level, and cannot be applied to understand the process of individual growth. This being said, growth curves remain a valid comparative instrument (for individuals and populations), provided that they are not interpreted as an optimum model of growth. As eloquently discussed by Lampl and Thompson (2007), using these curves as a depiction of ideal growth masks inter-individual variability and its intrinsic adaptive value. Furthermore, the curves represent static data, while individual growth is an ongoing, dynamic process.

An important contribution of the saltation-stasis model to our understanding of growth processes is the reappraisal of the adaptive meaning of individual variation. In this perspective, it is important to understand that different individuals may achieve their potential in different ways, due to variation in the regulation of stasis and saltation. For instance, two individuals could reach the same adult stature through entirely different processes: one could have frequent and modest growth spurts, while the other could have infrequent yet more substantial growth spurts. Experimental evidence indicates that this variation does occur in infancy (Lampl and Thompson, 2007), and individual variation in growth patterns seems to be already expressed in the fetus (Lampl et al., 2009). Viewing individual growth as the interface between the species and the environment, that is, the unit of selection, Lampl and collaborators underlined the importance of understanding individual variation and its adaptive meaning. Contrary to a continuous growth model, in which the organism simply responds to its environmental milieu, saltatory growth allows the individual to interact and constantly adjust its growth rates to environmental factors.
2.4.2.1 Potential Mechanisms of Growth Saltation

Growth saltation implies the existence of controlling mechanisms, which through inhibitory and promoting actions regulate the periodicity observed. In particular, it is possible to hypothesize the existence of a biological clock that would alternatively induce or suppress growth through differential gene expression and message transduction. Biological rhythms have been identified in several developmental processes such as shell deposition in mollusks and enamel formation in mammals (Pannella and MacClintock, 1968; Dean, 1987), and there are no reasons to exclude a possible role of rhythmic phenomena in human longitudinal growth. Within the human body, circadian rhythms have been observed in the plasmatic concentration of several hormones (Berne et al., 1998) and it is plausible that these complex mechanisms may have a role in suppressing or promoting bone growth at the growth plate. It is tempting to see GH secretion as the crucial event regulating the periodicity of longitudinal growth. In particular, it has been observed that GH levels fluctuate in response to a variety of factors, including low glucose levels, low free fatty acids, arginine, starvation, exercise and phase VI of the sleep cycle (Berne et al., 1998). In relation to resting time, Noonan and colleagues (2004) found that in animal models (lamb) growth is not continuous, and occurs primarily during recumbency. Based on these results and the evidence of “growing pains” during sleep, these authors suggested that the majority of child growth might take place during sleep. Interestingly, the fact that growing pains in children generally occur only in the lower limb could suggest that mechanical loading may have an immediate negative effect on cell proliferation at the growth plate, and that removal of such loading might reactivate longitudinal growth. This control mechanism could be explained by cartilage modeling.
(Frost, 1999, 2003). A possible role of loading in promoting longitudinal growth is supported by the evidence of retarded growth observed in children with some forms of cerebral palsy resulting in immobilization (Kong et al., 1999). To date, it is not possible to delineate a simple straightforward mechanism of saltatory growth regulation, which most likely results from the interrelation of endogenous and exogenous factors.

2.4.2.2 Saltation and Faltering

It is appropriate to explore the implications of the saltation-stasis growth model for the concept and assessment of growth faltering. On one hand, the data presented by Lampl and collaborators (1992) call into question the validity of classic growth models, therefore implying that the assessment of growth faltering also needs reconsideration. On the other hand, by highlighting individual variation in growth and its potential adaptive value, the new model may be misinterpreted. Indeed, it would be easy to dismiss any discussion of growth faltering as a discrepancy between individual growth and inadequate reference standards.

Hence, how can the adaptive potential of growth saltation and growth faltering be reconciled? I argue that the dissonance between the two is only apparent and primarily due to the different scale of the observations. The mechanism of saltatory growth might indeed be discontinuous, but at the end it results in cumulative growth that can be evaluated in comparison with other individuals. Even in the extreme scenario in which any specific point of the growth process is not representative of the process itself, it is indisputable that the end result of growth (i.e., adult stature and proportions) is unique and clearly comparable. Evidence indicates that growth faltering occurs, and its results are visible as reduced adult stature and associated health consequences (Beaton, 1989).
The new growth model does not alter the meaning of abundant data on growth faltering, and it can be argued that while it might confer adaptive value in normal circumstances, there is no real difference between this and old models under severe growth perturbations. After all, if growth is arrested, it is irrelevant whether it is continuous or alutatory.

The question that remains unanswered is how to assess growth faltering during growth. Also, there is a clear duality of interests in the issue: from an evolutionary perspective it is relevant to posit questions on the adaptive value of growth and its mechanisms; from a policy perspective it is essential to be able to recognize and intervene on the effects of growth faltering. Based on the data presented by Lampl and colleagues, growth retardation assessment at the individual level necessarily needs to rely on improved insights on the process of alutatory growth and appropriate individual measurements. In this way, the alteration of growth patterns would be determined not in relation to standards, but to an internal reference. Even though this method would certainly provide accurate indications of the timing, duration and severity of growth faltering, it is also clear that its application is limited by practical considerations, such as the frequency of measurements and the relatively unknown degree of intra-individual variation.

In conclusion, the conflict between the alutatory model and growth faltering is only superficial. Similarly to classical models, also in this model growth faltering results from a pathological interruption of normal physiological processes. The implications of the alutatory model for the assessment of growth faltering are important in methodological and policy terms, and require reconsidering the way faltering is
commonly assessed. In this latter regard, the improved understanding of the mechanisms of saltation and its intra-individual variability will certainly prove beneficial, and will possibly be used to develop new methods combining individual and aggregate level observations in the diagnosis of growth faltering.
CHAPTER 3: DEVELOPMENTAL ORIGINS OF VARIATION IN STATURE AND BODY PROPORTIONS

A proper interpretation of the variation patterns observed in stature and body proportions in populations across the globe requires an understanding of the mechanisms that allow for biological variation to be expressed. Clearly, being the basis for selection, biological variation has an essential role in evolution, and is promoted by both genetic and developmental variation. In this chapter, following a brief introduction of important concepts relating to the expression of biological variation, I first review the role of genes and environment in determining the pattern of variation observed in human stature and body proportions. Subsequently, I review how growth perturbations, as well as the recovery from growth insults, play a role in determining adult phenotypes.

3.1 Plasticity, Adaptation and Norms of Reaction

Due to its importance for selection and evolutionary change, biological variation is promoted starting at the genetic level, where different molecular forms (alleles) of the same gene may exist. Different genetic combinations, constantly generated through meiotic divisions and sexual reproduction, lead to genomic variation. Furthermore, the
interaction between genes and environment generates phenotypic variation on which selective pressures exert their action.

The term *phenotypic plasticity*, or simply *plasticity*, is commonly employed to indicate the ability of a genotype to produce different phenotypes in different environments. According to its classic definition, phenotypic plasticity is expressed during growth and development as a response to environmental stimuli and is the developmental basis for variation (Sultan and Stearns, 2005). Such phenotypic “adjustment” is generally interpreted as adaptive: for instance, accelerated growth rates following growth perturbations have been seen as the organism’s adaptive response to reduce instability. In fact, if resources are scarce, developmental acceleration implies earlier reproduction and increases the probability of gene transmission to the next generation. Clearly, the meaning of plasticity is that of regulating growth in relation to environmental conditions in order to maximize the adult organism’s success. Different models have been proposed to explain the evolution of human developmental plasticity, which ultimately hinges on adjusting phenotypic expressions in response to environmental constraints (Gage, 2003; Bateson et al., 2004). Compared to that of other primate and mammal species, human growth and development is not only extremely long, but it is also characterized by a prolonged childhood phase, typically absent in other taxa (Bogin, 1999). Childhood growth, being prolonged and energetically relatively inexpensive, allows humans to exhibit a great degree of plasticity and to reach adulthood in spite of environmental adversity. It has been estimated that, compared to mammalian species lacking a childhood phase, which on average raise to adulthood only 10 percent of their offspring, between 10% ad 30% of the offspring of social mammals with a
childhood stage reach adulthood (Lancaster and Lancaster, 1983). Thanks to the addition of a childhood phase and the consequent plastic reaction to the environment of the growing individual, traditional human societies are able to raise to adulthood approximately 50 percent of their offspring (Lancaster and Lancaster, 1983).

Even though the principle of plasticity is adaptive, an organism’s response to environmental stress always represents a compromise aimed at maintaining homeostasis. A relevant question is therefore to what extent a plastic response to environmental stress may be considered adaptive. Scrimshaw and Young (1989:21) define adaptation as a “long-term, steady state [that] can be achieved while function is maintained within an “acceptable” or “preferred” range.” According to this definition, adaptation may imply a certain degree of compromise by which certain processes and functions may be altered or lost. When functional compromises are too excessive to be considered adaptive, according to these authors it is more appropriate to talk about accommodations, that is, “responses that, while they favor survival of the individual, result simultaneously in significant losses in some important functions” (Scrimshaw and Young, 1989:22). At what point, therefore, does growth retardation stop to be an adaptive response and becomes accommodation? This question is particularly important in terms of nutrition policy and has accordingly received notable attention.

In the 1980s, the economist David Seckler argued that the reduction in height observed in developing countries is an adaptive response that allows humans to avoid functional impairment as the result of malnutrition (Seckler, 1982). Seckler argued that height reduction was a no cost adaptation to environmental conditions and individuals would be “small but healthy” (Seckler, 1982). However, research in human biology has
shown that severe reduction in height-for-age, defined as a z-score below two negative standard deviations (stunting) is a major sign of poor health. Indeed, stunting has been shown to be associated with compromised immune competence, poor psychological performance, diminished productivity, reduced reproductive potential, and increased mortality risk (Beaton, 1989; Martorell, 1989; Goodman, 1993; Norgan, 2000; Paajanen et al., 2010).

It is important to understand, therefore, that even though the human body is able to respond to environmental stressors by altering its growth, such plastic response may come at a cost. As such, the variation generated by plastic responses to the environment is not infinite, and is actually restricted to viable phenotypic niches. The range of possible phenotypic expressions for a given genotype across different environments is defined as norm of reaction (Hoffman and McKenzie, 2005). Even though a genotype may in theory be able to express different phenotypes in response to different environmental conditions, in practice the range of phenotypic variation is constrained by a number of intrinsic and extrinsic factors that limit an individual’s survival and/or its ability to produce viable offspring. In such cases, developmental stability allows an organism to keep the phenotype constant in spite of environmental perturbations (Hoffman and McKenzie, 2005). At an aggregate level, developmental stability leads to canalization of an adaptive trait, which is therefore going to exhibit low levels of intrapopulation variation (Hoffman and McKenzie, 2005).

This implies that the observable variation in stature and body proportions is going to be constrained and limited to a range of norms of reactions that allow individual survival. It is unclear to what extent growth retardation may affect adult stature and body
proportions prior to meeting a non-viability threshold. It is also unclear whether different body segments are more canalized than others. For instance, sitting height may be more canalized in size than leg length due to the fact that the chest and abdomen house vital organs. In order to understand and advance explanations for variation in growth outcomes, it is essential to be mindful of the factors that contribute to it: genes and the environment.

3.2 Genes and Environment

The existence of developmental plasticity implies that growth is not a predefined, immutable process entirely orchestrated by solipsistic genes. Rather, it is more like a dynamic dialogue between hereditary components, which set the general instructions and tools for assembling the body, and the environment, which supplies the energy and materials necessary. Understanding the relative contributions of genes and environment in determining growth is therefore a crucial point for understanding the origins of variation in stature and body proportions.

3.2.1 Genetic Controls of Human Growth

Different lines of evidence have been employed to investigate the nature and the extent of the control that hereditary factors have on longitudinal growth. On the one hand, pedigree analyses and genetic models have been employed to determine the proportion of inter-individual phenotypic variation in stature and other anthropometric variables that can be explained by hereditary factors. On the other hand, the direct analysis of allelic
and genomic variation has allowed the identification of genes that are involved in the regulation of adult stature and proportions.

3.2.1.1 Heritability of Stature and Proportions

Several authors employed pedigree analyses to examine the correlation between anthropometric variables of related individuals and to estimate the genetic component of adult growth outcomes (Tambs et al., 1992; Devor et al., 1986a, 1986b; Livshits et al., 1995; Ginsburg et al., 1998). Their results indicate that a great part of inter-individual variation in stature, possibly up to 80% may be explained by genetic factors (Lettre, 2009). Even though evidence of genetic controls of body proportions is not as abundant, a recent study suggests that hereditary factors may account for a substantial portion of observed variation (Livshits et al., 2002). Livshits and colleagues (2002) carried out a pedigree analysis on two different samples to detect familial correlations in anthropometric variables, proportional indices of their elaboration, as well as the first two factors obtained through factor analysis of indices. Additionally, they employed genetic analyses to evaluate the extent to which inter-individual variation in the factors considered is explained by genetic and shared environmental variables. The results showed that, while correlations of traits between spouses was close to zero and non-significant, positive significant correlations were detected between parents and offspring as well as between siblings. The results of the study indicate that hereditary factors may explain between 40% and 75% of the inter-individual variation observed in the body proportions under examination.
3.2.1.2 Genes Involved in Stature Control

Thanks to the advances in human genetics, in recent years the study of allelic and genomic variation has complemented classic pedigree analyses in determining the specific genes involved in the control of stature and body proportions. Among all gene sets involved in development control, HOX genes deserve particular attention. HOX genes are characterized by the presence of a highly conserved nucleotidic sequence defined *homeobox*, which is virtually ubiquitous in all metazoans (Mark et al., 1997). In vertebrates, HOX genes occur in four clusters (HOXa, HOXb, HOXc, HOXd) and are responsible for defining body axes of the developing organism. Differential spatial and temporal expression of HOX genes produces molecular gradients that are fundamental in providing proper spatial information to the developing tissues, allowing for the proper development of different anatomical structures. In humans, the homeobox-containing gene SHOX, situated in the pseudo autosomal region of the X and Y chromosomes, has been linked to short stature in several pathological conditions including Turner Syndrome and Leri-Weill dyschondrosteosis (Attie, 2000; Binder et al., 2000; Clement-Jones et al., 2000; Rappold et al., 2002; Sabherwal et al., 2007). Even though the specific function of the SHOX gene transcript has not yet been identified, it is extremely abundant in osteoprogenitor cells (bone marrow fibroblasts), suggesting a direct role of this gene in controlling normal bone growth (Attie, 2000). Even though pathological alterations of the SHOX gene have been shown to be related to short stature, it is unclear what role this gene may have on stature in normal development.

 Thanks to relatively recent investigation techniques, such as the analysis of single nucleotide polymorphism (SNP) and genome-wide associations (GWA) it is now possible
to test the association between certain genotypic make-ups and specific phenotypic traits, such as stature (Weedon and Frayling, 2008; Lettre, 2009). Several studies employing these techniques have fostered a wealth of information on a plethora of genes that are involved in the control of adult stature (Liu et al., 2003; Sammalisto et al., 2005; Lettre et al., 2008; Axenovich et al., 2009). To date, over 50 genes have been identified, which show small but additive effects on stature, explaining up to 5% of the total variation observed (Lettre, 2009; Axenovich et al., 2009). The genes identified are involved in chromatin structure, extracellular proteins of bone and cartilage, BMP signaling, cell cycle controls, and hedgehog signaling (one of the primary determinants of body plan in the embryo).

3.2.1.3 Genetic Bases for Sex Differences in Growth

There is evidence for genetic differences between the sexes in the regulation of growth and resulting in sexual dimorphism. For instance, Ogata and Matsuo (1997) observed that, even in patients failing to develop sexually, sexual dimorphism in growth outcomes is still visible. Therefore, they argued that the mechanism leading to adult dimorphism lies in the expression of genes located on the non-recombining (long) arm of the Y chromosome, Yq. On purely theoretical grounds, they advanced the idea that genes on Yq may control sexual dimorphism by regulating the growth pattern observed in childhood. These genes would be specifically involved in the regulation of the prolonged duration of childhood growth in males. If this gene were to mutate, the male growth pattern would then revert to a female one and the difference between males and females would be obliterated. These authors did not test this hypothesis, but gathered some clinical evidence supporting it.
Following the lead of Ogata and Matsuo, Ellis and colleagues (2001) explored the relationship between normal variation in the non-recombinant portion of the Y chromosome and adult stature in individuals of European ancestry. Using analyses of restriction fragment-length polymorphism (RFLP) in Yq, these authors were able to detect a positive significant association between genotypic variants and phenotypic variation in stature. Additionally, the same authors investigated whether similar associations existed between stature and allelic variation in the aromatase gene. Aromatase is an enzyme coded by the CYP19 gene, located on the long arm of chromosome 15, which is responsible for the conversion of androgens into estrogens. Given the fact that estrogens have been shown to play an important role in growth cessation, aromatase mutations are characterized by pathological alterations of stature. Ellis and colleagues investigated whether allelic variation in the CYP19 gene shows correlations with stature in normal individuals. The results of the study highlighted an association between allelic variation in CYP19 and stature only in males and not in females, suggesting the existence of differential hormone sensitivity and regulation during development in the two sexes.

Sex differences in developmental patterns have been invoked to explain the differences in stature and proportions exhibited by adult men and women. Specifically, on average male stature exceeds female stature by over 10 cm. However, it should be noted that the mechanisms underlying the expression of sexual dimorphism among primates are complex (Frayer and Wolpoff, 1980; Plavcan, 2001), and environmental factors can affect the degree of dimorphism (Gray and Wolfe, 1980; Stinson, 1985). In
particular, there seems to be a general tendency for an increase in stature sexual
dimorphism under positive life conditions.

Sexual dimorphism in height has been shown to be mainly due to differences in
leg length rather than trunk length (Wells, 2007). In agreement with this notion, there is
evidence indicating that even within the same population males and females tend to have
different trunk/leg proportions, with males exhibiting relatively longer legs than females
(Leonard and Katzmarzyk, 2010). These differences in stature and proportions are not
present throughout infancy and childhood and arise during adolescence as a result of the
different growth patterns exhibited by the sexes. On average girls enter adolescence about
two years prior to boys. This means that on average boys experience childhood growth
for more years than girls thus maturing sexually and skeletally at a later age. It has been
debated whether the differences observed between the sexes are due to a delayed onset of
puberty in boys, a more intense puberty spurt in boys than girls, or both (Gasser et al.,
2000). Gasser and colleagues (2000) addressed this question by examining change in
several anthropometric variables during adolescence in a longitudinal study. Their results
indicate that different parts of the body achieve their adult size and shape in different
ways. Specifically, the delayed pubertal spurt in males accounts for 63.6% of the adult
sex difference in leg length and only 45.8% of differences in sitting height. In contrast, a
more intense pubertal spurt in boys was found to be responsible for 48.7% of the
differences in sitting height and only 17.3% of the difference in leg length.

In summary, pedigree analyses and genetic studies have shown that human
longitudinal growth outcomes are regulated by a large number of different genes and that
sex-based differences in hereditary factors determining adult body size and proportions exist. It is also clear that the polygenic control of stature and body proportions allows for great developmental plasticity and that growth outcomes, loosely defined genetically, largely depend on contingent environmental influences on the growing body.

3.2.2 Environmental Influences on Human Development

Even though the maximum growth potential in stature and body proportions is controlled genetically, variation has been observed even within closely related groups (Karlberg et al., 1994; Bogin et al., 2002). The origins of such variation are generally considered to be environmental in nature, that is, resulting from constraints that the environment exerts on the growing body. Growth outcomes have been shown to vary among human populations in relation to a variety of environmental factors, including climatic conditions, diet, socio-economic status, and disease (Rona and Chinn, 1991; Waterlow and Schürch, 1993; Bogin, 1999; Wadsworth et al., 2001; Bogin et al., 2002; Mascie-Taylor and Lasker, 2005). In this section, I briefly review the major environmental factors known to affect growth, as well as the evidence for sex differences in the response to environmental stress.

3.2.2.1 Climate and Ecogeographic Rules

A well-known aspect of human variation is the fact that modern humans inhabiting different parts of the globe have different physical appearance. This phenetic variation is the result of millennia of microevolution, which selected the most successful traits for specific climatic conditions. The effects of climate on endothermic organisms have been described in two ecogeographic rules, Bergmann’s and Allen’s, which explain
how body shape changes to improve thermoregulation (Bergmann, 1847; Allen, 1877). Bergmann’s rule postulates that body size of endothermic species is inversely proportional to mean annual temperature (1847). Therefore, organisms inhabiting colder climates are expected to be bulkier than closely related organisms living in warmer climates. Thirty years after the publication of Bergmann’s principle, Joseph Aleph Allen published his observations regarding the different proportions of animals’ body parts in relation to climate. In brief, Allen’s rule posits that the length of an endothermic organism’s appendices shows a directly proportional relation with mean annual temperatures. Therefore, animals living in colder climates will have shorter limbs and tails than their relatives from warmer climates (Allen, 1877). The biological basis for these two ecogeographical principles is the necessity of an endothermic organism to optimize thermoregulation. Greater body size and shorter limbs have the benefit of reducing the volume/surface area ratio and consequently of improving heat retention in colder climates. Conversely, in warmer climates, where heat dispersion is more important than heat retention, an organism with smaller body size and increased surface area has a selective advantage. Since their initial formulation, these ecogeographic principles have been validated in several taxa (Ashton et al., 2000) and experimentally reproduced in laboratory animals (Riesenfeld, 1973; Serrat et al., 2008).

The effects of climate on body proportions in relation to Bergmann’s and Allen’s rules have been extensively documented and described in both extinct and living humans (Schreider, 1950; Roberts, 1953; Newman and Munro, 1955; Stinson, 1990; Ruff, 1994; Holliday, 1997; Holliday and Ruff, 1997; Katzmarzyk and Leonard, 1998; Ruff, 2002; Weinstein, 2005; Temple et al., 2008; Holliday and Hilton, 2010; Wells, 2012). Eugene
Schreider (1950) is credited for publishing the first report of the relationship between geographic distribution and the body-weight/body-surface ratio in human populations. However, the first systematic test of Bergmann’s rule in humans was conducted by Roberts (1953), who investigated the association between body size and mean annual temperature in a large number of human populations from different geographic proveniences. The results indicated a strong, significant negative correlation between body mass and mean annual temperature, while the relationship between stature and temperature was not significant. Similarly, Ruff (1994) demonstrated that body weight also shows a significant positive relationship with absolute latitude. In 1998, Katzmarzyk and Leonard (1998) re-examined the relationship between climate and body size and shape on data published since Roberts’ original publication. Additionally, they expanded previous investigations by examining the body mass index (BMI = mass (kg)/stature (m²)) and relative sitting height (RSH = sitting height/height) in addition to body weight, hence introducing body proportions in the analysis. Consistently with previous studies, they observed a significant negative association between body mass (and BMI) and mean annual temperature, as well as a negative relationship between RSH and temperature. However, the associations observed were more modest than those found by Roberts (Katzmarzyk and Leonard, 1998). This discrepancy was interpreted in terms of secular trend in body mass in several populations, which attenuated the effect of climate on human body size. In a recent study, Wells (2012) provided evidence to explain the mechanisms leading to the association between body fat and mean annual temperatures. Specifically, his results indicate that colder environments favor an increase in both lean (heat producing) and fat (insulating) mass.
It should be noted that some striking exceptions to the general ecogeographic pattern exist. As already observed by Roberts (1953:553), certain Oceanic populations exhibit somatotypes in sheer contrast with climatic expectations. Such discordance with a generally valid pattern has subsequently been explained on a genetic basis by Bindon and Barker (1997) and as the outcome of several contingent biocultural factors by Wells (2012). Regardless of the specific factors involved in this specific case, this research indicates that, even though climate clearly plays a role in generating part of the phenotypic variation observed in body size and shape of populations across the globe, other environmental factors, such as increased acculturation and improved nutrition in the developing world have moderated their influence.

This evidence suggests that the effects of climate and other environmental factors on stature and body proportions differ in nature and scale. On the one hand, changes in body size and shape in relation to climate are the result of long-term microevolutionary change. As such, the selection of specific somatotypes in relation to ecogeographic pressures leads to changes in a population’s genetic makeup and can explain the interpopulation variation in growth patterns observed across the globe. On the other hand, contingent environmental pressures play a role in determining short-term adaptive responses by adjusting individual growth. While important in determining adult phenotypes and generating variation at the intrapopulation level, due to their mercurial nature, contingent environmental factors typically do not lead to evolutionary change. Consequently, while climatic adaptation may largely explain differences at the interpopulation level, it is unlikely to be informative of the causes and patterns of variation in stature and body proportions at the intrapopulation level. In this latter case,
other factors such as nutrition, disease, and social inequality appear to play a major role in determining variation in individual growth outcomes.

3.2.2.2 Nutrition, Disease, and Social Inequality

Nutritional stress and disease are among the contingent environmental factors having the greatest impact on the growing body. Clearly, adequate nutrition is necessary for a growing organism because it provides energy and nutrients necessary not only to meet basal metabolic requirements and maintain homeostasis, but also to promote growth and development. To support proper growth, an organism requires a variety of essential macronutrients (carbohydrates, protein, and fat) and micronutrients (minerals, vitamins), which the body is unable to synthesize and must therefore acquire through diet (Bogin, 1999). Evidence indicates that deficiencies of single nutrients occur rarely and single nutrient supplementation in case of growth faltering has consequently had inconsistent results (Allen, 1994). This suggests that growth faltering in human populations is often related to multiple, concomitant deficiencies (Allen, 1994).

Infectious disease and parasitic infestations may further affect human growth in a large number of ways by interfering with disparate metabolic processes and exacerbating the effects of nutritional stress. In fact, to the extent that disease and parasitic infestations affect growth, their action is commonly mediated by nutritional imbalance, either through nutrient malabsorption or reduced appetite (Allen, 1994). The interaction between nutrition and disease is often circular, with each factor contributing to the expression of the other (Scrimshaw et al., 1968; Subcommittee on Nutrition and Diarrheal Diseases Control, 1992; Ambrus and Ambrus, 2004). Specifically, by compromising immune competency malnutrition and undernutrition increase the susceptibility to disease, which
in turn may further promote nutrient malabsorption or limit food intake (Keusch and Farthing, 1986; Ullrey, 1993). Therefore, the effects of nutritional stress and disease on the human body are often tethered in such a way that their respective contributions to growth retardation may not be teased apart. Nonetheless, they can be considered but two aspects of the same overall environmental stressor, which affects growth by altering energy balance and limiting the raw materials needed to sustain growth. The interrelation between nutritional stress and growth is so strong and so well documented (see Bogin, 1999), that growth information such as height-for-age or weight-for-age is commonly employed to assess the nutritional status of living populations. Abundant literature on this topic has unequivocally shown that individuals exposed to suboptimal environmental conditions during growth (malnutrition, infectious disease and parasitic infestations) always suffer from growth retardation and exhibit smaller body size than individuals who did not experience similar stressors (Malina et al., 1986; Bogin, 1991; Dettwyler and Fishman, 1992; Crooks, 1999; Orr et al., 2001; Foster et al., 2005; Benefice, 2006; Piperata, 2007; Welch et al., 2009).

Even though in some cases growth retardation may be directly related to single environmental factors, it is most commonly the outcome of a variety of co-present and concomitant factors that constitute the overall environmental milieu of an individual. Typically, the same socio-cultural factors that lead to malnutrition and undernutrition are associated with poor hygiene and increased exposure to pathogens. Social inequality is often at the root of different environmental conditions experienced by members of the same population (Smith, 1996; Brunner, 1997; Krieger, 1999). However, social inequality is not simply a proxy for nutrition and disease; rather, it is a complex and
subtle concept, which may exist on the basis of gender, age, biological ancestry, hierarchy, religion, and a multitude of other biocultural factors. Even though such a complex situation may not be entirely comprehensible or evident, in most human societies it is commonly expressed at least in terms of socio-economic status (SES). SES variation is typically interpreted as differential access to resources, including food, health care and education, exposure to disease, and differential workload (Bogin, 1999). The existence of distinct SES groups in a variety of human populations has allowed human biologists, bioarchaeologists, economists, and historians to study biological variation in stature (and much less frequently in body proportions) within closely related groups in relation to different environmental conditions over time (Boas, 1912; Bogin and McVean, 1983; Dufour et al., 1994; Johnston et al., 1985; Steckel, 1986, 1992; Larsen, 1997; Schutkowski, 2000; Bogin et al., 2002; Wadsworth et al., 2002; Godoy et al., 2005; Bassino, 2006; Mays et al., 2009). This literature shows that by altering the eco-biocultural milieu in which individuals grow, social inequality translates into biological inequality. Consequently, higher status individuals tend to mature earlier and to have greater body size and longer limbs than their low status counterparts (Bogin, 1999).

3.2.2.3 Other Environmental Factors

Over the years, several other environmental factors have been shown to influence growth, including altitude and seasonality. Human prenatal and postnatal growth at high altitude has been demonstrated to be somewhat retarded compared to that of populations living at sea level (Barker, 1978; Stinson, 1982; Bogin, 1999). High altitude is stressful because it is characterized by low temperature and hypoxia, due to the inverse relationship between atmospheric partial pressure of oxygen and elevation above sea
level. The classic view was that hypoxia, limiting oxygen intake, was the primary cause for growth retardation; however, two lines of evidence suggest that that other factors may be responsible for growth faltering at high altitude. First, the human body has the ability to adapt to hypoxia by adopting both short and long term strategies, involving oxygen intake, erythropoiesis and alteration of metabolic processes (Young and Reeves, 2002). Second, Stinson (1982), investigating the relationship between growth faltering and residence at high altitude, found that the growth retardation attributable to altitude was relatively small (approximately 2.5 cm), hence unable to explain the short stature observed in high altitude populations. A possible explanation for the actual growth faltering observed may be found in the co-occurrence of other stressors at high altitude (Bogin, 1999). High altitude environments are known for their low productivity compared to terrestrial ones (Scott and Billings, 1964; Billings and Mooney, 1978) and it is therefore reasonable to assume that they may not be able to provide all nutrients necessary to sustain human growth. A recent analysis of Andean skeletal populations from low and high altitudes supports the idea that changes in body size and proportions may result from a combination of both climatic and nutritional stressors (Weinstein, 2005).

Seasonality is another factor that may affect human growth (Bogin, 1999). Rather than being a direct climatic stressor, seasonality is likely to exert its influence on human growth by altering ecological factors, which in turn will affect food availability and disease risk (Shell-Duncan, 1995; Singh et al., 2001). As such seasonality may be a proxy for other, more causative factors.
Numerous other factors, including psychosocial adversity, cultural practices and workload can be considered part of the broader biocultural environment that is typically embodied by SES. Therefore, the understanding and examination of these additional factors require an understanding of the complex biological, ecological, cultural, social and ideological world people live in. To this end, biocultural approaches have been introduced into human biology (Dufour, 2006).

3.2.2.4 Environmental Stress and Mechanisms of Linear Growth Retardation

It is clear that environmental pressures can affect longitudinal growth outcomes. An important question, then, is: what are the mechanisms by which environmental stress can affect longitudinal growth? Since linear growth is the outcome of cell proliferation at the growth plate, its retardation has to be caused by an alteration of the normal physiology of the growth plate. In a relevant discussion of the topic, Frost and Schönau (2001) compare the sequence of ENOS phases to a train, whose locomotive is represented by the precursor cells of the germinative zone. In normal conditions the rates of cell proliferation, differentiation and degeneration are equal, therefore maintaining the thickness of the growth plate constant. When proliferation slows down and the other phases do not, the end result is the complete ossification of the growth plate, which signals skeletal maturity. Hence, disruptions of growth result from the inhibition of one of the ENOS phases or lack of synchrony between them (Frost and Schönau, 2001).

A relevant question is therefore how can malnutrition and disease disrupt the physiology of the growth plate. Unfortunately, there is no direct answer to this question. However, evidence indicates the existence of paracrine and endocrine responses to both malnutrition and disease, which eventually alter normal growth patterns.
It has long been observed that nutritional deficiencies can have detrimental effects on longitudinal growth (Eveleth and Tanner, 1990; Allen, 1994; Bogin, 1999). The exact mechanisms by which malnutrition affects longitudinal growth are not known, in part due to the fact that malnutrition is rarely the result of single-nutrient deficiencies. It is possible to conceive the effects of malnutrition as either direct or indirect. Direct effects can be observed when a specific nutrient, involved in the process of ENOS, is not available. A clear example is represented by rickets, a disease resulting from Vitamin D deficiency (Pettifor, 2002). Since Vitamin D is fundamental in the calcification of matrix vesicles, in its absence calcification does not occur and bone growth is slowed down and accompanied by deformity (Wharton and Bishop, 2003; Dimitri and Bishop, 2007). Similarly, deficiency of specific nutrients needed for the production of certain hormones can induce stunted growth. For example, iodine deficiency reduces the organism’s capability of producing thyroid hormones, therefore interfering with cell maturation in the growth plate (Allen, 1994). In most cases it is not possible to find a clear association between a specific deficiency and growth retardation, while strong associations with overall diet quality exist (Allen, 1994). In such circumstances, the mechanisms by which malnutrition affects growth are indirect and less clear. For instance, even though it has been demonstrated that growth hormone (GH) production is increased in starved individuals (Ho et al., 1988), severe malnutrition has long been known to induce growth faltering (Eveleth and Tanner, 1990; Bogin, 1999). Additional evidence indicates that IGF levels are notably reduced in severe malnutrition (Clemmons et al., 1985; Unterman et al., 1985), and it has been proposed that this might be the limiting factor on linear growth (Waterlow and Schürch, 1993).
The mechanisms by which infectious diseases interfere with normal growth are even more obscure, as they involve several inflammatory signals, which exert their actions at both paracrine and endocrine levels. In particular, several cytokines produced by inflammatory processes (IL-1, TNF, TGF-β) are known to play a role in controlling bone resorption and formation, and may contribute to the onset of growth retardation (Price et al., 1994; Skerry, 1994).

3.2.2.5 Sex Differences in Environmental Susceptibility

Human growth outcomes are molded by the interaction of genetically set growth trajectories and contingent environmental constraints. A commonly held notion is that the sexes exhibit differences not only in anatomy and body size, but also in terms of longevity, susceptibility to disease and mortality. Indeed, long-standing observations across a large number of taxa suggest the existence of sex differences in the adaptive response to environmental stress (DeRousseau and Reichs, 1987; Magwere et al., 2004; Kalmbach et al., 2005). Heterogameity, larger size, and sex-specific hormonal interactions with physiological functions are among different possible causes for such differences (Sheldon et al., 1998; Jones et al., 2009). This being the case, do human males and females respond differently to environmental stress during growth? On purely theoretical grounds, greater male susceptibility to stress during growth may be expected because growth patterns and rates differ between the sexes. Specifically, males exhibit both a longer childhood phase and a more intense adolescent growth spurt, which would justify greater growth retardation following environmental perturbation (see Section 3.3).

Starting in the late 1960’s, a growing literature on sex differences in environmental response has provided evidence to support the idea that the sexes may in
fact interact with their milieu differently. Stini (1969) was the first to observe sexual differences in human responses to environmental conditions. Studying the effects of nutritional stress on the growth of children from Heliconia, Colombia, Stini (1969) observed that boys and girls exhibited different adaptive responses to malnutrition, except in extremely severe cases of deprivation. Specifically, while females tended to recover from malnutrition in the preadolescent period, males showed no recovery and consequently expressed more compromised growth outcomes.

Stinson (1985) conducted a systematic literature review to further investigate this topic. She found that while there is empirical evidence to support the hypothesis of female buffering during the prenatal period, data collected during the period of postnatal growth in a range of human populations were mixed with some showing evidence of female buffering and others providing equivocal information. According to Stinson (1985), one reason for these mixed results may be found in the confounding effects of the preferential treatment of sons observed in many human societies, which may therefore mask underlying biological differences between the sexes.

Similarly, ambivalent conclusions were also the outcome of a symposium held in 1994 with the goal of further exploring the issue of sex differences in environmental sensitivity. The symposium, entitled “Female Biological Superiority – Fact or Fiction?” included eleven contributions that examined a variety of different biological phenomena, from growth and development to morbidity, longevity and mortality (Brooks and Brooks, 1994; Katz and Armstrong, 1994; Konigsberg and Grant, 1994; Lazenby and Pfeiffer, 1994; The symposium, organized by Patty Stuart-Macadam, was held during the sixty-third annual meeting of the American Association of Physical Anthropologists, which took place in Denver, CO between March 30th and April 2nd, 1994.)
Some contributions did in fact support the hypothesis of different sex sensitivity, while others did not. Interestingly, only the studies examining differences in developmental stress and growth outcomes did, at least in part, support the hypothesis. More recently, Guatelli-Steinberg and Lukacs (1999) reviewed the literature on different sex responses to environmental stress to evaluate how it may affect the expression of enamel hypoplasias in human and non-human primates. In agreement with previous studies, these authors concluded that the evidence in support of the hypothesis of different environmental sex susceptibility is not conclusive, even though some results may in fact indicate greater female buffering to environmental stress. Guatelli-Steinberg and Lukacs (1999) concluded that “both cultural practices as well as environmental influences must be understood in order to evaluate if and how a hypothesized greater female resistance to stress relates to the by sex distribution of enamel hypoplasias within a population” (1999:118).

In summary, due to the difficulties of collecting multiple lines of evidence and understanding the numerous, often subtle factors that may contribute to sex variation within a population, the hypothesis of greater male sensitivity/female buffering requires additional investigation.
3.3 Timing and Duration of Growth Perturbations

As reviewed above, a large number of genetic and environmental factors contribute to molding the adult phenotype. In a vacuum, an individual’s skeletal growth would follow a genetically predetermined trajectory and would result in adult height and body proportions typical of the individual’s population of origin. However, in reality, environmental conditions interact with an individual’s genotype in determining actual growth trajectories and end results (Sultan and Stearns, 2005). Consequently, intra-population variation arises because each individual’s height and body proportions are the outcome of a unique life history.

The heterochronic nature of growth suggests that, depending on their duration and timing, environmental insults may play a major role in shaping the adult phenotype (Martorell, 1989; Martorell et al., 1994). Perturbations suffered during different phases of development are in fact expected to have a different impact on the growing skeleton, not only compromising overall body size but also altering body proportions.

Particularly interesting in this regard are the theoretical expectations formulated by Karlberg and colleagues (1994) in relation to childhood-onset retardation. Despite the fact that this model was developed for later childhood onset due to congenital conditions, it exemplifies well the potential effects of even small perturbation of early development on adult stature. As shown in Figure 3.1, delays in childhood onset (or the cessation of growth during childhood) have the potential of reducing final growth outcomes in a measure that is proportional to their duration and their timing.
3.1. Effect of severe nutritional deprivation on childhood onset. In conditions of severe deprivation childhood growth is retarded and can potentially result in permanent reduction of adult size. After Karlberg et al., (1994).

3.3.1 Duration of the Perturbation

On the basis of its duration, a growth perturbation may be considered acute and episodic (short-term) or chronic (long-term) (Lovejoy et al., 1990). Intrinsic in this distinction is the idea that the former type of insult is intense, discrete and non-recurring, whereas the latter is the summation of milder and recurring insults over time, which in practical terms can be considered as a continuous stress episode. It has been suggested
that chronic growth insults may have more severe long-term effects on skeletal growth than single stress episodes (Lovejoy et al., 1990; Golden, 1994).

Based on the existence of different growth rates for different body segments during different growth phases (see Section 2.3), it is expected that even short-term insults will have large impacts on total growth if they occur during fast-growth phases. Hence, it is expected that earlier (intra-uterine and infancy) perturbations of growth will have more dramatic effects than insults later in life. This seems indeed to be the case (Martorell, 1989; Falkner, 1993; Cameron, 2007). The earliest phases of growth would therefore represent a first critical period, during which even minor events can have dramatic effects on the adult phenotype.

The fact that undisturbed intrauterine and infancy growth and development is fundamental for later well-being is not limited to linear growth. In the mid 1990s, David Barker advanced the hypothesis that nutritional stress experienced during prenatal and infant development determines an individual’s predisposition to develop cardiovascular disease in adulthood (Barker, 1995; Barker, 1997). According to this hypothesis, also known as “Barker hypothesis,” “fetal programming,” or “predictive adaptive response” (Cameron, 2007), the fetus adapts to earlier nutritional stressors by altering irreversibly its metabolic responses to the environment (Barker, 1995). However, such an adaptive response is inadequate once nutritional stress is removed and does in fact predispose individuals to disease later in life. A growing literature on the topic has indeed confirmed the link between early nutritional stress and adult coronary disease, and has demonstrated the fetal origin of several other diseases (Barker et al., 2002; Cameron and Demerath, 2002).
More generally, adopting auxological and epidemiological approaches, Cameron and Demerath (2002) argued that the predisposition to diseases of aging (such as diabetes, obesity, and cardiovascular diseases) results not only from fetal programming, but also from cumulative factors over the entire life and in particular during critical periods. Critical periods are disseminated throughout growth and development, and tend to coincide with phases of fast growth.

In spite of the greatest sensitivity of intrauterine and infancy growth, only extreme environmental perturbations seem to have dramatic, irreversible effects on the infant (Miller, 1992; Warshaw, 1992; Stein et al., 2004), and chronic conditions during childhood are generally invoked to explain the majority of linear growth retardation (Karlberg et al., 1994). This discrepancy between observations and theoretical expectations is only apparent, and is explained by the unique characteristics of the fetal/neonatal environment. During the first phases of life, the maternal body represents the individual’s entire environment. The maternal body tends to buffer the fetus/infant against earlier insults by providing adequate nutrition and antibodies through lactation. However, these factors are no longer available after weaning, therefore exposing the growing child to malnutrition and disease. Rather than a distinct life history episode, weaning may be considered to be a process that leads the child to be nutritionally independent from the mother. By removing nutritional and immunological buffers, weaning exposes the child to increased environmental stress. Consequently, poor nutrition and diarrheal disease, which is most common in the first two years of life, are the most common causes of growth retardation at the time of weaning (Martorell, 1989). This suggests that maternal buffering in the first two years is crucial for survival and
long-term wellbeing and that it would be adaptive to wean children after the completion of infancy. In fact, and contrary to modern clinical advice, on evolutionary bases the complete cessation of dependence on breast milk in humans should occur between 2.5 and 6.5 years of age (Dettwyler, 1995). However, weaning in human populations takes place at very different times based on a variety of biocultural factors. As a consequence, infant feeding practices may play a major role in determining adult growth outcomes by exposing the growing body to stressors it is not yet ready to cope with (Dettwyler and Fishman, 1992).

3.3.2 Timing of the Perturbation

Timing of environmental perturbations is also critical. Several lines of evidence indicate that, due to intra-skeletal heterochrony of growth (Humphrey, 1998), the timing of environmental perturbations affects different parts of the skeleton in unequal ways (Bass et al., 1999; Bradney et al., 2000; Nyati et al., 2006). Using anthropometric methods, Bass and collaborators (Bass et al., 1999; Bradney et al., 2000) demonstrated that in both sexes growth rates of limb bones remain constant until puberty and then drop dramatically, while the trunk shows slower rates until puberty, when it peaks and then accelerates after puberty. Hence, sitting height grows slower than limbs until puberty, when it finally catches up. Based on the data presented in these studies, the authors argue for a model of human growth in which the tempo (rates) of growth is region-specific. Also, they indicated how insults during different phases of growth will have different outcomes: reduced limb length (prepuberty) or reduced trunk length (puberty).
On this basis, it can be theorized that perturbations of growth resulting in altered rates and/or duration of the each growth phase will produce different growth outcomes in terms of both stature and body proportions. This seems to be indeed the case.

3.4 Catch-up Growth

Further complicating the understanding of the mechanisms involved with determining adult growth outcomes is the potential for catch-up growth, that is, the reversal of earlier growth retardation. Martorell and colleagues (1994) reviewed the evidence of catch-up growth as observed in three different situations: 1) continued residence in the environment that gave rise to stunting; 2) continued residence in the same environment with improvements in nutrition; 3) relocation from the environment that gave rise to stunting. Evidence indicates that the potential for catch-up growth depends on several factors, but mostly on age at onset of stunting and age at the time environmental conditions are improved. Both stunting and catch-up growth are more common in the first phases of growth since this is the period of fastest growth.

Catch-up growth has been documented in several populations, but its mechanisms are not entirely known (Martorell et al., 1994). In general, it is thought that in response to improved environmental conditions, stunted children can – at least in part – recover from linear growth retardation through increased growth rates and/or delayed maturation (Golden, 1994; Martorell et al., 1994; Gafni and Baron, 2000). However, delayed maturation is generally not such that complete recovery can take place, and faster growth rates in improved environment might actually anticipate maturation, hence reducing the potential for catch-up growth. In a review of the literature on the topic, Golden (1994)
discusses the possibility of complete catch-up growth in stunted children. In particular, evidence tends to indicate two possibilities: 1) once the perturbation has occurred catch-up growth is not possible; 2) catch-up growth is possible but requires notable changes in the environment, which are unlikely. This latter explanation seems particularly appropriate to explain the discrepancies reported in the literature on catch-up growth occurrence (Handa and Peterman, 2009). Additionally, catch-up growth potential is determined by the entity, duration or recurrence of the insult, and the mechanisms by which it mediates growth retardation.

Admitting that catch-up growth is indeed possible, how can it be measured? In theory, it would be possible to evaluate whether there is a reduction of growth retardation between consecutive measurements of the same individuals. This has been done using either raw data or z-scores, with apparently conflicting results (Martorell, 1994; Adair, 1999). In a review of the assessment of catch-up growth, Cameron and coworkers (2005) discussed the problem represented by regression-to-the-mean, which is a tendency of sampling data to converge toward the mean of the actual population. In practice, regression to the mean is an inverse relationship between initial height and later height gain, that is, on statistical grounds it predicts that shorter individuals will tend to show larger height increases over time. In this case, an increase in stature may not be due to actual catch-up growth, but to the statistical distribution adopted and the effects of consecutive sampling. Regression-to-the-mean is particularly insidious because, albeit for totally different reasons, it is expected to produce the same results of catch-up growth. Hence, how can catch-up growth be distinguished from regression-to-the-mean? Cameron and coworkers (2005) demonstrated that catch-up growth is better assessed
through the use of z-scores rather than raw data. This conclusion is supported by several facts. First, the strength of the correlation between early stature and later gains in terms of raw data is confounded by changes of stature distributions with age. Raw data are therefore not readily applicable, while z-scores are, since by their very calculation they incorporate information on stature for age. Second, catch-up growth can only be demonstrated in comparison to expected values of a reference population, and that is exactly the purpose of z-scores. Lastly, through the computation of z-scores, it is possible to identify and remove the effects of regression-to-the-mean, therefore evaluating catch-up growth only. As a consequence, catch-up growth can be defined as a change in z-score over time beyond what is predicted by regression-to-the-mean. It is therefore possible to calculate catch-up growth using the equation \((z_2 - rz_1)\), that is, the difference between observed \((z_2)\) and expected \((rz_1)\) height at follow-up, where \(z_2\) and \(z_1\) are the z-scores observed at the time of the two consecutive measurements and \(r\) is the correlation between them. If the value provided by the equation is positive, it can be concluded that catch-up growth has occurred.
CHAPTER 4: LONGITUDINAL GROWTH, STATURE, AND INFERENCES ON EARLY LIFE CONDITIONS IN THE PAST

From the foregoing review of the mechanisms of longitudinal growth and its disruptions, three important concepts emerge: 1) longitudinal growth is a complex physiological process finely regulated by several hormones, and its disruption results in linear growth retardation; 2) periods of faster growth are more susceptible to environmental perturbations; 3) intra-skeletal heterochrony determines differential susceptibility of body regions to environmental perturbations during different growth phases. Based on these concepts, it is clear that – even though the specific nature of the environmental stressors may not be determined – adult stature and body proportions may provide useful inference on the degree of environmental stress experienced by an individual during growth. Specifically, from the discussion above follows that within a population, shorter individuals will have likely suffered from insults earlier in life and/or for a longer time. In fact, due to its well-known association with environmental quality, stature is commonly used as an indicator of overall environmental quality in both living and archaeological populations (Martorell, 1989; Frisancho, 1990; Larsen, 1997; Larsen, 2002; Steckel, 2004; Maat, 2005; Piperata, 2007; Frisancho, 2008).
However, while observations of stature in relation to environmental stress in living populations are typically substantiated by rich biological, ecological, social and cultural data, similar information is typically not available in studies of past populations. Indeed, the study of growth in the past and the use of stature as an indicator of environmental quality of ancient populations are fraught by specific theoretical and methodological complications. First, the study of past populations hinges on the assumption that the analysis of skeletal remains can foster information that is comparable to that obtained on living populations. The validity of this assumption and the reliability of the information drawn from skeletal remains have therefore been matter of intense debate within the discipline (Wood et al., 1992; Wright and Yoder, 2003). Second, even when such assumptions are met, the study of life in the past is hindered by matters of preservation and lack of contextual data, which have been addressed by developing multidisciplinary approaches to the excavation and analysis of human remains from archaeological contexts (Larsen, 1997, 2002; Buikstra and Beck, 2006). This chapter reviews the theoretical and methodological issues intrinsic in the study of growth and inference on environmental conditions from human skeletal remains, which have led to the formulation of the research presented in this dissertation.

4.1 Growth in the Past: Useful Inferential Tool or Paradoxical Evidence?

4.1.1 Stature and the “Osteological Paradox”

Because early life conditions in the past are not easily assessed directly, bioarchaeologists routinely rely on skeletal growth as an indicator of overall health status during growth (Saunders and Hoppa, 1993; Larsen, 1997; Pietrusewsky et al., 1997;
Exemplary cases of stature variation over time and in relation to major population events (subsistence shifts, population contact, climate change) have been reported and demonstrated the value of skeletal growth for reconstructing accounts of life in the past (Cohen and Armelagos, 1984; Larsen, 1994, 1995; Gerhards, 2005; Formicola and Holt, 2007; Gustafsson et al, 2007). Nonetheless, the relationship between early life conditions and growth in skeletal populations is often equivocal (Larsen, 1997; Temple, 2008; Klaus and Tam, 2009), likely due to the fact that variation in stature depends on a large number of factors.

Being a sensitive indicator of developmental stress, stature undergoes natural selection. It may be selected directly in relation to specific metabolic or climatic adaptations, or indirectly because it is associated with other undesirable growth outcomes. Considering the general relationship between overall well-being and stature, the expectation is that selection will eliminate short-statured individuals from the population. The implication of this selective pressure is that the stature distribution in the survivor group may not be representative of the entire variation within a population. In fact, the observed variation, as screened by natural selection is contingent on environmental conditions. This implies that, when overall stress is elevated, selection on stature should be more evident due to an overall increase in mortality. In contrast, when overall stress levels decrease, natural selection is milder and mortality decreases, hence increasing the observable variation in stature. On theoretical grounds, it is possible to predict that under stricter selection the mean stature of the survivor group will be greater than in phases of milder selection. This counterintuitive conclusion was eloquently
illustrated by Wood and colleagues (1992) in their formulation of the “osteological paradox.”

In a paper that has become a major milestone within the discipline, Wood and colleagues (1992) questioned the classic interpretations of osteological evidence in paleodemography and paleopathology. They brought attention to three major problems in osteological data, which pose a model identification problem and require particular interpretive attention. Specifically, such problems are: 1) *demographic non-stationarity* - real populations are not static or avulse from context, hence it is necessary to evaluate the effects of fertility variation on age-at-death distributions; 2) *selective mortality* - since death is a selective process, death composition samples are always biased and not representative of the living, surviving group; 3) *hidden heterogeneity in risk* – populations are composite of individuals with different frailty and mortality risks, that are unfortunately not know *a priori* and therefore indiscernible in skeletal samples. As a result, these authors questioned the validity of classical interpretations of skeletal pathology and demographic profiles of past populations and offered alternative interpretations. In particular, they argued that the manifestation of skeletal lesions may reflect better, rather than worse health. In brief, since expression of bone lesions requires a long time, lesions will only be found in individuals who survived the pathology (at least for a certain time), while they will be absent in the skeletons of those individuals who died immediately. Hence, “better health makes for worse skeletons” (Wood et al., 1992:356). Wood and colleagues concluded that, while classic interpretations of skeletal evidence may still be valid, it is essential to consider alternative, possibly less straightforward explanations.
When applied to stature, the osteological paradox warns us from reaching simplistic conclusions simply based on absolute bone lengths. More generally, the paradox stresses the fact that the study of skeletal growth in past populations is fraught with complications intrinsic to the nature of skeletal assemblages, such as small sample size, poor preservation, minimal knowledge of the factors contributing to environmental quality, and composition biases of mortuary samples. All such difficulties are particularly present in the study of subadult skeletal growth in skeletal populations, because the individuals under examination are the non-survivors of the population. As a consequence, information on skeletal growth in subadult populations may be counterintuitive and not easily interpreted. The study of adult stature is less problematic, provided that proper consideration is given to the issues raised by the osteological paradox and multiple lines of evidence are employed to interpret the observed pattern of variation.

It should be noted that, even though the selective model proposed by Wood and colleagues (1992) is certainly possible, it is not clear whether it is probable. In fact, evidence of high level of stunting among adults in developing countries seems to suggest that high selective pressures on stature are not the rule. A relevant question, then, is what are the environmental factors that lead to increased mortality and selection, and how can they be quantified in archaeological contexts. To date this is an issue that remains largely unanswered and requires further, multidisciplinary research.
4.1.2 Beyond the Paradox: New Approaches to the Study of Stature in Skeletal Populations

Even though it is undeniable that the analysis of growth and life history in the past is complicated by the inherent limitations of skeletal samples, since the formulation of the osteological paradox new approaches have been advanced that attempt to overcome them. In a commentary on the “paradox” paper, Byers (1994) proposed a way to assess whether a population is undergoing selection for stature. Assuming – as is generally the case – that stature in human populations is approximately normally distributed, the removal of shorter individuals at young ages should produce a skewed distribution in the adult population (both living and dead). This fact provides a way to statistically test the hypothesis that the population is being selected for stature: if selection is present, the distribution will deviate from normality. Such deviations from normality can be evaluated based on the degree of skewness and kurtosis. A complication of this test – which is absolutely sound in theoretical terms – is that significance of such statistical parameters requires either large sample size or massive deviations, conditions that are not typically satisfied by archeological samples. Byers proposed a way to circumvent these statistical issues, namely relying on numerous skeletal elements and applying simple tests (Student’s t and chi-square - $\chi^2$) in order to determine whether trends and deviations do in fact exist. Wood and Milner (in Cohen et al., 1994) later proposed the use of conditional distributions of stature among survivors as a way to estimate the trait’s effective mortality employing maximum-likelihood methods. Nonetheless, this approach also rests on rather theoretical grounds and is not easily applied. The methods proposed by these authors are theoretically meaningful, but their use in the study of archaeological collections is limited
due to small sample size and sample composition. Rather, an integrated, multidisciplinary approach to skeletal samples may be more applicable and help to overcome these theoretical issues and foster meaningful results in bioarchaeological analyses (Larsen, 2006). Indeed, numerous bioarchaeological investigations now incorporate information drawn from multiple lines of evidence and progressively more sophisticated research methods. For instance, more traditional osteometric and paleopathological data are increasingly more frequently examined and interpreted in relation to biocultural information drawn from a variety of interdisciplinary methodological approaches including biochemical analyses of mineralized tissues, biomechanical analyses of long bones, and genetic and immunological analyses (Sealy and Pfeiffer, 2000; Tung and Knudson, 2008; Tung, 2008; Vercellotti et al., 2008; Kemp et al., 2009).

### 4.2 Methodological Aspects of Stature Estimation From Skeletal Remains

Even when contextual information is available and the validity of assumptions and the interpretation of the evidence can be incontrovertibly tested, there still remain practical and methodological issues associated with the study of stature (and more in general growth) in the past.

One of the major obstacles to the proper analysis of stature in the past is the fact that the preservation of skeletal material in bioarchaeological context is often suboptimal (Gordon and Buikstra, 1981; Walker et al., 1988). A variety of taphonomic factors, including soil chemistry and faunal alterations are known to alter bone preservation. Additionally, funerary practices may also be at the basis of differential preservation and therefore alter the representativeness of skeletal assemblages. As a consequence, only
partial skeletons and/or fragmentary skeletal remains may be available for the analysis. Clearly, this sets a number of problems for the study of stature, which is a characteristic of the individual emerging from the sum of multiple skeletal elements and soft tissues.

An expedient approach to circumvent this issue is to examine only long bones known to exhibit a strong correlation with stature, such as the femur and tibia (DeWitte and Hughes-Morey, 2012). This research strategy has the major advantage of being applicable to partial and even comingled skeletal remains and does therefore allow for the collection of data on larger sample sizes. However, the analysis of long bones provides only partial information on body size. Therefore, it is common practice to use methods that allow reconstructing living stature from one or more skeletal elements.

Three methods may be used to reconstruct stature from skeletal remains: the measurement of length in the grave, the anatomical method, and regression formulae.

Length in the grave consists in the measurement of the length of a skeleton in supine position at the time of excavation (Boldsen, 1984; Petersen, 2005, 2011). Petersen (2005) evaluated the accuracy of the measurement compared to other methods for stature estimation and found that length in the grave allowed reconstructing living stature with no bias. However, in a re-evaluation of the previous work, Petersen (2011) suggested that this method may actually underestimate living stature by approximately 2.5 cm, and that the addition of 2.5 cm to the measured length in the grave produces improved, unbiased estimates. As pointed out by Petersen (2005), this method has the advantage of relying on intrinsic properties of the skeleton examined and of being entirely independent from reference population information. However, its application is limited to supine and complete, undisturbed burials.
Accurate stature estimates are best obtained with the anatomical method, first advanced by Fully (1956) and recently revised by Raxter and colleagues (2006, 2007). In this method, living stature is approximated as the sum of measurements of all skeletal elements contributing to height, namely skull, trunk, lower limb bones (all together referred to as skeletal height), and a corrective factor for soft tissues. After extensive systematic evaluation of the technique, Raxter and colleagues (2006, 2007) developed an improved version of Fully’s method, which refines the measurements to be taken, provides better soft tissue corrective factors and accounts for age-related stature changes. This new technique estimates living stature from skeletal height by means of two formulae, used differentially when age at death is known or unknown. As noted by Raxter and colleagues (2007), even though age estimates for bioarcheological remains are inevitably imprecise, it is advisable to incorporate them into living stature reconstruction in order to avoid systematic underestimation in younger individuals. The anatomical method provides highly accurate estimates (±2.05 cm) and should be employed whenever complete skeletons are available (Krogman and İşcan, 1986; Klepinger, 2006). Nonetheless, it is not applicable when dealing with partly incomplete skeletal remains. In such cases, it is possible to estimate stature from the length of one or few skeletal elements through regression techniques. Regression formulae are mathematical models, which allow stature prediction on the basis of its covariation with long bone length. Most techniques are developed from recent samples for which intra vitam stature is known (Krogman and İşcan, 1986; Klepinger, 2006), but are commonly applied when living stature of a specific population is not available. In the latter case, regression equations can be developed from reconstructed living stature obtained through the anatomical
method. This technique has been successfully used to develop specific regression formulae for bioarcheological populations (Sciulli et al., 1990; Sciulli and Giesen, 1993; Formicola and Franceschi, 1996; Sciulli and Hetland, 2007; Raxter et al., 2008).

Due to their applicability to incomplete remains and easy computation, regression formulae are most commonly employed both in forensic and bioarcheological contexts. Nonetheless, their use is not risk-free. A calculated estimate's accuracy is affected by several biological factors, in particular genetic similarity and ecogeographic adaptations (i.e., limb length proportions). As a consequence, using a formula on a sample inconsistent with the population it was calibrated on may result in poor estimates (Konigsberg et al., 1998). Regression formulae selection requires careful examination in the context of the specific population of interest.

In deciding the most suitable equation for stature estimation in a bioarcheological context, it is general practice to seek methods devised from modern populations deemed to be genetically similar to the one under study. However, ancestry alone may not be a good predictor of which stature equations to use. In fact, since adult stature attainment is mediated by environmental factors, genetic affinity per se is only indicative of growth potential and has limited predictive value on actual body size or proportions. This problem could be minor if the environment affected only body size, maintaining the same body proportions. In such a case it could be argued that the effects of isometric changes on regression equation accuracy could be negligible because the ratios between body segments would likely remain the same. However, several studies on genetically similar populations exposed to different environments indicate that allometric changes do occur and secular trends in stature are accompanied by changes in body proportions (Tanner et
Consequently, regression formulae should be chosen cautiously for bioarchaeological remains. Recently, the accuracy of traditionally used regression methods and their usefulness in reconstructing past populations’ life conditions has been questioned (Formicola, 1993, 2003; Petersen, 2005; Giannecchini and Moggi-Cecchi, 2008) and new, more accurate, population-specific techniques are being sought (Hanson, 1992; Raxter et al., 2008; Vercellotti et al., 2009).

Lastly, as pointed out by Konigsberg and colleagues (1998), issues exist with the very statistical methods employed for developing regression equations. Beginning with Pearson (1899), all mathematical models employed in stature reconstruction were based on inverse calibration techniques, estimating stature from bone lengths. Inverse calibration does provide accurate estimates if the specimen analyzed fits in the stature distribution of the reference population (Konigsberg et al., 1998). This a priori condition cannot always be satisfied and in such cases classic calibration techniques (i.e., regression of bone length(s) on stature) are preferable (Ross and Konigsberg, 2002). Although applying classic calibration may produce estimates with higher standard errors, it avoids the risk of drawing conclusions based on biased estimates (Konigsberg et al., 1998). Inverse calibration methods remain highly valuable when the above-mentioned condition is satisfied. This is particularly true when regression formulae are developed on specific bioarchaeological samples and applied to fragmentary remains within the same population, or to populations known to exhibit similar body proportions.

Besides the well-known issues with the selection of appropriate regression formulae for the reconstruction of stature from skeletal remains, these mathematical methods have
additional limitations when they are used to infer life conditions in the past. Specifically, regression formulae have the tendency to minimize variation within the population by producing converging estimates based on the average relationship between variables. In reality, the relationship between the element(s) used to calculate stature and actual stature is never the same for all members of a population and individuals deviate more or less from the expected pattern. As a consequence, while the inferences on life conditions based on reconstructed stature may be valid at an aggregate level, they fail to capture and depict intrapopulation variation in stature as the outcome of individual and unique life histories. In this regard, the heterochrony of growth and differential susceptibility of the human skeleton suggest that body proportions could provide additional information on life conditions during growth.

4.3 Body Proportions and Inference on Life Conditions in the Past

In spite of their potential value in interpreting past life conditions (Bogin and Rios, 2003), body proportions are relatively unexplored at the bioarchaeological level. Additionally, the inferential value of body proportions is limited by the fact that the relationship between early life conditions and growth remains largely untested in skeletal populations. In an effort to address these issues, Boldsen (1998) examined the correlation between early growth disruptions, as determined from linear enamel hypoplasia (LEH), and stature and body proportions in a Medieval Danish population. No correlation was found between LEH episodes and stature, but body proportions (long bones to stature) changed in response to early growth disruptions. Boldsen (1998) suggested that such changes in body proportions might have taken place as a consequence of catch-up growth
following the stress episode that caused LEH. Additionally, he highlighted the fact that, lacking any contextual information besides the sex of each individual, it was virtually impossible to explore the role of other confounding factors on growth. This study clearly indicated that body proportions have the potential to complement stature as indicators of life conditions in the past, but their analysis requires the evaluation of multiple factors.

Prompted by similar considerations, Schweich and Knüsel (2003) explored male physique in the Middle Ages in relation to socio-economic circumstances. Specifically, they examined stature and body mass (both calculated through regression formulae), the body mass index, and body proportions (indicated by relative leg length – (femur+tibia/stature)) in five samples of different socio-economic and health status. Their results indicated that stature variation in these groups was accompanied by changes in relative leg length, and reflected variation in the biocultural milieu. In order to increase sample size, this study employed regression formulae for the estimation of stature from femoral length and used lower limb length to define relative limb proportions. It is unclear whether this methodological approach masked or otherwise interfered with some of the biological variation in the variables examined. In any case, this study showed the great potential of complementing stature with other indicators of environmental quality during growth.

Given the promising results of these studies, it is surprising that no further attempts have been made to investigate how body proportions vary in relation to different biocultural factors in human populations. Clearly, an improved understanding of this aspect of human biological variation can provide useful insights on how humans adapt to their specific socio-bio-cultural milieu and allow reconstructing more accurate accounts
of life conditions experienced by past populations. A relevant question is, therefore, why only a handful of studies have examined body proportions in past populations. A likely reason for such a limited literature on the topic is that the investigation and interpretation of biological variation in the past is fraught by several intrinsic limitations. Specifically, poor skeletal preservation, small sample sizes, and the lack of accurate contextual biocultural information represent major hindrances to the study of body proportions in skeletal assemblages. Consequently, the primary and most crucial obstacle to be overcome when approaching this kind of study is the identification of a collection suitable for the analysis. Minimally, such a collection must include complete, well-preserved individual burials, and be accompanied by extensive contextual information. Additionally, any study of growth in the past should incorporate and examine models of variation developed on living populations for which extensive contextual biocultural information is available. All such complications have undoubtedly hindered the study of growth outcomes in the past in relation to specific biocultural factors.

In this study, I attempt to overcome such limitations and to improve our understanding of human variation in response to the biocultural milieu across time and space. To this end, as will be discussed in the following chapters, I adopt strict criteria for sample and method selection, and combine evidence from both living and biorchaeological populations in tandem.
CHAPTER 5: PURPOSE OF THE STUDY AND RESEARCH DESIGN

5.1 Purpose of the Study

This study explores the patterns of variation in stature and body proportions at the intra and interpopulation level in both living and bioarchaeological populations. Even though an association between biocultural factors and stature has been long observed in human biology, it is unclear how the same factors may impact body proportions. I explore differences in skeletal growth outcomes within populations in relation to sex, severe growth retardation, and differential access to resources. Additionally, I explore the interpopulation variation among bioculturally and geographically distinct populations. It is expected that significant differences exist because – in spite of intragroup biosocial inequality – all members of a population share most aspects of the same biocultural environment.

This study is unique in that it addresses the same research questions in both living and bioarchaeological populations in tandem and has the potential of shedding light on the mechanisms underlying variation in growth outcomes in both living and past populations.

The specific research questions addressed in this study are:
1) Do males and females within the same population exhibit different body proportions?

2) Is growth retardation associated with changes in body proportions?

3) Is differential access to resources associated with changes in stature and body proportions?

4) Do stature and body proportions allow us to differentiate between populations exposed to different environmental conditions?

5.2 Research Design

Few studies have investigated the degree of variation in body proportions within a population, and no previous attempt has been made to examine such variation in both living and past populations at once. This is the objective of this dissertation. The decision to address the same research questions in both living and bioarchaeological populations in the same study emerges by the realization that the investigation and interpretation of biological variation in past human populations is inevitably limited by several difficulties. First, skeletal material from archaeological contexts is generally too incomplete or fragmentary to allow for the analysis of body proportions involving the relationship between trunk length and other body parts. Second, when the material is suitable for the analysis sample sizes tend to be very small. Third, the interpretation of evidence from archaeological sites requires a wealth of biocultural information that may simply not be available due to preservation issues and selective investigation of different aspects of the same excavation. All such difficulties are not typically encountered in human biology studies. Therefore, the evidence gathered on living populations has the potential to
provide useful insights and draw instructive parallels between present and past populations’ biological variation.

5.2.1 Biocultural Approaches in Human Biology

In this study, to improve the understanding of the causes and mechanisms of variation in stature and body proportions, I seek to complement growth data with biocultural information. Biocultural approaches in human biology recognize that culture is an intrinsic aspect of human nature and plays an integral role in shaping the environment in which growth and development take place (McElroy, 1990; Dufour, 2006; Khongsdier, 2007). Consequently, recording and measuring both biological and cultural variables is essential for improving the understanding of the causes of biological variation.

As pointed out by Dufour (2006), the adoption of biocultural approaches encounters some challenges related to the definition, operationalization and multifactoriality of biocultural variables. Referring to her work with the women from Cali, Colombia, included in this study, Dufour (2006) points out how even seemingly common constructs such as “work” or “poverty” may be difficult to define and operationalize. Specifically, a construct such as poverty is neither simple nor universal. First, there are multiple components to what makes somebody “poor”, which go beyond simple material wealth. In fact, poverty is a multidimensional condition that is not limited to material possession, but extends to how an individual feels about his or her role in society and how he or she interacts with others. Second, poverty is a concept that is culturally mediated and as such its perception is not universal. This aspect is particularly important because limited or
partial understanding of the cultural framework may bias how an external observer
defines and records poverty, hence affecting the validity of the observations. Biocultural
approaches recognize that these challenges exist and set to address them by openly
addressing the interrelation between culture and biology in human populations.

In the following section I provide some definitions of how variables are defined and
interpreted in this study. The specific details on how these variables and additional
variables included in the interpretation of the results were assessed in each sample are
provided in Chapter 6.

5.2.2 Definitions

The following concepts are at the basis of the formulation of the research
questions addressed in this dissertation. It is therefore important to clearly indicate how
they are used throughout this study.

*Intrapopulation Variation.*

In this study, I define intrapopulation variation as the biological variation
observable within a single population, which is relatively homogeneous in terms of
environmental, biological and cultural factors. In this sense, a suitable population for this
kind of analysis is a population whose individual members: 1) are exposed to the same
environmental conditions – with no major variation in climatic, geophysical and
ecological conditions; 2) share a similar biological history and exhibit biological
continuity – affected by minimal external gene flow – for an extended period of time; and
3) show relative cultural stability, with no sudden changes in social organization,
subsistence strategy and cultural beliefs. According to this definition, the subject of intra-population studies may not be restricted to a cross-sectional examination of biological variation at a specific point in time, but may also examine variation in the same population over time, provided that there are no major changes in the population’s eco-bio-cultural milieu. This is particularly true when studying variation within past human populations, where limited sample size and dating issues may not allow researchers to restrict the analysis to a specific point in time.

Interpopulation Variation.

In contrast with the previous definition, interpopulation variation is the biological variation observed between populations that are ecologically, biologically, socially and/or culturally distinct. The concept explored in this research is that the unique combination of environmental characteristics experienced by each population is reflected in unique and identifiable growth outcomes.

Sex and Gender.

The terms sex is used strictly to refer to an individual’s biological sex. In this regard, individuals are referred to as males and females. In contrast, gender expressions (men, women, boys, girls) are employed to refer to cultural roles assigned to males and females. In this study, the investigation of sex-related differences in body proportions is based on the concept that differential environmental sensitivity is due to strictly
biological factors. Nonetheless, gender roles and behaviors are considered in the interpretation of the results.

**Severe Growth Retardation (Stunting).**

Severe growth retardation, also referred to as stunting, is identified by means of z-scores on the basis of stature values falling below -2 standard deviations of the population distribution. Typically, stunting is determined by standardizing individual data by the parameters (mean and standard deviation) of an international growth reference (Frisancho, 2008).

**Access to Resources.**

In this study, access to resources includes different factors that may cause social inequality and consequently differential access to resources. Specifically, the factors examined include socio-economic status (SES) as well as relative isolation. SES is primarily based on differences in social hierarchy and wealth; relative isolation is defined in terms of proximity to a road connecting different communities. Details on how status and isolation groups were assigned are discussed in Chapter 6.

**Stature and Height.**

The term stature and height are frequently used interchangeably in the human biological literature, while the term stature appears almost exclusively in the literature regarding skeletal remains. In this study, stature is used for both living and skeletal populations; conversely, height is used specifically to refer to the anthropometric variable
measured directly on a living subject. Similarly, sitting height refers to the anthropometric variable, while the term trunk is used more broadly. Lastly, leg length is typically used to indicate the anthropometric variable calculated based on height and sitting height; lower limb, femur and tibia are the terms preferentially employed in regard to skeletal remains.

5.2.3 Sample Selection

One of the main goals of this study is to assess variation in body proportions in relation to biocultural variables in both living and past populations. This implies the need to identify suitable samples that allow addressing the different research questions posited. Clearly, collecting anthropometric data and detailed biocultural information for different living and bioarchaeological populations goes beyond what can be achieved by a single individual. Therefore, this study includes both data directly collected on skeletal material, and datasets previously collected by other authors on living populations.

The archaeological collections were selected based on several criteria including skeletal completeness, availability of contextual information, and historical contemporaneity. Skeletal completeness is crucial because the analysis of stature and body proportions in the past requires the presence of all components of stature. This is particularly problematic because skeletal elements rich in trabecular bone, such as the vertebral bodies and tarsal bones, have the tendency to be poorly preserved. As a consequence, the number of individuals suitable for analysis within a population is relatively low and sample sizes typically small. Conceptually, it would be possible to carry out the analyses on pooled samples from the same geographic area and time period.
However, the extent and nature of the impact of environmental factors on body proportions has not been previously examined at the intrapopulation level. It is therefore unknown whether smaller samples may be pooled together without confounding the variation pattern to be examined.

Even when skeletons are well preserved and complete, the interpretation of intrapopulation variation hinges on the ability to distinguish clear biocultural differences in regard to sex and access to resources. While sex is easily estimated from complete adult remains, the identification of social inequality is much more subtle and must rely on multidisciplinary studies on the population under examination. Such rich contextual information is not commonly available, especially for archaeological sites that have not been completely excavated. Lastly, in order to allow for comparative analyses among populations, the samples selected must be relatively contemporaneous, that is, dated to the same historical period. The application of such criteria led to the selection of two skeletal samples from medieval Europe (1 from Italy and 1 from Poland). Both samples satisfy the completeness requirement; contextual information from excavation and analyses is available for both samples, although not in equal measure. Samples are described in detail in Chapter 6.

The selection of the living samples was based on the availability of measurements of both stature and sitting height in order to allow for the analysis of body proportions, on the availability of biocultural information, and similar geographic provenience. Additionally, samples from developing countries, experiencing environmental conditions arguably more similar to those of past populations than industrialized populations, were sought. The samples included are all from South America (1 from rural Brazil, 1 from
rural Guyana, 1 from urban Colombia – see Chapter 6). While all datasets employed feature the same anthropometric variables, they vary in terms of representation of the sexes, biocultural information and differential access to resources.

5.2.4 A Note on Comparisons Between Living and Bioarchaeological Populations

This dissertation is founded on the idea that examining and comparing the patterns of variation observed in living and past populations can provide improved insights than either area of investigation alone.

At the same time, the variables measured and analyzed in human biology and bioarchaeology, while representative of the same biological relationships, are not exactly the same because of the relative presence/absence of soft tissues. This implies that data collected on living and past populations cannot be compared directly. A possible solution to this problem may be that of estimating anthropometric variables from osteometric measurements. This is typically done in the case of stature, where regression methods are employed to estimate living stature from skeletal measurements introducing a corrective factor for soft tissues (Fully, 1956; Raxter et al., 2006, 2007). The application of regression methods to the estimation of other living anthropometric variables, such as sitting height, from skeletal measurements is problematic. Such estimation may be based on published data or developed directly from cadaveric samples. In either case, the estimation of variables from their relationship in other populations implies that the actual pattern of variation may be altered in at least two ways. First, by assuming that the same relationship between variables is the same across populations, the use of an external reference may mask the actual pattern of intrapopulation variation. Second, the use of
regression methods has the tendency to minimize variation within the population by producing converging estimates based on a best-fit model for the relationship between variables.

The research questions addressed in this study have not been previously tested and the degree of intrapopulation variation in body proportions is largely unknown. Given the fact that there is no evidence that the same biological relationships may be valid for all human populations across time and space, and in light of the potential confounding factors that may be introduced in the analysis by reconstructing variables under such assumption, in this study anthropometric and osteometric data are not analyzed together. Rather, the same questions are addressed in both living and archaeological populations and the patterns emerging from such analyses compared in interpretive and theoretical terms.
CHAPTER 6: MATERIALS AND METHODS

6.1 Materials

6.1.1 Materials I: Living Populations

Three samples from as many living populations are included in the study: 1) *Ribeirinhos* inhabiting rural communities in the Brazilian state of Pará; 2) Makushi from the savannahs of interior British Guyana; and 3) urban citizens of the city of Cali, Colombia.

6.1.1.1 *Ribeirinhos*

Extensive anthropometric and biocultural data collected by Barbara Piperata starting in 2002 (Piperata, 2005, 2007) make Brazilian *Ribeirinhos* an excellent sample in which to explore intrapopulation variation in stature and body proportions. The sample includes individuals living in upper-land (*terra firme*) communities located in and around the Caxiuanã National Forest in the State of Pará (Fig. 6.1) (Piperata, 2007). The local people self-identified as *Ribeirinhos* but are also referred to as *Caboclos* in the literature (for a review of the terms see Piperata, 2005). They are a mixed ethnicity (Amerindian/Portuguese and to a lesser extent African) group formed during the colonization of the Amazon region by the Portuguese in the 16th century (Harris, 1998).
The region, in general, is considered part of a black-water river system (Costa et al., 2002). Such ecosystems are characterized by acidic water and soils and are known for their low productivity relative to other Amazonian ecosystems (Moran, 1993).

Figure 6.1. Location of the Ribeirinhos communities included in the study. Image courtesy of Barbara Piperata, Ph.D.

People and Field Site

At the time of data collection, the communities were rural, had no electricity or running water, and only a few households had pit toilets. The majority of households used the forest and river for waste disposal. Water for cooking and drinking was collected from the river or, in a few cases, from hand-dug wells, and trash was burned, buried, or
dumped in the river. While people were aware of public health messages regarding the transmission of disease via water, efforts to treat drinking water were uncommon and, when practiced, inconsistent. For example, Piperata (2005) observed the use of chlorine drops to treat drinking water in a small number of households. However, the amount of chlorine used was insufficient for the volume of water, household members drank treated and untreated water on the same days and, the results of a household survey revealed that no household reported purchasing or using chlorine, or any other type of water treatment, on a regular basis. No local study of water quality is available; however, the fact that gastrointestinal infections were the second most commonly reported cause of morbidity implies that water-borne illnesses are an issue in these communities.

Homes built on stilts, were made of wood and covered with one of three materials, palm fronds, ceramic tile, or an industrialized, fire retardant material referred to as Brasilite. Most households consisted of a nuclear family but some included extended kin. Average household size was 7.6 (range: 3-15). All the people practiced slash and burn agriculture with bitter manioc (Manihot esculenta) as their staple crop. Manioc was consumed primarily in the form of farinha, a toasted meal, and was the most important source of calories and carbohydrates in the diet (Murrieta et al., 2008; Piperata et al., 2011b). Fish and, to a lesser extent, hunted game were the most important sources of protein, and açaí (Euterpe oleracea), a local palm fruit consumed primarily in the form of a juice, was an important seasonal source of calories (Piperata et al., 2011b). While the people cultivated, fished, hunted, and collected the majority of the food they consumed, they were also actively involved in and dependent upon the regional market economy. Men and women shared the work associated with the cultivation and processing of
manioc, which included clearing the forest, burning, planting, weeding, harvesting and finally, processing the roots into *farinha*. Fishing, hunting and the collection of *açaí* were primarily male activities, although women cleaned and prepared the fish and game and extracted the *açaí* juice. Women were also responsible for all housework and childcare.

**Access to Medical Care and Disease**

Access to medical care was limited. The closest clinic and hospital were located in the town of Portel, which was an eight-hour boat ride from the communities. Due to the costs of fuel and what were described by the local people as poor services due to limited medical staff and medications, trips to town for care were limited to what were perceived as emergency situations (i.e., snake bites and broken bones). As part of a household survey conducted in 2002, people were asked to list the most common causes of illness. Their responses indicated that respiratory infections (i.e., flu, sinus congestion), gastrointestinal problems (i.e., diarrhea, vomiting, parasitic infections), skin related issues (i.e., rashes, itching) and general aches and pains related to heavy labor and/or arthritis were the most common causes of morbidity. Distance to town also limited the access to pre- and postnatal health services. The majority of women relied on a local midwife to assess their condition during pregnancy and assist with birth. Hospital births were rare (<10%) and were limited to instances where the fetus was identified as being breach by the midwife or, in a few cases, where the mother was young (14-15 years) and her parents, out of fear, paid to have her transported to town to deliver her first child.

Follow-up neonatal care was also limited and typically ceased after the infant was fully
vaccinated. Overall, Ribeirinhos are subject to chronic stress – as evidenced by high rates of growth retardation – which has been associated with nutritional stress during growth and development and poor access to healthcare (Silva and Crews, 2006; Murrieta et al., 1998; Giugliano et al., 1981, 1984).

Previous Studies on Growth Outcomes

Piperata (2007) assessed the nutritional status of children and adult Ribeirinhos from these communities from anthropometric measurements including stature, weight, skinfolds and circumferences. She found that, with the exception of children younger than 3 years, all age groups in the population exhibited signs of growth retardation, with average z-scores falling below -2 standard deviations of the international reference. In particular, 60% of adult men and 70% of adult females were found to be stunted and no significant secular trend in stature was observed. Based on this evidence, Piperata (2007) concluded that environmental conditions affected growth in this population and no significant environmental change had taken place over the last few generations.

The Sample

This study included a total of 172 (88 female; 84 male) adults between 18 and 77 years of age, which represent a subset of the larger sample analyzed by Piperata (2005, 2007). These individuals were included in the study based on the availability of measurements of stature and sitting height, as well as age. This population was particularly suited to address the research questions posited in this study because
extremely detailed biocultural data regarding dietary practices, differential treatment of male and female offspring, and female reproductive histories are available.

6.1.1.2 Makushi

The Makushi are Amerindians inhabiting savannas and rain forests in Guyana and Brazil. Starting in 1996, the Guyanese government established a program aimed at preserving biodiversity while promoting the development of the interior. This led to the creation of a new national Park - the Iwokrama International Centre for Rainforest Conservation and Development -, and to the creation of a road connecting the rainforest to the coast of the country, therefore increasing exposure of the natives to outsiders (Wilson, n.d.). These changes have since been threatening and altering the traditional lifestyle of the Makushi living in Guyana. To evaluate the impact of the new developments in the region on the Makushi, a project entitled ‘Culture change and health among the Makushi’ was initiated in 1999 (Wilson, n.d.). As part of this broader research endeavor, anthropometric data and information on diet and feeding practices, morbidity and healthcare, and on Makushi culture were collected. Given the fact that differences in access to healthcare and market integration have been observed among Makushi communities (Wilson et al., n.d.), these data are well-suited for an investigation of the potential impact that differential access to resources may have on adult growth outcomes.

People and Field Site

The Makushi a Carib-speaking Amerindian tribe found along the border between Guyana and Brazil. Their presence in Guyana is documented starting at the end of the 18th century, when they are thought to have migrated into the region from the banks of
the Orinoco (Edwards and Gibson, 1979). It is estimated that at this time approximately 9000 Makushi inhabit the Rupununi region in the interior of Guyana (Forte, 1996), a geographic area delimited by the Siparuni River in the north, the Essequibo River in the east, the Kanaku Mountains in the south, and the Takatu and Ireng Rivers in the west along the international border with Brazil (Wilson et al., 2006). Makushi are also present in the Brazilian state of Roraima, although there is little formal contact between the Brazilian and Guyanese communities (Wilson et al., 2006).

This study includes data collected on individuals inhabiting 11 communities in the North Rupununi region (Figure 6.2).

Figure 6.2. Map of Guyana. The detailed map shows the location of the Makushi villages from the North Rupununi region included in the study in relation to the Georgetown-Lethem road and the Essequibo River. Image courtesy of Warren Wilson, Ph.D.
The region is characterized by a multiplicity of ecosystems, including savannas, rainforests and both nutrient-depleted black-water and nutrient-rich white-water river systems (Mistry et al., 2004). Both savannas and tropical forests experience a dry season from October to April, when precipitation decreases drastically, especially in the savannas to the south (Wilson et al., 2006). Over periods of 6-10 years, seasonality in the region is accentuated by climate changes associated with El Niño souther oscillation (ENSO) (Iwokrama International Centre for Rainforest Conservation and Development, 2003).

The Makushi of Guyana live in villages located in the savannas and maintain farms in nearby forests, even though it is not uncommon for farms to be at least a one-hour walk away. Houses are built with wattle-and-daub or clay bricks and have thatched roof (Forte, 1996). The Makushi are exogamous and patrilineal and traditionally practiced cross-cousin, matrilocal unions (Wilson et al., 2011). It is not uncommon for extended families to share the same house. Until recent years, the Makushi traditional subsistence practice consisted in slash-and-burn agriculture for the cultivation of high-cyanide bitter manioc (Manihot esculenta). In order to reduce its toxicity, high-cyanide manioc requires extensive, labor-intensive processing (Dufour, 1989; Elias et al., 2000). The processed manioc results in a loose-grained cereal named “farine”, but may be also used to make bread or fermented drinks (Forte, 1996). The cultivation and processing of the manioc are almost the exclusive responsibility of the women, possibly assisted by older children. Men are generally responsible for hunting and fishing, activities that are performed year-round, although there are seasonal fluctuations (Mistry et al., 2004). In general, fishing provides the majority (49%) of the proteins in the Makushi diet (Palmer,
Palmer (2009) reports that even after increased contact the Makushi are still mostly independent from market economy and their daily diets consisted mainly of manioc, cereals, nuts, fish, fruits and vegetables, and only to a lesser extent by meat and dairy products. Drinking water is drawn from rivers, streams and wells and rarely boiled (Wilson et al., 2006).

Access to Medical Care and Disease

Overall life conditions during growth among the Makushi appear to be fairly poor. High infant (93/1000 live births) and child (169/1000) mortality rates (Wilson et al., 2006) as well as dietary inadequacy (Palmer, 2009) have been reported. Additionally, water sources are frequently contaminated by organic pollutants (KPMG 1999; Guyana Water Incorporated 2003, cited in Wilson et al., 2011) and diarrhea and parasitic infestations widespread (Wilson et al., 2011). Additionally, malaria and dengue fever are endemic in the villages located along rivers (Wilson et al., n.d.).

Investigations of the nutritional status in children and adolescents found that, while stunted in comparison to non-Amerindian Guyanese peers, growth among the Makushi is less severely affected than that of other Amerindian populations (Wilson et al., 2011). Additionally, examining growth outcomes in adult Makushi, Wilson and colleagues (n.d.) found that stature increased over time between 1920 and 1980, likely due to improvements in health care and possibly genetic admixture.

The Makushi of Guyana suffered greatly from early contact with non-Amerindians, who introduced several diseases in the area. In the early 1900s, several epidemics brought the Makushi to the brink of extinction and their numbers kept
declining until 1946, when the British government started a program to protect the native tribes of the country (Butt-Colson, 1971). Following the establishment of medical outposts and hospitals, as well as improved hygiene and vaccination campaigns, the Makushi population progressively increased in number, with a notable demographic increase in the 1960s (Wilson et al., 2006). Following a failed insurgenge for Rupununi independence, in 1969 access to the region was restricted for decades and medical care limited, causing a decline in the Makushi’s overall health (Baines, 2005). Today, all villages included in this study have a health post and a community health worker trained in diagnosing and treating common ailments. The local health post refers patients to a regional health post, where health workers typically have training equivalent to that of a nurse in several areas. The regional post is located anywhere between 1 and 80 km away from the villages it serves. While the regional health worker should visit all villages on a monthly basis to administer vaccinations and treat acute illnesses, such visits are not always performed, especially to isolated villages that are not easily accessed by means of a road (Wilson et al., 2006).

Intrapopulation Differences in Access to Resources

The Rupununi region is connected to the coast by a 570 km road between the capital, Georgetown, and the interior city of Lethem. The road is in very poor condition and may be traveled only by means of large off-road vehicles only (Wilson et al., 2011). Furthermore, villages vary in their relative isolation, that is, distance from the road. Of the eleven villages included in this study, only 7 have access (at least seasonally) to the road, while the rest are dispersed along the Rupununi River and lack any link to the road.
Isolation is expected to be a determining factor on growth outcomes because it reflects different life conditions and access to resources. On the one hand, isolated villages are expected to have: 1) better diets because they are located in areas with a more nutrient-rich soil, 2) a certain buffer from cultural change and related distress; and 3) some protection against the introduction of infectious disease. On the other hand, individuals living in the isolated villages typically have limited access to trade and health care, which may be particularly relevant given the fact that malaria is endemic in isolated, but not in non-isolated, villages. Lastly, wage labor opportunities are more frequent in non-isolated villages, which are only one day’s bicycle ride away from the Brazilian city of Normandia, where the Makushi may find employment as ranchers or agricultural laborers (Wilson et al., 2011).

The Sample

A total of 532 (126 male; 406 female) individuals from 11 Makushi villages from the North Rupununi region of Guyana were included in this study. Based on access to the Georgetown-Lethem road, these individuals were assigned to relative isolation subsamples for a total of 236 isolated (75 male; 161 female) and 296 non-isolated (51 male; 245 female) individuals. All individuals were of ages ranging between 19.5 and 82 years and were included in the study based on the availability of measurements of stature and sitting height. All data were collected by Wilson and collaborators between 2000 and 2007.
Over the past century, increasing urbanization has dramatically changed the demographic profiles and subsistence activities in Colombia. Once a primarily agrarian society, due to migration from rural areas to the cities, by 1990 68.3% of Colombia’s entire population lived in urban areas (World Bank, 1990). In the city of Cali, fast urbanization, characterized by the concentric growth around the city center was accompanied by an increase in social stratification and inequality. In the late 1980’s Dufour and colleagues (1994) initiated a project to evaluate the how urbanization impacted the physiology, anthropometry and nutrition of women of different socioeconomic status (SES) living in the city of Cali, Colombia (Figure 6.3).

In the late 1980s Cali counted approximately 2 million inhabitants and was the third largest urban center in the country, following the capital, Bogotá, and Medellín. The city is located in a valley in the interior of the country, approximately 100 km from the coast and at an altitude exceeding 1,000 m above sea level. Savannah-like plains extend to the north and the south of the city, which is bordered by the Cauca River in the east and by a mountain range in the west. The climate is semi-tropical, with only modest fluctuations in temperature and precipitation during the year, because of the proximity to the equator.
Figure 6.3. Map of Colombia showing the geographic location of Cali (black dot).
Inequality in Cali

Socioeconomic inequality in the city is marked and typically reflected in the city’s spatial organization in *barrios* (Dufour et al., 1994; Departamento Administrativo de Planeación – Alcaldía de Santiago de Cali, 2010), which is still evident in official reports (Figure 6.4).

At the time of data collection, low SES *barrios* were characterized by recent urbanization, reflected by their peripheral location, unpaved streets, no access to public transportation, and precarious nature of residential units. Indeed, several houses were either under construction or built with temporary, recycled materials. Most units did not have access to water, electricity, telephone lines, and sewage and waste disposal services. However, in several cases the residents of the *barrios* had devised “unofficial” connections to water and electric sources (Dufour, 1994). Mid-low SES *barrios* were typically older settlements with some paved roads and access to public transportation.
Figure 6.4. Spatial organization in barrios corresponding to different socioeconomic status (SES) in Cali, Colombia. Yellow = Extremely Low SES; blue = Low SES; pink = Mid-Low SES; grey = Mid SES; orange = Mid-High; purple = High SES; green = non-residential. Source: Departamento Administrativo de Planeación – Alcaldía de Santiago de Cali, 2010
Houses in these neighborhoods were typically made of bricks or cement blocks and had water, electricity and sewerage connections through the city; only few homes had phones (Dufour et al., 1994, 1997). In contrast, high SES barrios were characterized by private homes or condominiums, benefitted from all city services including phones, and had access to city parks and green zones (Dufour et al., 1994). Besides differences in residential unit type and access to services through the city, striking and significant ($p = 0.001$) socioeconomic differences among status groups were also evident in regard to degree of education and employment (Dufour et al., 1994). As a consequence of these differences, in spite of the general food availability in Cali, many low SES women reported food insecurity due to uncertain income (Dufour et al., 1997). Access to healthcare was available to the majority of the population through government-sponsored health posts located in the barrios, even though high SES individuals could take advantage of the services provided by costly clinics (Spurr et al., 1992).

Previous Studies on Growth Outcomes

Previous analyses of anthropometric data by Dufour and colleagues (1994) revealed that differences in adult stature exist between SES groups, with high SES individuals being on average $5.0$ cm taller than their low/mid-low status counterparts. Additionally, an inverse relationship was found between body fatness and SES, consistent with data from other affluent societies. Additionally, these differences in body fatness across groups decreased with age (Dufour et al., 1994).
The Sample

A total of 1568 women from the original dataset collected by Dufour and colleagues (1994) in 1988-1989 are included in this study. These women were assigned to three SES groups (Low = 517; Mid-Low = 592; High = 458) based on barrio of residence and information on sociodemographic variables obtained by interview (Dufour et al., 1994). All individuals were of ages between 18 and 44 years and were included in the study based on the availability of measurements of stature and sitting height.

6.1.2 Materials II: Bioarchaeological Populations

Two populations from archaeological settings are included in this study: 1) the socioeconomic diverse group inhabiting Trino Vercellese (Italy) during the Middle Ages; and 2) the medieval population from Giecz, Poland.

6.1.2.1 Trino Vercellese

Historical sources indicate that social stratification and inequality were aspects of everyday life in medieval Europe. Nonetheless, in spite of the existence of socioeconomic differences during life, due to egalitarian funerary practices Christian medieval cemeteries seldom reflect the sociocultural complexity of the time. The cemetery of San Michele’s church, Trino Vercellese (VC), Italy (Figure 6.5) is an exception to this general rule. Thanks to the clear spatial and cultural distinction between the burials of high and low status individuals, San Michele’s cemetery offers the opportunity to explore biocultural differences between groups of the same population.
Figure 6.5. Map of Italy showing the location of Trino Vercellese (black solid circle) and the planimetry of the site (modified from Negro Ponzi Mancini, 1999). In the map of the site, the dark gray area represents the church of San Michele, the light gray area represents the cemetery outside the church, and the black line indicates the fortification walls.
The Medieval Population from Trino Vercellese

Written documents dating back to the 10th century (Codex Vaticanus 4322, cited in Ferraris, 1938) mention San Michele’s church in Trino as one of the earliest pievi of the region, that is, rural churches characterized by a baptistery and cemetery, upon which other churches depended for baptismal and funerary functions. Due to its role as pieve and the consequent obligatory interment of the whole population on its grounds, starting around the 8th century and until the 13th century AD, the church of San Michele became the funerary epicenter of a well-defined area surrounding the urban center of Trino Vercellese. Excavations carried out by the University of Torino between 1980 and 1994 led to the recovery of a total of 749 burials located inside and outside the church (Negro Ponzi Mancini, 1999). The majority of the burials (688) dated to the Middle Ages (8th-13th centuries), while a minority of the burials recovered inside the church was post-medieval (14th century). Among the medieval burials, 585 (85%) were adults and 103 (15%) juveniles. It has been noted that such a low proportion of juveniles is unlikely representative of actual subadult mortality in medieval Trino, and seemingly in conflict with the notion that the entire population was being buried in the grounds of the pieve (Negro Ponzi Mancini, 1999). It is possible that the obligatory interment in the plebeian cemetery was limited to adults, and that only a portion of the juvenile population from Trino was buried in the cemetery of the church as a consequence of differential mortuary treatment. In fact, the custom of burying children in dedicated areas separated from the adult cemetery is documented in Italy during both Antiquity and Middle Ages (Ginatempo, 1988), and there are no reasons to doubt that may have been the case also in medieval Trino. Additionally, juvenile burials in Trino’s cemetery were typically
positioned along the margins of adult burials and consequently more likely to be
disturbed by successive inhumations. It is therefore possible that, despite their potential
original abundance, subadult burials may have been highly disturbed, to the point that the
majority of them ended up being unrecognizable as individual units and therefore not
included in the demographic profiles of the population. This notwithstanding, the general
presence of men and women of different ages both inside and outside the church has been
interpreted as evidence that the majority of the population was buried in the cemetery of
San Michele, leading to the conclusion that the skeletal collection is a representative
sample of Trino Vercellese’s adult inhabitants during the Middle Ages (Negro Ponzi
Mancini, 1999).

Additionally, it has been advanced that the skeletal sample recovered from Trino
is representative of the socio-economic variation expressed by the population during the
Middle Ages. Indeed, several lines of evidence suggest that groups of different social
status were buried in different areas of San Michele’s cemetery. In particular, the
existence of status differences in mortuary treatment is supported by 1) burial location, 2)
burial typology, and 3) grave good typology. First, San Michele’s cemetery (Fig. 1)
shows a spatial organization that is highly suggestive of an underlying hierarchical order,
with the most obvious differences existing between burials located within and without the
church. Of the 688 medieval burials from San Michele, 273 individuals (205 adults; 68
juveniles) were recovered inside the church, while 415 (380 adults; 35 juveniles) were
excavated in the grounds surrounding the church. Starting in the Early Middle Ages
(circa 5th century), it was not uncommon for privileged families, philanthropists and the
clergy to be buried inside sacred buildings, whereas the rest of the population was
generally interred in the area outside the church (Negro Ponzi Mancini, 1999; Chavarria Arnau, 2007). The archaeological evidence from Trino indicates that San Michele’s church was no exception to this general custom, documented for this region in the writings of Attone, Bishop of Vercelli in the 10th century AD. The burials closest to the altar were primarily single interments of adult males – likely important members of the clergy –, while further from the altar were identified family burials containing the remains of multiple individuals, including women and children. This latter evidence is consistent with the custom of burying within churches local noble families, whose presence is documented in Trino starting at least in the 10th century (Rao, 2003). In fact, at this time, the local nobles erected fortifications all around the urban center and the church, which effectively become part of the castle (Negro Ponzi Mancini, 1999).

Second, burial typology differs notably between interments inside and outside the church. Most burials located in the external grounds of the cemetery consisted of simple earth ditches, rarely placed within wooden or masonry walls, and occasionally delimited by pebbles and/or bricks on the top level. In sharp contrast with this simple interment, all burials within the church, including those of juveniles, were placed in well-defined masonry (rarely wooden) cases, often of large dimensions. Lastly, the presence and typology of objects in the grave can help to shed light on an individual’s status within the community. Even though the interpretation of grave goods as status indicator is complicated by a plethora of cultural factors (James, 1989), they have the potential of corroborating other lines of evidence and unveiling subtle nuances of past populations’ social organization. Even in Christian cemeteries, which are typically characterized by a general paucity of grave goods, the presence of simple objects, such as parts of an
individual’s garments, can foster valuable information on individual status. In San Michele’s cemetery, the burials inside the church exhibit a greater (even though not significant \( p = 0.09 \)) abundance of buckles, brooches and, in general, metal objects than the burials located in the external grounds. In particular, the exclusive presence of gold threads – likely part of garments – in the burials of both men and women inside the church has been interpreted as unequivocal evidence in support of status differences (Negro Ponzi Mancini, 1999).

Extensive archaeological, archaeozoological, palaeobotanical, and paleopathological studies have been carried out on the site, allowing for an extremely detailed reconstruction of environmental conditions and lifestyle of the medieval population inhabiting Trino Vercellese (Accorsi et al., 1999; Aimar et al., 1999; Caramiello et al., 1999; Celoria, 1999; Ferro, 1999; Girotti and Doro Garetto, 1999; Negro Ponzi Mancini, 1999; Porro et al., 1999).

Overall, this research indicates that throughout the medieval period the area surrounding Trino Vercellese was characterized by hardwood forests, the extension of which was progressively reduced by anthropic deforestation in favor of pastures and crops (Caramiello et al., 1999). Primary crops were represented by cereals (including wheat, rye, and millet), legumes, and aromatic plants (Umbelliferae) (Accorsi et al., 1999). The local economy was centered on livestock breeding, destined not only for local consumption but also for regional trade. Faunal remains at the site indicated that the most abundant domestic species were swine, cattle and sheep/goats, followed by horses and domestic fowl (Ferro 1999). Based on butchery marks and age-at-death profiles, it was determined that swine and cattle were mostly bred for meat and hides, while sheep and
goat were primarily a source of wool and milk (Aimar et al., 1999). The consumption of wild ungulates, primarily red deer and roe deer (*Cervus elaphus* and *Capreolus capreolus* respectively) also was commonplace, since these animals were sought for their antlers and hides, valued for several crafts. Fish remains are also documented, although aquatic resources were probably not a major component of the everyday diet.

Anthropological analyses indicated that the medieval population from Trino Vercellese experienced relatively good life conditions, without major growth disruption and an overall varied and rich diet. Porro and colleagues (1999), drawing demographic profiles and carrying out craniometric and paleopathological analyses, concluded that throughout the Middle Ages the population exhibited relative numerical stability and biological continuity. Based on metric analyses, these authors determined that the population showed consistent skeletal growth profiles, with only moderate growth disruptions. Stature estimates from long bones were employed to support the notion that the population benefited from overall positive environmental conditions during growth, even though stature differences attributable to social status (Table 6.1) suggested a certain degree of variation in early life conditions within the population.

Table 6.1. Mean estimated stature and LEH frequencies based on the total number (N) of teeth examined in the high and low status subsamples from Trino Vercellese (from Girotti and Doro-Garetto, 1999; Porro et al., 1999).

<table>
<thead>
<tr>
<th></th>
<th>High Status</th>
<th>Low Status</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td>Mean Estimated Stature(cm)</td>
<td>171.59</td>
<td>159.54</td>
</tr>
<tr>
<td></td>
<td>N=35</td>
<td>N=24</td>
</tr>
<tr>
<td>LEH (%)</td>
<td>31.1</td>
<td>41.3</td>
</tr>
<tr>
<td></td>
<td>N=443</td>
<td>N=293</td>
</tr>
</tbody>
</table>
Celoria (1999) investigated the presence of growth disruptions in the population by examining several indicators of stress, such as the presence of Harris lines, metabolic diseases (porotic hyperostosis, cribra orbitalia, scurvy, rickets/osteomalacia), and non-specific periostitis. This analysis was conducted on a subsample of 93 individuals (4 juveniles; 89 adults) that could be examined for all of the indicators. The results of this investigation revealed low frequencies of Harris lines for the time period (females: 41.7%; males: 57.6%), a general absence of metabolic disorders, and moderate presence of non-specific periostitis (females: 14.28%; males: 36.36%). This analysis focused primarily on adult skeletons and is consequently most informative of growth disruptions only in individuals surviving childhood. While the results of this study may not be informative in respect to actual prevalence of pathological conditions in the population as a whole, they are relevant to the present study, which focused on adult survivors only. It should be noted that Celoria (1999) did not distinguish between individuals buried in different areas of the cemetery and her study is therefore not informative of biological differences between individuals of different social status. Lastly, Girotti and Doro-Garetto (1999) examined the dentition of 206 individuals (82 buried inside and 124 outside the church) for tooth loss, dental caries, and linear enamel hypoplasia (LEH). These authors determined that oral health of the population was typical for the time period, characterized by fairly high LEH frequencies (Table 6.1), moderate tooth loss, and abundant carious lesions, affecting approximately 70% of individuals examined and seemingly more common among the elderly. By comparing these dental indicators among population subgroups, the same authors detected the presence of significant differences attributable to sex and status. All indicators show significant differences between status
samples (p<0.01), mainly attributable to greater developmental stress and poor oral conditions suffered by low status males. Indeed, while the differences between male status subsamples are always significant (p=0.0001), only LEH frequencies differ significantly between female subsamples (p=0.002).

Since multiple lines of evidence pointed to the existence of status differences within the population of Trino Vercellese, this collection is particularly suitable for investigating intrapopulation biological differences in stature and body proportions at the bioarchaeological level.

The Sample

All complete adult individuals from Trino Vercellese’s medieval population are included in the study, for a total of 52 (20 female, 32 male) skeletons. The sample is subdivided in two groups of different status, as determined from archaeological evidence (burial location and typology, and grave goods typology): 1) High status (6 female; 14 male); 2) Low status (14 female; 18 male).

6.1.2.1 Giecz

The medieval population from Giecz, Poland, is well-suited for the investigation of stature and body proportions in relation to environmental factors thanks to abundant contextual information and because the preservation of the skeletal material is truly outstanding.
The Giecz Collection

The medieval site of Gz. 4, is located just outside of the small farming village of Giecz. The settlement is located in the birthplace of the Polish state, generally referred to as Weilkopolska (Greater Poland) (Figure 6.6).

Figure 6.6. Map of Poland showing the location of Giecz (black solid circle) and the planimetry of the site (modified from Kostrzewski, 1964). The map of the site shows the outline of the medieval stronghold and the location of the medieval cemetery and the lake that extended to the north of the fortifications during the Middle Ages.

Until the 10th century, the Polish population was organized in nomadic or semi-nomadic tribes that practiced a variety of pagan religions (Barford, 2001). In AD 996,
Prince Mieszko I unified the tribes and founded the first Polish state, at the same time converting to and establishing Christianity as the state religion (Lerski, 1996). At this time of major sociopolitical change, Mieszko I erected several strongholds to defend and administer the newly founded state. The settlement of Giecz was founded at the center of Weilkopolska, approximately 30 km southeast of Poznań and 25 km southwest of Gniezno and Ostrów Lenicki. A fortified stronghold was built at Giecz in a strategic location comprised between a lake (now entirely dried up) and a swampy valley (Kostrzewski, 1964). A village and market flourished just to the north of the fortifications. The first mention of the settlement of Gdech as one of the major royal strongholds contributing to the military prowess of king Bolesław dates to 12th century (Chronicle of Poland, author anonymous). Later mentions of the settlement occur in the Chronicle of Polish Princes and Chronicle of the Czech by Kosmas. This latter document reports the invasion of Poland by the Czech prince Břetislav and how, in AD 1039, the inhabitants of Giecz surrendered in front of the preponderance of the enemy forces. Following the surrender, the inhabitants of the village were relocated to Czech territories and the stronghold and village destroyed. Following these events, the settlement at Giecz lost its geopolitical importance and remained as a rural village. The church and the castle were rebuilt in the second half of the 11th century and the southern part of town within the fortified perimeter was destined to peasant residential quarters. The area of the previous settlement, located north-west of the stronghold, was employed as a cemetery by the populace throughout the 11th and 12th centuries (Krysztofik, 2005; 2007).

Given its historical importance as one of the major fortified centers of the rising Polish state, Giecz has been the object of extensive archaeological investigations starting
in 1949 (Kostrzewski, 1952). These investigations led to the identification of the major architectural structures (castle, church, fortifications), the recovery of numerous artifacts (pottery, metal objects, ornaments) and the discovery of several graves, many of which were damaged by agricultural activities (Kostrzewski, 1964).

Palynological analyses revealed that in medieval times the area surrounding the settlement was characterized by mixed deciduous forest and marshes, with a progressive increase of meadows and pastures resulting from anthropic deforestation throughout the Middle Ages (Milecka 1991; Polcyn and Wierzbicki, 1991; Polcyn et al., 1994; Polcyn, 2000). Paleocarpological evidence suggests the cultivation of a variety of grains, in particular millet and, in smaller proportions, wheat, rye and barley (Indycka, 2000). Archaeological evidence of farming tools, scales, craft implements and furnaces with associated metal slag, suggests that the local population was mainly engaged in subsistence activities such as farming, smelting, handicraft and trade (Koztrewski, 1964).

Extensive faunal remains document the presence of domestic animals and the abundance of fish scales and fishing implements suggests that aquatic resources were exploited as well.

The cemetery followed conventional Christian funerary practices in the deposition and orientation of the bodies (Krysztowiak, 2008), even though the presence of grave goods such as personal objects (combs, ornaments) suggests the persistence of pagan beliefs and practices. Overall, the spatial disposition and typology of the burials tends to exclude the existence of social stratification at the cemetery site and it is likely that individuals of higher status were buried elsewhere.
Skeletal materials composing the Giecz Collection were excavated in field seasons from 1999 to 2008 and are presumably genetically restricted and representative of the population as a whole (Justus, 2005). Remains are curated at the Rezerwat Archeologiczny Gród Piastowski w Gieczu (Giecz, Poland). These skeletons are excellently preserved although some have sustained taphonomic damage due to modern agricultural (plowing) activities. The Giecz Collection currently includes 277 burials. The majority (64.4%) of individuals died after maturity and these adults are represented by 103 males (58%), 56 females (32%), and 18 (10%) of indeterminate sex. Most adults (47%, n= 84) died in middle adulthood, classically defined as 35-49 years, with fewer younger adults (29%, n=52) and older adults (6%, n=10) represented. Due to the high degree of fragmentation, it was not possible to estimate age at death beyond adulthood for several individuals (18%, n=31).

Preliminary paleopathological examination of the collection revealed high frequencies of common indicators of environmental stress such as cribra orbitalia, porotic hyperostosis and linear enamel hypoplasia (LEH). Among adult individuals excavated by 2006, over 80% exhibited signs of porotic hyperostosis and 50% of sampled teeth were affected by LEH, indicating that the population was exposed to high levels of environmental stress during growth. No significant differences in the frequency of stress indicators were observed between men and women. It is unknown, however, if sex differences exist in the degree of expression of such indicators.

3 The incidence of stress indicators in Giecz is determined from unpublished data collected as part of the Global History of Health Project and kindly provided by Amanda Agnew, Ph.D. Analyses are limited to subadults and adults of known sex for whom a given trait could be scored.
Paleodietary isotope analyses conducted by Reitsema and colleagues (2010) indicate that the medieval population inhabiting the settlement had a mainly terrestrial, omnivorous diet. The evidence of faunal remains at the site is consistent with regular meat consumption and the reliance on plants utilizing both $C_3$ (wheat, rye) and $C_4$ (millet) photosynthetic pathways is supported by archaeobotanical findings (Indycka, 2000). However, while fish remains as well as fishing implements were recovered at Gz. 4, isotopic values of the individuals examined provide little support of regular fish consumption. This notwithstanding, isotopic signatures of three male individuals suggest that they may have consumed small amounts of marine fish. Additionally, Reitsema and colleagues (2010) identified sex-related differences in diet in the population from Giecz: male diets featured more meat and millet-based foods than female diets. These authors advanced several explanations for these findings, primarily in terms of differential access to resources based on sexual division of labor, different adherence to religion customs, or sex-related inequality (Reitsema et al., 2010).

Sample
A total of 66 (20 female; 46 male) complete skeletons are included in this study. All individuals were between 20 and 55 years old at the time of death (mean = 39.9; SD = 8.4).
6.2 Methods

6.2.1 Methods I: Living Populations

6.2.1.1 Anthropometry and Contextual Information

To assess variation in stature and body proportions in living populations, linear growth outcomes (height, sitting height, and leg length) were evaluated in different population subsamples and among populations.

Ribeirinhos

Height and sitting height for all individuals included in this study were collected by Piperata (2005, 2007) in 2002. All measurements were taken following standardized procedures (Lohman et al., 1988) and recorded to the nearest 0.1 cm using a Seca portable stadiometer. Anthropometric measurements were taken at either the local schoolhouse or in individual homes. The schoolhouses had level, cement floors. When anthropometric data were collected in an individual’s home, a level was used to find the most appropriate area for taking the measurements. All women who were in the final trimester of a pregnancy were measured multiple times pre- and post-partum. Anthropometric data recorded two months after birth are used in this study to avoid methodological issues associated with height variation due to vertebral compression and postural changes during pregnancy (Scholl et al., 1993).

Adult ages were based on the individual’s recall and, when available, were crosschecked with legal documents such as government-issued identification cards.
Structured interviews were used to gather detailed biocultural data on the individual participants including household size and composition and women’s reproductive histories. Reproductive histories were conducted with each of the 88 adult women and included information on age at menarche, age at birth of first child, parity and date of birth of each child. The birth dates of the individual children were used to calculate inter-birth intervals and their average. This information is used to interpret sex differences in growth outcomes. Semi-structured and unstructured interviews with adult women and men, along with ethnographic data collected via participant observation, were used to gather information on daily life and local beliefs regarding gender (work and access to resources). Detailed dietary data collected in 2002 on a sample of 23 lactating women (Piperata and Dufour, 2007) and dietary data collected in 2009 on a sample of 52 children (unpublished) are used to complement the observational data on gender and access to resources mentioned above.

Makushi

This study includes data on height and sitting height of Guyanese Makushi collected between 2000 and 2007 by Wilson and colleagues (n.d.), as part of a broader study entitled ‘Culture change and health among the Makushi’ initiated in 1999. Measurements were taken according to standard protocols (Lohman et al., 1988) using portable equipment and recorded to the nearest 0.1 cm. Measurements were taken in a central location of each village included in the project. Data for pregnant women are included in this study only if the measurement was not taken during the third gestational trimester.
Ages of all participants were calculated from their date of birth, which was determined in interviews with each individual and verified using records kept at the local health post. For individuals older than 40 years, official records reported only the year of birth and no information on day and month. In some cases, elderly individuals did not recall their year of birth, which was then determined from discussions with other household members (Wilson et al., n.d.).

The Makushi anthropometric data are examined and interpreted on the basis of contextual information recorded by Wilson and colleagues (n.d.) such as relative isolation, birth season (wet/dry), birth order, number of children in the household, and information regarding household income and subsistence means. Individuals are assigned to relative isolation groups (isolated/non-isolated) based on whether their village of residence had direct access to the Georgetown-Lethem road or not at the time the data were collected. Individuals who moved to other communities are either assigned to the isolation group corresponding to their village of origin or excluded from isolation analyses in case of provenience from communities not included in the study. Birth season is determined from month of birth (October-April = Dry Season; May-September = Wet Season). Additionally, dietary information collected by Palmer (2009) in these communities is used to complement observations on growth outcomes. Lastly, ethnographic information on Makushi marital practices and gender roles (Wilson et al., 2011) are employed to interpret patterns of variation observed between males and females.
Cali

The anthropometric data for the Cali sample employed in this study (height and sitting height) were collected by Dufour and colleagues (1994) in 1988-1989 as part of the broader project aimed at assessing the impact of sudden urbanization on Colombian women’s health. Two trained technicians with over 10 years of experience took all measurements with a Harpenden anthropometer, following standard procedures (Lohman et al., 1988). Measurements were recorded to the nearest 0.1 cm.

The participants of the study were volunteer, non-pregnant, non-lactating women of ages comprised between 19 and 44 years. Information regarding the subjects’ socioeconomic status as well as dietary intake and cultural approaches to food availability in the lower SES groups were collected by trained technicians through both direct observations and structured interviews (Dufour et al., 1994, 1997a, 1997b, 1999). Additionally, physical activity levels and underlying behaviors were also determined (Spurr et al., 1992, 1996; Dufour et al., 2003). This contextual information is used to interpret the patterns of variation among SES groups in Cali.

Human Subjects Research

All data included in this study were collected as part of research projects approved by appropriate institutional review boards. Specifically:

1) All data collection methods for the study of Brazilian Ribeirinhos were reviewed and approved by the Human Research Committee at the University of Colorado-Boulder (HRC no. 1001.2) and by similar committees in Brazil;
2) The ongoing project “Culture change and health among the Makushi” was approved by Conjoint Faculties Research Ethics Board at the University of Calgary, Guyana’s Ministry of Amerindian Affairs, Guyana’s Environmental Protection Agency, and the North Rupununi District Development Board;

3) The investigation of urbanization impacts on women’s health was reviewed and approved by the Human Research Review Committee of the Medical College of Wisconsin and the Research Committee of the Universidad del Valle, Colombia.

6.2.1.2 Data Analysis

To explore the existence of differences in growth outcomes within living populations, I examine height and the relationship between height, sitting height, and leg length (leg length = height – sitting height) in different population subsamples based on sex, growth retardation (stunting) and differential access to resources.

Sex differences are explored in both Ribeirinhos and Makushi, and in this latter case not only in the entire population, but also within isolation groups. Proportional differences in relation to stunting are assessed in all living population samples (Ribeirinhos, Makushi, Cali) and subsamples (sex, isolation, SES). Differences related to differential access to resources are investigated among the Makushi and the inhabitants of Cali. The Makushi are subdivided into relative isolation subsamples (isolated/non-isolated), while the women from Cali are subdivided into three SES subgroups (High, Mid-Low, Low).

Sexual dimorphism in growth outcomes within each sample is determined by examining the regions on non-overlap of the distributions of a given trait in the two sex
subsamples (Chakraborty and Majumder, 1982). Dimorphism is expressed in terms of “D”, a value ranging between 0 (no dimorphism) and 1 (complete dimorphism). Given the existence of sexual dimorphism in body size, height, sitting height, and leg length are compared only between same sex groups, both within and between populations. Non-parametric tests – Mann-Whitney or Kruskal-Wallis tests, depending on the number of subsamples being compared – are used to test for differences in the distribution of anthropometric variables across subsamples. These non-parametric tests are preferable to the parametric ANOVA because they are applicable even when the distribution of the data departs from normality (Zar, 1999).

The existence of differences in body proportions in relation to sex, growth retardation, and differential access to resources is explored by means of the “Quick-Test” devised by Tsutakawa and Hewett (1977). This test has been used to identify differences in body proportions in a range of taxa (Swartz, 1997; Maie et al., 2007; Temple et al., 2008). Simply, the “Quick-Test” allows testing differences in the distributions of two or more samples in relation to a line fitted to the combined sample. For each comparison presented in this study, natural log-transformed sitting height and height data are employed to calculate a fit line with a slope of 1.0 passing through the grand mean of the combined samples being compared. This fit line represents a perfectly isometric relationship between the variables under examination for the pooled samples. Upon calculation of the appropriate fit line for each comparison, the “Quick-Test” is employed to test the null hypothesis that the joint distribution of data points above and below the fit line is the same for distinct samples (Tsutakawa and Hewett, 1977).
Raw and log-transformed data, rather than z-scores, are used in all analyses. While z-scores have the advantage of standardizing raw data by sex and age, using raw data are used in order to avoid masking part of the biological variation within the population by standardizing it by means of an extraneous reference sample. A potential problem with using raw data lies in possible age-related changes in height and sitting height, primarily due to vertebral compression. To evaluate the potential effects of age on the data, differences in age distributions across subsamples are evaluated using non-parametric tests. In the case significant differences are found, their impact on the analyses results is evaluated. In any case, data are not age-corrected to avoid introducing a potential source of error in the pattern of intrapopulation variation. In fact, the process of age-related stature reduction itself is not entirely understood (Galloway, 1988; Cline et al., 1989; Chandler and Bock, 1991; Giles, 1991) and the application of age correction methods vexed by several limitations, including age at onset of stature change, sex, and population differences in stature loss entity and timing. Given the fact that growth outcomes are not compared across age groups, as long as differences in age distributions are taken into considerations, they do not represent a major impediment to this study.

Stunting categories (stunted/non-stunted) are based on z-scores. Individual z-scores for height-for-age (HAZ) are calculated using the National Health and Nutrition Examination Surveys (NHANES III) reference values provided in Frisancho (2008). In agreement with common practice in human biological research, stunting is defined as a low HAZ (z-score < -2) (WHO, 1995). The international reference includes a broad range of variation encompassing most of the variation observed even in developing countries and has been argued to be applicable without limitations of ancestry. Furthermore, it has
been observed that z-scores falling below -2 characterize individuals whose growth is compromised beyond adaptive levels (i.e., being accommodation). In these cases, the organism’s function is compromised and short stature is associated with compromised immune competence, poor psychological performance, diminished productivity, reduced reproductive potential, and increased mortality risk (Martorell, 1989; Paajanen et al., 2010).

The assessment of differences in the degree of variation of all variables in each sample is assessed by means of the coefficient of variation (CV = standard deviation/mean). Additionally, interpopulation differences are further explored by a one-way ANOVA (F-test) on height, sitting height, and leg length of the living populations included in the study. Non-parametric analogues of ANOVA (Kruskal-Wallis test or Mann-Whitney test) are used in case the F-test assumptions are not met. The analyses are conducted on sex-specific samples only. Lastly, differences in body proportions between populations are investigated using the “Quick-Test.”

6.2.2 Methods I: Bioarchaeological Populations

6.2.2.1 Demographic data

Sex and age-at-death of all individuals included in the study were estimated from sexually dimorphic features of the pelvis (Phenice, 1969; Buikstra and Ubelaker, 1994) and morphological alterations of the os pubis’ articular face (Brooks and Suchey, 1990) and ilium auricular surface (Lovejoy et al., 1985). Age structures of population subsamples examined are compared by Mann-Whitney or Kruskal-Wallis tests.
6.2.2.2 Osteometry

The skeletal elements analyzed include upper limb bone maximum lengths (radius, humerus) and all elements contributing to living stature: cranial height (basion-bregma), skeletal trunk height (measured as the sum of all vertebral heights between C2-S1), bicondylar femur length, tibia condylo-malleolar length and foot height, measured as the height of talus and calcaneus in articulation as prescribed by the anatomical method devised by Fully (1956) as modified by Raxter and colleagues (2006, 2007). All long bones were measured using a portable osteometric board (Paleotech Concepts) to the nearest 0.1 cm; basion-bregma height was measured with a spreading caliper (GPM, DKSH Switzerland Ltd) and recorded to the nearest 0.1 cm; a sliding caliper (GPM, DKSH Switzerland Ltd) was used to measure vertebral body heights, which were recorded to the nearest 0.1 cm.

Skeletal height is calculated as the sum of all elements above, excluding upper limb bones. Missing vertebral elements’ height is reconstructed from their relative contribution to total column length in the individual’s sex and status subsample (Sciulli et al., 1990; Vercellotti et al., 2009). In order to increase sample size, foot height of 7 individuals is reconstructed from its relative contribution to skeletal height in the individual’s sex and status subsample. If specimens presented an extra lumbar vertebra, it is included in skeletal height calculation, as recommended by Raxter and Ruff (2010). Living stature estimates are calculated from skeletal height using the regression formulae devised by Raxter and colleagues (2006). As recommended by Raxter and colleagues (2007), age-corrected equations are used to avoid stature underestimation in younger individuals due to the age structure of the sample employed to develop the regression
equations for stature estimation from skeletal height. It should be noted that only skeletal height was employed in statistical analyses, and that stature estimates are provided for comparisons only.

6.2.2.3 Data Analysis

Intrapopulation body size variation is assessed by testing the presence of absolute dimensional differences in individual skeletal elements and skeletal height among sex and status subsamples. Given the fact that males and females exhibit sexual dimorphism in stature, these comparisons are limited to same-sex samples (Trino Vercellese). Additionally, overall morphological patterns are estimated by means of multivariate analysis on all skeletal elements contributing to stature. These comparisons are performed both between males and females (Trino Vercellese, Giecz) and status groups (Trino Vercellese) within the same population.

The existence of differences in absolute element size among status subsamples is tested by Monte Carlo analysis, a resampling method that allows testing differences between relevant statistics when sample size is small, with minimal assumptions regarding the underlying distribution of the data (Metropolis and Ulam, 1949; Gotelli and Ellison, 2004). Monte Carlo methods can be used to create a probability distribution of a variable of interest by resampling the data at random for a large number of iterations. Once such a distribution is obtained, it is possible to test the significance of differences observed in the original dataset. A one-tailed test with 1000 iterations is used to test the presence of significant differences between each variable’s mean in the social status subsamples.
Body proportions' variation is estimated by segmental proportions indices:
Brachial Index = Radius/Humerus; Crural Index: Tibia/Femur; and Trunk-to-Leg Index = Trunk/(Tibia+Femur). The indices are subject to two-tailed Monte Carlo analyses with 1000 iterations to detect significant differences in body proportions among population sex and status subsamples, as well as between populations.

Overall proportional differences are further explored by means of multivariate analyses in order to depict overall morphological variation within each population. Overall size and shape are analyzed by Principal Components Analysis (PCA) according to the method developed by Darroch and Mosimann (1985). This method allows examining the patterns of morphological variation in biological populations in regard to both size and shape. “Log size-and-shape data”, obtained by natural log-transforming raw data, are submitted to PCA and provide information on the overall morpho-dimensional pattern in the population. Purely morphological differences are assessed by submitting to PCA “Log shape” variables, which are created by taking the natural logarithm of an individual’s measurements (cranial height, trunk, femur, tibia, and foot height) standardized by their geometric mean, which has been argued to be the measure that best represents an individual’s overall size (Darroch and Mosimann, 1985). In a recent paper Auerbach and Sylvester (2010) argued that stature is a better scaling factor to employ in analyses of morphology. The two methods were tested in a preliminary PCA carried out on the samples included in this study, whose data were standardized by their geometric mean and by skeletal height. The two scaling methods provided equivalent outcomes; hence, for continuity with the literature on the topic, standardization by the geometric mean is used in this study. PCA is carried out on the variance-covariance matrix of both
log size-and-shape and log shape variables for all elements contributing to skeletal height (cranial height, skeletal trunk height, femur length, tibia length and foot height) of both skeletal populations analyzed. Intrapopulation comparisons of overall dimensional and morphological variation are performed by comparing the outcomes of PCA on each sample. Interpopulation comparisons are based both on PCA results and Monte Carlo analyses of segmental indices in sex-specific subpopulations.

Statistical analyses are performed using SAS/STAT 9.0, SPSS 19.0, PAST (PAleontological Statistics - Hammer et al., 2001) and Microsoft Excel 2007. Statistical significance is defined as p≤0.05.
CHAPTER 7: RESULTS

7.1 Sex differences

Based on the fact that the sexes exhibit different growth patterns (Bogin, 1999) and may be differently sensitive to environmental stress (Stinson, 1985), sex-related differences in body proportions are expected. If males are in fact more sensitive to growth perturbations, then they are expected to exhibit relatively shorter legs than females. Furthermore, if males exhibit more compromised growth outcomes, then the degree of sexual dimorphism in the population is expected to decrease (Gray and Wolfe, 1980).

This section reports the results of the analyses of body proportions and sexual dimorphism among Brazilian Ribeirinhos, Guyanese Makushi and the medieval populations from Trino Vercellese and Giecz.

7.1.1 Ribeirinhos

Descriptive statistics for Ribeirinhos anthropometric data and age by sex subsamples are reported in table A.1. A certain degree of sexual dimorphism in stature is evident ($D = 0.732$). When the components of height are examined individually, it
emerges that they contribute differently to overall sexual dimorphism. Specifically, sitting height is less dimorphic \( (D = 0.551) \) than leg length \( (D = 0.645) \).

The “Quick-Test” is employed to investigate whether males and females exhibit differences in body proportions in response to similar environmental stress. Since there is no significant difference in age distributions of males and females \( (p = 0.14; \text{ see also Figure B.1}) \), log-sitting height is plotted over log-height for males and females and the joint distribution is fitted by a line of slope equal to \( 1.0 \) through the grand mean of the male and female samples.

The “Quick-Test” result is significant \( (p = 0.0001) \), indicating that the relationship between height and sitting height in the sample was significantly different between the sexes. Specifically, males tend to cluster below the line, indicating they are characterized by relatively longer legs (Table 7.1 and Figure C.1).

<table>
<thead>
<tr>
<th>Sample</th>
<th>Line Equation</th>
<th>Sex</th>
<th>( n ) Above Line</th>
<th>( n ) Below Line</th>
<th>( p ) (^1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>( y = x - 0.6437 )</td>
<td>Females</td>
<td>55</td>
<td>33</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Males</td>
<td>28</td>
<td>56</td>
<td></td>
</tr>
</tbody>
</table>

\(^1\) Highlighted p-values are significant at 0.05 level.

7.1.2 Makushi

The existence of sex differences in response to similar environmental stress among the Makushi is investigated in the entire population, as well as within isolation
subsamples (isolated/non-isolated). Table A.2 reports the descriptive statistics for height, sitting height, leg length, and age for each subsample included in the analysis. When isolation subsamples are combined, the observed degree of sex dimorphism in stature equals 0.711, while dimorphism in sitting height and leg length is 0.746 and 0.023 respectively. Similar degrees of dimorphism are observed within the isolation subsamples (Isolated: height $D = 0.679$; sitting height $D = 0.697$; leg length $D = 0.264$; Non-Isolated: height $D = 0.777$; sitting height $D = 0.842$; leg length $D = 0.174$). Age distributions in all sex subsamples are not significantly different (Figures B.2-B.4)

Sex differences in body proportions in each sample are assessed by fitting each subsample pair with an isometric line and by examining distributions by the “Quick Test” (Table 7.2). The results of the test are significant in all subsamples considered. Males consistently cluster above the line and females below the line, indicating that females in this population have relatively longer legs than their male counterparts (Figures C.2-C.4).

<table>
<thead>
<tr>
<th>Sample</th>
<th>Line Equation</th>
<th>Sex</th>
<th>$n$ Above Line</th>
<th>$n$ Below Line</th>
<th>p$^1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>$y = x -0.6692$</td>
<td>Females</td>
<td>200</td>
<td>206</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Males</td>
<td>109</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>Isolated</td>
<td>$y = x -0.6599$</td>
<td>Females</td>
<td>84</td>
<td>77</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Males</td>
<td>62</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>Non-Isolated</td>
<td>$y = x -0.67650$</td>
<td>Females</td>
<td>114</td>
<td>131</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Males</td>
<td>40</td>
<td>11</td>
<td></td>
</tr>
</tbody>
</table>

$^1$ Highlighted p-values are significant at 0.05 level.
7.1.3 Trino Vercellese

Descriptive statistics for all skeletal segments measured and skeletal height for sex and status subsamples of the medieval population from Trino Vercellese are reported in Table A.3. The age structures of the four subsamples (see Figure B.5) are compared by Kruskal-Wallis test and found to show no significant differences (p = 0.354). Sexual dimorphism values for all skeletal elements and skeletal height are also reported (Table A.3).

It can be noted that the degree of sexual dimorphism expressed by the two status groups differs; high status individuals express stronger differences in overall size (D = 0.988) than low status individuals (D = 0.773). Differences in the degree of expression of sexual dimorphism in both samples suggest the existence of differences in body proportions between males and females.

Sex differences in body proportions are investigated by means of Monte Carlo analyses performed on segmental indices in both pooled and distinct status subsamples. Descriptive statistics for the four indices examined are reported for sex and status subsamples (Table A.4). The results of the analyses indicate that significant differences in body proportions exist between males and females (Table 7.3). In the combined status sample males and females exhibit significant differences in the brachial (p = 0.006) index, due to the fact that females have proportionally shorter radii than males in this population. Additionally, in the pooled status sample males and females also exhibit significantly different trunk/lower limb proportions (p = 0.025), due to the fact that females have relatively shorter legs than males. When the sexes are examined within
status subsamples, significant differences are found only in the brachial index (high status: p = 0.03; low status: p = 0.047).

Table 7.3. P-values for Monte Carlo analyses of proportional indices between male and female individuals from Trino Vercellese.

<table>
<thead>
<tr>
<th>Test</th>
<th>Radius/Humerus</th>
<th>Tibia/Femur</th>
<th>Trunk/(Femur+Tibia)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males v. Females</td>
<td>0.006</td>
<td>0.085</td>
<td>0.025</td>
</tr>
<tr>
<td>High Status M vs. F</td>
<td>0.030</td>
<td>0.092</td>
<td>0.133</td>
</tr>
<tr>
<td>Low Status M vs. F</td>
<td>0.047</td>
<td>0.367</td>
<td>0.071</td>
</tr>
</tbody>
</table>

1 Highlighted p-values are significant at 0.05 level.

7.1.4 Giecz

The existence of sex differences in growth outcomes is also investigated in the medieval sample from Giecz, Poland. Table A.5 reports the descriptive statistics for all skeletal elements considered in the study as well as skeletal height and sexual dimorphism. Adults from this population are characterized by tall mean stature (female: 157.2 cm; males: 172.37) for the time period. Indeed, average male stature falls just below the value of average stature of the modern reference and female stature is just below the 25th percentile (Frisancho, 2008). The distribution of age is non-significantly different between male and female samples (p = 0.888; see also Figure B.6). The degree of sexual dimorphism appears consistent across all skeletal elements (0.636 < D < 0.815). Segmental indices (Table A.6) are used to investigate sex differences in body proportions
by Monte Carlo analyses. No significant differences are found in any of the indices examined (Table 7.4).

Table 7.4. P-values for Monte Carlo analyses of proportional indices between male and female individuals from Giecz.

<table>
<thead>
<tr>
<th>Test</th>
<th>Radius/Humerus</th>
<th>Tibia/Femur</th>
<th>Trunk/(Femur+Tibia)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males v. Females</td>
<td>0.292</td>
<td>0.142</td>
<td>0.081</td>
</tr>
</tbody>
</table>

1 Highlighted p-values are significant at 0.05 level.

7.2 Stunting

Severe growth retardation (stunting) has been argued to impact the lower limb more than the trunk, hence altering body proportions (Bogin et al., 2002). This allometric change is expected to occur similarly in the sexes.

This section presents descriptive statistics and information on stunting prevalence in each of the samples examined and reports the results of the analyses of body proportions in stunted and non-stunted individuals in three living populations (Ribeirinhos, Makushi and Cali).

7.2.1 Ribeirinhos

The existence of different body proportions between stunted and non-stunted Ribeirinhos is tested by means of the “Quick-Test” both in sex-combined and sex-specific samples (Table 7.5). The overall prevalence of stunting among Ribeirinhos is
48% and the mean HAZ for the combined sex sample is -2.0. The mean HAZ in the male and female sub-samples are -1.9 and -2.2, respectively. A significantly higher rate ($\chi^2 = 5.31; p = 0.02$) of stunting is detected in females (50/88 = 57%) than in males (32/84 = 38%). The result of the Mann-Whitney test on age distributions of stunted and non-stunted individuals in the sample is significant ($p = 0.03$; Figure B.7). This is attributable to a higher frequency of stunting among older individuals. As a consequence, stunted individuals may have shorter trunks due to age-related compression of the vertebral bodies. If this were the case, stunted individuals would have proportions biased in favor of relatively longer legs, contrary to the expectation that stunted individuals have relatively shorter legs than non-stunted individuals. This consideration is evaluated in the interpretation of the results. Log-height is plotted over log-sitting height for the sex-combined sample and the joint distribution fitted by a line of slope equal to 1.0 through the grand mean of the samples (Table 7.5).

Table 7.5. “Quick-Test”: isometric line equations, distributions and p-values for differences in body proportions associated with stunting among Ribeirinhos.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Line Equation</th>
<th>Stunting</th>
<th>$n$ Above Line</th>
<th>$n$ Below Line</th>
<th>$p^1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>$y - x - 0.6431$</td>
<td>Stunted</td>
<td>47</td>
<td>35</td>
<td><strong>0.02</strong></td>
</tr>
<tr>
<td></td>
<td>Non-Stunted</td>
<td></td>
<td>35</td>
<td>55</td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>$y = x - 0.6320$</td>
<td>Stunted</td>
<td>28</td>
<td>22</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td>Non-Stunted</td>
<td></td>
<td>14</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>$y = x - 0.6554$</td>
<td>Stunted</td>
<td>18</td>
<td>14</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>Non-Stunted</td>
<td></td>
<td>25</td>
<td>27</td>
<td></td>
</tr>
</tbody>
</table>

$^1$ Highlighted p-values are significant at 0.05 level.
The results of the test are significant \((p = 0.02)\). As expected, stunted individuals tended to fall above the line, indicating that they had relatively shorter legs (Figure C.5). Considering the hypothesis that males and females may be differentially affected by environmental stress, the relationship between stunting and proportions is also addressed in the sex-specific subsamples. Age distributions between stunted and non-stunted individuals in the population is tested using the Mann-Whitney test and reveals a significant difference in the male subsample \((p = 0.04\); Figure B.8\). This difference is due to the higher occurrence of stunting among older individuals. When the oldest individual in the population (77 years old) is removed from the comparison, the age distributions of the two subsamples are not significantly different \((p = 0.07)\). Therefore, differences in the relationship between log-sitting height and log-height for stunted and non-stunted males are tested (Table 7.5). The results indicate no difference in the relationship between height and sitting between stunted and non-stunted males \((p = 0.51)\). In other words, stunting (or the process of stunting) appears to be isometric and not accompanied by detectable changes in sitting height/height proportions (Figure C.6).

The difference in the age distribution of stunted and non-stunted females in the population is non-significant \((p = 0.09\); Figure B.9\). Figure C.7 is the scatter plot of log-sitting height over log-height of stunted and non-stunted *Ribeirinha* women. The result of the “Quick-Test” is non-significant \((p = 0.08)\) meaning there is no significant difference in the relationship between height and sitting height in stunted and non-stunted females (Table 7.5).
7.2.2 Makushi

Differences in body proportions between stunted and non-stunted individuals are carried out in several population subsamples based on sex and relative isolation. Overall stunting prevalence among the Makushi is 39% (Table 7.6).

Table 7.6. Summary statistics for the prevalence of stunting among Guyanese Makushi by sex and isolation subsamples.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Stunted n</th>
<th>Non-stunted n</th>
<th>Total N</th>
<th>Percent Stunted</th>
<th>Average Z-score</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>208</td>
<td>324</td>
<td>532</td>
<td>39</td>
<td>-1.8</td>
</tr>
<tr>
<td>Females</td>
<td>145</td>
<td>261</td>
<td>406</td>
<td>36</td>
<td>-1.9</td>
</tr>
<tr>
<td>Males</td>
<td>63</td>
<td>63</td>
<td>126</td>
<td>50</td>
<td>-1.8</td>
</tr>
<tr>
<td>Isolated (M, F)</td>
<td>104</td>
<td>132</td>
<td>236</td>
<td>44</td>
<td>-1.9</td>
</tr>
<tr>
<td>Non-Isolated</td>
<td>104</td>
<td>192</td>
<td>296</td>
<td>35</td>
<td>-1.7</td>
</tr>
<tr>
<td>Isolated F</td>
<td>61</td>
<td>100</td>
<td>161</td>
<td>38</td>
<td>-1.8</td>
</tr>
<tr>
<td>Isolated M</td>
<td>43</td>
<td>32</td>
<td>75</td>
<td>57</td>
<td>-2.0</td>
</tr>
<tr>
<td>Non-Isolated F</td>
<td>84</td>
<td>161</td>
<td>245</td>
<td>34</td>
<td>-1.7</td>
</tr>
<tr>
<td>Non-Isolated M</td>
<td>20</td>
<td>31</td>
<td>51</td>
<td>39</td>
<td>-1.8</td>
</tr>
</tbody>
</table>

Furthermore, sex differences are evident, with males exhibiting higher rates of stunting than females in the entire population ($\chi^2 = 7.65; p = 0.006$) and in the isolated sub-sample ($\chi^2 = 7.08; p = 0.008$). Even though a greater proportion of males than females within the non-isolated subsample is stunted, this difference in non-significant ($\chi^2 = 0.26; p = 0.61$). Table A.2 reports the descriptive statistics for Makushi anthropometric data and age by sub-sample.

All population subsample pairs are examined for differences in body proportions by the “Quick-Test.” The age distributions of stunted and non-stunted individuals are significantly different ($p = 0.000$) in four samples (entire sample, all females, isolated
sexes combined, isolated females). This is due to the fact that in all of these samples stunting is more common among older individuals (Figures B.10, B.11, B.13, B.15). This result may imply that stunted individuals may have shorter trunks due to age-related compression of the vertebral bodies. If this were the case, stunted individuals would have proportions biased in favor of relatively longer legs. The expectation is that stunted individuals actually have relatively shorter legs than non-stunted individuals. This consideration is evaluated in the interpretation of the results (see chapter 8). Age distributions are not significantly different in all other subsamples (Figures B.12, B.14, B.16-B.18).

The results of the “Quick-Test” point to the existence of significant differences in body proportions in association with stunting in four samples (entire sample, all females, all isolated, all non-isolated). In these samples, stunted individuals tend to cluster above the line, as expected for individuals with relatively shorter legs. Non-stunted individuals are equally present above and below the line, indicating greater variability in the relationship between trunk and legs. All other subsamples (all males, isolated females, isolated males, non-isolated females and non-isolated males) do not show any significant difference in body proportions between stunted and non-stunted individuals (Figures C.8-C.16). Isometric line equations, proportions of individuals falling above and below the line in each subsample and test p-values are shown in Table 7.7.
Table 7.7. Quick-Test™: isometric line equations, distributions and p-values for differences in body proportions associated with stunting among Guyanese Makushi.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Line Equation</th>
<th>Stunting</th>
<th>n Above Line</th>
<th>n Below Line</th>
<th>p^1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sexes Combined</td>
<td>[y = x - 0.6812]</td>
<td>Stunted</td>
<td>148</td>
<td>60</td>
<td>0.0003</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Stunted</td>
<td>179</td>
<td>145</td>
<td></td>
</tr>
<tr>
<td>All Females</td>
<td>[y = x - 0.6945]</td>
<td>Stunted</td>
<td>92</td>
<td>53</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Stunted</td>
<td>131</td>
<td>130</td>
<td></td>
</tr>
<tr>
<td>All Males</td>
<td>[y = x - 0.6384]</td>
<td>Stunted</td>
<td>33</td>
<td>30</td>
<td>0.284</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Stunted</td>
<td>26</td>
<td>37</td>
<td></td>
</tr>
<tr>
<td>Isolated, Sexes Combined</td>
<td>[y = x - 0.6669]</td>
<td>Stunted</td>
<td>80</td>
<td>24</td>
<td>0.045</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Stunted</td>
<td>85</td>
<td>47</td>
<td></td>
</tr>
<tr>
<td>Isolated Females</td>
<td>[y = x - 0.6804]</td>
<td>Stunted</td>
<td>40</td>
<td>21</td>
<td>0.321</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Stunted</td>
<td>57</td>
<td>43</td>
<td></td>
</tr>
<tr>
<td>Isolated Males</td>
<td>[y = x - 0.6359]</td>
<td>Stunted</td>
<td>22</td>
<td>21</td>
<td>0.816</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Stunted</td>
<td>15</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>Non-Isolated, Sexes Combined</td>
<td>[y = x - 0.6928]</td>
<td>Stunted</td>
<td>64</td>
<td>40</td>
<td>0.015</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Stunted</td>
<td>89</td>
<td>103</td>
<td></td>
</tr>
<tr>
<td>Non-Isolated Females</td>
<td>[y = x - 0.7038]</td>
<td>Stunted</td>
<td>50</td>
<td>34</td>
<td>0.060</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Stunted</td>
<td>75</td>
<td>86</td>
<td></td>
</tr>
<tr>
<td>Non-Isolated Males</td>
<td>[y = x - 0.6403]</td>
<td>Stunted</td>
<td>14</td>
<td>6</td>
<td>0.084</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Stunted</td>
<td>13</td>
<td>18</td>
<td></td>
</tr>
</tbody>
</table>

^1 Highlighted p-values are significant at 0.05 level.

7.2.3 Cali

The effects on stunting on body proportions among Cali women are explored both in the entire population and in socioeconomic (High, Mid-Low, Low) subsamples.
Descriptive statistics for stunted and non-stunted individuals in each sample are reported in Table A.7. Overall stunting in the population is 16%, but clear differences in stunting prevalence are evident across SES subsamples (Table 7.8).

Table 7.8. Summary statistics for the prevalence of stunting among Cali women by status subsample.

<table>
<thead>
<tr>
<th></th>
<th>Stunted n</th>
<th>Non-Stunted n</th>
<th>Total N</th>
<th>Percent Stunted</th>
<th>Average Z-score</th>
</tr>
</thead>
<tbody>
<tr>
<td>All SES Groups</td>
<td>245</td>
<td>1322</td>
<td>1567</td>
<td>16</td>
<td>-1.0</td>
</tr>
<tr>
<td>High SES</td>
<td>17</td>
<td>441</td>
<td>458</td>
<td>4</td>
<td>-0.4</td>
</tr>
<tr>
<td>Mid-Low SES</td>
<td>118</td>
<td>474</td>
<td>592</td>
<td>20</td>
<td>-1.2</td>
</tr>
<tr>
<td>Low SES</td>
<td>110</td>
<td>407</td>
<td>517</td>
<td>21</td>
<td>-1.2</td>
</tr>
</tbody>
</table>

Specifically, the rate of stunting among High SES individuals is only 4%, while it amounts to 20% and 21% in the Mid-Low and Low SES samples. Mann-Whitney tests of age distributions across categories of stunting in each sample reveal significant differences (p <0.01) among all samples, with the exception of Mid-Low SES women. These differences are attributable to a greater incidence of stunting among older women (Figures B.19-B.22) and are evaluated in the interpretation of the results.

The relationship between log-height and log-sitting height in stunted and non-stunted individuals is examined in different population subsamples by the “Quick-Test” (Table 7.9). Significant (p < 0.004) differences in body proportions between stunted and non-stunted individuals are found in all samples examined. Consistently with expectations, stunted individuals are more abundant above the line and non-stunted
individuals below it, indicating that stunted individuals have relatively shorter legs than non-stunted ones (Figures C.17-C.20).

Table 7.9. Quick-Test*: isometric line equations, distributions and p-values for differences in body proportions associated with stunting among Cali women.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Line Equation</th>
<th>Stunting</th>
<th>n Above Line</th>
<th>n Below Line</th>
<th>p^1</th>
</tr>
</thead>
<tbody>
<tr>
<td>All SES groups</td>
<td>y = x - 0.5761</td>
<td>Stunted</td>
<td>174</td>
<td>71</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Stunted</td>
<td>455</td>
<td>867</td>
<td></td>
</tr>
<tr>
<td>High SES</td>
<td>y = x - 0.5796</td>
<td>Stunted</td>
<td>12</td>
<td>5</td>
<td>0.0004</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Stunted</td>
<td>121</td>
<td>320</td>
<td></td>
</tr>
<tr>
<td>Mid-Low SES</td>
<td>y = x - 0.5771</td>
<td>Stunted</td>
<td>78</td>
<td>40</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Stunted</td>
<td>181</td>
<td>293</td>
<td></td>
</tr>
<tr>
<td>Low SES</td>
<td>y = x -0.5720</td>
<td>Stunted</td>
<td>81</td>
<td>29</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Stunted</td>
<td>147</td>
<td>260</td>
<td></td>
</tr>
</tbody>
</table>

^1 Highlighted p-values are significant at 0.05 level.

7.3 Differential Access to Resources

Differential access to resources has been linked to different stature outcomes, but it is unclear whether it is also associated with changes in body proportions. Given the fact that leg length is supposed to be more sensitive to environmental perturbations, individuals benefitting from better access to resources are expected to have not only greater overall stature, but also relatively longer legs than less privileged individuals.
This section reports the results of the comparisons between groups experiencing different access to resources within the same population, both in living (Makushi, Cali) and archaeological (Trino Vercellese) populations.

7.3.1 Makushi

The prevalence of growth retardation in groups experiencing different access to resources is reported in Table 7.6. When both sexes are pooled, isolated individuals exhibit a greater, significant ($p < 0.05$) rate of stunting (44%) than non-isolated individuals (35%). However, no significant differences are found in same-sex comparisons (Table 7.10).

Table 7.10. $\chi^2$ statistic and p-values for differences in stunting prevalence between Makushi subsamples.

<table>
<thead>
<tr>
<th>Test</th>
<th>$\chi^2$</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Isolated vs. Non-Isolated</td>
<td>4.03</td>
<td>0.045</td>
</tr>
<tr>
<td>Isolated F v Non-Isolated F</td>
<td>0.40</td>
<td>0.525</td>
</tr>
<tr>
<td>Isolated M v Non-Isolated M</td>
<td>3.29</td>
<td>0.070</td>
</tr>
</tbody>
</table>

1 Highlighted p-values are significant at 0.05 level.

The analysis of height, sitting height, and leg length between male subsamples reveals similar distributions for all growth indicators ($p > 0.07$) and no significant differences between their mean values ($p > 0.08$). The comparison between isolated and non-isolated females shows a different pattern. There are no significant differences between the groups in terms of both height distribution ($p = 0.137$) and mean height ($p = 0.057$).
0.054); however, significant differences (p < 0.02) are evident in both the distribution and mean values of both sitting height and leg length. This result suggests that different access to resources among Makushi women may be associated only with changes in body proportions. The age distributions of isolated and non-isolated individuals are tested by Mann-Whitney test and found to be significant among females (Figures B.24-B.25).

The “Quick-Test” is used to test the existence of differences in proportions between isolation subsamples (Table 7.11). Consistent with the results of absolute anthropometric data, significant differences (p = 0.014) are found only between females (Figure C.21-C.22). These differences are due to the fact that isolated females tend to have relatively shorter legs than non-isolated females, even though the latter are evenly distributed above and below the reference line used to test the presence of allometric differences (Figure C.21).

**Table 7.11. Quick-Test”: isometric line equations, distributions and p-values for differences in body proportions associated with relative isolation among Guyanese Makushi.**

<table>
<thead>
<tr>
<th>Sample</th>
<th>Line Equation</th>
<th>Isolation</th>
<th>n Above Line</th>
<th>n Below Line</th>
<th>p^1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females</td>
<td>y = x - 0.6974</td>
<td>Isolated</td>
<td>102</td>
<td>59</td>
<td><strong>0.014</strong></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Isolated</td>
<td>124</td>
<td>121</td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>y = x - 0.6390</td>
<td>Isolated</td>
<td>37</td>
<td>38</td>
<td><strong>0.857</strong></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-Isolated</td>
<td>24</td>
<td>27</td>
<td></td>
</tr>
</tbody>
</table>

^1 Highlighted p-values are significant at 0.05 level.
7.3.2 Cali

The association between access to resources and growth among the women from Cali is evaluated across SES population subsamples. Descriptive statistics for the three status subsamples are reported in Table A.7. Extremely significant (p = 0.000) differences in height, sitting height, and leg length are found between High SES and both Mid-Low and Low SES individuals. No significant differences (p > 0.29) are found in any of the variables between Mid-Low and Low SES women. Age distributions are significantly different between Low SES and the other groups, while no significant differences are found between High and Mid-Low SES (Figures B.25-B.27).

Differences in the relationship between height and sitting height are examined across SES samples with the “Quick-Test” (Table 7.12).

Table 7.12. Quick-Test”: isometric line equations, distributions and p-values for differences in body proportions associated with socioeconomic status among Cali women.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Line Equation</th>
<th>SES</th>
<th>n Above Line</th>
<th>n Below Line</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>High vs. Mid-Low</td>
<td>y = x - 0.5875</td>
<td>High</td>
<td>188</td>
<td>270</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mid-Low</td>
<td>371</td>
<td>221</td>
<td></td>
</tr>
<tr>
<td>High vs. Low</td>
<td>y = x - 0.5864</td>
<td>High</td>
<td>179</td>
<td>279</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Low</td>
<td>326</td>
<td>191</td>
<td></td>
</tr>
<tr>
<td>Mid-Low vs. Low</td>
<td>y = x - 0.5811</td>
<td>Mid-Low</td>
<td>294</td>
<td>298</td>
<td>0.022</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Low</td>
<td>293</td>
<td>224</td>
<td></td>
</tr>
</tbody>
</table>

1 Highlighted p-values are significant at 0.05 level.
The results indicate that the two lower SES groups differ moderately from each other ($p = 0.022$) and they are both significantly ($p = 0.0001$) different from the High SES group. In agreement with expectations, relatively shorter legs characterize individuals of relatively lower SES (Figures C.23-C.25).

7.3.3 Trino

Absolute dimensional differences of all skeletal elements and skeletal height between status subgroups are compared by Monte Carlo analyses. Significant differences ($p < 0.05$) are found in trunk and limb bones between high and low status males. Such differences are more pronounced in the lower limb – particularly in the distal segment – than in the trunk. No significant differences are found in skull height. No significant differences in any of the segments examined were found between high and low status females, with the only exception of foot height.

Differences in body proportions based on social status are evaluated in terms of segmental indices (see Table A.4) and overall morphotype by principal component analyses (PCA). No significant differences are found in the comparison of segmental indices by status subsamples (Table 7.13).

Table 7.13. P-values for Monte Carlo analyses of proportional indices between high and low status individuals from Trino Vercellese.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Radius/Humerus</th>
<th>Tibia/Femur</th>
<th>Trunk/(Femur+Tibia)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sexes Combined</td>
<td>0.914</td>
<td>0.111</td>
<td>0.795</td>
</tr>
<tr>
<td>Males</td>
<td>0.703</td>
<td>0.209</td>
<td>0.956</td>
</tr>
<tr>
<td>Females</td>
<td>0.924</td>
<td>0.601</td>
<td>0.360</td>
</tr>
</tbody>
</table>
However, PCA results reveal a distinct pattern in body size and shape variation in relation to status and sex. The first component (PC1) of size-and-shape variables for all the subsamples accounts for 76.24% of the total variance and reflects primarily size (as expressed by positive loadings of the eigenvectors – Table 7.14), while PC2 accounts for 9.43% of the total variance, and mainly contrasts trunk and foot height to tibia and femur length. When scores for all individuals are plotted (Fig. 7.1), it can be noted that high status individuals are generally bigger than their low status counterparts, with greater differences observed between the male subsamples. PC1 and PC2 of shape variables account for 42.83% and 32.68% of total variance, respectively (Table 7.14).


<table>
<thead>
<tr>
<th>Eigenvector Coefficients</th>
<th>Log Size-and-Shape</th>
<th>Log Shape</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PC1</td>
<td>PC2</td>
</tr>
<tr>
<td>Cranial Height</td>
<td>0.635</td>
<td>-0.124</td>
</tr>
<tr>
<td>Trunk</td>
<td>0.799</td>
<td>0.431</td>
</tr>
<tr>
<td>Femur</td>
<td>0.927</td>
<td>-0.322</td>
</tr>
<tr>
<td>Tibia</td>
<td>0.928</td>
<td>-0.308</td>
</tr>
<tr>
<td>Foot Height</td>
<td>0.904</td>
<td>0.327</td>
</tr>
<tr>
<td>Eigenvalues</td>
<td>0.018</td>
<td>0.002</td>
</tr>
<tr>
<td>%Total Variance</td>
<td>76.24</td>
<td>9.43</td>
</tr>
</tbody>
</table>
The first component contrasts trunk and cranial height to lower limb elements (femur, tibia and foot height), while the second component contrasts foot height and trunk to femur, tibia, and cranial height. The plot of individual scores highlights differences between high status males – falling right below the plot’s diagonal – and all the other subsamples, which fall above the diagonal (Fig. 7.2).

Figure 7.1. Scatter plot of individual scores for the first two principal components of Log Size-and-Shape Variables for individuals from Trino Vercellese, by sex and status.
Figure 7.2. Scatter plot of individual scores for the first two principal components of Log Shape Variables for individuals from Trino Vercellese, by sex and status.
7.4 Interpopulation Comparisons

7.4.1 Living Populations

Variance and coefficient of variation (CV) for height, sitting height, and leg length for all populations considered are reported in Table 7.15.

Table 7.15. Variance and coefficient of variation for height, sitting height, and leg length in Ribeirinhos, Makushi and Cali individuals, by sex.

<table>
<thead>
<tr>
<th></th>
<th>Coefficient of Variation</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Height</td>
<td>Sitting Height</td>
<td>Leg Length</td>
</tr>
<tr>
<td>Females</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ribeirinhos</td>
<td>0.038</td>
<td>0.038</td>
<td>0.067</td>
<td></td>
</tr>
<tr>
<td>Makushi</td>
<td>0.031</td>
<td>0.079</td>
<td>0.094</td>
<td></td>
</tr>
<tr>
<td>Cali</td>
<td>0.041</td>
<td>0.036</td>
<td>0.066</td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ribeirinhos</td>
<td>0.044</td>
<td>0.048</td>
<td>0.062</td>
<td></td>
</tr>
<tr>
<td>Makushi</td>
<td>0.034</td>
<td>0.039</td>
<td>0.059</td>
<td></td>
</tr>
</tbody>
</table>

Among the female samples, Ribeirinhos and Cali individuals exhibit a similar degree of variation in all anthropometric variables considered, while the Makushi exhibit a different pattern of variation. Specifically, even though total stature is less variable among Makushi women, its components are much more variable than they are in other samples. This finding is not mirrored by variation among males. In fact, male Makushi exhibit less variation in all anthropometric variables than the Ribeirinhos.

These differences are further explored by analysis of variance. Because in several comparisons the assumptions of normality and homoscedasticity are not met, non-
parametric tests are employed to test the existence of significant differences in the distributions of each variable in the different samples. The results of the Kruskal-Wallis test on female subpopulations revealed the existence of significant (p = 0.000) differences among populations in all variables considered. Pair-wise comparisons indicate that height is differently distributed among all populations, with Cali showing the greatest stature, followed by the Makushi and lastly by the Ribeirinhos. Sitting height is significantly different between Cali and the other two populations, but similar between Makushi and Ribeirinhos. Lastly, leg length is significantly different between the Makushi and the other two populations, but not between Cali and Ribeirinhos. These results point to the existence of differences both in total growth outcomes (height) and body proportions between the populations examined. These differences are visible in the scatter plot of log sitting height over log height for all female subpopulations (Figure 7.3).
The male subpopulations exhibit a different pattern of variation: while no differences between the groups exist in terms of total height, sitting height, and leg length are significantly different.

Differences in body proportions between populations are tested by the “Quick-Test” (Table 7.16). The results indicate that all populations examined differ significantly in their sitting height/height relationship. Specifically, female Ribeirinhos tend to have relatively shorter legs than Makushi women, even though Makushi women are equally distributed above and below the line. Both Amazonian populations exhibit relatively longer legs than the women from Cali, Colombia. Lastly, in contrast with the pattern
exhibited by females, male Ribeirinhos possess relatively longer legs than their Makushi counterparts (see also Figures C.26-C.29).

Table 7.16. Quick-Test: isometric line equations, distributions and p-values for differences in body proportions between populations.

<table>
<thead>
<tr>
<th>Line Equation</th>
<th>Population</th>
<th>n Above Line</th>
<th>n Below Line</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females</td>
<td>Ribeirinhos</td>
<td>73</td>
<td>15</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Makushi</td>
<td>196</td>
<td>210</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cali</td>
<td>1531</td>
<td>39</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Makushi</td>
<td>140</td>
<td>266</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ribeirinhos</td>
<td>21</td>
<td>67</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Cali</td>
<td>1265</td>
<td>305</td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>Ribeirinhos</td>
<td>34</td>
<td>50</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Makushi</td>
<td>81</td>
<td>45</td>
<td></td>
</tr>
</tbody>
</table>

1 Highlighted p-values are significant at 0.05 level.

7.4.2 Bioarchaeological Populations

Differences in overall morphology between the medieval individuals from Trino Vercellese and Giecz are evaluated on PCA eigenvalues of PCA run for each sample. The results of the PCA for Giecz are summarized in Table 7.17.
Table 7.17. Principal Component Analysis: first two principal components of Log Size-and-Shape and Log Shape variables for body proportions in Giecz.

<table>
<thead>
<tr>
<th></th>
<th>Eigenvector Coefficients</th>
<th>Log Size-and-Shape</th>
<th>Log Shape</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>PC1</td>
<td>PC2</td>
</tr>
<tr>
<td>Cranial Height</td>
<td>0.621</td>
<td>0.014</td>
<td>-0.104</td>
</tr>
<tr>
<td>Trunk</td>
<td>0.916</td>
<td>0.110</td>
<td>0.313</td>
</tr>
<tr>
<td>Femur</td>
<td>0.952</td>
<td>0.163</td>
<td>0.541</td>
</tr>
<tr>
<td>Tibia</td>
<td>0.907</td>
<td>0.334</td>
<td>0.796</td>
</tr>
<tr>
<td>Foot Height</td>
<td>0.805</td>
<td>-0.587</td>
<td>-0.943</td>
</tr>
<tr>
<td>Eigenvalues</td>
<td>0.016</td>
<td>0.003</td>
<td>0.003</td>
</tr>
<tr>
<td>%Total Variance</td>
<td>75.75</td>
<td>12.08</td>
<td>42.83</td>
</tr>
</tbody>
</table>

The first component (PC1) of size-and-shape explains 75.75% of the total variance, reflects mainly size and as such discriminates individuals based on sex. PC2 contrasts foot height to all other measurements and accounts for 12.08% of total variation. Figure 7.4 is a plot of the scores for size-and-shape variables in Giecz.
Figure 7.4. Scatter plot of individual scores for the first two principal components of Log Size-and-Shape variables for individuals from Giecz.

PC1 of log shape variables contrasts primarily tibial length and foot height and accounts for 42.38% of the total variance. Instead, PC2 contrasts cranial height and all other variables, accounting for 35.74% of total variation. Individual scores for log shape variables are plotted in Figure 7.5.
Figure 7.5. Scatter plot of individual scores for the first two principal components of Log Shape variables for individuals from Giecz.

The loadings of the PCA analyses on Log Size-and-Shape and Log Shape variables indicate that while overall size varies similarly in the two populations, morphology is not the same. Therefore, differences in overall stature and body proportions are explored by Monte Carlo analyses of segmental proportions of individuals from Trino Vercellese and Giecz. Given the fact that sex-related differences exist in some of the indices, these analyses are carried out on sex-specific population subsamples. The results of the analysis indicate the existence of differences in overall
stature between the two groups, with both sexes in Giecz exhibiting greater body size than their Italian counterparts. Additionally, body proportions differ between the two medieval populations, albeit the pattern of variation is different in the two sexes. Males differ only in the trunk/lower limb proportions, while females have significantly different brachial and crural indices but not differences in the relationship between trunk and lower limb (Table 7.18).

Table 7.18. P-values for Monte Carlo analyses of proportional indices between individuals from Trino Vercellese and Giecz.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Stature</th>
<th>Radius/Humerus</th>
<th>Tibia/Femur</th>
<th>Trunk/(Femur+Tibia)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td>0.003</td>
<td>0.581</td>
<td>0.991</td>
<td>0.016</td>
</tr>
<tr>
<td>Females</td>
<td>0.006</td>
<td><strong>0.011</strong></td>
<td>0.084</td>
<td><strong>0.01</strong></td>
</tr>
</tbody>
</table>

1 Highlighted p-values are significant at 0.05 level.

The difference between males is due to the fact that individuals from Trino Vercellese have relatively longer legs than those from Giecz, as evinced from a lower mean trunk/lower limb index. The differences in brachial and crural indices found between females result from the expression of relatively shorter radii and tibiae in the females from Trino Vercellese.
In summary, the results of this study demonstrated that:

1. Sex differences in body proportions are found in both living and bioarchaeological populations. However, the pattern of variation is not consistent. Among the *Ribeirinhos* males have relatively longer legs than females, while among the Makushi males have relatively shorter legs. Differences in the skeletal populations are only evident in Trino Vercellese, where males have relatively longer legs than females. No significant sex differences in body proportions are found in the Giecz sample.

2. Growth retardation is associated with allometric changes in body proportions in the Cali sample, where, in agreement with expectations, stunted individuals exhibit relatively shorter legs than their non-stunted counterparts. Contrary to this finding, no allometric changes are found among rural Amazonian populations in association with stunting.

3. Social inequality is associated with changes in stature and body proportions in both living and bioarchaeological populations. Specifically, in the Cali sample there is a significant positive association between overall stature and leg length and socioeconomic status. In Trino Vercellese, differences in stature and body proportions are found only between male status subsamples. High status individuals exhibit the greater stature and also relatively shorter legs. Lastly, no differences in growth outcomes are found between isolated and non-isolated Makushi.

4. Stature and body proportions allow the differentiation of populations exposed to different environmental conditions even within the same broad ecogeographic
zone. Among living populations significant differences in stature are found only among females, while significant differences in body proportions are found in both sex subsamples. Significant differences in both stature and body proportions are detected in both male and female skeletal samples.
CHAPTER 8: DISCUSSION

8.1 Sex Differences in Growth Outcomes

The first goal of this study is to investigate the existence of sex-related differences in body proportions at the intrapopulation level. According to the hypothesis of greater male sensitivity to environmental conditions, it is expected that when both sexes are exposed to the same overall environmental stress, males should exhibit more compromised growth outcomes. Specifically, males should have relatively shorter legs than females. This, in turn, should also lead to a reduction of size sexual dimorphism in the population.

The results of the analyses presented in Chapter 7 reveal that sex differences in growth outcomes do exist within all populations examined, but they vary greatly. In this section, I set to interpret the patterns observed in relation to the broader biocultural context of each population, as well as to draw some key elements of such variation.

8.1.1 Ribeirinhos

Significant sex differences in body proportions exist among the Ribeirinhos included in this study; however, contrary to expectations, males exhibited relatively longer legs than females, suggesting that males benefiting from overall better life
conditions during growth. These differences in trunk/lower limb proportions are consistent with a general pattern observed in analyses of worldwide variation in relative limb lengths, which have shown that males tend to have relatively longer lower limbs than females (Leonard and Katzmarzyk, 2010). Drawing on long-term ethnographic research conducted by Piperata (2005, 2007; Piperata and Dufour, 2007; Piperata and Gooden-Mattern, 2010; Piperata et al., 2011a, 2011b), which included data obtained via interviews and participant observation, and detailed dietary data, there are several possible factors that could be invoked to explain this finding, including differential access to resources between the sexes and sex-specific energetic stress associated with reproduction during adolescence.

8.1.1.1 Access to Resources Over the Period of Growth and Development

Stinson (1985) argued that a major confounding factor that may explain the weak support for female buffering during the postnatal period is the preferential treatment of sons, especially in terms of access to food and medical care, observed in many societies. Brazilian society, like those throughout Latin America, is patriarchal and exhibits male dominance (Neuhouser, 1989). Several studies of child health conducted in Latin America have found evidence of greater dietary adequacy (Frongillo and Bégin, 1993; Dewey, 1980), better access to healthcare (Delgado et al., 1982; Dewey, 1980, 1983; Larme, 1997), and better nutritional status (Frongillo and Bégin, 1993; Dewey, 1980, 1983) among boys. However, studies conducted in Brazil indicate that the pattern of parental-child investment is complex and there is little evidence of male bias in access to resources (Emerson and Souza, 2007; Silva and Crews, 2006; Thomas, 1994).
Ribeirinhos identify with the larger Brazilian society and can also be described as male dominant. However, data collected during long-term research in these communities provide little evidence for an increased desire for or preferential treatment of sons, especially during the period of most rapid growth (Piperata, pers. comm.).

As part of a reproductive history interview, women were asked about their ideal family size and composition. The most common response to the question “How many children do you want?” was “O que Deus quiser” or “What God wants or desires” (Piperata, pers. comm.). This response indicates that women felt they had little control over their total parity and this was due, in large part, to their limited access to birth control. Another common response to this question was “um casal” which literary translates as “a married couple” but in this context means “one girl and one boy.” Only in a few instances, where a woman was pregnant and already had a large number of children of one sex, was a preference for the opposite sex expressed.

The lack of preference for one sex over the other may be related to the fact that adults recognized the contributions of both boys and girls in the household. Girls provided significant support to their mothers from an early age, caring for younger siblings, hauling water and doing laundry. The contribution of boys started around 10-12 years when they began fishing and then later (~15 years) when they started to hunt and assist their fathers with heavy labor, such as clearing the forest to plant a new manioc garden, cutting wood, and hauling heavy loads.

Ribeirinhos do not observe a preferential residence pattern. Thus, upon marriage, it was equally likely for daughters and sons to choose to build their homes close to that of their parents. In cases where daughters lived near their parents, it was common to
observe mothers and daughters time their domestic and agricultural activities to coincide so that they could enjoy the company and assistance of one another as they worked. Sons, when living close to their natal home, often continued hunting and fishing with their fathers and fathers and sons assisted one another clear their respective manioc gardens. Fathers and sons also coordinated their economic activities and commonly traveled together to town to trade.

Long-term field research, including 22-months living in the communities, provided Piperata many opportunities to observe the ways boys and girls were treated. In terms of healthcare, there is little evidence to support preferential access for males. As mentioned earlier, access to healthcare was limited for all community members due to the distance between the communities and town and people only tended to seek medical care in emergency situations. Common illnesses, such as respiratory and gastrointestinal infections, were rarely treated with western medicine. Both types of illnesses were typically allowed to run their course although, in the case of gastrointestinal infections, mothers often prepared medicinal teas made from local plants to treat symptoms.

Direct observations of hundreds of meals provide no evidence of the preferential feeding of boys over girls. Dietary data collected in 2009 on 52 children aged 4-16 years support these observations as statistical analyses revealed no significant sex-based difference in energy (t = 1.2; p = 0.23) or protein (t = 1.1; p = 0.29) adequacy (Piperata, un-published). In addition, Piperata (2007) found no difference in average height-for-age z-scores or rates of stunting between male and female children and, in a longitudinal study, Piperata and collaborators (2011a) found no difference in the rates of catch-up growth between males and females during the childhood or juvenile stages. Taken
together these data provide little support for the preferential treatment of males in these communities, at least during the period of most rapid growth.

While there is no evidence for the preferential treatment of male children, there are two local practices or norms that could potentially induce sex-related differences in access to resources, specifically food, during adolescence that may explain the higher rates of stunting and proportionally shorter legs found among adult females. First, direct observations and interviews with mothers revealed a particular concern with the dietary intakes of their older, adolescent, sons. As mothers saw it, adolescent and adult males required more food than other members of the household due to the energy they expended in subsistence work including manioc cultivation, fishing and hunting. Adolescent boys, along with their fathers, were often served first at mealtimes and food was often set-aside for them if they were absent from the household when a meal was served. Even though this practice did not appear to compromise the dietary intakes of other children in the household, it is possible that adolescent males benefitted from improved nutrition and that this, in turn, allowed for catch-up growth during adolescence.

Second, adolescent males exhibited much greater mobility than their female counterparts and only males, including adolescents, participated in wage labor jobs. Houses in most communities were strung along the river’s edge and were anywhere between a five and 30 minute canoe ride from one another. It was far more common to see males traveling to other households than females and local custom dictated that visitors be offered food. While a highly sugared cup of coffee was the most common offering, a visitor that arrived during a meal was almost always invited to eat. Those employed in wage labor (e.g., small-scale timber operations, scientific field station) were
fed by their employers and these meals could be substantial such as large servings of rice and beans, along with farinha and tinned, fatty meats. Thus, both of these activities may have provided males the opportunity to secure resources outside of their own households, options unavailable to adolescent females.

In conclusion, even though male and female Ribeirinhos appear to be exposed to the same environmental conditions during infancy and childhood, potentially better access to resources for males during adolescence may explain some of the differences in body proportions observed in this study. Specifically, improved nutrition in adolescence may support catch-up growth in males that exhibited relatively longer legs than their female counterparts.

8.1.1.2 Longitudinal Growth and the Costs of Female Reproduction

An additional factor that may have contributed to the higher rates of stunting and sex differences in relative trunk/limb proportions observed among adults Ribeirinhos is the energetic stress of reproduction on females during the period of growth and development.

Several studies (Scholl et al., 1993; Scholl et al., 1994; Casanueva et al., 2006; Rah et al., 2008) have reported that early pregnancy can conflict with fetal growth. In these instances, the mother’s body may divert nutrients for its own use, including growth, leading to adverse birth outcomes (Frisancho et al., 1983; Scholl et al., 1994; Wallace et al., 2001; Duvan et al., 2010). Fewer studies have addressed the impact that early reproduction may have on maternal growth, especially under sub-optimal environmental conditions. Recent studies conducted among Mexican and Bangladeshi adolescents suggest that, in poorer settings, pregnancy during adolescence may lead to maternal
growth cessation (Casanueva et al., 2006; Rah et al., 2008). However, it is important to note that both studies were conducted over a relatively brief period during the postpartum (1-6 months). Thus, it remains unclear if maternal growth resumed at some later point. If growth does not resume, the costs associated with female reproduction may in fact explain the unexpected pattern of variation in body proportions observed among *Ribeirinhos*.

To explore whether female reproduction is a factor that could explain the sex differences observed, the association between the final outcome of linear growth and reproductive history parameters such as age at menarche, age at first birth and parity, are summarized in Table 8.1.

Table 8.1. Reproductive characteristics of *Ribeirinha* women (n=88).

<table>
<thead>
<tr>
<th></th>
<th>Min</th>
<th>Max</th>
<th>Mean</th>
<th>St Dev</th>
</tr>
</thead>
<tbody>
<tr>
<td>Menarche (years)</td>
<td>11</td>
<td>16</td>
<td>12.8</td>
<td>1.1</td>
</tr>
<tr>
<td>Age at First Birth (years)</td>
<td>13</td>
<td>24</td>
<td>17.8</td>
<td>2.3</td>
</tr>
<tr>
<td>Breastfeeding duration (months)</td>
<td>4.3</td>
<td>25.6</td>
<td>13.4</td>
<td>4.3</td>
</tr>
<tr>
<td>Inter-birth Interval (months)</td>
<td>10.75</td>
<td>73.0</td>
<td>27.5</td>
<td>10.7</td>
</tr>
<tr>
<td>Parity</td>
<td>1.0</td>
<td>15.0</td>
<td>6.2</td>
<td>4.0</td>
</tr>
<tr>
<td>Parity (women &gt; 45 yrs) (n= 15)</td>
<td>2.0</td>
<td>15.0</td>
<td>10.3</td>
<td>3.8</td>
</tr>
</tbody>
</table>

Average age at menarche is 12.8 ± 1.1 years and average age at the birth of the first child is 17.8 ± 2.3 years. On average, women breastfeed for 13.4 ± 4.3 months and the average inter-birth interval is 27.5 ± 10.7 months. Average total parity for women over the age of 45 is 10.3 ± 3.8 children. Age at first birth showed a significant decline over time (Figure 8.1) with the trend of younger women giving birth earlier than older
women (Kruskall-Wallis test, p = 0.02). Age at menarche did not differ among age
groups (p = 0.66). However, parity expectedly increased with age (p < 0.001).

Figure 8.1. Secular trend in mean age at first birth among Ribeirinha women.

The relationship between reproductive history parameters and growth outcomes is
explored by correlation analyses. Given the existence of a negative secular trend in age at
first birth among Riberinhos in the communities studied (Figure 8.1) and thus the
increased occurrence of pregnancy prior to the completion of skeletal growth, all analyses
are controlled for age.
The results of these analyses (Table 8.2) indicate that age at first birth is the only reproductive history parameter that is significantly correlated with the anthropometric variables examined. In particular, positive correlations exist between age at first birth and height ($r = 0.29; p = 0.01$) and age at first birth and total leg length ($r = 0.41; p = 0.001$). There is no relationship between age at first birth and sitting height ($r = -0.04; p = 0.72$). That is, those with earlier ages at first birth are shorter in stature and have proportionally shorter legs.

Table 8.2. Correlation analyses between anthropometric data and reproductive history parameters, controlled for age and age at first birth.

<table>
<thead>
<tr>
<th>Control Variable</th>
<th>Age at First Birth</th>
<th>Parity</th>
<th>Age at first birth</th>
<th>Inter-birth Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Correlation</td>
<td>Correlation</td>
<td>Correlation</td>
<td>Correlation</td>
</tr>
<tr>
<td>Age</td>
<td>0.195</td>
<td>-0.133</td>
<td>-0.135</td>
<td>-0.135</td>
</tr>
<tr>
<td></td>
<td>(2-tailed)</td>
<td>(2-tailed)</td>
<td>(2-tailed)</td>
<td>(2-tailed)</td>
</tr>
<tr>
<td></td>
<td>0.098</td>
<td>0.220</td>
<td>0.135</td>
<td>0.389</td>
</tr>
<tr>
<td></td>
<td>71</td>
<td>85</td>
<td>41</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>0.123</td>
<td>0.850</td>
<td>-0.134</td>
<td>0.392</td>
</tr>
<tr>
<td></td>
<td>0.158</td>
<td>0.180</td>
<td>-0.072</td>
<td>0.645</td>
</tr>
<tr>
<td></td>
<td>0.298</td>
<td>0.645</td>
<td>0.001$^2$</td>
<td>0.645</td>
</tr>
<tr>
<td></td>
<td>0.182</td>
<td>0.180</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.723</td>
<td>0.180</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.723</td>
<td>0.645</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.044</td>
<td>0.645</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.145</td>
<td>0.645</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.210</td>
<td>0.645</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.289</td>
<td>0.645</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.412</td>
<td>0.645</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^1$ Significant at 0.05 level.

$^2$ Significant at 0.001 level.

It has been argued that age at menarche, reflecting sexual maturation, may show an association with estrogen-induced epiphyseal closure and consequently with growth.
cessation (Porcu et al, 1994). However, no significant correlation between age at menarche and anthropometric variables is found. Nonetheless, this lack of relationship should be considered with caution as older women may not have been able to accurately recall their age at menarche and instead may have reported values similar to those of the younger women (daughters and granddaughters) around them who experienced the event more recently.

The positive correlation between age at first birth and total leg length suggests that early reproduction has a negative impact on the mother’s own skeletal growth. Even though correlation does not imply causation, it seems reasonable to attribute the observed relatively shorter lower limb in females to nutritional costs associated with pregnancy and lactation. Data collected between 2002 and 2009 indicate that adolescents in these communities become sexually active early in their teens (14-15 years) and, with limited access to contraception, teen pregnancy is common.

A detailed, longitudinal study of maternal dietary intake, energy expenditure and mobilization of body stores during lactation conducted in these same communities found that while women’s energy and protein intakes came close to meeting their normal daily energy needs, they were insufficient for meeting the additional energy demands of reproduction, especially lactation, forcing women to rely on their own energy reserves (Piperata and Dufour, 2007). Therefore, it is conceivable that women reproducing at a time when their own growth is not complete experience greater nutritional stress compared to their adolescent male counterparts.

Additional evidence to support this idea comes from comparisons of the rates of catch-up growth among male and female adolescents in this population. While Piperata
and collaborators (2011a) found no difference in the rates of catch-up growth among children and juveniles, marked differences were found among adolescents. Ninety percent of adolescent males compared with only 8% of adolescent females exhibited signs of catch-up growth. Reproductive histories reveal that most of the adolescent girls had been pregnant, at least once, during the study period leading Piperata and colleagues to suggest that the sex-related difference in catch-up growth during adolescence was likely attributable to the costs of pregnancy and lactation on the growing female body.

Lastly, it is conceivable that multiple pregnancies may be associated with more severe female growth retardation than a single pregnancy. To this end, correlation analyses are carried out on anthropometric variables and parity (controlling for age), as well as on anthropometric variables and inter-birth interval between first and second birth, controlling for age at first birth. In both cases, there are no significant correlations. These results suggest that the nutritional costs (and possibly the increased estrogen levels) associated with pregnancy and lactation, occurring concomitantly with skeletal growth, may inhibit any further gains in height.

It is interesting to note that among Ribeirinhos, growth retardation associated with early reproduction is limited to leg length, while sitting height is not affected. It has been argued that, based on growth heterochrony, different timing and duration of growth insults may result in altered adult body proportions (Bass et al., 1999; Bradney et al., 2000). Specifically, negative growth outcomes are expected to be greater for those body segments that are growing faster and/or are further from growth completion at the time of the insult. There is evidence indicating that the appendicular skeleton grows faster than the trunk during childhood, while the trunk growth velocity increases at the onset of
puberty (Bass et al., 1999; Bradney et al., 2000). On this basis, one would expect stress experienced later in growth – such as adolescent pregnancy and lactation – to have a greater impact on the axial rather than the appendicular skeleton. However, the findings of this study do not match expectations.

This discrepancy may be explained in terms of developmental plasticity and growth canalization. First, while the models reported above may be valid for individuals from affluent societies, they may not be applicable to individuals chronically exposed to environmental stress, such as those included in this study. It is possible that the human body responds to a more stressful environment by plastically adjusting growth rates and duration, as has been observed in other species (Bateson et al., 2004). This hypothesis finds support in the delayed maturation patterns observed in several populations from developing countries (Bogin, 1999). Therefore, the negative impact of reproduction on leg length may be due to the fact that, unlike their peers living in more affluent settings, adolescent mothers in the developing world are farther from having reached adult leg length. Second, regardless of the tempo of growth of different body segments, it is possible that sitting height may be more canalized, hence less variable, than leg length. Specifically, sitting height may be more constrained in size in relation to the size of the vital organs located in the chest and abdomen. Given the increased spatial demand in the torso associated with pregnancy, it seems reasonable to assume that leg length may be preferentially sacrificed.

To further examine this interpretation, I explored whether among Riberinhos trunk length was more canalized than leg length by using an F-test. The results indicate that the trunk is significantly more canalized than the leg among females (F = 1.955; p =
0.00008), but not among males (F = 1.988; p = 0.09). This evidence suggests that, at least in the sample examined, a greater canalization of trunk length may be associated with the specific demands of female reproduction.

8.1.2 Makushi

The results of the analyses on male and female Makushi reveal the existence of significant sex differences in growth outcomes. In agreement with the hypothesis of greater male sensitivity to environmental stress, males exhibit significantly higher rates of stunting than females. Furthermore, in all population subsamples males have relatively shorter legs than females. These findings appear to support the hypothesis of greater male sensitivity, however, a more in-depth investigation of the pattern of variation observed among the Makushi reveals that females do not simply have longer legs. In fact, both leg length and sitting height in the female subpopulation exhibit a bimodal distribution. Hence, this pattern of variation is explored further in relation to available biocultural data.

8.1.2.1 Different Morphotypes

An interesting aspect of intrapopulation variation among the Makushi is that in all population subsamples examined females exhibit a much greater range of variation in both leg length and sitting height than males (see Tables 7.15 and A.2 and Figures C.2-C.4). However, a similar degree of variation is found in total height. When the components of height for each individuals are plotted, it becomes apparent that among the Makushi there are two distinct morphotypes: one characterized by relatively long trunk and short legs and one displaying short trunk and long legs. In the following
discussion these morphotypes are referred to as morphotype 1 and 2 respectively. The latter morphotype is almost exclusively present among women (Figure 8.2).

![Figure 8.2. Scatter plot of sitting height over leg length of female (circles) and male (squares) Makushi. The line represents a perfect 1:1 relationship between the two variables.](image)

The two female morphotypes are distinguished by the fact that the relationship between trunk and legs is inverted, while mean height is the same. A correlation analysis of sitting height and leg length among females indicates a very strong negative relationship between the two variables ($r = -0.760; p = 0.000$), which are both positively
correlated with height (sitting height: \( r = 0.114; \ p = 0.022 \); leg length: \( r = 0.559; \ p = 0.000 \)). The existence of these two body types only among females appears to be at the origin of the differences in body proportions between males and females. To test this idea, a “Quick-Test” is run between males and females characterized by morphotype 1 (Figure C.30). The results indicate the absence of significant differences in body proportions between men and women (Table 8.3), even though males tend to be more frequent below the line. However, this result should be interpreted with caution, because significant (\( p = 0.000 \)) differences exist in the age distributions of the male and female Makushi included in this analysis. Specifically, males are on average significantly older than females. Given the fact that older individuals may have relatively longer legs due to vertebral body compression (Galloway, 1988; Cline et al., 1989; Chandler and Bock, 1991; Giles, 1991), it cannot be excluded that the lack of sex differences may be attributable to confounding factors such as aging.

Table 8.3. “Quick-Test”: isometric line equation, distributions and p-value for sex differences in body proportions among “morphotype 1” Makushi.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Line Equation</th>
<th>Sex</th>
<th>( n ) Above Line</th>
<th>( n ) Below Line</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>( y = x - 0.6358 )</td>
<td>Females</td>
<td>122</td>
<td>99</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Males</td>
<td>56</td>
<td>70</td>
<td></td>
</tr>
</tbody>
</table>
8.1.2.2 Association Between Environmental Factors and Morphotypes.

Previous studies (Bogin et al., 2002) have shown that improved life conditions result in the elongation of the lower limb, while trunk length does not vary. However, among the Makushi leg elongation is associated with a reduction of trunk length. This evidence suggests that, rather than being the outcome of improved overall conditions, the existence of two distinct morphotypes may be due to different growth processes and possibly related to different selective pressures. Therefore, two relevant questions to understand the differences observed between sexes among the Makushi are: 1) what produced the two distinct morphotypes and 2) why they are present only among women.

In order to answer these questions, the morphotypes are examined in relation to a number of variables including age, relative isolation, season of birth, and birth order as well as population customs and known changes in its biocultural milieu. A different prevalence of either morphotype in relation to age may provide information regarding secular trend in the population, which could possibly be related to known population history events. Relative isolation, based on relative proximity to the Gerogetown-Lethem road, plays a role in access to resources such as trade goods and healthcare services. Additionally, isolated villages tend to be closer to bodies of water and be more affected by malaria during the wet season. Therefore, isolation could possibly enlighten the causes of the differences in morphotypes if they reflected differences in overall environmental quality. Season of birth (dry/wet season) has also been argued to have an effect on Makushi growth in relation to the nature and timing of environmental stressors such as food availability and disease (Wilson et al., 2011). Birth order, as an indicator of relative
food and care availability within a household could also provide insights on the differences observed.

When the relationship between trunk and lower limb is examined in relation to the factors mentioned above, it becomes evident that the presence of the two different morphotypes is significantly different across age groups (Kruskal-Wallis test, \( p = 0.000 \)). In particular, morphotype 2 is rare among women aged 55 years and older, but it becomes progressively more common among younger age groups. Among female individuals aged 35 years and younger, the distinction between the two morphotypes is extremely well defined (Figure 8.3).

![Figure 8.3. Scatter plot of sitting height over leg length in female Makushi younger than 35. Note the complete distinction of the two different morphotypes observed in the population.](image)
Correlation and non-parametric analyses of morphotypes and all other variables considered indicate that there is no association (p >0.05) between morphotypes and isolation, birth season or birth order, even though morphotype 1 appears more frequent among isolated individuals than non-isolated individuals. This suggests that the factor(s) leading to increased expression of morphotype 2 involved the entire population to a similar extent, regardless of relative isolation, birth season and birth order. An important element in understanding what may have caused this change is the association between morphotype 2 and young age. Indeed, among women 35 and younger, 48% exhibit morphotype 1 and 52% exhibit morphotype 2. All individuals who were 35 and younger at the time of data collection were born after 1965, suggesting that some environmental change starting in the 1960s may underlie the change in body proportions observed among Makushi females.

The most conspicuous documented change in environmental conditions that took place in the 20th century is the establishment of health programs in the region by the British government first and then by the Guayana government following independence (Butt-Colson, 1971). Historical accounts of Makushi life conditions and health in the late 19th-early 20th century indicate that several epidemics dramatically affected the Makushi inhabiting the north Rupununi region. The earliest accounts of epidemics refer to the introduction of smallpox in the area in 1842, with devastating consequences on the Makushi population (Butt-Colson, 1971). In the early 20th century malaria was also introduced in the region, where it became one of the primary causes of mortality among the natives (Wilson et al, n.d.). Additional epidemics, including the influenza pandemic
in 1918 continued to vex the Makushi population, the numbers of which constantly declined, to the point to raise serious concerns regarding the tribe’s survival (Wilson et al., n.d.). The decline in the Makushi population was due not only to the losses attributable to disease, but also to the aggravating fact that sick individuals could not attend to their manioc fields and produce adequate food (Keary, 1930 in Wilson et al., n.d.). Such circumstances were mitigated by the establishment of Amerindian districts by the British, with the goal to safeguard the natives’ well-being (Butt-Colson, 1971). In response to multiple enterprises to improve the natives’ health, including the establishment of hospitals, a campaign to eradicate malaria and improve sanitation, and the introduction of powdered milk in schools, Makushi’s health improved even though not constantly due to sporadic epidemics. By the 1960’s the tribe had undergone notable population growth, further promoted by increased sedentarization in proximity to health posts and ongoing governmental health initiatives in the interior starting in the 1970s (Butt-Colson, 1971).

The improvement in sanitation and overall life conditions that started in the second half of the 20th century could explain, at least in part, the changes in body proportions observed among the Makushi. In particular, improvements of conditions during early (infancy/childhood) would explain a relative elongation of the lower limb, which grows faster than the trunk during the first phases of growth. Interestingly, leg elongation is accompanied by a reduction in trunk length, possibly suggesting that the improved conditions did not last beyond the first few years of life. However, the fact that the overall mean stature associated with the two morphotypes is not significantly different (p = 0.675) suggests other selective pressures may be at play. Additionally, if
improved sanitation is at the basis of changes in body proportions, why would it affect females and not males? The following section addresses this question by examining biocultural differences between male and female Makushi.

8.1.2.3 Biocultural Differences Between Males and Females

One of the questions investigated in this study is whether males and females respond differently to the same environmental milieu. As seen above, even though the differences in body proportions observed among the Makushi may support such hypothesis, the pattern of intrapopulation variation is more complex than originally posited. In particular, why do females in the same population show two different morphotypes and males only one? Possible explanations include differential treatment of male and female offspring and the existence of sex-specific selective pressures in response to changes in overall environmental conditions.

Interestingly, Wilson and colleagues note: “Two lines of ethnographic evidence and one line of theory indicate that, at least traditionally, daughters were favoured in Makushi households” (2011:9). Traditionally the Makushi practice matrilocal, cross-cousin unions (Im Thurn, 1883; Farabee, 1924; Myers, 1946). According to Myers (1993), when a union was arranged, the men had to live with the future bride’s family for a probationary period, during which he had to prove his worth to the bride’s father, assisting him in a variety of subsistence activities. Being instrumental in the acquisition of a valued “assistant and ally” to her father, a daughter was therefore considered more highly than her brothers. As such, it is conceivable that girls were accorded preferential treatment and benefitted from improved conditions compared to their male siblings. Additionally, among the Makushi women are responsible for the cultivation of manioc,
which represents the major dietary staple of the population (Palmer, 2009). Also for this reason, a girl’s status in the household may be elevated compared to that of boys. Lastly, it has been theorized that under adverse circumstances, it would be more adaptive for parents to invest in daughters than sons (Trivers and Willard, 1973; Cronk, 1991). Given the fact that the Makushi live in extremely poor conditions (Wilson et al., 2011; n.d.), it is possible that parents enact behaviors that, favoring daughters, lead to increased reproductive success.

An analysis of dietary adequacy among individuals between 1 and 20 years from these communities supports the existence of differential treatment of children by sex (Wilson and Bulkan, 2009). The favoring of daughters appears substantiated by different dietary intakes of boys and girls. In fact, females’ food intake is closer to the estimated average requirements (EAR) than males (females: 90% of EAR; males: 70% of EAR). In agreement with these data, Wilson and colleagues (2011) found higher rates of growth faltering among male individuals aged 0-20 years than among their female peers. This evidence suggests that, regardless of its proximate causes, inequality and preferential treatments of daughters among the Makushi exists. It is unclear to what extent this favoring of daughters may be expressed and as such it is difficult to evaluate its impact on the variation observed in terms of body proportions.

If improved nutrition, sanitation, and overall access to healthcare are at the root of the changes in morphology observed among the Makushi, then it should be concluded that the extent of offspring discrimination based on sex is such to exclude males entirely from the improved conditions. Arguably, if environmental conditions are poor and the limited benefits are passed on only to daughters, they would be the only ones exhibiting
changes in growth outcomes. However, across a continuum of differential access to resources, these individuals would be expected to express progressively larger size and elongation of the lower limb. Instead, among the Makushi even the female subpopulation is dichotomously divided in two different, well distinct morphotypes.

8.1.2.4 Selective Pressures on Females and Males

The bimodal distribution of trunk and leg length suggests that selection may act differently on the two morphotypes in relation to contingent levels of environmental stress. Under favorable environmental conditions selection is expected to be relaxed and intrapopulation variation to increase (Lahti et al., 2009). In regard to stature and body proportions, this implies that to the end of reproductive success it is marginally relevant whether individuals are short or tall, or whether they have long trunks or long legs. However, under increased environmental pressures, as in cases of malnutrition or disease, selection would favor morphotypes associated with other characteristics that have the potential to increase reproductive success. Specifically, if the energy that can be allocated to somatic growth is limited, it is more adaptive to allocate such energy to the development of vital organs (and by extension to the skeletal trunk), rather than to leg growth. Additionally, the ability to store fat upon completion of growth would also be selected because it provides females with energy reserves necessary to meet the increased energetic demands associated with pregnancy and lactation (Dufour and Sauther, 2002.). Indeed, a negative association between leg length and body fat has been observed in early growth retardation and is due to the inter-relatedness of physiological mechanisms involved in energetic efficiency and low fat oxidation, (Frisancho, 2007; Hoffman et al., 2000; Sawaya et al., 2004). In sum, a morphotype characterized by relatively short legs,
long trunk and greater body fat would be better suited for reproducing under adverse conditions and is expected to be selected.

Not surprisingly, these characteristics are found in what I have referred to as morphotype 1 among the Makushi. This is the phenotype that characterizes older women and all men in the population, and likely the only one that existed prior to the improvement of sanitation and healthcare access in the population. When these changes took place, it is conceivable that overall environmental stress declined and selection relaxed. As a result, more individuals survived to adulthood (as proven by the demographic increase documented starting in the 1950s) and women exhibited the second, latent morphotype 2. This morphotype, so distinctly opposite to the “traditional” one, may in fact have reproductive advantages in a more favorable environment. Increased leg length, associated with a short trunk, suggests more rapid (or intense) growth during childhood and a shorter adolescence, possibly leading to the achievement of overall adult size in a shorter time. This idea finds support in the documented association between more favorable growth conditions and earlier age at sexual maturation (Maclure et al., 1991; Onat and Ertem, 1995; Thomas et al., 2001; Sloboda et al., 2007). Therefore, if morphotype 2 were associated with earlier sexual maturation, then it could potentially increase reproductive success. Several life-history models have been advanced to explain the adaptive advantages of earlier reproduction resulting from precocious maturation (Day and Rowe, 2002; Gage 2003; McIntyre 2011). An important aspect of achieving early sexual maturity is that its advantages must outweigh the tradeoffs in the organism’s fecundity associated with a smaller body size at maturity (Day and Rowe, 2002). Interestingly, Day and Rowe advanced the concept of developmental
threshold, which is “a minimum size or condition that must be attained before a life-history transition can occur” (2002:339). In a literature review of the association between adult body size and age at menarche, McIntyre and Kacerosky (2011) noted that the Day and Rowe model could in fact explain the observed association between age at maturity and body size in humans. Therefore, if size thresholds apply to humans, morphotype 2 could allow reaching a minimum body size necessary for sexual maturation at an earlier age, hence proving to be an adaptive norm of reaction under improved environmental conditions.

If the two female morphotypes observed among the Makushi did in fact represent different norms of reactions in response to different selective pressures, the same kind of pressures and related adaptive advantages would not apply to males in the population. Indeed, with the exception of cases of severe intrauterine growth retardation and genetic diseases (Raboch and Reisenauer, 1976; Yunis et al., 1977; Toledo et al., 2011), there is no evidence to support the idea that male fertility may be related to adult size or age at maturity. Additionally, even though a positive association between male stature and reproductive success has been observed in western countries, primarily due to female choice selection (Pawlowski et al., 2000; Mueller and Mazur, 2001), similar associations may not be the norm in developing countries (Sear, 2006). If marital unions among the Makushi are arranged by the families, then sexual selection of specific male morphotypes is expected to be minimal. Under such circumstances, there would be no basis for the selection of morphotype 2 – less favorable under increased environmental stress – among males.
In conclusion, the morphological pattern observed among the Makushi points to differences between the sexes that may be attributed to preferential treatment of daughters and/or different selective pressures on men and women. In any case, whether the existence of two morphotypes is explained in terms of offspring sex discrimination or relative fitness and adaptive value, it is unclear what proximate causes and mechanisms may have led to its expression among the Makushi. Given the fact that morphotype 2 (re)appeared recently in response to improved conditions, in parallel with morphotype 1, it is conceivable that epigenetic controls may mediate early environmental stimuli in setting individual growth trajectories. Clearly, without more detailed, in-depth information on individual life histories as well as Makushi marital practices and mate selection practices it is not possible to draw definitive conclusions.

8.1.3 Trino Vercellese

Preservation issues and limited sample sizes complicate the investigation of differences in body proportions within bioarchaeological populations, especially when trunk/limb proportions are examined. In this study, Monte Carlo analyses are employed to overcome, at least in part, the issues. The results of the analysis on the medieval population from Trino Vercellese indicate that when social status groups are combined, significant sex-related differences in body proportions exist in both the brachial index and the relationship between trunk and the lower limb. However, only the difference in the brachial index persists within status-specific subsamples.

Sex differences in the brachial index have been observed by other authors (Trinkaus, 1981; Ruff, 1994; Holliday and Ruff, 2001) and have been explained in terms
of relative allometry of the different skeletal elements to overall size (Holliday and Ruff, 2001; Sylvester et al., 2008). Specifically, besides the fact that males are generally larger and therefore exhibit greater variability in element size than females, Sylvester and colleagues (2008) observed that the radius exhibits positive allometry with overall size, while the humerus shows a negatively allometric relationship with size. As a result, with overall size increase the distal segment of the upper limb is expected to be proportionally larger, hence producing higher brachial indices. The findings of the study seem to support this notion.

Similar sex-related differences are expected to be present also in the lower limb (Sylvester et al., 2008). The results of the analysis of the crural index (tibia/femur) on individuals from Trino Vercellese are non-significant. There are at least two possible explanations for this finding. First, Sylvester and colleagues (2008) noted that sex-related differences in the crural index are smaller and more difficult to detect because “males and females share a common set of allometry coefficients (i.e., slope) for the elements of the lower limb” (2008:380). It is, therefore, possible that the non-significance of the differences between sexes in the crural index may be due to the fact that the sample sizes for individuals from Trino Vercellese are small. Second, because the tibia is more sensitive to environmental stress than the femur, sex-related differences may be masked by different life histories and different responses of males and females to environmental conditions.

The significant difference in relative trunk length, due to the fact that females tend to have relatively shorter legs than males, may be interpreted in a similar fashion. On the one hand, such difference may be interpreted as related to allometric elongation of the
limbs (since females are characterized by smaller overall size they also have shorter legs). On the other hand, different developmental processes experienced by males and females in this population may explain this evidence. For instance, relatively shorter legs in females may indicate that they experienced less favorable life conditions that their male peers during development. Clearly, this evidence must be interpreted in the context of overall life conditions experienced by the sexes during growth. Thanks to rich contextual information available for the medieval inhabitants of Trino Vercellese, the relative importance of sample size effects and environmental conditions during growth can be explored. As discussed more in detail below, the results of overall morphotype analysis in Trino Vercellese suggest that the lack of sex-related differences in the lower limb and in the trunk/limb relationship may be due to different life histories experiences by males and females of different socio-economic status. A more complete picture of the pattern of variation in body size and proportions in Trino Vercellese in relation to both sex and status differences is presented in section 8.3.3.

8.1.4 Giecz

Stature estimates for individuals from Giecz reveal that this population was relatively tall for the time period. In particular, male average stature falls within average ranges of modern populations, and female stature is around the 25th percentile of the modern reference (NHANES III: Frisancho, 2008). Simply based on stature, it may be inferred that the population as a whole, and males more than females, experienced relatively positive overall life conditions during growth and development. If this were the case, then this population should therefore express sex-related differences in body
proportions. Specifically, if overall environmental stress was low, and males benefitted from relatively better life conditions than females, males are expected to have relatively longer legs than females. Additionally, the distal segments of the limbs should be longer in males than in females. However, none of the indices examined is significantly different between males and females from Giecz, indicating that the sexes in this population share the same body proportions.

There is no a priori reason why this population should defy the patterns of sex-related variation in body proportions observed across the globe (Leonard and Katzmarzyk, 2010). Rather than invoking some major deviation from the general rule, this unexpected finding may be explained in more conservative terms. First, preservation bias and methodological limitations are factors known to affect the validity of the analysis of remains from archaeological contexts. Second, the inadequacy of the assumption that tall stature implies good environmental quality during development must be considered.

8.1.4.1 Preservation Bias and Sample Size

If preservation bias existed, then it would be possible for the individuals analyzed not to be representative of the adult population inhabiting Giecz in the Middle Ages. The effects of preservation can be significant, especially when overall skeletal preservation is poor (Walker et al., 1988). It should be noted that the only selective criterion for inclusion of a skeleton in the study was completeness of all elements contributing to living stature. Preservation of undisturbed burials in Giecz is truly exceptional and it allowed including in this project 41% of the entire adult population unearthed from the medieval cemetery (Vercellotti et al., 2009). The remaining individuals were not included.
because they were damaged by agricultural activities, which appear to have involved all areas of the cemetery excavated. Hence, there is no reason to suspect that these disturbances were anything but random as far as preservation bias in population subsamples is concerned.

Even when samples can be deemed to be reasonably unbiased and representative of the entire population, bioarchaeological analyses are often affected by the fact that only small sample sizes are available. This is particularly true for studies such as this one, where skeletal completeness and availability of contextual information are needed. That said, small sample sizes are unlikely to be the reason for the lack of significant differences observed in this study. The total sample size for the analysis of proportional indices is 64 (19 female; 45 male) for the brachial index and 66 (20 female; 46 male) for crural and trunk/lower limb indices. Albeit not extremely large, these sample size are adequate for the analysis, especially in light of the fact that Monte Carlo re-sampling analyses with 1000 iterations were employed.

8.1.4.2 Stature in Giecz: Evidence of High Selective Pressures During Early Growth?

If methodological issues are not likely causes for the results presented above, then it is possible that the assumptions on which the expectations were founded are not met. Specifically, I argue that the tall stature observed in the population might not be a good indicator of early life conditions experienced by subadults in medieval Giecz. In fact, I argue that the tall stature observed in Giecz may reflect high levels of environmental stress early in life. At least two lines of evidence support this hypothesis.

First, a vast majority of adult individuals from Giecz show signs of LEH (sexes combined: 61%) and porotic hyperostosis (sexes combined: 90%), and to a lesser extent
cribra orbitalia (sexes combined: 31%). Even though these indicators are generic in nature and do not provide insights on specific stressors, they point out that nutritional deficiencies and growth perturbations were common in Medieval Giecz. In the survivor population, no sex differences exist in the prevalence of these conditions, even though males exhibited higher rates of LEH and porotic hyperostosis. Interestingly, the analysis of non-survivors (subadults) in the populations reveals that, while the prevalence of cribra orbitalia is significantly higher among deceased subadults ($\chi^2 = 4.48; p = 0.03$), porotic hyperostosis is more frequent among survivors ($\chi^2 = 46.29; p < 0.0001$). The discrepancy observed in the incidence of the two conditions may be due to the fact that orbital lesions, typically not extensive, likely healed in older survivors. A significant negative correlation between cribra orbitalia and age ($r = -0.28; p = 0.003$) supports this interpretation. Conversely, no significant association between porotic hyperostosis and age is found ($r = -0.04; p = 0.65$). In sum, this evidence implies that in Giecz overall environmental stress during development – and associated selective pressures – were high.

Second, data on subadult growth in this population support the notion that environmental stress experienced by the inhabitants of Giecz during early growth was extremely high and that tall stature in the survivor group is due to selection. Agnew and colleagues (2007) observed that subadults from Giecz exhibit severe growth retardation. Specifically, they noted that, when long bone diaphyseal length is plotted over dental age (Figure 8.4), subadults from Giecz consistently fall below modern size-to-age standards (Maresh, 1970).

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$^4$ Due to the fact that information on LEH in subadults was limited to a small number of individuals, LEH is not considered in the comparison between adults and subadults.
Clearly, the growth pattern of deceased subadults may not be representative of growth in the survivor group. Nonetheless, it provides evidence for high environmental stress, which in turn is extremely suggestive of high selection levels in this population. If environmental stress in Giecz was high, then as evinced from multiple lines of evidence, it is logical to conclude that small body size, as the byproduct of poor growth, was selected against. Consequently, the mean stature of the survivor group would be skewed toward higher values. This being said, it is important to recognize the fact that high selective pressures do not necessarily imply that the average stature of the survivor group will increase. There are at least two reasons why this is not necessarily the case. First, under poor environmental conditions, short stature is not selected directly, but it is merely a correlate of unsuccessful individual coping strategies rather than an intrinsically
undesirable trait in its own merit. Additionally, in this context short stature is a norm of reaction to poor growth conditions, which is determined by complex multigenic, epistatic, and epigenetic mechanisms. As such, short stature does not provide any information on the underlying genetic potential and variability. Hence the effects of selection are likely to end up being non-directional. A second, related consideration is that post-survival conditions must allow individuals to achieve tall stature. If the levels of environmental stress are high and constant throughout an individual’s entire growth period, then survival will not be associated with greater body size. Adult individuals from Giecz are in fact characterized by a relatively tall stature and this implies that the levels of environmental stress experienced by subadults in this population varied over time.

8.1.4.3 Catch-up Growth in Giecz?

The major shortcoming of stature as an indicator of environmental quality during growth is that it provides reliable information only when life conditions are the same for the entire growth period. Simply, when the environment changes, the organism responds. In particular, when life conditions improve, catch-up growth may take place. Catch-up growth following an earlier phase of high environmental stress may explain the tall stature observed in medieval Giecz. A key question is whether life conditions in Giecz could support catch-up growth. The evidence available to answer this question is quite scarce, especially inasmuch as life conditions are mediated culturally. There appears to be consensus among investigators working on skeletal remains from medieval Poland, that life conditions in the Middle Ages were less than favorable, in particular in rural settings (Jankowski, 1988; Łubocka, 2003 – both cited in Senator et al., 2006). Evidence of high prevalence of cribra orbitalia and Harris lines in several skeletal series from medieval
Poland is consistent with the high levels of stress inferred for Giecz (Gronkiewicz et al., 2001; Piontek and Kozlowski, 2002; Senator et al., 2009). Poor sanitation and infectious disease, rather than malnutrition and metabolic deficiencies, have been advanced as the more likely causes for the high levels of biological stress experienced during growth (Piontek and Kozlowski, 2002; Senator et al., 2009), but the bases for such reasoning are unclear. Similarly (and questionably), life conditions experienced by rural populations have been argued to be worse than those of people inhabiting major urban centers, primarily on the basis that famines would have had a greater impact on food security in rural settings (Senator, 2009).

Regardless of the causes of environmental stress attested in medieval Poland, the tall stature of the population from Giecz suggests that upon survival of earlier stressors, overall life conditions could support catch-up growth. In this regard, the isotopic analyses conducted by Reitsema and colleagues (2010) indicate that the adult population had a diverse, omnivorous diet, which likely included animal protein. Therefore, it would appear that adult diets could in fact allow for catch-up growth. It is unknown whether children’s diets in this population (and in general medieval Poland and medieval Europe) differed significantly from adult diets, hence it is difficult to reach definitive conclusions on the causes for high early stress followed by catch-up growth opportunities. Nonetheless, poor sanitary conditions, widespread infectious disease, and possibly nutrient-deficient diets are all factors that may have contributed to early growth retardation during childhood in Giecz. Conversely, upon survival of early stressors and infectious disease, the reduced risk of incurring further disease (justified by a “veteran” immune system) and possibly the adoption of adult diets at the end of childhood could
have promoted a reversal of growth retardation. Clearly, additional evidence on children’s diets and an improved understanding of the socio-cultural perception of children in medieval Poland are necessary to shed additional light on this matter.

Accepting the idea that catch-up growth was in fact possible for the medieval inhabitants of Giecz, how, then, would it affect body proportions? Unfortunately, there is no definitive answer to this question, because the nature and entity of catch-up growth vary in relation to the duration and timing of growth perturbations and environmental improvements. In general, the lower limb is expected to be more affected by growth retardation than the trunk, and distal elements more than proximal ones. Therefore, individuals of both sexes are expected to have relatively shorter legs than they would have in the absence of growth perturbations. Clearly, if life conditions were homogenously poor for the entire population, the presence of relatively shorter legs would need to be evaluated in relation to the body proportions of individuals who did not experience such stressors (e.g., different status groups; other populations).

Additionally, how could catch-up growth alter sex-related differences in body proportions? Assuming that stress levels are the same for both sexes, it may be argued that differences between males and females should remain unaltered. However, if males are more sensitive to environmental factors, then even the same stress levels could lead to the obliteration of males’ proportional limb elongation, particularly in the distal segment. The lack of significant differences observed between male and female body proportions in Giecz is consistent with this interpretation. Greater male sensitivity may also explain the significantly greater (Levene’s test, p = 0.035) variance observed in adult male skeletal height in this study (see Table A.5). Specifically, while female growth outcomes appear
to be more canalized, male size would vary more in relation to environmental factors. However, it should be noted that males’ greater variance may also be due to the fact that they have overall larger size. Furthermore, the difference in total variance may be interpreted as due to a significantly smaller variation in female size. In addition to being the result of canalization, a smaller range of variation among females may also be due to additional selective pressures related to the specific energetic demands of reproduction. In this regard, it is interesting to note that while catch-up growth led males to reach average stature values equivalent to modern day’s reference, females are smaller than the modern reference population. There is no reason to suspect that females may have a reduced potential for catch-up growth compared to males. However, it is possible that the burden of reproduction reduced the actual occurrence of catch-up growth in females. In this regard, it is reasonable to think that the timing of female reproduction could be culturally mediated to coincide with the achievement of an “ideal” adult size, defined as minimum body size compatible with successful reproduction. Clearly, further research on the specific impact of female reproduction on growth, as well as an improved understanding of the biocultural factors that may mediate it, are needed to clarify the relative contributions of different factors on the expression of sex-related differences in body proportions.

8.2 Growth Retardation and Body Proportions

The second goal of this study is to investigate whether severe growth retardation involves changes in body proportions. Several studies have shown that changes in life conditions are accompanied by changes in relative leg length (Tanner et al., 1982;
Siniarska and Wolanski, 1983; Bogin, 1999; Wolanski and Siniarska, 2001; Bogin et al., 2002). However, it is unclear whether differences in body proportions occur in absence of major environmental changes. This research question is addressed in three living populations by comparing differences in body proportions between stunted and non-stunted individuals. Clearly, the stature distribution of stunted and non-stunted individuals is different by definition (i.e., stunting is unusually small height-for-age) and is consequently not examined.

It should be noted that the definition of stunting in relation to an international reference might appear rather arbitrary and inadequate to assess variation within a specific population. In fact, the use of an external reference may mask or otherwise confound specific variation patterns and the determination of population-specific stunting patterns should be used instead. Nonetheless, this latter approach posits problems related to the identification of suitable cut-off points. In fact, when a population’s distribution parameters are used to normalize the data, that is, to calculate population-specific z-scores, the range of variation in z-scores is found to be fairly limited, with only a handful of individuals falling below -2 S.D. in each population examined. The populations under examination in this study are affected by high incidence of stunting by international standards (NHANES III, Frisancho, 2008). This implies that, since all individuals are short, only the most extreme cases of growth retardation are classified as “stunted” by population-specific criteria. Population-specific z-scores below -2 in these populations are almost non-existent, likely due to the fact that individuals with such short stature are likely not viable. This being the case, an alternative cut-off value should be identified. However, what this value should be is not straightforward. Furthermore, when examined
in the context of broader human variation in height, this approach appears limited and does not allow interpopulation comparisons. Based on these considerations, although not ideal, international references are adopted to define categories of stunting in this study.

Lastly, an objective of the project was to test differences in body proportions associated with stunting within both living and archaeological populations. However, the calculation of z-scores for individuals from archaeological settings (Trino Vercellese; Giez) revealed that only a handful of individuals from each collection fell below the cut-off of \( z = -2 \), making the comparison between stunted and non-stunted individuals not meaningful in these settings. This result is interesting because it highlights the fact that environmental stress in the past was not necessarily comparable to that experienced by modern populations. Hence, a proper understanding of environmental conditions in the past is crucial for verifying the validity of assumptions concerning biological variation in archaeological settings. As discussed in Sections 8.1.4 and 8.3.3, I argue that the lack of individuals that may be considered stunted by modern standards is due to extremely high levels of early environmental stress and later catch-up growth, which eliminated stunted individuals from the survivor group of each population.

8.2.1 Ribeirinhos

The analysis of body proportions between stunted and non-stunted Ribeirinhos meets only in part the expectation that allometric changes accompany severe stature reduction. A significant difference between stunted and non-stunted individuals exists in the sex-combined sample, with stunted individuals exhibiting significantly shorter legs than non-stunted individuals. This result matches expectations and is consistent with what
has been reported by other authors (Bogin et al., 2002). However, this result should be interpreted with caution in light of the absence of significant differences in the sex-specific samples (see below). In particular, given the significantly higher rate ($\chi^2 = 5.31; p = 0.02$) of stunting in females ($50/88 = 57\%$) than in males ($32/84 = 38\%$), it is possible that the differences observed may be attributable to sex-related differences in body proportions rather than body shape changes associated with growth retardation. The observed disparity in stunting rates between the sexes may be due, at least in part, to lack of catch-up growth, especially during adolescence, and/or increased nutritional stress associated with reproductive costs during growth experienced by females in this population (see Section 8.1.1).

The unexpected lack of significant differences in body proportions between stunted and non-stunted individuals in the sex-specific samples may indicate that height reduction in the population is rather isometric and that the stress leading to stunting affected trunk and lower limb length equally. For instance, this could happen if the stress experienced by stunted individuals was constant through the entire growth period.

Additionally, confounding factors such as age-related changes in trunk length and catch-up growth may also explain these findings. For example, even though the age distributions of stunted and non-stunted individuals did not significantly differ, stunting was more prevalent among older individuals. Numerous authors have reported age-related height reduction attributable to the compression of the vertebral column over time (Galloway, 1988; Cline et al., 1989; Chandler and Bock, 1991; Giles, 1991). This reduction varies in relation to a variety of factors, such as age at onset of height reduction due to age-related vertebral compression, sex, and population differences in the extent
and timing of height loss. According to Trotter and Gleser (1951 a, b), beginning at age 30, average loss in stature is approximately 0.06 cm per year. While negligible in the short term, this small annual reduction in stature would add up over decades leading to a noticeable decline in total height in older age. Age-related stature changes, being limited to the trunk, alter body proportions and shift an individual’s morphotype toward relatively longer legs. This phenomenon is exactly in the opposite direction of the allometric change associated with stature. Therefore, the effects of aging on vertebral heights could potentially obliterate the effects of stunting on body proportions and explain the lack of significant differences observed between stunted and non-stunted individuals. Additionally, catch-up growth during adolescence may partly reverse the effects of stunting, therefore eliminating differences in body proportions between the stunted and non-stunted sub-samples.

8.2.2 Makushi

The investigation of body proportions in relation to stunting among the Guyanese Makushi reveals a mixed pattern, with significant differences in some population subsamples and not others. In particular, significant differences exist in all sex combined samples and females (isolation groups combined). In light of the existence of different patterns of variation between males and females, the significant differences found are interpreted to be due to sex differences rather than to the process of stunting itself. Similarly, the significant result among females may be related to the existence of different morphotypes rather than to changes associated with stunting. Therefore, in order to verify if stunting is associated with changes in body proportions it is necessary to
examine each female morphotype individually. To this end, morphotype-specific population subsamples are tested by means of the “Quick-Test” (Table 8.4).

Table 8.4. “Quick-Test”: isometric line equations, distributions and p-values for differences in body proportions among stunted and non-stunted female Makushi, by morphotype and isolation.

<table>
<thead>
<tr>
<th>Line Equation</th>
<th>Stunting</th>
<th>( n ) Above Line</th>
<th>( n ) Below Line</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Morphotype 1</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All ( y = x - 0.6328 )</td>
<td>Stunted</td>
<td>55</td>
<td>36</td>
<td><strong>0.02</strong></td>
</tr>
<tr>
<td></td>
<td>Non-Stunted</td>
<td>57</td>
<td>73</td>
<td></td>
</tr>
<tr>
<td>Isolated ( y = x - 0.6304 )</td>
<td>Stunted</td>
<td>23</td>
<td>18</td>
<td>0.416</td>
</tr>
<tr>
<td></td>
<td>Non-Stunted</td>
<td>27</td>
<td>31</td>
<td></td>
</tr>
<tr>
<td>Non-Isolated ( y = x - 0.6347 )</td>
<td>Stunted</td>
<td>31</td>
<td>18</td>
<td><strong>0.032</strong></td>
</tr>
<tr>
<td></td>
<td>Non-Stunted</td>
<td>30</td>
<td>42</td>
<td></td>
</tr>
<tr>
<td><strong>Morphotype 2</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All ( y = x - 0.7715 )</td>
<td>Stunted</td>
<td>42</td>
<td>12</td>
<td><strong>0.0001</strong></td>
</tr>
<tr>
<td></td>
<td>Non-Stunted</td>
<td>50</td>
<td>81</td>
<td></td>
</tr>
<tr>
<td>Isolated ( y = x - 0.7632 )</td>
<td>Stunted</td>
<td>17</td>
<td>2</td>
<td><strong>0.0001</strong></td>
</tr>
<tr>
<td></td>
<td>Non-Stunted</td>
<td>14</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td>Non-Isolated ( y = x - 0.7758 )</td>
<td>Stunted</td>
<td>25</td>
<td>10</td>
<td><strong>0.005</strong></td>
</tr>
<tr>
<td></td>
<td>Non-Stunted</td>
<td>37</td>
<td>52</td>
<td></td>
</tr>
</tbody>
</table>

\(^1\) Highlighted p-values are significant at 0.05 level.

It should be noted that age distributions are non-significantly different between morphotype 1 samples, and significant between morphotype 2 samples (Figures B.29-B.34). The significant differences in this latter case are mainly attributable to the fact that
stunted women are older than non-stunted women exhibiting morphotype 2. In spite of these differences in age distribution, significant differences in body proportions are found in all morphotype 2 tests. These differences are due to the fact that stunted individuals have relatively shorter legs (Figures C.34-C.36) and suggest that age-related vertebral compression did not occur or was too modest to obliterate differences between stunted and non-stunted individuals.

The results of the analysis of morphotype 1 individuals are significant in two out of three cases. As expected, significant differences within the general and non-isolated samples are mainly attributable to a relative reduction of leg length among stunted individuals (Figures C.31, C.33). In contrast with this result, no differences are found between stunted and non-stunted individuals from isolated communities (Figure C.32). The similarity of age distributions suggests that this result may not be an artifact of age-related changes. Instead, the lack of changes in body proportions associated with stunting is suggestive that morphotype 1 isolated females experienced rather constant environmental stress during development, reducing the entire body rather than only leg length.

Similarly to isolated morphotype 1 females, no differences in body proportions are found in any of the tests carried out on male samples. Also in this case, stunting is associated with isometric changes, possibly due to constant stress throughout the entire period of growth.
8.2.3 Cali

The results of the analyses of body proportions in stunted and non-stunted individuals from Cali meet the expectations: in all samples stunted individuals have relatively shorter legs than their non-stunted counterparts. It is interesting that significant differences are found in spite of the existence of significant differences in age distributions. This is due to the fact that in this sample the reduction in leg length associated with stunting well exceeds age-related reduction in trunk height. The difference between stunted and non-stunted individuals in mean leg length exceeds 6 cm in all samples. Considering that the maximum age in the Cali population is 44 years, the degree of any age-related changes in trunk length would be negligible. For instance, according to the age correction method developed by Trotter and Gleser (1951a, b), stature change between ages 30 and 44 would amount to only 0.84 cm.

The fact that stunting in Cali is associated with relatively shorter legs suggests that environmental stress in this population is more severe during the earlier phases of growth and then possibly decreases at the end of childhood.

8.3 Differential Access to Resources, Stature and Body Proportions

Research in several areas of human biology has shown that, by influencing individual’s access to resources, social inequality translates into biological inequality. A goal of this project is to investigate whether significant differences in stature and body proportions exist between groups experiencing differential access to resources. To this end, absolute body size and proportions are examined in two living (Makushi, Cali) and one archaeological population (Trino Vercellese).
8.3.1 Makushi

Among Guyanese Makushi, differential access to resources is determined based on whether the villages are connected to the Georgetown-Lethem road or are dispersed in the interior along the Rupununi River. One of the major differences between isolation groups is that individuals living in isolated communities have less access to trade goods and healthcare. Consequently, isolated individuals are expected to exhibit poorer growth outcomes. This hypothesis seems to be supported by the fact that isolated individuals exhibit greater incidence of stunting than non-isolated individuals, even though significant differences are found only in sex-combined samples. When sex-specific samples are examined, no differences are found between isolated and non-isolated males in the distributions of height, sitting height, and leg length. Similarly, the “Quick-Test” points to the absence of differences in body proportions between isolation groups. Instead, the results of the analyses between female subsamples reported in Section 7.3.1 suggest the existence of significant differences. However, in light of the fact that two distinct female morphotypes have been observed among the Makushi, it is likely that such differences may be due to the unequal presence of such morphotypes in isolation samples. To clarify this issue, all analyses of absolute body size and proportions are carried out in morphotype-specific subsamples.

The results of these analyses show that the distribution of height, sitting height, and leg length between isolation groups are not significant (p>0.05) for either morphotype. Similarly, the results of the “Quick-Test” on morphotype-specific female
samples indicate that the body proportions of the isolation groups are not significantly different (Table 8.5 and Figures C.37, C.38).

Table 8.5. “Quick-Test”: isometric line equations, distributions and p-values for differences in body proportions among isolated and non-isolated female Makushi, by morphotype.

<table>
<thead>
<tr>
<th>Line Equation</th>
<th>Isolation</th>
<th>n Above Line</th>
<th>n Below Line</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>y = x - 0.6331</td>
<td>Isolated</td>
<td>55</td>
<td>45</td>
<td>0.344</td>
</tr>
<tr>
<td></td>
<td>Non-Isolated</td>
<td>58</td>
<td>63</td>
<td></td>
</tr>
<tr>
<td>y = x - 0.7782</td>
<td>Isolated</td>
<td>36</td>
<td>25</td>
<td>0.53</td>
</tr>
<tr>
<td></td>
<td>Non-Isolated</td>
<td>66</td>
<td>58</td>
<td></td>
</tr>
</tbody>
</table>

It should be noted that significant differences in age distributions are present between morphotype 1 isolation groups and not between morphotype 2 groups (Figures B.35, B.36). It is therefore possible that age-related changes in trunk length may have affected the analysis. However, the fact that no differences in either absolute size or body proportions exist in any of the samples examined suggests that relative isolation does not affect growth outcomes among the Makushi.

This lack of differences may be due to the fact that other characteristics of isolated communities offset the issues related to limited access to trade goods and healthcare. For instance, it has been advanced that individuals living in isolated villages may have better diets because they are located in areas with a more nutrient-rich soils and isolation may offer some protection against the introduction of infectious disease (Wilson
et al., 2011). Alternatively, it is possible that the monthly health services provided by health workers who visit the isolated communities may be sufficient to eliminate inequality in access to medication and treatment. Lastly, it is also possible that, while valid for younger generations, relative isolation may be a construct that does not well represent social inequality among the individuals included in this study. In particular, it is possible that at the time the individuals included in the analyses were growing, the differences between isolated and non-isolated villages were not conspicuous. There are at least to lines of evidence that suggest this may have been the case. First, Wilson and colleagues (2011) noted that the conditions of the Georgetown-Lethem road were such that it could only be travelled on off-road vehicles, at least until the full establishment of the Iwokrama International Centre for Rainforest Conservation and Development in the early 2000’s. This being the case, it is likely that in the past all villages were similarly isolated and intrapopulation differences in access to resources milder. Second, Wilson and coworkers (2011) found significant differences in stunting rates between isolated and non-isolated children and adolescents from these communities. This suggests that relative isolation may be a valid proxy for differential access to resources for those individuals who were growing at the time of the recent changes that have taken place in the region, and not for the older Makushi. This evidence stresses the importance of understanding the subtle differences in the type and degree of resources access experienced by individuals of the same population.
8.3.2 Cali

Socioeconomic status (SES) in Cali is a major determinant of relative access to resources experienced by individuals. Social inequality in Cali is so pronounced that the local administration recognizes up to 6 SES categories (see Figure 6.4). The results of the analyses on both absolute size and body proportions support the validity of this construct as an indicator of overall life conditions. High status individuals are taller and have longer trunks and legs than individuals from low status groups, which are not significantly different from each other. Based on this result, it may be concluded that differences in absolute sizes are particularly significant in proportion to the degree of inequality between the samples tested, but minimal if status differences are modest.

The analysis of the relationship between trunk height and leg length in different SES groups reveals that significant differences in body proportions exist between all groups examined and highlights a general positive association between social status and leg length. This holds true even between Mid-Low and Low SES groups, indicating that leg length may be so sensitive to environmental stress to detect even relatively small differences in overall life conditions. The differences in life conditions that could support the development of proportional changes between Low and Mid-Low SES women may be related to food security and sanitation.

Dufour and colleagues (1997a, b) showed that over 50% of low SES women in Cali experience food insecurity, due to not having the money to purchase food on a regular basis. These women enact several dietary strategies to cope with the inability to purchase food. These strategies include substituting meat with less “acceptable” animal parts, eliminating animal proteins, reducing portion sizes and, as a last resort, eliminating
meals or relying on support from others (Dufour et al., 1997a, b). Even though it is unclear to what extent food insecurity for children in Cali may be buffered by parental dietary practices and governmental subsidies, limited food availability is clearly a problem among lower SES groups.

One of the major differences between the two lower SES groups is that poorer barrios did not have access to water, electricity, and sewage and waste disposal services through the city. This implies that the sanitary conditions of these barrios were more precarious and that the transmission of infectious disease was possibly facilitated by the lack of proper sewage and waste disposal means. The impact of diarrheal disease on the growing body is typically more frequent in the earlier phases of life (Subcommittee on Nutrition and Diarrheal Diseases Control, 1992) and could therefore partially explain the relative reduction in leg length associated with progressively poorer life conditions.

8.3.3 Trino Vercellese

8.3.3.1 Status Differences in Absolute Bone Lengths

The results of the analysis of the medieval population from Trino Vercellese indicate a pattern of intrapopulation variation in body size and shape that is more complex than posited by previous research. In particular, while the male subsamples exhibit significant size differences in all post-cranial elements analyzed, only minor, non-significant differences are found between the female subsamples. The only exception to this general trend in the status subsamples is a significant difference in foot height
between female subsamples, which is likely the result of the limited sample sizes available for this measurement.

Overall, these results differ from those of previous research (Porro et al., 1999), which had identified differences between status groups of both sexes (Table 6.1). The reason for this discrepancy can be found in the different methodological approaches employed. While previous studies used regression formulae to estimate stature, I applied the anatomical method. This latter method is generally accepted to yield more accurate stature estimates, because it derives stature directly from the lengths of the skeletal elements that compose it. Based on the anatomical estimates, the mathematical ones reported by Porro and colleagues consistently overestimate actual living statures in the population from Trino Vercellese. In particular, mathematical estimates for low status individuals (both sexes) and high status females on average exceed anatomical estimates by over 4 cm. In clear contrast with this pattern, high status males’ average stature was overestimated by only 0.6 cm.

8.3.3.2 Stature Estimation in Trino Vercellese: A Cautionary Tale

However, the methodology employed by Porro and colleagues (1999) is unclear in regard to which formulae were employed and how estimates were obtained, and it is therefore difficult to draw definite conclusions on the causes of the discrepancies observed. Based on the information provided in an earlier preliminary report on the site (Masali et al., 1995) it would seem that the estimates published were obtained by employing a combination of Trotter and Gleser’s (1952; 1958) formulae for American whites’ different long bones. In order to gain insights on the differences observed between anatomical and mathematical estimates, I employ Trotter and Gleser’s (1952;
1958) formulae to calculate mathematical estimates for all individuals in the sample, which represent a subsample of the total individuals employed by previous researchers. Table 8.6 reports descriptive statistics for anatomical estimates and regression estimates derived from radius, humerus, tibia, and femur, as well as a “summary estimate,” obtained by averaging the estimates of the same individuals obtained with different formulae. Additionally, mean percent prediction errors (PPE) are computed to assess the deviation of mathematical estimates from anatomical ones. PPEs were calculated as \[100 \times \frac{\text{mathematical estimate} - \text{anatomical estimate}}{\text{anatomical estimate}}\] and their means are reported in table 8.6. In all cases Trotter and Gleser’s formulae overestimate anatomical stature in all sex and status subsamples. Overall, mean PPES indicate that Trotter and Gleser’s formulae perform better in the high status rather than low status subsamples. However, mean PPEs do not highlight a consistent performance pattern across all sex-status groups.
Table 8.6. Anatomical and mathematical stature estimates in the Trino subsamples: descriptive statistics and mean PPEs.

<table>
<thead>
<tr>
<th>SAMPLE</th>
<th>Anatomical Estimate^a</th>
<th>TG Humerus Estimate^b</th>
<th>TG Radius Estimate</th>
<th>TG Femur Estimate</th>
<th>TG Tibia Estimate</th>
<th>TG Summary Estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>High</td>
<td>Low</td>
<td>High</td>
<td>Low</td>
<td>High</td>
<td>Low</td>
</tr>
<tr>
<td>MALE</td>
<td>Mean</td>
<td>171.09</td>
<td>164.41</td>
<td>169.74</td>
<td>166.07</td>
<td>174.04</td>
</tr>
<tr>
<td></td>
<td>SD</td>
<td>4.19</td>
<td>4.90</td>
<td>3.28</td>
<td>3.58</td>
<td>3.69</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>14</td>
<td>18</td>
<td>14</td>
<td>18</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Mean PPE^c</td>
<td>---</td>
<td>---</td>
<td>-0.76</td>
<td>1.05</td>
<td>1.75</td>
</tr>
<tr>
<td>FEMALE</td>
<td>Mean</td>
<td>154.25</td>
<td>151.73</td>
<td>159.78</td>
<td>155.96</td>
<td>160.40</td>
</tr>
<tr>
<td></td>
<td>SD</td>
<td>2.58</td>
<td>5.65</td>
<td>4.68</td>
<td>5.07</td>
<td>4.05</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>6</td>
<td>13</td>
<td>5</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Mean PPE</td>
<td>---</td>
<td>---</td>
<td>2.97</td>
<td>2.95</td>
<td>3.37</td>
</tr>
</tbody>
</table>

^a Anatomical estimates were obtained applying the anatomical method devised by Fully (1956) and revised by Raxter and colleagues (2006). See text for details. All estimates are reported in centimeters.

^b Mathematical estimates were obtained applying the regression formulae developed by Trotter and Gleser (TG) for stature estimation from the maximum length of long bones (1952; 1958). Summary Estimate indicates the estimated stature obtained by averaging estimates from different long bones of the same individual.

^c PPE calculated as 100 x [(mathematical estimate – anatomical estimate)/anatomical estimate].
These summary estimates are consistent with those reported by previous authors, with estimates for high status males showing smaller deviations from anatomical estimates, while all other samples’ stature is overestimated by several centimeters. As noted by several authors, the divergence between anatomical and mathematical estimates observed in this study stresses the importance of applying caution when using regression formulae developed from recent samples on past human populations (Holliday and Ruff, 1997; Vercellotti et al., 2009; Auerbach and Ruff, 2010).

8.3.3.3 Sex and Status Differences in Body Proportions

Human biologists have reported that improved life conditions during growth result in an overall increase in stature, even though different body segments show differential increments, with length gains generally more pronounced in the lower limb and in distal elements in particular (Jantz and Jantz, 1999; Bogin et al., 2002). Therefore, different status groups are expected to exhibit different body proportions attributable to a relative elongation of the limb among high status individuals. While most significant absolute size variation occurs in lower limb distal segment (tibia length), based on the results of the Monte Carlo analyses on limb proportions, these dimensional changes in limb bones appear to be equally distributed and not causing significantly different inter and intra-limb proportions among the subsamples analyzed. This notwithstanding, the PCA results highlight the existence of differences in shape between high status males and all other subsamples.

Based on the loadings of the two principal components of shape (Table 7.14), the diagonal of the Log Shape variables plot (Figure 7.2) may be interpreted as the trajectory of normal growth for the population, characterized by a relative decrease of the trunk in
relation to the lower limb, and a relative increase of individual lower limb bones (tibia and femur) in relation to the trunk. Perpendicular deviations far above the diagonal identify individuals characterized by relatively long limb bones and short trunks, while deviations below the diagonal depict individuals characterized by short limb bones and long trunks. Based on this interpretation of the variation pattern, several low status individuals show deviations from the expected growth pattern that are mainly attributable to growth disruptions affecting primarily the trunk. On the contrary, a few high status males exhibit deviations that indicate stress episodes whose effects are mainly visible in the lower limb. This pattern is seemingly counterintuitive, since one would expect low status individuals to show greater evidence of lower limb growth stress compared to high status individuals (Bogin et al, 2002). This evidence could be explained by several different factors, including a possible allochthonous origin of high status males in the population, or the existence of different growth disruption patterns among different status subgroups. In this latter case, the absence of low status individuals below the line – and the general pattern observed – could be explained in light of the “osteological paradox” (Wood et al, 1992). On these premises, these results could suggest that the different body proportions observed between different status subsamples could emerge as the result of differential survival to stress episodes during growth. Regardless of the causes of such variation pattern, the fact that the tallest group examined (high status males) also exhibits the shortest relative lower limb indicates an interesting biological relationship. While all other studies on body proportions (Holliday, 1997; Jantz and Jantz, 1999; Sylvester et al, 2008; Auerbach and Sylvester, 2010) revealed a certain positive allometry in tibial length in taller groups, the findings of this study point out that longer tibiae are not an
indispensable condition for taller stature. This result stresses the importance of developmental plasticity in determining adult body proportions.

Several other factors can also be invoked to explain the patterns observed in stature and body proportion variation, including small sample sizes, biological differences between the sexes, and cultural practices.

First, the sample sizes employed are small due to the fact that only complete skeletons could be included in the analysis. Especially in the case of high status females, preservation conditions were such to yield only a small sample available for analysis. I have attempted to reduce the effects of small sample sizes by employing resampling techniques (i.e., Monte Carlo method) with a large number of iterations. While summary statistics (Table A.3) indicate that the high status female subsample is indeed characterized by slightly larger skeletal elements than its low status counterpart, the general trend indicated by the p-values points toward the absence of significant differences between female samples. Exception to this general observation is foot height, whose p-values can be interpreted as the outcome of a combination of small sample size and small sample variation. Previous research has shown that most variation resulting from different life conditions is expected to occur in limb bones (Bogin et al, 2002), especially in the distal elements and the tibia in particular (Jantz and Jantz, 1999). The lack of differences in the tibia between female subsamples would seem to reinforce the results of the resampling analysis. Regardless of the robustness of the Monte Carlo method, if an unforeseen preservation bias existed, which would make the subsamples not representative of their original population, the lack of significant differences between the female subsamples could be an artifact of sampling bias. While there is no evidence
this might be the case in the subsamples from Trino Vercellese, this possibility cannot be entirely excluded.

Second, several authors have argued for the existence of biological differences between the sexes in regard to their susceptibility to environmental perturbations during growth and development (Stini 1969; Stinson, 1985). According to this model, females would be less susceptible to growth insults than males, who would therefore express greater growth retardation under adverse circumstances (and, conversely, greater positive responses to improved conditions). The hypothesis of greater environmental male sensitivity could explain, at least in part, the variable pattern observed in medieval Trino Vercellese. In particular, the lack of significant differences between female subsamples could be interpreted as the result of higher “environmental buffering” of the female body, regardless of social status. If this were indeed the case, similar body size in the female subsamples would be due to the fact that low status females did not decrease in size even though they experienced inferior life conditions. In contrast, low status males would have suffered major, significant reduction in size in response to inferior environmental quality. This process and discrepancy between the sexes finds support in differential evolutionary constraints on human body size in relation to male and female reproduction. The hypothesis of greater male sensitivity can, at least in part, explain the variation observed in stature and body proportions, and is corroborated by the evidence emerging from dental indicators of stress in the population of Trino Vercellese. Indeed, LEH frequencies in the population (Girotti and Doro-Garetto, 1999) point to a different pattern of variation between social status groups (Table 6.1). In both status samples, males and females had significantly different LEH frequencies (high status: p=0.006; low status: p=0.02), and
high status individuals had significantly lower frequencies than their low status counterparts (p=0.0001). LEH frequency differences were stronger in males (p<0.0001) than in females (p=0.002) when status groups are compared. This emerging pattern, where males of different status show evidence of the highest and lowest levels of development stress while females show less extreme differences, could be explained by greater male environmental sensitivity.

Lastly, cultural practices associated with a patriarchal society could also contribute to the expression of the variation observed in Trino Vercelles. In agreement with theoretical expectations for stratified patriarchal societies, it is reasonable to assume that high status males benefited from better overall environmental quality during growth and development than all other groups, which allowed them to survive earlier growth insults and attain higher stature and larger adult body mass. Interestingly, Jankauskas and Kozlovskaya (1999) observed similar patterns of stature variation among Iron Age Lithuanians, where significant differences were observable only between high and low status males, while no differences were observed between the female subsamples. By examining trace elements in the population, the same authors observed that high status males were different from all other groups, and explained such a pattern as the outcome of “unequal access to animal protein products” within the population.

8.3.3.4 Sex, Status, and Age-Related Differences in Diet in Medieval Trino Vercellese

To explore whether resource allocation in medieval Trino Vercellese varied significantly in relation to sex, status, and age, Reitsema and Vercellotti (2012) carried out a dietary analysis of subadult and adult diets of 30 (20 male; 10 female) of the adult individuals included in the analysis of stature and body proportions. In order to gather
information on diet during childhood and adulthood, a second molar (the crown of which
develops between 3 and 7 years) and a rib were sampled for each individual, for a total of
60 samples that were employed for isotopic analyses. The results of the analyses indicate
that childhood diets did not vary significantly by sex and status, suggesting the existence
of a cultural buffer for children’s diets. In contrast, adult diets indicate that low-status
adult males differ considerably from women and high-status males in that they consumed
a diet with more millet and less meat, a difference that developed after childhood. While
the observed change in diet among low status males is in line with the evidence of growth
outcomes, it is interesting to note that the diet of high status males was not significantly
different from that of females. This result may be explained in terms of cultural buffering
of female diets – regardless of social status – possibly resulting from the recognition of
women’s energetic requirements associated with pregnancy and lactation. Alternatively,
the buffering of female diets may be related to the effort of providing food security for
children, with whom women may have spent more time day-to-day than men. Even
though it may not be possible to detect the behaviors that led to it, cultural and
ideological factors are most likely at the root of female dietary buffering. This idea is
strongly supported by the fact that millet is almost entirely absent from female (and high
status male) diets. In fact, while there is no nutritionally valid reason to avoid millet, the
cultural beliefs of the time deemed millet to be an inferior grain (Nada Patrone, 1981).
The fact that millet is clearly a major component of low status male diets at the same time
confirms the idea it was a low status food and supports the notion of female diet buffering
through differential food allocation within households.
It is interesting to note that, in spite of virtually identical diets, high status males and all females exhibit different morphological patterns. I argue that this may be due to differential response to environmental stress and overall different life histories, mediated by cultural practices and food ideology. Specifically, greater male sensitivity to disease during childhood may have contributed to the relatively shorter legs of high status males and later catch-up growth to their relatively long trunks. Instead, female growth trajectories appear to be more constrained, as seen in the fact that they tend to fall closely to the “ideal” growth trajectory of the population (Figure 7.2). Nonetheless, low status females show greater deviations from ideal pattern, possibly due to poorer sanitary conditions. The fact that females exhibit overall relatively longer legs than high status males may also be due to the fact that, in spite of good nutrition that would have supported it, they did not experience catch-up growth because they started reproducing in later adolescence.

8.4 Interpopulation Variation

It has been shown that body proportions vary across human populations in relation to ecogeographic rules (Katzmarzyk and Leonard, 1998) and as such they can discriminate between populations from different climatic zones (Holliday, 1997). However, as noted by Katzmarzyk and Leonard (1998), improvements in life conditions have the potential of attenuating ecogeographic patterning. Therefore, it is reasonable to assume that body proportions can provide more information than just climatic adaptation (Bogin and Rios, 2003). In this light, the last objective of this study is to explore whether at the aggregate level stature and body proportions, resulting from unique environmental
factors combinations, allow distinguishing between different populations. In this section, I discuss the results of the comparisons between the populations object of this study.

8.4.1 Living Populations

All of the living populations included in this study live in South America, but they are distinct in terms of ecological, biological, and cultural factors. Even though these populations live within the same broad subequatorial climatic zone, specific ecological settings differ. The Ribeirinhos live in a tropical forest, the Makushi inhabit a mosaic region with tropical forest and savannas, and the population from Cali resides in a region characterized by mid-altitude savannah-like plains. Biologically, these groups are diverse and range in their degree of admixture from almost exclusively Amerindian ancestry (Makushi) to multiethnic origins (Cali, Ribeirinhos). Subsistence strategies are similar for Makushi and Ribeirinhos, who practice manioc cultivation, hunting and fishing, even though with regional variation in dietary practices; the women from Cali are not engaged in subsistence activities and work in different areas and to a different extent to acquire the funds necessary for purchasing food. Culturally, the populations examined vary from tribal customs to a general identification with their respective national identities and practices. In sum, while similarities exist between these populations, overall they are each characterized by a unique set of eco-socio-biocultural conditions.

The examination of the degree of variation expressed by each population reveals some interesting general patterns. First, stature varies more in samples with greater overall stature and more among males than females, possibly in relation to greater canalization of female growth outcomes. Second, leg length is the anthropometric
parameter that exhibits the greatest variation in all populations, while trunk length is less variable. This finding supports the idea that leg length is more susceptible to environmental perturbations than trunk length and even stature itself, as argued by Bogin and colleagues (Bogin et al., 2002). It should be noted, however, that with the exception of female Ribeiinhos (see Section 8.1.1), there are no significant differences in the variance structures of sitting height and leg length in the samples examined.

When the distributions of height, sitting height, and leg lengths are investigated in sex-specific comparisons it is interesting to observe that stature is significantly different between all female subpopulations. The women from Cali have the tallest average stature, followed by the Makushi and lastly by the Ribeiinhos. These differences in absolute stature may be interpreted as the outcome of progressively worse overall life conditions. The population from Cali includes both low and high status individuals and the average stature of the population reflects the presence of well-off individuals. Height among Makushi females, while not equal to Cali, may be better relative to that of Ribeiinhos because this tribe appears to favor daughters, hence allowing females to express better growth outcomes. In contrast, sitting height and leg length are not different between all subpopulations, indicating the existence of different body proportions.

The “Quick-Test” results indicate that differences in body proportions exist between all populations examined. However, the Ribeiinhos overlap the Makushi distribution. Considering the existence of two specific morphotypes among the Makushi, the analysis of body proportions is run between Ribeiinhos and Makushi characterized by relatively short legs (morphotype 1) (Table 8.7)
Table 8.7. “Quick-Test”: isometric line equations, distributions and p-values for differences in body proportions between female *Ribeirinhos* and morphotype 1 Makushi.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Line Equation</th>
<th>Isolation</th>
<th>$n$ Above Line</th>
<th>$n$ Below Line</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females</td>
<td>$y = x - 0.6317$</td>
<td><em>Ribeirinhos</em></td>
<td>55</td>
<td>45</td>
<td>0.801</td>
</tr>
<tr>
<td></td>
<td>“Morphotype 1”</td>
<td><em>Makushi</em></td>
<td>58</td>
<td>63</td>
<td></td>
</tr>
</tbody>
</table>

The results are non-significant ($p = 0.80$), indicating that the morphotype 1 characterizes both Amazonian populations (Figure C.39). It is interesting that the more severely stunted Ribeirinhos exhibit this specific morphotype. This finding suggests that morphotype 1 may in fact have been selected as an ideal compromise between growth-limiting factors and the demands of reproduction in the Amazon. Clearly, when both morphotypes are considered together, the Makushi appear to be a distinct group from both *Ribeirinhos* and Cali. Additionally, the analysis of body proportions indicates that both Amazonian groups have relatively longer legs than the women from Cali. This result is particularly interesting considering the fact that the women from Cali appear to experience less environmental stress and exhibit taller stature. This result may be explained in at least two different ways. First, it is possible that the women from Cali experience higher stressors during infancy and childhood but benefit from catch-up growth later in life. Even though plausible, this idea is not supported by the evidence of extremely high stress levels among both Amazonian populations during the earlier phases of growth. A second, possibly more appropriate, explanation may be related to ecogeographic differences between the populations. Even among highly stunted
individuals, having relatively longer legs would represent a better adaptation for thermoregulation in the warm and humid environment of the Amazon basin. A similar somatotype is likely not as important at mid-altitude. Roberts (1953) and more recently Katzmarzyk and Leonard (1998) have shown that there is a positive correlation between leg length and mean annual temperature. Mean annual temperatures in the North Rupununi region are about 27.5 °C; 26 °C in Caxiuana Bay and 24 °C in Cali (Jansen-Jacobs and ter Steege, 2000; Silveira, 2002). Considering that both Amazonian populations are exposed to higher temperature than people in Cali, ecogeographic adaptation may explain the differences observed in body proportions.

The comparison between male subpopulations provides different results. There is no absolute difference in stature between Ribeirinhos and Makushi, while sitting height and leg length differ. This suggests the existence of differences in body proportions, which are in fact observed. The fact that the Ribeirinhos have relatively longer legs may be interpreted in terms of better overall life conditions experienced during the period of growth. The biocultural information available on these populations supports this idea. Indeed, while Ribeirinhos cultural practices somewhat favor males and support catch-up growth, Makushi customs appear to disfavor males and limit their growth potential.

8.4.2 Bioarchaeological Populations

The interpopulation comparison of stature and body proportions is carried out on the medieval populations from Trino Vercellese and Giecz. Both populations date to the middle ages, inhabited villages in the interior, and practiced similar subsistence activities and crafts. However, these populations are also different, not only in regard to their
geographic location (Italy and Poland), but also in terms of socioeconomic composition and overall health conditions. While Trino Vercellese features individuals of different socio-economic status and fairly good life conditions during development, the people from Giecz are deemed to represent only the general populace, exposed to high levels of environmental stress.

On these bases, it is expected that differences in total stature and body proportions may exist between these two populations. In particular, based on contextual information, one would expect the individuals from Trino Vercellese – who benefitted from better overall environmental conditions – to be taller and exhibit relatively longer legs. In fact, the pattern observed in growth outcomes in these populations does not match all expectations. First, both sexes from Giecz exhibit greater stature than the individuals from Trino Vercellese. This result, apparently counterintuitive, may actually be explained as due to different selective pressures on the two populations. As discussed above (see Section 8.1.4), the tall stature observed in Giecz may be interpreted as the outcome of directional selection that eliminated short individuals in relation to high levels of environmental stress. In contrast, if the overall life conditions in Trino Vercellese were better, at least for some segments of the population – as suggested by the indicators of stress – it is possible that relaxed selection allowed the expression of greater variation in the population. It is also possible that the differences observed might be in part due to genetic differences between the groups. Interestingly, differences in absolute body size between eastern and western European populations have been observed in Europe starting in the Mesolithic (Formicola and Giannecchini, 1999). Both gene flow and major environmental differences have been advanced to explain this pattern, but no conclusive
evidence has been advanced to explain it, likely due to the difficulty to tease apart genetic and environmental factors that may have contributed to the expression of stature variation. Lastly, different cultural practices, whose specific nature or extent unfortunately cannot be determined, may have differently affected not only the pattern of growth, but also the possibility of catch-up growth in these populations. While more in-depth contextual information is needed to understand the specific causes of variation observed between these populations, it is evident that stature alone does not reflect well individual and population life conditions during development.

In contrast, body proportions can provide additional information on the overall process of growth. When male subpopulations are examined, it becomes evident that the only significant difference in body proportions observed between the people from Trino Vercellese and Giecz is found in the relationship between trunk and lower limb length. The Italian population exhibits relatively longer legs, suggesting a difference in the level of stress to which individuals were exposed during the earlier phases of growth, as well as the potential for catch-up growth. Again, this different pattern may be interpreted as the outcome of different, unique selective pressures in the two distinct populations. Even though this idea cannot be entirely ruled out, given the fact that climatic and ecological conditions were quite similar at the two sites, it is unlikely that the differences observed may have ecogeographic origin. This notion is corroborated by the results of the analysis of female segmental proportions. While no differences are observed in trunk length, both brachial and crural indices indicate that the women from Trino had relatively shorter distal limb bones. This may be due to allometric scaling related to differences in the pattern of growth in these two populations. Positive allometry predicts that taller
individuals (i.e., Giecz) will have relatively longer distal limb elements (Sylvester et al., 2010). The results of this study seem to confirm this finding. It is possible that environmental and reproductive constrains selected substantially different female growth patterns in the two populations. In particular, the smaller size observed in Giecz may have resulted from earlier sexual maturation in response to overall better life conditions during childhood; conversely, the larger size in Giecz may be related to delayed reproduction and more extensive catch-up growth. Clearly, it is not possible to pinpoint specific factors as causative of the biological differences observed, even though an improved understanding of contextual biocultural information will undoubtedly allow testing specific hypotheses concerning the relationship between environmental/genetic factors and growth outcomes.

8.5 Different Angles: Comparisons Between Living and Archaeological Populations

The direct comparison of the pattern of variation in stature and body proportions between living and archaeological populations is fraught by numerous complications. First, even though the human body is the subject of investigation in both cases, the variables that can be observed and measured in the two circumstances are different and require different methodological approaches. Clearly, studying living populations allows collecting anthropometric and demographic data directly as well as gathering a wealth of contextual information on the complex multidimensional ecological, social and biocultural world people are immersed. The most crucial aspect of human biological studies is the identification of the variables necessary to address specific research questions and the definition and understanding of the biocultural constructs that are
meaningful to the interpretation of the biological variation observed. In contrast, the
study of past people is often more concerned with reconstructing valid and meaningful
variables from what is left by preservation and taphonomy. Simple concepts such as
height are deconstructed in skeletal analyses. Individuals bones may be available for
analysis, but too often individual completeness is not met, skeletal elements of different
individuals are preserved differently and possibly commingled and out of context.
Furthermore, even when it is possible to derive meaningful variables from their skeletal
proxies, there remains the substantial issue of reconstructing the intangible socio-cultural
dimension of human existence from its tangible archaeological traces. Recent theoretical
and methodological advances in bioarcheology, especially with an increased impetus
toward a multidisciplinary, integrated approach, allow reconstructing life conditions in
the past reasonably well. However, this is a long-term endeavor. Additionally, even when
skeletal material is available for the analyses and rich archaeological and cultural
information is available, often bioarchaeological analyses are vexed by small sample
sizes. All of these aspects of bioarchaeological investigations make exploring life in the
past both stimulating and challenging.

This study represents an effort to approach the same research questions in both
living and archaeological populations in tandem, so that parallels drawn between analyses
of present and past people may provide information on general patterns in human
variation across time and space. Unquestionably, the availability of biocultural
information allows informed interpretations of variation among the living, which may
enlighten the study of the human past. At the same time, the analysis of skeletal
populations can shed light on intraskeletal variability – typically difficult to examine in
the living – as well as on the human condition in the past and present. In this section, I revisit each research question addressed in this study trying to draw general conclusions from the information obtained from the analysis of living and archaeological groups.

8.5.1 Sex Differences

The analysis of the living and bioarchaeological populations included in this study reveals that sex-related variation in growth outcomes is extremely variable. First, like previous research, this study produced mixed results in regard to whether sex-related differences in environmental sensitivity exist. Among the living populations examined, male Ribeirinhos exhibit better growth outcomes than females, while among the Makushi males are more stunted and have relatively shorter legs. What do these results mean for the hypothesis of greater male sensitivity? Possibly not much. In fact, the exploration of sex differences to test the hypothesis of male sensitivity relied on the assumption that males and females would be subject to the same environmental stressors. This assumption, however, does not appear to be met in either of the living groups examined. In fact, the stressors experienced by males and females differed in relation to cultural practices favoring one sex and different energetic demands and possibly selective pressures associated with female reproduction. Interestingly, the evidence that provides greater support for female buffering comes from the medieval population from Trino Vercellese. This is due to the fact that, albeit cultural practices likely favored males, low status male individuals exhibit the relatively worse growth outcomes and highest incidence of stress episodes as inferred from linear enamel hypoplasia. Interestingly, this is the case in spite of the fact that childhood diets in the population were similar between
boys and girls. Examined all together, the results of the study suggest that the hypothesis of greater male sensitivity may be valid, but it is difficult to test because of the number, entity, and extent of possible confounding factors. Future investigations of the topic should be structured in a way to strictly verify whether environmental conditions are the same by incorporating biocultural variables in the selection of appropriate test samples. Regardless, the results of this study suggest that while biologically based sex differences in environmental sensitivity may exist, culture and sex-specific reproductive pressures may be more influential on the achievement of final growth outcomes.

In this regard, an interesting finding of this research is that differences in body proportions appear to be largely dependent on a population’s life conditions and cultural practices. Of particular interest is the finding that if a population enacts cultural practices that result in preferential access to food and resources by one sex more than the other, growth outcomes reflect such inequality in a direct way. Therefore, the evidence that male *Riberinhos* benefit from culturally-mediated opportunities for catch-up growth that are not available to females can explain the lower incidence of stunting among males and the fact that they have relatively longer legs than females. Conversely, in a group that traditionally favors daughters such as the Makushi the reverse pattern is observed, with females exhibiting lower stunting rates and relatively longer legs than males. Preferential treatment of males is also consistent with the pattern observed in Trino Vercellese, where high status males exhibit growth outcomes that are different from all other samples.

However, the origins of sex-related differences in growth outcomes are not restricted to favoring children of a given sex and other factors likely come into play. For instance, the clear association between leg length and later reproduction found among the
*Ribeirinhos* suggests that under poor environmental conditions females may show less desirable growth outcomes as a side-effect of early reproduction, which would be selected for as long as it does not compromise maternal survival. Unfortunately the lack of reproductive histories for Cali and Makushi women did not allow testing for the existence of associations between growth outcomes and female reproduction in any other sample. Nonetheless, the results of the correlation analyses conducted on female *Ribeirinhos* are highly suggestive that early reproduction can play an important role in determining adult stature. Even though reproductive information is not available for archaeological populations, it is reasonable to assume that also in the past selective pressures would be toward a compromise between female growth and survival, and the earliest age at reproduction possible.

### 8.5.2 Growth Retardation

Among other objectives, this study aimed at exploring whether severe growth retardation affects leg length more than trunk length, hence altering body proportions. As discussed above (see Section 8.2), the definition of growth retardation represents a compromise between finding a meaningful cut-off point and the risk of masking intrapopulation variation by adopting an external reference. The most commonly accepted cut-off point for stunting is -2 standard deviations of a multiethnic international reference (Frisancho, 2008). Alternative, population-specific cut-offs may be used, but it is unclear what criteria should be followed to define such parameters. Regardless, it is important to keep in mind that the definition of categories of stunting is always a compromise that reduces continuous variation in growth outcomes to workable discrete
variables. Conventional z-scores are used to define stunting in this study primarily for consistency with the existing literature and comparability of the results to those of other studies.

The results of the analyses indicate that the relationship between stunting and shorter leg length is generally verified within female samples, with the exception of Ribeirinhos and morphotype 1 isolated Makushi. Additionally, males of both Amazonian groups studied showed no differences in proportions in relation to stunting. This discrepancy may be due to the fact that overall life conditions experienced by these individuals are such to exert their limiting action over the entire growth period of the individual, hence affecting all body segments equally. In this case, growth reduction would be isometric and not limited to leg length. In contrast, life conditions in the samples exhibiting differences in body proportions associated with growth retardation may improve after childhood, hence limiting growth retardation to the lower limb. It is also possible that significant differences in Cali are found because sample sizes are much larger than those of the other groups examined, hence allowing for an improved identification of proportional differences. To test this idea, I examined differences in body proportions on random samples representing approximately 10% of the entire Cali population. The results of the analyses were consistent with those carried out on the entire population (p = 0.000), suggesting that differences in body proportions are detectable even in smaller random subsets of the population. Given the fact that there is no reason to suspect that samples of similar size for Ribeirinhos and Makushi are not representative of the population as a whole, it is reasonable to suspect that differences in body proportions in these settings do not exist between stunted and non-stunted
individuals. The fact that no differences are found among males may be related to different selective pressures on the sexes. Specifically, it is reasonable to assume that while trunk leg would be more constrained than leg length in females in relation to the increased space demands associated with reproduction. Similar pressures would clearly not exist for males, who could therefore express a dimensional reduction in all body segments. The findings of constraints in trunk length among the Ribeirinhos support this explanation.

It is interesting to note that while a notable proportion (approximately 20%-50%) of living individuals could be classified as stunted according to the distribution of the international reference, this was not possible for skeletal populations. In fact, only a handful of individual z-scores in each collection would fall below -2, making any analysis impractical. A relevant question is: why do stunted individuals not appear in the bioarchaeological collections examined? The contextual information available suggests that stress levels were high, at least for some segments of the populations from Trino Vercellese and Giecz. A likely explanation for this finding is that growth retardation might have been so severe to be lethal for most stunted individuals and that survivors would otherwise undergo catch-up growth. If this were the case, then it could be concluded that the life conditions experienced by the medieval populations included in this study were very different from those of the living groups examined. In a way, the high rates of stunting observed among the living suggest that while stressors exist and may be important, selective pressures on these populations may be more relaxed than those experienced by the medieval populations from Trino Vercellese and Giecz. Without a specific knowledge of the stressors in these past populations it is challenging to advance
explanations for stronger selection in these medieval populations than in modern groups from developing countries.

This notwithstanding, it may be suggested that different stressors may be responsible for the pattern observed. For instance, it is possible that infectious disease epidemics, well documented as a major cause of mortality during the Middle Ages, were a predominant cause of growth retardation in the past, while chronic malnutrition may be the primary growth limiting factor in modern populations. Clearly such a dichotomous distinction between stressors in unlikely, but it serves this discussion well.

Even though both disease and malnutrition may have similar effects on the growing body, it is possible to imagine important differences in their long-term effects on growth. First, infectious diseases may be contracted in spite of overall good nutrition. Second, infectious diseases tend to be acute episodic stressors with an impact on survival rather than long-term growth outcomes (obviously multiple acute episodes could have effects similar to those of prolonged chronic stress). Third, infectious diseases are probabilistically more likely to affect the growing body in earlier phases of life, when the immune system has not yet been exposed to them. Therefore, provided that an individual can survive earlier disease episodes, as he/she grows his/her likelihood of contracting the same diseases decreases in relation to the fact that immune system has been primed to face given pathogens. Consequently, if other environmental conditions and nutrition in particular are good, upon surviving diseases individuals may experience catch-up growth. The net result of this is that the weakest individuals die off and do not grow up to become stunted individuals.
In contrast, moderate malnutrition has the tendency to be a chronic stressor that exerts its action on the growing body for a prolonged time. The causes of malnutrition may be multiple and may involve not only dietary nutrient restriction, but also parasitic infestations. Except for the most extreme cases, malnutrition is not lethal, but can compromise growth to a great extent. Additionally, unless its causes are eliminated, which is rarely the case, malnutrition is a long-term stressor experienced throughout the entire period of growth. Under these circumstances, individuals may not die off and grow up to be stunted adults.

Obviously, infectious disease and malnutrition are likely to occur to various extents in most human populations, but their relative prevalence may lead to specific interactions between the growing body and the environment, hence altering growth patterns in predictable ways. It is possible that the importance of infectious disease and malnutrition varies in relation to ecological and climatic factors, as expected based on different ecosystems’ productivity and infectious diseases ecogeographic distribution. In this regard, additional research is needed to investigate the specific impacts of disease and malnutrition on the growing body in populations from different climatic regions.

8.5.3 Access to Resources

Differential access to resources is expected to produce different growth outcomes in both present and past populations. The results of this study show that differences in growth outcomes can indeed be detected between groups experiencing different access to resources, provided that the socio-cultural constructs employed are meaningful.
Expected differences in both total stature and body proportions were detected among Cali women, indicating that SES is positively associated with increases in leg length. Similarly, in the medieval population from Trino Vercellese high status individuals are characterized by greater stature and exhibit a morphotype that is different from all other subsamples in the population. A general pattern emerging from these results is that developmental plasticity is such to allow variation in growth outcomes to be expressed at the intrapopulation level.

As noted above, it is important to understand the complexity of social differentiation and inequality that leads to differential resource access. The fact that Makushi relative isolation was not associated with changes in growth outcomes is a cautionary tale that clearly demonstrates how social inequality – perceived or real – may be difficult to define and understand. This is particularly true for archaeological populations, whose socio-cultural milieu must be inferred from indirect evidence. Difficult as it may be, the recognition of social inequality is fundamental for the proper interpretation of biological variation at the intrapopulation level, as shown by Trino Vercellese.

As with the other aspects investigated above, while mostly concordant in the existence of differences in stature and body proportions in response to differential resource access, the patterns observed vary and highlight the complexity of the mechanisms leading to differences in longitudinal growth outcomes. Again, more information on the type of stressors experienced by different population subsamples is needed to expand the analyses beyond the recognition of significant biological differences.
8.5.4 Interpopulation Comparisons

Lastly, the comparisons of stature and body proportions at the interpopulation level show that differences in growth outcomes exist between different groups. These differences can be considered the populations’ response to the unique set of environmental conditions they are exposed to. The fact that significant differences were found between all groups, even those living in comparable geographical areas and practicing similar subsistence activities, is encouraging. In particular, by interpreting biological variation in relation to overall life conditions, this approach may complement ecogeographic analyses of body proportions and possibly lead to an improved understanding of the relative contributions of climatic, ecological, social, and cultural variables to the expression of adult body proportions across space.
CHAPTER 9: CONCLUSIONS

This study examined living and archaeological populations with the goal of addressing four research questions concerning the nature of inter and intrapopulation variation in stature and body proportions. The first goal was to determine whether sex-related differences in body proportions exist and to test the hypothesis of greater male sensitivity to environmental stress. Sex differences in growth outcomes were indeed found, but they revealed a situation that is more complex than expected. In particular, the inclusion of biocultural information in the interpretation of the analyses has allowed detecting the existence of cultural practices and behaviors that engendered different life conditions for males and females within the same population. Consequently, the assumption that both sexes were subject to similar environmental stress was found to be invalid and the hypothesis of greater male sensitivity non-testable. On these bases, most of the analyses do not provide evidence in support or refutation of the hypothesis. Nonetheless, this study underlines the importance of incorporating biocultural information in the determination of environmental stress similarity on the sexes in order to test the existence of sex-differences due to greater male sensitivity. The evidence from Trino Vercellese, which does at least in part support the hypothesis, suggests that if detecting truly egalitarian populations in regard to sex is impossible, it may be preferable
to focus future efforts on populations favoring males and experiencing high levels of environmental stress. In this case, the effect of male favoring and male sensitivity would be in opposite directions, hence allowing discrimination between their relative importance in determining adult growth outcomes.

In spite of the fact that the hypothesis of greater male sensitivity could not be incontrovertibly tested, sex differences were found in 3 out of 4 populations examined. This result is important in that it reveals the existence of sex-related differences in growth outcomes in relation to a population’s sex-biased customs and behaviors, as well as reproductive practices. In this regard, the existence of an association between age at first birth and leg length among the Ribeirinhos indicates that the conflict between early reproduction and maternal growth may be an important factor in determining female growth outcomes and sex-related differences in body proportions. The lack of reproductive histories for all female samples did not allow testing the hypothesis that the costs of reproduction have a negative impact on growth in all populations; however, it is reasonable to assume that this may be the case in all populations experiencing environmental stress and early reproduction. Future research focused on early pregnancy and maternal growth may enlighten the relationship between somatic growth and specific environmental conditions. This will be relevant both in terms of health policy and understanding of the specific evolutionary pressures and trade-offs between growth and reproduction.

In this regard, it is interesting that two different female morphotypes were found among the Makushi, while males did not exhibit similar variation. Among the other possible reasons advanced to explain this finding, one that deserves further investigation
is the fact that such type of intrapopulation variation may be the result of different selective pressures on female growth based on reproductive success. For instance, it is interesting to explore whether the two different morphotypes are associated with different female reproductive history parameters including age at menarche, age at first birth and overall fecundity. Further, a more in-depth investigation of possible biocultural correlates of these morphotypes is needed to understand what factors caused such a dramatic change in growth patterns in just one or two generations. Regardless of the causes underlying such variation, its expression is in itself an important finding. Indeed, while previous studies have reported a relative elongation of leg length in response to improved life conditions, there are no reports of trunk reduction accompanying leg elongation. This finding stresses the extremely plastic nature of human growth and the importance of investigating not only stature but also changes in body proportions in relation to environmental and biocultural data.

This result notwithstanding, the examination of body proportions in relation to severe growth retardation in most female samples matched expectations. In all samples but two, stunting was associated with a significant reduction in leg length – even in the morphotype 2 Makushi, who exhibit relatively longer legs than all other samples. The fact that stunting is not associated with allometric changes in proportions in two female samples and both male samples suggests the existence of isometric body size reduction as well. This may be the result of intense stressors affecting all body segments equally throughout the entire growth period. The sex difference in the changes in body proportions related to stunting suggests that trunk growth may be more constrained than leg growth only in females, in relation to the increased spatial demands of reproduction.
The evidence of canalization in trunk length among the *Ribeirinhos* supports this interpretation.

A surprising finding of this project is the extreme underrepresentation of stunted individuals in archaeological populations compared to living populations. This finding is unexpected because it is generally assumed that medieval populations experienced a variety of climatic, nutritional, hygienic, social, and cultural stressors likely to exceed the ones found among living people in developing countries. As a result, more compromised growth outcomes in the medieval populations were expected. Examined in the context of paleopathological, paleodietary and biocultural information, the high average stature observed is interpreted as the outcome of selective pressures that were possibly higher and different in nature from those experienced by the living populations examined. This interpretation, suggests that the life conditions of medieval Europe were substantially different and not comparable to those found nowadays in South America. Specifically, it is likely that geographic location and climatic differences may be at the root of differences in the relative importance of infectious disease and chronic malnutrition in the two settings. Future research should investigate the specific impacts of disease and malnutrition on the growing body in populations from different climatic regions.

Among the other causes of variation investigated in this study, differential access to resources was found to be associated with variation in body proportions in three of the samples examined. However, only in the Cali sample was a clear direct association between SES and leg length found. In the medieval population from Trino Vercellese, high status males are actually characterized by relatively shorter legs than all other population subsamples. This result, interpreted as due to differential stress levels and
potential for catch-up growth, highlights the importance of contextual information in the evaluation of growth outcomes in the past. Additionally, the fact that the tallest group examined (high status males) also exhibits the shortest relative lower limb indicates an interesting biological relationship. While all other studies on body proportions revealed a certain positive allometry in tibial length in taller groups, these findings point out that longer tibiae are not an indispensable condition for taller stature. This result stresses the importance of developmental plasticity in determining adult body proportions. The existence of intrapopulation variation in relation to socioeconomic diversity is important for the study of past populations and suggests that the failure to detect inequality can lead to the oversight of variation and consequently to missing the opportunity to make better inferences on life in the past. Furthermore, the inconsistent performance of regression equations in different population subsamples is a methodological cautionary tale that warns from overreaching conclusions on biological variation in the past based on inadequate methods.

In contrast with the significant results found in Cali and Trino Vercellese, no differences in body proportions were detected between Makushi isolation groups. This finding suggests that relative isolation is not a proper construct representing differential access to resources in that population. In particular, the existence of isolation effects on younger generations draws attention to how differential access to resources is defined within a population. In this regard, it is important to understand the complex nature of constructs such as isolation or social status. Especially in cases where access to resources is mediated by factors other than social inequality, it is essential to operationalize variables according to strict protocols. Future research should investigate what other
forms of social inequality are associated with changes in stature and body proportions in a variety of different settings, hence providing further insights in the adaptive potential of human growth.

Lastly, this study has shown that even within the same broad ecogeographic zone, the uniqueness of a populations’ eco-socio-biocultural milieu leads to recognizable patterns of variation that distinguish populations from each other. In this regard, an interesting future development of this research is to examine the impact of life conditions on the expression of ecogeographic patterns in body proportions and to understand the proper scale of observations for examining the effects if each factor on human growth.

In conclusion, this study represents a first attempt to examine variation in growth outcomes in both living and archaeological populations at the intrapopulation level. Being the first of its kind, this research project has provided several unexpected, interesting results and numerous stimuli for future research. Most of all, this study has shown that human variation in growth outcomes is even more complex than previously held and the potential for developmental plasticity truly impressive.
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APPENDIX A – DESCRIPTIVE STATISTICS
Table A.1. Descriptive statistics for *Ribeirinhos* anthropometric data and age by subsample.

<table>
<thead>
<tr>
<th>Ribeirinhos</th>
<th>Height (cm)</th>
<th>Sitting Height (cm)</th>
<th>Total Leg Length (cm)</th>
<th>Age (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Minimum</strong></td>
<td>122</td>
<td>70.9</td>
<td>43.8</td>
<td>18</td>
</tr>
<tr>
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<td>87.2</td>
<td>78.8</td>
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<td></td>
<td></td>
<td></td>
</tr>
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<td>88</td>
<td>88</td>
<td>88</td>
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<td>43.8</td>
<td>18</td>
</tr>
<tr>
<td><strong>Maximum</strong></td>
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<td></td>
<td></td>
<td></td>
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<td>40.1</td>
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<td>73.7</td>
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<td>94.7</td>
<td>66</td>
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<td></td>
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<tr>
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1 All measurements are reported in centimeters.
Table A.2. Descriptive statistics for Makushi anthropometric data and age by subsample.

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<tr>
<th></th>
<th>Height</th>
<th>Sitting Height</th>
<th>Total Leg Length</th>
<th>Age</th>
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<td>0.939</td>
<td>0.842</td>
<td>0.587</td>
<td>0.901</td>
</tr>
</tbody>
</table>

¹ All measurements are reported in centimeters.
² D is a measure of sexual dimorphism ranging between 0 (no dimorphism) and 1 (complete dimorphism).
Table A.4. Descriptive statistics for body proportions’ indices for males and females from Trino Vercellese.

<table>
<thead>
<tr>
<th>Trino Vercellese</th>
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<th>STH/ (F+T)</th>
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</thead>
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<td><strong>Females</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Minimum</td>
<td>0.699</td>
<td>0.733</td>
<td>0.587</td>
</tr>
<tr>
<td>Maximum</td>
<td>0.768</td>
<td>0.835</td>
<td>0.713</td>
</tr>
<tr>
<td>Mean</td>
<td>0.735</td>
<td>0.802</td>
<td>0.668</td>
</tr>
<tr>
<td>Std. Deviation</td>
<td>0.025</td>
<td>0.031</td>
<td>0.033</td>
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<tr>
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<tr>
<td><strong>Males</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Minimum</td>
<td>0.718</td>
<td>0.751</td>
<td>0.585</td>
</tr>
<tr>
<td>Maximum</td>
<td>0.792</td>
<td>0.873</td>
<td>0.744</td>
</tr>
<tr>
<td>Mean</td>
<td>0.757</td>
<td>0.816</td>
<td>0.644</td>
</tr>
<tr>
<td>Std. Deviation</td>
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<td>0.027</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Minimum</td>
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<td>0.789</td>
<td>0.639</td>
</tr>
<tr>
<td>Maximum</td>
<td>0.767</td>
<td>0.835</td>
<td>0.713</td>
</tr>
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<td>0.807</td>
<td>0.678</td>
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<td>0.027</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Minimum</td>
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<td>0.795</td>
<td>0.585</td>
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<td>Maximum</td>
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<td>0.846</td>
<td>0.744</td>
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<td>0.823</td>
<td>0.644</td>
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<tr>
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<td>0.733</td>
<td>0.587</td>
</tr>
<tr>
<td>Maximum</td>
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<td>0.835</td>
<td>0.712</td>
</tr>
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<td>0.035</td>
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<tr>
<td><strong>Low Status Males</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Minimum</td>
<td>0.718</td>
<td>0.751</td>
<td>0.595</td>
</tr>
<tr>
<td>Maximum</td>
<td>0.792</td>
<td>0.873</td>
<td>0.694</td>
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<td>0.810</td>
<td>0.644</td>
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<td>Std. Deviation</td>
<td>0.022</td>
<td>0.031</td>
<td>0.028</td>
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<td>N</td>
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<td>18</td>
</tr>
</tbody>
</table>

R = Radius; H = Humerus; F = Femur; T = Tibia; STH = Skeletal Trunk Height (C2-S1).
Table A.5. Descriptive statistics and sexual dimorphism for sex and status subsamples from Giecz.

<table>
<thead>
<tr>
<th></th>
<th>Cranial Height</th>
<th>Humerus</th>
<th>Radius</th>
<th>Vertebral Column</th>
<th>Bicondylar Femur</th>
<th>Condylo-malleolus Tibia</th>
<th>Foot Height</th>
<th>Skeletal Height</th>
<th>Stature</th>
</tr>
</thead>
<tbody>
<tr>
<td>FEMALE</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean 1</td>
<td>13.07</td>
<td>30.27</td>
<td>22.81</td>
<td>49.58</td>
<td>41.71</td>
<td>34.37</td>
<td>6.79</td>
<td>145.49</td>
<td>157.21</td>
</tr>
<tr>
<td>SD</td>
<td>0.37</td>
<td>1.17</td>
<td>0.95</td>
<td>2.03</td>
<td>1.44</td>
<td>1.34</td>
<td>0.34</td>
<td>4.41</td>
<td>4.54</td>
</tr>
<tr>
<td>N</td>
<td>20</td>
<td>20</td>
<td>19</td>
<td>20</td>
<td>20</td>
<td>20</td>
<td>20</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>MALE</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>13.89</td>
<td>33.56</td>
<td>25.77</td>
<td>55.36</td>
<td>45.99</td>
<td>37.5</td>
<td>7.5</td>
<td>160.55</td>
<td>172.37</td>
</tr>
<tr>
<td>SD</td>
<td>0.51</td>
<td>1.91</td>
<td>2.12</td>
<td>2.69</td>
<td>2.38</td>
<td>2.24</td>
<td>0.45</td>
<td>7.15</td>
<td>7.10</td>
</tr>
<tr>
<td>N</td>
<td>46</td>
<td>46</td>
<td>45</td>
<td>46</td>
<td>46</td>
<td>46</td>
<td>40</td>
<td>40</td>
<td>40</td>
</tr>
<tr>
<td>D^2</td>
<td>0.656</td>
<td>0.726</td>
<td>0.701</td>
<td>0.782</td>
<td>0.749</td>
<td>0.636</td>
<td>0.637</td>
<td>0.815</td>
<td>0.814</td>
</tr>
</tbody>
</table>

1 All measurements are reported in centimeters.
2 D is a measure of sexual dimorphism ranging between 0 (no dimorphism) and 1 (complete dimorphism).
Table A.6. Descriptive statistics for body proportions’ indices for males and females from Giecz.

<table>
<thead>
<tr>
<th></th>
<th>R/H</th>
<th>T/F</th>
<th>STH/ (F+T)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Females</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Minimum</td>
<td>0.730</td>
<td>0.795</td>
<td>0.618</td>
</tr>
<tr>
<td>Maximum</td>
<td>0.778</td>
<td>0.852</td>
<td>0.698</td>
</tr>
<tr>
<td>Mean</td>
<td>0.753</td>
<td>0.824</td>
<td>0.652</td>
</tr>
<tr>
<td>Std. Deviation</td>
<td>0.014</td>
<td>0.018</td>
<td>0.021</td>
</tr>
<tr>
<td>N</td>
<td>19</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td><strong>Males</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Minimum</td>
<td>0.711</td>
<td>0.764</td>
<td>0.613</td>
</tr>
<tr>
<td>Maximum</td>
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<td>0.866</td>
<td>0.741</td>
</tr>
<tr>
<td>Mean</td>
<td>0.762</td>
<td>0.815</td>
<td>0.664</td>
</tr>
<tr>
<td>Std. Deviation</td>
<td>0.031</td>
<td>0.023</td>
<td>0.026</td>
</tr>
<tr>
<td>N</td>
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<td>46</td>
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</tr>
</tbody>
</table>

R = Radius; H = Humerus; F = Femur; T = Tibia; STH = Skeletal Trunk Height (C2-S1)
Table A.7. Descriptive statistics for Cali women’s anthropometric data and age by subsamples.

<table>
<thead>
<tr>
<th>Subsample</th>
<th>Height</th>
<th>Sitting Height</th>
<th>Total Leg Length</th>
<th>Age</th>
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</thead>
<tbody>
<tr>
<td>All Stunted</td>
<td>Minimum 132.1</td>
<td>75</td>
<td>54</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>Maximum 148.7</td>
<td>89.3</td>
<td>69.2</td>
<td>44</td>
</tr>
<tr>
<td></td>
<td>Mean 145.1</td>
<td>82.6</td>
<td>62.5</td>
<td>30.9</td>
</tr>
<tr>
<td></td>
<td>Std. Deviation 2.6</td>
<td>2.3</td>
<td>2.5</td>
<td>7.5</td>
</tr>
<tr>
<td></td>
<td>N 245</td>
<td>245</td>
<td>245</td>
<td>245</td>
</tr>
<tr>
<td>All Non-Stunted</td>
<td>Minimum 147.8</td>
<td>75.4</td>
<td>57.8</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>Maximum 175.1</td>
<td>98</td>
<td>85.5</td>
<td>44</td>
</tr>
<tr>
<td></td>
<td>Mean 156.3</td>
<td>86.8</td>
<td>69.6</td>
<td>28.8</td>
</tr>
<tr>
<td></td>
<td>Std. Deviation 5.1</td>
<td>2.8</td>
<td>3.9</td>
<td>6.9</td>
</tr>
<tr>
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<td>N 1322</td>
<td>1322</td>
<td>1322</td>
<td>1322</td>
</tr>
<tr>
<td>High SES - Stunted</td>
<td>Minimum 141.5</td>
<td>79.7</td>
<td>58.6</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>Maximum 148.6</td>
<td>86.3</td>
<td>65.7</td>
<td>44</td>
</tr>
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<td>Mean 145.9</td>
<td>82.9</td>
<td>63.0</td>
<td>36.4</td>
</tr>
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<td></td>
<td>N 17</td>
<td>17</td>
<td>17</td>
<td>17</td>
</tr>
<tr>
<td>High SES - Non-Stunted</td>
<td>Minimum 147.8</td>
<td>79.2</td>
<td>59</td>
<td>19</td>
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<tr>
<td></td>
<td>Maximum 175.1</td>
<td>95.4</td>
<td>80.7</td>
<td>44</td>
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<td>Mean 158.9</td>
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<td>441</td>
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<tr>
<td>Mid-Low SES - Stunted</td>
<td>Minimum 132.1</td>
<td>76.5</td>
<td>54</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>Maximum 148.7</td>
<td>86.2</td>
<td>69.2</td>
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<td>Mean 144.9</td>
<td>82.1</td>
<td>62.8</td>
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<td>68.4</td>
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<td>Mean</td>
<td>Std. Deviation</td>
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<tr>
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<td>155.0</td>
<td>4.9</td>
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<td>6.9</td>
</tr>
<tr>
<td>High SES</td>
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<td>175.1</td>
<td>158.4</td>
<td>5.6</td>
</tr>
<tr>
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<td>95.4</td>
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<td>7.0</td>
</tr>
<tr>
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<td>153.1</td>
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</tr>
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<td>75.4</td>
<td>94.0</td>
<td>85.5</td>
<td>3.1</td>
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<td>7.1</td>
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</table>

1 All measurements are reported in centimeters.
APPENDIX B – AGE DISTRIBUTION TESTS
Figure B.1. Results of the Mann-Whitney U test on age distributions of female (F) and male (M) Ribeirinhos.
Figure B.2. Results of the Mann-Whitney U test on age distributions of female (F) and male (M) Makushi.
Figure B.3. Results of the Mann-Whitney U test on age distributions of female (F) and male (M) isolated Makushi.
Figure B.4. Results of the Mann-Whitney U test on age distributions of female (F) and male (M) non-isolated Makushi.
Figure B.5. Results of the Kruskal-Wallis test on age distributions among sex (M = male; F = female) and status (High; Low) subsamples from Trino Vercellese.

1. The test statistic is adjusted for ties.
2. Multiple comparisons are not performed because the overall test does not show significant differences across samples.
Figure B.6. Results of the Mann-Whitney U test on age distributions of female (F) and male (M) individuals from Giecz.
Figure B.7. Results of the Mann-Whitney U test on age distributions of stunted (1) and non-stunted (0) Ribeirinhos, sexes combined.
Figure B.8. Results of the Mann-Whitney U test on age distributions of stunted (1) and non-stunted (0) male Ribeirinhos.
Figure B.9. Results of the Mann-Whitney U test on age distributions of stunted (1) and non-stunted (0) female *Ribeirinhos*. 

<table>
<thead>
<tr>
<th>Statistic</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total N</td>
<td>88</td>
</tr>
<tr>
<td>Mann-Whitney U</td>
<td>1,149.500</td>
</tr>
<tr>
<td>Wilcoxon W</td>
<td>2,424.500</td>
</tr>
<tr>
<td>Test Statistic</td>
<td>1,149.500</td>
</tr>
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<td>Standard Error</td>
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</tr>
<tr>
<td>Standardized Test Statistic</td>
<td>1.682</td>
</tr>
<tr>
<td>Asymptotic Sig. (2-sided test)</td>
<td>.093</td>
</tr>
</tbody>
</table>
Figure B.10. Results of the Mann-Whitney U test on age distributions of stunted (1) and non-stunted (0) Makushi, sexes combined.
Figure B.11. Results of the Mann-Whitney U test on age distributions of stunted (1) and non-stunted (0) female Ribeirinhos.
Figure B.12. Results of the Mann-Whitney U test on age distributions of stunted (1) and non-stunted (0) male Makushi.
Figure B.13. Results of the Mann-Whitney U test on age distributions of stunted (1) and non-stunted (0) isolated Makushi.
Figure B.14. Results of the Mann-Whitney U test on age distributions of stunted (1) and non-stunted (0) non-isolated Makushi.

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<td><strong>Total N</strong></td>
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<td><strong>Standard Error</strong></td>
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</tr>
<tr>
<td><strong>Asymptotic Sig. (2-sided test)</strong></td>
<td>.219</td>
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Figure B.15. Results of the Mann-Whitney U test on age distributions of stunted (1) and non-stunted (0) isolated female Makushi.
Figure B.16. Results of the Mann-Whitney U test on age distributions of stunted (1) and non-stunted (0) isolated male Makushi.
Figure B.17. Results of the Mann-Whitney U test on age distributions of stunted (1) and non-stunted (0) non-isolated female Makushi.
Figure B.18. Results of the Mann-Whitney U test on age distributions of stunted (1) and non-stunted (0) non-isolated male Makushi.
Figure B.19. Results of the Mann-Whitney U test on age distributions of stunted (1) and non-stunted (0) females from Cali, Colombia, SES groups combined.
Figure B.20. Results of the Mann-Whitney U test on age distributions of stunted (1) and non-stunted (0) High SES females from Cali, Colombia.
Figure B.21. Results of the Mann-Whitney U test on age distributions of stunted (1) and non-stunted (0) Mid-Low SES females from Cali, Colombia.
Figure B.22. Results of the Mann-Whitney U test on age distributions of stunted (1) and non-stunted (0) Low SES females from Cali, Colombia.
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Figure B.24. Results of the Mann-Whitney U test on age distributions of isolated (1) and non-isolated (0) Makushi males.
Figure B.25. Results of the Mann-Whitney U test on age distributions of High SES (1) and Mid-Low SES (2) females from Cali, Colombia.
Figure B.26. Results of the Mann-Whitney U test on age distributions of High SES (1) and Low SES (3) females from Cali, Colombia.
Figure B.27. Results of the Mann-Whitney U test on age distributions of Mid-Low SES (2) and Low SES (3) females from Cali, Colombia.
Figure B.28. Results of the Mann-Whitney U test on age distributions of “morphotype 1” male (M) and female (F) Makushi.
Figure B.29. Results of the Mann-Whitney U test on age distributions of “morphotype 1” stunted (1) and non-stunted (0) female Makushi.
Figure B.30. Results of the Mann-Whitney U test on age distributions of “morphotype 1” stunted (1) and non-stunted (0) isolated female Makushi.
Figure B.31. Results of the Mann-Whitney U test on age distributions of “morphotype 2” stunted (1) and non-stunted (0) non-isolated female Makushi.
Figure B.32. Results of the Mann-Whitney U test on age distributions of “morphotype 2” stunted (1) and non-stunted (0) female Makushi.
Figure B.33. Results of the Mann-Whitney U test on age distributions of “morphotype 2” stunted (1) and non-stunted (0) isolated female Makushi.
Figure B.34. Results of the Mann-Whitney U test on age distributions of “morphotype 2” stunted (1) and non-stunted (0) non-isolated female Makushi.
Figure B.35. Results of the Mann-Whitney U test on age distributions of “morphotype 1” isolated (1) and non-isolated (0) female Makushi.
Figure B.36. Results of the Mann-Whitney U test on age distributions of “morphotype 2” isolated (1) and non-isolated (0) female Makushi.
APPENDIX C – “QUICK-TEST” SCATTER PLOTS
Figure C.1. Scatter plot of log sitting height over log height for male (M - squares) and female (F - circles) *Ribeirinhos*. The line has a slope of 1.0 and passes through the grand mean (5.031, 4.388) of the samples. Females tend to cluster above the line, and males below the line, indicating that they have relatively shorter legs than males (p = 0.0001).
Figure C.2. Scatter plot of log sitting height over log height for male (M - squares) and female (F - circles) Makushi. The line has a slope of 1.0 and passes through the grand mean (5.040, 4.370) of the samples. Males tend to cluster above the line, and females below the line, indicating that they have relatively longer legs than males ($p = 0.0001$).
Figure C.3. Scatter plot of log sitting height over log height for male (M - squares) and female (F - circles) Isolated Makushi. The line has a slope of 1.0 and passes through the grand mean (5.036, 4.376) of the samples. Males tend to cluster above the line, and females below the line, indicating that they have relatively longer legs than males ($p = 0.0001$).
Figure C.4. Scatter plot of log sitting height over log height for male (M - squares) and female (F - circles) Non-Isolated Makushi. The line has a slope of 1.0 and passes through the grand mean (5.044, 4.368) of the samples. Males tend to cluster above the line, and females below the line, indicating that they have relatively longer legs than males ($p = 0.0001$).
Figure C.5. Scatter plot of log sitting height over log height for stunted (squares) and non-stunted (circles) *Ribeirinhos*, sexes combined. The line has a slope of 1.0 and passes through the grand mean (5.029, 4.385) of the samples. Stunted individuals tend to cluster above the line while non-stunted individuals are more numerous below the line (p = 0.02).
Figure C.6. Scatter plot of log sitting height over log height for stunted (solid circles) and non-stunted (open circles) female (F) Ribeirinhos. The line has a slope of 1.0 and passes through the grand mean (4.990, 4.358) of the samples. The two samples are equally distributed above and below the line, indicating that there are no differences in body proportions between stunted and non-stunted individuals (p = 0.08).
Figure C.7. Scatter plot of log sitting height over log height for stunted (solid squares) and non-stunted (open squares) male (M) Ribeirinhos. The line has a slope of 1.0 and passes through the grand mean (5.068, 4.413) of the samples. The two samples are equally distributed above and below the line, indicating that there are no differences in body proportions between stunted and non-stunted individuals (p = 0.51).
Figure C.8. Scatter plot of log sitting height over log height for stunted (squares) and non-stunted (circles) Makushi, sexes combined. The line has a slope of 1.0 and passes through the grand mean (5.017, 4.336) of the samples. Stunted individuals tend to cluster above the line while non-stunted individuals are more numerous below the line (p = 0.0003).
Figure C.9. Scatter plot of log sitting height over log height for stunted (solid circles) and non-stunted (open circles) female (F) Makushi. The line has a slope of 1.0 and passes through the grand mean (4.998, 4.304) of the samples. Stunted individuals tend to fall above the line, while non-stunted ones are evenly distributed above and below the line. Stunted females have relatively shorter legs than their non-stunted counterparts (p = 0.012).
Figure C.10. Scatter plot of log sitting height over log height for stunted (solid squares) and non-stunted (open squares) male (M) Makushi. The line has a slope of 1.0 and passes through the grand mean (5.075, 4.436) of the samples. Stunted and non-stunted individuals exhibit similar distributions, suggesting that stunting among males is a rather isometric process (p = 0.284).
Figure C.11. Scatter plot of log sitting height over log height for stunted (squares) and non-stunted (circles) isolated Makushi, sexes combined. The line has a slope of 1.0 and passes through the grand mean (5.036, 4.376) of the samples. Stunted individuals tend to cluster above the line while non-stunted individuals are more numerous below the line (p = 0.045).
Figure C.12. Scatter plot of log sitting height over log height for stunted (solid circles) and non-stunted (open circles) isolated female (F) Makushi. The line has a slope of 1.0 and passes through the grand mean (4.995, 4.315) of the samples. Stunted and non-stunted individuals exhibit similar distributions ($p = 0.321$).
Figure C.13. Scatter plot of log sitting height over log height for stunted (solid squares) and non-stunted (open squares) isolated male (M) Makushi. The line has a slope of 1.0 and passes through the grand mean (5.074, 4.438) of the samples. Stunted and non-stunted individuals exhibit similar distributions, suggesting that stunting among males is a rather isometric process ($p = 0.816$).
Figure C.14. Scatter plot of log sitting height over log height for stunted (squares) and non-stunted (circles) non-isolated Makushi, sexes combined. The line has a slope of 1.0 and passes through the grand mean (5.014, 4.321) of the samples. Stunted individuals tend to cluster above the line while non-stunted individuals are more numerous below the line \((p = 0.015)\).
Figure C.15. Scatter plot of log sitting height over log height for stunted (solid circles) and non-stunted (open circles) non-isolated female (F) Makushi. The line has a slope of 1.0 and passes through the grand mean (5.001, 4.297) of the samples. Stunted and non-stunted individuals exhibit similar distributions ($p = 0.06$).
Figure C.16. Scatter plot of log sitting height over log height for stunted (solid squares) and non-stunted (open squares) non-isolated male (M) Makushi. The line has a slope of 1.0 and passes through the grand mean (5.075, 4.435) of the samples. Stunted and non-stunted individuals exhibit similar distributions, suggesting that stunting among males is a rather isometric process ($p = 0.084$).
Figure C.17. Scatter plot of log sitting height over log height for stunted (solid circles) and non-stunted (open circles) for women from Cali, all SES groups combined. The line has a slope of 1.0 and passes through the grand mean (5.014, 4.438) of the samples. Stunted individuals tend to fall above the line, while non-stunted ones are more abundant below the line, indicating they have relatively longer legs ($p = 0.0001$).
Figure C.18. Scatter plot of log sitting height over log height for stunted (solid circles) and non-stunted (open circles) High SES women from Cali. The line has a slope of 1.0 and passes through the grand mean (5.025, 4.446) of the samples. Stunted individuals tend to fall above the line, while non-stunted ones are more abundant below the line, indicating they have relatively longer legs ($p = 0.0004$).
Figure C.19. Scatter plot of log sitting height over log height for stunted (solid circles) and non-stunted (open circles) Mid-Low SES women from Cali. The line has a slope of 1.0 and passes through the grand mean (5.010, 4.433) of the samples. Stunted individuals tend to fall above the line, while non-stunted ones are more abundant below the line, indicating they have relatively longer legs ($p = 0.0001$).
Figure C.20. Scatter plot of log sitting height over log height for stunted (solid circles) and non-stunted (open circles) Low SES women from Cali. The line has a slope of 1.0 and passes through the grand mean (5.010, 4.438) of the samples. Stunted individuals tend to fall above the line, while non-stunted ones are more abundant below the line, indicating they have relatively longer legs ($p = 0.0001$).
Figure C.21. Scatter plot of log sitting height over log height for non-isolated (solid circles) and isolated (open circles) female (F) Makushi. The line has a slope of 1.0 and passes through the grand mean (5.005, 4.307) of the samples. Isolated individuals tend to cluster above the line, while non-isolated individuals are equally distributed above and below the line (p = 0.014).
Figure C.22. Scatter plot of log sitting height over log height for non-isolated (solid squares) and isolated (open squares) male (M) Makushi. The line has a slope of 1.0 and passes through the grand mean (5.076, 4.437) of the samples. Isolated and non-isolated show similar distributions ($p = 0.857$).
Figure C.23. Scatter plot of log sitting height over log height for high SES (circles) and mid-low SES (diamonds) women from Cali. The line has a slope of 1.0 and passes through the grand mean (4.979, 4.412) of the samples. High SES women are more abundant above the line and mid-low SES women below it, indicating they have different body proportions ($p = 0.0001$).
Figure C.24. Scatter plot of log sitting height over log height for high SES (circles) and low SES (triangles) women from Cali. The line has a slope of 1.0 and passes through the grand mean (4.980, 4.419) of the samples. High SES women are more abundant above the line and low SES women below it, indicating they have different body proportions ($p = 0.0001$).
Figure C.25. Scatter plot of log sitting height over log height for mid-low SES (diamonds) and low SES (triangles) women from Cali. The line has a slope of 1.0 and passes through the grand mean (4.977, 4.414) of the samples. Mid-low SES women cluster above the line and mid-low status women below it, indicating they have different body proportions ($p = 0.022$).
Figure C.26. Scatter plot of log sitting height over log height for Makushi and Ribeirinhos females. The line has a slope of 1.0 and passes through the grand mean (4.996, 4.331) of the samples. The Ribeirinhos cluster above the line, indicating they have relatively shorter legs than the Makushi ($p = 0.0001$).
Figure C.27. Scatter plot of log sitting height over log height for Ribeirinhos and Cali females. The line has a slope of 1.0 and passes through the grand mean (5.013, 4.406) of the samples. The Ribeirinhos cluster below the line, indicating they have relatively longer legs than the individuals from Cali ($p = 0.0001$).
Figure C.28. Scatter plot of log sitting height over log height for Makushi and Cali females. The line has a slope of 1.0 and passes through the grand mean (5.023, 4.380) of the samples. The Makushi cluster below the line, indicating they have relatively longer legs than the individuals from Cali ($p = 0.0001$).
Figure C.29. Scatter plot of log sitting height over log height for Makushi and Ribeirinhos males. The line has a slope of 1.0 and passes through the grand mean (5.076, 4.428) of the samples. The Ribeirinhos tend to cluster below the line, indicating they have relatively longer legs than the Makushi (p = 0.001).
Figure C.30. Scatter plot of log sitting height over log height for morphotype 1 Makushi females (F - circles) and males (M - squares). The line has a slope of 1.0 and passes through the grand mean (5.038, 4.402) of the samples. The sexes cluster equally above and below the line, indicating that they exhibit similar body proportions (p = 0.06).
Figure C.31. Scatter plot of log sitting height over log height for morphotype 1 stunted (solid circles) and non-stunted (open circles) Makushi females. The line has a slope of 1.0 and passes through the grand mean (4.996, 4.3636) of the samples. Stunted individuals tend to cluster above the line while non-stunted individuals are more numerous below the line (p = 0.02).
Figure C.32. Scatter plot of log sitting height over log height for morphotype 1 stunted (solid circles) and non-stunted (open circles) isolated Makushi females. The line has a slope of 1.0 and passes through the grand mean (4.994, 4.364) of the samples. Stunted and non-stunted individuals exhibit similar distributions above and below the line (p = 0.416).
Figure C.33. Scatter plot of log sitting height over log height for morphotype 1 stunted (solid circles) and non-stunted (open circles) non-isolated Makushi females. The line has a slope of 1.0 and passes through the grand mean (4.998, 4.364) of the samples. Stunted individuals tend to cluster above the line and non-stunted individuals below it ($p = 0.03$).
Figure C.34. Scatter plot of log sitting height over log height for morphotype 2 stunted (solid circles) and non-stunted (open circles) Makushi females. The line has a slope of 1.0 and passes through the grand mean (5.001, 4.229) of the samples. Stunted individuals tend to cluster above the line while non-stunted individuals are more numerous below the line (p = 0.0001).
Figure C.35. Scatter plot of log sitting height over log height for morphotype 2 stunted (solid circles) and non-stunted (open circles) isolated Makushi females. The line has a slope of 1.0 and passes through the grand mean (4.997, 4.233) of the samples. Stunted individuals tend to cluster above the line while non-stunted individuals are more numerous below it (p = 0.0001).
Figure C.36. Scatter plot of log sitting height over log height for morphotype 2 stunted (solid circles) and non-stunted (open circles) non-isolated Makushi females. The line has a slope of 1.0 and passes through the grand mean (5.003, 4.227) of the samples. Stunted individuals tend to cluster above the line and non-stunted individuals below it (p = 0.005).
Figure C.37. Scatter plot of log sitting height over log height for isolated (solid circles) and non-isolated (open circles) morphotype 1 female Makushi. The line has a slope of 1.0 and passes through the grand mean (5.001, 4.368) of the samples. Isolated and non-isolated individuals show similar distributions (p = 0.344).
Figure C.38. Scatter plot of log sitting height over log height for isolated (solid circles) and non-isolated (open circles) morphotype 2 female Makushi. The line has a slope of 1.0 and passes through the grand mean (5.010, 4.232) of the samples. Isolated and non-isolated individuals show similar distributions (p = 0.530).
Figure C.39. Scatter plot of log sitting height over log height for *Ribeirinhos* females (diamonds) and morphotype 2 female Makushi (triangles). The line has a slope of 1.0 and passes through the grand mean (4.994, 4.362) of the samples. Isolated and non-isolated individuals show similar distributions (p = 0.801).