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Secular Trends in Human Skeletal Growth: Stature
Change and Appositional Bone Development in a
19th and Early 20th Century Finnish Skeletal
Population

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2015

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Secular Trends in Human Skeletal Growth: Stature Change and Appositional Bone Development in a 19th and Early 20th Century Finnish Skeletal Population

Abstract

This thesis aims to examine secular changes in four skeletal growth parameters (recorded living stature, bone length, total cross-sectional area (TA) and twice average bending rigidity 'J' in femur, tibia and humerus) using adult male individuals from a 19th and early 20th century Finnish skeletal collection. Further objectives are to investigate whether the study individuals' prisoner status introduces variation in the skeletal parameters within the sample as well as to examine what environmental indicators may have a relationship with the examined parameters. Data on bone cross-sectional geometric properties (CSG) were collected using a desktop 3D laser scanner whilst environmental data were acquired using existing Finnish data sources. The results showed a significant secular increase in stature, which was also reflected in femur length. Humeral (CSG) properties showed a significant secular decrease. Individuals who were prisoners had significantly smaller TA and lesser J at 35% length of the humerus than non-prisoners. It is concluded that the changing living conditions of late 19th and early 20th century Finland seem to have affected both endochondral and appositional bone growth of this sample, whereby improvements in the country's disease and nutritional environment after the Finnish Famine could explain the found secular trend in stature and femur length. Changes in childhood loading history after the introduction of free elementary school in Finland are a possible explanation for the secular decrease in the humerus cross-sectional geometric properties, and might also be related to the found difference between prisoners and non-prisoners.

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Declaration

Some material in this thesis has been previously submitted for an undergraduate dissertation by the author at Durham University. The undergraduate dissertation served as a research proposal for this project and included content incorporated into the literature review of 19th century Finnish social history in this thesis. Preliminary results on stature were also reported in the dissertation and discussed with reference to the social history literature. All other work presented here is novel.

Statement of Copyright

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Acknowledgements

First and foremost I would like to thank my supervisors Dr Sarah Elton and Dr Ian Rickard for support and advice that was always available. Occasionally via Skype when we were not in the same country. I am certain the things you have taught me will continue to be valuable in the years to come.

I would also like to thank Dr Ilpo Hanski from the Finnish Museum of Natural History for allowing me access to the museum's collection of human skeletal material. I am grateful to Kati Salo from the Archaeology Department at the University of Helsinki for loaning me her personal measuring equipment and to Dr Jari Holopainen for patiently explaining to me the peculiarities of the grain figure data used in this study. Thank you to Dr Samuli Helle from the University of Turku for helping me track down historical infant mortality data.

At Durham, I would like to say many thanks to everyone associated with the Bioinformatics Lab for their help and for the productive chats, and also for making it fun to get to the lab in the morning. Dr Charlotte King – thank you for the last minute support, it was truly needed.

Finally, I would like to give special thanks to my family and to my friends both in Finland and in the UK.

1 Introduction

Humans, like other organisms, invest energy in growth. From a life history theory perspective, this investment is a part of the evolutionarily derived trade-offs made by individuals over their life course between growth, maintenance and reproduction (Bogin 1999; Stearns 1989). Energetic investments made by humans, such as the investment in growth, are influenced by a variety of environmental factors, including nutritional status, disease burden, and the physical environment, as well as societal and cultural context, such as social status (Bogin 1999; Tanner 1989). In past populations, human growth can be investigated using skeletal remains, with bone growth, both in length and width, recognised to be sensitive to environmental influences (Ruff et al. 2013). Recently, analyses comprising a range of skeletal parameters and including variables measuring the wider living environment of archaeological samples have been called for, as these can provide insights into both the functional and physiological bases of growth (Ruff et al. 2013). Prompted by this, the present study aims to look at secular trends in four skeletal growth parameters (recorded living stature; long bone length, total cross-sectional area (TA) and total resistance to bending (J)) in a well-preserved Finnish skeletal population from the 19th and early 20th century. This collection is unique in that information on the individuals' sex, age, recorded living stature, occupation, and prisoner status as well as cause of death accompanies the material, filed post mortem by medical professionals from the University of Helsinki (Söderholm 2002).

A subsample of individuals in this collection consists of prisoners and will be given particular attention in this study. Prisoner status is rarely known in archaeological skeletal populations and thus the present study provides a valuable opportunity to investigate its possible effects on skeletal parameters. Additionally, population level data in terms of historical GDP per capita index, infant mortality rate, annual average spring temperature and grain figures, are employed with the aim of forming

a comprehensive picture of both the ecological and social living environment of this population. I have not compared this collection with other skeletal populations because comparative samples with similar level of detail on individuals could not be obtained and the use of a poorly matched collection would lead to methodological inconsistencies. Instead, the present study uses literature sources to set context and draw comparisons.

This study also presents a novel approach in terms of examining secular trends in cross-sectional skeletal traits within an archaeological sample in combination with information on longitudinal bone growth and the social history of the population. It is unknown whether or how bone cross-sectional size and shape of many populations have changed within small time spans, notably the last 200 years, which have seen secular increases in stature in many European countries (Cole 2000). Thus far, secular trend research has been heavily concentrated on heights, whereas existing secular trend studies of human appositional bone growth and bone strength are focused on covering extensive time periods and multiple populations – largely providing information on species level patterns (e.g. Macintosh et al. 2014; Ruff et al. 1993; Ruff 2006; Ruff et al. 2015; Ryan and Shaw 2015).

The focus of the present study is on one small population, the Finns, during a key period in Finnish history. The late 19th century in Finland saw rapid economic growth and development of infrastructure, increasing life expectancy and decreasing mortality, as well as the introduction of new social policies, most notably, public elementary schooling (Heikkinen 1986; Kannisto et al. 1999; Kurth 2005; Turpeinen 1986). Following previous work on environmental effects on skeletal growth in populations undergoing changes in their disease and nutritional environment (Cole 2003; Garn et al. 1975; Hauspie et al. 1997; Mays et al. 2009; Tanner 1981) this study aims to inspect whether the improving living environment of Finns through late 19th and early 20th century was reflected in skeletal growth parameters of adult male individuals. Secular changes in height in Finland have been previously investigated for the 20th century (Silventoinen et al. 2000). The individuals included in the present study predate that, offering a rare insight into 19th century Finnish statures, combined with assessment of bone length and cross-sectional geometric (CSG) properties with the objective of including skeletal growth parameters that capture

aspects of both endochondral growth (growth in bone length) and appositional growth (growth in bone width and diameter).

1.1 Mechanisms of Human Growth

Three processes are responsible for an organism's growth: increase in cell number (hyperplasia), increase in cell size (hypertrophy) or increase in interstitial fluid (Tanner 1989). For tissues that are largely non-regenerative, growth occurs in three phases (Tanner 1989). In the first stage of tissue growth, cells divide and the cell number increases. In the beginning, these new cells consist almost entirely of nuclei with much fluid between cells; there is very little cytoplasm. In the second stage, the rate of cell division decreases but proteins continue to be synthesised at similar rate to stage one. Proteins enter the cytoplasm and cells become larger; at the same time inter cellular fluid decreases. New cells are still made but at a slower rate. In the third and final stage cell division ceases and growth occurs only in size. The timing of this depends on the tissue or organ in question and typically each organ starts to form at a particular developmental stage and follows a characteristic pattern before stopping at a predictable time (French 1989). After growth all cells have to renew their components leading to a continuous turnover of substances in the body, that is, there is an uninterrupted pattern of constituents going in and coming out; Tanner (1989) explains that it is this pattern of continuously changing molecules, which enables organisms, including humans, to adapt to changing environments, such as varying food stuffs. To pay for these processes and keep the turnover going, the body requires energy (Tanner 1989).

DNA functions as the template for growth, as it contains the code for the proteins required for the division and growth of cells. Important genes for growth are the homeobox genes, which specify the morphological identity of segmental morphological systems such as limbs and the vertebral column in a hierarchical order (Weiss et al. 1998). Mammals have 38 Hox genes on different chromosomes, and during the human embryonic period (first 8 weeks after fertilisation) these genes are responsible for cell division, cell adhesion and migration to create structures in the developing embryo (Ulijaszek 1998). Overall the embryonic period has 23 distinct morphological stages during which rapid changes in form take place – by

stage 13 between four and five weeks after fertilisation all four limb buds can be recognized (O’Rahilly and Müller 1998a) and limb length increases from about 2 millimetres (mm) in the fifth week to about 13 mm at eight weeks (O’Rahilly and Müller 1998b). Besides genes, prenatal growth is affected by a variety of maternal factors such as weight, caloric intake, blood pressure, smoking as well as alcohol intake whereas only 25-44% of variation in birth-weight can be explained by fetal genes (Mueller 1998; Wells and Stock 2011).

Hormones act as translators of genetic information as well as modify their actions depending on constraints imposed by the environment (Tanner 1989). They are specialist proteins secreted by glands located around the body and are responsible for the timing of growth events (Hindmarsch 1998; Tanner 1989). During gestation, insulin-like growth factors (IGFs) are key growth regulating hormones, whereby IGF-II is most expressed in early pregnancy and IGF-I in later pregnancy (Agrogiannis et al. 2014). The IGFs differ from hormones secreted by hormonal glands in that they are synthesized locally in different tissues, and act directly on cells that produce them (autocrine mode of action) or those in close proximity (paracrine mode of action) (Hernandez 1998). IGF serum levels have been found to be closely related to fetal growth, including length, and infants with IGF-I deficiency have been found to be severely growth retarded (Agrogiannis et al. 2014). IGFs are dependent on nutrition supply, both glucose and amino acids (Bloomfield et al. 2013) providing a link between fetal growth retardation and prenatal nutrition.

The endocrine system continues to control human growth after birth, and in addition to hormones the regulatory system comprises hormone binding proteins as well as hormone and growth-factor receptors (Karlberg 1998). Human growth hormone (GH) is responsible for growth during childhood, whereas growth during adolescence is due to both GH and sex hormones (testosterone in males and estrogens in females) (Karlberg 1998). GH also modifies its actions in the body depending on environmental constraints, for example by responding to starvation by taking fat out of deposits and allowing it to be metabolised to provide energy, sparing carbohydrates which are stored in muscle (Tanner 1989; Weiss et al. 1998). GH as well as the sex hormones are important in achieving skeletal maturity (Karlberg 1998). IGF-I remains important for growth after intra-uterine life, amongst other things, as an intermediary of GH to initiate bone growth and is produced both

locally at the growth plates of bones and in the liver (Tanner 1989). Other hormones that have a vital role in the growth process include thyroxine, the stress hormone cortisol, adrenal androgens as well as hormones from the pituitary gland, such as thyroid-stimulating hormone (TSH) (Hindmarsch 1998; Weiss et al. 1998).

1.1.1 Growth of Bone Tissue

Bone tissue originates from the mesoderm, which is one of the three germ layers of the embryo. Early in development, bones of the cranial vault, parts of the mandible as well as the clavicle arise directly from mesenchyme stem cells through a process called intramembranous ossification (ossification refers to the process of bone formation) (Stini 1998). The origin of these few bones differs from most of the skeleton in that they do not have a cartilaginous precursor, that is, a cartilage model of bone that later becomes ossified (Stini 1998). This latter process is called endochondral ossification and it is through this that most skeletal elements such as long bones as well as the vertebra are formed (Stini 1998). The cartilaginous precursors are sheathed in vascularized tissue envelopes called the perichondrium (Stini 1998). The bone-forming cells, the osteoblasts, form an organic matrix called osteoid by secreting collagen, which becomes covered in crystalline mineral consisting of calcium hydroxyapatite (Robling et al. 2006; Figure 1.1). Collagen and calcium hydroxyapatite are the main building materials of bone and give it its structural properties. The mineral component gives bone hardness and rigidity, whilst the collagen allows for bending (White et al. 2011). Because the bone matrix calcifies soon after being produced, bone cannot grow through cell hypertrophy, so new bone material needs to be added (White et al. 2011).

Bone formation begins to take place at specific sites around the body, the primary and secondary ossification centres, early in development – the first mainly appear during the fetal period and the latter after birth (Stini 1998). Around the time of birth so-called epiphyseal growth plates are formed. These are cartilaginous discs that extend across the cross-section of a bone between the primary and secondary centres of ossification, that is, between the metaphysis and the epiphysis (White et al. 2011; Figure 1.2). Because skeletal elements need to remain functional during growth, it is essential for bones to keep their basic shape while their size increases. Thus the newly added bone material from the growth plates thickens, changes in

consistency and is moved along the epiphysis away from the epiphyseal plate; the original growth plate material is temporary and becomes resorbed by bone removing cells, the osteoclasts (Rauch 2005; Robling et al. 2006). During growth this process of adding and removing bone tissue to accommodate changing requirements is called bone modelling, during rest of life, the continuous process of removal and replacement of bone is called remodelling (White et al. 2011). Bone formation and resorption are both influenced by hormones; Figure 1.3 shows key hormonal influences on bone (Walsh 2015).

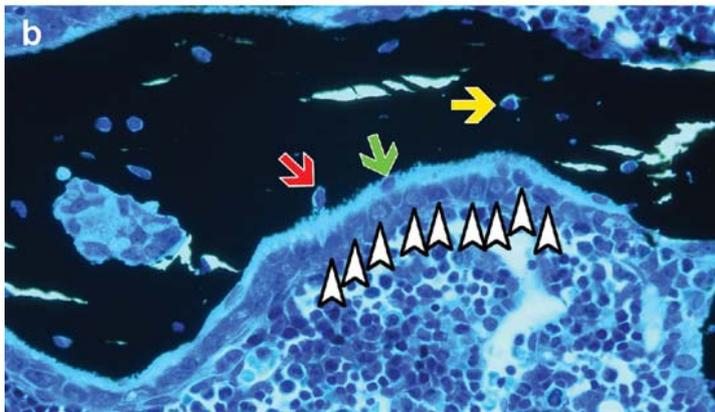


Figure 1.1 Thin section (4 μm) of a rat tibia showing bone formation by osteoblasts (= white arrowheads, bone = black, soft tissue and cells = blue), after Robling et al. (2006). Between mineralized bone and osteoblasts is a pale blue strip of tissue (osteoid), which is freshly deposited matrix that has not yet mineralized. As this continues some of the osteoblasts get trapped in their own matrix (green arrow), which subsequently gathers mineral (red arrow), leading to a former osteoblast surrounded by mineralized bone (yellow arrow), the cell is now considered an osteocyte.

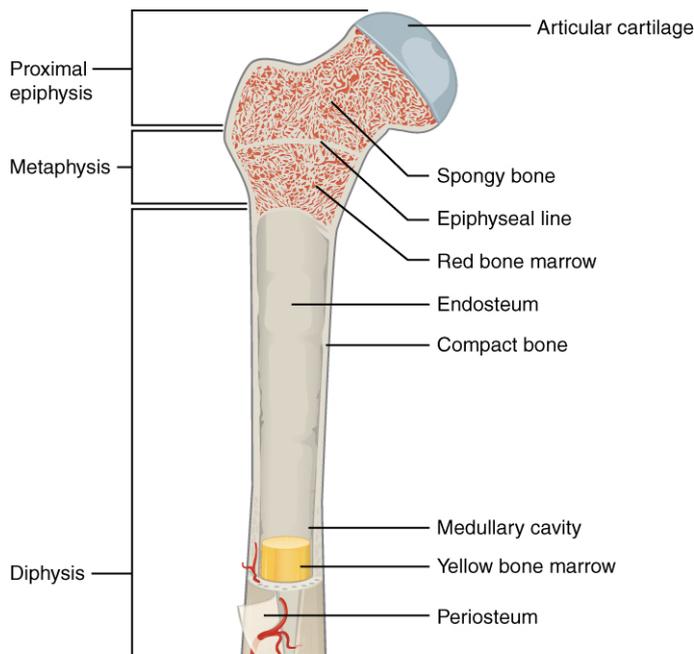


Figure 1.2 Anatomy of a human proximal femur (CNX 2015)

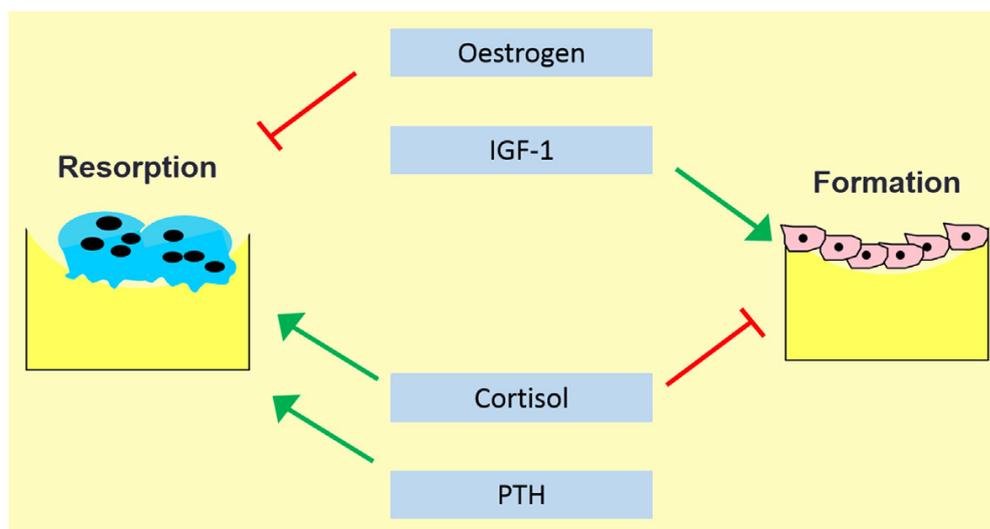


Figure 1.3 Hormonal influences on bone formation and resorption. Green arrows= promote, red= inhibit, after Walsh (2015)

After osteoblasts become surrounded by bone (Figure 1.1) they are considered osteocytes, that is, cells permanently entombed in the bone matrix (Robling et al. 2006). How this process is regulated is partly unknown, however at least three levels of control can be observed: systemic (hormonal) control, since the growth of both sides of the body is synchronized; local control, as different growth plates show different activity; and mechanical control, as bone growth responds to mechanical forces (Rauch 2005). Any disturbance to longitudinal bone growth has to either

directly or indirectly influence the growth plate cartilage (Rauch 2005) as it is the site of ossification. Besides the epiphyseal plate, bone growth also occurs on the periosteal (outer) surface of bone through a process called periosteal apposition (1.1.2) leading to bone growth in width and diameter (Rauch 2005). The growth at the epiphyseal plate, called endochondral or longitudinal growth and periosteal apposition, called appositional growth are two distinct biological processes (Rauch 2005).

Figure 1.4 presents an idealized pattern of human growth in height gained (in cm) per year at different ages for boys and girls (Bogin 1999) whilst Figure 1.5 shows a human tibia at different ages, from a newborn to an individual aged eighteen (White et al. 2011). Most individuals do not follow growth curves exactly, and the figures merely give an indication of how a child of mean birth length grows at mean velocity. Similarly, the tibia and other bones of the body show much variation in appearance and size at different ages and thus the figure only provides an example of what a tibia can look like at different ages. As will be discussed in the following pages there are many factors that influence the growth process and lead to growth outcomes differing from the general pattern. Different parts of the body grow with different gains, rates and timings during different growth phases, for example gains in sitting-height generally occur in infancy and puberty and gains in leg length in childhood (Karlberg 1998). This leads to young children having long legs compared to their torso. After puberty the lower limbs stop growing faster than the upper segment of the body. Overall, nine per cent of final height in males is gained during puberty (Karlberg 1998).

Growth stages are defined through changes in hormonal function whereby the transition from infancy to childhood growth phase takes place when GH begins to regulate growth significantly and a rise in GH dependent IGF-I is observed (Hochberg and Albertsson-Wikland 2008). Infancy and early childhood have been identified as periods during which endochondral growth is especially sensitive to environmental disturbances, and a delayed onset of childhood growth stage is often thought to be an important explanatory factor of shortness – short stature for age in children with normal birth weight and no endocrine disease is explained by a delayed childhood stage in 44% of cases in developing countries (Hochberg and Albertsson-Wikland 2008; Karlberg 1998). In children with delayed onset of

childhood, there is a delay in the rise of GH dependent IGF-I (Hochberg and Albertsson-Wikland 2008). The transition between the growth stages requires a positive energy balance, and can be delayed by both disease and undernutrition (Hochberg and Albertsson-Wikland 2008). Catch up growth is a process where stunted children (those who are more than two standard deviations (SD) shorter for a given age than the mean) return to normal height for their age as conditions improve (Victora et al. 2008). However there is evidence that even with catch up full growth potential in stature might not be reached (Guerrant et al. 2008). With the sample of the present study, which consists only of adult individuals, bone growth at different life stages cannot be measured; however observed differences in adult height and bone lengths through time might be related to disturbances in endochondral growth during growth.

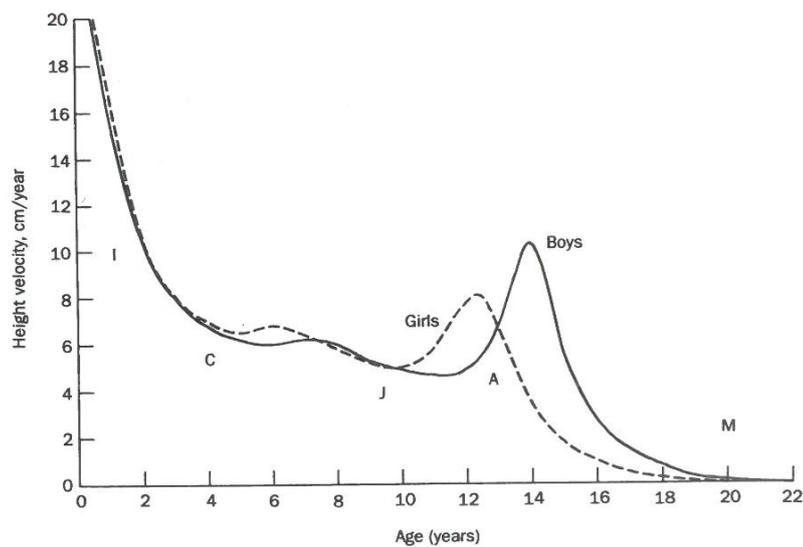


Figure 1.4 Human height velocity (cm/year) for boys and girls at different developmental periods, after Bogin (1999). I=Infancy, C=Childhood, J=Juvenile, A=Adolescent, M=Mature



Figure 1.5 Bone Growth. Left human tibia (from newborn to 18 years), after White et al. (2011)

1.1.2 Appositional Bone Growth

Appositional growth occurs via periosteal apposition and endosteal absorption whereby osteoblasts add mineralized tissue on the outer surface of the bone, the periosteum, and osteoclasts remove it from the inner, endosteal surface (Rauch 2005; White et al. 2011; Figure 1.2). This allows for the bone shaft to maintain its dimensions while it grows in size – as the diameter increases due to periosteal apposition, the size of the medullary cavity enlarges in proportion due to the bone-removing actions of the osteoclasts. Beginning with adolescence, bone growth can also occur at the endosteal surface, often in response to physical activity (Mays et al. 2009; Pearson and Lieberman 2004). Periods of most rapid appositional growth correspond well with periods of high height velocity in boys (Tanner et al. 1981; Rauch 2007). Figure 1.6 shows average perisosteal apposition rates in the human humerus and femur until age five (Rauch 2005). Growth velocities in humerus and

tibia widths of UK boys and girls from age three to 18 show that during puberty, an individual's peak growth velocity in height coincides with peak growth velocity in bone width, most commonly around age 14 (Tanner et al. 1981). These figures are important in terms of the present study, as they indicate key periods of periosteal apposition during growth and the ages at which environmental influences on appositional growth parameters might be strongest. This information will be used to select the ages for which environmental data are included in analysis; all rates are high during the first few years of life as well as puberty in boys. Similarly to endochondral growth, different skeletal elements grow at different rates depending on developmental period, for instance, at 33 months, periosteal apposition is nearly four times as fast at the femur than at the humerus, which is thought to be related to increased mechanical requirements of the femur compared to the humerus due to the child having begun to walk (Rauch 2005; Ruff 2003). A longitudinal study on long bone strength (calculated from diaphyseal breadth measurements) from infancy to late adolescence showed that both femoral and humeral strength velocities were highest at puberty but also during first few years of life (Ruff 2003). The sample was quite limited at 20 individuals but still gives an indication that long bone strength velocity follows a similar pattern as stature and the periosteal apposition rates of these bones.

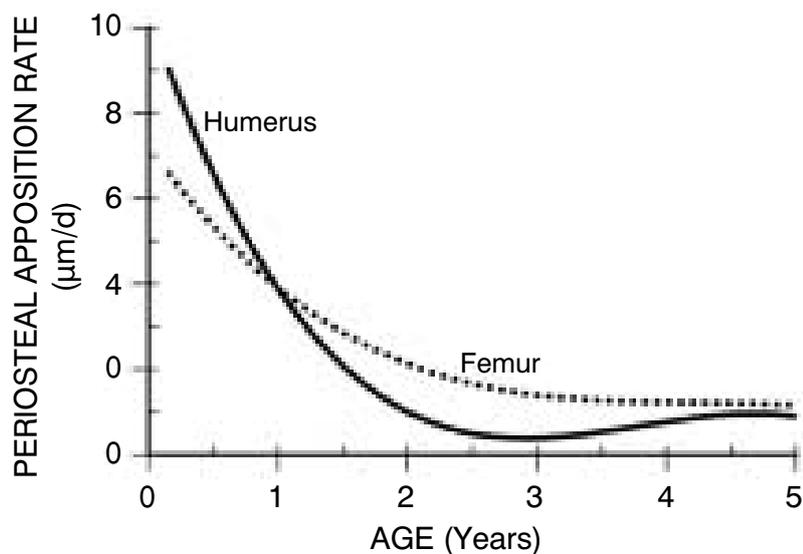


Figure 1.6 Periosteal apposition rates of femur and humerus by age in boys until 5 years, after Rauch (2005)

Bone cells can respond to mechanical stimuli, and it is widely understood that osteocytes act as mechanosensors, mediating a relationship between appositional bone growth and mechanical loading (Robling et al. 2006; Skerry 2006). Robling et al. (2006) describe the suitability of these cells by noting that osteocytes are abundant throughout bone tissue and can communicate with other bone cells; furthermore, strain causes extracellular fluid flow which interacts with the bone cells allowing the conversion of a physical force into a cellular response (mechanotransduction). However some caution is warranted as not all effects of mechanical stimuli on bone are necessarily functional, because many other cells in the human body are mechanosensitive without filling a specific mechanical purpose (Skerry 2008). The idea that physical activity influences bone growth relates to the concept of the mechanostat (Currey 2002; Frost 2003; Skerry 2008), a mechanism by which bone responds to changes in loading and habitual exercise through structural changes in bone architecture (Skerry 2006). This is related to an idea put forward already in the 19th century by Julius Wolff, today known as 'Wolff's Law', which states that change in the form and function of a bone, or in the function alone, is followed by alterations in internal architecture and external conformation of bone in accordance with mathematic laws (Skerry 2006). Wolff's Law is also important in understanding what is often called 'functional adaptation' that is, optimal size and strength of weight-bearing tissue: the skeleton of any animal needs to be strong enough to support its weight and to allow for habitual activity without fractures, but also light enough as to not waste energy in its growth and maintenance (Skerry 2006). In literature, the term functional adaptation is confusingly used to describe both the species/population level adaptation of the skeleton to physical requirements and the individual level responses in bone to physical activity (Wolff's Law), however it is important to keep in mind that these two are distinctly different processes.

The 'mechanostat', a term coined by Harold Frost, describes in detail the dynamic process that takes effect in bones throughout an individual's life, not just during the growth period. The catalyst is thought to be strain stimuli, that is, mechanical force directed at bone and a minimum strain is required before bone remodelling occurs (Currey 2002). Strain stimuli are complex and vary between parts of the skeleton and as such, there is no one 'mechanostat' (Skerry 2006). Since the future requirements of a bone are not known at the moment of growth, it is not surprising

that such a dynamic feedback system to regulate bone growth exists (Skerry 2006). If a growing bone is not exposed to loading, it does not take the expected or usual form, for example, the tibia of an inactive person will grow to be round at cross-section instead of the usual triangular shape (Robling et al. 2006).

Under normal circumstances, it is not possible to quantify the force inflicted on bone directly; its presence and magnitude must be inferred through measurements of deformations (Skerry 2008). Furthermore, there are no absolute measures of bone's response to strain, as the amount of deformation due to mechanical force is always divided by the original parameter of the same unit (Skerry 2008). This can be understood by imagining that a load is applied on a portion of bone, which causes it to shorten by a small amount. The effect of the shortening (strain) is understood in terms of length lost in relation to the original length of the portion (Skerry 2008). Magnitude of strain is the key target at which bone's response is aimed (Skerry 2006). Figure 1.7 describes the response of bone to changes in levels of strain compared to the 'customary strain stimulus', that is, the magnitude, rate, frequency and duration of strain in previous loading history (Skerry 2006). This highlights the complexity of the mechanical environment and posits how the response of each bone is relative to its starting point, that is, previously experienced loads.

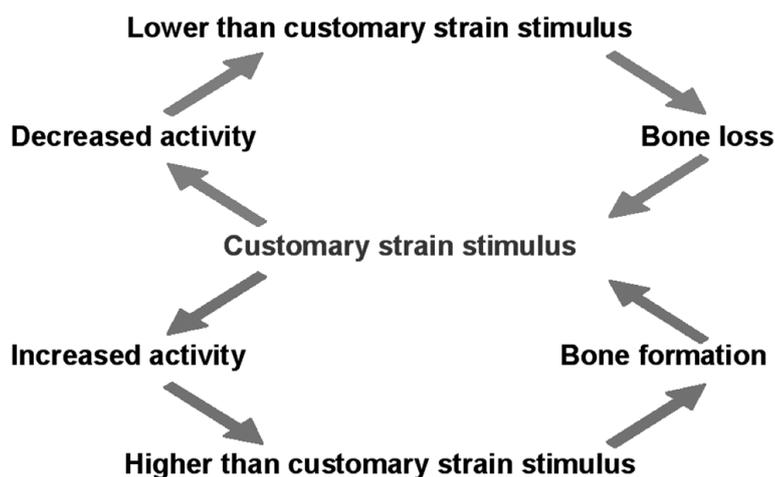


Figure 1.7 Regulation of bone by strain, after Skerry (2006)

The regulation of bone by strain is related to how changes in bone in response to activity or inactivity are perceived. If an increase in bone mass as response to use is

taken as desirable, then bone loss due to disuse is not pathological but merely an adaptive response (Skerry 2006). As such, disuse depends on the previous activity level of the individual (Skerry 2008). As will be discussed later on in this chapter nutrition also influences appositional bone growth, however, there is no simple relationship whereby an increase in nutrition would automatically result in increased appositional bone growth because available nutrition does not control the bone's response to activity, it merely enables or limits it (Skerry 2006). Still, improved nutrition can lead to increases in body size, such as increased stature, which can change the mechanical requirements of bone and may result in periosteal apposition. In the absence of loading and with adequate nutrition, it is presumed that there is a genetically determined minimum bone mass (Skerry 2008).

1.1.3 Genetics and the Heritability of Skeletal Traits

Before a discussion of environmental effects on bone growth, it is important to acknowledge that genes influence all human traits, including the endochondral and appositional growth parameters investigated in this study and as such, much of the variation in skeletal traits observed between individuals is caused by genetic variation. The extent of the influence of genes on growth is a debated topic as growth is controlled by a large variety of genes (Wells and Stock 2011; Zemel et al. 1997) with recent evidence suggesting that growth in stature is influenced by hundreds of genetic variants at at least 180 loci (Lango Allen et al. 2010). Recent twin studies of modern European populations give a heritability estimate of 80-90% for observed adult height (Wells and Stock 2011). However, the standard of living in Europe is relatively high and might lead to overestimations of the role of genes on stature, as there is less environmental variability that would lead to larger differences in attained height (Wells and Stock 2011). Complicating the matter are complex gene-environment and gene-gene interactions (Wells and Stock 2011; Lango Allen et al. 2010). Phenotypic plasticity, even during the intrauterine life of monozygotic twins, has been found to influence height – for instance in one Finnish twin study where one twin was at least 15% heavier than the other at birth, the heavier twin became on average 1.7cm taller at 16 years than the lighter twin (Pietiläinen et al. 2002).

A debate on the extent of the influence of genes on growth persists, as there is disagreement as to what extent change in a skeletal trait within a population is considered to be due to environmental factors. As mentioned the expression of genetic potential might vary when environmental conditions differ. It is widely accepted that there has been an increase in heights over the last 150 years in many Western populations, a trend which has been assigned to drastically improved living conditions (Cole 2000; Cole 2003; Hauspie et al. 1997; Komlos 1995). Still, it has been suggested that in Switzerland, increases in adult height within the last 150 years might be the result of decreases in adaptive pressures for smaller bodies after better nutrition became available (Rühli et al. 2008). Further, it is suggested that decreasing regional variance in Swiss statures between 19th century and 2005 might be due to increases in mobility, which have led to genetic exchange (Rühli et al. 2008). It is also acknowledged that alternatively, the lesser variance in statures between Swiss cantons might be due to increasing environmental homogeneity (Rühli et al. 2008). The first two arguments may be countered, as drastic changes in height related gene frequencies seem to be suggested within very short time periods. According to a recent calculation, if the secular trend in heights of another European population, the Dutch, was mainly genetic in origin, it would mean that 30% of the of the shortest individuals in the population must fail to reproduce, a selection pressure which is considered implausible (Stulp and Barrett 2014). Thus secular increases in stature are for most part the result of individuals achieving their genetic growth potential to a higher extent in better nutritional environments, and within population secular stature increase can be taken as an example of developmental plasticity (Wells and Stock 2011). Further, natural selection does not act on the final trait, such as height, but on the fitness consequences of the overall growth strategy, which in humans is complex and includes many other traits besides height, such as birth size and timing of puberty (Wells and Stock 2011). Still it is worth noting that a small part of the Dutch secular trend might be attributable to natural selection, as although Dutch heights follow the general pattern of increased height in improved growth environment, recent evidence suggests that additionally, taller Dutch men have more children and also higher child survival, despite their later age of first reproduction (Stulp et al. 2015).

Studies of genetic influences on appositional bone growth have concentrated on Quantitative Trait Loci (QTL) analysis, which is used to identify gene sequences that

might be influential in determining traits, in this case the mechanical properties of bones. Traits such as femoral structure and cross-sectional area have been found to be highly heritable (Klein et al. 2002; Koller et al. 2001). In an extensive study by Lang et al. (2005) QTLs for measures such as bone width, cortical thickness and cross-sectional area mapped on to nearly every chromosome implying that similarly to longitudinal bone growth, appositional bone development is influenced by a large number of genes. Quantitative Trait Loci for body weight, as well as height, often mapped to the same regions as those for the inspected skeletal traits suggesting that genes influencing bone growth could be mediated by body size (Lang et al. 2005; Masinde et al. 2003). However Blank (2014) notes that it is still unknown whether the observed pleiotropy between bone and muscle mass is due to a gene affecting just one trait (bone), which then mediates a response in the other (muscle), or the other way around. Further, there are limitations to QTL studies, as although several specific genetic markers that influence femoral cross-sectional shape and size have been found the molecular pathways the genes work through remain unknown (Volkman et al. 2003). Genes controlling bone mechanical properties and appositional growth have been found to be different to those influencing bone mineral density (BMD)(Klein et al. 2002).

Heritability estimates are another way of assessing the extent of genetic influence on skeletal traits. These, however, change through an individual's life span as the estimated genetic control over a trait can be different at different life stages (Duren et al. 2013). Mechanisms through which genetic contributions might operate at different life stages include developmental timing of gene action and epigenetic action of bone-related genes (Duren et al. 2013). In a group of 1761 subjects from 250 nuclear and extended families who took part in the Fels Longitudinal study, the genetic control of bone length remained relatively stable throughout an individual's growth period, but the genetic control of bone width fell from the teenage years and continued to do so throughout adulthood, possibly owing to larger activity related differences between individuals as variance due to factors such as weight, sex and age was also high during these life stages (Duren et al. 2013). This shows that in contrast to stature, heritability estimates of appositional growth are more challenging, as through its response to physical activity the mechanical demands of bone strongly affects traits measured.

Since there are differences in height and skeletal robusticity between populations (Katzmarzyk and Leonard 1998; Stulp and Barrett 2014), it is important to consider the genetic history of the study population used here, the Finns, to evaluate whether treating them as a single population is appropriate. The inspection of environmental influences on skeletal traits is based on the assumption that a population under study is similar enough genetically that observations are to likely not due to genetics. There is a wealth of literature on the genetic make-up of Finns, originally inspired by the unusual prevalence of certain genetic disorders in the population, often called the Finnish Disease Heritage (de la Chapelle 1993). It is widely accepted that the land area now belonging to Finland was first inhabited after the last glacial maximum, around 10 000 BC (Lappalainen et al. 2006) when the retreating ice sheet allowed hunter gatherers to populate the area. This small founding population was later joined by two significant migrant populations, estimated around 4000 and 2000 years ago (Varilo et al. 2003). Both of these migrant populations comprised a relatively small number of individuals who settled in the southern and southwestern coastal regions of the country. A permanent settling of the northern and northeastern part of the country occurred very late, around mid-17th century and the descendants of the original founding population, the Saami, were pushed further North into Lapland (Varilo et al. 2003).

There is evidence of a genetic boundary between Eastern and Western Finland due to a very localised population structure in what is a scarcely populated country, however these two subpopulations are more closely related to each other than either are to other Europeans, such as the English or the Germans (Salmela et al. 2008). Caution has still been warranted against treating Finns as a single population in genetic association studies (Salmela et al. 2008). There is evidence of an Eastern-Western divide in statures of Finnish men born in early 20th century, which is commonly assigned to differences in nutritional environment and especially to the lower socio-economic situation of Eastern Finns, but an underlying genetic explanation cannot be ruled out (Forsén et al. 2000). Therefore, the population structure of the Finns needs to be taken into consideration in this study, as whether genetic or environmental in origin, residence in Eastern or Western Finland might have affected skeletal growth, especially in stature.

1.1.4 Effects of Nutrition and Disease on Skeletal Growth

In the present study changes in the nutritional environment of late 19th and early 20th century Finns are considered factors, which possibly influenced the skeletal growth parameters of the population. In this section existing literature on nutritional effects on both endochondral and appositional growth will be discussed. Stature is often linked to overall living conditions (Komlos et al. 1995) and adequate nutrition has long been acknowledged as a requirement for normal longitudinal bone growth (Garn et al. 1975; Leonard 1989; Tanner 1981). Within a given population, adult height has been argued to represent a historical record of cumulative nutritional status, indicating the intake of nutrients minus basal metabolic costs, energy expenditure and disease burden (Komlos 1995). Therefore, stature can be used as a variable to measure a population's standard of living. Stunting, especially in the first years of life, predicts higher risk for later life diseases (Davey Smith et al. 2000; Gunnell et al. 1998). This makes height an extremely useful variable for examining population health. The height of individuals during their childhood cannot be analysed using a skeletal collection consisting of adults, however stunting in early life can be the cause of observed differences in adult heights as population level trends in adult heights have been found to mirror those of children (Cole 2003). For instance in Japan, mean birth length has not shown significant changes in the last 40 years, however, mean height at age two has increased by 10mm/per decade and this is identical to the mean height increase observed in adults (Cole 2003). This indicates that the secular increase of adult height in Japan (around 4cm between 1950 and 1990) was present already at age two, and there were no further height increases between age two and adulthood during the study period (Cole 2003). Following this it is reasonable to assume that adult heights of past populations might be similarly related to their childhood height, which in turn is in part a reflection of the childhood living environment.

The body requires sufficient amounts of both macro- and micronutrients, which can influence bone development both directly, by modifying bone turnover, and indirectly through changes in hormone secretion (Rizzoli 2008). For example, Insulin-Like Growth Factor I (IGF-I) is recognised as essential for longitudinal bone growth and acts as an important controller of both calcium and phosphate, the main minerals in bone (Niu and Rosen 2005; Rizzoli 2008). Dietary protein restriction has been

shown to lower IGF-I in rats which induced osteoblast resistance to IGF-I and thus hindered bone formation (Bonjour et al. 2013; Bourrin et al. 2000). Further, it seems that this process is moderated by calcium and phosphate intake, whereby lower intake attenuated the effect of low protein diet on IGF-I levels (Fournier et al. 2014). Milk is often used as an example of a foodstuff that is especially beneficial for bone growth, as it includes protein, calcium, and vitamins. It does not by itself, however, contain sufficient amounts of Vitamin D for the normal function of calcium and phosphate during bone formation (Bonjour et al. 2013) and therefore additional sources of Vitamin D are needed during growth. Milk also contains IGF-I and increases in serum IGF-I have been recorded after consumption (Wiley 2012). This could be either because protein consumption promotes IGF-I production, or as some have argued, directly by the IGF-I present in milk (Wiley 2012). In the latter case, the IGF-I would need to survive digestion (Wiley 2012). Children aged 3-10 years from New Zealand who had avoided milk through childhood had low stature for their age and although some catch-up growth occurred, remained smaller than their peers after two years (Rockell et al. 2005). In Japan, there has been an acceleration in growth in height since the 1960s, which is argued to be related to strong increases in milk consumption in a population that previously consumed very little milk (Takahashi 1984).

Nutrition also influences appositional bone development, whereby malnutrition, especially protein calorie deficiency leads to reduced bone strength in humans as well as in animal experiments (Bonjour et al. 2013; Bourrin et al. 2000; Fournier et al. 2014; Garn et al. 1975; Himes et al. 1975). Much of the human evidence comes from the 1970s when radiographic studies on the bone development of children were still conducted (e.g. Garn et al. 1975; Himes et al. 1975). Lampl et al. (1978) supplemented the diets of a group of New Guinean children with protein (skim milk powder) for eight months and found significantly increased growth in periosteal breadth in the second metacarpal compared to a control group. The children also showed a significant increase in height (Lampl et al. 1978). Equally to endochondral growth, appositional bone development is dependent on the micronutrients needed for bone growth; calcium supplementation combined with increased physical activity increases appositional bone growth in children (Specker and Binkley 2003). Considering this, it is possible that the individuals in the study by Lampl et al. (1978)

did not just benefit from the protein supplementation but also from the calcium present in the milk powder.

Iodine and selenium are further micronutrients required for normal growth due to their role in thyroid hormone function – iodine is a constituent of both thyroid hormones, thyroxine (T4) and triiodothyronine (T3), whereas enzymes that are dependant of selenium convert T4 to T3 (Ren et al. 2007; Zimmermann 2011). Thyroid hormones promote human growth hormone expression as well as directly affect epiphyseal bone growth (Zimmermann 2011). Similarly, IGF-I is dependent on thyroid hormone function, both indirectly through GH secretion and by direct effects (Zimmermann 2011). An experimental animal study has shown that iodine and selenium deficient diets led to lesser bone growth due to impaired function of the growth plate cartilage (Ren et al. 2007). Iodine deficiency is an important factor causing cretinism, a condition characterised by both physical and mental growth defects (Zimmermann 2011). Both iodine and selenium are found in soil as well as marine water, however quantities are very small in many parts of the world and iodine needs to be added to table salt in many countries. In Finland, the ground is particularly deficient in both minerals, as the soil is ancient bedrock (Aro 2015). Goitre, a condition caused by abnormal function of the thyroid gland and in many cases related to iodine deficiency was historically very common in Finland; in the 1940s iodine began to be added to salt (Aro 2015). Today, goitre is a rare disease across age groups in Finland. Although more abundant in soil than iodine, in Finnish soil selenium only exists in insoluble form due to its acidic and ferrous consistency (Aro 2015). Apart from China and New Zealand, estimates of selenium intake in Finland from the 1970's were lowest in the world and this led to selenium being added to plant fertilizers (Aro 2015). This means that Finnish diets in the 19th as well as early 20th century were likely deficient in both minerals and although beyond the scope of the present study, this possibly had an effect on the population's bone growth.

Similarly to nutrition, there is much literature on the effects of the disease environment on bone growth. In this section, some of the studies highlighting the relationship between diseases and skeletal growth will be discussed; later in this chapter the disease environment of late 19th century Finland will be examined as it possibly influenced the study population's skeletal growth. The role of disease in

bone growth is often connected to the role of nutrition as studies have shown that there is a complex interplay between nutritional and disease environments (Schaible and Kaufmann 2007). Especially childhood diseases associated with diarrhoea result in reduced capacity to utilise the nutrients in food and lead to hindered skeletal growth (Dillingham and Guerrant 2004; Guerrant et al. 2008). Children from areas with a large disease burden tend to be more stunted (Checkley et al. 2004; Dillingham and Guerrant 2004; Guerrant et al. 2008; Sharpe 2012), and in a study conducted in northeast Brazil diarrhoeal diseases in the first two years of life resulted in persistent 3.6cm shortage in stature (Moore et al. 2001). Some researchers argue that malnutrition can be considered an infectious disease in itself, and its combined effect with especially intestinal diseases worsens growth shortfall (Guerrant et al. 2008). However, it needs to be noted that although the effects of malnutrition are often mediated by pathogens or leave the body more vulnerable to these, malnutrition itself does not inherently include or introduce pathogens. In the context of understanding skeletal growth in general, it is worth considering both the disease and nutritional environment of a population as, even if one is adequate, failures in the other might lead to growth retardation. With this in mind, the present study aims to include factors measuring both the disease and nutritional environment (see 2.2). In addition to the link with nutrition, infectious disease load and hindered skeletal growth might be connected through the body's inflammatory response during infection. Cytokines, which are hormones that modulate the immune response and are released by many different cell types once the immune system is activated, also stimulate the activity of the hypothalamic-pituitary-adrenal (HPA) axis (Silverman et al. 2005). The HPA axis is key in the body's reaction to stressors ('fight or flight' response). Once in circulation, the cytokines cause the release of corticotrophin-releasing hormone (CRH), which in return leads to the release of adrenocorticotrophic hormone (ACTH) and stress hormone cortisol, which as discussed previously, inhibits bone growth (Walsh 2015).

Communicable diseases such as tuberculosis (TB) can affect bone development. A recent study by Sparacello et al. (2015) found that young individuals from the Neolithic who died of TB were relatively gracile, that is, had weaker bones for their size than the rest of the sample. The authors conclude that more research is required into the effects of TB on factors such as total cross-sectional area and limb long bone rigidity, as it remains unclear whether TB influences these parameters via

reduced activity in the individual or causes either a direct or indirect metabolic effect (Sparacello et al. 2015). It is possible that the discussed link between the inflammatory response and HPA axis function could be involved because as a bacterial disease TB can be expected to cause an immune response and thus the release of cytokines, which in turn could lead to reduced bone growth due to cortisol secretion. Tuberculosis was a common cause of death before the wider introduction of antibiotics and a group of individuals in the Finnish skeletal collection used in the present study had this cause of death according to the records accompanying the material. Further background to the collection and the reliability of this information is discussed in 1.3; however, due to the finding that TB might influence bone cross-sectional geometric properties, cause of death will be considered in this study.

There are also conditions, which can affect the growing skeleton without the introduction of pathogens. Hyperparathyroidism is a disease that increases bone turnover due to the excess production of parathyroidhormone (PTH), leading to loss of cortical bone and thus making skeletal elements more prone to fracture (Mosekilde 2008). Diseases such as this are rare at the population level, but can create differences in skeletal parameters between individuals that are difficult to identify when studying a skeletal collection. Especially if a skeletal sample consists of only a few individuals, there is always a chance that any observed pattern is due to individual differences such as an illness that cannot be diagnosed from the skeletal remains, as neither soft tissue nor medical records are available. Even if a disease does leave notable or identifiable marks on the skeleton, these are often highly similar between different conditions, for instance, skeletal lesions can be a sign of a number of different conditions (Wood et al. 1992). This is closely related to the osteological paradox – only individuals who died at a certain age can be inspected in a skeletal collection, those who survived are not represented (Wood et al. 1992). This creates inherent bias in the sample and a skeletal collection is never representative of a society at large. With regard to pathology, conclusions cannot be drawn about the incidence of a disease in the population merely based on evidence of those who died, and individual factors play a large role as susceptibility to disease can differ depending on a person's underlying vulnerability to a specific illness (Wood et al. 1992). In terms of the skeletal sample studied here, it is likely not representative of the general population, not least because a subsample of the

collection consists of prisoners and it is probable that their background and social circumstances differed from most of the population (see section 1.3)

1.1.5 Effects of Physical Activity on Skeletal Growth

The relationship between mechanical loading and skeletal growth was discussed with reference to the concept of the mechanostat earlier in this chapter. This section will look at the relationship between physical activity and bone growth in detail, because an important aspect of the present study is an investigation of the cross-sectional geometric (CSG) properties of the skeletal sample. CSG properties are widely understood to be particularly affected by habitual activity patterns (Ruff 2008). Endochondral and appositional bone growth are differentially affected by physical activity (Rauch 2005). Mechanical control of longitudinal bone growth is less researched; however, there are some examples of how loading influences bone length (Rauch 2005). Rauch (2005) discusses how historically it was thought that compressive force decreases longitudinal bone growth and tensile force increases it (labelled the Hueter-Volkmann law in the 19th century). Today, it is recognized that the impact of compression on bone length is more complex, and Rauch (2005) goes on to explain this using the mild version of the disease genu varum. This condition is found in toddlers, whose medial part of the tibial growth plate is more compressed by walking than the lateral. If, as the Hueter-Volkman law states, compression always led to decreased length, the condition would get gradually worse (Rauch 2005). However, the opposite is observed, and in mild cases the deformation corrects itself by increased growth in the more compressed medial growth plate (Rauch 2005). Only in severe cases does this negative feedback mechanism not work and surgery is required to fix the effects of the deviation. Rauch (2005) relates this back to the concept of the mechanostat whereby strain stimulus increases growth until a threshold is exceeded after which growth ceases (Figure 1.8, after Rauch (2005)).

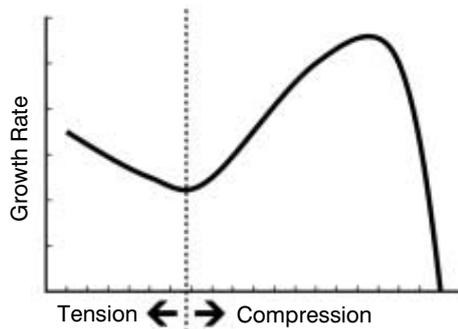


Figure 1.8 Growth rate in response to tensile and compressive force, after Rauch (2005)

There is a broad range of literature on the effects of activity on appositional growth in the fields of medicine, archaeology and anthropology (reviewed in Pearson and Lieberman 2004). In anthropology, the work of Christopher Ruff is widely cited and his biomechanical application of ‘beam theory’ to inspect structural changes in bone in response to physical activity includes work on many modern and past populations (Ruff et al. 1993; Ruff 2000; Ruff et al. 2006; Ruff 2008; Ruff et al. 2013; Ruff et al. 2015). Beam theory builds on the assumption that long bones are similar to construction beams in their mechanical qualities, and therefore their strength and resistance to bending can be measured using the same functions engineers apply to beams (Ruff 2008). Physical activity inflicts strain on bone and according to beam theory, its response relates to its structural properties. A key consideration here is the length and the width of the beam (or bone); for example a doubling of the length, keeping width constant, results in reduction of strength by a factor of 8 (Rauch 2005). This is because the doubling in one dimension has to be raised to the power of 3 as strength is the product of the three dimensional volume. Following this, for bone to keep its mechanical strength and resistance to bending during longitudinal growth, it also has to grow in width (Rauch 2005).

The effects of physical activity on appositional bone growth are often measured using cross-sectional geometry, whereby the cross-section of the bone measured at any point along the diaphysis is assumed to have similar properties to the cross-section of a beam at the same position. Table 1.1, modified after Ruff (2008) shows CSG properties with units of measurement.

Property	Abbreviations	Units	Definition
Cortical area	CA	mm ²	compressive/tensile strength
Total subperiosteal area	TA	mm ²	area within outer surface
Medullary area	MA	mm ²	area within medullary cavity
Percent of cortical area	%CA	%	(CA/TA) x 100
Second moment of area about M-L (x) axis	I _x	mm ⁴	anterior-posterior bending rigidity
Second moment of area about A-P (y) axis	I _y	mm ⁴	medial-lateral bending rigidity
Polar second moment of area	J	mm ⁴	torsional and (twice) average bending rigidity

Table 1.1 Cross-sectional geometric properties, modified after Ruff (2008)

Timing is important in terms of the response of bone to physical activity (Kontulainen et al. 2002). The cross-sectional properties of the humeri of young female tennis and squash players were more asymmetric in bone size measures (reflected as stronger forehand in comparison to backhand) if the subjects had started playing before puberty compared to late beginners (Kontulainen et al. 2002). Similar findings have also been presented by Haapasalo et al. (2000) and Bass et al. (2002), the latter conclude that loading before puberty increases bone cross-sectional size whilst loading after puberty results in bone growth on the endosteal surface, that is, the inner surface of the bone. This does not increase bone's resistance to bending (J) to any great extent, as that is mainly related to the size of the surface area at cross-section (Sparacello and Pearson 2010). These studies indicate that physical activity during childhood and adolescence has a stronger effect on bone strength and total cross-sectional area than later life activity. It has been shown that bones upon which forces are inflicted, such as those of the lower and upper limb, can remodel after maturity has been reached, albeit to a much lesser extent than during growth and mainly through changes that do not increase periosteal size, such as Haversian remodelling (HR) (Pearson and Lieberman 2004; Ruff et al. 2006). Haversian remodelling refers to turnover of cortical bone whereby osteoclasts and osteoblasts are activated in a coordinated way: first, osteoclasts resorb bone in a tunnel-like manner and then osteoblasts deposit bone within the tunnel around a vascular channel forming a 'Haversian system' (Pearson and Lieberman 2004). Haversian bone is stronger than old bone with microcrack

damage and it might strengthen bone by orientating more collagen along axes of tension (Pearson and Lieberman 2004). If bones experience strains below the customary level, bone mass decreases (Pearson and Lieberman 2004). An example of this comes from studies with astronauts, who lose on average 11% of the bone mass in their proximal femora during a four – six month space flight (Lang et al. 2006). However, it is important to note that this loss occurs via thinning of the cortices and no significant reductions in bone size measures are observed due to decreased loading (Lang et al. 2006). This is because thinning of the cortices occurs via endosteal resorption; total area at cross-section is a measure of periosteal growth.

Some debate remains concerning the influence of physical activity on appositional bone growth (Pearson and Lieberman 2004). Whilst it is agreed that bone responds to strains through modelling and Haversian remodelling, the so-called trade-off model has been proposed to be better suited to predict bone's response to strains than Frost's mechanostat (Pearson and Lieberman 2004). The main difference between these models is that the trade-off model predicts that HR is induced in response to high strain in distal elements of the limbs (Pearson and Lieberman 2004). The mechanostat predicts HR is inhibited by high strains (Pearson and Lieberman 2004). Although for most parts the models are in agreement, experimental evidence from juvenile sheep highlights that bone location is an important factor when considering bone's response to high loads as HR rates were higher in distal limb elements (tibia, metatarsals) but not in the proximal (femur) (Lieberman et al. 2003). This is possibly related to distal tapering, which is common amongst mammals and refers to thinner distal limb elements in comparison to proximal ones to save energy by reducing the limb's moments of inertia (Lieberman et al. 2003). However, this means that when the limb is under high strain the distal elements are less strong in comparison to the proximal. The trade-off model suggests that to balance distal tapering with ability to resist high loads, modelling rates (periosteal apposition) decrease from proximal to distal midshafts whilst HR rates increase from proximal to distal midshafts (Lieberman et al. 2003). Haversian remodelling does not increase periosteal diameter and therefore would not affect distal tapering. Work on other animals besides sheep is needed before the trade-off model can be fully supported, as are studies investigating within element changes in modelling and HR rates. Still, based on the evidence from juvenile sheep, it seems

that distal limb elements respond less to mechanical loading and thus proximal elements (femur, humerus) might be better indicators of loading environment during growth (Lieberman et al. 2003). This is of importance for studies inferring activity patterns from skeletal material, as it highlights that different elements might show different responses to the same activity.

Reconstructing activity patterns from skeletal remains has received some criticism, notably from Jurmain (1999). He notes that caution is warranted when links between activity patterns and changes in bone architecture are made, especially in cases where there is no information on age and sex of the individuals; for instance, hormonal differences between the sexes have been found to influence age related changes in bone whereby older females show more endosteal absorption (Jurmain 1999). This is related to the actions of sex hormone estrogen, which prevents bone resorption (Walsh 2015). After menopause, estrogen levels decrease in women and this can lead to increased bone turnover and a remodelling imbalance (Walsh 2015). It is also difficult to ascertain from past populations whether activity levels were within 'normal ranges' and thus not expected to result in marked differences (Jurmain 1999); what constitutes normal range is dependant of the previous loading history of an individual (Skerry 2006). As discussed, bone location is of further importance, and strain thresholds might be both variable and site specific (Jurmain 1999). Overall, since there is limited clinical data linking specific activities to specific bone architectures in humans, Jurmain (1999) argues that conclusions about the strenuousness of different subsistence strategies from bone parameters should not be made. The inference of activity patterns from bone morphology has been further questioned, as differences in locomotor behaviour during growth did not result in different bone morphologies in a sample of captive and wild chimpanzees (Morimoto et al. 2011). Whilst these results are very interesting, the activity patterns of the samples were not known but instead referred from literature of both wild and captive chimpanzee behaviour. Furthermore, the samples used were quite small, each group comprising around 25 individuals, which were further divided into three developmental categories (Morimoto et al. 2011). Overall, the discussed critique in regard to inferring activity from bone morphology needs to be kept in mind and factors such as age and sex controlled for (Jurmain 1999). Further, whilst differences in physical activity patterns might explain observed variation in bone morphology to some extent, genetic and nutritional factors also need to be

considered as these influence bone's response to activity during growth (Skerry 2006).

1.1.6 Effects of the Physical Environment on Skeletal Growth

A further environmental factor, which might have influenced the bone growth of the present study population, is the physical environment. The physical environment influences human growth parameters through climate and seasonality (Deleamarre-van de Waal 1993; Pomeroy et al. 2014; Simondon et al. 2007; Watson and McDonald 2007). Studies have found that growth is fastest in the spring (Deleamarre-van de Waal 1993) and that birth season has significant effects on several life history traits, including growth in stature (Pomeroy et al. 2014). The mechanisms are for large part still unknown; however it has been proposed that exposure to sunlight or seasonally varying micronutrient levels in foodstuffs might play a role (Pomeroy et al. 2014).

From a broader perspective, the physical environment, especially climate, has likely been one of the key forces resulting in differences in skeletal parameters observed today between populations, assuming that these differences are not related to current living standards (Katzmarzyk and Leonard 1998). Populations living in colder climates tend to have relatively shorter limbs and be more robust whilst populations living in hot arid climates have longer limbs and are more gracile, as predicted by Bergmann's and Allen's rules (Katzmarzyk and Leonard 1998). Some caution regarding these conclusions is warranted because of allometry – the observed increase in limb proportions in taller individuals might include an allometric effect, as limbs have positive allometry with stature (Auerbach and Sylvester 2011), which itself does not co-vary with climatic factors (Ruff 1994). This means that the observed relationship between limb length and stature could be functional and exist independently from climate.

A study on the relationship between British military recruit statures from the 18th century and 'climate', categorised based on early 20th century average January temperatures of different localities in the UK, found that individuals from warmer areas were significantly shorter, possibly due to a biological response to cold or associated food resources (Stegman 1985). This is supported by the evidence that

human populations in colder climates have larger body size (Katzmarzyk and Leonard 1998), however stature is not a very good measure of overall size because individuals of similar height can have very different body proportions and weights. As mentioned, stature by itself has not been found to co-vary with climate (Ruff 1994) and therefore body breadth would need to be considered, as unlike stature, it influences the surface area per mass ratio in humans, which is central to the prediction of Bergmann's rule that populations in colder climates have a lower ratio than those in warmer climates (Ruff 1994). The afore discussed studies do not directly link to the study population nonetheless they do have implications when considering appropriate methods to control for the effects of body mass using skeletal measures, as it is important that body mass is estimated using appropriate formula. Ruff et al. (2005) found that the body mass of Finnish males was underestimated by functions based on a previous reference sample that included data of individuals from 54 different populations but only few that were from high latitudes. Finnish males were found to have particularly broad bodies and exceed the sizes of previous reference samples, which is not surprising for a population inhabiting a cold climate (Katzmarzyk and Leonard 1998). In the body mass estimation of the present study population, the findings of Ruff et al. (2005) will be taken into consideration.

It has been proposed that in addition to effects on final body size, climate, especially temperature in terms of environmental heat load might influence birth weight in humans (Wells and Cole 2002). This is supported by a study of 140 human populations, which found that increased heat stress is associated with reduced birth weight, more specifically, the climatic effects seem to influence the proportion of population born with relatively low birth weights (under 2500g) (Wells and Cole 2002). The reasoning behind this is that low birth weight in hot climates might be an adaptation to environmental stress whereby associations between maternal size, fatness, heat production as well as size and composition of the fetus function to mediate the effects of the heat load (Wells 2002). Wells (2002) notes that this is the case with many animals and has been shown by experimental models; however, with reference to humans data are lacking and more evidence would be needed before conclusions can be made. The relationship between cold temperatures and birth weight in humans is unclear – in a sample of 12 500 Aberdeen children born in the 1950s reduced birth weight was associated with winter births, however it is

unknown whether this was related to exposure to low temperatures in the third trimester of pregnancy, high temperatures during first trimester or both (Lawlor et al. 2005). Extreme temperatures, both cold and hot can cause disturbances in human blood flow and have been shown to lead to excess cardiovascular deaths (Lawlor et al. 2005). Therefore, it is possible that fetal blood flow could also be disturbed by extreme weather conditions and seasonal patterns in birth weight might be explained by temperature effects at different stages of pregnancy (Lawlor et al. 2005). In the present study birth season is not investigated, however it is possible that some variation in the skeletal parameters of the study population is related to birth month effects on infant size as birth weight is one predictor of adult height (Cole 2000).

In addition to the more direct influences climate might have on human body size and birth weight, yearly weather patterns strongly influence the availability of food in populations that are reliant on domestic agricultural produce (Holopainen & Helama 2009) and thus a link might exist between skeletal growth and spring temperature during key developmental periods. Further, measures of yearly grain yields can be used as an added variable to inspect the nutritional environment of an agricultural population. Grain figure data from 19th century Finland have been used to analyse the effects of food shortages on mortality, and Hayward et al. (2012) found that in years of poor harvest, there was increased mortality among the lowest social classes in southwest Finland. The Hayward et al. (2012) study did not measure the effects of the food shortage on growth parameters, but it does suggest that grain figure data can capture variation in the nutritional environment, which influences fitness related traits in humans. Therefore, both the Finnish grain figure and spring temperature data will be used in the present study as measures of the population's nutritional environment (see Chapter 2).

1.1.7 Intra-household Factors and Skeletal Growth

Factors operating at the household level can affect growth as the amount of food available for individuals can differ within a household. As will be discussed, such factors cannot be investigated in the present study, but their potential influence is important to remember; this section will review some of the literature indicating that household factors can affect human growth. Some cultures place more importance

on males, with female children expected to be less active and eat less, leading to smaller size (Messer 1997). In India, females can be denied highly nutritious foods within household, such as milk and fruit while also being denied access to healthcare (Messer 1997). A further factor creating differential access to nutrition in members of the same household is age, as data from some traditional Indian, Mexican and African societies show bias towards either elderly males or elderly of both sexes. In other cases the opposite is observed, and food is allocated to the most 'productive' members of the household, in terms of earning wages (Messer 1997). In a study into food security in Niger it was found that many households had detrimental childcare practices and sick children were not given special treatment to assist in recovery and high quality foods such as meat were often reserved for the male head of the household (Hampshire et al. 2009). This is understandable within a framework of managing risks in a chronically deprived environment as all within-household decisions need to be balanced against costs to livelihood and effects to the rest of the family (Hampshire et al. 2009). Since studies on intra-household food allocation for 19th century Finland do not exist, these factors cannot be accounted for or examined. However, the sample in this study is limited to males and this might remove some possible gender-related bias, as Finland was historically a patriarchal society.

Number of children in a family has a significant effect on stature across social classes in the UK (Tanner 1981) and this is likely related to more scarce resources when the number of people to feed per earning member of the family increases. In a study using a comprehensive sample of contemporary British families, sibling number had significant effects on stature in the first decade of life even when a large range of other factors, such as income and educational level were considered (Lawson and Mace 2008). The height cost was also higher for later born siblings (Lawson and Mace 2008). Thus, even in well-nourished environments, reduced parental investment due to multiple siblings has an effect on height, and likely also other factors such as IQ and overall health (Lawson and Mace 2008).

Factors such as birth order or number of siblings are difficult to measure or account for in past populations, because they operate at the individual level and the identities of people in archaeological collections are often unknown. Even if their name is known, detailed data on the person's family history and everyday life is not.

Zooming out to the population level from individual level information is not straightforward, and variation caused by unknown factors in each individual's life is always a possible explanation for what is observed, especially when sample sizes are small. Remodelling of bone after the growth period can occur throughout life (Pearson and Lieberman 2004), but should have very limited effect on the skeletal parameters inspected in this study, as periosteal dimensions are for most part not affected by remodelling and cortical area is not looked at in the present study. Therefore, most of what is investigated in this study is tied to childhood and adolescent events, and changes related to old age should not create much bias in these data.

1.1.8 Effects of Social, Economic and Political Factors on Skeletal Growth

The final environmental factors to be considered in the present study are largely unique to humans and related to the wider living environment of populations. In humans, social, economic and political factors influence access to resources by setting the framework in which access to food, health care and other resources are determined. The relationship between malnutrition, disease, poverty and socioeconomic and political instability has been described as synergistic, as these variables often have interacting effects on each other (Schaible and Kaufmann 2007; Figure 1.10) . This can be understood in terms of a cycle, where population and individual level factors meet and interact. A change for the worse in any one factor can lead to further negative consequences in the others. Larger scale phenomena such as economic instability might lead to disturbances in food distribution or prices, causing malnutrition. This in turn impairs child development, compromises immunity and makes an individual more susceptible to infection and disease. Because of this it can be argued that economic and political factors are highly important in exposing populations to direct causes of growth retardation such as malnutrition. During famines, ecological factors such as agricultural production have been found less related to food security within households than economic and socio-political processes (Misselhorn 2005).

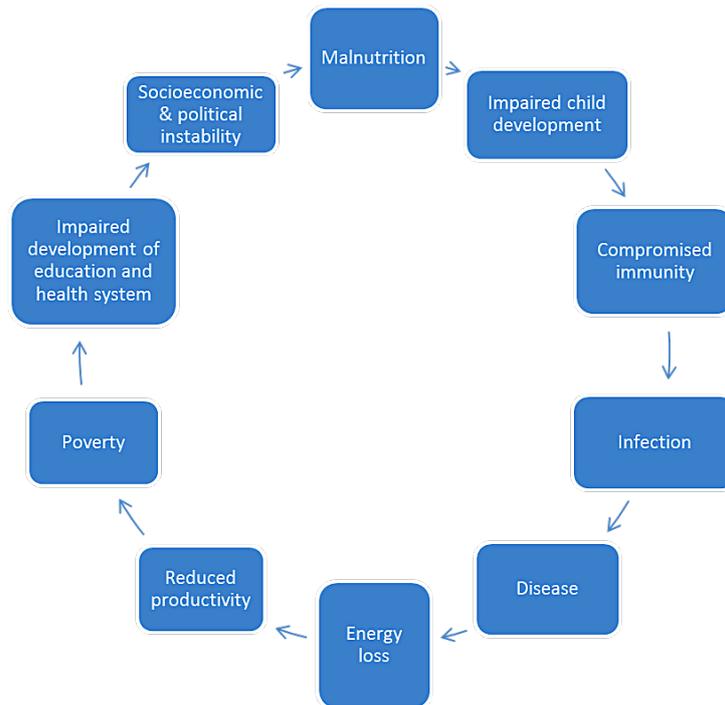


Figure 1.9 Synergistic relationship between child development and environmental factors, after Schaible and Kaufmann (2007)

As well as creating differences in the growth environment between populations, economic and political factors, especially socioeconomic status, create variation within populations. There is often differential access to resources for individuals within a society, and significant alterations in mean stature between social classes have been found in modern (Cavelaars et al. 2000; Lawson and Mace 2008; Peck and Lundberg 1995; Tanner 1981) and historical populations (Komlos 1998). As early as 1833 a British doctor inspecting a factory in Manchester noted that the factory class seemed to have much lower statures compared to the ‘national standard’ (Floud et al. 1990) whilst a French doctor, L. R. Villerme, was ahead of his time in the 1820s by assigning differences in growth to low levels of income, poor housing, clothing and nourishment (Tanner 1981). In the 1970s, results from the UK National Child Development Study showed that children in professional and managerial families were on average 3.3cm taller than children whose fathers were classified as unskilled manual workers (Tanner 1981). This, for the first time, provided evidence of discrepancy in height between social classes on a national scale (Tanner 1981).

There is a wealth of research demonstrating the effects of economic factors on human growth (Bogin 1999; Komlos 1995; Komlos 1998; Sharpe 2012; Steckel 2008; Tanner 1981). These have been argued to be more important than the disease environment (Komlos 1998), but due to the synergistic variable relationships (Figure 1.9) it is difficult to draw apart the relative effect of a single factor. Additionally, there is some evidence that caution is warranted when using economic indicators, such as a country's income level per capita, to inspect stature trends: in African countries, unlike in the rest of the world, GDP per capita and height are negatively correlated (Deaton 2007). Further, other commonly used factors that tend show a relationship with stature, such as infant mortality rate or maternal education level, do not show the predicted associations in any of the 27 inspected African countries (Deaton 2007). This is not the case with European or Asian populations and the explanation for tall Africans despite poor living conditions remains unknown (Deaton 2007). This should not be an issue in the present study; however, it does show that aspects of environmental influences on height are still poorly understood in certain populations.

In many parts of the world, occupation is – to an extent – a proxy for an individual's social class, and there are differences in stature between occupations (Floud et al. 1990; Tanner 1981). In early 19th century Britain there were notable differences in height between occupations, whereby men working in commerce or in white collar jobs were much taller compared to manual labourers, domestics and textile workers (Floud et al. 1990). This probably relates to access to resources but possibly also to psychosocial stress linked to deprivation (Delemarre-van de Waal 1993) as stress-hormone cortisol inhibits bone growth (Walsh 2015). Emotional stress might be linked to poorer childhood growth and children in boarding schools have been found to grow more whilst at home for the holidays (Mascie-Taylor 1991). Both childhood social class and psychosocial living conditions affect adult stature in Sweden (Peck and Lundberg 1995). The proportion of short individuals, classified as height one standard deviation below mean, was larger amongst manual and unskilled workers compared to non-manual employees (Peck and Lundberg 1995). Furthermore, the group of individuals who reported dissent in the family and thus had likely experienced psychosocial stress during childhood had a larger proportion of short people (Peck and Lundberg 1995). In an archaeological population, social class influenced cortical bone growth but not bone length in a 19th century Birmingham

sample (Mays et al. 2009). Children from higher social class had thicker cortices than children from lower social classes, possibly indicating that they had a better nutritional environment compared to their poorer peers (Mays et al. 2009). No difference was observed in bone width, which supports the argument, because if the difference were due to higher physical activity levels in the more well-off children, it should have been reflected in periosteal apposition (Mays et al. 2009). A further possibility would be that the results are related to the poorer children having experienced more psychosocial stress during childhood, as cortisol also promotes bone resorption (Walsh 2015).

In developing countries, level of education is a further social factor, which is connected to adult stature. The Human Development Index (HDI; UN 2015), which shows a positive relationship with the mean stature of a population, includes literacy rate as a measure of a country's educational environment (Bogin et al. 2007; Currie and Vogl 2013). This could be related to better-educated children also having educated parents who are able to offer more resources for their offspring. A similar finding has been made in a comparison of statures and educational level in 10 European countries, whereby lower educated men and women were shorter than those who were more highly educated (Cavelaars et al. 2000). The study puts forward three possible mechanisms for this observation. First, educational level might reflect childhood living conditions via social class, which itself influences among other things diet, disease risk, housing and psychosocial stress, which affect growth (Cavelaars et al. 2000). Second, the relationship might reflect a selection effect, which means that some of the adverse childhood circumstances leading to short stature also led to lower attained education and downwards social mobility (Cavelaars et al. 2000). Third, social factors of height might have a genetic origin, whereby taller individuals who have a likelihood of being upwardly socially mobile 'accumulate' in the higher social classes (Cavelaars et al. 2000).

In relation to appositional growth, the relationship with literacy rate and also educational level might be more complex, as learning to read and going to school might change childhood activity patterns and lead to less physically active children. The more sedentary the activity, the lower the 'physical activity ratio', which is the amount of energy as multiples of the basal metabolic rate (BMR). Activities children are involved with at school, such as reading and writing, have an activity ratio of

around 1.36 (Ulijaszek 1995) and thus require much less energy than activities children might otherwise be occupied with, such as active play, helping with farm work or other domestic chores (Table 1.2; James and Schofield 1990). Therefore, going to school could lead to less appositional bone growth, as lower physical activity induces less strain on bones, which as discussed, leads to smaller cross-sectional size and lower bending rigidity.

Energy cost of different activities gives as physical activity ratio (measured as multiples of BMR), after James and Schofield (1990)	
Activity	Physical activity ratio
Shopping firewood	4.1
Household chores	1.8-3.7
Feeding animals	3.6
Collecting and spreading manure	5.2
Clearing ground for crops	2.9-7.9
Cutting trees	4.8
Fishing with line	2.1
Sawing by hand	7.5

Table 1.2 Energy cost of different activities as multiples of BMR, after James and Schofield (1990).

1.2 Secular Trends

“The secular trend in human physical growth is a natural experiment which highlights the complex interplay between genes, physiology and environment in determining the size and shape of individuals from one generation to the next.” (Cole 2003: 165)

As briefly discussed in the section on genetic influences on growth, a population experiencing environmental changes can show changing patterns in skeletal traits through time, which do not have a genetic origin. Commonly, the measure of these changes is stature and the observed change is called a secular trend (Hauspie et al. 1997). Secular trends relate to changes in the nutritional and disease environment as well as economic and political factors. Changes through time can be observed by examining statures between groups within the population or in the population as a whole. What is evident from the literature is that there is no uniform context in which

a secular change in height occurs but a variety of improving conditions that result in an increase in the standard of living in a population or worsening conditions that result in a decrease (Cole 2003; Floud et al. 1990; Hauspie et al. 1997; Komlos 1995). Published studies on secular trends with regard to appositional bone growth are limited and tend to focus on change over extensive periods of time, such as thousands (Macintosh et al. 2014; Ruff et al. 2015) or even millions of years, covering the entire *Homo* lineage (Ruff 2006). The general pattern in these studies has been gracilisation over time, which is argued to be related to changes in subsistence related activity patterns. Recently, Ruff et al. (2015) presented evidence that in Europe, the last notable decrease in bone strength and resistance to bending occurred during the beginning of the Neolithic. Some signs of gracilisation were observed through the Iron and Roman periods but no further changes were observed in more recent populations, latest of which were from the 20th century. The Finnish population studied here is included in Ruff et al.'s (2015) sample of 'very recent' humans. However, they use it just as a single data point as part of a pooled 19th and 20th century European comparative sample, and they do not take into account variation through time within the Finnish population, which is the focus of the current study.

Variation in the nutritional and disease environment seem to be important drivers of secular change in height (Mays et al. 2009) and this has been demonstrated for example by Bogin (1999) in his research on the Maya of Guatemala and the children of Maya immigrants brought up in the USA, who showed increased stature compared to their parents' generation. The Maya children living in the US had access to better nutrition as well as lesser disease burden early in life (Bogin 1999). This intergenerational difference in height also provides strong evidence for the argument that within population height differences are not entirely due to changes in gene frequencies but at least in part response to an improved living environment. A further example of the effect of socio-economic change on stature comes from Papua New Guinea, where a significant secular increase in children's statures was observed among the small-scale Mountain Ok population after the opening of a mine, which greatly increased the population's wealth and access to nutrition (Adhikari et al. 2011). Secular change has also been studied using skeletal remains, for instance, the long bone lengths of both Black and White Americans were inspected using multiple collections dated up to the 1970s (Jantz and Jantz 1999).

The study found that the lower limb long bones showed secular changes more clearly than the upper limb, and that changes were stronger in men than in women. It concludes that the cumulative environmental conditions the study individuals were exposed during growth have improved over the last 200 years (Jantz and Jantz 1999). This supports the evidence from historical studies on secular changes in Western countries, discussed below.

In the Western world, the general trend of secular change in growth has been an increase in stature and growth velocity since the 19th century (Cole 2000). This follows, to an extent, the demographic and subsistence change from agrarian societies towards industrialised states (Hauspie et al. 1997). The industrial revolution itself, however, was followed by a decrease in stature in many European countries in late 18th and early 19th century (Cole 2000), as despite a rapidly growing economy (Komlos 1998), increasing numbers of people lived in overcrowded and poorly sanitized cities without adequate nutrition (Komlos 1995). The epidemiological transition occurred in many European countries well after industrialisation and English cities, for example, suffered from cholera outbreaks until the 1860s (Sharpe 2012). Thus, despite steady economic growth, the health of especially the poorest part of the population was not improved. The epidemiological transition takes place when there are changes in specific demographic markers, notably, when a population's life expectancy starts to increase and mortality rate starts a permanent decline (Omram 1971). Figure 1.10 shows patterns of stature change in a sample of Western countries from 1790 to 1930, after Treme and Craig (2013). From this graph the mentioned decrease in heights in Europe and also the US is evident, as is the continuous secular increase in the heights of many European populations after the late 19th century. Secular trends in stature in Finland and neighbouring countries will be discussed in Chapter 2. The following pages discuss the skeletal collection I have used in detail, as well as the social history of 19th century Finland.

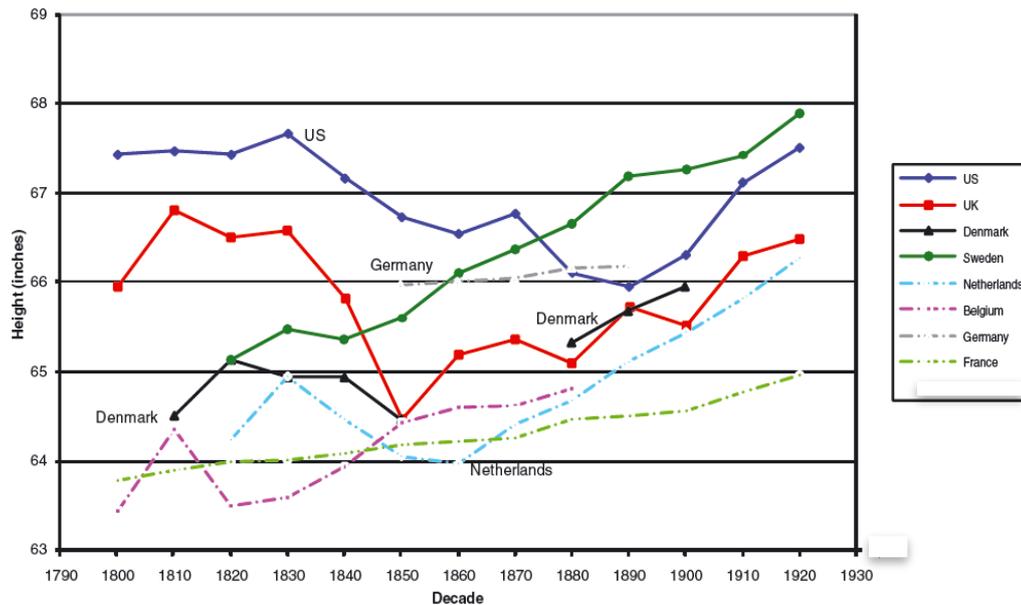


Figure 1.10 Secular change in stature in selected Western countries from 1790-1930, after Treme and Craig (2013)

1.3 Study Population

1.3.1 Historical Context of the A-series Collection of Human Remains

In the early decades of the 20th century, Finnish medical examiners sent partial skeletons of cadavers to the Department of Anatomy, University of Helsinki to be used for teaching and research purposes (Söderholm 2002). This material is now housed at the Finnish Museum of Natural History in Helsinki, and forms a mixed-sex skeletal collection called the ‘A-series’ of 201 adult individuals with accompanying demographic data including, for many individuals, their name, age at death, recorded living stature, place of birth, cause of death and occupation. These data were recorded by medical examiners and then transferred onto cards by the doctor receiving the samples at the Department of Anatomy, University of Helsinki (Figure 1.11). Skeletal elements are numbered as are the accompanying cards allowing identification of the individuals. Söderholm (2002) arranged the collection to meet modern curation standards and reviewed the labelling procedure. Due to the historical nature of the records, some error is likely to remain and factors such as cause of death cannot be confirmed using modern disease classifications. Still, it is

assumed here that the records are more reliable than estimations based on individual skeletal elements would be. Since the individuals are identified by name and for many there are detailed data such as date of birth, it is fair to assume that large part of what was recorded by the medical professionals of the time is reliable. The composition of the collection is as follows: 143 individuals have a recorded living stature and year of birth, 113 are males and 40 are females. The years of birth of the individuals vary between 1840 and 1914 for males and 1838 and 1911 for females; age at death ranges from 18 to 91, with the oldest male being 83 years. Place of residence is known for approximately half of the sample, and individuals from all historical Finnish municipalities are present. Thirty four of the males were prisoners at time of death. There are no skulls in the collection and very few pelvises. Although in very good condition, all individuals only have a few skeletal elements present, mainly either the upper or lower limb bones; further details on the samples chosen for the present study are given in Figure 1.13 and under 2.2, 3.2 and 4.2. It needs to be noted that the area referred to as 'Finland' in the text is not the same as Finland's current area and borders but instead includes the area and people that were first part of the autonomous Grand Duchy of Finland (1809-1917) and later the Republic of Finland (1917 onwards, pre-World War II borders).

The mid-19th to early 20th century was a highly interesting time in the history of the then autonomous Grand Duchy of Finland, which was, both culturally and geographically, the most Western part of the Russian Empire. Within this period the Finnish population underwent gradual industrialisation after a devastating famine in 1866-68 (Alanen 1995; Turpeinen 1986). The living conditions of the working population slowly improved after the 1870s with politically motivated investments in welfare programs and basic infrastructure (Turpeinen 1986; Turpeinen 1991). These changes coincide with the end of the first epidemiological stage in Finland estimated around 1875 (Kannisto et al. 1999). This is when the population's life expectancy started to increase and mortality rate started a permanent decline (Turpeinen 1977). These are two demographic markers of the transition between the first and the second epidemiological stage - the first stage is characterised by high and fluctuating mortality, the second, known as 'The Age of Receding Pandemics', shows a trend towards a lower mortality and higher life expectancy at birth (Omram 1971). The period over which the A-series was collected spans the time of transition, as oldest male individual in sample was born in 1840 and the youngest

1911. The changing living conditions of 19th century Finland are discussed in detail in the following pages.

HELSINGIN YLIOPISTON
ANATOMINEN LAITOS

Kortti N:o 198. V. 19. 35.

Merkki N:o 86. Laitoksen jatkuva N:o 270.

Nimi [redacted]

Ammatti Työmiehe.

Kirjoissa Novoristen seurak. Käpylään k.

Asunto Pitkämäen sairaal. * A 270

Syntymäpaikka [redacted]

Syntynyt (ikä) 6. III - 1887.

Kuollut 28. II - 1935. (Typhoidus paratyphosus et sim.)

Kuolemansyynä Kehohäiriö (Typhoidus paratyphosus et sim.)

Saapunut laitokselle 16. III - 1935.

Viisä Pitkämäen sairaal.

Yhteys ei mitään.

Muistut. Sitten formalisoitu. Kuumehöyryä.

lattu Tällä 18. III - 1935. Eklund.

lattu 30. I - 36.

Figure 1.11 Example of an identification card from the A-series (anonymised)

1.3.2 The Finnish Famine of 1866-1868

As late as 1866-1868, Finland suffered a large-scale mortality crisis in form of the Great Finnish Famine, resulting in the deaths of over 100,000 people of a population of 1.8 million (Grada 2001). The country had suffered from weather related crop failures and gradually worsening economic conditions from 1862 onwards, and this led to the famine after the nearly complete crop failures in 1865 and 1867 (Pitkänen and Mielke 1993; Jäntti et al. 2006). Mortality rates peaked in 1868 with 77.6 deaths per 1000 inhabitants (Grada 2001). Many deaths were not directly caused by starvation but instead by the spread of infectious diseases, leading to deaths in the population, which had been weakened by under-nutrition and denuded by large-scale migration (Pitkänen and Mielke 1993; Kannisto et al. 1999). The main diseases affecting the population were typhoid fever, typhus, dysentery and relapsing fever, a vector borne bacterial disease carried by lice and ticks (Pitkänen and Mielke 1993). The localized agricultural subsistence strategy of the majority of the Finnish population throughout the 19th century left the country susceptible to food shortages and probably had an impact on the long duration of the first epidemiological stage, as access to health care was poor and thus advances of medical research were out of reach for the majority of the population. People had a

direct dependency on crops, whereby bad years resulted in forced migration and hunger (Turpeinen 1986), and there was almost a complete lack of state-level support systems and infrastructure. This included a lack of road and rail networks that could be used to transport grain to secluded municipalities (Turpeinen 1991). Poor economic status and preindustrial subsistence strategies of many 19th century Finns were further reasons why the Finnish Famine had such catastrophic results (Häkkinen 2004). A large part of the population belonged to the social underclass, which included landless wage-labourers and urban poor who were very vulnerable to fluctuations in the economy and food availability (Häkkinen 2004). Less than 40% of households in the countryside were landowning families (Alanen 1995). Agricultural practices were very simple (Grada 2001) and 'burn-beating' (a type of slash-and-burn agriculture) was still common especially in eastern parts of the country (Holopainen & Helama 2009). Major technological advances only came after the famine years, which have later been considered a turning point of history (Alanen 1995).

Even without famine, the nutritional environment of early to mid-19th century Finland was poor and low in protein (Vihola 1994), an essential macronutrient for growth. Vihola (1994) reports that around 80% of the nutrition of workmen and maidservants consisted of vegetarian foods, mainly rye and potato, with meat and fish making up about 10% and milk products the remaining 10% of the food intake. Foods such as butter and sugar likely played a minimal part in the population's nutrition, as sugar consumption was not high enough to be recorded in the documents used by Vihola (1994), and butter was a highly valuable merchandise. People living in the first half of the 19th century are actually thought to have had worse quality nutrition in terms of consumption of sufficient amounts of fats and proteins than people living in the 16th and 17th century, as the increase in overall population size meant further reliance on agriculture, as opposed small-scale subsistence farming combined with hunting and gathering (Vihola 1994).

1.3.3 Industrialisation and Improving Living Conditions in Finland

Finland followed a non-traditional pattern of industrialisation. Compared to other Western European countries, Finland industrialised very late. By the beginning of the 20th century it was still a sparsely populated agricultural society (and not an

independent state but part of the Russian Empire until 1917 as the autonomous Grand Duchy of Finland). Industrialisation began slowly in the late 19th century and tracked a growing foreign need for wood produce. However, this did not have a large impact on the population in terms of urban versus rural habitation because sawmills and paper factories were mainly located in the countryside (Alanen 1995). Finland was well suited to developing a forestry industry as in the mid-19th century only 8% of the total land mass was cultivated for agricultural use (Grada 2001; Figure 1.13). As late as 1907 80% of the population still worked in the primary sector and only 1/7 in working class occupations, of whom half were factory employees (Kurth 2005).

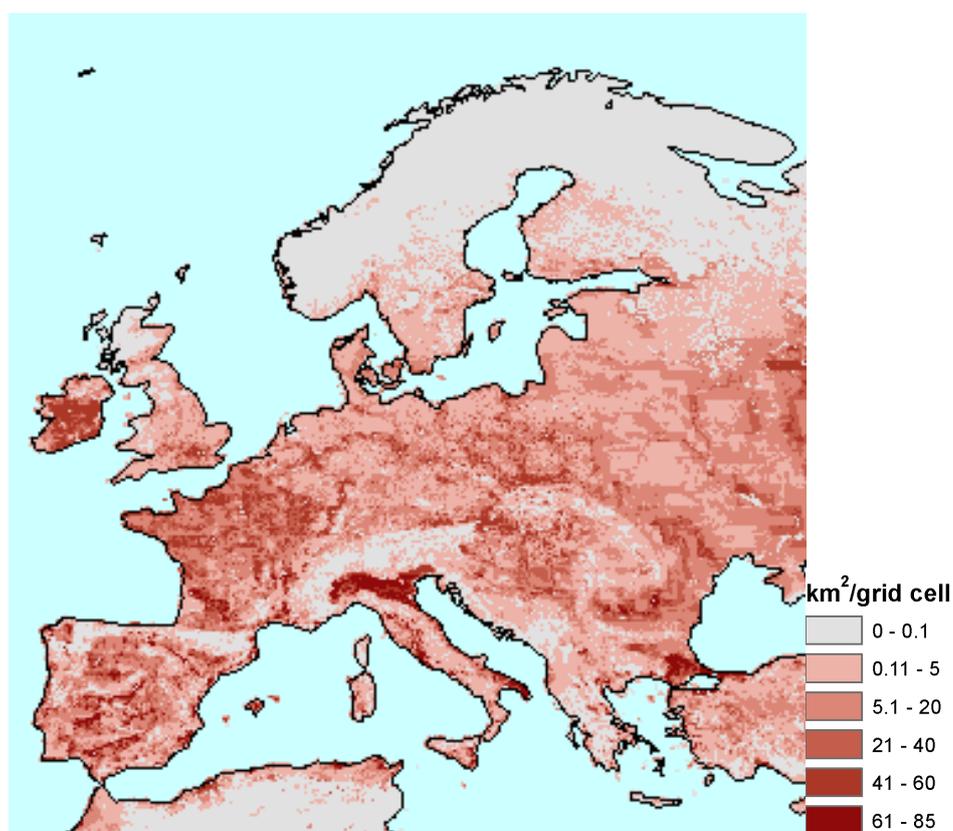


Figure 1.12 Estimated percentages of cultivated land (crops) per km² in Europe in year 1800 (Goldewijk et al. 2011), available at http://themasites.pbl.nl/tridion/en/themasites/hyde/download/download_form.html

In some countries, such as the UK, the health of urban populations suffered during industrialisation in the late 18th century, as infections and an insufficient diet led to poor growth (Komlos 1995). Finland industrialised in the decades following the famine and after the epidemiological transition (Kannisto et al. 1999), parallel with political efforts to develop the country (Turpeinen 1991). These included

investments in roads, rail and telegraph networks (Turpeinen 1991). In 1859, trade outside cities became free in Finland meaning that slowly, and occurring by the end of the 19th century, people's access to food was less limited by their own crop yields as food could be bought locally from tradesmen (Turpeinen 1991). For the poor, a marked improvement in food availability came through organized state (and private) relief committees that brought food and clothing directly to the areas that were affected by bad crop years, preventing migration (Turpeinen 1991) and probably the spread of infections. These committees were often led by women and this paved the way for women's rise in politics and election to Parliament in the elections of 1907 (Turpeinen 1991).

Building elementary schools in the countryside was a further part of the relief operations after the famine and the literacy of the population strongly increased towards the end of the 19th century, surpassing that of any other part of the Russian Empire (Turpeinen 1991). The number of elementary schools in the country increased over 100-fold between 1865 and 1921, whereby in 1865 there was one school for every 100 000 inhabitants and in 1921 one for every 1000 (Table 1.3). The Education Act of 1866 for the first time introduced public elementary schools in the country (Kurth 2005). J.V. Snellman, a senator and leading Fennoman politician (Klinge 2015), who was also one of the initial promoters of a public school system stated that "it is not relevant to discuss how much knowledge for example a farmer needs. As things stand currently, he needs to know as much as a priest, and then some" (Kurth 2005: 38). The Fennomans were a political movement who argued for an independent Finland, wanted to raise the status of Finnish language and culture as well as were opposed to both the Tsar's regime and the Swedish speaking upper classes. The quote from Snellman shows how education was perceived as something highly necessary, and it was viewed a vital part of the development of a modern European civil society (Kurth 2005). Special attention was given to the selection and education of teachers, who had to be 'model citizens' (Kurth 2005). Still, as late as 1898, two thirds of Finnish children did not attend school at all and the geographical spread of schools around the country remained uneven; in 1886 109 of 345 local councils did not have schools at all (Kurth 2005; LocalFinland.fi 2015). In 1898 a new act was put forward requiring every municipality to establish elementary schools in areas with at least 30 children (Kurth 2005). The substantial increase in the number of schools at the turn of the century was related to the

eventually ineffective efforts of the Tsar's regime to make the population more pro-Russian (Kurth 2005). Although in practice education had become compulsory in Finland by 1921, it was only then made into a law (Kurth 2005). The changes in the Finnish education environment in late 19th and early 20th century were reflected in the literacy rates both in the population at large and among prisoners, who as mentioned, form a subsample in the present study (Table 1.4, after Markussen (1990). The percentage of illiterate individuals is larger amongst prisoners compared to the rest of the population, which might be related to the overall low social status of Finnish prisoners in the 19th century (Aho and Karsikas 1980).

Year	Number of elementary schools in the country	Per capita
1865	20	.00001
1880	457	.00022
1895	1273	.00051
1900	1873	.00071
1911	2903	.00097
1921	3773	.00118

Table 1.3 Number of elementary schools in Finland 1865-1921, after Kurth (2005). Per capita values calculated using official population statistics (Statistics Finland).

Year	Number	Neither read nor write %	Read only %	Both read and write %
Literacy of members of Evangelical Lutheran Church of Finland				
1880	1,592,593	1.3	86.3	12.4
1900	2,177,633	0.8	60.6	38.6
1930	2,285,915	0.7	15.2	84.1
Literacy of a sample of male prisoners in Finland				
1891	276	4	55	40
1900	586	5	53	40
1915	928	1	40	56

Table 1.4 Literacy rates in Finland between 1880 and 1930, after Markussen (1990)

The mean life expectancy at birth in Finland for males dramatically increased from 30.7 years in 1861-70 to 41.3 years in 1881-90 and then to 50.2 years in 1921-30 (Kannisto et al. 1999). Between 1850 and 1950, total mortality rate dropped from 24.3 to 15.9 per thousand, and as mentioned, started a permanent decline after 1875 (Turpeinen 1977). This has often been interpreted to be a consequence of

industrialisation, but Turpeinen (1977) notes that change in the disease environment needs to be considered, as infant and childhood mortality, both of which are related to infectious disease (Sharpe 2012), decreased in particular. Also, advances in bacteriology started to change the hygiene practices and treatment policies of Finnish doctors in the late 19th century (Turpeinen 1986). The Health Care Act of 1879 is thought of as the first successful campaign to raise hygiene awareness of Finnish medical professionals whereby local and national statistics on population health and living conditions begun to be used as measures of success of the new policies (Harjula 2007). A new focus on preventive medicine in terms of communicable disease control was perceived as important in late 19th century Finland and also a marker of a civilised European nation (Harjula 2007). Health was commonly discussed in terms of the effects that mortality and disease have on the economy through the loss of workdays and labourers (Harjula 2007).

Still, at the end of the 19th century Finland had much higher mortality rates than neighbouring Sweden and Norway and communicable diseases were prevalent. 13.5% of all deaths in the country were due to tuberculosis between 1891-1900, with 'fever diseases', including typhoid, accounting for a further 9.4% and measles and scarlet fever combined for 7.9% of deaths; 2/3 of deaths were ambiguously classified as 'other disease' (Harjula 2007). Consequently, it is not surprising that the main aim of health policies in late 19th century Finland was to prevent the spread of infectious disease by maintaining hospitals for epidemic diseases and keeping cholera epidemics outside Finnish borders (Harjula 2007).

Public health campaigns became a method for spreading information about hygiene and disease risk factors and, in 1893, 25,000 copies of the first public information leaflet about tuberculosis entitled (when translated from the Finnish) "Information and guidelines for prevention of lung disease (tuberculosis)" were printed (Harjula 2007). The main message of public hygiene campaigns was an emphasis on lifestyle factors, such as avoiding dirt and disorder and fostering cleanliness and tidiness – these values were meant to reach all aspects of family life from the home to child care practices and nutrition (Harjula 2007). However, it was acknowledged, that a single person or family has no control over certain aspects of their living environment, such as air or water quality. Therefore, the Health Care Act of 1879 also included the mandatory appointment of a Board of Health in every city and

municipality whose responsibility it was to measure and record population health; every locality also had to produce a sewage plan within 10 years and as far as feasible, guarantee access to clean water (Harjula 2007). As discussed previously, childhood infections and especially diarrhoeal disease is connected to both stunting as well as access to appropriate water sources and sanitation (Checkley et al. 2004; Dillingham and Guerrant 2004). The decrease in infant mortality rate through the end of the 19th century and the 20th century and implies that both public and professional awareness of hygiene improved in Finland. Smallpox was nearly eradicated in Finland by 1883 after a successful mandatory vaccination campaign (Harjula 2007).

Although a welfare state was not created in Finland until the decades following World War II, state level political efforts of late 19th and early 20th century (Turpeinen 1991) tackled some of the social and structural issues that led to an inadequate growth environment during industrialisation in many other countries. Finland also survived further bad crop years after the famine (especially in 1891-93) without a population crisis. The investments to public welfare can be partly explained by the objectives of the nationalistic Fennoman movement, which in their endeavour to raise the status of Finnish language (mainly used at the time by peasants) and culture profited from everyone, including the poor, supporting the Finnish autonomous regime instead of the Swedish speaking upper classes or the Russians (Klinge 2015; Turpeinen 1991).

Social historians have examined changes in the standard of living in the Finnish population after the famine in comparison to early 19th century living standards. Using historical economic data, Heikkinen (1986) has estimated that private consumption per capita in Finland doubled between 1860 and 1912. The pattern of consumption also changed and, for example, expenditure on food, as a proportion of overall expenditure, decreased from 65% to 57% (Heikkinen 1986). At the same time, expenditure on items such as shoes and clothing increased. Within food consumption, the total share of grain fell and share of imported grain increased (Heikkinen 1986). Use of milk and butter grew rapidly and was reflected in agricultural production, with grain growing partly replaced by dairy production (Heikkinen 1986). The fastest growth was in coffee (threefold increase) and sugar (ninefold increase) consumption. Heikkinen (1986) estimates that between 1860

and 1912 the estimated daily intake of energy per capita rose from 1900 kcal to 3000 kcal. He notes that the latter figure is higher than actual consumption – this is due to biases caused by inferring per capita consumption from historical records that do not actually include any record of intake, merely what was purchased. Thus the energy intake figures should be treated as very rough estimates, which act to highlight an overall pattern of better food availability. The proportions of foodstuffs in the population's diet remained similar to the situation before the famine, whereby grain and other plant produce made up two-thirds and animal products one-third of the diet (Heikkinen 1986).

Silventoinen et al. (2000), using data from the Finnish Twin Cohort Study, found that the average body height of the population increased steadily between 1900 and 1957. The average heights for males and females in the sample born before 1928 are 171.3 and 159.2 cm and for the sample born between 1947 and 1957 are 176.6 and 163.5 cm (Silventoinen et al. 2000). Many of the individuals in the present study were born before 1900 and since the living conditions in Finland started to improve already after the 1880s (Kannisto et al. 1999; Turpeinen 1991), it will be investigated in this study whether Finnish statures started to increase before the turn of the century.

1.3.3.1 Prisoners in 19th century Finland

Given that a subsample of the individuals in the skeletal collection used in this study were prisoners at time of death and as such belonged to a social grouping different from the population at large, the Finnish prison population of late 19th century needs to be discussed. The demographics of the Finnish prisoners during this time period have been studied by Aho and Karsikas (1980) in a special research publication as part of the "Prison administration 100" project. They report that around 75% of prisoners at the end of the 19th century were males, of whom two-thirds were 21–40 years old. Adolescents formed a very small part of the prisoners, whereby only 0.5% were part of the youngest age category of 15–17 years in 1885 and a further 5% were 18–20 years old (Aho and Karsikas 1980). These data on the prisoners' ages mean that an individual was unlikely to become a prisoner in 19th century Finland before skeletal growth had finished, in terms of longitudinal growth and periosteal apposition. Therefore, the poor living conditions of prisons, such as frequently used

additional punishments in form of a low nutrition diet ('bread and water') should not have affected the skeletal parameters inspected in this study to great extent. Still, other factors, which might result in a difference between prisoners and the rest of the sample, need to be considered. Most importantly, the social background of prisoners was different to that of the rest of the population. Aho and Karsikas (1980) report that overall, around 50% of prisoners were individuals without occupations or permanent work, labelled as 'idlers' and 'vagrants' in the prison records. The spread of occupations amongst Finnish prisoners was similar to the overall population; however, the proportion of people with less respected and temporary occupations as well as low social class individuals was larger. In 1885, 42 to 76% of prisoners were idlers, depending on type of prisoner, as especially those sent to labour imprisonment were often sentenced for 'idleness' (Aho and Karsikas 1980). Many of these prisoners were re-offenders with previous criminal as opposed to vagrancy related sentences, revealing a pattern of unsuccessful rehabilitation of convicts into society. Overall, Aho and Karsikas (1980) describe the typical Finnish prisoner of the late 19th century as a young man without family or means of permanent living. As mentioned earlier, the proportion of illiterate individuals is larger amongst prisoners compared to the rest of the population (Markussen 1990) indicating that a greater proportion of prisoners lacked formal education compared to the population at large. In the 1890s the overall amount of prisoners in Finland doubled compared to the previous decade as a newly introduced criminal law made robbery and theft punishable by prison sentence (Aho and Karsikas 1980). It is also likely that individuals suffering from mental health issues ended up in prisons due to a lack of knowledge about mental illness and facilities for treatment (Aho and Karsikas 1980).

1.4 Aims and Objectives

This study aims to investigate growth in stature and appositional bone development using adult male individuals from a 19th and early 20th century Finnish skeletal collection (A-series). The study has three objectives:

(1) To test whether a secular trend in skeletal growth parameters (the recorded living stature, long bone length, total cross-sectional area (TA) and twice average bending rigidity “J”) is present in the sample. Bone length, TA and J will be investigated in femur, tibia and humerus.

(2) To investigate whether the study individuals’ prisoner status introduces variation in the examined skeletal parameters within the sample.

(3) To examine what environmental indicators may have relationships with the skeletal growth parameters. It needs to be noted that individual level conclusions cannot be drawn from larger scale changes in the population’s living environment.

The A-series does not consist of full skeletons: most individuals are only represented by either upper or lower limb bones. This causes a sample size restriction, as although stature data are available for 113 adult males, the other skeletal parameters can only be investigated in reduced samples (Figure 1.13). Sample sizes were deemed sufficient for femora, tibiae and humeri so these were included in analysis. At time of death 34 individuals in the collection were prisoners.

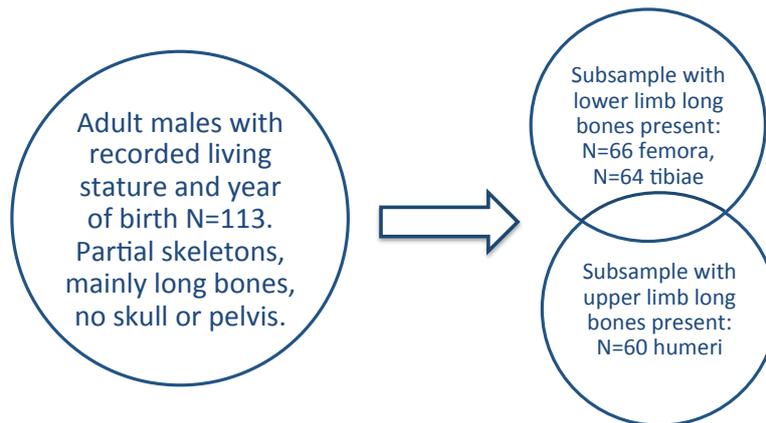


Figure 1.13 Summary of samples from the A-series used in this study. Stature is investigated for the full sample of 113 individuals, with long bone lengths and cross-sectional properties assessed in the two subsamples. Sixteen individuals are represented in both the tibia and humerus samples, with 18 individuals represented in both the femur and the humerus samples.

1.4.1 Outline of Chapter 2: Recorded Living Stature

In Chapter 2 I analyse and discuss the three objectives of this study with reference to the recorded living stature of adult male individuals in the A-series. A secular trend in stature is reported widely across Europe around the time my study sample was alive, I contextualise this in the chapter introduction by introducing studies on stature trends from countries close to Finland and by citing some of the debate surrounding the secular trend literature. A significant positive secular trend is reported and it is concluded that this could be related to the drastic changes in the living environment of late 19th and early 20th century Finns, as the country tried to prevent further population disasters after the devastating famine of 1866-68. Prisoner status and the examined environmental variables did not have a significant relationship with recorded living stature.

1.4.2 Outline of Chapter 3: Lower Limb: Femur and Tibia Length and CSG Properties

In Chapter 3 I analyse and discuss the three objectives of this study with reference to femur and tibia length and cross-sectional geometric (CSG) properties. The chapter presents a novel approach in terms of examining whether lower limb long bone CSG properties changed through time in an industrialising European population. Data were collected on 66 femora and 64 tibiae using a desktop 3D laser scanner. A significant secular trend in femur length is reported. There were no significant secular trends in tibia length or in the examined CSG properties. Prisoner status did not have a significant relationship with any of the investigated skeletal parameters. The average grain figure for rye, barley and oat in Finland for the first two years of life had a significant relationship with the examined CSG properties. This is a puzzling finding, as the grain figure did not show a significant relationship with the other examined traits; it will be discussed with reference to literature on the effects of nutritional insults on both endochondral and appositional growth.

1.4.3 Outline of Chapter 4: Upper Limb: Humerus Length and CSG Properties

In Chapter 4 I analyse and discuss the three objectives of this study with reference to humerus length and CSG properties. The humerus is included in this study because as a non-weight bearing skeletal element it may show different patterns in comparison to the lower limb bones, in the introduction I contextualise this by introducing literature on humeral CSG properties and habitual activity patterns. Data were collected on 60 humeri. There was a significant secular decrease in the humeral CSG properties and a significant relationship between prisoner status and TA and J. These findings are discussed with reference to literature on the introduction of public elementary schools in Finland in the late 19th century, as schooling might have influenced the upper limb loading environment of children in the country. There was no significant secular trend in humerus length. The examined environmental variables had no significant relationships with either humerus length or CSG properties.

1.4.4 Outline of Chapter 5: General Discussion

In Chapter 5 I focus on the question why the results for the skeletal parameters examined in this study revealed different patterns by situating the results in the literature on both the social history of Finland and on the biological variability between skeletal elements. It is concluded that the large-scale changes in the living environment of the 19th and early 20th century Finns offer a possible explanation for the observed trends. Further, there is a need for future research investigating appositional growth parameters during Industrialisation.

2 Recorded Living Stature

2.1 Introduction

This chapter aims to investigate whether there is a secular trend in the recorded living stature of adult male individuals in the A-series. The average body height of both males and females steadily increased in Finland between 1900 and 1957 (Silventoinen et al. 2000) but whether this trend had begun before the turn of the century is unknown. A further aim of this chapter is to examine whether the study individuals' prisoner status or residency in East versus West Finland has an association with final attained height. Additionally, the possible influences of environmental variables (GDP per capita index, infant mortality rate, annual average spring temperature and annual grain yields for rye, barley and oat) on stature are considered. The motives for selecting these variables, although in part referred to in Chapter 1, will be discussed in this introduction.

Stature is largely a measure of endochondral bone growth (Mays et al. 2009), with bone tissue accounting for 97-98% of a person's height (Malina et al. 1991; Table 2.1, after Raxter et al. 2006). In historical populations, stature trends are commonly studied using military or prisoner records (Floud et al. 1990; Komlos 1998; Maloney and Carson 2008). Increases and decreases in European and North American statures over the last 200 years have been explained using multiple factors – for instance, economic conditions and business cycles, exposure to sunlight, disease burden and the availability and quality of nutrition (Carson 2011; Floud et al. 1990; Komlos 1995; Sharpe 2012; Woitek 2003). The relationship between stature and economic growth has received special attention from both anthropologists and economists and a widely accepted conclusion is that whilst European and US statures show a general increase from the late 19th century onwards, there was a notable dip in adult heights during the mid-19th century despite economic growth (Komlos 1998; Treme and Craig 2013). This trend of decreasing statures in growing

economies, commonly assigned to the poor living conditions of overcrowded cities, has been labeled the 'antebellum puzzle' and has been revealed by studies using height records from the UK, the US, Denmark, Netherlands and Belgium (Komlos 1998; Treme and Craig 2013), although as discussed below the 'puzzle' is not universally accepted. Interestingly, in two countries close to Finland, Sweden and Estonia, mean statures in the 19th century do not follow the pattern of the other European countries and the US (Lintsi and Kaarma 2006; Sandberg and Steckel 1997). Estonian heights increased 0.7cm per decade between 1811 and 1886; mean statures of Estonian 17-year-old boys rose from 160.7 to 179.11cm between 1811-2003 (Lintsi and Kaarma 2006). Swedish males saw an increase of mean height from 167 to 179.3 cm between 1820-1965 (Sandberg and Steckel 1997). There was a small dip in Swedish statures in the 1840s, although they recovered quickly (Sandberg and Steckel 1997). Urbanization was slow in Sweden until the 1870s and this might have been beneficial to population health as living conditions in cities were poor at the time (Sandberg and Steckel 1997). After the 1870s, Sweden industrialized very rapidly and conditions in cities improved markedly, quickly becoming one of the most developed countries in Europe (Sandberg and Steckel 1997).

Although Finland is geographically and culturally close to Sweden, living conditions differed between the two countries in the late 19th century and therefore the stature trend of Sweden should not be assumed to apply to Finland also. As discussed in Chapter 1, Finnish industrialization followed an unusual pattern. Similarly to Sweden, the process began very late by European standards but was much slower. Finland did not see rapid urbanization and technological development. Instead forestry became the main industry in the country (Alanen 1995; Hjerppe 1989). Change from small-scale subsistence farming to more technologically advanced forms of agriculture was slow. Agriculture also held its position as the main subsistence strategy in Finland, employing 80% of the population as late as 1907 (Alanen 1995; Grada 2001; Hjerppe 1989). Economic development until the 19th century had also been slower in Finland compared to Sweden and in 1860, the GDP per capita of Sweden was nearly double that of Finland (Hjerppe 1989). A further difference between Finland and Sweden in terms of overall development of the countries in the late 19th century was in educational attainment. In Sweden in 1890 all but 1% of army conscripts could both read and write, whereas in Finland in 1900

60.6% of members of the Lutheran church could only read and 38.6% could both read and write (Markussen 1990). This probably limited occupational options and access to resources for many Finns in comparison to the neighboring Swedes. Considering these differences and the unique pattern of industrialization in Finland, a specific direction for a secular trend in stature in this study will not be hypothesised. Based on the literature reviewed extensively in Chapter 1, living conditions in terms of disease burden, access to nutrition and education seem to have improved in Finland throughout the study period and thus the population could have seen an increase in statures. However, it is also feasible that Finnish statures might have stagnated until the beginning of the 20th century due to slower industrialization in comparison to the other Western European countries. It is considered less likely that Finnish statures would have decreased over the time period, although a Finnish version of the antebellum puzzle cannot be completely ruled out. The data used in the present study is not sufficient to test whether the antebellum puzzle exists in Finland. However if Finnish statures did decrease at any point in the 19th century, that might prevent the data from showing a secular trend.

Complicating the matter of 19th century stature trends is a recent argument that questions the existence of the antebellum puzzle (Bodenhorn et al. 2013). Since the studies that have observed this pattern of decreased statures use both conscript and convict records, it has been proposed that inherent sample selection bias might be driving the results, as who chooses to become a soldier or turn to a life of crime can change through time as economic conditions and opportunities for work fluctuate (Bodenhorn et al. 2013). This means that the part of the population in prisons or enlisting in the military can vary – for instance in bad times taller individuals of somewhat higher social class might decide to enlist in the army or turn to crime as a means of living. These are choices they might not consider under normal circumstance. Similarly during good economic times when work is plentiful, it is plausible that only the poorest (and shortest) in a society choose to become soldiers or turn to crime (Bodenhorn et al. 2013). These individually motivated behavioral choices could explain the observed pattern of short statures in growing economies when data used consist of military recruits and prisoners. As of yet, this hypothesis has not been tested using the original data sets showing the mid-19th century stature decreases (Bodenhorn et al. 2013). Still, this argument is of interest for the present study as the study sample includes both prisoners and non-prisoners

and thus conflicting stature trends might be present. Also, as prisoners in 19th century Finland tended to come from the poorest social backgrounds (Aho and Karsikas 1980) their heights might have differed from the rest. For these reasons this study will compare prisoner and non-prisoner heights before the data are analyzed further. To examine the possible relationship between economic growth and Finnish statures, data on historical GDP per capita indices will be employed in the study.

Besides the economic environment, disease burden was identified in Chapter 1 as an important factor influencing bone growth. To examine the possible link between the disease environment and height in this sample, infant mortality rate will be included in analysis. Historical data on infant mortality in Finland is available for 19th and 20th century and shows a general pattern of decrease starting around 1880 (Kannisto et al. 1999). Whereas in 1865 infant mortality in Finland was 193.7 it had decreased to 153.1 in 1900 and to 96.7 per 1000 live births by 1920 (Statistics Finland 2015). Infant mortality might contribute to a secular stature trend directly in this population – infectious diseases, which are major determinants of infant mortality are connected to shorter stature in modern developing populations (Dillingham and Guerrant 2004; Moore et al. 2001). In historical samples the childhood disease environment has been used as a possible explanatory factor of short statures in 19th century English cities, and amongst 19th century US soldiers, the mortality rate of the area in which an individual spent their infancy and early childhood had a negative relationship with adult stature (Haines et al. 2003; Sharpe 2012). Further, early childhood mortality rates were found to be a good negative predictor of height in a large sample of American World War I recruits (Haines and Steckel 2000), indicating that historical infant mortality rates capture an aspect of the early growth environment.

To include measures of the nutritional environment during growth in this study, data on yearly weather patterns and grain yields will be analysed with reference to height. As discussed in Chapter 1, yearly weather patterns strongly influence the availability of food in populations that are reliant on domestic agricultural produce (Holopainen & Helama 2009) and thus a link might exist between skeletal growth and spring temperature during key developmental periods. Grain yields were chosen as a further factor measuring food availability. Grain figure data from 19th

century Finland have been used to analyse the effects of food shortages on mortality, and Hayward et al. (2012) found that in years of poor harvest, there was increased mortality among the lowest social classes in southwest Finland. The effects of food shortages on growth parameters were not measured (Hayward et al. 2012) but the study does suggest that grain figure data can capture variation in the nutritional environment, which influences fitness related traits in humans. Spring temperatures and grain figures are not assumed to contribute to any secular trend directly in this population but might be responsible for inter-annual variation around a general trend in recorded living stature.

As noted in the introductory chapter, there is a difference in 20th century statures between East and West Finland. This might be due to a genetic difference, related to poorer living conditions in the eastern parts of the country at beginning of 20th century or reflect a combination of both genetic and environmental influences (Forsén et al. 2000). Therefore, the present study will investigate whether there is a difference in recorded living stature of A-series individuals according to whether they resided with in East versus West Finland. These data do not exist for the entire sample and consequently has to be investigated using a subsample.

When examining the recorded living statures, it is important to keep in mind that the link between stature and endochondral bone growth is complex, as the timing and velocity of growth differs between both bones and individuals (Karlberg 1998; White et al. 2011). When investigating how environmental change affects longitudinal bone growth, distinction between stature and bone length is important as an adverse living environment might differentially affect the growth of certain bones, most notably the tibia (Sohn 2015). Recently, research has become increasingly focused on comparison of specific skeletal elements and body proportions and comparing these with height (Pomeroy et al. 2012; Padez et al. 2009; Bogin and Baker 2012; Sohn 2015). However, in archaeological populations, living stature is often unknown and therefore comparisons of growth between different skeletal elements and stature are difficult, as in these cases stature is often predicted using bone length meaning it is not an independent measure. The population under study is an exception to this, as the individuals in the A-series have a recorded living stature. Whilst this chapter focuses on recorded living stature, following chapters will

investigate measures of both endochondral and appositional bone growth in specific skeletal elements (femur, tibia, humerus).

Skeletal elements adding to height			
Cranium	From 2 nd cervical to 5 th lumbar vertebra		1 st sacral vertebra
Femur	Tibia	Talus	Calcaneus

Table 2.1 Skeletal elements adding to height, after Raxter et al. 2006

2.2 Methods

2.2.1 Study sample

All adult male individuals from the 19th to early 20th century A-series collection of human skeletal remains, housed at the Finnish Museum of Natural History, Helsinki, with a recorded living stature and year of birth were selected for analysis. These data were available for 113 individuals. Each individual in the collection has an associated datasheet (Söderholm 2002), which allowed the estimation of biological maturity using the recorded age at death of the individuals together with assessing epiphyseal fusion of present limb long bones. Only individuals with fully fused long bones were included, even if their recorded chronological age at death was over 18. This was done to minimize any bias that could result from analysing recorded living stature data of individuals whose longitudinal bone growth had not finished. The name of each individual in the collection is known and was used to assign sex. There were no individuals for whom the recorded name could belong to either sex. To ensure anonymity, the names of the individuals were removed from the data set. In addition to name, stature and age, data were available for most individuals on cause of death, occupation and place of residence. Throughout the study, the ethical guidelines of the British Association for Biological Anthropology and Osteoarchaeology (BABA0 2015) were followed.

Only individuals with a recorded stature were included in the analysis – no attempts were made to estimate stature using the skeletal material because of the errors

these methods introduce. Population specific equations using long bone length to predict stature give different values depending on which bone is used (Kozak 1996). The anatomical method for stature estimation (Hauser et al. 2005) is more precise than those based on individual bone lengths, however, it could not be used in the present study as the method requires measuring all height additive skeletal elements and these were not present. Further, since the living stature is known for many individuals in the collection, an estimated stature for some would create an inconsistency within the sample.

2.2.2 Year of Birth Categories

The sample individuals were divided into three year of birth categories to allow a closer examination of possible change in mean statures between selected time periods. Table 2.2 shows the chosen year of birth categories with number of individuals.

<i>Time Period</i>	<i>N</i>
<1870	24
1870-1900	57
>1900	32

Table 2.2 Year of birth categories with number of individuals. First category includes individuals born before and during the Finnish Famine, second category includes individuals born after the famine but before the turn of the century. Third category includes individuals born after 1900.

2.2.3 Environmental Data

Prisoner status, GDP per capita index, infant mortality rate, historical annual spring temperature and grain figures were used in analysis. These data were included from each individual's birth year. Additionally, an average of the first two years of life was added for variables that show great inter-annual variation, that is, spring temperature and the grain figures. As discussed in Chapter 1, the first two years of life are a critical period in terms of bone growth (Cole 2000; Cole 2003; Pomeroy et al. 2014; Rauch 2007). Calculating an average for the first two years of life was deemed an unnecessary procedure in terms of the GDP per capita index and infant

mortality rate as these show much less inter-annual variation and thus the value for the birth year was assumed to be representative of the early growth period. Since an important increase in stature occurs during the pubertal growth spurt, data for individuals' 14th year of life was included – because this is when on average pubertal growth is at its fastest in males (Tanner 1981). There is much individual variation in the timing of the pubertal growth spurt but for the purposes of this study and considering the limitations of working with a skeletal collection, choosing an age that probably saw increased growth in stature in most individuals in this population was deemed acceptable.

2.2.3.1 Prisoner Status

To inspect whether prisoner status influenced growth in stature in this population the sample was divided into three categories based on information from the collection records: “Prisoner” (N=34), “Non-prisoner” (N=64) and “Unknown” (N=15). The “Non-prisoner” category includes many individuals whose occupation is recorded as “Workman”. Some had more specific titles such as “Carpenter”. Most occupations in the category were working class and would have involved manual labour. Four individuals in the sample had occupations suggesting a somewhat higher social standing compared to the labourers: two salesmen, one former clerk and one tailor. However this sample was too small to be analysed separately from the manual labourers and both were included in the “Non-prisoner” category.

2.2.3.2 GDP per Capita Index

Annual historical GDP per capita indexes for Finland have been published by the Bank of Finland (Hjerppe 1989) and were included in the analysis. These data provide information about the general economic conditions of the country encompassing most of the study period.

2.2.3.3 Infant Mortality Rate

Historical annual data on Finnish infant mortality rates have been published by Statistics Finland (2015) and were included in analysis.

2.2.3.4 Spring Temperatures

Data on historical annual average reconstructed spring temperatures (February to June) in °C for southwest Finland were taken from Holopainen et al. (2009) and included in analysis. Although the temperature data are for a specific locality, southwest Finland, they are believed to be representative of broad weather patterns that affected the country, as comparisons made by Holopainen et al. (2009) show that the year-by-year spring weather in Southern Sweden and St. Petersburg followed very similar patterns.

2.2.3.5 Grain Figures

Data on yearly grain figures for Finland for rye, barley and oat were available for individuals in the collection born after 1860 (Holopainen & Helama 2009) and included in analysis. Grain figures for domestic wheat were not available for a large part of the study period and so were excluded from analysis. The grain figure is a measure of the yearly productivity of crops in a field, farm or an area whereby the yields of seeds is adjusted for the number sowed. In Finland grain figures were measured in barrels until the mid-1880s when the unit of measurement was changed to hectolitres. For the years 1876 and 1877 data were missing. A combined grain figure, whereby the grain figures of rye, barley and oat for Finland were added together was calculated for the birth year, the first two years of life (average) and for age 14. Amounts of grain imports from abroad were unknown, so could not be accounted for in the analysis.

2.2.4 East versus West Finland

As an attempt to take into account the possible influence of residence in East or West Finland on stature, individuals with a known place of residence were placed in either the “East” (N=28) or “West” (N=25) category following the linguistic boundary between Eastern and Western Finnish dialects (Paunonen 2007, Figure 2.1) that has been found to roughly track the genetic boundary between Eastern and southwestern Finns (Barbujani and Sokal 1990, Figure 2.2 after Salmela et al. 2008).

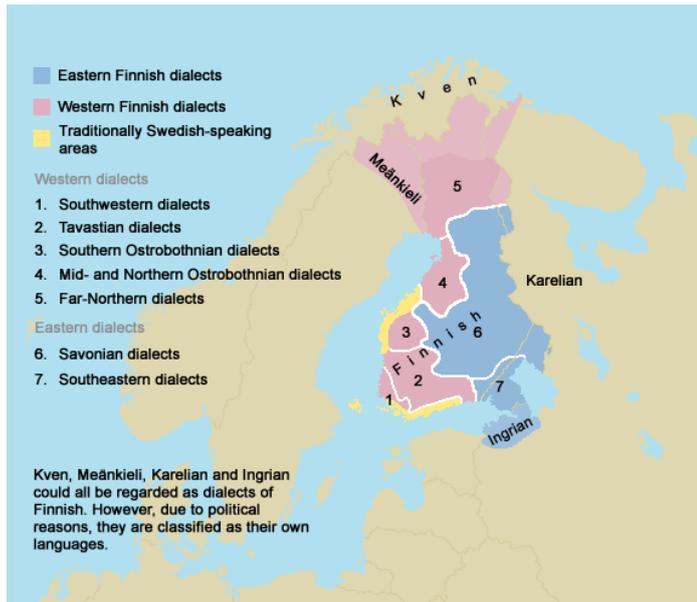


Figure 2.1 Geographical boundaries of Finnish dialects, after Mikkola et al. 2005.

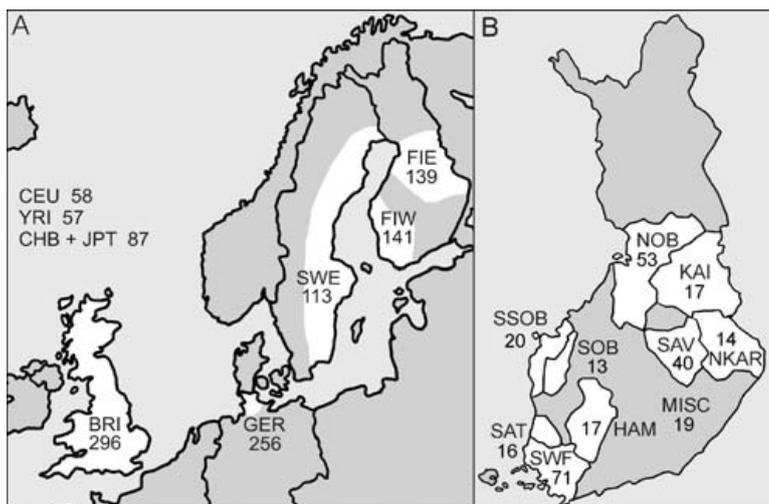


Figure 2.2 Map of the genetic division between Eastern and Western Finns, after Salmela et al. (2008)

2.2.5 Statistical Analysis

Statistical analyses were performed in SPSS 20. The relationships between recorded living stature and year of birth, the environmental variables and residence in East and West Finland were investigated. Variables were tested for normality using Shapiro-Wilk's tests. The relationships of stature and the first two years of life (average) grain figures and spring temperatures were similarly examined. Two-tailed

Pearson's correlations were used to test the significance and strength of the relationship of stature with year of birth and the environmental variables. The procedure was repeated for stature and the environmental variables at estimated year of adolescent growth spurt. An independent samples t-test was performed to test whether place of residence significantly influenced stature. A One-Way ANOVA was conducted to test for effect of prisoner status on stature as well as to investigate the relationship of the year of birth categories and stature. This relationship was further examined using a Bonferroni post hoc test. Temporal trends in the environmental variables were tested using two-tailed Pearson's correlations. Regression analyses were performed in a General Linear Model (GLM) to further inspect the effects of the environmental variables on recorded living stature. Due to the time series nature of the data set, year of birth was included in analyses as a way to de-trend the data (Cameron 2005). A cut off point of $p < 0.25$ (for the univariate relationships) was used to select variables further inspected in GLM. This course of action was taken because choosing only variables significant at the $p < 0.05$ level for multivariate analysis can lead to a failure to identify important factors (Bursac et al. 2008).

2.3 Results

2.3.1 East versus West Finland

There was no significant difference in mean recorded living stature between individuals from East and West Finland ($t_{(51)}=0.949$, $p=0.347$). The data were analysed further without consideration of place of residence. The mean stature of Western Finns was 172.8cm and the mean stature of Eastern Finns was 171.29cm.

2.3.2 Prisoner Status

There was no statistically significant difference in mean recorded stature between prisoners, non-prisoners and individuals of unknown occupation ($F_{(2)}=2.805$, $p=0.065$; Figure 2.3). The data were analysed further without consideration of prisoner status.

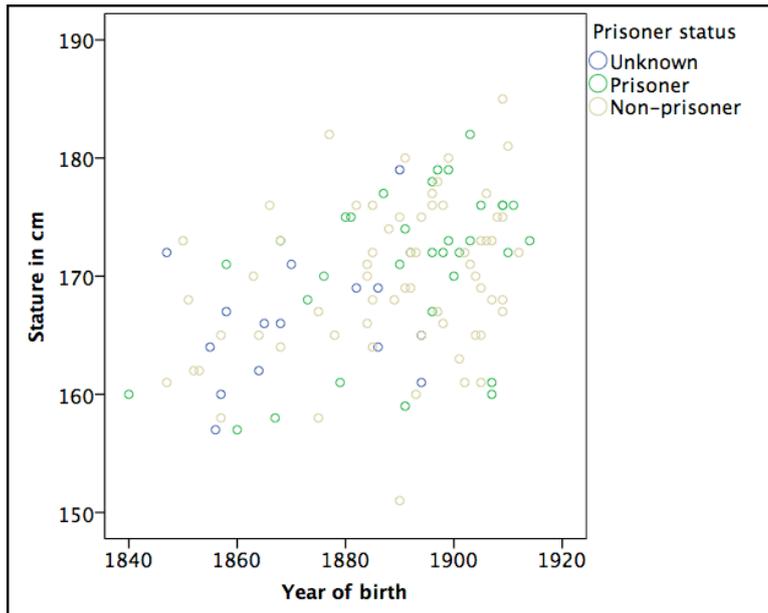


Figure 2.3 The relationship between stature and year of birth, with prisoner status indicated. Prisoners, as well as individuals without known prisoner status were represented across the time period. The figure also points towards an overall secular increase in stature.

2.3.3 Year of Birth

Individuals born later were significantly taller than individuals born earlier ($r=0.390$, $p<0.01$). Mean statures significantly differed between the year of birth categories ($F_{(2)}= 7.412$, $p<0.01$). A Bonferroni post hoc test confirmed that there was a significant increase in mean stature from the earliest year of birth category consisting of individuals born <1870 to the middle category, that is those born 1870-1900. Similarly individuals who were born 1870-1900 had a significantly lower mean stature than those born >1900 ($p<0.01$; Figure 2.4).

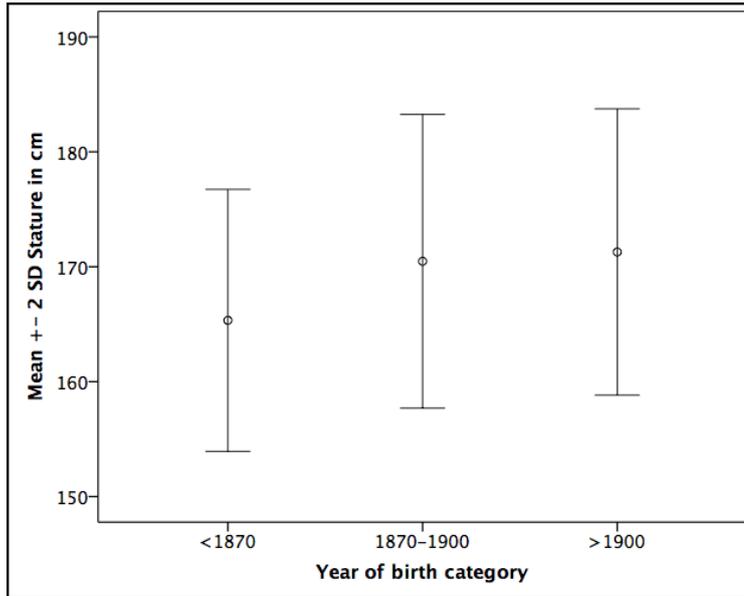


Figure 2.4 Mean statures in cm and standard deviations by year of birth category. Mean stature of individuals born <1870 = 165.33cm (N=24); 1870-1900 = 170.47cm (N=57); >1900 = 171.28cm (N=32).

There were significant correlations between recorded living stature and some of the environmental variables at year of birth and first two years of life (Table 2.3; Table 2.4). All environmental variables showed a significant temporal trend (Table 2.4). Regression analysis of the variables in GLM did not show significant effects on recorded living stature when year of birth was included in the model to de-trend the data (Table 2.5). Figure 2.5 illustrates the lack of relationship between stature and the environmental variables after de-trending, whereby stature was modelled against de-trended GDP per capita for birth year.

	Grain figure for rye, barley and oat for birth year	GDP per capita index for birth year	Infant mortality rate for birth year	Springtime temperatures (Feb-Jun) °C for birth year
Stature in cm	0.184 (N=96)	0.273* (N=99)	-0.182 (N=113)	0.224 (N=113)
Year of birth	0.472* (N=107)	0.966* (N=111)	-0.592* (N=126)	0.463* (N=126)

Table 2.3 Pearson's correlations of stature, year of birth and environmental variables at birth year. Bold type denotes statistical significance ($p < 0.05$; asterisk (*) denotes $p < 0.01$). Sample size is given in brackets.

	Grain figure for rye, barley and oat (first 2 years of life average)	Springtime temperatures (Feb-Jun) °C (first 2 years of life average)
Stature in cm	0.353 (N=94)	0.219 (N=113)
Year of birth	0.541* (N=105)	0.611* (N=126)

Table 2.4 Pearson's correlations of stature, year of birth and environmental variables in first two years of life. Bold type denotes statistical significance ($p < 0.05$; asterix (*) denotes $p < 0.01$). Sample size is given in brackets.

Variable	F	df	B	Sig.
GDP per capita index (birth year)	0.161	1	0.080	0.689
Infant mortality rate (birth year)	0.943	1	0.016	0.334
Spring temperature (birth year)	0.863	1	0.578	0.355
Spring temperature (first 2 years of life)	1.003	1	-1.037	0.319
Year of birth	0.399	1	0.188	0.529
R²: 0.092 (adjusted 0.044)				

Table 2.5 Results of GLM. Dependent variable recorded living stature (N=99). Year of birth is included in the model to de-trend the data.

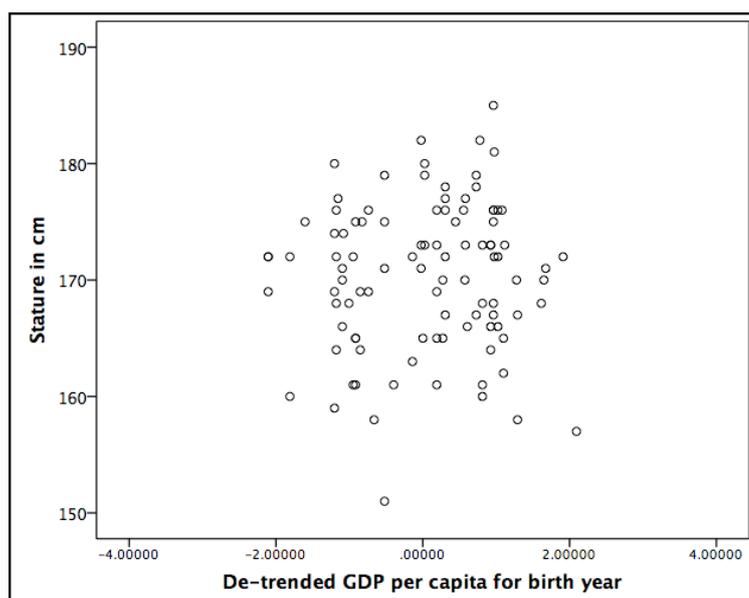


Figure 2.5 The relationship between recorded living stature in cm and de-trended GDP per capita for year of birth

2.3.4 Adolescence

There were significant correlations between recorded living stature and several of the environmental variables at estimated year of adolescence, that is, age 14 (Table 2.6). Regression analysis of the environmental variables in GLM did not show significant effects on recorded living stature when year of adolescence was included in the model to de-trend the data (Table 2.7).

	Grain figure for rye, barley and oat (14 years)	GDP per capita index (14 years)	Infant mortality rate (14 years)	Springtime temperatures (Feb-Jun) °C (14 years)
Stature in cm	0.051 (N=99)	0.398* (N=112)	-0.353* (N=113)	0.157 (N=113)
Year of adolescence (14 years)	0.290* (N=112)	0.896* (N=125)	-0.824* (N=126)	0.184 (N=126)

Table 2.6 Pearson's correlations of stature and environmental variables at estimated year of adolescence. Bold type denotes statistical significance ($p < 0.05$; asterix (*) denotes $p < 0.01$). Sample size is given in brackets.

Variable	F	df	B	Sig.
GDP per capita index (14 years)	2.012	1	0.131	0.159
Infant mortality rate (14 years)	0.005	1	-0.003	0.946
Spring temperature (14 years)	0.959	1	0.379	0.330
Year of adolescence	0.078	1	0.022	0.781
R²: 0.167 (adjusted 0.135)				

Table 2.7 Results of GLM. Dependent variable: recorded living stature in cm (N=112). Year of adolescence is included to de-trend the data.

2.4 Discussion

The results show a significant positive secular trend for stature, which is also reflected in the significant increases in mean statures between the year of birth categories. The GDP per capita index for birth year, the average spring temperature for birth year, and the average spring temperature for first two years of life show significant positive relationships with stature. At year of estimated adolescent growth spurt infant mortality rate and GDP per capita have significant relationships with recorded living stature. However, all these correlations appear to be driven by the underlying temporal trend. The significant increases through time in GDP per capita, average grain figure for Finland and average spring temperature, as well as the significant decrease through time in infant mortality rate, imply that the overall living environment in Finland improved, as has been argued by Finnish historians (Heikkinen 1986; Kannisto et al. 1999; Turpeinen 1986; Turpeinen 1991). A significant stature increase in the Finnish population has been reported by Silventoinen et al. (2000) for the 20th century, but the results of the current study imply that the trend predates their study and started in the first years of industrialization in mid- to late-19th century.

Owing to the historical nature of the data used in this study it is important to consider what each variable does and does not represent. The reconstructed annual spring temperature gives an indication of the climatic conditions in the country at the time and would have affected everything that was growing whereas the grain figure included those domestic crops for which data were available, that is rye, barley and oats. Wheat could not be included in the grain figure as data were missing for the earlier years. The lack of data may be due to the relative lack of importance of wheat in the Finnish economy in the early 19th century (Heikkinen 1986). After 1860, the proportion of both domestic and imported wheat grew and the share of traditional local crops decreased (Heikkinen 1986). Therefore, the variable used in this study did not capture an increasing part of grain available in Finland. Although still considered a reasonable measure of overall grain yields, error might have been introduced due to differences in local availability as well as preference. For example, barley and rye are more resistant to cold than wheat or oat and can be better cultivated in the colder regions of the country (Soveri et al. 1956). Therefore their relative importance might be higher. Controlling for this and similar factors was not

feasible with the data and sample size available. Surprisingly, both the temperature and the grain figures showed a significant, albeit relatively weak positive temporal trend (and are themselves correlated). This is interesting and could have helped boost the country's economy in addition to the social and political changes promoted by the government. Increases in the grain figures through time could also reflect technological advances in agricultural practice.

The results of the stature analysis seem unlikely to be caused by sample bias. This study controlled for factors that often leave considerable room for error in studies on skeletal collections, such as the sex and age of the study individuals. All individuals analyzed were adult males and had occupations that can be assumed to belong to a similar, relatively low, social class. Prisoners and labourers had very similar mean statures. Individuals with unknown prisoner status were not excluded from the analyses on stature, as although their social class cannot be inferred, their mean stature did not significantly differ from the rest. Importantly, they did not show higher statures to the rest of the sample, which might have indicated differential access to resources during growth and thus create bias in the data, especially if they were later born individuals. There are no signs based on the occupational data that the secular increase in height in this sample is caused by later born individuals having been born to families of higher social class. Prisoners were also represented throughout the study period. Instead, the living conditions of the lower social classes seem to have improved through this time period in Finland. This is supported by the work of Turpeinen (1991), who argued that after the Great Famine of 1866-68, the Finnish government introduced policies that improved the living conditions of especially the poorest in the population. Free elementary school was introduced in 1866 (Kurth 2005) alongside heavy investments in infrastructure (Turpeinen 1991). These included new road and rail networks, which enabled grain transport to more secluded municipalities in bad crop years (Turpeinen 1986). Before and during the famine, food aid was limited and relied mainly on Russia and a few other European countries. In the 1890s, a telegraph network was established which together with the improved transport links allowed grain imports from as far as America (Turpeinen 1991). The proportion of imported grain, mainly wheat, grew dramatically between 1860 and 1912 making the Finnish population less dependent on domestic crops and vulnerable to fluctuations in weather (Heikkinen 1986). Private consumption per capita showed great increases throughout the study period

(Heikkinen 1986). These can be taken as significant improvements in the country's living conditions and by increasing people's access to food, childhood growth environments likely improved as well. This fits well with the significant secular trend in stature presented here. After the famine, no large scale population crises occurred in the country until the Civil War of 1918 and then, World War II (Kannisto et al. 1999).

No significant differences in living stature were found between East and West Finland, which suggests that although the Western Finns in this population had a marginally higher average stature, place of residence did not introduce marked bias to this sample. The difference between Eastern and Western Finnish statures has been seen to result from different standards of living, whereby Eastern Finland is considered to be more deprived overall than the West (Forsén et al. 2000). This study did not aim to distinguish between a possible environmental or genetic difference in Eastern and Western Finnish statures. The fact that no significant difference was found here does not mean that geographical location did not introduce some geographic bias in to the data. The difference between East and West could only be tested using the subsample of individuals for whom place of residence was known. It is possible that the rest of the sample was biased in either direction or that there were more Western Finns amongst the later born individuals, which would could have resulted in the observed pattern of later born individuals being taller than earlier born individuals and thus reflect geographic rather than temporal differences. However this may be considered unlikely, because in the subsample the place of residence was known, the distribution of old and young individuals across localities appears random. Furthermore, it may be argued that there is no reason to believe based on the report on the skeletal collection by Söderholm (2003) that sampling procedures had a set geographical component or varied through time.

Per capita calorie consumption increased substantially between 1860 and 1912 in Finland (Heikkinen 1986) and this measure of the nutritional environment supports the findings of this study, as adult stature is influenced by childhood malnutrition, especially undernutrition (Victora et al. 2008). The measure of early life disease burden used in this study, infant mortality rate, showed a significant secular decrease. Although as with the other environmental variables, the relationship

between infant mortality rate and stature was explained by the overall secular trend, the results show that the disease environment in Finland improved over the study period. The nutritional and disease environment have a synergistic relationship with growth, and this study showed an improvement through time in both. GDP per capita index showed the strongest temporal trend out of all the environmental variables, which is large part explained by industrialization (Hjerppe 1989). Although no continuous data on literacy rate could be found, much can be said about the social and political environment of Finland in the 19th century, and as discussed in Chapter 1, major leaps were made in terms of population welfare and educational policy (Kurth 2005; Turpeinen 1991). Elementary schooling became more common throughout the end of the 19th and beginning of 20th century, based on historical data on both number of elementary schools in the country (Kurth 2005) as well as on increased literacy rate (Markussen 1990). This probably allowed better access to resources through access to better jobs and also benefitted the following generation as increases in social class are reflected in increased child stature (Delemarre-van de Waal 1993; Mascie-Taylor 1991; Peck and Lundberg 1995; Tanner 1981). The individuals born towards the end of the study period likely had parents who were born after the introduction of the elementary school and some of them might have thus benefitted from having literate and better-educated parents compared to the previous generations.

The relationship between recorded living stature and the environmental variables at adolescence showed very similar results to those at birth year, and similarly, once the data were de-trended, there were no significant relationships between the environmental variables and stature. Hence, no conclusions can be drawn here about the relative importance of these two developmental periods on growth in stature in terms of environmental effects. Factors such as intra-household food allocation or number of children in the family could have created unknown variation in statures in this sample. The substantial improvements in the living standards are a plausible explanation for the observed significant secular change in stature in this population. Still, it is important to keep in mind that zooming out to population level phenomena from the relatively small sample of individual level data inspected here means that caution must be exercised when speculating about causal relationships. This is often the case with archaeological and skeletal populations but it is argued here that a consideration of a broad range of factors in combination with studies

from other disciplines provides valuable descriptive data on the populations living environment at large, even if statistical value is limited.

Finally, to set the stature results of this study in broader context and to assess whether the statures of this rather small sample seem anomalous, the mean statures of each year of birth category are compared with Swedish male statures of 19th and early 20th century as reported by Sandberg et al. (1997). For the latest year of birth category the A-series statures are also compared with previously reported early 20th century Finnish male statures (Silventoinen et al. 2000). The mean height of the individuals in the A-series born before 1870 was 165.33 cm whilst in Sweden it was 169 cm in 1865 (Sandberg and Steckel 1997). In the year of birth category 1871-1900, the mean stature in the A-series was 170.47 cm, which is within two centimeters of Swedish statures in 1885 (171.5cm). The A-series individuals born after 1900 have a mean stature of 171.28 cm, which is again shorter than that of Swedes in 1910 (172.9 cm) but remarkably close to the mean stature of Finnish monozygotic male twins born between 1900-1928, whose mean stature is 171.3cm (Silventoinen et al. 2000). This indicates that at least for the two later year of birth categories the mean statures in the A-series do not seem abnormally high or low, which they might do if the sample was poorly representative. Instead, the mean statures in the A-series are close to the Swedish mean statures. In the last year of birth category the mean stature of the A-series individuals is nearly identical to that of the large sample of Finnish male twins investigated by Silventoinen et al. (2000). Overall, the comparisons show a pattern of shorter Finns compared to Swedes, which is supported by the literature on living conditions in these two countries in the 19th century. As noted in the chapter introduction, Sweden became very quickly one of the most developed countries in Europe at the end of the 19th century, whilst Finland remained in comparison a relatively poor agricultural society. Both countries saw an improvement of living conditions but in addition to starting worse off, development was less steady Finland (Hjerppe 1989). Therefore, it is unsurprising that Swedish statures started off higher and remained so in the late 19th and early 20th century. Also, it is important to keep in mind that there are genetic differences between the two populations and these might have some effect on mean statures. The statures of the earliest year of birth category are quite low in comparison to the Finns born later and the difference between the Finnish and Swedish statures is largest in this group. There are two possible explanations for this. First, it could be

that partly due to the relatively low sample size of this group, individual variation causes the low mean stature in the first category and the actual mean stature of Finnish males born within this period is higher than what is reported here. This would not alter the finding of a positive secular trend in height in 19th century Finland, as the increase in mean height was significant also between the two latest year of birth categories. Alternatively, if the living conditions in Finland before and during the famine were much worse in comparison to Sweden (and to the later periods in Finland), the mean height reported here for individuals born before and during the famine could be representative. The present study does not provide sufficient evidence to support either conclusion, but this could be an interesting area for further research, if more data on mid-19th century Finnish statures are found.

This chapter investigated the recorded living statures of A-series individuals and found a significant secular trend in height. This trend was discussed with reference to the changing living conditions of 19th century Finland, as well as in comparison to neighboring Sweden. It is concluded here that in terms of the first endochondral growth parameter examined in the present study, recorded living stature, the improving standards of living in the country are a possible explanation for the found trend. Whether this trend is also reflected in individual bone lengths and in cross-sectional geometric properties of long bones will be investigated in the following chapters.

3 Lower Limb: Femur and Tibia Length and CSG Properties

3.1 Introduction

This chapter aims to investigate whether there are secular trends in the length and cross-sectional geometric (CSG) properties (total cross-sectional area and twice average bending rigidity 'J' at midshaft) of the femur and tibia of adult male individuals in the A-series. Secular trends in bone lengths and CSG properties have not been previously examined in Finnish skeletal populations. A further aim of this chapter is to examine whether the study individuals' prisoner status, residency in East versus West Finland or death from tuberculosis (TB) has an association with the skeletal parameters. As in Chapter 2, the possible influences of environmental variables (GDP per capita index, infant mortality rate, annual average spring temperature and grain figures) are considered. The motives for examining the relationship of skeletal parameters and place of residence in East versus West Finland, prisoner status as well as the environmental variables were discussed in Chapter 2.

The bones of the human lower limb have important mechanical functions in terms of bearing the weight of the individual and facilitating walking and other physical activity. The lower limb long bones, like other skeletal elements, need to fulfill their mechanical purpose throughout development while their size increases (Rauch 2005). Endochondral growth in the femur and the tibia adds to stature, while appositional growth determines their strength and resistance to bending. The basic biological mechanisms of endochondral and appositional growth as well as the use of 'beam theory' to examine mechanical influences on bone were discussed in Chapter 1. In studies on archaeological populations the beam theory has been applied to infer different activity patterns within and between populations by comparing their CSG properties (Nikita et al. 2011; Shaw and Stock 2013; Stock and Pfeiffer 2001). Mobility and subsistence strategy of a group or subgroup are

often used to explain observed differences (Sparacello and Marchi 2008; Stock 2006; Ruff et al. 2006). For instance, a pastoral subsistence strategy in combination with a rugged terrain is thought to explain the robust lower limbs of a Neolithic Italian sample (Marchi 2008) whilst transition to agriculture is associated with lesser bone strength and robusticity in European populations, probably due to reduced activity (Macintosh et al. 2014). Within populations, CSG properties have been examined, for instance, with reference to sexual dimorphism, and observed differences are potentially linked to different activity patterns between males and females in past societies (Nikita et al. 2011; Pomeroy and Zakrzewski 2009; Weiss 2003). Despite the interesting findings related to mobility patterns and subsistence strategies, a challenge for many of the studies is a lack of information about the populations' nutrition and disease environment during growth (Jurmain 1999). Thus, a recent examination of bone structural properties with reference to tuberculosis, a disease that has affected human populations for millennia (Sparacello et al. 2015) is a welcome addition to the discussion. The study, as mentioned in Chapter 1, found evidence that individuals whose skeletons showed signs of TB were more gracile than those whose did not (Sparacello et al. 2015). This finding is relevant for the present study, as some individuals in the A-series died of TB. Therefore, the possible relationship between tuberculosis and CSG properties will be tested in the present study before the data are analyzed further.

Studies on secular trends in bone cross-sectional geometry are scarce and thus far temporal trends in CSG properties have been mainly investigated between populations and over extended time periods of thousands or even millions of years (Macintosh et al. 2014; Ruff et al. 1993; Ruff 2006; Ruff et al. 2015; Ryan and Shaw 2015). Still, some evidence of within population changes in bone strength over smaller time frames can be found – for instance, in the American southwest a decrease in total cross-sectional area at midshaft and resistance to bending between the 12th and the 13th and late 14th century has been reported (Brock and Ruff 1988). A possible explanation for the trend comes from the archaeological record, which indicates that the native American population had a more sedentary lifestyle in late 14th century in comparison to the 12th and 13th centuries, which were characterized by difficult living conditions (Brock and Ruff 1988). Another archaeological study found that the femora of 15th century Swedish females were thicker (as well as had higher bone density) than those of a late 20th century

comparative sample, possibly due to lesser physical activity during growth in the modern sample (Ekenman et al. 1995). In England the rate of bone loss in both pre- and postmenopausal women was lower in 18th and 19th century compared to a modern sample, which similarly to the results of the Swedish study could be due to differences in female physical activity patterns between the examined time periods (Lees et al. 1993). These two findings are interesting in terms of the present study, as they imply that activity related differences might cause negative secular trends in skeletal parameters that are influenced by mechanical loading, despite the likely better nutrition available during growth in the late 20th century. As discussed in Chapter 1, available nutrition does not control bone's response to activity, it merely enables or limits it (Skerry 2006), thus inactivity in better nutritional environments might result in weaker bones in comparison to higher physical activity combined with poorer nutrition, as long as the nutritional constraints are not so severe they prevent appositional bone growth. In the light of the studies discussed above, and similarly to recorded living stature, a direction will not be specified for any secular trend in CSG properties in the present study. It is possible that there is a positive secular trend in bone cross-sectional area and resistance to bending in the A-series due to the improvements in the overall living conditions in Finland. On the other hand, the above studies imply that modern, relatively sedentary lifestyles result in negative trends in activity related skeletal parameters (Ekenman et al. 1995; Lees et al. 1993). Although the present study population can by no means be considered modern, the physical activity levels of Finnish boys might have decreased in the late 19th and early 20th century, for instance due to the larger percentage of the population attending school. This could lead to adults with less robust bones; as discussed in Chapter 1, the physical activity ratios of activities children take part in school are much lower than activities 19th century children might have otherwise been occupied with, such as farm work (James and Schofield 1990). Further, a study has found that school children taking part in a sports initiative had increased bone strength compared to controls whose school days remained 'normal' (Macdonald et al. 2007), indicating that even moderate changes in the amount of physical activity children take part in can lead to differences in CSG properties.

In the present study, the cross-sectional geometric properties will focus on total cross-sectional area in mm² (TA) and the twice average bending rigidity in mm⁴ (J), which gives an indication of the total resistance to bending at a bone location (Ruff

2008). These two variables are well suited for the present study because they measure overall size and resistance to bending. This study does not aim to separate between different activity patterns and therefore variables, which give an indication of the direction of mechanical force inflicted on bone, are not included. Both TA and J are influenced by the size and shape of the individual and need to be body size standardized (Ruff 2000). Ideally, both body mass and bone length need to be considered, as individuals with the same body mass can have very different body shapes (Ruff 2000). Thus, in the lower limb sample of the present study the body mass of each individual will be estimated to allow for adequate size standardization of the CSG properties (see Methods for procedure).

The Introduction to this chapter has thus far concentrated on CSG properties; however, there are factors to consider in relation to the endochondral growth parameters investigated here, that is, the maximum bone lengths of both femur and tibia. Certain skeletal proportions, such as tibia length, lower limb length or the cormic index (lower limb length to height ratio), have been argued to be particularly sensitive to environmental influences during growth (Bogin et al. 2007; Pomeroy et al. 2012; Sohn 2015). However, others have found this not to be the case; in Mozambique relative leg length was not sensitive enough to distinguish between two living environments (slum and town center) although there was a significant difference in stature (Padez et al. 2009). Interestingly, the discrepancy in results between studies might be due to differences in the overall level of economic development in particular populations, whereby in more developed countries, environment has a more pronounced effect on leg length than on stature, whilst in less developed countries, stature is a better measure of the growth environment (Sohn 2015). The results of the above studies are somewhat conflicting and there is no agreement about which is the best endochondral parameter to investigate environmental conditions. Therefore, the present study examines multiple endochondral growth parameters, which in this chapter include both femur and tibia length. These results will be contrasted with the results on recorded living stature in the chapter Discussion.

3.2 Methods

3.2.1 Study Sample

All adult male individuals from the A-series with complete femora (N=66) and tibiae (N=64) and a recorded year of birth were selected for analysis. For most individuals, the bone from the left side of the body was chosen, however, in the few cases it was not present (N=4 femora, N=3 tibiae), the right side was analysed instead. See 2.2.1 for the procedure by which maturity and sex were assessed. Any bones showing signs of healed fractures or other clear deformations were excluded from analysis. The lower limb sample equals roughly half of the individuals that made up the stature sample (2.2.2). The remaining individuals from the stature sample had only the upper limbs present, examined in Chapter 4.

3.2.2 Data Collection Procedure

3.2.2.1 Bone Measurements

The maximum lengths of femora and tibiae were measured manually using an osteometric board following the standard measuring procedure as defined by White et al. (2011). Femoral head diameter measurements were taken using a Sylvac sliding caliper following the guidelines given in Ruff and Scott (1991).

3.2.2.2 3D Scanning

3D scanning of the sample took place at the Finnish Museum of Natural History between July and September 2014, and December 2014 – February 2015. A Desktop Next Engine 3D laser scanner was used. Two full 360-degree scans with the High Definition (HD) setting were taken of each femur to capture the entire length of the bone. Additionally, three to four HD single scans were taken to ensure that the epiphyses were recorded, as the program later used to analyse the scans can automatically calculate bone length if the model is complete. Due to the smaller

size of the tibia, one 360-degree HD scan per bone was sufficient. Further HD single scans were taken to capture the shape and size of the epiphyses of the tibiae.

The scans were processed in Scan Studio, a computer program designed for the Next Engine. The trim feature was used to clear the scans of any excess material, such as images of the metal stand used to hold the bone in place during scanning. After trimming, the 360-degree scans were aligned with the single scans. This process involves manually identifying at least three matching features on the two scans, which the program then uses to attach the scans together. Alignments were accurate to within a margin of 0.25 mm. Following alignment the scans were volume merged. This eliminates overlap from multiple scans and creates a single mesh. After, the fuse feature was used to create a watertight model. Some bones had a black marking along the diaphysis with the bone's identification number, which the scanner read as surface variation. These minor rises were smoothed with the buff function in Scan Studio. Finally, each scan was orientated using the CAD feature following the guidelines given in Ruff (2002), whereby the bone was set to face the screen in upright posterior view. The models were saved in the .xyz format.

3.2.2.3 Attainment of CSG Properties

The models were analysed using a specialist computer program called AsciiSection (instructions for acquiring this program are available at <http://www.pave.bioanth.cam.ac.uk/software.html>) following the method by Davies et al. (2012). The program calculated five cross-sectional properties at 50% of bone length: total area (TA), I_{max}, I_{min}, I_x and I_y bending rigidities. Within AsciiSection, a command line program called *gnuplot* created black and white images of each cross-section (Figure 3.1).

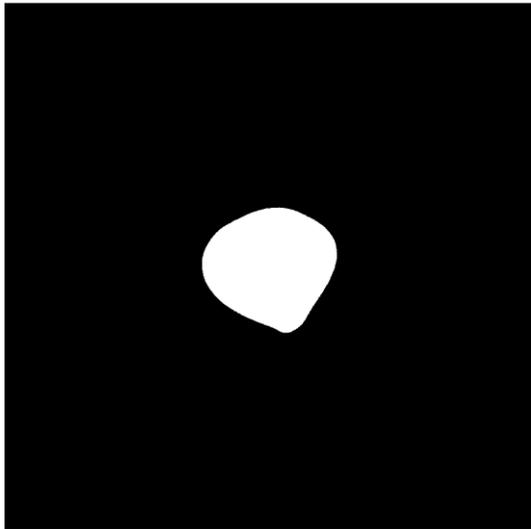


Figure 3.1 An example image of a cross-section at femur midshaft from AsciiSection

3.2.2.4 Size Standardisation of CSG Properties

Bone total cross-sectional area and the twice average bending rigidity at midshaft were size standardised. Table 3.1 shows each variable together with the size standardisation method used. Due to the very partial nature of the skeletons in the collection, body mass (BM) could not be estimated using the method preferred in the literature, that is, a regression formula using stature and bi-iliac breath (Ruff et al. 2005). Instead, body mass was estimated using the femoral head (FH) diameter measurements and the formula by Grine et al. (1995). This formula was chosen because it was assumed to be particularly suited for estimating the BM of Finns, as they are considered a large bodied population (see 1.1.6; Auerbach and Ruff 2004; Ruff et al. 2005). Overall, this method has been shown to correlate reasonably well with real body mass and produce results comparable to the bi-iliac method (Auerbach and Ruff 2004).

Property	Unit	Description	Size Standardisation
Total area (TA) 50	mm ²	Total area at midshaft	TA / BM x 100 (Sparacello and Marchi 2008)
J (= I_{max} + I_{min})	mm ⁴	(Twice) average bending rigidity at midshaft	J ^{0.73} / BM x bone length (Stock 2006)

Table 3.1 Cross-sectional properties measured and size standardisation method used

3.2.3 Sensitivity Analysis

The procedure by which the models were orientated prior to running them in AsciiSection is very subjective, even following the guidelines given in Ruff (2002). Therefore a sensitivity analysis was conducted with a subsample of 10 femur scans. The orientation of each bone was altered slightly on two axes and the new models were saved. The total cross-sectional areas in mm² at midshaft (TA) of these altered models were then compared with the originals. To assess the reliability of the orientation, both the technical error of measurement and the coefficient of reliability were calculated following Lewis (1999), whereby the variance in the TA introduced by the researcher was compared to the variance that already exists (standard deviation). The results gave a reliability coefficient of 0.97 for this sample, which means an error of less than 5% and was thus concluded to be acceptable.

3.2.4 Suitability of the Davies et al. (2012) Method

To assess the suitability of the Davies et al. (2012) method for calculating cross sections in the present study, a comparison was made after the first stage of data collection between a subsample of the femoral and tibial cross-sectional data acquired using the Next Engine, and data previously collected by the author for an undergraduate dissertation.

In the undergraduate project, which also functioned as a pilot for this Master's, cross-sectional area was calculated using two manual measurements taken with a Sylvac sliding caliper (anterior-posterior (a-p) and medial-lateral (m-l) diameters at midshaft). The cross-sectional areas were imagined as ellipses (Demes et al. 1991) whereby the area in mm² equals $\pi \times a \times b$ (with a and b being half of the measured a-p and m-l diameters in mm). This method is much faster in comparison to 3D scanning, however, it was also assumed to be less precise at capturing shape variation at midshaft as real bones rarely match precise mathematical forms such as ellipses. This assumption was supported by a comparison of the total areas

calculated using the two methods as independent samples t-tests showed significant differences in mean total area both at femur ($t_{(34)}=3.471$, $p<0.01$) and tibia midshaft ($t_{(32)}=5.068$, $p<0.01$). For both the femora and the tibiae, all areas were estimated to be larger by the pilot method. The difference in measured area was relatively consistent in the femora sample ranging from 30 to 108 mm². In the tibiae, there was more variation in the difference in total area measured with a range of 46 to 242 mm². This is to be expected as the tibia cross-sectional shape at midshaft deviates more strongly than the femur from the elliptical form assumed by the pilot study method. In the light of these results, it was concluded that using the more precise 3D scanning method to estimate total area is preferable.

3.2.5 Environmental Data

The environmental variables inspected were the same as with recorded living stature and described in detail in 2.2.2.

3.2.5.1 Cause of Death (Tuberculosis)

Following the recent study by Sparacello et al. (2015), individuals in the collection whose cause of death had been determined as tuberculosis (14 femora, 13 tibiae) by the medical examiner needed to be investigated for possible effects of the disease on cross-sectional geometry. Therefore, an additional variable was created whereby cause of death from TB was either coded as 'Yes' or 'No' (52 femora, 51 tibiae).

3.2.5.2 Prisoner Status

For the analyses of the lower limb, the prisoner status was categorised as with stature (see 2.2.2.1). There were 21 prisoners, 9 individuals without known prisoner status and 36 non-prisoners in the femora sample (34 in the tibia sample). Due to the small sample size of the "Unknown" prisoner status category these individuals were not analysed separately, instead being excluded from the analysis of prisoner status on bone length and cross-sectional properties.

3.2.6 East versus West Finland

The possible effect of place of residence was investigated as with recorded living stature and described in detail in 2.2.3.

3.2.7 Statistical Analysis

To assess the possible influences of tuberculosis as cause of death, residence in East or West Finland as well as prisoner status on bone length and cross-sectional properties, independent samples T-tests were performed. The relationships between the environmental variables and the three outcome variables (measured bone maximum length, TA and J at midshaft) for both the femora and the tibiae were examined. Variables were tested for normality using Shapiro-Wilk's tests. Two-tailed Pearson's correlations were used to test the significance and strength of these relationships. Regression analyses were performed in a General Linear Model (GLM) to further inspect the effects of the environmental variables on the outcome variables. Due to the time series nature of the data set, year of birth was included in analyses as a way to de-trend the data (Cameron 2005). Similarly to Chapter 2, a cut-off point of $p < 0.25$ (for univariate analyses) was used to select variables that were further examined in GLM.

3.3 Results

3.3.1 Cause of Death Tuberculosis (TB)

Individuals who died of TB had smaller total cross-sectional areas (TA) and lower bending rigidity (J) at femur and tibia midshaft compared to individuals who did not (Table 3.2). Figure 3.2 and Figure 3.3 show graphs of the mean TAs for both groups. Due to the significant differences in mean TA and J between individuals who died of TB and those who did not, the individuals with cause of death TB were excluded from all further analyses on cross-sectional outcome variables.

Variable	T	df	Sig.
TA femur midshaft	-2.195	64	<0.05
J femur midshaft	-2.179	64	<0.05
TA tibia midshaft	-1.626	62	0.109
J tibia midshaft	-1.140	62	0.259

Table 3.2 Results of Independent Samples T-tests of cross-sectional properties (TA, J) between cause of death (TB) categories “Yes” N=14 femora, N=13 tibiae and “No” N=52 femora, N=51 tibiae. Bolding denotes statistical significance (p<0.05).

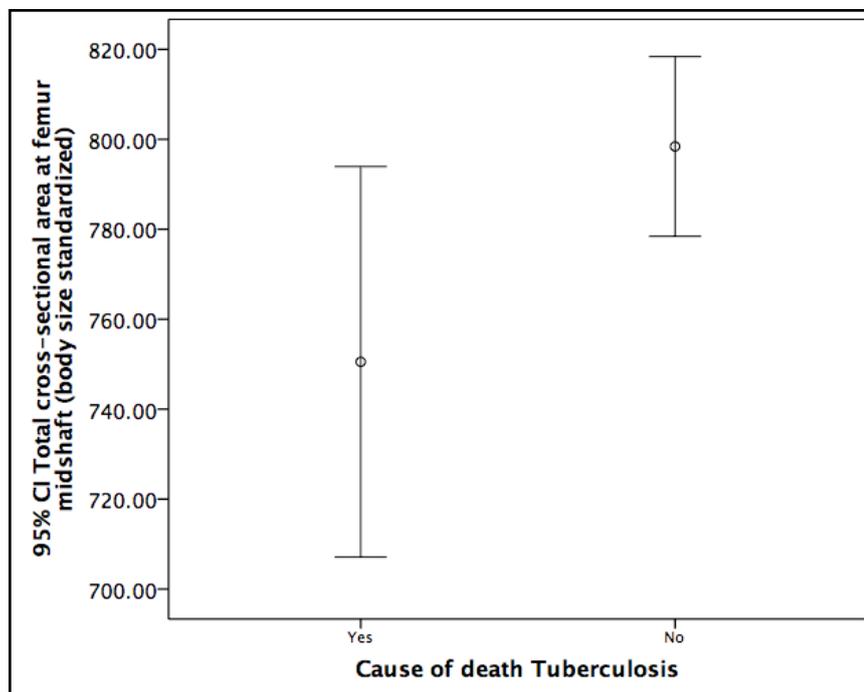


Figure 3.2 Cause of death (TB) and mean TA at femur midshaft with 95% confidence intervals, “Yes” N=14, “No” N=52

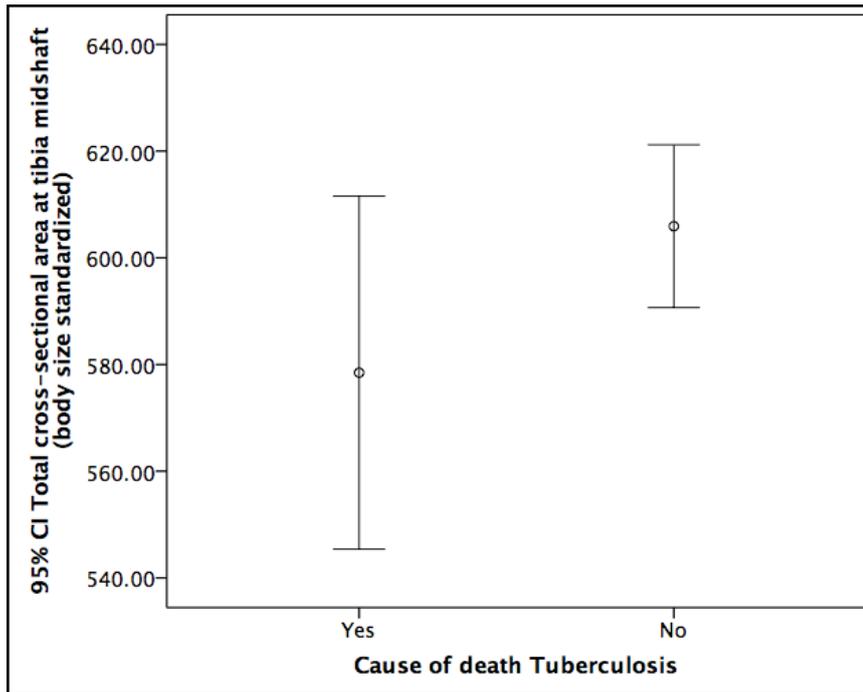


Figure 3.3 Cause of death (TB) and mean TA at tibia midshaft with 95% confidence intervals, “Yes” N=13, “No” N=51

For comparison, the relationship of TB with endochondral growth parameters, that is, femur and tibia maximum length was also examined. No significant differences were present between mean maximum length of either the femur or the tibia in individuals who died of TB and those who did not (Table 3.3). Individuals with cause of death TB were not excluded from analyses on bone length.

Variable	T	df	Sig.
Femur max length in mm	0.431	64	0.668
Tibia max length in mm	-0.999	62	0.322

Table 3.3 Results of Independent Samples T-tests between Cause of death TB categories “Yes” N=14 femora, N=13 tibiae and “No” N=52 femora, N=51 tibiae and bone maximum length

3.3.2 East versus West Finland

There were no significant differences in mean maximum lengths of femora and tibiae, or cross-sectional properties at femur or tibia midshaft between individuals

from East and West Finland (Table 3.4). For the TA and J at tibia midshaft the p-value was less than 0.25 and would have thus warranted further inspection in GLM; however the sample size (N=24) did not allow this. The data were analysed further without consideration of place of residence.

Variable	T	df	Sig.
TA femur midshaft	0.232	22	0.819
J femur midshaft	0.129	22	0.898
TA tibia midshaft	2.042	22	0.053
J tibia midshaft	1.429	22	0.167
Femur maximum length (N=13 West, N=16 East)	-0.260	27	0.797
Tibia maximum length (N=13 West, N=16 East)	0.222	27	0.826

Table 3.4 Results of Independent Samples T-tests between cross-sectional properties, bone length of the femur and tibia and place of residence. East Finland N=11 and West Finland N=13, TB individuals were excluded from CSG analyses.

3.3.3 Prisoner Status

Independent samples t-tests showed no significant difference in the mean bone length of femur and tibia or mean total cross-sectional area or J at femur or tibia midshaft between prisoners and non-prisoners (Table 3.5). The data were analysed further without excluding any individuals based on prisoner status.

Variable	T	df	Sig.
Femur max length	1.224	55	0.225
Tibia max length	0.163	53	0.871
TA Femur midshaft	0.786	42	0.436
J Femur midshaft	0.210	42	0.835
TA Tibia midshaft	0.404	41	0.688
J Tibia midshaft	-0.205	41	0.839

Table 3.5 Results of Independent Samples T-tests of bone length (femur, tibia), cross-sectional properties (TA, J) between prisoners and non-prisoners.

3.3.4 Femur

3.3.4.1 Bone Length Femur

Individuals born later had significantly longer femora than individuals born earlier (Pearson's $r=0.364$, $p<0.01$) and there was a significant correlation between femur maximum length (FML) and springtime temperature at year of birth (Table 3.6, Figure 3.4). The p -value was below the $p<0.25$ threshold for GDP per capita index, infant mortality rate and average spring temperature for first two years of life. These variables were chosen for further analysis in GLM. Regression analysis of the variables for year of birth in GLM did not show significant effects (Table 3.8) on FML.

There were significant correlations between FML and environmental variables at adolescence (Table 3.6). Regression analysis of the environmental variables for the year of adolescent growth spurt in GLM did not show significant effects (Table 3.9) on femur maximum length.

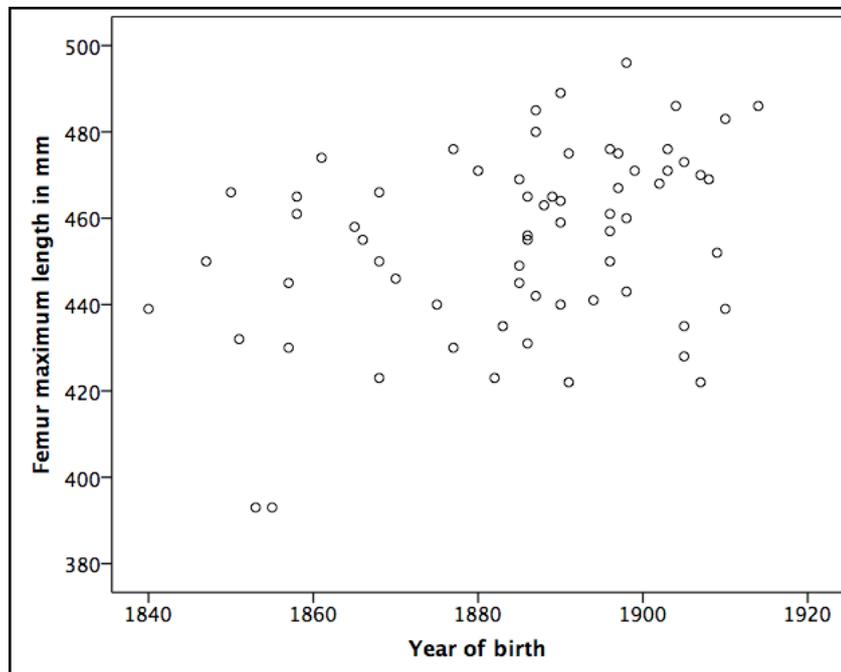


Figure 3.4 Year of birth and femur maximum length in mm (N=66, $r^2=0.133$)

	Grain figure for rye, barley and oat for birth year	GDP per capita index for birth year	Infant mortality rate for birth year	Springtime temperature (Feb-Jun) °C for birth year	Average grain figure for rye, barley and oat for first two years of life	Average springtime temperature (Feb-Jun) °C for first two years of life	Grain figure for rye, barley and oat (at 14 years)	GDP per capita index (at 14 years)	Infant mortality rate (at 14 years)	Springtime temperatures (Feb-Jun) °C (at 14 years)
Femur length	0.043 (N=54)	0.199 (N=56)	-0.228 (N=66)	0.298 (N=66)	-0.046 (N=53)	0.180 (N=66)	0.095 (N=60)	-0.354* (N=65)	-0.385* (N=66)	0.152 (N=66)

Table 3.6 Pearson's correlations of FML and environmental variables at birth year/first two years of life/at adolescence. Bold type denotes statistical significance ($p < 0.05$; asterix (*) denotes $p < 0.01$). Sample size is given in brackets.

	Grain figure for rye, barley and oat for birth year	GDP per capita index for birth year	Infant mortality rate for birth year	Springtime temperature (Feb-Jun) °C for birth year	Average springtime temperatures (Feb-Jun) °C for first two years of life	Grain figure for rye, barley and oat (at 14 years)	GDP per capita index (at 14 years)	Infant mortality rate (at 14 years)
Femur TA at midshaft	0.256 (N=41)	-0.119 (N=43)	-0.059 (N=52)	-0.039 (N=52)	-0.029 (N=52)	-0.045 (N=48)	-0.049 (N=51)	0.148 (N=52)

Table 3.7 Pearson's correlations of TA at femur midshaft and environmental variables at birth year/first two years of life/at adolescence. Bold type denotes statistical significance ($p < 0.05$; asterix (*) denotes $p < 0.01$). Sample size is given in brackets.

Variable	F	df	B	Sig.
Spring temperature (birth year)	0.798	1	2.359	0.376
Spring temperature (first two years)	0.747	1	-3.563	0.392
GDP per capita (birth year)	0.251	1	0.483	0.629
Infant mortality rate (birth year)	0.319	1	-0.034	0.575
Year of birth	0.043	1	-0.197	0.837

R²: 0.072 (adjusted -0.021)

Table 3.8 Results of GLM. Dependent variable femur maximum length, N=66.

Variable	F	df	B	Sig.
Infant mortality rate (14 years)	1.273	1	-0.213	0.264
Spring temperature (14 years)	0.267	1	0.976	0.607
GDP per capita index (14 years)	0.031	1	0.072	0.861
Year of adolescence	0.113	1	0.117	0.738

R²: 0.155 (adjusted 0.099)

Table 3.9 Results of GLM. Dependent variable femur maximum length, N=66.

3.3.4.2 Total Area Femur

There was no significant relationship between body size standardized TA at femur midshaft and year of birth (Pearson's $r=-0.134$, $p=0.34$; Figure 3.5). The p-values for the relationships between the average grain figure for rye, barley and oat in Finland for first year of life as well as for first two years of life and TA at femur midshaft were below the $p<0.25$ threshold (Table 3.7). Due to the limited sample size only one of these variables was investigated further in GLM – the first two years of life average was chosen as it had a higher correlation and a much lower p-value with body size standardized TA at femur midshaft (Pearson's $r=0.283$, $p=0.076$). Due to a significant temporal trend in the grain figure year of birth was included in the model to de-trend the data. The relationship between average grain figure for first two

years of life and TA at femur midshaft was significant after de-trending (Figure 3.6; Table 3.10).

To further investigate the relationship between femur TA and the grain figure in early life, first two year of life averages were calculated for each crop. TA and the three new variables (an average of rye in first two years of life, an average of barley in first two years of life and an average of oat in first two years of life) were examined in GLM. Again, year of birth was included to de-trend the grain figures. Model reduction was based on predictor specific p-values whereby non-significant predictors were left out of the model one by one, starting with the least significant. A Likelihood Ratio Test was not used, as no full model included multiple significant predictors. The final model showed a significant relationship between TA at femur midshaft and the average grain figure for oat in the first two years of life (Table 3.11). There were no notable ($p < 0.25$) relationships between TA at femur midshaft and the other environmental variables at year of birth (Table 3.7).

For year of adolescence the average spring temperature had a $p < 0.25$ relationship with body size standardized TA at femur midshaft (Pearson's $r = 0.243$, $p < 0.083$). This relationship was further examined in GLM however, it was not significant after year of adolescence was included in the model to de-trend the data (Table 3.12). Other environmental variables showed no notable ($p < 0.25$) relationships with body size standardized TA at femur midshaft (Table 3.7).

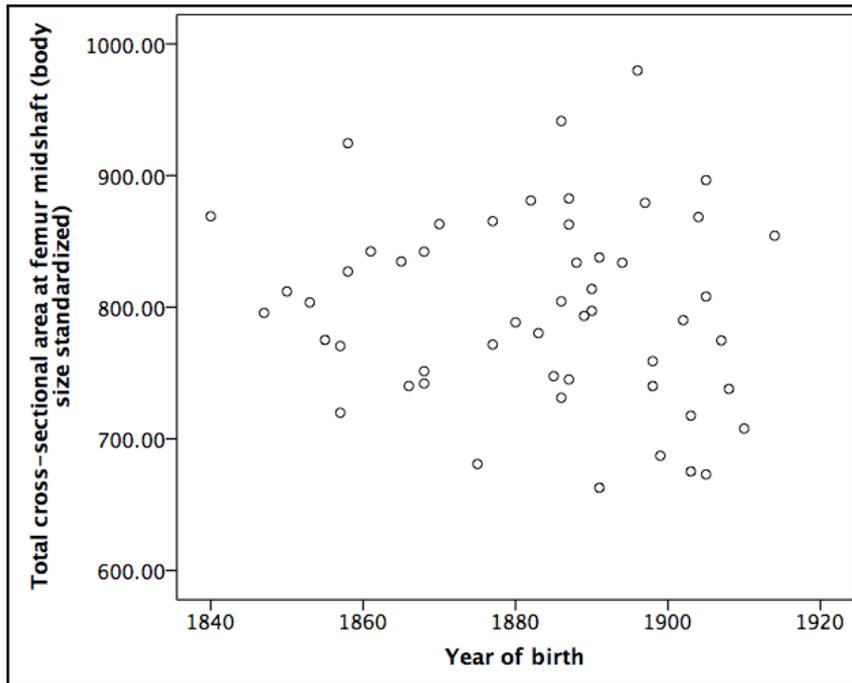


Figure 3.5 Body size standardized TA at femur midshaft and year of birth (N=52)

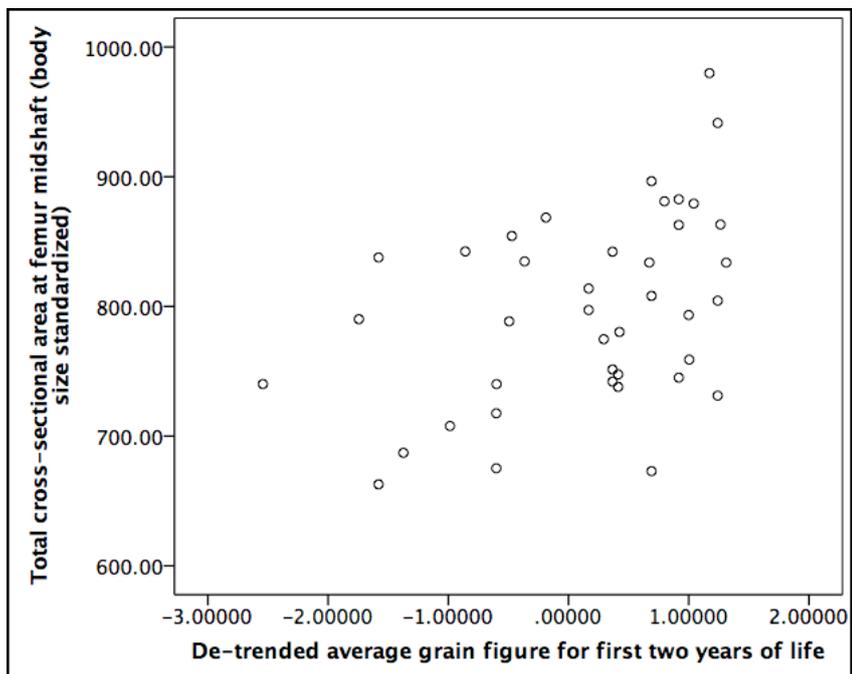


Figure 3.6 De-trended average grain figure for first two years of life and body size standardized TA at femur midshaft (N=40)

Variable	F	df	B	Sig.
Average grain figure rye, barley, oat (first two years of life)	8.223	1	22.829	<0.01
Year of birth	5.456	1	-2.167	<0.05

R²: 0.198 (adjusted 0.115)

Table 3.10 Results of GLM. Dependent variable: body size standardised TA at femur midshaft (N=40). Year of birth is included in the model to de-trend the data. Bold type denotes statistical significance.

Variable	F	df	B	Sig.
Average grain figure for oat (first two years of life)	9.136	1	78.587	<0.01
Year of birth	5.507	1	-2.108	<0.05

R²: 0.214 (adjusted 0.172)

Table 3.11 Results of GLM. Dependent variable: body size standardised TA at femur midshaft (N=40). Year of birth is included in the model to de-trend the data. Bold type denotes statistical significance.

Variable	F	df	B	Sig.
Springtime temperature (Feb-Jun) in °C (14 years)	3.949	1	15.063	0.053
Year of adolescence	1.732	1	-0.693	0.194

R²: 0.091 (adjusted 0.54)

Table 3.12 Results of GLM. Dependent variable: body size standardised TA at femur midshaft (N=52). Year of adolescence is included in the model to de-trend the data. Bold type denotes statistical significance.

3.3.4.3 J Femur

There was no significant relationship between body size standardized twice average bending rigidity (J) at femur midshaft and year of birth (Pearson's $r=-0.241$, $p=0.085$; Figure 3.7). There was a $p<0.25$ relationship between average grain figure for rye, barley and oat in Finland for first two years of life and J at femur midshaft (Pearson's $r=0.235$, $p=0.145$). The relationship was examined in GLM and it was significant after de-trending (Table 3.13). It was investigated further as with TA at femur midshaft. The results of the final model are presented in Table 3.14 and show that similarly to TA, the grain figure for oats had the strongest relationship with J. Other environmental variables showed no significant or $p<0.25$ relationships with J at birth year or in the first two years of life (Table 3.15).

For year of adolescence infant mortality rate had a $p<0.25$ relationship with body size standardized J at femur midshaft (Pearson's $r=0.235$, $p<0.093$). This relationship was further examined in GLM however, it was not significant after year of adolescence was included in the model to de-trend the data (Table 3.16). Other environmental variables showed no notable ($p<0.25$) relationships with body size standardized TA at femur midshaft (Table 3.15).

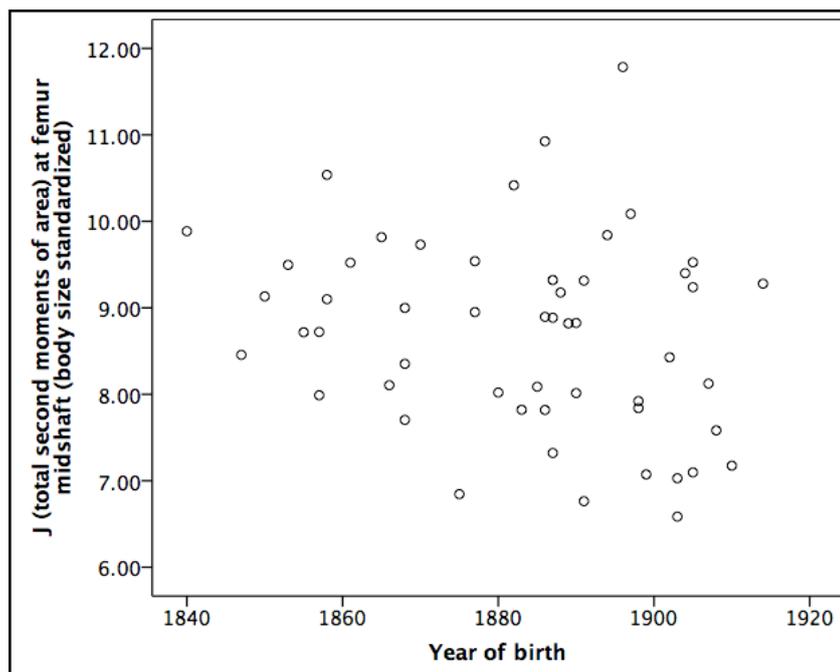


Figure 3.7 Body size standardized J at femur midshaft and year of birth (N=52)

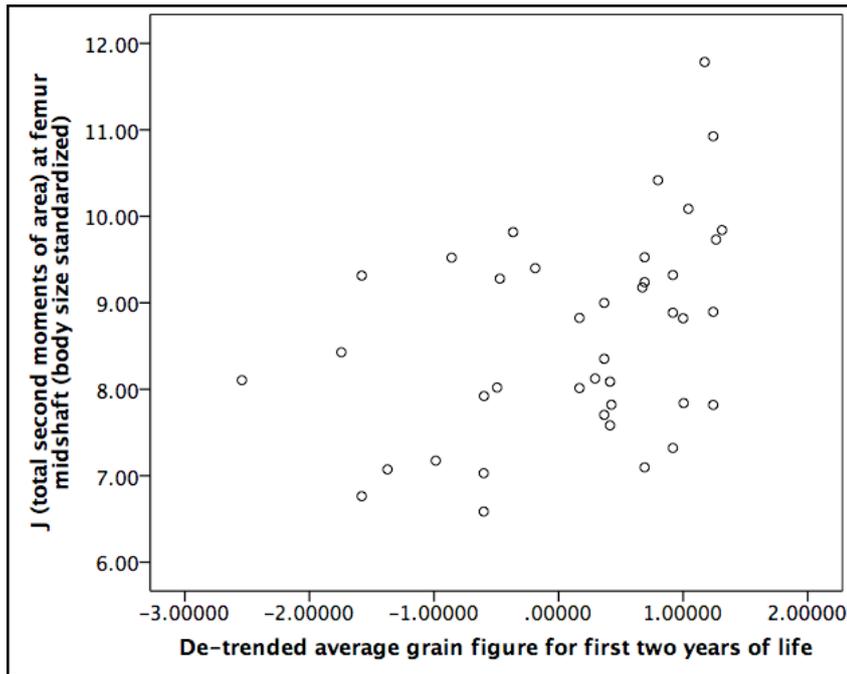


Figure 3.8 De-trended average grain figure for first two years of life and body size standardized J at femur midshaft (N=40)

Variable	F	df	B	Sig.
Average grain figure rye, barley, oat (first two years of life)	7.435	1	0.345	<0.05
Year of birth	6.736	1	-0.038	<0.01

R²: 0.201 (adjusted 0.157)

Table 3.13 Results of GLM. Dependant variable: body size standardised J at femur midshaft (N=40). Bold type denotes statistical significance.

Variable	F	df	B	Sig.
Average grain for oat (first two years of life)	9.799	1	1.271	<0.01
Year of birth	7.641	1	-0.039	<0.01

R²: 0.241 (adjusted 0.200)

Table 3.14 Results of GLM. Dependant variable: body size standardised J at femur midshaft (N=40). Bold type denotes statistical significance.

	Grain figure for rye, barley and oat for birth year	GDP per capita index for birth year	Infant mortality rate for birth year	Springtime temperatures (Feb-Jun) °C for birth year	Average springtime temperatures (Feb-Jun) °C for first two years of life	Grain figure for rye, barley and oat (at 14 years)	GDP per capita index (at 14 years)	Springtime temperatures (Feb-Jun) °C (at 14 years)
Femur J at midshaft	0.185 (N=41)	-0.173 (N=43)	0.004 (N=52)	-0.128 (N=52)	-0.042 (N=52)	-0.114 (N=48)	-0.139 (N=51)	0.154 (N=52)

Table 3.15 Pearson's correlations of J at femur midshaft and environmental variables at birth year/first two years of life/at adolescence. Sample size is given in brackets.

Variable	F	df	B	Sig.
Infant mortality rate (14 years)	0.338	1	0.006	0.564
Year of adolescence	0.483	1	-0.009	0.491

R²: 0.065 (adjusted 0.026)

Table 3.16 Results of GLM. Dependent variable: body size standardised J at femur

midshaft (N=52). Year of adolescence is included in the model to de-trend the data.

3.3.5 Tibia

3.3.5.1 Bone Length Tibia

The relationship between maximum tibia length and year of birth was not significant (Pearson's $r=0.263$, $p=0.062$; Figure 3.9). There were no significant relationships, or relationships with $p<0.25$, between tibia maximum length and the environmental variables at year of birth or in the first two years of life (Table 3.17). For year of adolescence, GDP per capita and infant mortality rate had relationships with $p<0.25$ with tibia maximum length. These were further examined in GLM but non-significant after year of adolescence was included in the model to de-trend the data (Table 3.18). Other environmental variables had no notable ($p<0.25$) relationships with tibia maximum length at year of adolescence (Table 3.17).



Figure 3.9 Tibia maximum length in mm and year of birth, N=51

	Grain figure for rye, barley and oat for birth year	GDP per capita index for birth year	Infant mortality rate for birth year	Springtime temperatures (Feb-Jun) °C for birth year	Average grain figure rye, barley, oat (first two years of life)	Average springtime temperatures (Feb-Jun) °C for first two years of life	Grain figure for rye, barley and oat (at 14 years)	GDP per capita index (at 14 years)	Infant mortality rate (at 14 years)	Springtime temperatures (Feb-Jun) °C (at 14 years)
Tibia length	0.086 (N=53)	0.059 (N=55)	-0.142 (N=64)	0.119 (N=64)	-0.014 (N=52)	0.001 (N=64)	0.003 (N=58)	0.175 (N=63)	-0.221 (N=64)	0.109 (N=64)

Table 3.17 Pearson's correlations of tibia length and environmental variables at birth year/first two years of life/at adolescence.

Sample size is given in brackets.

Variable	F	df	B	Sig.
Infant mortality rate (14 years)	1.197	1	-0.239	0.278
GDP per capita (14 years)	0.099	1	0.147	0.278
Year of adolescence	0.209	1	-0.182	0.649

R²: 0.050 (adjusted 0.002)

Table 3.18 Results of GLM. Dependant variable: tibia maximum length (N=63). Year of

3.3.5.2 Total Area Tibia

There was no significant relationship between body size standardized TA at tibia midshaft and year of birth (Pearson's $r=-0.1$, $p=0.49$). Similarly to the femur midshaft, the relationships between TA at tibia midshaft and the average grain figure for year of birth as well as the first two years of life had a p-value less than 0.25. Due to the limited sample size only the relationship between TA at tibia midshaft and the grain figure for the first two years of life was examined in GLM, as this was the stronger relationship and had a lower p-value (Pearson's $r=0.288$, $p=0.076$). When the underlying time trend was controlled for, the average grain figure had a significant relationship with TA at tibia midshaft (Figure 3.10; Table 3.19). This relationship was investigated further following the same procedure as with femur TA (and J); results for the final model are presented in Table 3.20.

There were no notable ($p<0.25$) relationships between tibia TA at midshaft and the other environmental variables at year of birth, in the first two years of life or at adolescence (Table 3.21).

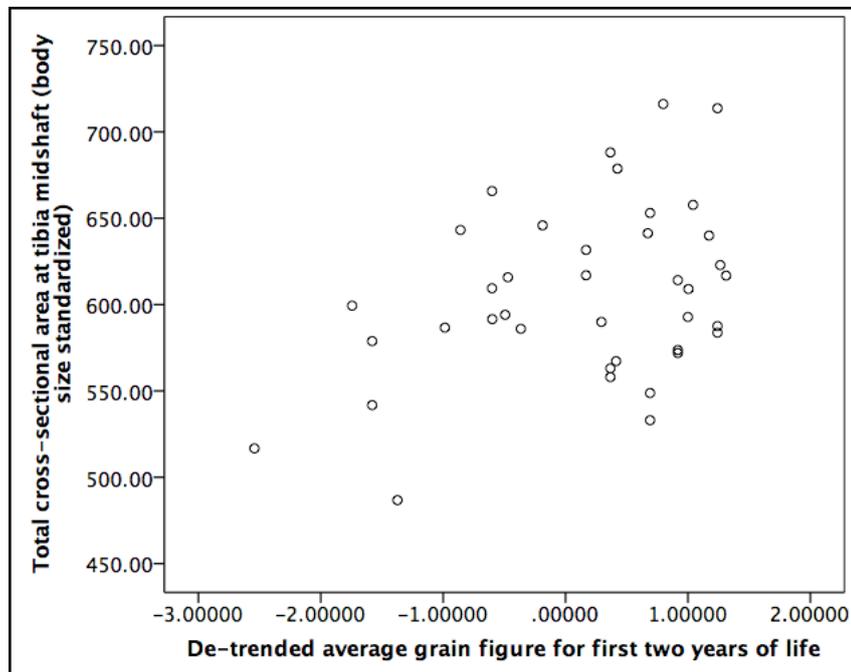


Figure 3.10 Body size standardized TA at tibia midshaft and de-trended average grain figure for first two years of life (N=39).

Variable	F	df	B	Sig.
Average grain figure rye, barley, oat (first two years of life)	6.053	1	13.787	<0.05
Year of birth	2.735	1	-1.082	0.107

R²: 0.147 (adjusted 0.1)

Table 3.19 Results of GLM. Dependent variable: body size standardised TA at tibia midshaft (N=39). Year of birth is included in the model to de-trend the data.

Variable	F	df	B	Sig.
Average grain figure for oat (first two years of life)	4.518	1	40.013	<0.05
Year of birth	1.984	1	-0.918	0.168

R²: 0.115 (adjusted 0.066)

Table 3.20 Results of GLM. Dependent variable: body size standardised TA at tibia midshaft (N=39). Year of birth is included in the model to de-trend the data.

	Grain figure for rye, barley and oat for birth year	GDP per capita index for birth year	Infant mortality rate for birth year	Springtime temperatures (Feb-Jun) °C for birth year	Average springtime temperatures (Feb-Jun) °C for first two years of life	Grain figure for rye, barley and oat (at 14 years)	GDP per capita index (at 14 years)	Infant mortality rate (at 14 years)	Springtime temperatures (Feb-Jun) °C (at 14 years)
Tibia TA at midshaft	0.255 (N=40)	-0.028 (N=42)	-0.050 (N=51)	0.066 (N=51)	0.145 (N=51)	0.055 (N=47)	-0.039 (N=50)	-0.008 (N=51)	0.064 (N=51)

Table 3.21 Pearson's correlations of TA at tibia midshaft and environmental variables at birth year/first two years of life/at adolescence. Sample size is given in brackets.

	Grain figure for rye, barley and oat for birth year	GDP per capita index for birth year	Infant mortality rate for birth year	Springtime temperatures (Feb-Jun) °C for birth year	Average springtime temperatures (Feb-Jun) °C for first two years of life	Grain figure for rye, barley and oat (at 14 years)	GDP per capita index (at 14 years)	Infant mortality rate (at 14 years)	Springtime temperatures (Feb-Jun) °C (at 14 years)
Tibia J at midshaft	0.146 (N=40)	-0.061 (N=42)	-0.021 (N=51)	0.011 (N=51)	0.153 (N=51)	0.059 (N=47)	-0.091 (N=50)	-0.004 (N=51)	0.032 (N=51)

Table 3.22 Pearson's correlations of J at tibia midshaft and environmental variables at birth year/first two years of life/at adolescence. Sample size is given in brackets.

3.3.5.3 J Tibia

There was no significant relationship between body size standardized J at tibia midshaft and year of birth (Pearson's $r=-0.159$, $p=0.267$). There was a positive relationship with $p<0.25$ between J at tibia midshaft and the average grain figure for the first two years of life (Pearson's $r=0.226$, $p=0.167$). In GLM this relationship was significant when the temporal trend was controlled for (Figure 3.11; Table 3.23). This relationship was investigated further following the same procedure as with femur TA (and J and tibia TA), results for the final model are presented in Table 3.24.

There were no further notable relationships ($p<0.25$) between body size standardized J at tibia midshaft and environmental variables at year of birth, in the first two years of life or at year of adolescence (Table 3.22).

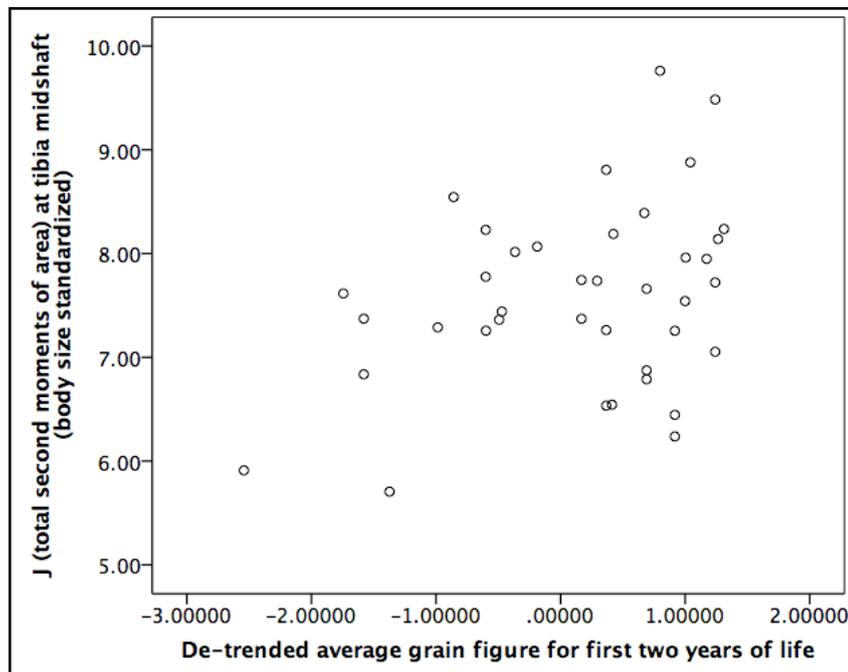


Figure 3.11 Body size standardized J at tibia midshaft and de-trended average grain figure for first two years of life (N=39).

Variable	F	df	B	Sig.
Average grain figure rye, barley, oat (first two years of life)	4.855	1	0.218	<0.05
Year of birth	3.366	1	-0.021	0.075

R²: 0.147 (adjusted 0.1)

Table 3.23 Results of GLM. Dependent variable: body size standardised J at tibia midshaft (N=39). Year of birth is included in the model to de-trend the data. Bold type denotes statistical significance.

Variable	F	df	B	Sig.
Average grain figure for barley (first two years of life)	5.557	1	0.624	<0.05
Year of birth	0.675	1	-0.008	0.417

R²: 0.147 (adjusted 0.099)

Table 3.24 Results of GLM. Dependent variable: body size standardised J at tibia midshaft (N=39). Year of birth is included in the model to de-trend the data. Bold type denotes statistical significance.

3.4 Discussion

The results for the endochondral growth parameters investigated in this chapter show a significant secular increase in femur length ($r=0.36$, $p<0.01$), similar to that found with regard to recorded living stature, but no significant secular increase in tibia length was evident. This implies that femur length increased more consistently with stature than did tibia length. The tibia is believed to be more sensitive to environmental changes (Duyar and Pelin 2003) and this could partly explain the result, as the scale of individual variation in tibia length might have been stronger than in femoral length. The results presented here are unlikely to be caused by an allometric effect, as the tibia shows more positive allometry with stature than the femur (Auerbach and Sylvester 2011). This means that the positive scaling relationship the tibia has with stature is stronger than the one femur has with stature and therefore it is unlikely that longer femora in comparison to tibiae of tall

individuals were due to an underlying scaling relationship (allometric effect). Furthermore, Pomeroy et al. (2012) reported that zeugopod (distal) lower limb elements responded more strongly to environmental stressors than total limb length (femur + tibia) or autopod elements (feet). In the tibia, there were no significant relationships between the environmental variables and bone length, likely due to the lack of a significant time trend in tibia length.

The body size standardized CSG properties showed no significant relationship with year of birth. The relationship between the average grain figure for the first two years of life in Finland and TA and J at both femur and tibia midshaft warranted further inspection in GLM. When the underlying time trend in the grain figure was accounted for, the studied CSG properties had a significant positive relationship with the grain figure and a significant negative relationship with year of birth. Additional investigation of individual crops in relation to the CSG properties revealed that for three out of four examined outcome variables (femur TA, femur J and tibia TA), the most important predictor was the average grain figure for oat in the first two years of life. Appositional growth is most intense during the first two years of life (Rauch 2005) and thus environmental influences can be expected to be stronger during this time. Why the average grain figure, or the grain figure for oats specifically, would have a relationship with the CSG properties and not stature or bone length is unclear. A possible explanation is that the results are a Type I error as sample sizes are relatively small. If however, the results reflect an underlying biological relationship, the average grain figure captured an aspect of the nutritional environment that positively affected the appositional but not endochondral bone growth of these individuals. If so, this would indicate that environmental disturbances more strongly affect appositional than endochondral growth. This could be the case if endochondral growth was more important for individual fitness in humans; under adverse environmental conditions humans might secure an investment in endochondral growth in the short term (for instance to appear more attractive and gain higher status) instead of placing resources into the underlying structure of bones to ensure long-term resistance to mechanical forces. However, evidence from studies on bone growth and malnutrition in children seems to argue against such a conclusion. In a study on Guatemalan children hospitalized for protein-calorie malnutrition, the outer widths of metacarpals were not diminished despite other growth failures, which implies that under adverse conditions periosteal

bone growth can sometimes continue (bone width is similarly to TA a measure of appositional growth) (Garn et al. 1969). The metacarpals are also non-weight bearing bones and have limited mechanical requirements, thus any bias in the results related to different activity levels between the children should be minor. However, the results from a study on children with coeliac disease are in contrast with the Guatemalan data. One-year-old Swiss children who had experienced a six-month period of malnutrition before diagnosis were equally behind in measures of both endochondral and appositional growth parameters for age (Barr et al. 1972). Thus, whilst the first study implies that appositional growth is somewhat better buffered against environmental disturbances, the second implies that periosteal and endochondral growth is equally affected by nutritional insult. Neither study found endochondral growth to be less influenced by malnutrition. Thus, the relationship found in the present study between CSG properties and the grain figures remains puzzling. To solve the question whether it is possible that appositional growth is positively influenced by some aspect of the nutritional environment, whilst endochondral growth is not, controlled studies into the effects of nutritional stress on both endochondral and appositional bone growth would be needed; currently the evidence is somewhat conflicting. Equally, further studies employing the historical grain figure data to examine possible associations with human growth parameters would be useful as at the moment the results presented here are difficult to set in context. Finally, why oats should stand out in comparison to the other crops is unknown. In the 19th century, porridge and bread, along with potato, were the main food stuffs of poor people and also fed to babies (Moring 1998). However it is not known whether oats were preferred over other grains.

Individuals in this study with death due to TB were excluded from analyses on cross-sectional geometric properties, as these males had significantly smaller TA and J at femur midshaft than individuals with another cause of death. Younger TB individuals had smaller TA and J than the older ones, which possible indicates that the younger individuals might have caught TB before skeletal growth ceased. The average infection time of TB in 19th century Finland has been reported to be around seven years (Harjula 2007). However, due to the slight negative trending between CSG properties and year of birth (these relationships were non-significant but r was consistently negative) in this population this conclusion might be erroneous as younger individuals were also those born later in this sample. Since no further

skeletal elements, such as the ribs or vertebrae are present in the collection possible skeletal markers left by TB cannot be investigated or assumed to exist. Instead, it is plausible that individuals who died of TB were more biologically 'frail', as Wood et al. (1992) have discussed in relation to the osteological paradox. The individuals who caught and died of TB might have had smaller TA and lesser J to begin with, for example due to a weaker immune systems, which in addition to making them more susceptible to TB might have exposed them to more growth hindering childhood infections and perhaps left them less physically active than other children. As frequent infections and biological 'frailty' could be expected to result in lesser endochondral growth as well, the bone maximum lengths of the TB individuals were compared with the rest of the sample. This did not reveal significant differences between these two groups in mean maximum femur or tibia length. The reason for this is unclear, but could be related to endochondral catch up growth during childhood, as discussed with reference to the grain figure results above, this has been shown to occur even when an improvement in the growth environment is not sufficient for catch up growth in bone width (Mays 1995). With the information available in the present study, the relationship between TB and CSG properties could not be examined further. However this could be an area of further research, for instance whether these individuals differed in terms of cortical thickness from the rest of the sample is currently unknown. Thin cortices in adult individuals indicate resorption of bone and hint at either reduced activity or nutritional restriction, both of which could occur during long-term illness.

Neither prisoner status, nor place of residence, had a significant relationship with CSG properties or bone length and were not considered in later analyses. Some questions remain about the effect of East/West residence on the cross-sectional properties at tibia midshaft, unfortunately, the sample size did not allow further examination. Besides the average grain figure for the first two years of life, no environmental variables showed significant relationships with CSG properties. The strong temporal trend in the environmental variables that tracked the positive trend in stature and femur length was not reflected in the CSG properties, which had no significant relationships with year of birth. However, the correlation coefficients between the examined CSG properties in both the femora and the tibiae and year of birth were consistently negative, implying a slight negative trend. This will be

discussed together with the results of the relationship between CSG properties of the humerus and year of birth in the following chapter.

Unfortunately, there was no access to computed tomography (CT) scans or radiographs in this study, which could have been used to collect data on endosteal bone parameters such as cortical area. This limitation affects the extent to which the data can be analysed, as environment or age-related losses in cortical thickness or area could not be examined. As discussed, this would be of particular value in regard to the individuals who died of TB. Also, data on the size of the medullary cavity and endosteal contours of the bones could be used to investigate whether there is any temporal trend in bone thickness in terms of percentage of cortical area. Some authors have concluded that especially in terms of nutritional effects on bone growth this is an important factor, and the studies by Mays et al. (2009), Garn et al. (1964; 1975) as well as Himes et al. (1975) show that children seem to respond to nutritional stress particularly through thinning of the cortices. As mentioned in Chapter 1, many individuals from this collection were included in the recent study by Ruff et al. (2015), for which the individuals were CT scanned. Access to these images is at the moment not possible; however, the authors have indicated that all of their material will be made open access within the next two years. This will provide an opportunity to take a closer look at the sample examined here.

In this chapter the relationships between year of birth and the bone lengths of femur and tibia as well as CSG properties were examined. There was a significant secular trend in femur length, which was similar to that found with regard to recorded living stature, and could also reflect the overall improvement in living conditions experienced by the Finnish population in late 19th and early 20th century. There was no significant trend in tibia length and as discussed, this could be because the scale of individual variation in tibia length might have been stronger than in the femur length due to the tibia being more sensitive to environmental influences (Pomeroy et al. 2012). The CSG properties had no significant relationship with year of birth. The average grain figure for first two years of life, particularly the grain figure for oat, had significant relationships with CSG properties. The reason for this remains unclear but as discussed, future research could shed some light on the matter.

4 Upper Limb: Humerus Length and CSG Properties

4.1 Introduction

This chapter aims to investigate whether there are secular trends in the length and cross-sectional geometric (CSG) properties (total cross-sectional area and twice average bending rigidity 'J') of the humerus of adult male individuals in the A-series. A further aim of this chapter is to examine whether the study individuals' prisoner status, residency in East versus West Finland or death from tuberculosis (TB) has an association with the skeletal parameters. As in previous chapters the possible influences of environmental variables (GDP per capita index, infant mortality rate, annual average spring temperature and grain figures) are considered.

The long bones of the upper limb are neither weight-bearing nor add to stature. This makes endochondral and appositional growth in the arm interesting to study, as although the overall size of the body influences the size of these skeletal elements (Ruff 2000), environmental influences such as physical activity might differentially affect the arms compared to the lower limbs. Studies on humeral strength and resistance to bending often concentrate on sideal asymmetry, that is, significant differences in any measured parameter between the left and the right side of the body. In Finnish tennis players, who were known to have sideal asymmetry in humerus strength, exercise induced gains were related to increases in size and not bone density, which remained similar between players and controls (Haapasalo et al. 2000). Similar findings have been presented in another study, which found significant differences in humerus strength and cross-sectional size between tennis players who started before puberty and those who had started later (Kontulainen et al. 2002). Studies such as these are examples of how the mechanical loading induced by exercise is related to greater growth of bone periosteal size and also support the use of total cross-sectional area as an indicator of activity during growth. However, as discussed in Chapter 1, inferring activity patterns from bone CSG properties in uncontrolled settings can be problematic if factors such as the age and sex of the individuals are not known (Jurmain 1999) and therefore in archaeological contexts where age and sex have to be estimated it is likely that some bias always remains. Despite these limitations, finding evidence of sideal asymmetry in past

populations can give an indication about habitual activity. For instance, amongst the Native American Arikara, sideal asymmetry of the humerus increased in males between the 16th and the 19th century, largely due to the individuals from the later period having stronger right humeri (Wescott and Cunningham. 2006). This is possibly related to the population's increased reliance on firearms for hunting and warfare, which placed the right (dominant) arm under increased loads (Wescott and Cunningham 2006). No temporal changes in the TA or strength of the femur were present indicating that lower limb activity patterns of the Arikara did not drastically change between the studied periods. Similar evidence of a relationship between habitual activity and the mechanical properties of the humerus comes from a comparison of 19th century indigenous Andaman Islanders who practiced fishing and heavily relied on marine transport and southern African foragers from Later Stone Age (LSA) who likely had very mobile terrestrial activity patterns (Stock and Pfeiffer 2001). The foragers had significantly stronger lower limbs than the Andamanese, however the pattern was reversed in the humerus possibly because the subsistence activities of the latter, offshore fishing, swimming and canoeing, require greater upper body strength than the foraging lifestyle of the LSA Africans (Stock and Pfeiffer 2001). Unlike in the controlled studies on tennis players, where it is clear why one arm is stronger than the other, in archaeological studies the sideal asymmetry in the humerus is assumed to result from handedness when performing activities. Whilst true that the majority of modern day humans are right handed, assuming this was the case in past populations might be erroneous, as patterns of handedness in modern humans have been shown to vary with age and between populations (Ubelaker and Zarenko 2012). Thus, research that uses sideal differences to infer activity patterns should carefully examine why asymmetry is expected (or not) in the sample. In the present study sideal differences are not examined, because no predictions are made about specific habitual activities. Still, to limit the bias that could be introduced without controlling for side, the left humeri were chosen for analysis, with the exception of two individuals. The two individuals for whom the right humerus was analysed otherwise filled the sample selection criteria and were included as the sample size is already relatively restricted in the present study (see Methods).

As discussed in the previous chapters, the sample investigated in the present study includes prisoners. Humeral cross-sectional geometry has been examined in a

sample of 18th century Quebec prisoners of war in comparison to early to mid-20th century urban New Mexicans from the Maxwell Museum Collection (Weiss 2005). The study found no difference in total cross-sectional area or resistance to bending between the two groups, which may indicate that the intensive labour to which the prisoners were subjected did not result in differences in CSG properties in comparison to the urban New Mexicans whose lifestyle is assumed to have been relatively sedentary. The prisoners of war were known to take part in heavy labour and are thought to come from mainly farming backgrounds whilst the New Mexicans represented many different occupations (Weiss 2005). However, whether the two groups truly differed in terms of physical activity patterns during growth years is not discussed in the study. Also, the representativeness of the Maxwell Museum Collection of the wider New Mexican population has been examined and the collection was found to mainly consist of individuals who did not self-donate but whose remains were donated by next of kin. This means that lower social classes were over-represented because unlike self-donations that tend to come from relatively well-off educated individuals, donations are often made by the next of kin of poorer individuals (Komar and Grivas 2008). It was noted in the study on the humeral CSG properties that only two of the individuals selected had occupations requiring hard physical labour (Weiss 2005), but it is not known whether this was the case also during the study individuals' growth years. A Federal law to restrict child labour was only passed in 1938 in the US (Grossman 1978), and thus it is possible that the sample individuals, especially those from the lower social classes, worked as children. If so, their childhood activity patterns might have been relatively similar to the farmers who later enlisted in the military and then died as prisoners of war. Overall, the study shows that comparing occupations or physical activity levels of adults might not be useful when creating hypothesis about activity effects on CSG properties. In the present study, the occupational data, which includes the prisoner status, are not used to separate between individuals who took part in intense versus light physical activity in adulthood. Instead, these data are taken as possible indicators of social class, which is discussed with regard to the historical information of the childhood living conditions of these groups. In the lower limb sample, no significant differences were found between prisoners and non-prisoners (the labourers). This chapter will investigate whether this is also true for the humerus sample.

The CSG properties investigated in this chapter cannot be size standardized using the method preferred in the literature, using a combination of body mass and bone length, because for the individuals in the humerus sample of the present study only upper limb elements are present – as noted in the previous chapter, body mass estimation requires a femoral head diameter measurement or a preserved pelvis that can be used for the measurement of bi-iliac breadth. The lack of a body mass estimate for the individuals in the humerus sample is a limitation in terms of how much of allometric variation can be controlled for in the present study, however Ruff (2008) notes that in cases where no femur or pelvis is present, CSG properties can be size standardized using powers of bone length (see Methods for procedure). Further, since the sample studied here can be considered to stem from one population, this procedure should not greatly bias the results, as the importance of controlling for mass in the upper limb is related to differences in the relationship of bone length to body shape that exist between populations (Ruff 2000). The overall body shapes of Finnish males can be assumed reasonably similar, even when allowing for some genetic difference between East and West Finland.

Endochondral growth in the arm is less studied than appositional growth and research is mainly concentrated on body proportions and relative limb length (Pomeroy et al. 2012). Upper limb length has been shown to respond to environmental stress similarly to lower limb length (Pomeroy et al. 2012), although, as discussed in Chapter 3, there is variation in the responses of limb elements, such as tibia length. In forensic and archaeological contexts the length of the humerus can be used to estimate stature similarly to the long bones of the lower limb (Trotter and Gleser 1952). The stature estimation methods introduce some error and are population specific (Trotter and Gleser 1952) but they still show that long bone length in the arm scales with overall stature similarly to the lower limb long bones. Therefore it can be assumed here that the secular increase observed in height is not just reflected in the height additive skeletal elements but might also be present in humerus length.

4.2 Methods

4.2.1 Study sample

All adult male individuals from the A-series with complete humeri (N=60) and a recorded year of birth were selected for analysis. For most individuals the bone from the left side of the body was chosen, however for two individuals it was not present, so the right side was analysed instead. The upper limb sample equals roughly half of the individuals that made up the recorded living stature sample (2.2.2). The remaining half had only the lower limbs present and was examined in the previous chapter.

4.2.2 Data Collection Procedure

Data collection followed the same procedure as in Chapter 3. The maximum length of the humerus was measured manually using an osteometric board following standard measuring procedure as defined by White et al. (2011). The variables used to examine the cross-sectional properties of the humerus were same as with the femur and the tibia (see 3.2.6). However, for the humerus, 35% of bone length was used instead of the midshaft to avoid the individual variation caused by the location and size of the deltoid tuberosity, as suggested by Ruff (2008). For the humerus, sample body mass could not be estimated, as for most individuals no lower limbs or pelvis were present. Therefore, humerus maximum length was used as body size control following Ruff (2008). See Table 4.1 for size standardisation methods used for the CSG properties.

Property	Unit	Description	Size Standardisation
Total area (TA) 35	mm ²	Total area at 35% of bone length	TA / (bone length ³) x 10.000 (Ruff 2008)
J 35 (= I_{max} + I_{min})	mm ⁴	(Twice) average bending rigidity at 35% of bone length	J / (bone length ^{5.33}) x 10.000 (Ruff 2008)

Table 4.1 Cross-sectional properties measured and size standardisation method used

4.2.3 Environmental data

The environmental variables examined were the same as with recorded living stature and described in detail in 2.2.2. In the humerus sample there were 15 individuals who died of tuberculosis. There were 18 prisoners, 37 non-prisoners and two individuals with unknown prisoner status, the latter were excluded from analyses.

4.2.4 Statistical Analysis

To assess the possible influences of tuberculosis as cause of death, residence in East or West Finland, as well as prisoner status, on humerus length and cross-sectional properties, independent samples t-tests were performed. The relationships between the environmental variables and the three outcome variables (measured humerus maximum length, TA and J at 35% of bone length) were investigated. Variables were tested for normality using Shapiro-Wilk's tests. Two-tailed Pearson's correlations were used to test the significance and strength of these relationships. Regression analyses were performed in General Linear Model (GLM) to further inspect the effects of the environmental variables on the outcome variables. Due to the time series nature of the data set, year of birth was included in analyses as a way to de-trend the data (Cameron 2005). Similarly to Chapter 2, a cut-off point of $p < 0.25$ (for univariate analyses) was used to select variables that were examined in GLM.

4.3 Results

4.3.1 Cause of Death Tuberculosis (TB)

Individuals who died of tuberculosis had significantly smaller mean TAs and lower mean J at 35% length of the humerus (Table 4.2; Figure 4.1). The mean maximum length of the humerus did not differ significantly between the two categories. Due to the significant differences in mean TA and J between individuals who died of TB

and those who did not, the individuals with TB were excluded from all further analyses on cross-sectional outcome variables. These individuals with were not excluded from analyses on bone maximum length.

Variable	T	df	Sig.
TA humerus 35	-2.341	54	<0.05
J humerus 35	-2.230	54	<0.05
Humerus maximum length	1.480	55	0.145

Table 4.2 Results of Independent Samples t-tests of bone length and cross-sectional properties between cause of death (TB) categories “Yes” N=15 and “No” N=41 (N=42 for humerus length). Bolding denotes statistical significance (p<0.05).

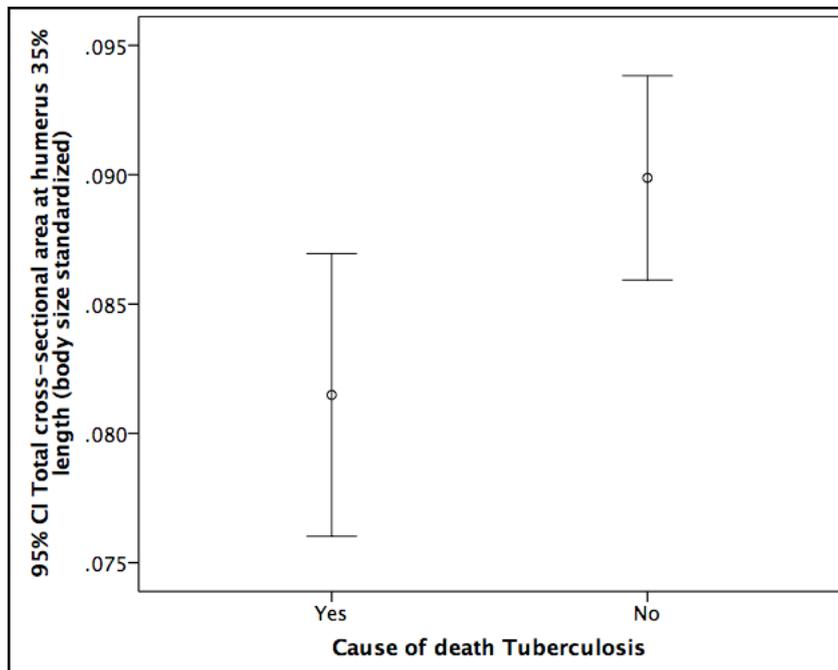


Figure 4.1 Cause of death (TB) and mean TA at 35% length of humerus with 95% confidence intervals, “Yes” N=15, “No” N=41

4.3.2 East vs. West Finland

There were no significant differences in mean maximum length of the humerus or in the examined cross-sectional properties between individuals from East and West

Finland (Table 4.3). The data were analysed further without consideration of place of residence.

Variable	T	df	Sig.
TA humerus 35% length	0.488	21	0.631
J humerus 35% length	0.419	21	0.680
Humerus maximum length	0.233	27	0.818

Table 4.3 Results of Independent Samples t-tests between cross-sectional properties and length of the humerus and place of residence (East versus West Finland). Individuals with cause of death were excluded from analyses on TA and J.

4.3.3 Prisoner Status

There was a significant difference in the size standardised mean total cross-sectional area and J at 35% length of the humerus between prisoners and non-prisoners (Table 4.4). Therefore, in all GLM analyses of cross-sectional outcome, the variable “prisoner status” was included in the model as a fixed factor. There were no significant differences in mean maximum length of the humerus between prisoners and non-prisoners, so humeral length data were analysed further without consideration of prisoner status.

Variable	T	df	Sig.
TA Humerus 35	-2.693	38	<0.01
J Humerus 35	-2.759	38	<0.01
Humerus maximum length	1.568	53	0.123

Table 4.4 Results of Independent Samples t-tests of cross-sectional properties and maximum length of the humerus between prisoners (N=13; N=18 for max length) and non-prisoners (N=27; N=37 for max length). Bolding denotes statistical significance ($p < 0.05$). Individuals with cause of death TB were excluded from CSG analyses.

4.3.4 Humerus

4.3.4.1 Bone Length Humerus

Individuals born later did not have significantly longer humeri than individuals born earlier (Pearson's $r=0.231$, $p<0.12$; Figure 4.2). There were no significant relationships between humerus maximum length and the environmental variables at year of birth (Table 4.5; Table 4.6). The p-value for humerus maximum length and average spring temperature for the first two years of life was below $p<0.25$. This relationship was further examined in GLM but there was no significant relationship after the data were de-trended (Table 4.7).

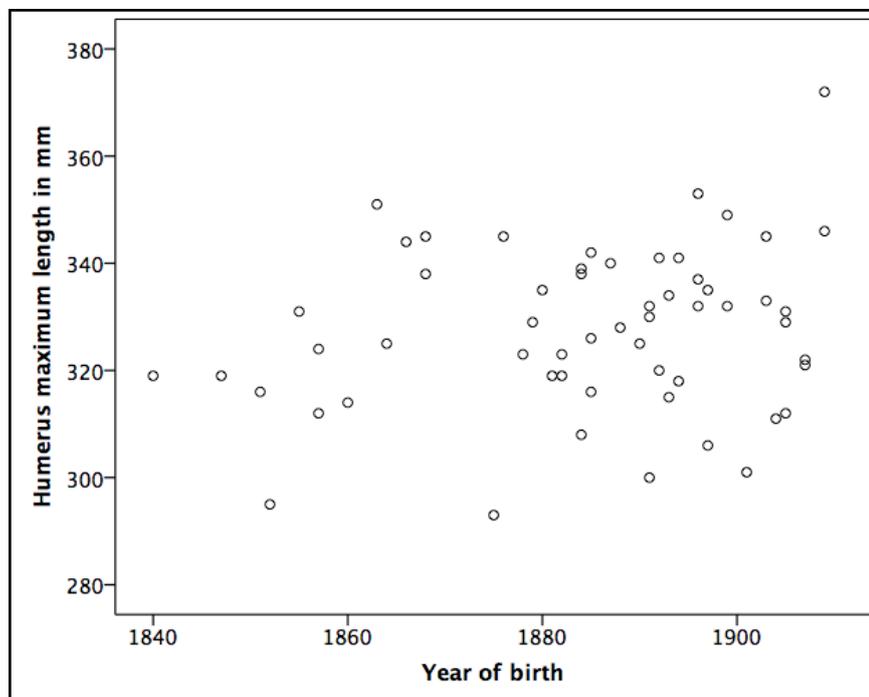


Figure 4.2 Humerus maximum length in mm and year of birth (N=57)

	Grain figure for rye, barley and oat for birth year	GDP per capita index for birth year	Infant mortality rate for birth year	Springtime temperatures (Feb-Jun) °C for birth year
Humerus maximum length	0.086 (N=48)	0.063 (N=50)	0.060 (N=57)	0.078 (N=57)

Table 4.5 Pearson's correlations of humerus maximum length and environmental variables at birth year. Sample size is given in brackets. All p-values are <0.25.

	Average grain figure for rye, barley and oat (first 2 years of life average)	Average springtime temperatures (Feb-Jun) °C (first 2 years of life average)
Humerus maximum length	0.020 (N=47)	0.180 (N=57)

Table 4.6 Pearson's correlations of humerus maximum length and environmental variables in the first two years of life. Sample size is given in brackets. Both p-values are <0.25.

Variable	F	df	B	Sig.
Average spring-time temperature (Feb-Jun) in °C (first two years average)	0.246	1	1.252	0.622
Year of birth	0.981	1	0.143	0.326

R²: 0.050 (adjusted 0.014)

Table 4.7 Results of GLM. Dependent variable: humerus maximum length (N=57). Year of birth is included in the model to de-trend the data.

There was a significant relationship between humerus maximum length and the GDP per capita index at adolescence, as well as a relationship below $p < 0.25$ between humerus maximum length and infant mortality rate at adolescence (Table 4.8). Examination of these variables in GLM did not show significant effects on humerus length when the underlying time trend was controlled for (Table 4.9).

	Grain figure for rye, barley and oat (at 14 years)	GDP per capita index (at 14 years)	Infant mortality rate (at 14 years)	Springtime temperatures (Feb-Jun) °C (at 14 years)
Humerus maximum length	0.086 (N=48)	0.272 (N=56)	-0.250 (N=57)	0.078 (N=57)

Table 4.8 Pearson's correlations of humerus maximum length and environmental variables at year of adolescence. Sample size is given in brackets. Bolding denotes statistical significance ($p < 0.05$)

Variable	F	df	B	Sig.
Infant mortality rate (at 14 years)	0.193	1	-0.070	0.663
GDP per capita (at 14 years)	1.466	1	0.438	0.231
Year of adolescence	0.600	1	-0.215	0.442

R²: 0.085 (adjusted 0.033)

Table 4.9 Results of GLM. Dependent variable humerus maximum length (N=56).

4.3.4.2 Total Area Humerus

The individuals born later had significantly smaller TAs at 35% length of the humerus than individuals born earlier (Pearson's $r = -0.350$, $p < 0.05$; Figure 4.3). This significant temporal trend remained when prisoner status was included in GLM as a fixed factor (Table 4.10).

TA at 35% length of the humerus and the average spring temperature for the first two years of life had a significant relationship and the relationship between TA and the average spring temperature for birth year had a relationship with $p < 0.25$ (Table 4.13). Due to the stronger relationship and lower p-value, the former was chosen for further investigation in GLM with year of birth included in the model to de-trend the data and prisoner status included as a fixed factor. The results show no significant

relationship of average spring temperature in the first two years of life on TA at 35% length of the humerus (Table 4.11).

For adolescence, GDP per capita index had a significant relationship with TA at 35% length of the humerus; the relationship between TA and infant mortality rate was below the threshold of $p < 0.25$. These variables were investigated in GLM whereby year of adolescence was included in the model to de-trend the data and prisoner status was included as a fixed factor. The results show there was no significant relationship between either variable and the TA at 35% length of the humerus (Table 4.12). Remaining environmental variables had no $p < 0.25$ relationships with TA at 35% length of the humerus (Table 4.13).

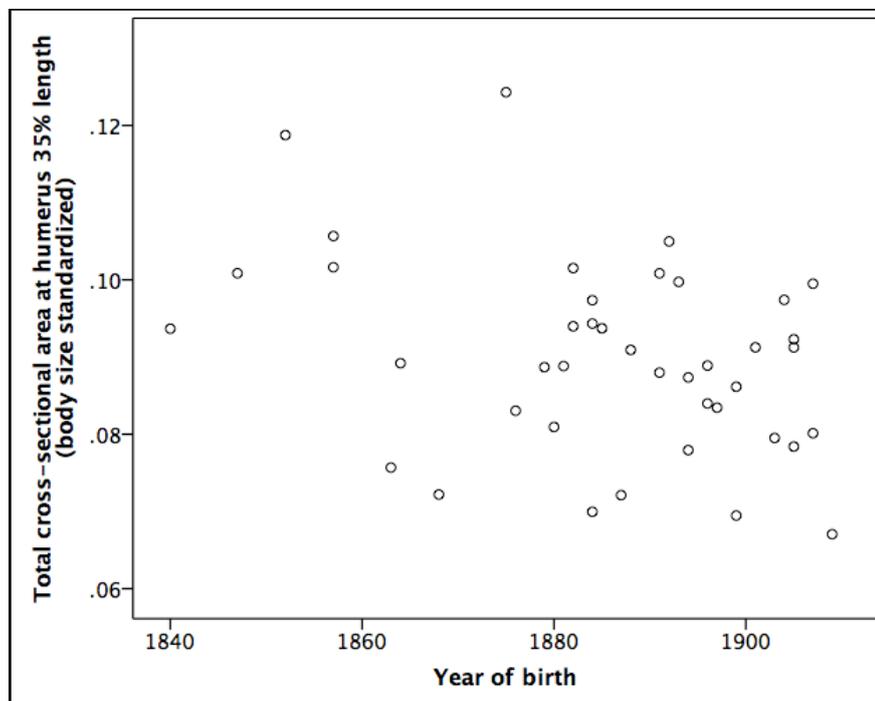


Figure 4.3 Size standardised TA at humerus 35% length and year of birth (N=40)

Variable	F	df	B	Sig.
Year of birth	6.297	1	0.000	<0.05
Prisoner status	8.258	1	-0.011	<0.01

R²: 0.282 (adjusted 0.244)

Table 4.10 Results of GLM. Dependent variable body size standardized TA at humerus 35% length (N=40). Bolding denotes statistical significance.

Variable	F	df	B	Sig.
Average spring temperature for first two years of life	3.395	1	-0.004	0.336
Year of birth	0.950	1	0.000	0.074
Prisoner status	10.509	1	-0.012	<0.01

R²: 0.344 (adjusted 0.290)

Table 4.11 Results of GLM. Dependent variable body size standardized TA at humerus 35% length (N=40). Bolding denotes statistical significance.

Variable	F	df	B	Sig.
GDP per capita (14 years)	3.252	1	-0.004	0.080
Infant mortality rate (14 years)				
Year of adolescence	0.067	1	0.000	0.797
Prisoner status	9.093	1	-0.012	<0.01

R²:0.345 (adjusted 0.268)

Table 4.12 Results of GLM. Dependant variable body size standardized TA at humerus 35% length (N=39). Bolding denotes statistical significance.

	Grain figure for rye, barley and oat for birth year	GDP per capita index for birth year	Infant mortality rate for birth year	Springtime temperatures (Feb-Jun) °C for birth year	Average grain figure for rye, barley and oat for first two years of life	Average springtime temperatures (Feb-Jun) °C for first two years of life	Grain figure for rye, barley and oat (at 14 years)	GDP per capita index (at 14 years)	Infant mortality rate (at 14 years)	Springtime temperatures (Feb-Jun) °C (at 14 years)
Body size stand. TA at humerus 35% length	-0.177 (N=35)	-0.129 (N=36)	-0.056 (N=41)	-0.303 (N=41)	-0.103 (N=34)	-0.341 (N=41)	-0.028 (N=38)	-0.405* (N=40)	0.304 (N=41)	-0.088 (N=41)

Table 4.13 Pearson's correlations of body size standardized TA at humerus 35% bone length and environmental variables at year of birth/first two years of life/at adolescence. Bolding denotes statistical significance ($p < 0.05$, asterix (*) = $p < 0.01$). Sample size is given in brackets.

	Grain figure for rye, barley and oat for birth year	GDP per capita index for birth year	Infant mortality rate for birth year	Springtime temperatures (Feb-Jun) °C for birth year	Average grain figure for rye, barley and oat for first two years of life	Average springtime temperatures (Feb-Jun) °C for first two years of life	Grain figure for rye, barley and oat (at 14 years)	GDP per capita index (at 14 years)	Infant mortality rate (at 14 years)	Springtime temperatures (Feb-Jun) °C (at 14 years)
Body size stand. J at humerus 35% length	-0.193 (N=35)	-0.149 (N=36)	-0.073 (N=41)	-0.341 (N=41)	-0.111 (N=34)	-0.366* (N=41)	-0.015 (N=38)	-0.417* (N=40)	0.304 (N=41)	-0.093 (N=41)

Table 4.14 Pearson's correlations of body size standardized J at humerus 35% bone length and environmental variables at year of birth/first two years of life/at adolescence. Bolding denotes statistical significance ($p < 0.05$, asterix (*) = $p < 0.01$). Sample size is given in brackets.

5 General Discussion

Over the course of the 19th and early 20th Century, the Finnish population experienced substantial changes in its living environment (Grada 2001; Häkkinen et al. 2001; Kannisto et al. 1999; Turpeinen 1991). Elsewhere in Europe, such changes were reflected in secular increases in height (Cole 2003). The current study aimed to test whether secular trends in recorded living stature and other skeletal growth parameters were evident in a sample of adult Finnish males from the A-series collection of skeletal remains. A second objective was to investigate the relationship between prisoner status and the skeletal parameters (stature, bone length, total cross-sectional area and twice average bending rigidity in femur, tibia and humerus) in the same sample. Finally, a third objective of this study was to identify which environmental indicators might have a significant relationship with the examined skeletal traits. The key findings of this study are (1) there is a significant positive secular trend in height, which is also reflected in femur length, (2) there is a significant negative secular trend in size standardized bone cross-sectional size and bending rigidity in the humerus and (3) prisoner status had a significant relationship with the CSG properties in the humerus. See Table 5.1 for a summary of the key results.

Summary of results

Year of birth and skeletal parameter

Variable	Pearson's r	P	N	
Recorded living height	0.390	<0.01	113	
Femur length	0.364	<0.01	66 (Lower limb sample)	
Femur TA	-0.134	0.34	66 (Lower limb sample)	
Femur J	-0.241	0.09	66 (Lower limb sample)	
Tibia length	0.263	0.06	64 (Lower limb sample)	
Tibia TA	-0.1	0.49	64 (Lower limb sample)	
Tibia J	-0.159	0.27	64 (Lower limb sample)	
Humerus length	0.231	0.12	60 (Upper limb sample)	
GLM Humerus TA (N=40)	F	P	B	df
Year of birth	6.297	<0.05	0.000	1
Prisoner status	8.258	<0.01	-0.011	1
R²=0.282 (adjusted 0.244)				
GLM Humerus J (N=40)	F	P	B	df
Year of birth	7.125	<0.05	-0.033	1
Prisoner status	8.831	<0.01	-1.4	1
R² = 0.301 (adjusted 0.264)				

Table 5.1 Summary of results.

5.1 Differences in Secular Trends between Skeletal Growth Parameters

The key findings posit the question why the examined skeletal growth parameters show different temporal trends and relationships with the investigated variables (prisoner status, environmental variables) in this population. Whilst statures increased, the CSG properties showed no such trend, and in the case of the humerus CSG properties there are significant negative trends. An often cited reason for differences in CSG properties is loading history, for example, amount of physical activity during childhood (Kontulainen et al. 2002). As discussed in Chapter 3, there is some evidence from archaeological samples that bone traits that have a known relationship with physical activity, such as bone density and rate of bone loss, show temporal trends. Twentieth century individuals have reduced bone density and greater rates of bone loss in comparison to archaeological samples from 15th century Sweden and 18th century England (Ekenman et al. 1995; Lees et al. 1993).

For the present study population it was concluded (Chapter 4) that a change in loading history might have occurred due to the dramatic changes in the country's schooling environment, given that the number of schools in the country increased over 100-fold over the study period (Kurth 2005). This resulted in a significant increase in the number of children in education and was also reflected in the increased literacy rate, as reported by Turpeinen (1991) and Markussen (1990). Annual data on historical literacy rates in Finland do not exist, but from the data reported by Markussen (1990), it is evident that both the reading and writing ability of the Finnish population strongly increased between 1880 and 1930. Most of the adult population in Finland were members of the Evangelical Lutheran Church, whose records show that between 1880 and 1900, the percentage of church members who could both read and write increased from 12.4 to 38.6, before reaching 84.1 in 1930 (Markussen 1990). Within a time span of 50 years, these are quite remarkable figures – the number of church members for whom literacy rate was recorded went from 1.6 million of a total population size of 2 million to around 2.3 million of a total population size of 3.4 million (Statistics Finland 2015). Overall, the increasing number of children in education likely reduced the amount of physical labour Finnish children carried out and as discussed in Chapter 1, amount of mechanical loading during growth is connected to periosteal size as well as bending rigidity.

In contrast to the humerus, the lower limb CSG properties showed no significant secular decrease. It is possible that this can be explained by less change over time in the lower limb loading environment during growth. All of the study individuals lived before mass transport was available in Finland and thus walking and skiing would have been the main means of travel for individuals in the lower social classes and school journeys would have been made by foot; a maximum distance children had to walk (or ski) to school was only set in 1898 when it was decided that school journeys should not exceed five kilometres each way (Kurth 2005). Thus, although all four investigated lower limb CSG properties (femur TA, J and tibia TA, J) trended negatively, it seems reasonable to assume that the femoral and tibial results are real, after all, a similar sample size for the humerus was large enough to show a significant decrease through time.

Besides the above discussed socio-ecological explanation, there might be biological reasons for the different temporal trends found in the humerus and femur as well as between the endochondral and appositional growth parameters of the present study sample. Growth velocities differ between skeletal elements, and although growth overall is under systemized hormonal control, part of the regulation of bone growth occurs locally, as different growth plates show different activities (Rauch 2005). This could mean that different bones also show varying responses to environmental change. Variability in the growth of limb elements has been reported between populations with different subsistence strategies. A Greek Neolithic sample showed more inter-limb differences in growth attainment than a Mesolithic Georgian sample (Pinhasi et al. 2011), implying that subsistence strategy might influence whether similar or different patterns of growth are observed between bones. Also, bone dimensions-for-age in the Greek sample were most similar to a modern day Denver sample between two and four years of age, whilst the dimensions of the Mesolithic sample resembled the Denver sample most between ages eight to ten (Pinhasi et al. 2011). It is unknown whether these differences in growth trajectories are related to subsistence strategy and particularly to the transition to agriculture; however, they do show that both overall growth patterns as well as patterns between limbs can vary between environments. A further study found that in medieval European populations there were differences between bones in the extent of inter-population variability, whereby during infancy, leg dimensions varied more than arm dimensions between the populations (Pinhasi et al. 2005). These findings could be related to population level genetic differences. It is also possible that genetic constraints, particularly during infancy, are not identical in the upper and lower limb (Pinhasi et al. 2005). Thus, the different patterns observed in the Finnish humeral and lower limb samples could be due to the skeletal elements responding differently to environmental conditions during different stages of growth. Some support for such a conclusion comes from a study on the integration (modularity) of human limb development, which found that compared to monkeys, humans and other great apes show greater independent evolvability of fore- and hindlimbs likely due to the divergent functions of human limbs (Young et al. 2010). This means that whilst the lower limbs needed to adapt for bipedalism, the upper limbs have acquired functions related to tool use and other manual tasks (Young et al. 2010). Thus, unlike in many primates that have four limbs with very similar functions, in humans, the lower and upper limbs are under less shared genetic constraint. Despite human limbs being

inter-correlated to large extent, 29% of variation in limb bone lengths of children aged three to ten years is not explained by the lengths of their other bones (Smith and Buschang 2004). Different developmental trajectories have also been found elsewhere in the human skeleton. The thorax shows different development in shape between the upper and lower ribs whereby the development of the upper thorax seems to be tied to that of the lungs, whilst the lower thorax responds to the lengthening of the abdomen (Bastir et al. 2013). Thus depending on the function of the skeletal element as well as the functions of the other tissues in proximity, bones can develop following different trajectories.

5.2 Differences in the Relationship with Prisoners Status between Skeletal Growth Parameters

Similarly to year of birth, prisoner status showed diverse relationships with the investigated growth parameters. There were no significant differences in stature, bone lengths or the CSG properties of the femur and the tibia between prisoners and non-prisoners. In the humerus, the prisoners had lower TA and J than the non-prisoners. In terms of endochondral growth, the results indicate that the nutritional and disease environment during growth of these two groups did not differ to an extent that would result in significant differences in the examined parameters, despite the fact that many of the prisoners were likely of somewhat lower social status than the labourers. As discussed, in 19th century Finland a disproportionately high number of very vulnerable people, such as vagrants and those suffering from mental health problems were sentenced to prison because in addition to actual crimes, idleness could result in a prison sentence (Aho and Karsikas 1980). The results imply that there were improvements in the growth environment of the poorest members of the Finnish society. The literature reviewed in Chapter 1 supports such a conclusion and in terms of nutritional environment, food security greatly improved in Finland after the famine years as in addition to the domestic crops that were included in the grain figure variable used in the present study, foreign grain imports became important supplements to domestic agricultural produce by the end of the 19th century (Heikkinen 1986; Turpeinen 1991). This increased the population's access to food during shortages, as local yields could be subsidised using the foreign produce. Improved transport networks gave secluded municipalities better

access to grain, and relief committees were set up around the country to arrange food aid to localities suffering from bad crop years (Turpeinen 1991). From around 1880, infant mortality rates strongly decreased in Finland due to advances in medicine combined with better hygiene practices, which improved population health (Harjula 2007; Turpeinen 1991) and probably led to decreased disease loads in young children. Neither the grain figures nor the infant mortality rate showed significant relationships with the investigated endochondral growth parameters in the present study after the data were de-trended, however, both showed significant secular changes. This is in line with previously published studies on these factors as well as with the historical literature describing change in living conditions in the late 19th century (Heikkinen 1986; Kannisto et al. 1999; Kurth 2005; Turpeinen 1991).

Why lower limb CSG properties did not differ between the prisoners and non-prisoners could be related to the overall similar terrestrial mobility patterns between the groups. Even if some of the individuals in the prisoner sample were vagrants before incarceration, and as discussed in Chapter 4 might therefore had limited opportunities for work as children, it is still likely that they travelled considerable distances by foot looking for food or shelter. It has been reported that the Finnish Famine increased the number of displaced people in the country, as masses left their homes in search of food and work (Turpeinen 1986). It is feasible that even after the famine years, those without permanent work or housing had to travel relatively long distances in order to survive. Despite the governmental relief operations that provided better access to food, vagrancy remained a crime and this could have created pressure not to stay in a single location for extended periods of time. Thus, individuals with a vagrant background might have spent large portions of their childhood on their feet. Such a travelling lifestyle could have loaded the lower limbs of vagrant children in a similar manner as working as a child, and could explain why the prisoner sample did not differ from the non-prisoners in terms of lower limb CSG properties. Another explanation would be that, similar to the results of the secular trends discussed above, the discrepancy in the relationship between prisoner status and the CSG properties in the lower limb bones and the humerus might be related to underlying biological differences in the developmental trajectories of these bones.

5.3 Differences in the Relationships between Environmental Variables and Skeletal Growth Parameters

The only environmental variable that showed a significant relationship with the examined skeletal parameters was the average grain figure for the first two years of life, which showed a significant positive relationship with femur and tibia TA and J. Such a relationship was not found in the humerus sample, in stature or in bone lengths. As discussed in Chapters 3 and 4, the significant relationship might be a type I error, as the sample size in the analysis of the relationship between the grain figures and CSG properties was relatively small, only 40 individuals. Small sample sizes are a common reason for results that do not reflect reality because low power increases the likelihood of a false result (Banerjee et al. 2009; Button et al. 2013). In addition, the effect size of the grain variable can be expected to be quite low; however, in the present study the effect size of the grain figure was constantly higher than that of year of birth and when combined in a model, these two variables seemed to explain as much as 20% of the variation in the examined CSG properties. Existing literature also poorly supports a conclusion that an early life nutritional factor would have a positive relationship with appositional but not endochondral growth. Rather, it seems that nutritional changes either have a similar influence on both endochondral and appositional growth (Barr et al. 1972) or more strongly affect endochondral growth (Garn et al. 1969). Thus, the reason for the discrepant results between the endochondral and appositional growth parameters and the grain figures remains unclear, though as concluded in Chapter 3, future research into the effects of early life nutritional insults on bone growth as well as into grain figures might help shed light on the matter.

As mentioned, the average grain figure for rye, barley and oat for first two years of life did not show a significant relationship with humeral CSG properties. This is easier to conceive than the lack of relationship with endochondral growth parameters, as in addition to the different sample individuals, periosteal apposition rates differ between the femur and the humerus in the first two years of life. This rate is high in both bones within this period, but starting around 12 months of age the periosteal apposition rate of the femur surpasses that of the humerus, which starts a decline (Rauch 2005); a nutritional disturbance might thus disproportionately affect the appositional growth of the femur after one year of age. It is also feasible

that in the second year of life a child might be less buffered against environmental nutritional insults (events such as poor crop years) because in comparison to the first year, a decreasing part of the child's nutrition comes directly from the mother in form of breast milk. Such an explanation is not unfeasible considering the low social class sample investigated in the present study, as in 19th century Finland breastfeeding was common amongst the poorest in the population because unlike land owners, they did not have access to cow's milk (Moring 1998). This idea that a differential access to weaning foods might influence the length of the period a child is breastfed has been used to explain observed variation in infant mortality in the archaeological record (Sellen and Smay 2001). It has been hypothesised that agricultural populations with access to weaning foods and dairy might end breastfeeding earlier than foraging populations (Sellen and Smay 2001). There is some support for this argument, although the associations between subsistence strategy and age at weaning are relatively weak; overall most preindustrial populations tend to feed similar foods during weaning and begin the introduction of both solid and liquid weaning foods by around nine months of age (Sellen and Smay 2001). As the Finnish study population can largely be considered preindustrial, the time at which weaning foods were introduced could have been similar. In archaeological samples, age at weaning can also be examined using stable isotope analysis of teeth, and it seems that breastfeeding and weaning behaviour have significant impact on the morbidity and mortality of infants (Beaumont et al. 2015; Eerkens et al. 2011). Future studies might examine whether there is also an association between age at weaning and skeletal growth parameters in archaeological populations.

In addition to the three objectives detailed at the start of this chapter, the present study found that individuals who died of tuberculosis in this population differed significantly in terms of their CSG properties from the individuals with other causes of death, whereby their mean total cross-sectional areas of the three examined long bones included in this study were smaller. The same pattern was observed with reference to twice average resistance to bending (J), a measure of bone rigidity. A similar relationship was not found in endochondral growth parameters, possible reasons for this were discussed in Chapter 3. That the study sample should have individuals who died of TB is not surprising, as discussed in Chapter 1, TB was a major public health concern in 19th century Finland and it was prevalent up until the

World War II years (Harjula 2007). Tuberculosis is a communicable disease, which today is treatable in most cases by antibiotics and has a low prevalence in many Western countries. The occurrence of TB in a population is related to political and social factors. As a common cause of death, it affected a considerable part of the Finnish population, causing 13.5% of all deaths between 1891-1900 (Harjula 2007). The eventual decline of TB infections can be considered related to broader societal changes ranging from better hygiene awareness in families to improvements in the provisioning of health care by the state. Although its interaction with bone appositional growth is as yet poorly understood (Sparacello et al. 2015), the fact that TB casualties differed from the rest of the sample in terms of CSG properties can be viewed as an example of the influence of human ecology on biomechanics. It is very unlikely that results similar to the ones of the present study would be found in a skeletal sample of late 20th century Finns, purely because TB no longer is a notable cause of death in the country and the few yearly cases reported very infrequently result in death. Largely, this is not because the disease or our physiological response to it is different rather due to good access to health care (including vaccinations) and overall high standards of living the disease has been nearly eradicated in the country. Overall the found significant relationship between the CSG properties and tuberculosis highlights the importance of considering a wide variety of variables when investigating appositional bone growth, not merely those that are indicators of habitual activity patterns.

5.4 Future Directions

This study incorporated a range of variables to examine the relationship between skeletal growth parameters and the nutritional, disease, economic, as well as social environment. Such aspects of human ecology are commonly studied with reference to changes in mean height through time (Cole 2003). The scarceness of such studies on CSG properties shows that the biomechanical literature has not yet made full use of an approach that encompasses the wider living environment of recent populations – it remains largely unknown whether the secular increases in statures in many European populations in the last 200 years were reflected in CSG properties. The results presented in this study indicate that CSG properties might show opposite trends to stature. However, the sample examined here was relatively

small and consisted of individuals from the lower social classes, therefore these results cannot be considered representative of the Finnish population at large. Thus, future studies are needed to establish whether similar patterns of appositional bone growth through time can be found in other skeletal populations, including those from neighbouring countries, such as Sweden and Estonia. Larger collections, for instance the sizable forensic skeletal collections in the US, could be used to investigate whether with more statistical power some of the environmental variables used in the present study, for instance GDP per capita index and infant mortality rate, might reveal significant relationships with both endochondral and appositional skeletal growth parameters.

Besides sample size, limitations of the present study include that it did not examine females, children or juveniles. The female sample in the A-series was not large enough for meaningful analyses, which is not surprising, as males tend to be overrepresented in skeletal collections that consist of donated individuals (Komar and Grivas 2008). This also means that overall there is a shortage of identified female skeletal remains with accompanying records on individual histories. Similarly in terms of stature, the widely reported trends on secular changes often come from samples of male conscript or prisoner records (Bodenhorn et al. 2013). Thus in future research, a particular focus on females might be worthwhile to investigate whether modern female study samples show similar responses to environmental changes as the data from the male dominated skeletal collections and historical records. Besides sex, the present study sample was limited by the fact that since there are no children or juveniles in the A-series the skeletal growth parameters were only examined using adult individuals. This meant that the study could not pinpoint ages when environmental disturbances to growth might have occurred. As there was no access to CT or X-ray facilities, possible indicators of nutritional insults during growth, such as Harris lines could not be examined (Mays 1995). Changes in the frequency of such markers through time could have provided important additional support for the found secular increase in height, although the reliability of using Harris lines as an indicator of environmental insults during growth has recently been questioned (Alfonso-Durruty 2011). The lack of access to higher quality imaging equipment was also reflected in that data on cortical thickness could not be collected. This was not a major limitation in terms of the objectives of this study

however, as discussed in Chapter 4, images of the inner contours of the bones would have been of particular interest in terms of the individuals who died of TB.

5.5 Conclusion

There is increasing interest in exploring the wider living environment of archaeological populations to gain insights into both the functional and physiological bases of bone growth (Ruff et al. 2013). This study shows the utility of such an approach, combining historical records that document the living environment with study of a well-contextualised skeletal sample. Relatively few studies have access to such a combination of data, and the research described in this thesis is also unusual in examining endochondral and appositional growth in several skeletal elements. The population examined in the present study underwent major environmental changes relating to the transition from an agricultural to an industrialised society, and the results indicate that such large-scale change across nutritional, disease, political and social environments leaves traces in skeletal parameters. From a wider perspective, the Industrialisation in Europe may be compared with the Neolithic Demographic Transition, as both were key periods of subsistence change in human populations. Both transitions also affected most aspects in populations' living environments. There is a large archaeological as well as biomechanical literature on the Neolithic Transition. Yet despite the similarity between these two transitions in terms of the extent of their influence on human societies, studies examining skeletal growth parameters during Industrialisation tend to focus only on heights. Thus, this study will conclude by emphasising the importance of future research that focuses on revealing patterns of change in skeletal traits other than stature within the period of Industrialisation. Since this transition happened in recent history, there are detailed environmental data available in form of historical records and population statistics. This should assist in testing detailed hypotheses about the relationships between environmental variables and both endochondral and appositional growth parameters and hopefully, future findings can be compared with the results of the present study.

6 References

- Agrogiannis, G.D., Sifakis, S., Patsouris, E.S., & Konstantinidou, A.E. 2014. Insulin-like growth factors in embryonic and fetal growth and skeletal development (Review). *Molecular Medicine Reports* 10: p.579–584.
- Aho, T., & Karsikas, V. 1980. *Vankien taustaan ja vankilukuun liittyviä tilastoja 1881-1978 (Statistical data relating to prisoners' background and to the prison population from 1881 to 1978)*. Helsinki: Vankeinhoidon historiaprojektin julkaisu n:o 3.
- Alanen, I. 1995. Finland as a peasant society and the agrarian reforms. In L. Granberg & J. Nikula (eds) *The Peasant State: The State and rural questions in 20th century Finland*, Rovaniemi: The University of Lapland Publications
- Alfonso-Durruty, M.P. 2011. Experimental assessment of nutrition and bone growth's velocity effects on Harris lines formation. *American Journal of Physical Anthropology* 145: p.169–180.
- Aro, A. 2015. Jodi ja seleeni (Iodine and Selenium). *Duodecim - Terveyskirjasto*. Available at: http://www.terveyskirjasto.fi/terveyskirjasto/tk.koti?p_artikkeli=skr00031 [Accessed August 17, 2015].
- Auerbach, B.M., & Ruff, C.B. 2004. Human body mass estimation: a comparison of 'morphometric' and 'mechanical' methods. *American Journal of Physical Anthropology* 125: p.331–42.
- Auerbach, B.M., & Sylvester, A.D. 2011. Allometry and apparent paradoxes in human limb proportions: Implications for scaling factors. *American Journal of Physical Anthropology* 144: p.382–391.
- BABAO. 2015. Ethics and Standards. Available at: <http://www.babao.org.uk/index/ethics-and-standards>.

- Banerjee, A., Chitnis, U.B., Jadhav, S.L., Bhawalkar, J.S., & Chaudhury, S. 2009. Hypothesis testing, type I and type II errors. *Industrial Psychiatry Journal* 18: p.127–131.
- Barbujani, G., & Sokal, R.R. 1990. Zones of sharp genetic change in Europe are also linguistic boundaries. *Proceedings of the National Academy of Sciences of the United States of America* 87: p.1816–1819.
- Barr, D.G., Shmerling, D.H., & Prader, A. 1972. Catch-up growth in malnutrition, studied in celiac disease after institution of gluten-free diet. *Pediatric Research* 6: p.521–527.
- Bass, S. et al. 2002. The effect of mechanical loading on the size and shape of bone in pre-, peri-, and postpubertal girls: a study in tennis players. *Journal of Bone and Mineral Research* 17: p.2274–2280.
- Bastir, M. et al. 2013. Differential Growth and Development of the Upper and Lower Human Thorax. *PLoS ONE* 8: p.e75128.
- Beaumont, J., Montgomery, J., Buckberry, J., & Jay, M. 2015. Infant mortality and isotopic complexity: New approaches to stress, maternal health, and weaning. *American Journal of Physical Anthropology* 157: p.441–457.
- Blank, R.D. 2014. Bone and Muscle Pleiotropy: The Genetics of Associated Traits. *Clinical Reviews in Bone and Mineral Metabolism* 12: p.61–65.
- Bloomfield, F.H., Spiroski, A.M., & Harding, J.E. 2013. Fetal growth factors and fetal nutrition. *Seminars in Fetal and Neonatal Medicine* 18: p.118–123.
- Bodenhorn, H., Guinnane, T.W., & Mroz, T. a. 2013. *Problems of Sample-Selection Bias in Historical Heights Literature: A Theoretical and Econometric Analysis*. New Haven.
- Bogin, B. 1999. *Patterns of Human Growth*. Cambridge: Cambridge University Press.
- Bogin, B., & Baker, J. 2012. Low birth weight does not predict the ontogeny of relative leg length of infants and children: An allometric analysis of the

- NHANES III sample. *American Journal of Physical Anthropology* 148: p.487–494.
- Bogin, B., Silva, M.I.V., & Rios, L. 2007. Life History Trade-Offs in Human Growth: Adaptation or Pathology? *American Journal of Human Biology* 19: p.631–642.
- Bonjour, J.-P., Kraenzlin, M., Levasseur, R., Warren, M., & Whiting, S. 2013. Dairy in adulthood: from foods to nutrient interactions on bone and skeletal muscle health. *Journal of the American College of Nutrition* 32: p.251–63.
- Bourrin, S., Ammann, P., Bonjour, J.P., & Rizzoli, R. 2000. Dietary Protein Restriction Lowers Plasma Insulin-Like Growth Factor I (IGF-I), Impairs Cortical Bone Formation , and Induces Osteoblastic Resistance to IGF-I in Adult Female Rats. *Endocrinology* 141(9): p.3149–3155.
- Brock, S.L., & Ruff, C.B. 1988. Diachronic patterns of change in structural properties of the femur in the prehistoric American Southwest. *American Journal of Physical Anthropology* 75: p.113–127.
- Bursac, Z., Gauss, C.H., Williams, D.K., & Hosmer, D.W. 2008. Purposeful selection of variables in logistic regression. *Source code for biology and medicine* 3: p.17.
- Button, K.S. et al. 2013. Power failure: why small sample size undermines the reliability of neuroscience. *Nature reviews. Neuroscience* 14: p.365–76.
- Cameron, S. 2005. Making Regression Analysis More Useful II: Dummies and Trends. In *Econometrics*, McGraw-Hill Education
- Carson, S.A. 2011. Was the 19th century stature-insolation relationship similar across independent samples? Evidence from soldiers and prisoners. *Journal of Socio-Economics* 40: p.199–207.
- Cavelaars, A.E. et al. 2000. Persistent variations in average height between countries and between socio-economic groups: an overview of 10 European countries. *Annals of Human Biology* 27: p.407–421.

- Checkley, W. et al. 2004. Effect of water and sanitation on childhood health in a poor Peruvian peri-urban community. *Lancet* 363(9403): p.112–8.
- Cole, T.J. 2000. Secular trends in growth. *Proceedings of the Nutrition Society* 59: p.317–324.
- Cole, T.J. 2003. The secular trend in human physical growth: a biological view. *Economics and Human Biology* 1: p.161–8.
- Currey, J.D. 2002. *Bones*. Princeton: Princeton University Press.
- Currie, J., & Vogl, T. 2013. Early-Life Health and Adult Circumstance in Developing Countries. *Annual Review of Economics* 5(1): p.1–36.
- Davey Smith, G. et al. 2000. Height and risk of death among men and women: aetiological implications of associations with cardiorespiratory disease and cancer mortality. *Journal of Epidemiology and Community Health* 54: p.97–103.
- Davies, T.G., Shaw, C.N., & Stock, J.T. 2012. A test of a new method and software for the rapid estimation of cross-sectional geometric properties of long bone diaphyses from 3D laser surface scans. *Archaeological and Anthropological Sciences* 4: p.277–290.
- Deaton, A. 2007. Height, health, and development. *Proceedings of the National Academy of Sciences of the United States of America* 104: p.13232–13237.
- Delemarre-van de Waal, H. a. 1993. Environmental factors influencing growth and pubertal development. *Environmental Health Perspectives Supplements* 101: p.39–44.
- Demes, B., Jungers, W.L., & Selpien, K. 1991. Body Size, Locomotion, and Long Bone Cross-Sectional Geometry in Indriid Primates. *American Journal of Physical Anthropology* 86: p.537–547.
- Dillingham, R., & Guerrant, R.L. 2004. Childhood stunting: measuring and stemming the staggering costs of inadequate water and sanitation. *Lancet* 363(9403): p.94–5.

- Duren, D.L., Seselj, M., Froehle, A.W., Nahhas, R.W., & Sherwood, R.J. 2013. Skeletal growth and the changing genetic landscape during childhood and adulthood. *American Journal of Physical Anthropology* 150: p.48–57.
- Duyar, I., & Pelin, C. 2003. Body height estimation based on tibia length in different stature groups. *American Journal of Physical Anthropology* 122: p.23–27.
- Eerkens, J.W., Berget, A.G., & Bartelink, E.J. 2011. Estimating weaning and early childhood diet from serial micro-samples of dentin collagen. *Journal of Archaeological Science* 38: p.3101–3111.
- Ekenman, I., Eriksson, S.A., & Lindgren, J.U. 1995. Bone density in medieval skeletons. *Calcified Tissue International* 56: p.355–358.
- Floud, R., Wachter, K., & Gregory, A. 1990. *Height, health and history: Nutritional Status in the United Kingdom, 1750-1980*. Cambridge: Cambridge University Press.
- Forsén, T. et al. 2000. Short stature and coronary heart disease: A 35-year follow-up of the Finnish cohorts of The Seven Countries Study. *Journal of Internal Medicine* 248: p.326–332.
- Fournier, C., Rizzoli, R., & Ammann, P. 2014. Low Calcium-Phosphate Intakes Modulate the Low-Protein Diet-Related Effect on Peak Bone Mass Acquisition: A Hormonal and Bone Strength Determinants Study in Female Growing Rats. *Endocrinology* 155: p.4305–4315.
- French, V. 1989. The control of growth and size during development. In J. Tanner & M. Preece (eds) *Physiology of Human Growth*, Cambridge: Cambridge University Press
- Frost, H.M. 2003. Bone's mechanostat: a 2003 update. *The Anatomical Record Part A* 275: p.1081–1101.
- Garn, S.M. et al. 1975. Nutrition, Growth, Development, and Maturation: Findings From the Ten-State Nutrition Survey of 1968-1970: Ad Hoc Committee To Review the Ten-State Nutrition Survey. *Pediatrics* 56: p.306–319.

- Garn, S.M., Guzmán, M., & Wagner, B. 1969. Subperiosteal gain and endosteal loss in protein-calorie malnutrition. *American Journal of Physical Anthropology* 30: p.153–155.
- Garn, S.M., Rohmann, C.G., Behar, M., Viteri, F., & Guzman, M.A. 1964. Compact Bone Deficiency in Protein-Calorie Malnutrition. *Science* 145: p.1444–1445.
- Goldewijk, K., Beusen, A., Van Drecht, G., & De Vos, M. 2011. The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. *Global Ecology and Biogeography* 20: p.73–86.
- Grada, C. 2001. Markets and famines: evidence from nineteenth-century Finland. *Economic Development and Cultural Change* 49: p.575–590.
- Grine, F.E., Jungers, W.L., Tobias, P. V., & Pearson, O.M. 1995. Fossil homo femur from Berg Aukas, Northern Namibia. *American Journal of Physical Anthropology* 97: p.151–185.
- Grossman, J. 1978. Fair Labor Standards Act of 1938. *United States Department of Labor*. Available at: <http://www.dol.gov/dol/aboutdol/history/flsa1938.htm> [Accessed September 8, 2015].
- Guerrant, R.L., Oriá, R.B., Moore, S.R., Oriá, M.O.B., & Lima, A. a M. 2008. Malnutrition as an enteric infectious disease with long-term effects on child development. *Nutrition reviews* 66(9): p.487–505.
- Gunnell, D.J. et al. 1998. Childhood leg length and adult mortality: follow up of the Carnegie (Boyd Orr) Survey of Diet and Health in Pre-war Britain. *Journal of epidemiology and community health* 52: p.142–152.
- Haapasalo, H. et al. 2000. Exercise-induced bone gain is due to enlargement in bone size without a change in volumetric bone density: A peripheral quantitative computed tomography study of the upper arms of male tennis players. *Bone* 27: p.351–357.
- Haines, M., & Steckel, R. 2000. *Childhood Mortality & Nutritional Status as Indicators of Standard of Living: Evidence from World War I Recruits in the United States*. Cambridge, MA.

- Haines, M.R., Craig, L. a., & Weiss, T. 2003. The Short and the Dead: Nutrition, Mortality, and the 'Antebellum Puzzle' in the United States. *The Journal of Economic History* 63: p.382–413.
- Häkkinen, A. 2004. Poverty and the Social Underclass during Finnish Industrialisation. In A.-M. Castren, M. Lonkila, & M. Peltonen (eds) *Between Sociology and History: Essays on Microhistory, Collective Action, and Nation-building*, Helsinki: Finnish Literature Society (SKS)
- Häkkinen, A., & Peltola, J. 2001. On the Social History of Unemployment and Poverty in Finland 1860-2000. In J. Kalela, J. Kiander, U. Kivikuru, H. A. Loikkanen, & J. Simpura (eds) *Down from the heavens, Up from the ashes: The Finnish economic crisis of the 1990s in the light of economic and social research*, Helsinki: Valtion taloudellinen tutkimuskeskus (from Finnish: Government Institute for Economic Research)
- Hampshire, K., Casiday, R., Kilpatrick, K., & Panter-Brick, C. 2009. The social context of childcare practices and child malnutrition in Niger's recent food crisis. *Disasters* 33: p.132–151.
- Harjula, M. 2007. *Terveyden jäljillä: Suomalainen terveystaloudellinen politiikka 1900-luvulla (After Health: Politics of Finnish Health Care in the 20th century)*. Tampere: Tampere University Press.
- Hauser, R., Smoliński, J., & Gos, T. 2005. The estimation of stature on the basis of measurements of the femur. *Forensic Science International* 147(2-3): p.185–90.
- Hauspie, R., Vercauteren, M., & Susanne, C. 1997. Secular changes in growth and maturation: an update. *Acta Paediatrica Suppl* 423: p.20–27.
- Hayward, A.D., Holopainen, J., Pettay, J.E., & Lummaa, V. 2012. Food and fitness: associations between crop yields and life-history traits in a longitudinally monitored pre-industrial human population. *Proceedings of the Royal Society B: Biological Sciences* 279: p.4165–4173.

- Heikkinen, S. 1986. On private consumption and the standard of living in Finland, 1860–1912. *Scandinavian Economic History Review* 34(2): p.122–134.
- Hernandez, M. 1998. Hormonal regulation of fetal growth. In S. Ulijaszek, F. E. Johnston, & M. A. Preece (eds) *The Cambridge Encyclopedia of Human Growth and Development*, Cambridge: Cambridge University Press
- Himes, J.H. et al. 1975. Patterns of Cortical Bone Growth in Moderately Malnourished Preschool Children. *Human Biology* 47(3): p.337–350.
- Hindmarsch, P. 1998. Endocrinological regulation of post-natal growth. In S. Ulijaszek, F. Johnston, & M. Preece (eds) *The Cambridge Encyclopedia of Human Growth and Development*, Cambridge: Cambridge University Press
- Hjerpe, R. 1989. *The Finnish Economy 1860 -1985: Growth and Structural Change*. Helsinki: Bank of Finland.
- Hochberg, Z., & Albertsson-Wikland, K. 2008. Evo-devo of infantile and childhood growth. *Pediatric Research* 64: p.2–7.
- Holopainen, J., Helama, S., et al. 2009. A multiproxy reconstruction of spring temperatures in south-west Finland since 1750. *Climatic Change* 92: p.213–233.
- Holopainen, J., & Helama, S. 2009. Little ice age farming in Finland: Preindustrial agriculture on the edge of the Grim reaper's scythe. *Human Ecology* 37: p.213–225.
- James, W.P.T., & Schofield, E.C. 1990. *Human Energy Requirements: A Manual for Planners and Nutritionists*. Oxford: Oxford University Press.
- Jääntti, M., Saari, J., & Vartiainen, J. 2006. *Growth and equity in Finland*.
- Jantz, L.M., & Jantz, R.L. 1999. Secular change in long bone length and proportion in the United States, 1800-1970. *American Journal of Physical Anthropology* 110: p.57–67.

- Jurmain, R. 1999. *Stories from the Skeleton: Behavioural Reconstruction in Human Osteology*. London: Taylor & Francis.
- Kannisto, V., Nieminen, M., & Turpeinen, O. 1999. Finnish Life Tables since 1751. *Demographic Research* 1.
- Karlberg, J. 1998. The human growth curve. In S. Ulijaszek, F. Johnston, & M. Preece (eds) *The Cambridge Encyclopedia of Human Growth and Development*, Cambridge: Cambridge University Press
- Katzmarzyk, P.T., & Leonard, W.R. 1998. Climatic influences on human body size and proportions: Ecological adaptations and secular trends. *American Journal of Physical Anthropology* 106: p.483–503.
- Klein, R.F. et al. 2002. Mapping Quantitative Trait Loci That Influence Femoral Cross-sectional Area in Mice. *Journal of Bone and Mineral Research* 17: p.1752–1760.
- Klinge, M. 2015. Snellman, Johann Vilhelm (1806-1881). *The National Biography of Finland*. Available at: <http://www.kansallisbiografia.fi/english/?id=3639>.
- Koller, D.L. et al. 2001. Genome screen for quantitative trait loci underlying normal variation in femoral structure. *Journal of Bone and Mineral Research* 16: p.985–991.
- Komar, D., & Grivas, C. 2008. Manufactured populations: What do contemporary reference skeletal collections represent? A comparative study using the Maxwell Museum documented collection. *American Journal of Physical Anthropology* 137: p.224–233.
- Komlos, J. 1995. The secular trend in the biological standard of living in the United Kingdom, 1730-1860. In J. Komlos (ed) *The Biological Standard of Living in Europe and America, 1700-1900*, Hampshire: Variorum
- Komlos, J. 1998. Shrinking in a Growing Economy? The Mystery of Physical Stature during the Industrial Revolution. *The Journal of Economic History* 58: p.779–803.

- Komlos, J., Tanner, J., Davies, P., & Cole, T. 1995. The growth of boys in the Stuttgart Carlschule, 1771-93. In J. Komlos (ed) *The Biological Standard of Living in Europe and America, 1700-1900*, Hampshire: Variorum
- Kontulainen, S., Sievänen, H., Kannus, P., Pasanen, M., & Vuori, I. 2002. Effect of Long-Term Impact-Loading on Mass, Size, and Estimated Strength of Humerus and Radius of Female Racquet-Sports Players: A Peripheral Quantitative Computed Tomography Study Between Young and Old Starters and Controls. *Journal of Bone and Mineral Research* 17(12): p.2281–2289.
- Kozak, J. 1996. Stature Reconstruction From Long Bones: The Estimation of the Usefulness of Some Selected Methods for Skeletal Populations from Poland. *Variability and Evolution* 5: p.83–94.
- Kurth, J. 2005. *Die Geschichte der finnischen Schule (The History of Finnish School)*. University of Dortmund.
- De la Chapelle, A. 1993. Disease gene mapping in isolated human populations: the example of Finland. *Journal of Medical Genetics* 30(10): p.857–865.
- Lampl, M., Johnston, F.E., & Malcolm, L.A. 1978. The effects of protein supplementation on the growth and skeletal maturation of New Guinean school children. *Annals of Human Biology* 5: p.219–227.
- Lang, D.H. et al. 2005. Quantitative trait loci analysis of structural and material skeletal phenotypes in C57BL/6J and DBA/2 second-generation and recombinant inbred mice. *Journal of Bone and Mineral Research* 20: p.88–99.
- Lang, T.F., Leblanc, A.D., Evans, H.J., & Lu, Y. 2006. Adaptation of the proximal femur to skeletal reloading after long-duration spaceflight. *Journal of Bone and Mineral Research* 21: p.1224–1230.
- Lango Allen, H. et al. 2010. Hundreds of variants clustered in genomic loci and biological pathways affect human height. *Nature* 467: p.832–8.
- Lappalainen, T. et al. 2006. Regional differences among the finns: A Y-chromosomal perspective. *Gene* 376: p.207–215.

- Lawlor, D., Leon, D., & Smith, G.D. 2005. The association of ambient outdoor temperature throughout pregnancy and offspring birthweight: findings from the Aberdeen Children of the 1950s cohort. *BJOG: An International Journal of Obstetrics and Gynaecology* 112: p.647–657.
- Lawson, D.W., & Mace, R. 2008. Sibling configuration and childhood growth in contemporary British families. *International Journal of Epidemiology* 37: p.1408–1421.
- Lees, B., Molleson, T., Arnett, T.R., & Stevenson, J.C. 1993. Differences in proximal femur bone density over two centuries. *Lancet* 341: p.673–675.
- Leonard, W.R. 1989. Nutritional determinants of high-altitude growth in Nuñoa, Peru. *American Journal of Physical Anthropology* 80: p.341–352.
- Lewis, S.J. 1999. Quantifying measurement error. In S. Anderson (ed) *Current and Recent Research in Osteoarchaeology: Proceedings of the 4th, 5th and 6th meetings of the Osteoarchaeological Research Group*, 54–55. Oxford: Oxbow Books
- Lieberman, D.E., Pearson, O.M., Polk, J.D., Demes, B., & Crompton, A.W. 2003. Optimization of bone growth and remodeling in response to loading in tapered mammalian limbs. *The Journal of Experimental Biology* 206: p.3125–3138.
- Lintsi, M., & Kaarma, H. 2006. Growth of Estonian seventeen-year-old boys during the last two centuries. *Economics and Human Biology* 4: p.89–103.
- LocalFinland.fi. 2015. The Association of Finnish Local and Regional Authorities. Available at: <http://www.localfinland.fi/en/contact/Pages/default.aspx> [Accessed August 21, 2015].
- Macdonald, H.M., Kontulainen, S.A., Khan, K.M., & McKay, H.A. 2007. Is a school-based physical activity intervention effective for increasing tibial bone strength in boys and girls? *Journal of Bone and Mineral Research* 22: p.434–446.
- Macintosh, A., Pinhasi, R., & Stock, J.T. 2014. Lower limb skeletal biomechanics track long-term decline in mobility across ~6150 years of agriculture in Central Europe. *Journal of Archaeological Science* 52: p.376–390.

- Malina, R.M., & Bouchard, C. 1991. *Growth, Maturation, and Physical Activity* 1st ed. Champaign: Human Kinetics Academic.
- Maloney, T.N., & Carson, S.A. 2008. Living standards in Black and White: Evidence from the heights of Ohio Prison inmates, 1829-1913. *Economics and Human Biology* 6: p.237–251.
- Marchi, D. 2008. Relationships between lower limb cross-sectional geometry and mobility: The case of a Neolithic sample from Italy. *American Journal of Physical Anthropology* 137: p.188–200.
- Markussen, I. 1990. The development of writing ability in the Nordic countries in the Eighteenth and Nineteenth centuries. *Scandinavian Journal of History* 15: p.37–63.
- Mascie-Taylor, C.G. 1991. Biosocial influences on stature: a review. *Journal of biosocial science* 23: p.113–128.
- Masinde, G.L. et al. 2003. Quantitative trait loci for periosteal circumference (PC): Identification of single loci and epistatic effects in F2 MRL/SJL mice. *Bone* 32: p.554–560.
- Mays, S. 1995. The Relationship between Harris Lines and other Aspects of Skeletal Development in Adults and Juveniles. *Journal of Archaeological Science* 22: p.511–520. Available at: <http://linkinghub.elsevier.com/retrieve/pii/S0305440385700490>.
- Mays, S., Ives, R., & Brickley, M. 2009. The effects of socioeconomic status on endochondral and appositional bone growth, and acquisition of cortical bone in children from 19th century Birmingham, England. *American Journal of Physical Anthropology* 140(3): p.410–6.
- Messer, E. 1997. Intra-household allocation of food and health care: current findings and understandings: Introduction. *Social Science & Medicine* 44: p.1675–1684.
- Mikkola, A. et al. 2005. Map of Finnish Dialects. *Äidinkieli ja kirjallisuus – käsikirja (WSOY)*: p.71. Available at:

https://en.wikipedia.org/wiki/Finnish_language#/media/File:FinnishDialects.png
[Accessed May 1, 2015].

- Misselhorn, A. a. 2005. What drives food insecurity in southern Africa? a meta-analysis of household economy studies. *Global Environmental Change* 15: p.33–43.
- Moore, S.R. et al. 2001. Early childhood diarrhoea and helminthiases associate with long-term linear growth faltering. *International Journal of Epidemiology* 30: p.1457–1464.
- Morimoto, N., De León, M.S.P., & Zollikofer, C.P.E. 2011. Exploring Femoral Diaphyseal Shape Variation in Wild and Captive Chimpanzees by Means of Morphometric Mapping: A Test of Wolff's Law. *Anatomical Record* 294: p.589–609.
- Moring, B. 1998. Motherhood , Milk , and Money: Infant Mortality in Pre-Industrial Finland. *The Society for the Social History of Medicine* 11: p.177–196.
- Mosekilde, L. 2008. Primary hyperparathyroidism and the skeleton. *Clinical Endocrinology* 69: p.1–19.
- Mueller, W.H. 1998. Genetic and environmental influences on fetal growth. In S. J. Ulijaszek, F. E. Johnston, & Preece M A (eds) *The Cambridge Encyclopedia of Human Growth and Development*, Cambridge: Cambridge University Press
- Nikita, E., Siew, Y.Y., Stock, J., Mattingly, D., & Lahr, M.M. 2011. Activity patterns in the Sahara Desert: an interpretation based on cross-sectional geometric properties. *American Journal of Physical Anthropology* 146(3): p.423–34.
- Niu, T., & Rosen, C.J. 2005. The insulin-like growth factor-I gene and osteoporosis: A critical appraisal. *Gene* 361: p.38–56.
- O'Rahilly, R., & Müller, F. 1998a. Developmental morphology of the embryo and fetus. In S. Ulijaszek, F. E. Johnston, & M. A. Preece (eds) *The Cambridge Encyclopedia of Human Growth and Development*, Cambridge: Cambridge University Press

- O’Rahilly, R., & Müller, F. 1998b. Growth of the human embryo. In S. Ulijaszek, F. E. Johnston, & M. A. Preece (eds) *The Cambridge Encyclopedia of Human Growth and Development*, Cambridge: Cambridge University Press
- Omram, A.R. 1971. The epidemiologic transition: a theory of the epidemiology of population change. *Milbank Memorial Fund Quarterly* 83: p.509–538.
- Padez, C., Varela-Silva, M.I., & Bogin, B. 2009. Height and relative leg length as indicators of the quality of the environment among Mozambican juveniles and adolescents. *American Journal of Human Biology* 21(2): p.200–9.
- Paunonen, H. 2007. *Lounaismurteiden asema suomen murteiden ryhmityksessä*. Helsinki. Available at: <https://helda.helsinki.fi/bitstream/handle/10224/4091/paunonen249-268.pdf?sequence=1>.
- Pearson, O.M., & Lieberman, D.E. 2004. The aging of Wolff’s ‘law’: ontogeny and responses to mechanical loading in cortical bone. *American Journal of Physical Anthropology Suppl* 39: p.63–99.
- Peck, M.N., & Lundberg, O. 1995. Short stature as an effect of economic and social conditions in childhood. *Social Science & Medicine* 41: p.733–8.
- Pietiläinen, K.H., Kaprio, J., Räsänen, M., Rissanen, A., & Rose, R.J. 2002. Genetic and environmental influences on the tracking of body size from birth to early adulthood. *Obesity Research* 10: p.875–884.
- Pinhasi, R., Stefanovi, S., Papathanasiou, A., & Stock, J.T. 2011. Variability in Long Bone Growth Patterns and Limb Proportions Within and Amongst Mesolithic and Neolithic Populations From Southeast Europe. *Human Bioarchaeology of the Transition to Agriculture*: p.177–202.
- Pinhasi, R., Teschler-nicola, M., Knaus, A., & Shaw, P. 2005. Cross-population analysis of the growth of long bones and the os coxae of three Early Medieval Austrian populations. *American Journal of Human Biology* 17: p.470–488.

- Pitkänen, K.J., & Mielke, J.H. 1993. Age and sex differentials in mortality during two nineteenth century population crises. *European Journal of Population* 9: p.1–32.
- Pomeroy, E. et al. 2012. Trade-Offs in Relative Limb Length among Peruvian Children: Extending the Thrifty Phenotype Hypothesis to Limb Proportions. *PLoS ONE* (12).
- Pomeroy, E. et al. 2014. Birth month associations with height, head circumference, and limb lengths among peruvian children. *American Journal of Physical Anthropology* 154: p.115–124.
- Pomeroy, E., & Zakrzewski, S.R. 2009. Sexual Dimorphism in Diaphyseal Cross-sectional Shape in the Medieval Muslim Population of Ecija, Spain, and Anglo-Saxon Great Chesterford, UK. *International Journal of Osteoarchaeology* 19: p.50–65.
- Rahikainen, M. 2001. Children and ‘the right to factory work’: child labour legislation in nineteenth-century Finland. *The Scandinavian Economic History Review* 49(1): p.41–62.
- Rauch, F. 2005. Bone Growth in Length and Width: The Yin and Yang of Bone Stability. *Journal of Musculoskeletal and Neuronal Interactions* 5(3): p.194–201.
- Rauch, F. 2007. Bone accrual in children: adding substance to surfaces. *Pediatrics* 119 Suppl: p.S137–S140.
- Raxter, M.H., Auerbach, B.M., & Ruff, C.B. 2006. Revision of the fully technique for estimating statures. *American Journal of Physical Anthropology* 130: p.374–384.
- Ren, F.L. et al. 2007. Effects of selenium and iodine deficiency on bone, cartilage growth plate and chondrocyte differentiation in two generations of rats. *Osteoarthritis and Cartilage* 15: p.1171–1177.
- Rizzoli, R. 2008. Nutrition: its role in bone health. *Best Practice & Research Clinical Endocrinology & Metabolism* 22: p.813–829.

- Robling, A.G., Castillo, A.B., & Turner, C.H. 2006. Biomechanical and molecular regulation of bone remodeling. *Annual Review of Biomedical Engineering* 8: p.455–98.
- Rockell, J.E.P. et al. 2005. Two-year changes in bone and body composition in young children with a history of prolonged milk avoidance. *Osteoporosis International* 16: p.1016–1023.
- Ruff, C. 1994. Morphological adaptation to climate in modern and fossil hominids. *American Journal of Physical Anthropology* 37: p.65–107.
- Ruff, C. 2000. Body size, body shape, and long bone strength in modern humans. *Journal of Human Evolution* 38(2): p.269–90.
- Ruff, C. 2003. Growth in bone strength, body size, and muscle size in a juvenile longitudinal sample. *Bone* 33: p.317–329.
- Ruff, C., Holt, B., Sládek, V., et al. 2006. Body size, body proportions, and mobility in the Tyrolean 'Iceman'. *Journal of human evolution* 51(1): p.91–101.
- Ruff, C., Holt, B., & Trinkaus, E. 2006. Who's Afraid of the Big Bad Wolff?: "Wolff's Law" and Bone Functional Adaptation. *American Journal of Physical Anthropology* 129: p.484–498.
- Ruff, C., Niskanen, M., Junno, J.A., & Jamison, P. 2005. Body mass prediction from stature and bi-iliac breadth in two high latitude populations, with application to earlier higher latitude humans. *Journal of Human Evolution* 48: p.381–392.
- Ruff, C.B. 2002. Long bone articular and diaphyseal structure in old world monkeys and apes. I: locomotor effects. *American Journal of Physical Anthropology* 119: p.305–42.
- Ruff, C.B. 2006. Gracilization of the Modern Human Skeleton: The latent strength in our slender bones teaches lessons about human lives, current and past. *American Scientist* 94: p.508–514.

- Ruff, C.B. 2008. Biomechanical Analyses of Archaeological Human Skeletons. In M. Katzenberg & S. Saunders (eds) *Biological Anthropology of the Human Skeleton*, 183–206. New Jersey: Wiley-Liss
- Ruff, C.B. et al. 2015. Gradual decline in mobility with the adoption of food production in Europe. *Proceedings of the National Academy of Sciences Early Edit*. Available at: <http://www.pnas.org/lookup/doi/10.1073/pnas.1502932112>.
- Ruff, C.B., Garofalo, E., & Holmes, M. a. 2013. Interpreting skeletal growth in the past from a functional and physiological perspective. *American journal of physical anthropology* 150(1): p.29–37.
- Ruff, C.B., & Scott, W.W. 1991. Articular and Diaphyseal Remodeling of the Proximal Femur With Changes in Body Mass in Adults. *American Journal of Physical Anthropology* 86: p.397–413.
- Ruff, C.B., Trinkaus, E., Walker, A., & Larsen, C.S. 1993. Postcranial Robusticity in Homo. I: Temporal Trends and Mechanical Interpretation. *American Journal of Physical Anthropology* 53: p.21–53.
- Rühli, F., Henneberg, M., & Woitek, U. 2008. Variability of height, weight, and body mass index in a Swiss Armed Forces 2005 census. *American Journal of Physical Anthropology* 137: p.457–468.
- Ryan, T.M., & Shaw, C.N. 2015. Gracility of the modern Homo sapiens skeleton is the result of decreased biomechanical loading. *Proceedings of the National Academy of Sciences* 112: p.372–377.
- Salmela, E. et al. 2008. Genome-wide analysis of single nucleotide polymorphisms uncovers population structure in Northern Europe. *PLoS one* 3: p.e3519.
- Sandberg, L.G., & Steckel, R.H. 1997. Was Industrialization Hazardous to Your Health? Not in Sweden! In R. Steckel & R. Flouds (eds) *Health and Welfare during Industrialization*, 127–160. Chicago: University of Chicago Press
- Schaible, U.E., & Kaufmann, S.H.E. 2007. Malnutrition and infection: complex mechanisms and global impacts. *PLoS medicine* 4(5): p.e115.

- Sellen, D.W., & Smay, D.B. 2001. Relationship Between Subsistence and Age at Weaning in 'Preindustrial' Societies. *Human Nature* 12: p.47–87.
- Sharpe, P. 2012. Explaining the short stature of the poor : chronic childhood disease and growth in nineteenth-century England. *Economic History Review* 65(4): p.1475–1494.
- Shaw, C.N., & Stock, J.T. 2013. Extreme mobility in the Late Pleistocene? Comparing limb biomechanics among fossil Homo, varsity athletes and Holocene foragers. *Journal of Human Evolution* 64(4): p.242–9.
- Silventoinen, K., Kaprio, J., Lahelma, E., & Koskenvuo, M. 2000. Relative Effect of Genetic and Environmental Factors on Body Height: Differences Across Birth Cohorts Among Finnish Men and Women. *American Journal of Public Health* 90: p.627–630.
- Silverman, M., Pearce, B., Biron, C., & Miller, A. 2005. Immune Modulation of the Hypothalamic-Pituitary-Adrenal (HPA) Axis during Viral Infection. *Viral Immunology* 18: p.41–78.
- Simondon, K.B. et al. 2007. Seasonal variations and trends in weight and arm circumference of non- pregnant rural Senegalese women , 1990-1997. *European Journal of Clinical Nutrition*.
- Skerry, T.M. 2006. One mechanostat or many? Modifications of the site-specific response of bone to mechanical loading by nature and nurture. *Journal of Musculoskeletal and Neuronal Interactions* 6: p.122–127.
- Skerry, T.M. 2008. The response of bone to mechanical loading and disuse: fundamental principles and influences on osteoblast/osteocyte homeostasis. *Archives of Biochemistry and Biophysics* 473: p.117–23.
- Smith, S.L., & Buschang, P.H. 2004. Variation in longitudinal diaphyseal long bone growth in children three to ten years of age. *American Journal of Human Biology* 16: p.648–657.
- Söderholm, N. 2002. *Den Anatomiska Bensamlingen vid Helsingfors Universitet*. University of Helsinki.

- Sohn, K. 2015. Is leg length a biomarker of early life conditions? Evidence from a historically short population. *American Journal of Human Biology* 00: p.n/a–n/a.
- Soveri, J., Ulvinen, A., & Kalliola, R. 1956. Historiallinen maatalous: Peltoviljely (Historical Agriculture: Field crops). Available at: <http://www.helsinki.fi/kansatiede/histmaatalous/peltoviljely/peltokasvit.htm> [Accessed August 1, 2015].
- Sparacello, V., & Marchi, D. 2008. Mobility and subsistence economy: A diachronic comparison between two groups settled in the same geographical area (Liguria, Italy). *American Journal of Physical Anthropology* 136: p.485–495.
- Sparacello, V., Roberts, C.A., Canci, A., & Marchi, D. 2015. Insights on the paleoepidemiology of ancient tuberculosis from the structural analysis of Ligurian Neolithic postcrania. In press.
- Sparacello, V.S., & Pearson, O.M. 2010. The importance of accounting for the area of the medullary cavity in cross-sectional geometry: A test based on the femoral midshaft. *American journal of physical anthropology* 143(4): p.612–24.
- Specker, B., & Binkley, T. 2003. Randomized Trial of Physical Activity and Calcium Supplementation on Bone Mineral Content in 3- to 5-Year-Old Children. *Journal of Bone and Mineral Research* 18(5): p.885–892.
- StatisticsFinland. 2015. Official Statistics of Finland. Available at: http://www.stat.fi/tup/tilastotietokannat/index_en.html.
- Stearns, S.C. 1989. Trade-Offs in Life-History Evolution. *Functional Ecology* 3: p.259–268.
- Steckel, R.H. 2008. *Heights and Human Welfare: Recent Developments and New Directions*. Cambridge, MA.
- Stegman, A.T. 1985. 18th Century British Military Stature: Growth Cessation, Selective Recruiting, Secular Trends, Nutrition at Birth, Cold and Occupation. *Human Biology* 57: p.77–95.

- Stini, W.A. 1998. Skeletal development. In S. J. Ulijaszek, F. E. Johnston, & M. A. Preece (eds) *The Cambridge Encyclopedia of Human Growth and Development*, Cambridge: Cambridge University Press
- Stock, J., & Pfeiffer, S. 2001. Linking structural variability in long bone diaphyses to habitual behaviors: foragers from the southern African Later Stone Age and the Andaman Islands. *American Journal of Physical Anthropology* 115(4): p.337–48.
- Stock, J.T. 2006. Hunter-gatherer postcranial robusticity relative to patterns of mobility, climatic adaptation, and selection for tissue economy. *American Journal of Physical Anthropology* 131: p.194–204.
- Stulp, G., & Barrett, L. 2014. Evolutionary perspectives on human height variation. *Biological Reviews of the Cambridge Philosophical Society* 44.
- Stulp, G., Barrett, L., Tropf, F.C., Mills, M., & Stulp, G. 2015. Does natural selection favour taller stature among the tallest people on earth? *Proceedings of the Royal Society of Biological Sciences* 282: p.1–9.
- Takahashi, E. 1984. Secular Trend in Milk Consumption and Growth in Japan. *Human Biology* 56: p.427–437.
- Tanner, J. 1989. *Foetus into Man: Physical Growth from Conception to Maturity*. Herts: Castlemead Publications.
- Tanner, J.M. 1981. *A History of the Study of Human Growth*. Cambridge: Cambridge University Press.
- Tanner, J.M., Hughes, P.C.R., & Whitehouse, R.H. 1981. Radiographically determined widths of bone, muscle and fat in the upper arm and calf from age 3-18 years. *Annals of Human Biology* 8: p.495–517.
- Treme, J., & Craig, L. a. 2013. Urbanization, health and human stature. *Bulletin of Economic Research* 65: p.130–141.
- Trotter, M., & Gleser, G. 1952. Estimation of stature from long bones of American Whites and Negroes. *American Journal of Physical Anthropology*: p.463–514.

- Turpeinen, O. 1977. Causal Relationships between Economic Factors and Mortality. In *Finnish Yearbook of Population Research XV*, Helsinki: Väestöliitto
- Turpeinen, O. 1986. Näлкä vai tauti tappoi? Kauhunvuodet 1866-1868 (Was it Hunger or Disease that Killed? Years of Terror 1866-1868). In *Historiallisia tutkimuksia 136*, Helsinki: Societas Historica Finlandiae
- Turpeinen, O. 1991. *Näläntorjunta ja hyvinvointivaltion perusteet (Prevention of Hunger and the Premise of a Welfare State)*. Helsinki: Valtion painatuskeskus.
- Tveit, K. 1991. The Development of Popular Literacy in the Nordic Countries: A Comparative Historical Study. *Scandinavian Journal of Educational Research* 35: p.241–252.
- Ubelaker, D.H., & Zarenko, K.M. 2012. Can Handedness be Determined from Skeletal Remains? A Chronological Review of the Literature. *Journal of Forensic Sciences* 57: p.1421–1426.
- Ulijaszek, S. 1998. The genetics of growth. In S. Ulijaszek, F. E. Johnston, & M. A. Preece (eds) *The Cambridge Encyclopedia of Human Growth and Development*, Cambridge: Cambridge University Press
- Ulijaszek, S.J. 1995. *Human energetics in biological anthropology*. Cambridge: Cambridge University Press.
- UN. 2015. Human Development Index. Available at: <http://hdr.undp.org/en/content/human-development-index-hdi>.
- Varilo, T. et al. 2003. The interval of linkage disequilibrium (LD) detected with microsatellite and SNP markers in chromosomes of Finnish populations with different histories. *Human Molecular Genetics* 12: p.51–59.
- Victora, C.G. et al. 2008. Maternal and child undernutrition: consequences for adult health and human capital. *Lancet* 371(9609): p.340–57.
- Vihola, T. 1994. Mitä ihminen tarvitsi elääkseen (What man needed to live on). In P. Karonen & A. Häkkinen (eds) *Pane leipään puolet petäjäistä: Näлкä ja*

pulavuodet Suomen historiassa (Put Half Pine Bark into Bread: Hunger and Years of Distress in Finnish History), Jyväskylä: Jyväskylän yliopisto

- Volkman, S.K. et al. 2003. Quantitative trait loci for femoral size and shape in a genetically heterogeneous mouse population. *Journal of Bone and Mineral Research* 18: p.1497–1505.
- Walsh, J. 2015. Normal bone physiology, remodelling and its hormonal regulation. *Surgery* 33: p.1–6.
- Watson, P.E., & McDonald, B.W. 2007. Seasonal variation of nutrient intake in pregnancy: effects on infant measures and possible influence on diseases related to season of birth. *European Journal of Clinical Nutrition* 61(11): p.1271–80.
- Weiss, E. 2003. Effects of rowing on humeral strength. *American Journal of Physical Anthropology* 121: p.293–302.
- Weiss, E. 2005. Humeral cross-sectional morphology from 18th century Quebec prisoners of war: Limits to activity reconstruction. *American Journal of Physical Anthropology* 126: p.311–317.
- Weiss, K., Stock, D., & Zhiyong, Z. 1998. Homeobox genes. In S. Ulijaszek, F. Johnston, & M. Preece (eds) *The Cambridge Encyclopedia of Human Growth and Development*, Cambridge: Cambridge University Press
- Wells, J.C.K. 2002. Thermal Environment and Human Birth Weight. *Journal of Theoretical Biology* 214: p.413–425.
- Wells, J.C.K., & Cole, T.J. 2002. Birth Weight and Environmental Heat Load: A Between-Population Analysis. *American Journal of Physical Anthropology* 119: p.276–282.
- Wells, J.C.K., & Stock, J.T. 2011. Re-examining heritability: genetics, life history and plasticity. *Trends in endocrinology and metabolism* 22(10): p.421–8.

- Wescott, D.J., & Cunningham, D.L. 2006. Temporal changes in Arikara humeral and femoral cross-sectional geometry associated with horticultural intensification. *Journal of Archaeological Science* 33: p.1022–1036.
- White, T., Black, M., & Folkens, P. 2011. *Human Osteology*. Berkeley: Academic Press.
- Wiley, A.S. 2012. Cow milk consumption, insulin-like growth factor-I, and human biology: A life history approach. *American Journal of Human Biology* 24: p.130–138.
- Woitek, U. 2003. Height cycles in the 18th and 19th centuries. *Economics and Human Biology* 1: p.243–257.
- Wood, J.W. et al. 1992. The Osteological Paradox: Problems of Inferring Prehistoric Health from Skeletal Samples. *Current Anthropology* 33: p.343–370.
- Young, N.M., Wagner, G.P., & Hallgrímsson, B. 2010. Development and the evolvability of human limbs. *Proceedings of the National Academy of Sciences* 107: p.3400–3405.
- Zemel, B.S., Riley, E.M., & Stallings, V.A. 1997. Evaluation of methodology for nutritional assessment in children: anthropometry, body composition, and energy expenditure. *Annual Review of Nutrition* 17: p.211–35.
- Zimmermann, M.B. 2011. The role of iodine in human growth and development. *Seminars in Cell and Developmental Biology* 22: p.645–652.