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Legs and Hills

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Abstract

Relatively longer leg length is a feature of the genus *Homo* that is often argued to have evolved due to selective pressures from a greater reliance on endurance running. Within the genus *Homo*, however, Neanderthals had relatively short legs with shorter tibiae – a characteristic that has been hypothesized to be a hindrance for running yet advantageous for locomoting on sloped terrains. This thesis tests three hypotheses relating to lower limb proportions and running performance: does morphological variability correspond with a) speed on flat and uphill terrain during a workout completed by cross-country athletes, or b) athletic performance during a 5-stage ultra-marathon, or c) lab measured running efficiency? The findings show no relationships, or weak non-significant relationships between leg length and crural index with measurements of athletic performance. This suggests that the variability in leg length among *Homo sapiens* does not have significant energetic consequences.

Key words: Evolution, morphology, endurance running, terrain, anthropometrics, 3D body scanning, human athletic paleobiology.

Summary

Anthropologists have theorized that relatively longer leg length evolved in the genus *Homo* approximately 2 million years ago as part of a general adaptation to endurance running. However, within the genus *Homo*, the Neanderthals presented relatively shorter leg lengths, a feature which has led some researchers to theorize that Neanderthals were inefficient at running, and perhaps locomotion in general. Researchers have used experimental evidence from contemporary humans walking and running on flat treadmills to support these theories, however, Neanderthals frequently lived in mountainous and hilly environments. It has been hypothesized that the unique morphology of Neanderthal lower legs and their short calves relative to total leg length would have been beneficial for climbing sloped terrain – however this has never been directly tested.

This thesis employs three tests to examine how leg length, and calf length relative to total leg length correspond with characteristics of running speed and efficiency on flat and uphill terrain. The first test examines how variation in the leg lengths among cross-country runners relates to how fast they run on flat and uphill segments during a workout. The second test examines how variation in the leg lengths of ultra-runners corresponds with how fast they run during a 5-day race through the Andalucía region in Spain. The third test considers how the leg lengths of the ultra-runners relates to the amount of energy used while running on a treadmill. From these tests, there were no findings to support the theory that longer leg length aids in faster and more efficient locomotion. There were also no findings which supported the theory that relatively shorter calves are advantageous for running uphill. Instead, I suggest that the variability in leg lengths among contemporary humans is not significant enough to display differences in running performance. The greater differences in leg length between species may lead to such energetic differences, but this is not directly testable through experimental methods.

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Chapter 1 – Introduction

The evolutionary significance of variation in human limb proportions has been the focus of several theories relating to the influence of climate and bipedalism. Following our African origin, modern humans managed to colonize almost every corner of the world. Our capacity to adapt to new climates through biological and cultural means has been the foundation of the success in the global dispersal of our species. Over the last 7 million years, hominins[1] have also been developing the capacity to walk and run through structural changes in our musculoskeletal anatomy. From the fossil record to present day, there remains a wealth of phenotypic diversity within and between populations. This inter-population variability has been of great interest to anthropologists trying to understand the evolutionary and adaptive significance of the human phenotype, with much of this interest being devoted to the impact of climate and bipedalism on human evolution.

Like other mammals, human body proportions appear to be strongly influenced by climatic factors as described by Bergmann's and Allen's rules. Bergmann's (1847) rule is based on the relationship between body weight and climatic temperature – where in colder climates Bergmann's rule would expect to see higher body masses, and in warmer climates lower body masses. Allen's (1877) rule is based around body proportions. Allen's rule holds that shorter limbs are expected to be found in cold climates, and longer limbs are expected to be found in warm climates. Bergmann's and Allen's rules have been repeatedly tested and verified among mammals, and humans generally conform to these rules as well.

Roberts (1953, 1978) originally applied Bergmann's and Allen's rules to humans, showing that human body mass and relative sitting height (sitting height / stature) exhibit strong negative relationships with mean annual temperature. Subsequent research has confirmed this relationship, though it is not as strong as originally reported (Katzmarzyk & Leonard, 1998). Katzmarzyk and Leonard (1998) found that there had been a secular increase in body mass in the 40 years between Roberts (1953) study and their own –

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[1] I use the term *hominin* throughout this thesis to refer to the bipedal great apes of the taxonomic tribe *Hominini*. Although chimpanzees are technically apart of this tribe, and are not habitually bipedal, the term *hominin* is a nice shorthand for the bipedal apes – past and present – when discussing the evolution of bipedalism.

particularly in tropical populations where there was considerable variability in body mass. Their study suggests that climate has had a strong evolutionary influence on body proportions and body mass, but it is also important to consider factors external to climate – such as nutrition and lifestyle changes – when examining the morphology of contemporary humans. There is additional evidence showing that other climatic variables like mean annual precipitation might have an effect on body proportions among humans (Wells et al., 2019), and the stress associated with growing up in a hypoxic environment has some impact as well (Payne et al., 2018; Pomeroy et al., 2012). Over the course of evolution, however, many authors have reported that climatic factors likely had the strongest influence on the evolution of body mass and limb length.

Research has shown that the body morphology of fossil hominids varies in accordance with thermoregulatory principles put forth by Allen and Bergmann, with factors like nutritional stress and precipitation explaining less of the observable variation in the human fossil record (Ruff, 1994; Will et al., 2021). In the context of the fossil record, Neanderthals conform exceptionally well to Bergmann's and Allen's rules. As exemplified by their high body mass and relatively short lower limbs which can be inferred from their large femoral heads, broad pelvises, and relatively short tibiae – Neanderthals display several traits which are consistent with a cold-adapted morphology (Holliday, 1997; Weaver, 2009). In comparison to contemporary human populations, Neanderthals appear to be even more cold-adapted than high latitude populations, with researchers suggesting that their phenotype was *hyperpolar* (Holliday, 1997).

In the evolutionary sense, body proportions and climate are most relevant to one another as body proportions can accurately be reconstructed from skeletal remains, and climatic variation has been a persistent factor in evolutionary history. At the same time, the evolution and refinement of bipedal locomotion has also been a major trend within the hominin lineage, as one of the defining characteristics of hominins is their striding bipedalism – which humans have become quite efficient at. And like climate, the evolution of bipedalism can be reconstructed and inferred through the hominin fossil record.

The contributing factors to the origins of bipedalism remain a mystery, but the fossil evidence has given excellent clues about when and where it arose. The earliest evidence of bipedalism comes from a *Sahelanthropus tchadensis* skull dating to 7 million years ago (MYA), which had an antero-inferiorly located foramen magnum – a feature indicative of an upright posture and bipedalism (Zollikofer et al., 2005). The characteristically bipedal femur of *Orrorin tugenensis* dating to 6 MYA (Richmond & Jungers, 2008), and a wealth of post-cranial fossils from the genus *Australopithecus* - spanning 4.9 – 2.0 MYA show the continuation, variation, and refinement of bipedal locomotion over the course of human evolution. Then the hominin fossil record covering the last 2 million years demonstrates that the fossil representatives of the genus *Homo* were likely habitually bipedal, walking and running in a manner similar to modern humans (Bramble & Lieberman, 2004; Hunt, 1994). With the progression of knowledge on the origins of bipedalism arose an interest from biological anthropologists in understanding how efficient hominins were at walking and running.

Efficiency is somewhat loosely defined among biological anthropologists, but it can be generally understood as the mass-specific cost to perform a task. Efficiency has typically been estimated in lab settings with modern human study participants by taking VO_2 (oxygen consumption) measurements while the participants are walking or running, and studying the results in conjunction with anthropometric data – especially leg length. These sets of metrics are then compared and extended to the fossil record (e.g., Raichlen et al., 2011; Steudel-Numbers & Tilkens, 2004; Steudel-Numbers et al., 2007). Locomotor efficiency (the anthropological term) is somewhat similar to the kinesiological term running economy, which is defined and measured by VO_2 consumption while running at a given velocity (Anderson, 1996). However, kinesiologists and engineers have recommended against associating limb lengths with how well people can walk or run (Kramer & Eck, 2000; Lacour & Bourdin, 2015), with previous research finding no evidence of a relationship between leg anthropometrics and running economy (Williams & Cavanagh, 1987). Though when considering interspecific comparisons, limb lengths are some of the only metrics available to readily predict locomotor efficiency.

In a study of humans walking on treadmills, Steudel-Numbers and Tilkens (2004) found that among their participants subjects with longer legs had a significantly lower cost of locomotion when walking. They extended this finding to interpret that fossil hominins such as Lucy (*Australopithecus afarensis*) and Neanderthals would have experienced energetically costly locomotion and reduced efficiency when walking due to their short lower limbs. The authors also suggested that Neanderthals would have had an energetic cost of locomotion 30% greater than modern humans due to their short but robust stature. Steudel-Numbers et al. (2007) later extended their research to running, investigating the relationships between limb lengths and locomotor efficiency. It was observed that people with relatively longer legs tended to spend less energy running than those with shorter legs – when relative leg length was standardized to body mass. They suggested that the elongation of limbs in the genus *Homo* likely contributed to greater running efficiency, but the short limbs of Neanderthals would have contributed to inefficient running (Steudel-Numbers et al., 2007).

There is further evidence to indicate that calcaneal tuber length and Achilles tendon moment arm length are closely related to VO2 max and running efficiency. Research has shown that having a shorter heel corresponds with having a shorter Achilles tendon moment arm, allowing for a greater release of energy in the Achilles tendon, and therefore greater running efficiency (Raichlen et al., 2011; Scholz et al., 2008). As humans have shorter calcaneal tubers and Achilles tendon moment arms compared to Neanderthals, they have more power transfer in their Achilles tendons when running – allowing for greater running efficiency (Raichlen et al., 2011; Scholz et al., 2008). Raichlen et al. (2011) used this line of evidence to suggest that Neanderthals would have been hindered in their running abilities by less energetic release from their Achilles tendons.

Many of the arguments surrounding Neanderthal locomotion suggest that their morphologies were cold-adapted, but not necessarily suited for the levels of locomotor efficiency seen in *Homo sapiens*. There are, however, several lines of evidence showing that Neanderthals had high activity levels – which means they would have engaged in some walking or running (Lieberman & Shea, 1994; Ruff et al., 1993; Shaw & Stock, 2013; Snodgrass & Leonard, 2009; Sorensen & Leonard, 2001). There is also recent research indicating that thermal-adapted morphologies may be beneficial for competing in hot and cold climate ultra-marathons (a race longer than a marathon, can be lengths of 50km to multi-week runs across the United States). Longman et al. (2019, 2021) found that finishers of ultra-endurance races in hot climates tended to have relatively longer lower limbs, and lower BMIs (i.e., traits typical of a hot-adapted population) than finishers of cold climate races, who tended to have higher BMIs and shorter lower limbs.

With these studies on hominin locomotor efficiency, researchers have taken diverse experimental approaches to predict how well Neanderthals would have been at walking and running. However, the experimental research has been conducted in labs with participants walking and running on flat treadmills, whereas Neanderthals frequently occupied mountainous and hilly environments. As climate and locomotor efficiency have been two factors considered heavily in studies on Neanderthal morphology, Higgins and Ruff (2011) suggested that terrain relief be considered in these sorts of studies as well. To address the influence of terrain on locomotion they generated a mathematical model comparing the leg lengths of modern humans and Neanderthals to explore how well they would walk uphill. Of particular interest to the authors was how the relatively short tibiae and lower crural indices (a metric reflective of the length of the tibia relative to the length of the femur) of Neanderthals would have impacted their uphill hiking capabilities. Their models tested how the limb lengths of humans and Neanderthals would impact step length at a given hip excursion angle, and hip excursion angle at a fixed step length. The calculation and functional significance of hip excursion angle remains loosely defined by Higgins and Ruff, though their results still provided interesting insights on the potential functional significance of short limbs and lower crural indexes for uphill locomotion. They found that humans, on average, have longer steps on flat terrain courtesy of their longer leg lengths. However, on sloped terrain that effect disappeared as Neanderthals were predicted to have similar step lengths to modern humans. As this paper used a mathematical approach to their research questions, Higgins and Ruff (2011) recommended that an experimental approach was required to better address their theory.

Research projects in this realm of biological anthropology typically use biomechanics labs to help test their hypotheses, though there have been a few studies in recent years using GPS data and the social media app Strava to explore human locomotion and physiology in field settings (e.g., Best & Braun, 2017; Furusawa, 2012). As well, researchers have advocated for the use of 3D body scanning in research interested in morphological variation in limb segments (for example, the volume and length of the thigh) (Treleaven & Wells, 2007). With these methods in mind, this thesis uses three approaches to study human locomotion from an evolutionary perspective. The first research project presented is a test of how variation in limb segment length and volume corresponds with the step parameters (i.e., step length, step rate) and speed on flat and uphill terrains during a workout completed by Western's varsity cross-country team. The second research project from this thesis examines how limb segment length and volume correspond with stage finishing time across a 5-day ultra-endurance race in Andalucía, Spain. For the third test, running economy data collected in a controlled laboratory setting from a subgroup of the ultra-runners are analyzed. With these experiments, I can present the following hypotheses:

i. Following the predictions of Higgins and Ruff (2011) that lower crural indices are advantageous for uphill locomotion, positive relationships will be observed between athletic performance and crural index on the uphill segment of the cross-country workout, and on stages of the ultra-marathon with greater levels of elevation gain than descent.

ii. In accordance with the theory that relatively longer legs are advantageous for more efficient running, negative relationships will be observed between relative leg length and stage finishing time throughout the five stages of the ultra-marathon.

iii. Similarly, positive relationships will be observed between relative leg length and running economy among the ultra-runners.

Chapter 2 – Literature Review

This chapter will review the literature relevant to my thesis, ranging from human evolution to experimental approaches to studying physical activity. The chapter begins by examining the influence of climate on human evolution. It then goes on to explore the evolution of bipedalism over the last 7 million years. The section covering bipedalism concludes by discussing the influence of terrain on bipedal locomotion, and then goes on to highlight the influence of terrain on biomechanics. I then review experimental approaches to studying physical activity which inspired the methodologies used in this thesis. This chapter concludes by examining the components of the body – beyond just legs – involved in bipedal locomotion.

2.1 Climate and Human Evolution

2.1.1 The Influence of Climate on Evolution

Bergmann's (1847) and Allen's (1877) rules are two of the oldest and most foundational theories in understanding how mammalian species adapt to their environments. These two theories hold that the morphology of mammals varies systematically in accordance with climate, latitude, and mean annual temperature. Bergmann's (1847) rule is based around the relationship between body mass and temperature. It predicts that in areas with colder annual temperatures you will find animals with higher body masses, whereas in hotter and tropical climates you will find animals with lower body masses. Allen's (1877) rule is based on the relationship between body proportions and climate. This rule holds that in areas with colder annual temperatures, you will find individuals with shorter legs, shorter arms, and a greater sitting height relative to total stature. In hotter climates, this rule holds that longer legs, arms, and a shorter sitting height will be found. Bergmann's and Allen's rules are often explored and applied together, and they help to explain the thermoregulation of mammals. As someone with a shorter stature and higher body mass – or someone you may expect to find in a cold environment – will be able to both hold in and generate heat more efficiently, and someone with longer limbs, a greater stature, and lower relative body mass would be able to dissipate heat more readily.

Research in anthropology has demonstrated that human morphology is generally in accordance with Bergmann's and Allen's rules. Roberts (1953) originally described the application of Bergmann's rule to humans, finding that there is a strong correlation between body mass and mean annual temperature among a global sample of body-mass-index (BMI) data. He later extended these findings to Allen's rule as well, showing that people living in colder regions have shorter legs and greater relative sitting heights than people living in warm regions (Roberts, 1978). In re-evaluating these findings and principles, Katzmarzyk and Leonard (1998) found that these rules apply to humans, though the relationship is not as strong as originally reported, or in data that comes from after 1950 – as there are an array of nutritional and environmental factors which also contribute to human morphological variation. Katzmarzyk and Leonard (1998) also noted there had been a secular increase in body weight among tropical populations in the time between Robert's publications and their own, which had contributed to changes in statistical relationships.

Among living humans, stature, weight, sitting height, and BMI are the more commonly tested variables used to understand the relationship between anthropometrics and climate or mean annual temperature, as these data are readily available from anthropologists and public health databases (Foster & Collard, 2013; Katzmarzyk & Leonard, 1998; Leonard & Katzmarzyk, 2010). However, among fossil humans, the relationship can be more readily tested with the array of variables available from the skeleton (but greater creativity is also required to understand these relationships as the fossil record is inherently incomplete).

Ruff (1994) developed one of the first tests on the application of thermoregulatory principles to fossil hominin morphology, finding that it varies systematically in accordance with Bergmann's and Allen's rules. His work included anthropometrics derived from contemporary humans, the remains of Lucy (AL 288-1), three early modern human fossils, and four Neanderthal (*Homo neanderthalensis*) fossils, with analogies drawn between the fossils and modern humans (*Homo sapiens*). In 2021 with a greatly expanded dataset, Will et al. (2021) sought to test how different environmental variables predict observable increases or changes in brain and body size in the genus *Homo*. They found that body size among the genus *Homo* over the last million years does vary in accordance with climate and the thermoregulatory rules put forth by Bergmann. While factors such as nutritional stress and proxies for precipitation correlated with brain size but did not fully explain the observable variation.

2.1.2 Neanderthals and Cold Adaptation

Beyond papers examining broader trends in hominin evolution there have been many projects looking at the anatomy of Neanderthals as it pertains to the adaptive significance of their morphology. Neanderthal morphology is of interest as they bear great similarity to humans morphologically, genetically, and temporally (Green et al., 2010; Sykes, 2020; Trinkaus, 1986), while there are a few key differences as well – such as the absence of a mental eminence, barrel-shaped thoraces, and a hyper-robust morphology. The functional significance of Neanderthal's unique morphology has been of interest to understand how this species was able to survive for nearly 500 thousand years in an array of environments, including the cold glacial climate of Pleistocene Eurasia.

Neanderthals had relatively shorter statures, yet they also had large femoral heads and broad pelvises, indicating they likely had high body masses for their stature (Holliday, 1997). They also had relatively long and wide torsos, and short distal limb segments (lower leg and forearm) relative to trunk height and limb lengths (Holliday, 1997). These anatomical features have led researchers to conclude that Neanderthals conform exceptionally well to the thermoregulatory laws put forth by Bergmann and Allen (Holliday, 1997; Ruff & Holliday, 1997; Steegmann & Holliday, 2002; Weaver, 2003, 2009).

Researchers have also predicted the total energy expenditure (TEE) of Neanderthals during summer and winter, calculating that Neanderthals would have been spending significantly more energy in a day than modern humans. Predictions of TEE for Neanderthals have suggested that males would have had a basal metabolic rate (BMR) of around 1800kcal/day and been spending 4000-5000 kcal/day during summer months, and 5300-6700 kcal per day during winter months (Snodgrass & Leonard, 2009). Females were predicted to have had a BMR of about 1400 kcal per day, with a TEE of 2900-4000 kcal/day during the summer, and 3800-5200 during the winter (Snodgrass & Leonard, 2009). The higher values from the winter months reflect the metabolic upregulation that occurs in cold environments, alongside the authors' prediction that more protein would have been consumed during the winter. To make a comparison to humans, TEE has been measured using doubly labelled water among Yakuts, an Indigenous population living in high-latitude Siberia with a mix of subsistence and urban lifestyles. These measurements indicated that during the winter, males had an average TEE of 3100 kcal/day with a BMR of 1800 kcal/day, and females had an average TEE of 2300 kcal/day with a BMR of 1500 kcal/day (Snodgrass et al., 2006). The differences in BMR and TEE between Neanderthals and modern humans reflect Neanderthals having higher activity levels, as well as relatively higher body masses for their stature.

Alongside research on Neanderthal physiological thermoregulation has been research on their potential cultural buffers against the cold. Some researchers, such as Holliday (1997) think that Neanderthals had insufficient cultural buffers against the cold, hence their hyperpolar morphology. Other authors such as Sykes (2020) and Ocobock et al. (2021) have argued that cultural adaptability was key to Neanderthal survival and that the archaeological record reflects adaptive changes in culture occurring in conjunction with climatic changes. Beyond material culture, researchers have stated that high activity levels – as reflected in the skeletal biomechanics of Neanderthals – would have served as a necessary cultural buffer against the cold (Ocobock, 2016; Sykes, 2020), with the thermic effect of food stemming from high protein diets contributing to elevated metabolic rates as well (Richards et al., 2000; Snodgrass & Leonard, 2009).

2.1.3 The Energetics of Thermoregulation

Many have considered the broader impacts of climate on the evolution of the human body form, though there has also been some attention devoted to understanding the more nuanced ways that the body copes with changes in temperature. These research projects have used field and lab settings to experimentally study how human morphological variation impacts heat dispersal or athletic performance. These sorts of experimental papers begin to illustrate the importance of considering the integration of bodily systems, and the complexity underlying the interactions between human biology and the natural environment.

Cross et al. (2008) studied how differences in body segment sizes impact the ways people thermoregulate, and how different limb segments contribute to different levels of heat dispersal. Prior to this study, many researchers had considered simple models of thermoregulation which viewed the entire body as a cylinder, with the key dimensions of height and body breadth defining the surface area to volume relationship and thermoregulatory properties of the body. Each portion of the body is, however, individually exposed to the environment, and they interact with the environment in different ways – depending on their size and how they move. With these differences in morphology and movement in mind, Cross et al. (2008) recognized that there is the potential for there to be subtle differences in thermoregulation capacities between different parts of the body. Differences in body size and shape will contribute to how much the limbs move through the air during locomotion, or how much heat can be dissipated during locomotion based on skin surface area. Different parts of the body will also move varying amounts during locomotion (for example, the lower arm moves 25% more than the torso during walking). As such, the authors conducted a study of people walking on treadmills in various temperatures. Cross et al. (2008) found that the head and torso contribute to the highest levels of heat dissipation during locomotion at all temperatures. Among the limbs, the thigh contributes to the highest level of heat dissipation at 20-30^{O}C. However, at 35ºC it was found that the arms, hands, and lower legs contribute to high levels of heat loss, with the thighs contributing the least. This paper illustrated that it is important to consider the body as more than a cylinder when discussing thermoregulation, and highlighted the individual importance of the head, torso, arms, and legs in thermoregulation during locomotion.

The influence of differences in body size on thermoregulation has been considered in the study of ultra-endurance runners taking part in hot and cold climate events. Ultra-endurance races offer unique opportunities for the study of human adaptation as participants willingly subject themselves to high degrees of energetic stress, which in turn has profound effects on their metabolic and physiological systems (Longman et al., 2020). Longman et al. (2018) first applied the predictions of life history theory to examine how male ultra-runners differentially allocate energy to their immune systems and reproduction systems before and after a 100-mile race. The authors found that the investment into immune function is raised slightly following the race, with investment into the reproductive system decreasing substantially following the energetic stress of running 100 miles.

In subsequent publications, Longman et al. (2019, 2021) sought to examine the application of Bergmann's and Allen's rules to ultra-endurance runners taking part in races in hot and cold climates. Longman et al. (2019) first observed that males who finished races in hot climates had longer relative leg lengths, as well as lower BMIs compared to those who finished cold races. It was later observed that females may have stronger associations between athletic performance and phenotype than males as females who finished races in hot climates had significantly lower weights, body mass indices, and greater leg lengths than those who finished cold climate races (Longman et al., 2021). In both these papers, the authors claimed that these differences in morphology between hot and cold climate racers may be evidence that some self-selection occurs among participants to enter races in climates which may be more suitable for their morphology.

The energetics of thermoregulation have been studied among Indigenous populations, and people participating in wilderness expeditions. Research among the Yakuts of Siberia has shown that resting metabolic rate and total energy expenditure increase significantly in the winter months, particularly among those that maintain herding and farming activities in the winter (Leonard et al., 2014; Snodgrass et al., 2006). The costs of thermoregulation in hot environments are a little less studied, but have been examined among the participants of outdoor education programs and wilderness expeditions. Ocobock (2016) found that among outdoor educations participants in hot, cold, and temperate conditions, those participating in the cold climate had the highest basal metabolic rates and predicted total energy expenditure. Ocobock noted that this is likely due to the high energetic costs of thermoregulating in cold conditions – coupled with the fact that the cold environment participants had the highest activity levels.

2.2 Evolution of bipedalism

Alongside research on the impact of climate on human evolution has been research on bipedalism. Wheeler (1984, 1991) was one of the first to examine the evolutionary influences of climate and bipedalism on humans, arguing that standing and walking on two feet would have allowed humans to get less direct exposure to the sun, lose their body hair, forage more efficiently, and gain thermoregulatory advantages. The theories and evidence underlying these ideas have become more refined as more fossil evidence has been discovered, and experimental methods have become increasingly intricate. This section will explore the evolution of walking and running abilities as assessed through fossil evidence and experimental methods with modern humans.

Many researchers have suggested that the human form of bipedalism is the more refined and efficient form of bipedalism, and that it likely arose with *Homo erectus* (Bramble & Lieberman, 2004; Holliday & Falsetti, 1995; Isbell et al., 1998; Jungers, 1982; Lieberman et al., 2006; Steudel, 2005; Steudel-Numbers et al., 2007; Steudel-Numbers & Tilkens, 2004). These claims are based on the authors' interpretations of the relationship between leg length and the energetics of locomotion. The claim is that longer legs will allow an individual to take longer steps, generate greater momentum, and therefore walk or run faster without carrying any extra energetic burden. Some researchers have found correlations between leg length and oxygen consumption rates during walking and running, in which people with longer legs tend to consume relatively less oxygen when walking or running (Steudel-Numbers et al., 2007; Steudel-Numbers & Tilkens, 2004). As humans and many other members of the genus *Homo* have longer legs than other hominins, this idea that longer legs equate to greater locomotor efficiency is held among many paleoanthropologists.

Early research on bipedalism and locomotor efficiency estimated step lengths and rates among hominins based on their skeletal proportions. Jungers (1982) predicted that Lucy (*Australopithecus afarensis*) would have had to take short and slow steps to move around. He suggested that Lucy likely had a "strolling behaviour" and had not fully adapted to contemporary bipedalism (Jungers, 1982: 677). Other authors such as Stern and Susman (1983) proposed that the locomotor anatomy of *Au. Afarensis* was indicative of a transitional form of locomotion between arboreality and habitual bipedalism. With implications that australopiths, particularly *Au. Afarensis*, may have been slow walkers, Kramer and Eck (2000) sought to challenge assumptions that the form of bipedalism practiced by the genus *Homo* was optimal, and those that came before it were transitional. Kramer and Eck (2000) compared the predicted energetic cost of locomotion for Lucy with that of a modern woman and found that the two would have had similar costs of locomotion, though due to her stature, Lucy would have taken shorter steps. As such, the authors suggested that *Au. Afarensis'* shorter limbs may have been a part of a slow-foraging niche with limited daily travel distances. Further, the authors noted that long limbs are not the inevitable product of successful bipedalism, so they questioned what selective pressures led to the long legs commonly observed in the genus *Homo*.

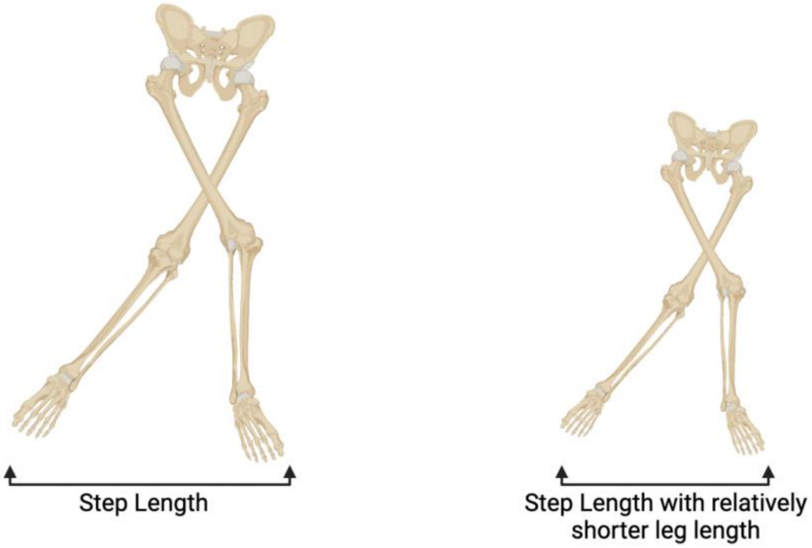

Figure 2.1 Representation of step lengths from an individual with longer legs, and an individual with shorter legs. Created with BioRender.com

Beyond just having longer legs and greater locomotor efficiency, however, there must have been some evolutionary explanation as to why longer legs arose in the genus *Homo* – to which there have been many suggestions. Aside from the influence of climate on the evolution of limb proportions, it has been argued that the relatively long limbs which arose in the genus *Homo* may have been to satisfy larger daily ranges, daily travel distances, and to satisfy the necessity for more efficient foraging (Isbell et al., 1998). A more widely discussed theory, due to its public appeal and its repeated validation, is that many features of contemporary human anatomy and physiology arose to satisfy a greater reliance on endurance running as a part of our ecology.

An influential paper was published by Bramble and Lieberman (2004) claiming that human beings evolved to be efficient distance runners, with alterations arising in our physiology and anatomy to satisfy this. There were many elements of human anatomy and physiology noted in this paper which may help humans be better runners – for example, a reduction in body hair, the capacity to sweat, long Achilles tendons, and long legs. The original paper stated that endurance running capabilities likely arose with *Homo erectus* about 2 million years ago, as the fossil record shows them as long legged and fully bipedal. Though with many features of the human body noted as being functionally significant for endurance running, many researchers began to look further into elements of our anatomy which may have evolved due to running. And this was done with new (to anthropology) experimental methods in laboratory settings using contemporary humans as analogies.

Steudel-Numbers & Tilkens (2004) found that leg length had a significant positive effect on the rate of oxygen consumption while walking. They found people with longer limbs and higher levels of lean mass took longer steps and spent less energy when walking when the data were controlled for body size. These authors have used their findings to infer that fossil hominins with shorter stature (e.g., Neanderthals, australopiths) and lower levels of lean mass would have been less efficient than other hominins possessing long limbs, such as those in the genus *Homo*. In examining the relationship between limb length and the cost of transport when running, Steudel-Numbers et al. (2007) observed partial positive correlations between the cost of transportation and limb length relative to body mass. Again, the authors took these findings to infer that hominins with shorter limbs, like Neanderthals and members of the genus *Australopithecus*, would have been inefficient at running, but hominins with longer limbs would have been more efficient.

Two more specific anatomical traits that have been reported to have evolved into their present-day form to satisfy endurance running have been the gluteus maximus and the Achilles tendon. The human form of the gluteus maximus was argued by Lieberman et al. (2006) to have evolved exclusively in response to a greater reliance on endurance running. They described the human form of the gluteus maximus in comparison to that of chimpanzees as being much larger relative to body size and lacking the insertion in the iliotibial tract that is seen in chimpanzees. The experimental portion of their study found that the gluteus maximus was largely inactive among their research participants when walking on a treadmill, but highly active when running. With these results, the authors discussed the anatomy and evolutionary trajectory of the pelvis and gluteus maximus of chimpanzees, australopiths, and humans. They proposed that the gluteus maximus was long and suited for climbing among chimpanzees, but the *Australopithecus* form appeared to be transitional between humans and chimpanzees and was therefore not suited for endurance running.

The other anatomical trait that has been argued to have evolved for enhanced endurance running capabilities has been the Achilles tendon. Achilles tendons are longer in humans, and act like a spring while running. Lengthened Achilles tendons are coupled with shortened calcaneal tubers, which allows for greater releases of energy when striding. There have been two research papers that have demonstrated shorter heels correlate with VO_2 during running and are associated with greater running efficiency (Raichlen et al., 2011; Scholz et al., 2008). Raichlen et al.'s (2011) study also included some comparisons between Neanderthals and humans. Although calcanei are not often preserved in the fossil record, Raichlen et al. (2011) presented the data of a few Neanderthal calcanei, and suggested that as Neanderthals possessed relative larger calcanei, they would not have been able to get the same energetic release from the tendons as humans and would have been less efficient at running.

In the papers reviewed above, the authors have generally argued that the Neanderthals would have been inefficient at walking and running. As Neanderthals had relatively short but robust statures, short legs, and apparently robust calcaneal tubers as well, researchers have suggested that their anatomy would have made bipedal locomotion energetically costly (Holliday & Falsetti, 1995; Raichlen et al., 2011; Steudel-Numbers et al., 2007; Steudel-Numbers & Tilkens, 2004). However, in the experimental portions of these papers they have studied participants walking and running on flat treadmills, whereas Neanderthals most often lived in hilly or mountainous environments.

To address this mismatch in experimental conditions, Higgins and Ruff (2011) developed a mathematical model to predict Neanderthal and modern human biomechanical characteristics while walking uphill. Of specific interest to the authors was how the crural index (figure 2.2) and relatively short tibiae of Neanderthals would have impacted their step length and step rate over different terrain. Higgins and Ruff's model was able to confirm that on flat terrains, *Homo sapiens* have longer steps on average courtesy of their long legs. However, on inclines, that effect disappeared. Their model

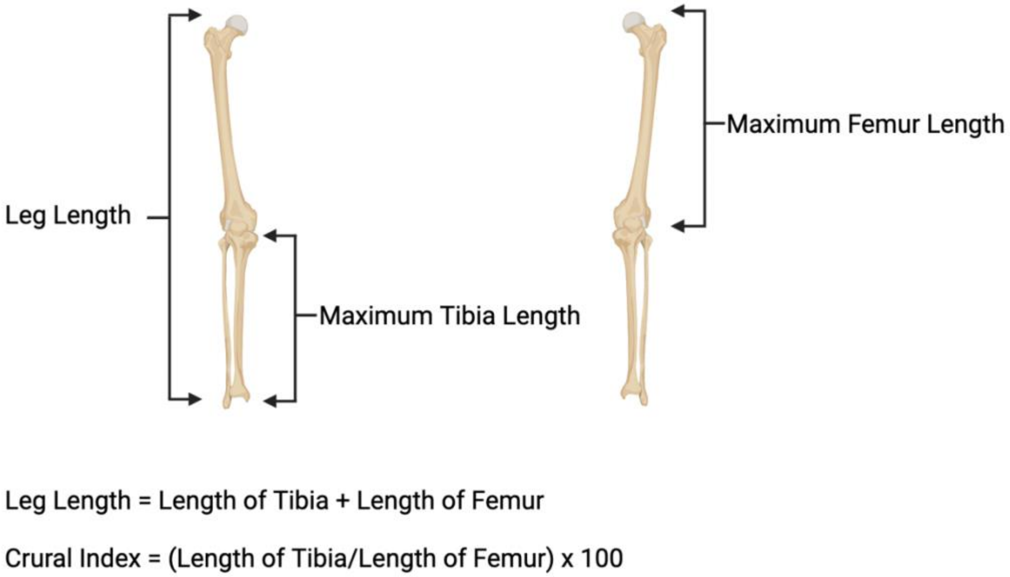

Figure 2.2 Diagrammatic representation of the measurements of leg length, femur length, and tibia length on the skeletal lower limbs. Image created in BioRender.com.

predicted that Neanderthals and modern humans would have had similar step rates, excursion angles at the hips, and step lengths when locomoting on sloped terrain. Higgins and Ruff (2011) suggested that at a given hip excursion angle shortened distal limb segments may have been an advantageous trait for climbing rugged, hilly, or mountainous terrains, but that more experimental work was needed. Figure 2.3 presents a diagrammatic representation of this theory (in Higgin's and Ruff's analysis of crural indices and locomoting uphill, they kept leg length and excursion angle at the hip controlled, with the crural indices representative of that of humans and Neanderthals).

Some have cautioned that the anthropometric data used in these experimental studies, especially limb lengths, are not a great predictor of locomotor efficiency as there are so many components involved in locomotion which should be considered as well (Kramer, 1999; Kramer & Eck, 2000). In addition, the daily energy budgets for fossil hominins cannot be accurately predicted simply by comparing limbs lengths and energy expenditure of living humans walking or running on treadmills (Higgins & Ruff, 2011). And although the energy expenditure of humans locomoting on treadmills is likely similar to that of outdoor locomotion, there are different muscles used in treadmill

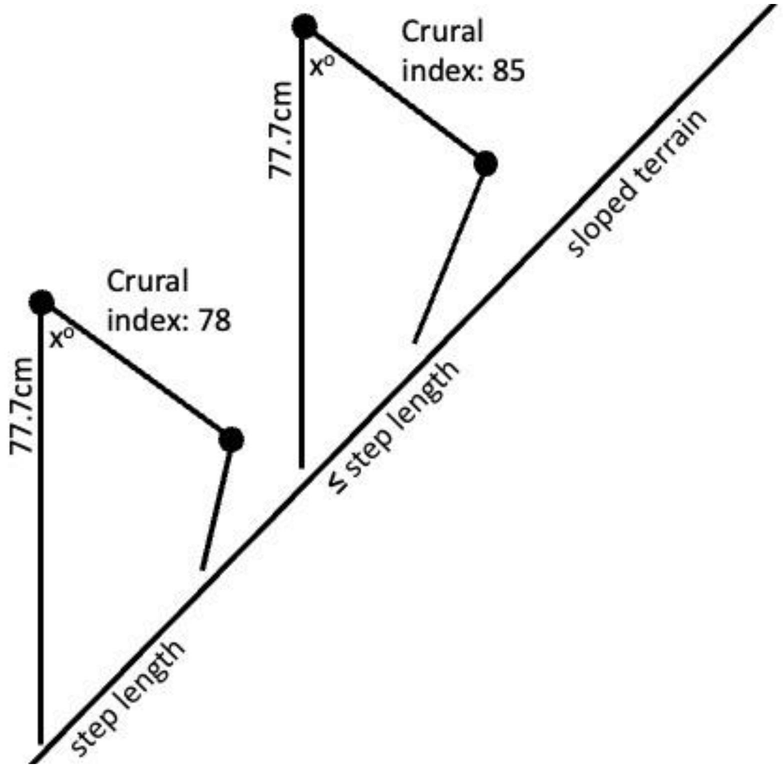

Figure 2.3 Interpretation of Higgins and Ruff's (2011) schematic drawing of their theory that animals with relatively longer distal leg segments should have a relatively shorter step length on sloped terrain for a given excursion angle at the hip (x).

locomotion, and VO_2 is not impacted by wind resistance (Saunders et al., 2004). However, when trying to understand the locomotor efficiency of fossil hominins, there are limitations on the data that can be used given that only the skeleton is preserved in the fossil record.

2.3 Biomechanics

This section will explore what is known about the relationships between bipedal locomotion and sloped terrains. I first outline the impact of activity levels and variable terrains on skeletal biomechanics. I then discuss how mountainous and hilly environments pose different challenges for walking and running, and how the body responds to locomoting uphill or up mountains. This section concludes by looking at Neanderthal skeletal robusticity.

2.3.1 Biomechanics on Different Terrains

Skeletal robusticity, as understood by the size and shape of a bone, is generally representative of the mechanical loading and stressors that have been experienced in the skeleton through the life course. The relationships between mechanical loading and bone functional adaptation remain somewhat complex as bone re-modelling can be confounded by an array of factors (e.g., diet, genetics, sex) (Pearson & Lieberman, 2004). However, experimental evidence has demonstrated that bone cross-sectional geometry can be used to understand habitual activity among past and present populations (Ruff et al., 2006, Shaw & Stock, 2013). Skeletal robusticity has been studied at length by biological anthropologists trying to understand human behaviour and evolution within and between populations and species. Biomechanical analyses within populations have been used to understand activity levels, mobility patterns, and to interpret the presence of repetitive tasks. For comparisons between populations and species, biomechanical analyses are used to understand how changes in species or lifestyles contribute to differences in bone mechanics.

Although activity levels are often considered in biomechanics, for the purposes here it is important to consider variation in terrain (e.g., flat, hilly, mountainous) which pose different challenges for walking and running around different environments. Holt and Whittey (2019) examined the influence of terrain from a global biomechanics dataset containing samples from hunter-gatherer, agricultural, and industrialized populations. Their analysis categorized the locations from which these samples were drawn as either flat, hilly, or mountainous. Holt and Whittey (2019) found that populations from mountainous environments had higher degrees of femoral strength than those from hilly or flat environments. The samples from hilly and mountainous environments had higher degrees of femoral anteroposterior loading than those from flat terrains. This effect was most pronounced among the hunter-gathers included in this study due to the high mobility nature of their lifestyle. This paper broadly addresses why mountainous and hilly terrains could result in higher levels of strength in bones, but it can be better understood through archaeological studies of mountainous sites.

Least cost path analyses of archaeological sites comparing distances between lithic chert sources and mountainous sites have demonstrated that people would have had to walk substantially further than the way the crow flies to reach the sources. For example, Rissetto's (2012) least cost path analysis of archaeological sites from the Cambria region in Spain found that the least cost distances would have ranged from 4-83km away from the source to site, whereas the straight-line distances were between 3 and 47km. The least-cost paths, or the paths of least resistance, would circumnavigate mountainous peaks and provide the most energetically conscious path to get from chert sites to home base. Straight lines are shorter at the basic level, but they may be more difficult than least-cost paths as they could climb multiple mountain peaks and be less efficient.

The energy expenditure of locomoting uphill was reported by Ulijaszek (1995) to be 2.5x greater than locomoting downhill, and for people who live in mountainous areas, locomoting uphill would therefore take up a larger portion of their daily energy expenditure than locomoting on flat or downhill terrains. Research has also shown that when walking uphill, humans will stake shorter but more frequent steps at a given speed (Padulo et al., 2013; Vernillo et al., 2017). Due to the energetic burden of fighting gravity, as well as moving up an incline, the leg muscles increase their activation, perform more work, and therefore incur a larger energetic cost of locomotion. Vernillo et al. (2017) found that it is the muscles of the hip which incur the largest increase in activation when running uphill. It has also been shown that locomoting on uneven surfaces will increase the energetic cost of transport by up to 24% when walking, and 5% while running (Voloshina et al., 2013; Voloshina & Ferris, 2015). Moving on uneven terrain results in increased muscle activation, particularly in thighs and hamstrings, to aid in both balance and movement. Voloshina and Ferris found that step rate and step length do not alter significantly on uneven terrain, though the ankle decreases its range of motion – likely to aid in stability.

Biomechanical analyses of Neanderthal limb bones have shown that they were highly active during their life courses (Ruff et al., 1993; Shaw & Stock, 2013). Aside from the theoretical work of Higgins and Ruff (2011), there have been no direct studies of Neanderthal biomechanics as it relates to locomoting through mountainous or hilly environments. Many researchers have examined their bones as it relates to high activity levels, as the bones present thick cortical area, robust muscle attachment sites, and are bowed at the proximal ends. These features have been attributed to high levels of mechanical loading through the life course, rather than differences in growth and development (Abbott et al., 1996; Ruff et al., 1993, 1994). Interestingly, the post-cranial skeleton of Neanderthals is more robust that contemporaneous Pleistocene *Homo sapiens*, and more robust than contemporary cross-country athletes running up to 160km per week (Ruff et al., 1993; Shaw & Stock, 2013). Several authors have interpreted that Neanderthals would have been highly mobile as a part of their hunting strategies, and to stay warm in the cold glacial climate that they lived in (Lieberman & Shea, 1994; Ruff et al., 1993; Snodgrass & Leonard, 2009; Sorensen & Leonard, 2001).

It is worth mentioning the potential of an underlying genetic component to skeletal robusticity as reported by Wallace et al. (2012) from their study of high activity/low activity mice with a history of over 80 generations. Wallace et al. (2012) found that mice who had been artificially selected for high amounts of endurance running had larger diaphyseal dimensions at 1 week of age than control mice. As their sample included mice who had an (artificial) evolutionary history of 80 generations – they suggested there may be an evolutionary signal for stronger limb bone geometry for groups with a deep history of high activity levels, and the potential for an underlying genetic cause for higher limb robusticity.

2.4 Experimental ways of studying physical activity

This section now moves away from the study of human evolution to how human evolution and biology can be studied in unique experimental ways. As I was constrained in how my thesis research could be carried out, this section reviews the papers which inspired the methodology used in this thesis. I present studies from anthropologists who have used athletes, GPS trackers, social media, and unique approaches to Bergmann's and Allen's rules to help study human biology and adaptability.

2.4.1 Experimental Methods with Athletes

Athletes have served as useful study participants for several experimental studies of human adaptation and evolution. Longman et al. (2020) outlined the many benefits of using athletes to experimentally test questions about human evolution with the recently defined field of human athletic paleobiology. Athletes are beneficial in this regard as they have undergone the same selection processes as any other human on their anatomical features such as leg length, and they also have higher than average physical fitness levels that serve as a good model when making comparisons to past hominins who would have also had high activity levels. Additionally, the amount of variation in stature and limb proportions among living humans is comparable to the variation among fossil hominins (Will et al., 2017). Though, morphological variation within sports and events follows different patterns of variation depending on the sport. For example, male soccer athletes follow similar levels of variation in height and weight when compared to healthy age-matched males, however, sprinters tend to be more similar in morphology – typically having shorter statures (O'Connor et al., 2007).

2.4.2 Application of GPS data and social media in studies of human activity

Above, I have already reviewed several studies which used athletes as study participants (e.g., Lieberman et al., 2006; Longman et al., 2018, 2019, 2021; Raichlen et al., 2011). Below, I will review two papers to examine experimental methods which are relevant to my thesis. But first, a quick explanation of GPS fitness trackers.

GPS (Global Positioning System) fitness trackers track exactly where people are on earth, how fast they are going, and how far they have gone. In addition, they commonly come in watch form and can provide heart rate and step rate data. GPS watches and trackers have been used to study things like movement and migration patterns among animals. Among humans, GPS trackers have been used in tandem with heart rate data to explore physiological stress and physical effort during tasks and athletic activity.

GPS trackers and heart rate data have been employed among the Roviana of the Salomon Islands. Roviana engage in a fisher-horticulturalist subsistence strategy, and as such Furusawa (2012) sought to explore variability in heart rate and physical activity patterns among Roviana engaging in shore-based and open water fishing activities. He found that participants had the highest heart rates while paddling at the reef edge – where participants were likely paddling at higher speeds, and recommended that GPS is a useful tool for studying physical activity patterns during food gathering activities. Similarly, Best and Braun (2017) tested the application of the social media for athletes app Strava to understand human physiology during mountain and road races. The authors located athlete data from four races (two mountain races and two road races) and gathered several metrics of performance. These metrics included race finish time, time to complete the first/second half of the race, average heart rate over the first/second half, and maximum heart rate (Best & Braun, 2017). The authors found that mountain runners showed little change in heart rate over the first and second half of their races, and they tended to slow down significantly over the second half of their races. Road runners showed an increase in heart rate over the second half of their races, coupled with a slight reduction in pace. Best and Braun (2017) provided some theoretical causes for the changes they observed and recommended that Strava may be used in future studies for the initial stages of physiological research, which may then inspire further lab research.

2.5 Are legs the end of the story?

Much of this review has been devoted to understanding the functional significance of legs and step length from an evolutionary perspective. However, there are many other factors which contribute to running efficiency beyond just leg morphology or step length. This section will briefly conclude the chapter by first discussing the relevance of step length to running efficiency, and then discuss the physiological and mechanical factors relevant to efficient bipedalism.

2.5.1 Step length and running efficiency

Aside from the papers discussed above, research on step length is not well represented in the anthropological literature. Research on step length from kinesiologists has revealed interactions between stature, speed, and step length. Forensic researchers have also tried to estimate stature from foot length and step length (e.g., Jasuja et al., 1997; Kanchan et al., 2015), and some researchers have been interested in step length modifications to understand joint loading and to make recommendations for injury prevention (e.g., Baggaley et al., 2020; Bowersock et al., 2017).

Step length is naturally dictated by the height, mass, and leg length of an individual. While humans are free to choose their step lengths, research has shown that natural step length is not always the most efficient way to locomote (Danion et al., 2003; Sekiya et al., 1997). Artificially dictating step length and rate by having study participants sync their stride to a metronome has shown that altering natural step length can result in more efficient walking and running, as many people tend to overstride in their natural locomotion (Danion et al., 2003; Sekiya et al., 1997).

In publications from kinesiologists looking at the relationships between anthropometrics, step length, and running performance, some variability in results has been observed, though none of them have stated that longer legs equate to being a faster runner. Williams and Cavanagh (1987) did not observe any relationships between running economy and step length nor step length as a percentage of height among trained distance runners. Among elite mid-distance runners, Brisswalter et al. (1996) observed that step length correlated closely with leg length, mass, height, and VO2 max when running at 9 km/h, but at 15 km/h step length correlated with body mass and height, but not VO_2 max. Among sprinters, step length correlates with sprint speed, but step rate does not (Hunter et al., 2004). However, as sprinters increase their speed, they increase their step rate, with step length staying constant. Additionally, Hunter et al. (2004) found that step length and step rate follow a negative correlation independent of leg length – in which shorter step lengths correspond with higher step rates and *vice versa*. These papers on step length do not conclude that having longer legs equates to greater running efficiency. Rather they assess that there are some observable associations between anthropometrics, running economy, and step length, though they cannot be confidently associated with how efficient a runner is.

2.5.2 Do leg dimensions correspond with variation in running performance?

Many of the anthropologists cited here have posited that longer leg length is related to increased running efficiency and that long legs evolved in the genus *Homo* to help improve walking and running capabilities (e.g., Bramble and Lieberman, 2004; Steudel-Numbers & Tilkens, 2004; Steudel-Numbers et al., 2007). The skeleton is all that is preserved in the fossil record, but the relationship between the lengths the femur and tibia with locomotor efficiency has perhaps been overstated in some instances (e.g., Steudel-Numbers et al., 2007). Although longer legs are theoretically able to generate greater momentum while running (Anderson, 1996), Williams and Cavanagh (1987) found that leg segment lengths and volumes showed no relationship with running economy among their research group of trained distance runners. Even with the mechanical and physiological parameters collected from their research participants, they concluded that there is no one characteristic of runners which appears to make them more efficient, but rather it is the sum of characteristics which contributes to improved efficiency.

Biomechanical efficiency is of course inherently relevant to running efficiency as well, with the morphology of a runner contributing to the efficacy of such. Anderson (1996) suggested that average or below average height is beneficial for improved biomechanical effectiveness among males, whereas above average height for females is beneficial. He also suggested that leg morphology with greater levels of mass towards the hips, and narrower pelvises are favourable for improved biomechanical efficiency. There are many mechanical factors contributing to efficient running, including lower peak ground reaction forces, low vertical oscillation of the torso, and having more acute knee angle during swing (Anderson, 1996; Williams & Cavanagh, 1987; see Saunders et al., 2004 for review).

Aside from the anthropometrics and the mechanics of runners, the physiology and aerobic capacity of runners are of importance as well. Maximum oxygen uptake (VO_{2MAX}) is typically higher among elite runners than non-elite runners, but there is little variation among top level runners (Foster, 1983; Noakes et al., 1990; Saunders et al., 2004). Increased blood volume, capillary density, and mitochondrial density are all factors which contribute to increased VO_{2MAX} (Thompson, 2017). Running economy as understood by VO_2 at sub-maximal running velocity, is additionally associated with overall running performance – but is still subject to variability among runners (Anderson, 1996; Thompson, 2017). While there is some evidence that running economy and VO_{2MAX} can be improved with training (with subsequent improvements enhancing race performance), there are still an array of factors which contribute to peak physical fitness among runners. But even then, this type of science is relevant for competitive runners, and not necessarily hunter-gatherers from the Pleistocene. And unlike leg length, the mechanics and physiology of bipedal hominins cannot be readily tested in the fossil record.

Although these mechanical and physiological factors are beyond what I can study in the methods presented below, it is important to remember that humans are complex biological systems. With the many different systems of the human body engaged in every single task that people do, it is important not to get lost in the complexity of something like running by narrowing down theories to the simple components involved – such as legs.

Chapter 3 – Methods

This section will describe the methods and materials used in the research project analyzing how morphological variability in limb segments corresponds with step parameters and athletic performance across flat and uphill terrains of a workout the Western cross-country team completed in the fall of 2021.

3.1 Participant Recruitment

Participants were recruited from the Western University cross-country team (N=6, 1 female, 5 males). Participants were recruited by asking the coach of the cross-country team to forward recruitment information, with potential participants being asked to contact the researcher for more information and to set up a study time. Participants were asked to wear compression clothing or tight gym wear for full accuracy in the body scanner. All data were collected in the PAVE Lab. Participants were given a letter of information and written consent form. After obtaining informed consent, the participants completed a body scan, had their stature measured, bio-impedance data collected, and provided a 3D body scan.

3.2 Ethics

Ethical approval for this research project was obtained by the Health Sciences Research Ethics Board at Western University (Project ID: 119361; Review Reference: 2021-119361-58056). Participants were given a letter of information, and informed written consent was obtained at the start of the study session from all participants.

3.3 Body Scanning

Body scans were obtained using the Size Stream 3D Body Scanner (Cary, North Carolina), a scanning booth that uses infrared depth sensors to provide 3D diagrammatic representations of people and their morphology. Participants were requested to wear compression clothing to ensure the highest accuracy possible when scanning. Participants were instructed to stand in the middle of the scanning booth and hold the booth’s handholds with their palms facing forward, so the scans were orientated in standard anatomical position. Scanning was initiated by the researcher, at which point the computer program provided additional instructions for the participant to stand still, facing forward, relax their shoulders, and indicated when the scanning had started and completed. The researcher then waited for the scan to finish processing to ensure that no significant errors had occurred.

3.4 Stature

Stature was measured using the Seca 274 stadiometer (Hamburg, Germany). Participants were be asked to remove their shoes and socks, and stand in the stadiometer with their heels and shoulders positioned against the stadiometer. They were asked to lower their chin such that their head was positioned in the Frankfurt Position – in which the inferior portion of the orbits are in line with the external auditory meatus. The researcher then placed the headpiece against the scalp, locked the headpiece in place, and recorded their height to the nearest millimeter.

3.5 Body composition analysis

The body composition of participants was estimated using the Seca mBCA 515 bioimpedance analysis system (Hamburg, Germany). Bioimpedance was analyzed using the 8-point system on this device, in which participants stood upright with the knees slightly bent. The participants were barefoot, wearing light clothing, and standing with their forefoot and heel positioned in line with the electrodes as seen in figure 3.1. The hands grasped handheld electrodes with the handhold spacer separating the middle and ring fingers as seen in figure 3.2. The measurement sequence was initiated by the researcher.

Figure 3.1 Foot placement on the base of the seca mBCA 515.

Figure 3.2 Hand placement on the handles of the seca mBCA 515.

Bioimpedance analysis treats the body as an electrical conductor in an alternating current circuit. The alternating current resistance, or impedance, is measured. There is an array of formulas that have been developed for calculating anthropometric parameters from bioimpedance data. However, seca has developed their own formulas which calculate total body water, extracellular water, fat-free mass, and skeletal muscle mass for the arms, legs, torso, and whole body. These values are automatically generated by the seca mBCA 515 and are presented in this study. Body mass index (BMI) is calculated by the machine after the researcher inputs the participant's stature. This is done using the standard calculation of weight (kg) / stature^2 (m^2).

3.6 Study Runs

Over the months of September and October 2021, the Western Varsity cross-country team ran kilometer repeats at Weldon Park, Arva – completing 6-8 in a single workout. This loop contains topographic change with downhill, uphill, and flat sections. The downhill's steepest grade is -5% and the uphill's steepest grade is 9%. As runners commonly have GPS watches with high accuracy, the research team requested that the participants forward the .TCX files containing the data from this workout.

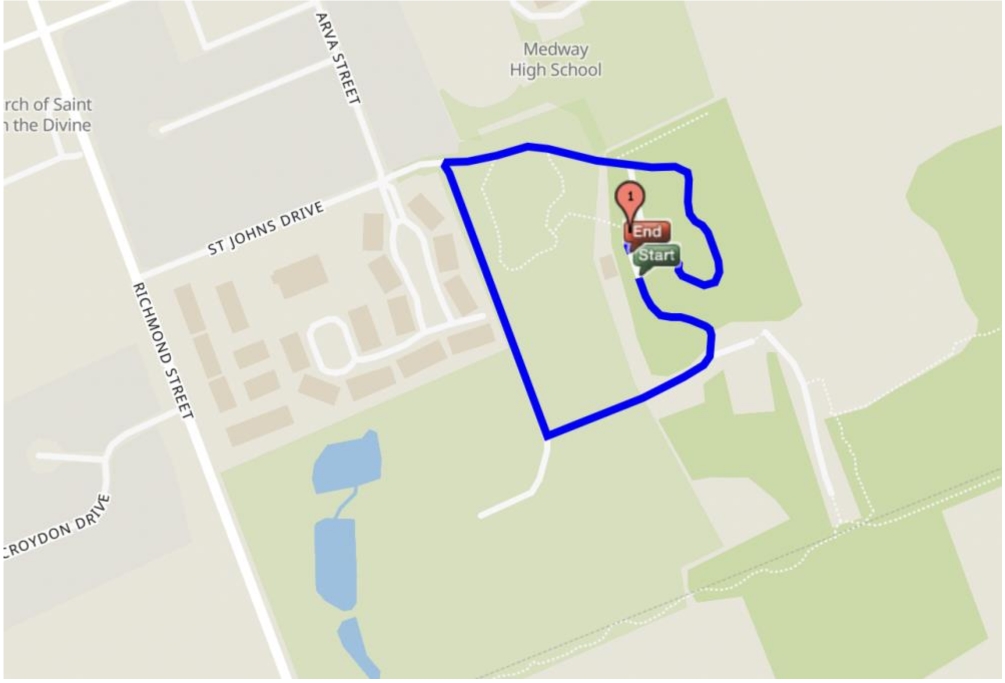

Figure 3.3 Map of the start and finish points of the 1000m loop that the Western cross-country team completes. Image courtesy of gmap-pedometer.com.

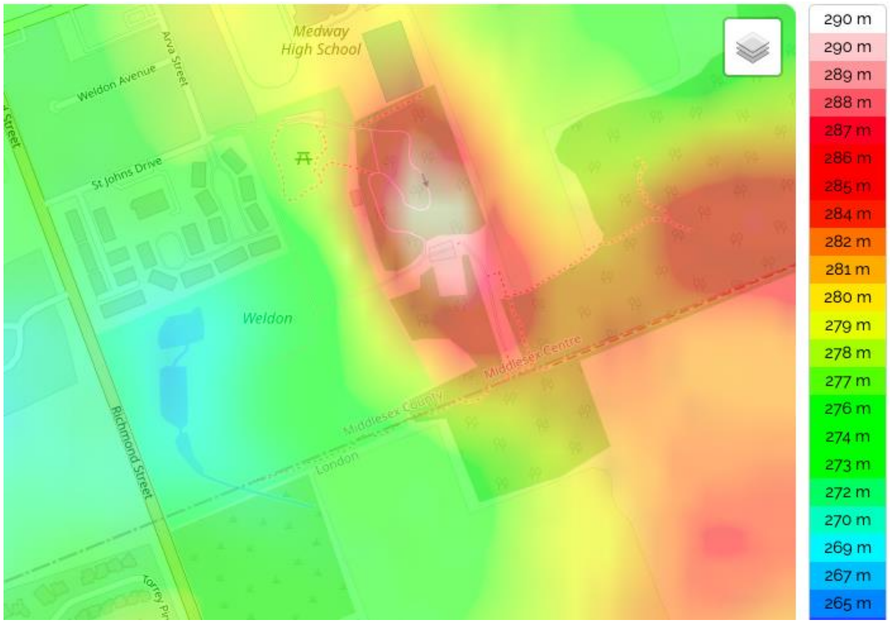

Figure 3.4 Topographic map of the area in which the Western cross-country team runs the 1600m loop. Image courtesy of: en-ca.topographic-map.com.

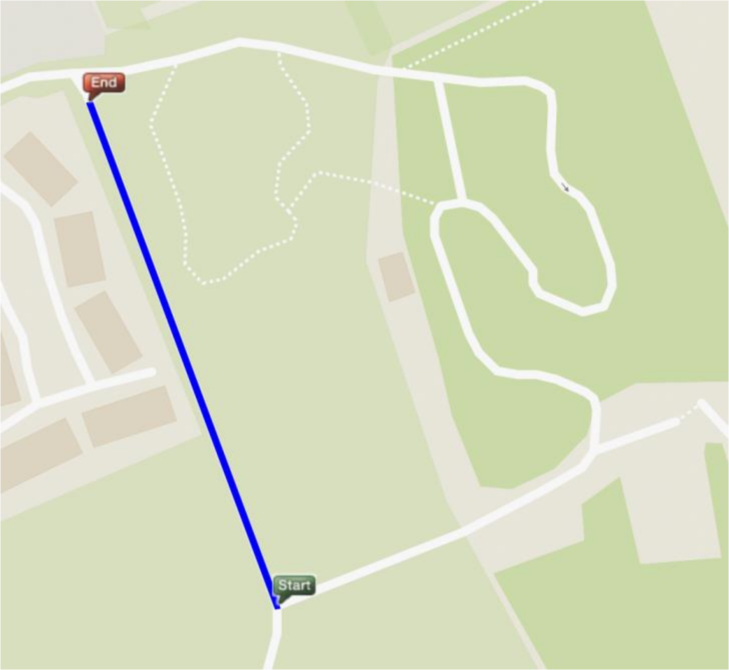

Figure 3.5 The flat segment of the 1000m loop. This segment is approximately 250m as measured by gmap-pedometer.com.

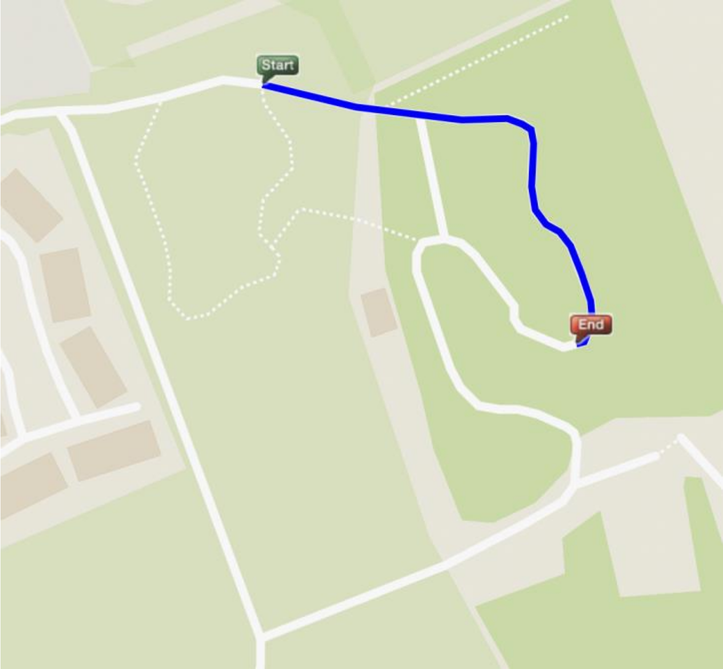

Figure 3.6 The ascending segment of the 1000m loop. This segment is approximately 250m as measured by gmap-pedometer.com.

3.7 Analysis of Study Runs

Participants were asked to email the researcher a copy of the TCX file which held the GPS and performance metric data from their workout. However, only one participant forwarded their TCX file. Instead, I obtained their GPS data on the social media for athletes app Strava. Using the analysis feature on activities, I identified the segments and calculated time and cadence by hand for the flat and uphill segments of the first and last repeats completed by the athletes. As the individuals completed between six and eight repeats of the kilometer loop, I analyzed the last repeat that the athlete completed during this workout – depending on the athlete this could have been their sixth, seventh, or eighth. Time was calculated by subtracting the segment start time from the segment finish time. Cadence was calculated by recording the cadence observed at eight points during the segment and averaging these eight observations. Step length was calculated using the formula distance covered divided by steps taken. In order to calculate steps taken, the duration of the segment was calculated as a ratio (total seconds/60), this value was then multiplied by the average cadence which gave me the value of average step length. Due to a low sample size, I identified other publicly available uploads using the “Group

Activity” feature on Strava showing who else ran with the athletes who participated in this study.

One drawback of this method is that the participants used their own GPS watches, which were of different makes and models. Different GPS watches have different protocols for receiving and logging GPS signals, and different watches have different levels of accuracy. These differences result in minor discrepancies over short distances (e.g., inaccuracies of 2-10m across 1km – resulting in 0.25 to 3 seconds of time variability).

Splits

KM	Pace	Elev
1	5:48 /km	-7 m
2	4:44 /km	0 m
3	4:40 /km	0 m
4	3:30 /km	1 m
5	3:34 /km	-1 m
6	3:01 /km	-1 m
7	3:05 /km	0 m
8	3:07 /km	0 m
9	3:11 /km	-1 m
10	2:57 /km	8 m
11	5:22 /km	-10 m
12	5:05 /km	0 m

18:52
Dist: **4.0 km**
Elev: **275 m**
Grade: **3.1%**
Pace: **3:10/km**
Cadence: **172 spm**

Figure 3.7 The analysis interface on Strava showing my cursor placed at the start of the uphill segment on the first repeat of the workout.

3.8 Body Scan Correction

Body scans were segmented using the software MeshMixer created by AutoDesk. Scans were visually inspected for the presence of errors. Common errors from scans are pooling of the feet (figure 3.8) or webbing between the thighs (figure 3.9). Where thigh webbing was identified, the triangle polygons of the webbing artifacts were removed, using visual landmarks as a guide. The holes that resulted from this process were corrected using the bridge and inspector tools. Pooling of the feet was simply corrected by removing the feet from the scan, as they were not necessary to the analysis.

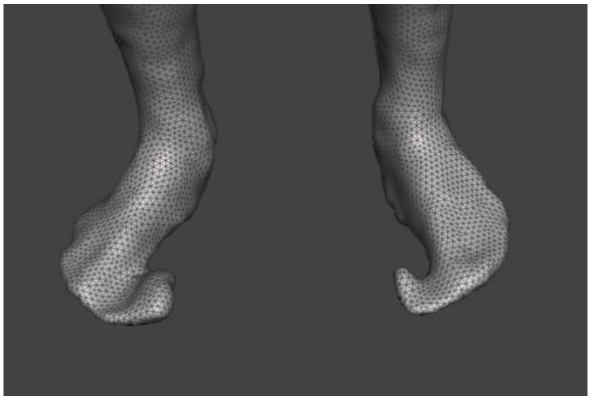

Figure 3.8 An example of pooling at the feet on a 3D body scan.

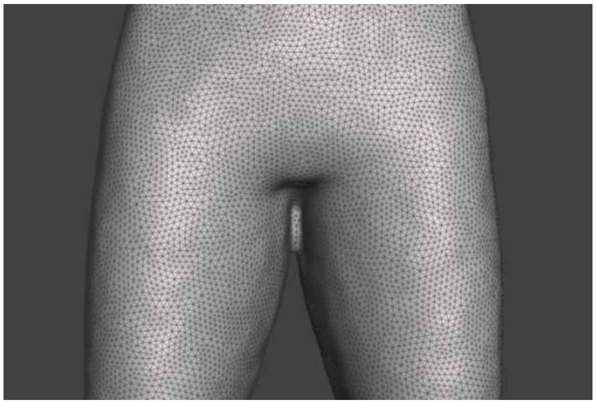

Figure 3.9 An example of webbing between the thighs on a 3D body scan.

3.9 Body Scan Segmentation

This thesis employs standards developed by McConville et al. (1980) for the segmentation of 3D body scans. Three planes of segmentation were used for the segmentation of the thigh and calf:

Hip plane: originates at the center of the groin and passes laterally between the antero-superior iliac spine and the trochanteric landmarks along the lines of the right and left inguinal ligaments.

Knee plane: passes through the lateral femoral epicondyle landmark parallel to the standing surface.

Ankle plane: originates at the sphyrion landmark and passes through the ankle parallel to the standing surface.

When combined, these planes generated six segments for my analysis: left leg, right leg, left thigh, right thigh, left calf, right calf. I then collected the surface area and volume of each of these segments.

Figure 3.10 The resultant limb segments from my analysis.

Using the identification instructions provided by McConville et al. (1980), I visually identified the landmarks on each of the body scans, and generated the six segments in MeshMixer. volume and surface area measurements were generated in the software and recorded. The length of the thigh, and the length of the calf were obtained by examining the maximum length of the thigh and calf segments among the 21 participants who provided scans. As the standards for the segmentation of 3D body scans use the same landmarks as measuring the length of the femur and length of the tibia, this serves as a proxy for femur length and tibia length to calculate crural index. Crural index was calculated by calf length / thigh length x 100. Volume index was additionally used in my analyses to estimate the size of the participant's calves relative to their thighs. Volume index was calculated by calf volume / thigh volume x 100.

3.10 Statistical Analyses

The relationships between anthropometric variables and race times were investigated using Pearson’s Correlation Coefficient. All statistical analyses were conducted in R, and ggplot2 was used for data visualization (Wickham, 2016). As there were both male and female participants, statistical analyses were first conducted with all participants pooled to investigate trends. The analyses with all participants pooled can be found in appendix three. In chapter four, the analyses contain data from only male participants (as the sample of female participants was low). The variables examined for this project are presented with definitions in table 3.1. As this section conducts several regression analyses, a Bonferroni Correction was performed to adjust the alpha value to 0.00104 to prevent the chance of a type-I error in the 48 comparisons.

Table 3.1 Anthropometric and running related variables which are examined in this project.

Anthropometric Variables	**Variable Definition**
Right Leg Volume (cm^3)*	Volume of the participant's right leg in cm^3
Right Thigh Volume (cm^3)	Volume of the participant's right thigh in cm^3
Right Calf Volume (cm^3)	Volume of the participant's right calf in cm^3
Right Leg Length	Length of the participant's right leg in cm
Crural Index*	(Calf length ÷ Thigh length) x 100
Volume Index*	(Calf volume ÷ Thigh volume) x 100
Running Variables	
Cadence	Participants' average step rates on the flat and uphill segments presented in steps per minute
Step Length	The average length of participants' steps on the flat and uphill segment presented in centimeters
Segment Time	Time it took participants to complete flat and uphill segments presented in seconds

*Denotes variables that are analyzed in both research projects in this thesis.

Chapter 4 – Results

This chapter presents the analyses of anthropometric data, and performance data collected from five members of Western's cross-country team. Anthropometric data was collected from body scans using the Size Stream 3D body scanner, and performance data was collected from Strava – analysing a workout the team did in Weldon Park, Arva.

4.1 Descriptive Statistics

Table 4.1 Descriptive statistics of participants who provided both GPS and anthropometric data (n = 5; * denotes n = 4)

Variable	**Mean (SD)**
Stature (cm)	180.62 (10.03)
Weight (kg)	71.94 (14.10)
BMI (kg/m^2)	21.86 (2.48)
Right Leg Volume (cm^3)	11078.29 (1792.59)
Right Thigh Volume (cm^3)	7841.73 (1157.97)
Right Calf Volume (cm^3)	3238.32 (658.55)
Crural Index	91.76 (3.79)
Volume Index	41.04 (2.91)
Flat Cadence (spm) (first repeat)*	181.63 (7.79)
Flat Step Length (cm) (first repeat)*	181.75 (15.59)
Flat Time (s) (first repeat)	45.60 (2.30)
Uphill Cadence (spm) (first repeat)*	178.94 (9.42)
Uphill Step Length (cm) (first repeat)*	166.50 (10.47)
Uphill Time (s) (first repeat)	48.80 (0.84)

4.2 Relationships between anthropometric and performance variables

Looking at correlations between performance data and anthropometric data presented in tables 4.2 and 4.3, there were few relationships observed between anthropometrics and athletic performance on the first repeat. Cadence on the flat segment showed a negative relationship with right leg volume (R = -0.98, p = 0.024), and time from the flat segment showed a negative relationship with crural index (R = -0.88, p =

0.05). Right leg volume also displayed a negative trend with cadence on the uphill segment (R = -0.95, p = 0.048).

Table 4.2 Regressions values of performance metrics from the flat segment of the first repeat of the workout and anthropometrics

Flat Cadence (first repeat)	**R**	**p**
Right Leg Volume	-0.98	0.024
Volume Index	-0.37	0.63
Crural Index	-0.38	0.62
Flat Step Length (first repeat)		
Right Leg Volume	0.85	0.15
Volume Index	0.84	0.16
Crural Index	0.81	0.19
Flat Time (first repeat)		
Right Leg Volume	-0.41	0.49
Volume Index	-0.63	0.25
Crural Index	-0.88	0.05

Table 4.3 Regression values of performance metrics from the uphill segment of the first repeat and anthropometrics

Uphill Cadence (first repeat)	**R**	**p**
Right Leg Volume	-0.95	0.048
Volume Index	-0.35	0.65
Crural Index	-0.41	0.59
Uphill Step Length (first repeat)		
Right Leg Volume	0.78	0.22
Volume Index	0.18	0.82
Crural Index	0.41	0.59
Uphill Time (first repeat)		
Right Leg Volume	0.55	0.33
Volume Index	0.024	0.97
Crural Index	-0.026	0.97

A few trends emerged when analyzing anthropometrics and performance variables from the last repeat completed by the athletes – these results and be seen in table 4.4 and 4.5. Crural index displayed a negative relationship with step length on the flat segment (R = 0.96, p = 0.043) and the uphill segment (R = 0.98, p = 0.024). Right leg volume also showed a negative trend with cadence on the flat (R = -0.3, p = 0.073) and uphill segments (R = -0.93, p = 0.071). Volume index also showed a positive trend with step length on the flat segment (R = 0.95, p = 0.052). All other analyses yielded non-significant results.

Table 4.4 Regression values of performance metrics from the flat segment of the last repeat and anthropometrics

Flat Cadence (last repeat)	**R**	**p**
Right Leg Volume	-0.93	0.073
Volume Index	-0.26	0.74
Crural Index	-0.34	0.66
Flat Step Length (last repeat)		
Right Leg Volume	0.60	0.40
Volume Index	0.95	0.052
Crural Index	0.96	0.043
Flat Time (last repeat)		
Right Leg Volume	-0.26	0.67
Volume Index	-0.74	0.15
Crural Index	-0.86	0.063

Table 4.5 Regression values of performance metrics from the uphill segment of the last repeat and anthropometrics

Uphill Cadence (last repeat)	**R**	**p**
Right Leg Volume	-0.93	0.071
Volume Index	-0.34	0.66
Crural Index	-0.43	0.57
Uphill Step Length (last repeat)		
Right Leg Volume	0.56	0.44
Volume Index	0.83	0.17
Crural Index	0.98	0.024
Uphill Time (last repeat)		
Right Leg Volume	0.41	0.49
Volume Index	-0.11	0.86
Crural Index	-0.47	0.42

4.3 Relationships between performance variables

Table 4.5 Descriptive statistics of performance data gathered from Strava. (n = 11, * denotes n = 10).

Variable	Mean (SD)
Flat Cadence (spm) (first repeat)*	185.64 (9.48)
Flat Step Length (cm) (first repeat)*	174.36 (13.03)
Flat Time (s) (first repeat)	46.33 (1.67)
Uphill Cadence (spm) (first repeat)*	182.20 (9.09)
Uphill Step Length (cm) (first repeat)*	163.73 (11.68)
Uphill Time (s) (first repeat)	49.17 (1.19)
Flat Cadence (spm) (last repeat)*	186.57 (8.52)
Flat Step Length (cm) (last repeat)*	177.91 (11.41)
Flat Time (s) (last repeat)	45.58 (2.91)
Uphill Cadence (spm) (last repeat)*	184.63 (8.86)
Uphill Step Length (cm) (last repeat)*	168.82 (9.37)
Uphill Time (s) (last repeat)	48.17 (2.12)

Testing the relationships between running variables on the flat and uphill segments using only data collected from Strava, four notable relationships were observed. On the first repeat of the workout cadence and step length on the flat segment showed a strong negative relationship ($R = -0.87$, $p < 0.001$) as seen in figure 4.1. Similarly, time and step length following a close negative relationship on the flat segment of the first repeat. ($R = -0.76$, $p < 0.01$) as seen in figure 4.3. However, time and cadence did not show any relationship – as displayed in figure 4.2. On the uphill segment of the first repeat, no relationships were observed between running metrics – as can be seen in figures 4.4 to 4.6. Looking at the relationships between running variables on the last repeat of the workout revealed two relationships. Step length and time on the flat segment showed a close relationship ($R = -0.73$, $p = 0.01$) as seen in figure 4.9. Cadence and step length on the uphill segment showed a partial negative relationship ($R = -0.62$, $p = 0.044$) as displayed in figure 4.10. However, all other correlations from the last repeat of the workout revealed non-significant results which can be seen in figures 4.7, 4.8, 4.11 and 4.12.

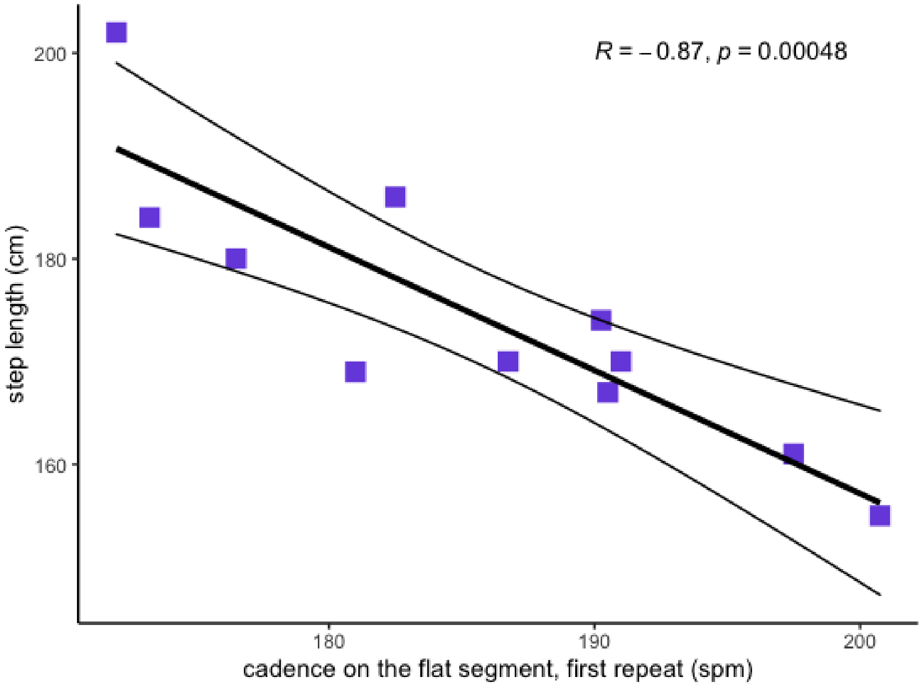

Figure 4.1 Scatterplot showing the relationship between cadence and step length of the flat segment of the first repeat of the workout

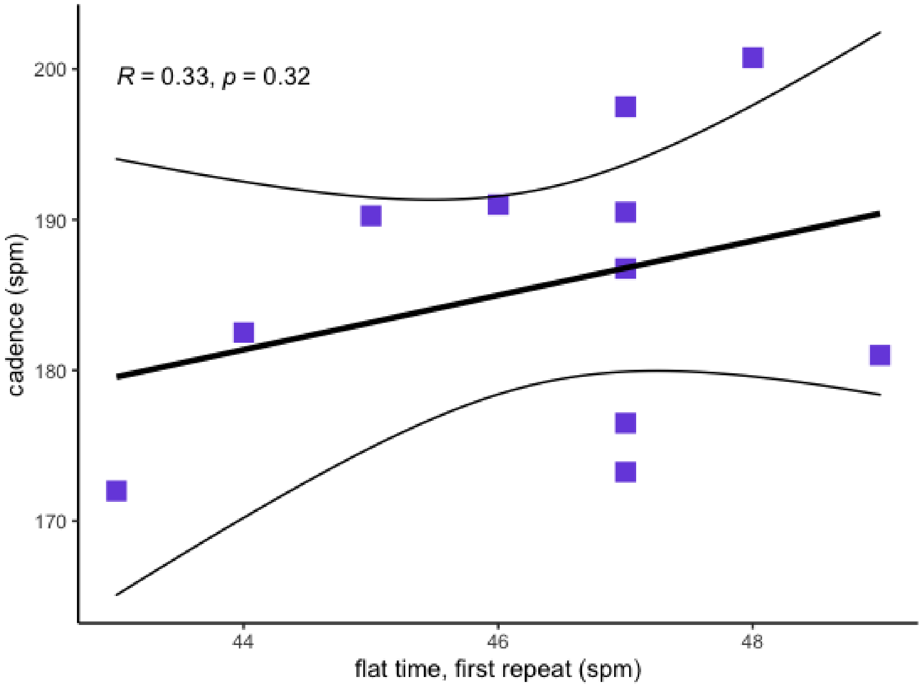

Figure 4.2 Scatterplot showing the relationship between time and cadence on the flat segment of the first repeat of the workout

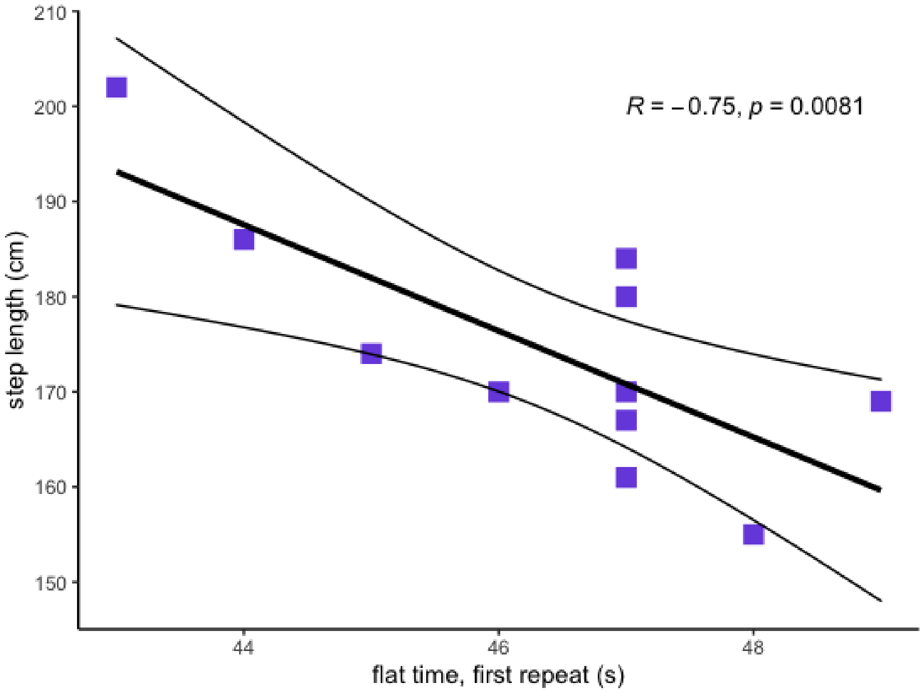

Figure 4.3 Scatter plot showing the relationship between time and step length among males on the flat segment during the first repeat of the workout.

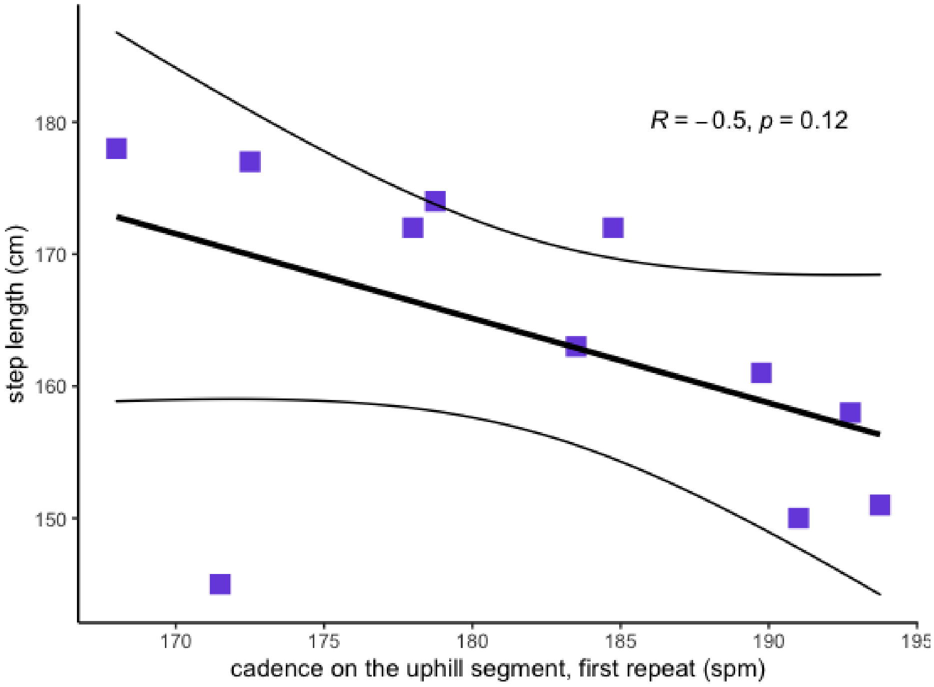

Figure 4.4 Scatterplot showing the relationship between cadence and step length on the uphill segment of the first repeat of the workout

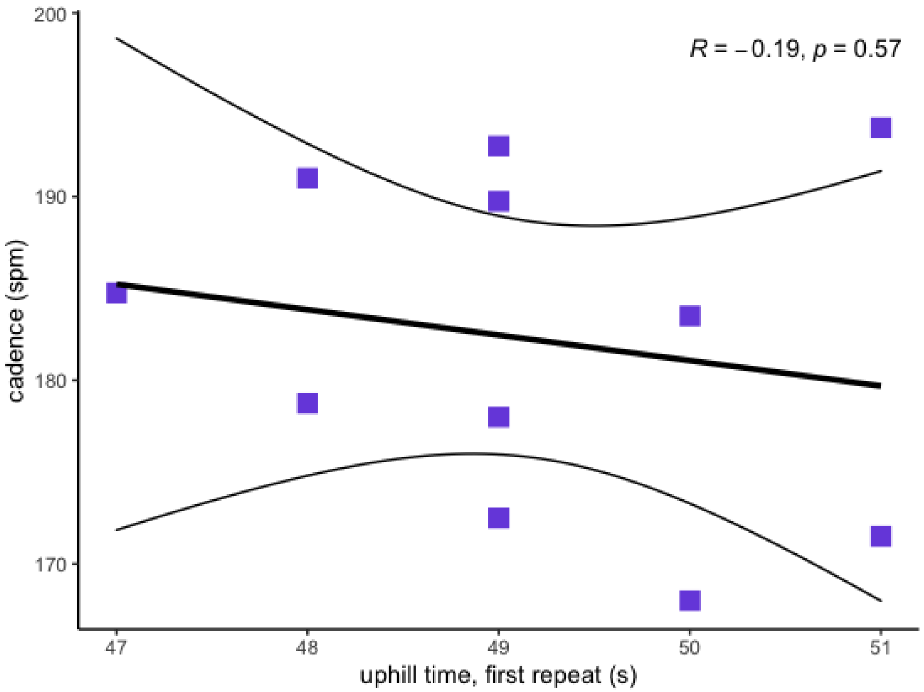

Figure 4.5 Scatter plot showing the relationship between time and cadence on the uphill segment of the first repeat of the workout

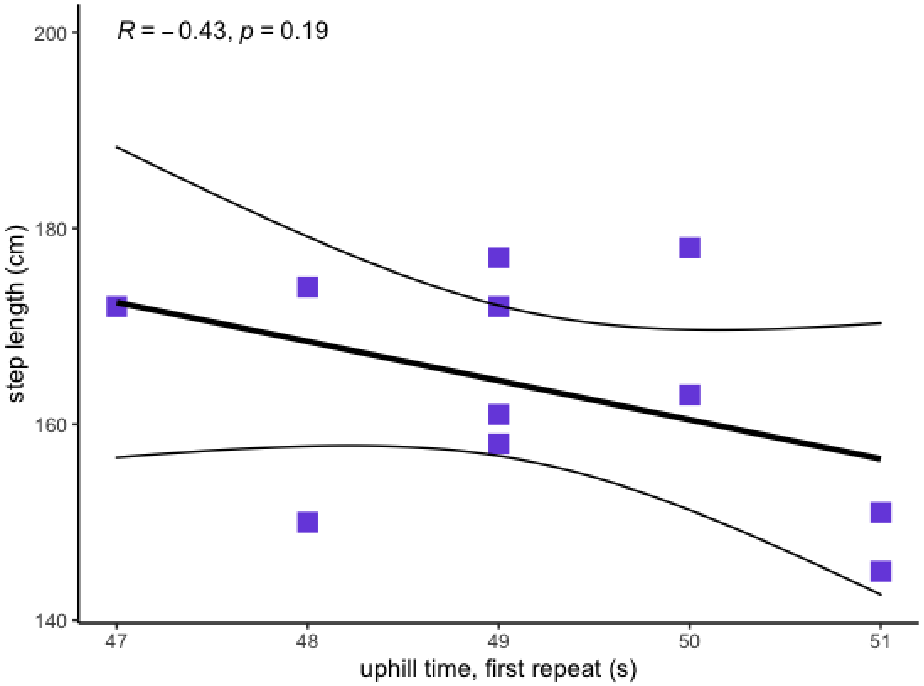

Figure 4.6 Scatter plot showing the relationship between time and step length among males on the uphill segment during the first repeat of the workout.

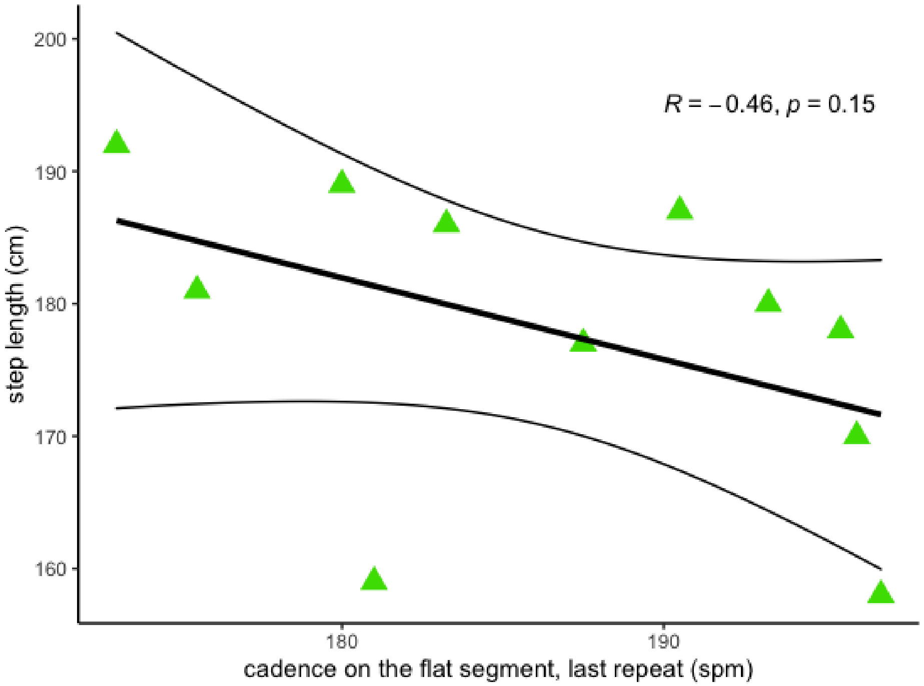

Figure 4.7 Plot showing the relationship between cadence and step length on the flat segment from the last repeat of the workout

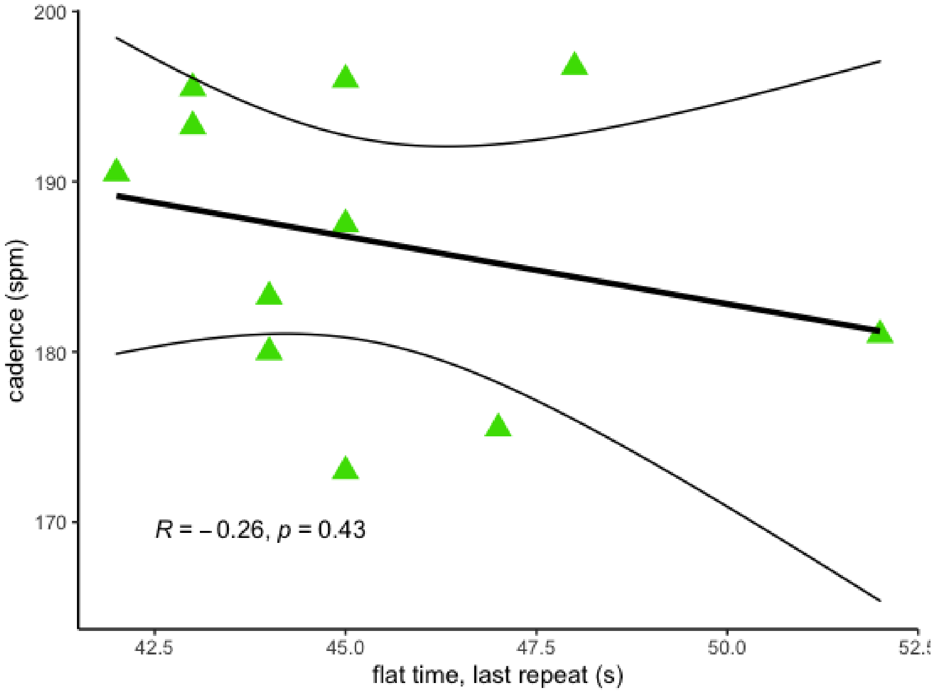

Figure 4.8 Plot showing the relationship between time and cadence on the flat segment from last repeat of the workout

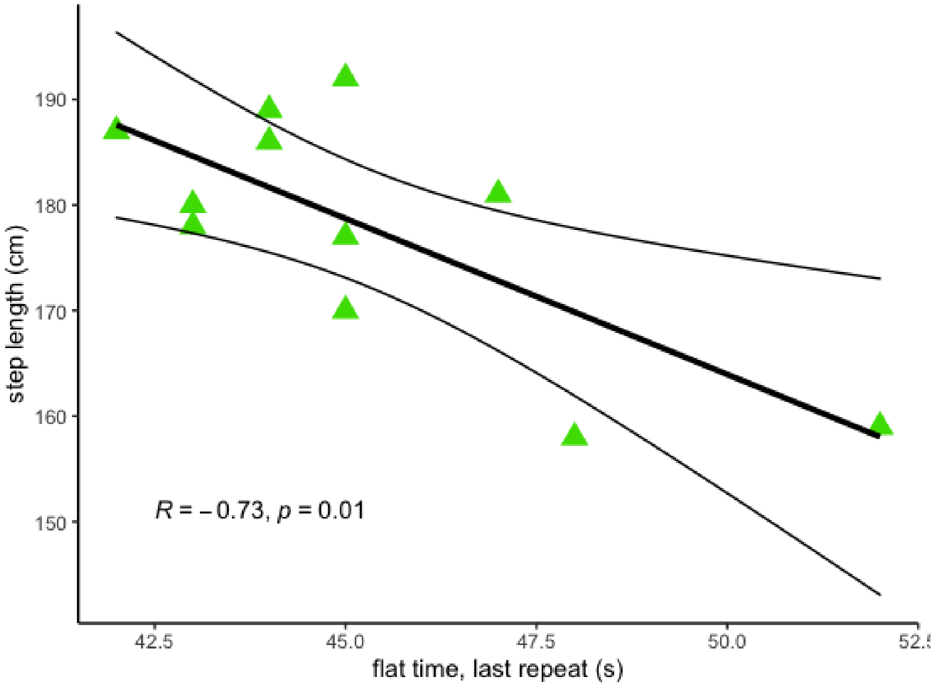

Figure 4.9 Plot showing the relationship between time and step length among males on the flat segment during the last repeat of the workout.

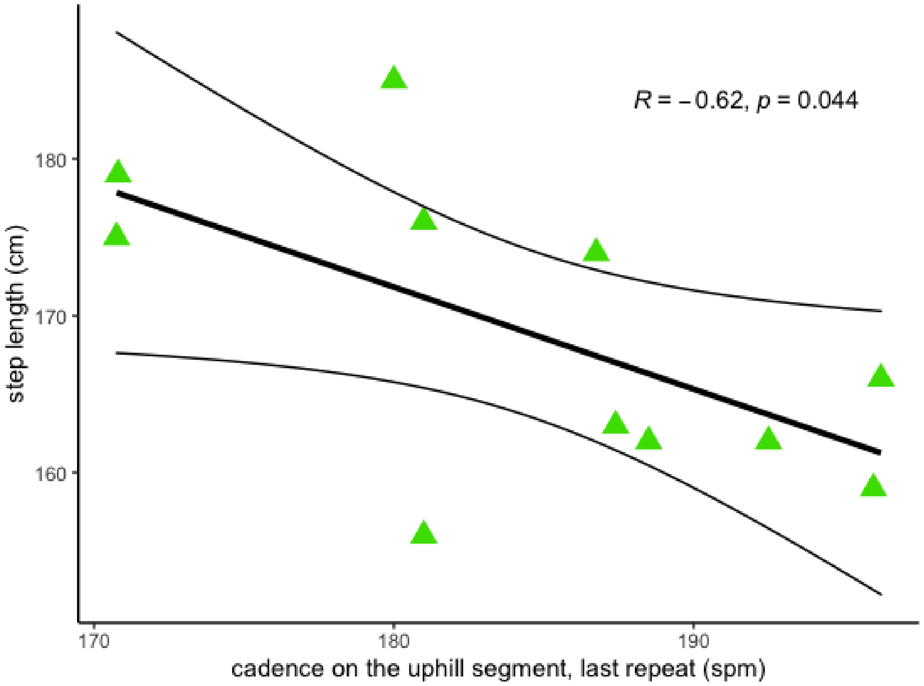

Figure 4.10 Plot showing the relationship between cadence and step length on the uphill segment during the last repeat of the workout

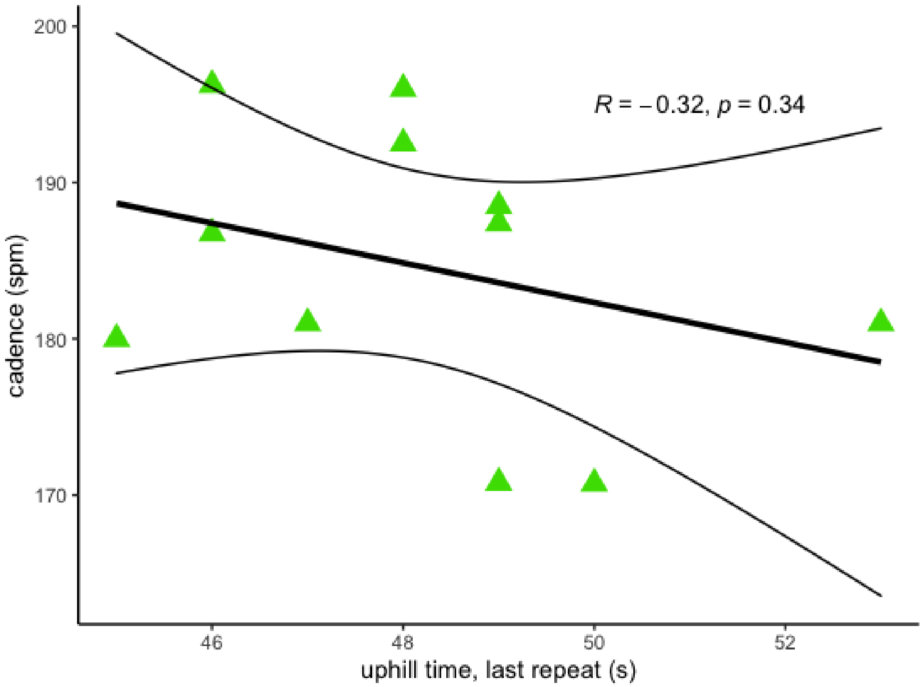

Figure 4.11 Plot showing the relationship between time and cadence on the uphill segment during the last repeat of the workout

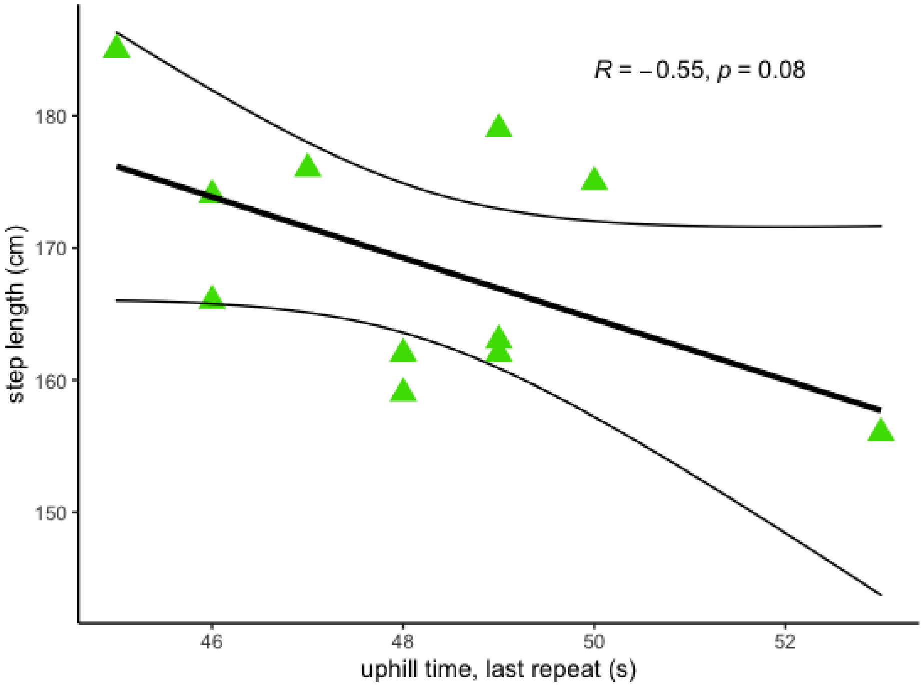

Figure 4.12 Scatter plot showing the relationship between time and step length among males on the uphill segment during the last repeat of the workout

Chapter 5 - Discussion

In this section, I present a test of theories from biological anthropologists by integrating two unique data sources. 3D body scans were collected from runners on Western University's cross-country team, and data on their running performance was gathered from their Strava profiles. Using these data, I was able to test how variation in lower limb morphology corresponds with cadence, step length, and speed over flat and uphill terrains.

5.1 Anthropometrics and athletic performance

Despite the sample size, some general trends can be noted from comparing athletic performance with anthropometrics among the cross-country runners. The relationships observed between leg volume with cadence and step length confirm the principle that leg morphology will generally dictate the length and frequency of people's steps when running (Brisswalter et al., 1996; Danion et al., 2003; Hunter et al., 2004). Though with generally weak relationships revealed in the analysis, it is difficult to use the results to confirm any results and theories put forth by Steudel-Numbers et al. (2007) or Higgins and Ruff (2011). There were no results to affirm Higgins and Ruff's (2011) theory that relatively short tibiae may be advantageous for locomoting uphill. The analysis of crural indices showed negative relationships with segment time on the flat segments of the first and last repeat of the workout, but no relationships were observed between crural index and uphill segment times.

The analyses looking at the running variables collected from Strava demonstrated that there were strong, negative relationships between time and step length on the flat segment of the first and last repeats. On the uphill segment, the analyses revealed the absence of relationships between the running variables. The negative relationships between step length and time observed on the flat segment may only be indicative of faster runners taking larger steps (Brisswalter et al., 1996; Hunter et al., 2004). On uphill terrain, the absence of a trend between step length and time could indicate that step length has less of an impact on overall speed. But without the evidence of anthropometrics, it is difficult to comment on any theories put forth by Higgins and Ruff (2011) that the effects of leg length are negated on sloped terrains or that relatively short tibiae may be advantageous for locomoting uphill.

Chapter 6 – Methods

This study investigates the relationships between athletic performance and anthropometrics from participants of the 2016 and 2017 editions of the Al Andalus Ultimate Trail – a 5-day ultra-marathon that takes place in Al Andalucía, Spain. This ultra-marathon takes place across a mountainous area of Southern Spain, with each stage having between 850 and 1500m of elevation gain. This study will also explore how variability in leg lengths corresponds with the running economy of a sub-group of the ultra-runners who participated in the race.

6.1 Study Race

Al Andalus Ultra Trail is an annual five-day, five-stage, semi-supported, multi-stage race covering a total of 234 km that takes place during July in Andalucía, Spain. The race conditions are typically hot, dry, and offers very little shade coverage throughout. The race organizers report that average temperatures in the daytime range from 30-35 degrees Celsius. Maps of each of the stages are presented in figure 6.1, and a topographic map of the area which this race takes place in is available in figure 6.2. Stage 1 starts in the town of Loja and covers 38 km with 1170 m of ascent, and 920 m of descent. The stage begins at an elevation of about 540 m, with the first 11 km covering a climb up to 1460 m of elevation. The stage continues to undulate through the Andalus mountains, finishing in Alhama de Granada. Stage 2 then begins in Alhama de Granada, covering 48 km with 1440 m of climbing, and 1350 m of descent. This stage undulates throughout, with a steep mountain climb in the middle, and finishes at Játar. Stage 3 then picks up from Játar, covering 39 km with 850 m of ascent and 915 m of descent. The stage begins on municipal and farm roads, moving to the mountains 1l km in to spend the last 28 km in the Sierras de Tejeda, ultimately finishing at the El Bacal Campsite, outside of Jayena. Stage 4 is the longest stage of the race, beginning at the El Bacal Campsite, and covering 67 km with 1500 m of ascent and 1540 m of descent. The stage has three difficult ascents throughout and covers farm roads, tarmac, and singletrack throughout, ultimately finishing at El Motor campsite, just outside of Alhama de Granada. And on the final day, stage 5 begins where stage 4 left off, covering 42 km with 970 m of ascent with 1290 m of descent, finishing back in Loja. The stage includes an 11 km ascent beginning at 20 km, with the race finishing on an 11 km descent, back down the mountain that the ultra-challenge started with on the first stage. Altogether, the race has 5930 m of ascent, and 6015 m of descent across a total of 234 km.

Stage 1: starts in the town of Loja and covers 38 km with 1170 m of ascent, and 920 m of descent

Stage 2: covers 48 km with 1440 m of climbing, and 1350 m of descent

Stage 3: covers 39k m with 850 m of ascent and 915 m of descent

Stage 4: the longest stage of the race, covering 67 km with 1500 m of ascent and 1540 m of descent

Stage 5: covers 42 km with 970 m of ascent and 1290 m of descent

Figure 6.1 Maps showing the routes for the five stages of the Al Andalus Ultimate Trail. The green arrows represent the start points, and the checkered flags represent the finishes.

Figure 6.2 Topographic map of region of Spain in which the Al Andalus Ultimate Trail takes place

6.2 Data Collection

Data from the Al Andalus race was collected by Danny Longman at the 2016 and 2017 editions of the race. Ethical approval was granted by the Cambridge Human Biology Ethics Committee. The aims of the study were to test components of human adaptability in real-world conditions, rather than in a laboratory, and to document life history trade-offs associated with locomotion under extreme conditions. Longman collected anthropometrics before and after the races, alongside biological samples such as blood and saliva. Race participants received an email prior to the start of the race explaining the study to them and inviting them to participate. Participants were also invited to go to the PAVE Imaging and Performance Laboratory at the University of Cambridge for a series of tests following the races, including taking a 3D body scan. Here, I will present the anthropometrics obtained from participants before the race (n=58), and a subset of those who also provided body scans and running economy data at the PAVE Lab (n=15).

6.3 Anthropometric Methods

Stature was assessed to the nearest 0.1cm using a Leicester stadiometer. Participants removed their socks and shoes and stood with their heels, buttocks, and shoulders in contact with the stadiometer, with their head placed in the Frankfurt Plane. Body mass was measured to the nearest 0.1kg using a seca (Hamburg, Germany) portable scale. Waist and hip circumferences, and sitting height were measured according to the standards put forth in the *International Standards for Anthropometric Assessment* (2001). A proxy for leg length was obtained by subtracting sitting height from total stature. Relative leg length was calculated by dividing leg length by stature.

For body scanning, the methods used for body scan collection and segmentation in this section are the same as those described in sections 3.3, 3.8 and 3.9 of this thesis. The length of the thigh, and the length of the calf were obtained by examining the maximum length of the thigh and calf segments among the 21 participants who provided scans. As the standards for the segmentation of 3D body scans use the same landmarks as measuring the length of the femur and length of the tibia, this serves as a proxy for the two measurements in examining the relationship between crural index and athletic performance. Crural index was calculated by taking calf length / thigh length x 100. Volume index was additionally used in my analyses to estimate the size of the participant's calves relative to their thighs. Volume index was calculated by calf volume / thigh volume x 100.

Additionally, I included the metric leg length / weight, as Steudel-Numbers et al. (2007) used this metric in their analysis of the impact of leg length on the energetic cost of transport so that they could “more carefully document the relationship between [cost of transport] and lower-limb length with the effect of body mass removed” (2007: 193).

6.4 Defining athletic performance

For this study, I have defined athletic performance as race finishing time across the 5 stages, and the overall time. Race time has previously been used as a measure of athletic performance by Longman et al. (2015), and Longman et al. (2019, 2021) used race finisher status (i.e. whether someone finished a race) as a metric of athletic performance. For the majority of cases in this study, I have only included stage times from people who completed the race, except for 5 individuals who did not complete the entire race but did provide body scans. I wanted to maximize the number of body scan participants, which necessitated the inclusion of their stage results, but their stage times were also included in the general anthropometric analyses.

For stage times, the overall time was recorded in the hh:mm:ss format, and then converted to decimal format as a fraction of 24 (i.e., the number of hours in a day, for example, 0.25 would be equal to six hours.). This was done to convert all the times to a number that R can read.

6.5 Submaximal and Maximal Treadmill Protocol Tests

Participants completed an incremental treadmill test at the Cambridge Centre for Sport and Exercise Science with the following protocol:

> Each participant completed a submaximal incremental speed-based protocol for the determination of lactate threshold 1 (LT1), lactate turn-point 2 (LT2), and running economy (RE) (Gordon et al., 2017). The starting speed was selected on an individual basis to coincide with a speed that the participant would normally warm-up at, and thereafter was increased by 1 km·h−1 every 3 min. Throughout the test, the gradient was kept constant at 1%. After each 3-minute increment, there was a 1-minute break where upon the participant was asked to stand astride of the treadmill to facilitate the collection of a capillary fingertip blood sample (20 μL) for the immediate determination of blood lactate concentrations. Once the sample was collected, the participants were asked to ease themselves back onto the treadmill and complete the remaining time of the 1-minute recovery at walking pace (4 km·h−1). Throughout the test, individual blood lactate responses (mmol·L−1) were plotted against exercise intensity (km·h−1) for the determination of lactate LT1 and LT2. Identification of LT1 was based on the first initial rise above baseline, whilst LT2 was the sudden and sustained increase in blood lactate, determined through visual inspection of the blood lactate curve (Bourdon, 2000; Gordon et al., 2017). Two physiologists present in the laboratory independently validated both LT1 and LT2. The test was terminated once the participant had reached LT2. Gas exchange responses were recorded throughout all trials on a breath-by-breath basis with a pre-calibrated metabolic

> cart (MetaLyzer 3B-R2, Cortex Ltd, Germany) and [heart rate] responses were tracked using a telemetric system (T31 heart rate strap, Polar, Kempele, Finland). Oxygen consumption at LT1 and LT2 was used to provide the measure of RE used in subsequent analyses (Longman et al., 2022: 84).

Following the completion of the incremental treadmill test and a 7-minute rest period, participants were asked to run an incremental test to voluntary exhaustion to assess VO_{2MAX}. The following protocol was employed:

> The running speed was based on the speed at which LT2 occurred in the previous protocol and kept constant throughout. Every minute, the gradient was increased by 1% (starting at 1%) until volitional exhaustion was reached, or when the participant was unable to maintain a predetermined position at the front of the treadmill. Verbal encouragement was provided towards the end of the test to facilitate a maximal effort of the participant. Immediately after completion of the $\dot{V}O_{2max}$ test, a capillary blood sample (20 µL) was collected for the determination of post-exercise blood lactate and glucose concentrations. Throughout the trial, expired air was recorded on a breath-by-breath basis and [heart rate] responses were documented using a telemetric system (Longman et al., 2022: 84).

6.6 Statistical analyses

The relationships between anthropometric variables and race times were investigated using Pearson's Correlation Coefficient. All statistical analyses were conducted in R, and ggplot2 was used for data visualization (Wickham, 2016). As this section conducts several regression analyses, a Bonferroni Correction was performed to adjust the alpha value to 0.00104 to prevent the chance of a type-I error in the 48 comparisons.

6.7 Hypotheses to explore

Hypothesis 1: Following the results presented by Steudel-Numbers et al. (2007) that relatively longer leg length results in more efficient and economical running, there will be negative relationships between relative leg length, or leg length controlled for body mass on all stages, and in overall finishing time. Then by testing running economy data, there will be a positive relationship between running economy at LT1 and LT2 with relative leg length.

Hypothesis 2: Following the predictions put forth by Higgins and Ruff (2011) that relatively short tibiae would be advantageous for climbing sloped terrains, I hypothesize the following: crural index will positively correlate with stage time on race stages with more elevation gain than loss. I also hypothesize that volume index (right calf volume / right thigh volume x 100) will positively correlate with stage times on stages with more elevation gain than loss. A lower volume index would be indicative of someone having relatively smaller lower limb segments relative to thigh volume. This, in turn, could also be indicative of relatively shorter calves relative to thighs, and/or more voluminous thighs relative to calves.

Hypothesis 3: As this race also took place in hot climatic conditions, it is worth exploring the results put forth by Longman et al. (2019, 2021) that the performance of ultra-runners corresponds with Bergmann's and Allen's rule. Here we can explore the hypothesis that there will be a negative relationship between relative leg length and stage times if athletes with longer legs are more efficient at locomotion in heat, and a positive relationship between sitting height ratio and stage time if those with greater trunk sizes are less efficient at locomotion in hot environments.

6.8 Variables analyzed for this study

Table 6.1 presents the anthropometric and physiological variables analyzed in this study with their definitions alongside them. Excluded from this table are the stage times, as the stage times represent the time it took participants of the Al Andalus Ultimate Trail to finish the stages.

Table 6.1 List of anthropometric and physiological variables analyzed for this project with their definitions.

Anthropometric Variables	**Variable Definition**
Leg Length	Calculated by subtracting sitting height from stature
Relative Leg Length	Leg length (cm) divided by total stature (cm)
Leg Length/Weight	Leg length (cm) divided by weight (kg)
Sitting Heigh Ratio	Sitting height divided by total stature
Right Leg Volume (cm^3)*	Volume of the right leg assessed from 3D body scans
Crural Index*	(Calf length ÷ Thigh length) x 100
Volume Index*	(Calf volume ÷ Thigh volume) x 100
Physiological Variables	
Economy at LT1	Volume of air respired (mL) per kilogram of body mass each minute while running at lactate threshold
Economy at LT2	Volume of air respired (mL) per kilogram of body mass each minute while running at lactate turn point
Economy at 11 km/h	Volume of air respired (mL) per body per kilogram of body mass each minute while running at 11 km/h

*Denotes variables that are analyzed in both research projects in this thesis.

Chapter 7 – Results

A total of 58 participants were recruited from the 2016 and 2017 Al Andalus trail runs, with 37 of those participants completing the races. Their summary statistics are presented in table 7.1. I first present the results from the statistical analyses of the race stage finishing times compared with anthropometrics. The comparisons of anthropometrics to running economy data are then presented. Lastly, I compare athletic performance with the limb segment lengths and volumes of the ultra-runners who provided body scans.

Table 7.1: The summary statistics of the participants from the Al Andalus Trail Races in the form of mean (standard deviation)

Variable	Males (n=38)	Females (n=20)
Age (Years)	49.18 (9.73)	45.10 (9.10)
Height (cm)	180.31 (6.85)	166.12 (5.16)
Weight (kg)	78.55 (8.76)	61.69 (7.31)
BMI	24.13 (2.06)	22.34 (2.32)
Leg Length (cm)	90.17 (4.33)	81.66 (3.64)
Relative Leg Length	0.50 (0.01)	0.49 (0.01)
Sitting Height	90.13 (4.13)	84.47 (2.76)
Number of Race Finishers	24	13
Overall Race Time	32:41:21 (0.19)	33:47:57 (0.17)

7.1 Correlation analyses between anthropometric variables of interest and stage and overall finishing times

Hypothesis 1: Following the results presented by Steudel-Numbers et al. (2007) that relatively longer leg length results in more efficient and economical running, there will be negative relationships between relative leg length, or leg length controlled for body mass on all stages and in overall finishing time. Then by testing running economy data, there will be a positive relationship between running economy at LT1 and LT2 with relative leg length.

Comparisons of leg anthropometrics and stage times resulted in a mix of relationships, with the significant results in this context only being observed among males with the alpha level of 0.05 – with the Bonferroni Corrected alpha level of 0.00104 no significant results were returned. It was observed that leg length does not correlate with any of the stage times, nor the overall time among either males or females. Relative leg length (leg length/height) only correlated with stage 4 time among males, with a partial negative correlation observed ($R = 0.41$, $p < 0.05$). Relative leg length did not correlate with stage times nor overall time when the data from the females' race was explored. In examining leg length controlled for weight (leg length/weight), statistical relationships were observed when exploring males stage times, but only on stages three ($R = -0.44$, $p < 0.05$), five ($R = -0.42$, $p < 0.05$), and in the overall time ($R = -0.42$, $p < 0.05$). Leg length controlled for weight did not correlate with stage one time ($R = -0.15$, $p = 0.45$), stage two time ($R = -0.36$, $p = 0.071$), or stage four time ($R = -0.33$, $p = 0.12$). Again, this relationship between leg length/weight and stage time was observed among males but not females.

Beyond the metrics related to legs[3], I also explored the relationships between stage times and overall time and sitting height ratio. These results are also presented in tables 7.2 and 7.3. The only correlation observed when comparing sitting height ratio and stage times was among males when regressed against stage four time ($R=0.41$, $p<0.05$).

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[3] Additional analyses between anthropometrics and stage times are presented in graph form in Appendix B. There were significant positive correlations observed between estimated fat weight and fat as a percentage of total body weight with stage times among men but not women. These results were interesting but were excluded from this section as I had not done prior research on fat for this thesis.

Table 7.2 Correlation values comparing anthropometric variables to stage times among male participants of the Al Andalus Ultimate Trail

Stage 1 Time (n=27)	R	p	Stage 4 Time (n=24)	R	p
Leg Length	-0.089	0.66	Leg Length	0.036	0.87
Relative Leg Length	-0.24	0.23	Relative Leg Length	-0.41	<0.05
Leg Length/Weight	-0.15	0.45	Leg Length/Weight	-0.33	0.12
Sitting Heigh Ratio	0.24	0.23	Sitting Heigh Ratio	0.41	<0.05
Stage 2 Time (n=26)			Stage 5 Time (n=25)		
Leg Length	0.061	0.77	Leg Length	0.21	0.31
Relative Leg Length	-0.14	0.5	Relative Leg Length	-0.19	0.35
Leg Length/Weight	-0.36	0.071	Leg Length/Weight	-0.42	<0.05
Sitting Heigh Ratio	0.14	0.5	Sitting Heigh Ratio	0.19	0.35
Stage 3 Time (n=26)			Overall Time (n=24)		
Leg Length	0.052	0.8	Leg Length	0.082	0.7
Relative Leg Length	-0.17	0.41	Relative Leg Length	-0.31	0.14
Leg Length/Weight	-0.44	<0.05	Leg Length/Weight	-0.42	<0.05
Sitting Heigh Ratio	0.17	0.41	Sitting Heigh Ratio	0.31	0.14

Table 7.3 Correlation values comparing anthropometrics variables to stage times among female participants of the Al Andalus Ultimate Trail

Stage 1 Time (n=15)	R	p	Stage 4 Time (n=13)	R	p
Leg Length	0.016	0.96	Leg Length	0.064	0.84
Relative Leg Length	0.086	0.76	Relative Leg Length	0.16	0.6
Leg Length/Weight	-0.27	0.32	Leg Length/Weight	-0.22	0.48
Sitting Heigh Ratio	-0.086	0.76	Sitting Heigh Ratio	-0.16	0.6
Stage 2 Time (n=15)			Stage 5 Time (n=14)		
Leg Length	0.12	0.66	Leg Length	0.011	0.97
Relative Leg Length	0.074	0.79	Relative Leg Length	0.12	0.68
Leg Length/Weight	-0.32	0.25	Leg Length/Weight	-0.37	0.19
Sitting Heigh Ratio	-0.074	0.79	Sitting Heigh Ratio	-0.12	0.68
Stage 3 Time (n=15)			Overall Time (n=13)		
Leg Length	0.16	0.57	Leg Length	0.073	0.81
Relative Leg Length	0.2	0.46	Relative Leg Length	0.15	0.63
Leg Length/Weight	-0.19	0.49	Leg Length/Weight	-0.22	0.46
Sitting Heigh Ratio	-0.2	0.46	Sitting Heigh Ratio	-0.15	0.63

7.2 Relationships between running economy and leg length

To evaluate the relationship between relative leg length and measures of running economy in hypothesis 1, correlation analyses were performed comparing relative leg length and leg length relative leg length with running economy at lactic threshold (LT1), lactate turn point (LT2), and economy at 11km/h among male participants (n = 14). Female participants were excluded from these analyses due to a low sample size. The summary statistics of participants who provided running economy data are presented in table 7.2.

Table 7.4 Summary statistics of the Al Andalus Ultimate male participants (n = 14) who provided running economy and body scan data in a follow up study

Variable	**Mean (SD)**
Height (cm)	181.00 (6.17)
Weight (kg)	78.26 (10.00)
Age	47.80 (7.74)
Right Leg Volume (cm^3)	12842.72 (2558.51)
Right Thigh Volume (cm^3)	9124.47 (2042.21)
Right Calf Volume (cm^3)	3737.31 (632.27)
Crural Index	85.16 (20.04)
Volume Index	41.88 (6.93)
Speed at LT1 (km/h)	10.33 (1.05)
Economy at LT1 (ml/kg/min)	34.65 (2.85)
Speed at LT2 (km/h)	12.67 (1.72)
Economy at LT2 (ml/kg/min)	41.02 (5.28)

No significant results were returned when relative leg length was correlated against economy at LT1 (figure 7.1) , or economy at LT2 (figure 7.2), however a partial correlation was observed when relative leg length was correlated with economy at 11 km/h (R = 0.55, P = 0.04, as seen in figure 7.3). Leg length relative to body mass revealed non-significant results when correlated against running economy data, as can be seen in figures 7.4 to 7.6.

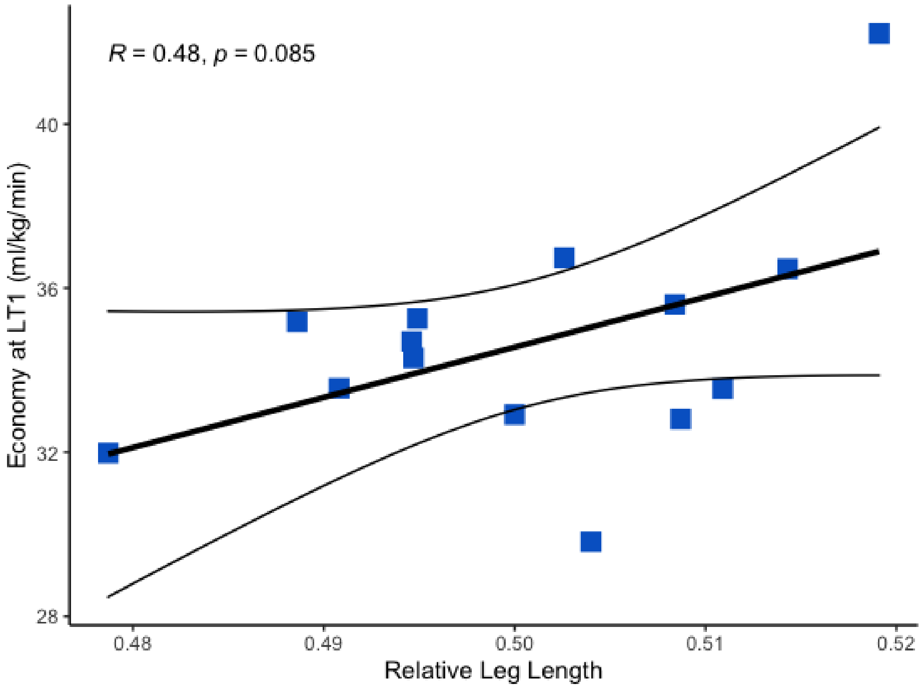

Figure 7.1 Scatterplot showing the relationship between relative leg length and economy at LT1

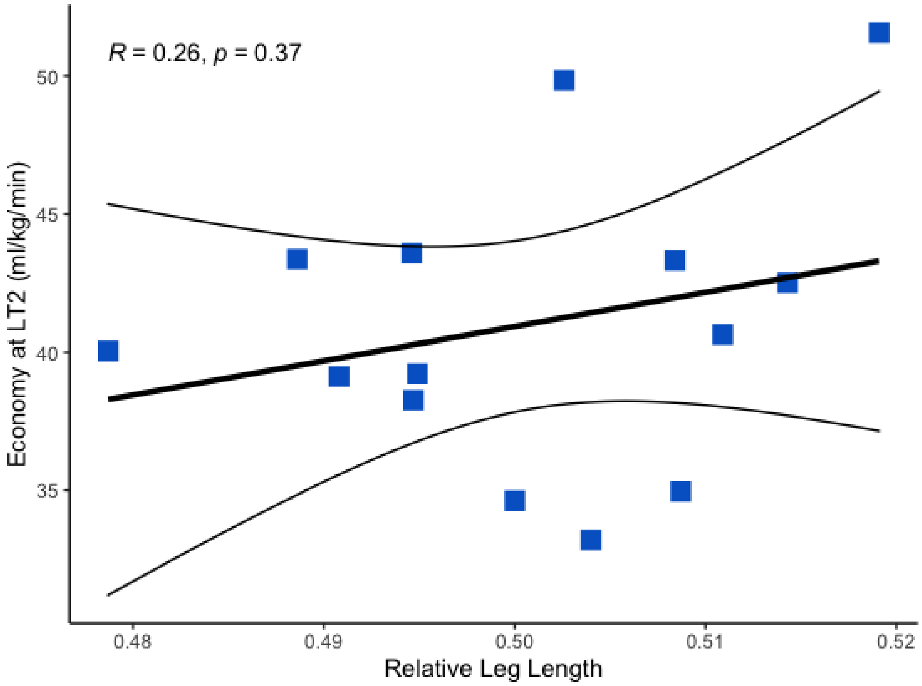

Figure 7.2 Scatterplot showing the relationship between relative leg length and LT2

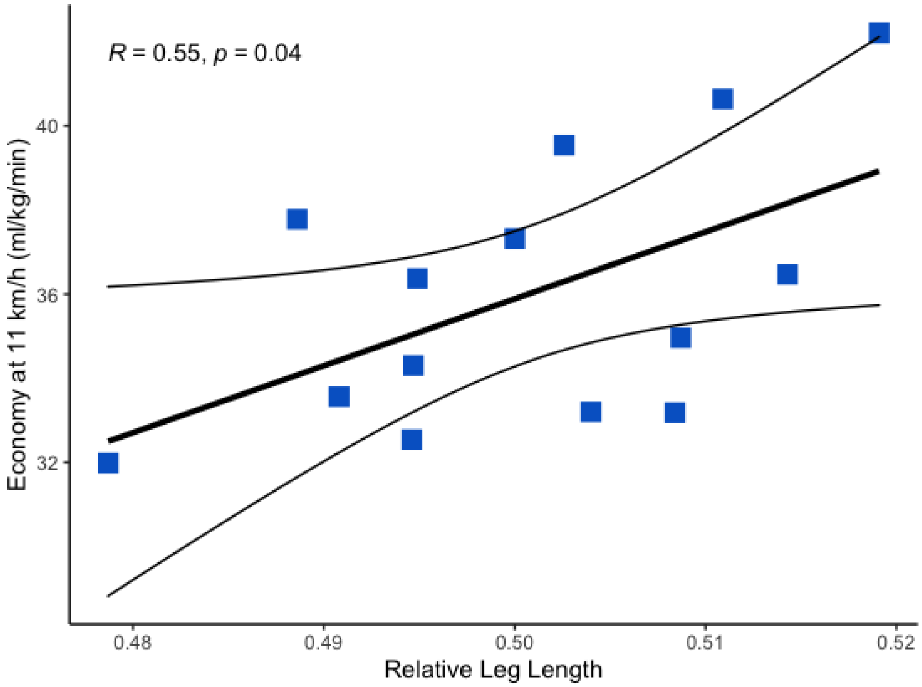

Figure 7.3 Scatterplot showing the relationship between relative leg length and economy at 11km/h

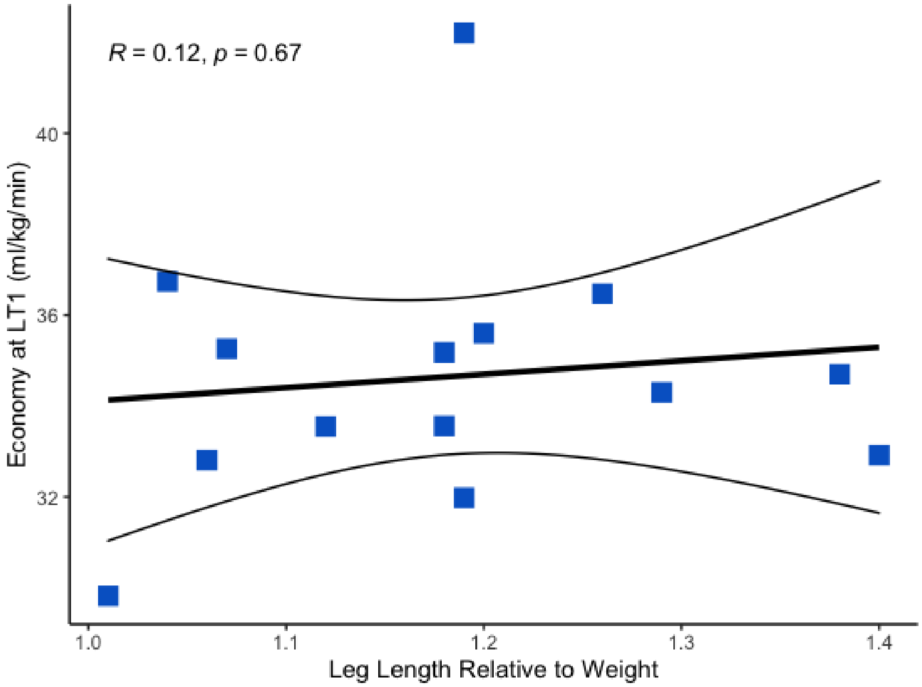

Figure 7.4 Scatterplot showing the relationship between leg length relative to weight and LT1

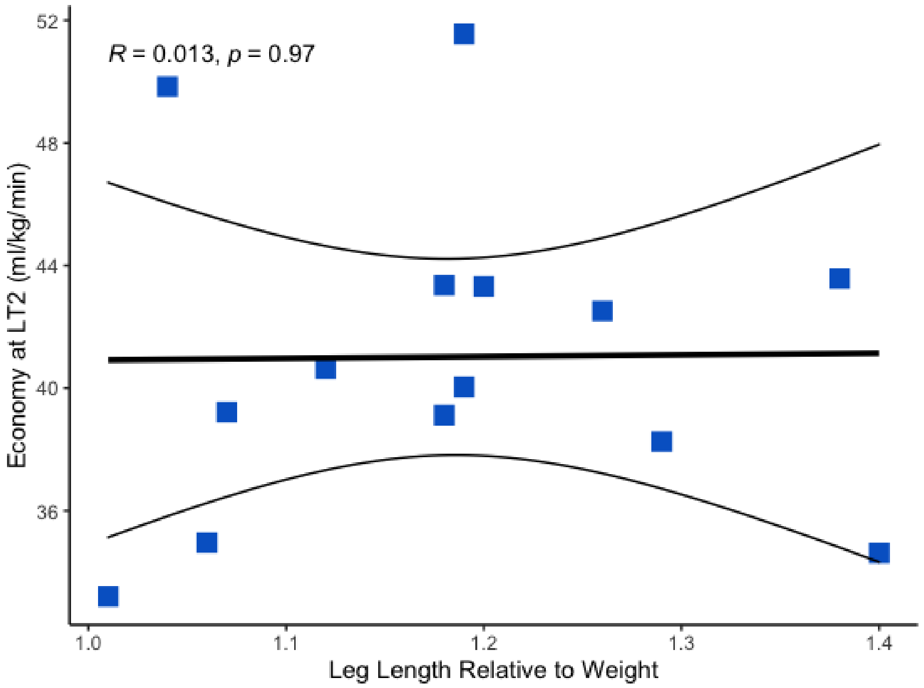

Figure 7.5 Scatterplot showing the relationship between leg length relative to weight and LT2

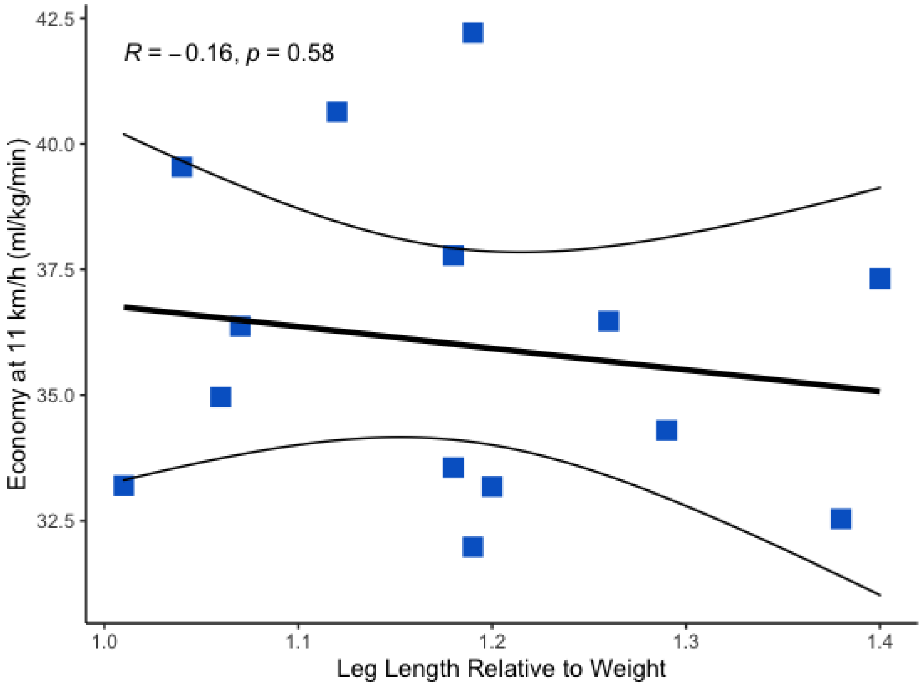

Figure 7.6 Scatterplot showing the relationship between leg length relative to body weight and economy at 11 km/h

7.3 Comparing Sizestream data to Al Andalus stage times

Hypothesis 2: Following the predictions put forth by Higgins and Ruff (2011) that relatively short tibiae would be advantageous for climbing sloped terrains, I can hypothesize the following: crural index will positively correlate with stage time on race stages with more elevation gain than loss. If there is not a significant relationship, yet this relationship is true, there will be evidence of a marginal energetic gain of having a short tibia.

From the correlations presented in table 7.5, no significant results were returned. Right leg volume showed no relationship with stage times. Volume index did not either. And crural index did not display any significant results either. These results do little to confirm the hypotheses that I set out to test, nor any of the claims made by Higgins and Ruff (2011).

Stage 1 (n=21)	R	p
Right Leg Volume	0.22	0.43
Volume Index	-0.31	0.26
Crural Index	-0.32	0.25
Stage 2 (n=20)		
Right Leg Volume	0.43	0.13
Volume Index	-0.42	0.13
Crural Index	-0.30	0.31
Stage 3		
Right Leg Volume	0.37	0.19
Volume Index	-0.37	0.20
Crural Index	-0.40	0.16
Stage 4 (n=16)		

Table 7.5 Correlation values from comparing stage times and overall times to anthropometric variables.

Right Leg Volume	0.18	0.57
Volume Index	-0.005	0.99
Crural Index	-0.023	0.94
Stage 5 (n=19)		
Right Leg Volume	0.38	0.18
Volume Index	-0.25	0.40
Crural Index	-0.30	0.30
Overall time (n=19)		
Right Leg Volume	0.41	0.18
Volume Index	-0.28	0.37
Crural Index	-0.15	0.64

7.3 Energetic relationships between athletic performance and Bergmann’s and Allen’s rules

Hypothesis 3: as this race also took place in hot climatic conditions, it is worth exploring the results put forth by Longman et al. (2019, 2021) that the performance of ultra-runners corresponds with Bergmann’s and Allen’s rules. Here we can explore the hypothesis that there will be a negative relationship between relative leg length and stage times if athletes with longer legs are more efficient at locomotion in heat, and positive relationship between sitting height ratio and stage time if those with greater trunk sizes are less efficient at locomotion in hot environments.

Looking at the relationships between relative leg length and stage times, there was only one correlation observed with stage 4 times among males ($R = -0.41$, $p < 0.05$). No other significant results were returned. When comparing sitting height ratio to stage times, the only relationship observed was again on stage 4 among males ($R = 0.41$, $p <0.05$). However, these values are not low enough to be considered significant based on the Bonferroni corrected alpha level of 0.00104.

Chapter 8 – Discussion

With this study, I present a test of theories from biological anthropologists in real-world conditions. Many of the papers which originally inspired this research project took place in labs, the running analyzed for this project took place across a 5-day ultra-endurance race in the Andalucía region of Spain. Through combing anthropometrics and stage finishing times, I was able to test how differences in anthropometric variables correspond with athletic performance across each of the stages, and with the overall finishing times. With the inclusion of running economy data as well, I was able to better contextualize the data from the ultra-runners with previous research from biological anthropologists.

8.1 Leg length and relative leg length

Many anthropologists have suggested that relatively longer leg length is an evolved trait in the genus *Homo* that has a relationship with enhanced running efficiency and performance (Bramble & Lieberman, 2004; Jungers, 1982; Steudel-Numbers et al., 2007; Sussman, 1983). There was little in this study to support that. Leg length did not correlate with stage time at any point, nor with overall time. This is not surprising, as leg length is a somewhat raw metric that is given more context when standardized to another anthropometric – such as height. That said, relative leg length (leg length / height) did not correspond with stage times, nor overall time. It was only leg length relative to weight that showed a negative relationship with some of the stage times among males – stages three, five, and overall times.

No significant results were found when analyzing the relationships between running economy at LT1 and LT2 with relative leg length and leg length relative to body weight. Economy at LT1 and LT2 was a metric used by Gordon et al. (2017) and Longman et al. (2022) to determine individual-specific speeds at which participants reach lactate threshold (LT1) and lactate turn point (LT2), with running economy being the volume of oxygen consumed per minute at the participants' relative speeds. This is in opposition to having standardized speeds at which people runs and provides a more relative approach to understanding running economy. Yet, this study was unable to demonstrate any associations between leg anthropometrics and running economy at LT1 or LT2, and only showed a partial correlation between leg length and running economy while the participants were running at 11 km/h.

Leg length relative to weight was a metric used by Steudel-Numbers et al. (2007) in their analysis of the relationship between leg length and running economy. For their research, running economy was understood as VO_2 at 2.83 m/s (6 mi/h or about 9.65 km/h) on the treadmill. They used the term relative leg length throughout their discussion but were referring to leg length relative to weight – not height. The only other study that appears to use this metric is Christiansen (2002), who studied the relationship between leg length, body mass, and peak running velocity among mammals. They found positive correlations between limb length and peak speed but noted that it does not make sense for the evolution of a species to lead to leg morphology being optimized to run extremely fast, but rather for evolution to optimize the energetic cost of locomotion at all speeds. According to Christiansen, this is because animals do not spend much of their time locomoting by way of running, but rather walking. Even still, Christiansen noted that it is rare for mammals to optimize their morphology to maximize the energetic efficiency of locomotion. In relation to the metric leg length standardized to weight, this paper noted that standardizing mammals' leg length measurements to weight improved the correlations. While I cannot find any other functional explanations for the relevance of leg length to body weight, it is likely that Neanderthals would have very low values if this were calculated for them – given their short legs and higher body masses.

Although there were correlations observed here between leg length relative to body mass among males and their times on stages 3, 5 and overall times, it is difficult to discern the functional and evolutionary significance of longer legs relative to body weight. Stages 3 and 5 both had more elevation loss than gain, so it could be a possibility that having longer legs relative to weight helps when running downhill – but there is little to base this claim on from the previous literature. Although body proportions and anthropometrics demonstrated some relationships with athletic performance at the Al Andalus Ultimate Trail, there are a wealth of other factors which contribute to running performance in the real world – which will be discussed later in this chapter.

8.2 Crural index, volume index, and leg volumes

I was unable to directly test the theory that relatively shorter lower limb segments are potentially advantageous for locomoting up sloped terrains by examining the individual climbs of the Al Andalus race. However, I was still able to test this theory using stage finishing times – where there were noticeable differences in total elevation gain and loss within stages. However, no significant results were returned in comparing crural index and volume index to stage times. These findings support those of Sheehan and Gottschall (2014), who observed that segment lengths correlated with few walking parameters when their research participants were walking on an incline. Although ultra runs involve lots of running, they also involve lots of walking – as walking helps to conserve energy, and at inclines steeper than 10 or 15 degrees some runners prefer to transition to walking as this too helps conserve energy and climb more efficiently (Brill & Kram, 2021).

The incorporation of 3D body scan data to study the relationships between leg volume and athletic performance did not demonstrate any significant relationships. There are a few potential reasons for this. The first being that this method simply looked at the volume of the participants' legs. There are many factors which influence the size of one's legs, and the performance that one can achieve from having legs. Leg volume in this example is partially influenced by length, while it is also influenced by muscle size and fat content in the segments. The lengths of limbs and limb segments that are observable in adulthood are influenced by many things through growth and development including sex, early childhood environments, nutrition, and participation in physical activity throughout the life course (Bogin & Varela-Silva, 2010). As well, previous research has shown that limb segment lengths and volumes show no associations with running efficiency (Williams & Cavanagh, 1987).

8.3 Energetic relationships with Bergmann's and Allen's rules

Longman et al. (2019, 2021) proposed that participation and performance in ultra-endurance races in hot and cold environments may be partially driven by Bergmann's and Allen's rules. Although these papers included data from the participants of the 2016 and 2017 Al Andalus trail races, Longman et al. looked at the relationships between race finisher status and anthropometrics, whereas I explored how the individual stage times correspond with relative leg length and sitting height ratio. The only significant results between stage time and these two anthropometrics were observed among males on stage 4 time – the longest stage of the race. Although the results were generally non-significant, and the results were limited by a smaller sample size, it remains a possibility that the energetic advantages of thermal-adapted morphologies are only present over longer durations, such as the 64km that was stage 4 of the Al Andalus Ultra. And although Longman (2021) originally suggested that the relationships between Bergmann's and Allen's rules and ultra-endurance athletic performance may be stronger among females than males, there were no significant results returned among female athletes.

8.4 What are the effects of variation in lower limb morphology?

Of course, legs are inherently involved in bipedal locomotion, but it took about 5 million years of hominin evolution for there to be a noticeable elongation of leg length in the fossil record. In the genus *Australopithecus* there was a mosaic of traits functionally relevant to locomotion among the species – some suited for climbing, some suited for walking, with many species likely capable of both. But Little Foot (STW 573, species uncertain) is the only fossil specimen of *Australopithecus* who presented relatively longer legs than other members of the genus. Two million years ago, relative leg lengths increased with the origin of *Homo erectus*, but there remains considerable variability among the genus *Homo.* The most notable anomaly of the genus *Homo* being the short and robust statures present among the Neanderthals.

There are many compelling arguments for why longer legs may have evolved to make bipedalism more efficient, but length alone does not appear to be the product of selective pressures from bipedal locomotion (Kramer & Eck, 2000). Researchers have suggested that species or individuals will locomote in a way that is most energetically efficient relative to their own anatomy and capabilities (Christiansen, 2002; Kramer, 1999; Sheehan & Gottschall, 2014). It also remains rare in mammalian evolution for species to evolve morphological features which minimize the energetic cost of locomotion (Christiansen, 2002). Even if a species would have taken relatively shorter steps as a product of their relatively shorter legs – that is not to say that they were in any way compromised or inefficient. And although the evidence which has been examined in this thesis is far separated in time and theory from the hominin fossil record, there has been no consistent or reliable evidence that leg length is associated with running performance in the real world.

Many of the papers cited throughout this thesis employ research conducted in biomechanics labs to help test the hypothesis that longer legs evolved to help make bipedal locomotion more efficient, yet if a hypothesis is true, it should also be observable outside of laboratories. Such studies have provided interesting results, yet leg length does not explain running performance among living humans running an ultra-endurance event in this study, nor among the running economy data gathered from a sub-group of the ultra-runners. Physiology and mechanics are of great importance to athletic performance as well. However, we cannot see the physiology of hominin species in the fossil record, it can only be inferred by drawing comparisons with living species – most often from humans and chimpanzees. Perhaps, this is why so much attention has been drawn towards leg length and bipedalism – as length can be readily drawn from elements preserved in the fossil record. Combined with the fact that elongated leg length is one of the defining features of the genus *Homo*, it becomes an important focal point of evolutionary theories. Yet in real world athletic performance, the effect of training history, and the biomechanical and physiological aspects of the human body will provide a greater contribution to how fast someone can run (Saunders et al., 2004; Williams & Cavanagh, 19*87*).

Chapter 9 – Conclusion

This thesis first set out to test how variability in the volume and lengths of limb proportions correspond with locomotor efficiency on sloped terrains through the analysis of anthropometric data collected from the Sizestream 3D Body Scanner and performance data collected from Strava. With a hypothesis drawn from Higgins and Ruff (2011) that relatively short lower limb lengths would confer a locomotor advantage on sloped terrain, I sought to test how variability in limb segment lengths and volumes corresponded with performance metrics from a workout completed by Western's cross-country team at a park in Arva. Although the participant numbers were low, I found general trends that limb segment volumes correlate with step rate and step length on flat terrain, with no correlations observed between limb segment volumes and time on flat terrain. On uphill terrain, the trends mostly disappeared, with there being no consistent relationship between limb volumes and the performance metrics gathered. It was also observed that crural index displayed a negative trend with time on both the flat and uphill segments on the first repeat of the workout, while the relationship weakened on the last repeat of the workout.

I then extended this thesis to examine how anthropometrics correspond with athletic performance at a 5-stage ultra-marathon taking place in the Andalucía region of Spain. This section also incorporated running economy data from a sub-group of the ultra-runners to test the hypothesis from anthropologists that longer leg length is associated with enhanced running economy (albeit with the previous findings from kinesiologists that leg length has no association with running economy).

With anthropometric data collected from the race participants via more traditional methods, and a sub-group of race participants providing 3D body scans, I sought to explore how variation in leg length and volume correspond with performance over the five stages and in the overall times. Although I was limited to the finishing times from the stages and could not look at the participants' performance over individual climbs, I extended my original hypotheses to test if there was an energetic advantage of having relatively shorter tibiae or relatively lower calf volume on stages with greater levels of elevation gain. I also sought out to test if having anatomical features that had previously been hypothesized to be advantageous for running (such as relatively longer legs) would have been advantageous over the course of the race. There was little to be found from this portion of my analyses. The only correlations found that were relevant to my original hypotheses were between leg length relative to body weight and times on stages 3, 5 and overall times among men. Leg length relative to body weight is a rarely used metric in sports science and anthropology, but it improved the correlations between relative leg length and stage times in this study. Despite these correlations, the relationships between leg morphology and running performance are sparse in this experimental approach to human evolutionary theory. Additionally, the inclusion of running economy data from a subset of the participants further revealed no relationships between leg length and oxygen consumption at various speeds.

By using two real-world tests of bipedalism in the forms of a cross-country workout, a 5 stage ultra-marathon, as well as the analysis of running economy data, this thesis has been unable to confirm any hypotheses from human evolutionary theory that longer legs evolved to aid in more efficient running, or that longer legs result in a more efficient form of bipedalism. Differences between the paleoanthropological and biomechanics literature are worth noting here. While paleoanthropologists describe a strong relationship between leg length and running economy, kinesiologists have often reported the absence of a relationship – as displayed in the results of this thesis. There are two potential reasons for this. There may an error in paleoanthropologists describing the adaptive significance of relatively longer leg length as being beneficial for faster and more efficient locomotion. The second reason may be that paleoanthropologists are correct in discussing the broader interspecific dynamics of the energetics of leg length, but within species the differences in leg length are too subtle to consistently validate theories on the evolution and energetics of leg length. Although the approach here largely focussed on time as a metric of running performance – which tests a real-world outcome of running a race rather than the physiological characteristics of runners – the inclusion of running economy data from ultra-runners further demonstrated the absence of a relationship between leg length and economy.

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Appendix

Appendix A: Ethics approval letter

Date: 14 October 2021
To:
Project ID: 119361
Study Title: Modern human locomotion on sloped terrain: With implications for the fossil record
Application Type: HSREB Initial Application
Review Type: Delegated
Meeting Date / Full Board Reporting Date: 02/Nov/2021
Date Approval Issued: 14/Oct/2021
REB Approval Expiry Date: 14/Oct/2022

Dear Professor [Redacted]
The Western University Health Science Research Ethics Board (HSREB) has reviewed and approved the above mentioned study as described in the WREM application form, as of the HSREB Initial Approval Date noted above. This research study is to be conducted by the investigator noted above. **All other required institutional approvals and mandated training must also be obtained prior to the conduct of the study**.
Documents Approved:

Document Name	Document Type	Document Date	Document Version
Medical and Activity History Questionnaire	Paper Survey	17/Aug/2021	1
attema_reb_application_2	Protocol	28/Sep/2021	2
Instructions for downloading TCX files	Other Data Collection Instruments	04/Oct/2021	1
Recruitment_Email_For_soccer_rowing_swimming_2	Email Script	28/Sep/2021	2
classroom recruitment script for controls	Email Script	28/Sep/2021	1

Recruitment_Email_for_XC_LWTFC_2	Email Script	28/Sep/2021	2
Letter of Information and Consent for Sedentary Controls 3	Written Consent/Assent	04/Oct/2021	3
Letter of Information and Consent for Swimming Soccer Rowing Teams 1	Written Consent/Assent	04/Oct/2021	1
Letter of Information and Consent Sheet For XC-LWTFC Athletes 3	Written Consent/Assent	04/Oct/2021	3

Documents Acknowledged:

Document Name	Document Type	Document Date	Document Version
References_for_rationale	References	02/Aug/2021	1

No deviations from, or changes to, the protocol or WREM application should be initiated without prior written approval of an appropriate amendment from Western HSREB , except when necessary to eliminate immediate hazard(s) to study participants or when the change(s) involves only administrative or logistical aspects of the trial.

REB members involved in the research project do not participate in the review, discussion or decision.

The Western University HSREB operates in compliance with, and is constituted in accordance with, the requirements of the TriC ouncil Policy Statement: Ethical Conduct for Research Involving Humans (TCPS 2); the International Conference on Harmonisation Good Clinical Practice Consolidated Guideline (ICH GCP); Part C, Division 5 of the Food and Drug Regulations; Part 4 of the Natural Health Products Regulations; Part 3 of the Medical Devices Regulations and the provisions of the Ontario Personal Health Information Protection Act (PHIPA 2004) and its applicable regulations. The HSREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000940.

Please do not hesitate to contact us if you have any questions. Sincerely,

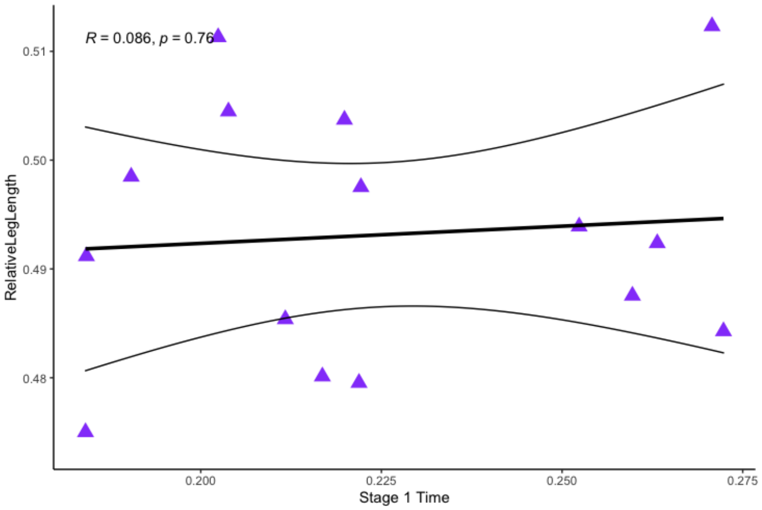
[Redacted], Ethics Officer ([Redacted]@uwo.ca) on behalf of Dr. [Redacted], HSREB Vice-Chair

Note: This correspondence includes an electronic signature (validation and approval via an online system that is compliant with all regulations

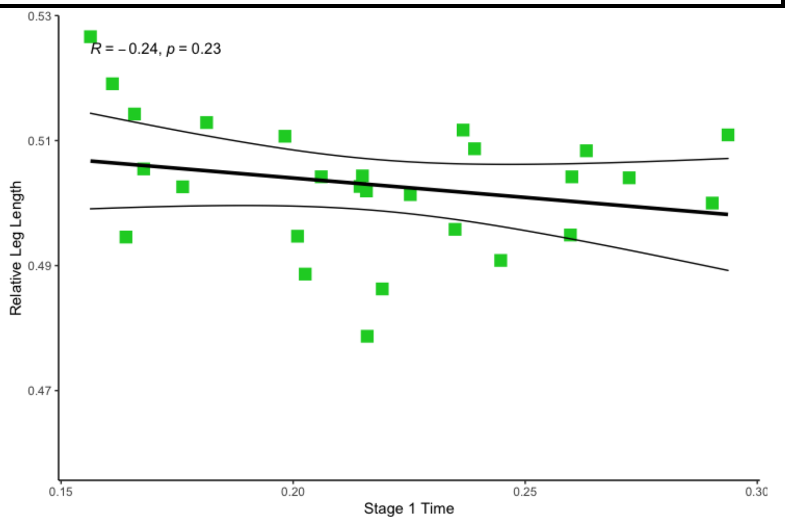
Appendix B: Scatterplots of analyses from chapter 7.

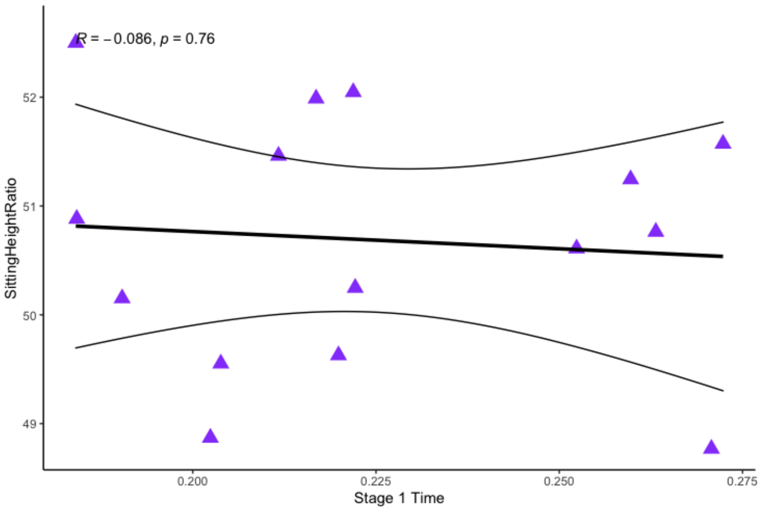
Stage 1 Times

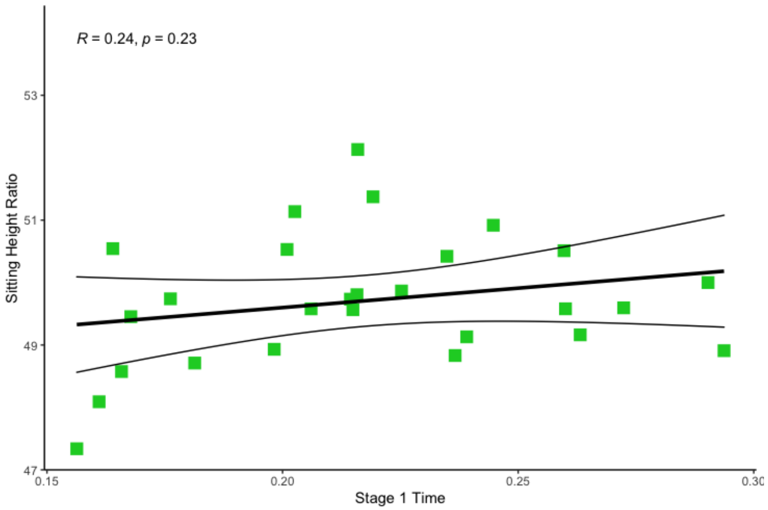
Females

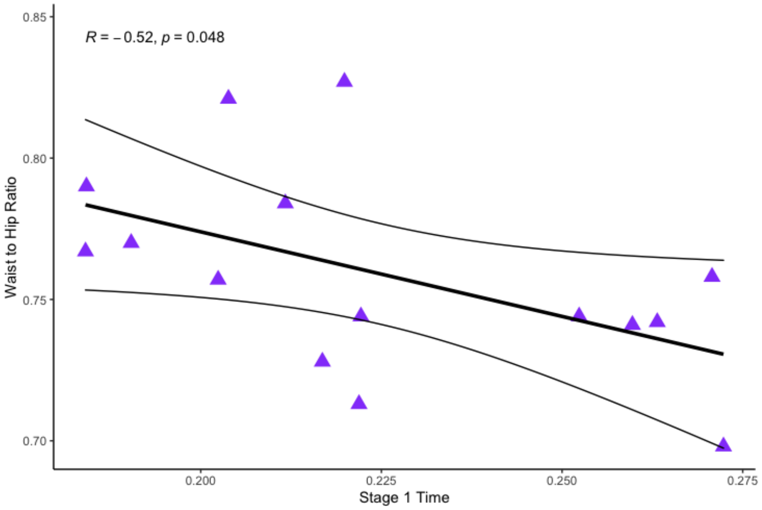


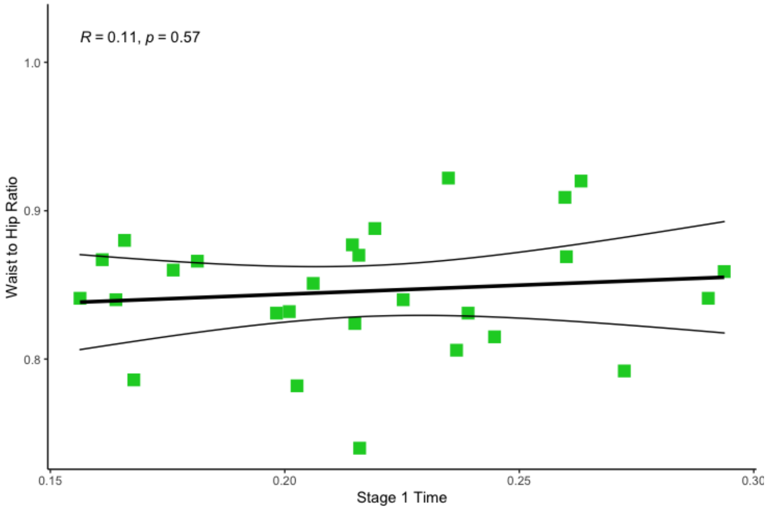
Males

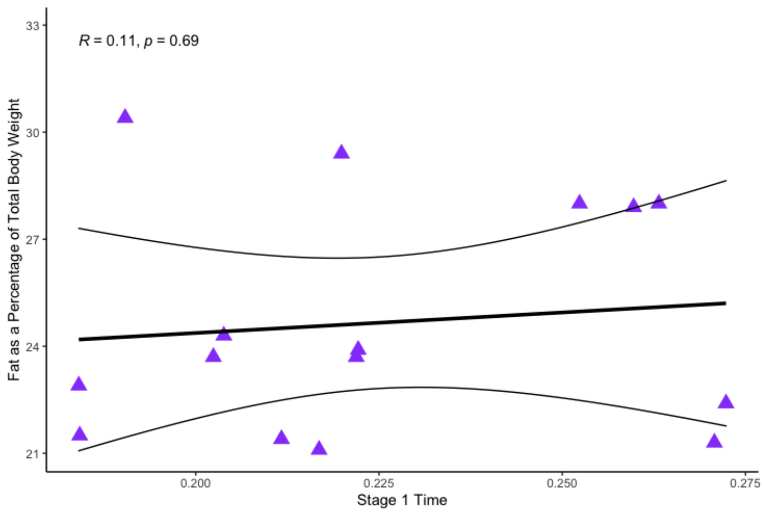



R = −0.086, p = 0.76
SittingHeightRatio
52
51
50
49
0.200
0.225
0.250
0.275
Stage 1 Time

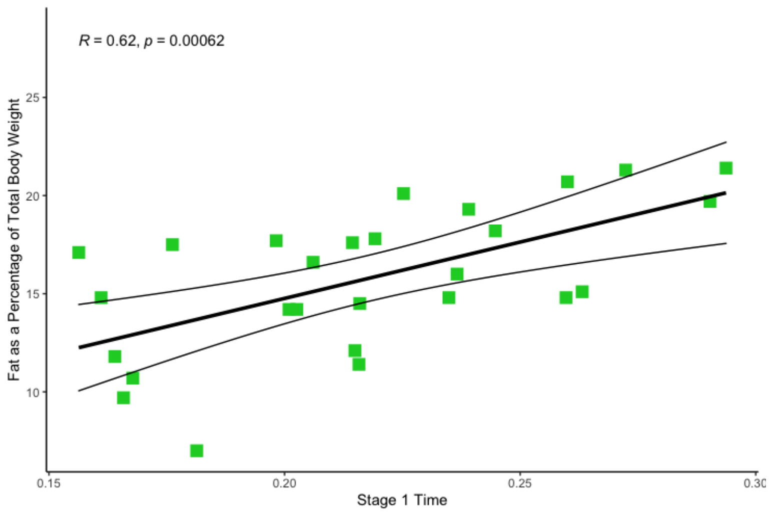

R = 0.24, p = 0.23
Sitting Height Ratio
53
51
49
47
0.15
0.20
0.25
0.30
Stage 1 Time


R = −0.52, p = 0.048
Waist to Hip Ratio
0.85
0.80
0.75
0.70
0.200
0.225
0.250
0.275
Stage 1 Time

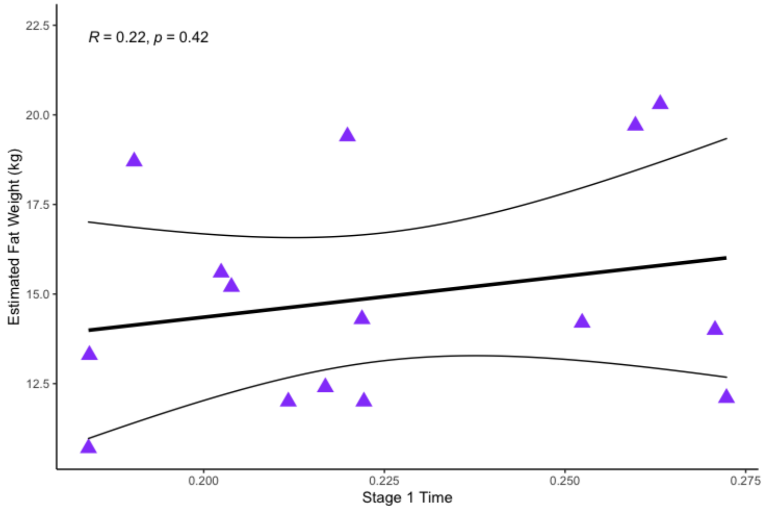

R = 0.11, p = 0.57
Waist to Hip Ratio
1.0
0.9
0.8
0.15
0.20
0.25
0.30
Stage 1 Time



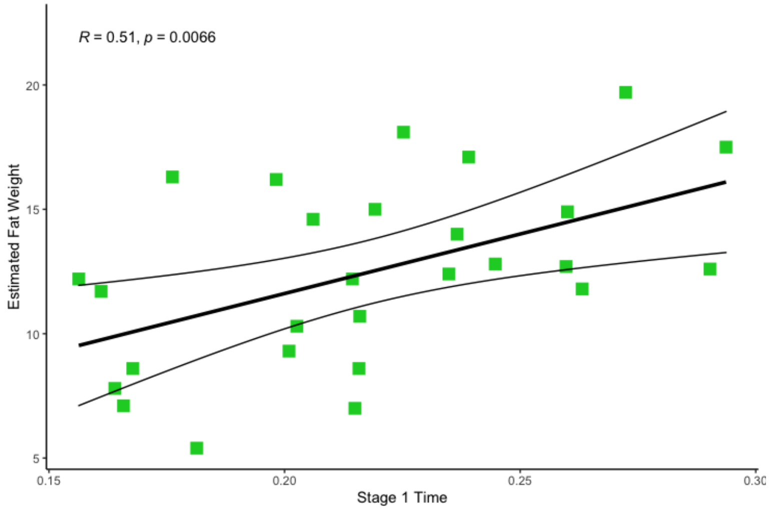
R = 0.11, p = 0.69
Fat as a Percentage of Total Body Weight
33
30
27
24
21
0.200
0.225
0.250
0.275
Stage 1 Time



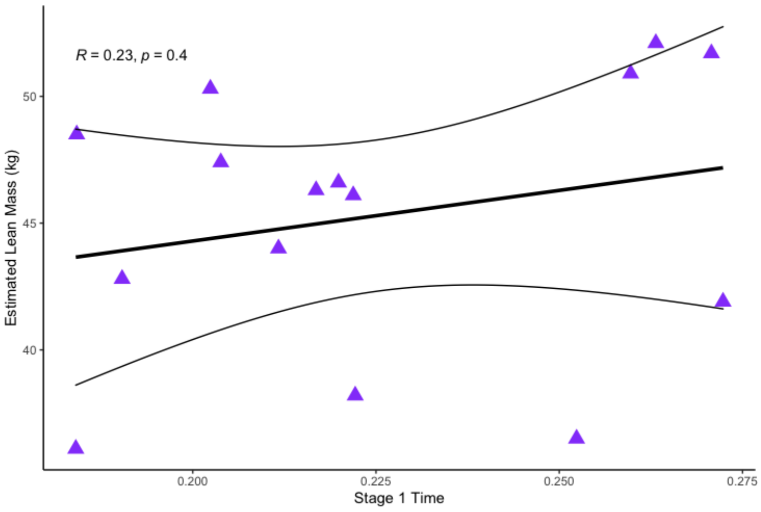
R = 0.62, p = 0.00062
Fat as a Percentage of Total Body Weight
25
20
15
10
0.15
0.20
0.25
0.30
Stage 1 Time

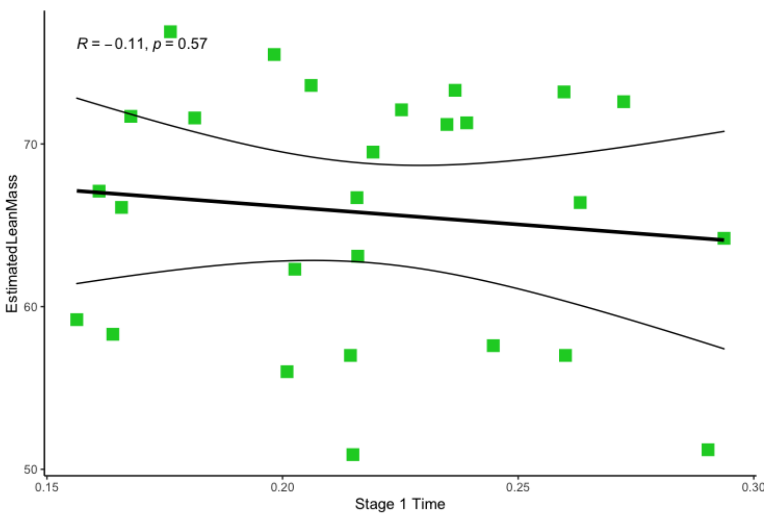


R = 0.22, p = 0.42
Estimated Fat Weight (kg)
22.5
20.0
17.5
15.0
12.5
0.200
0.225
0.250
0.275
Stage 1 Time



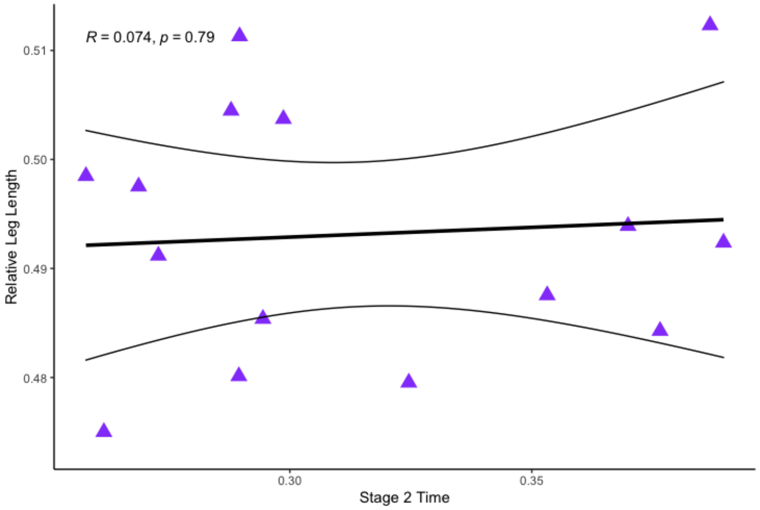
R = 0.51, p = 0.0066
Estimated Fat Weight
20
15
10
5
0.15
0.20
0.25
0.30
Stage 1 Time

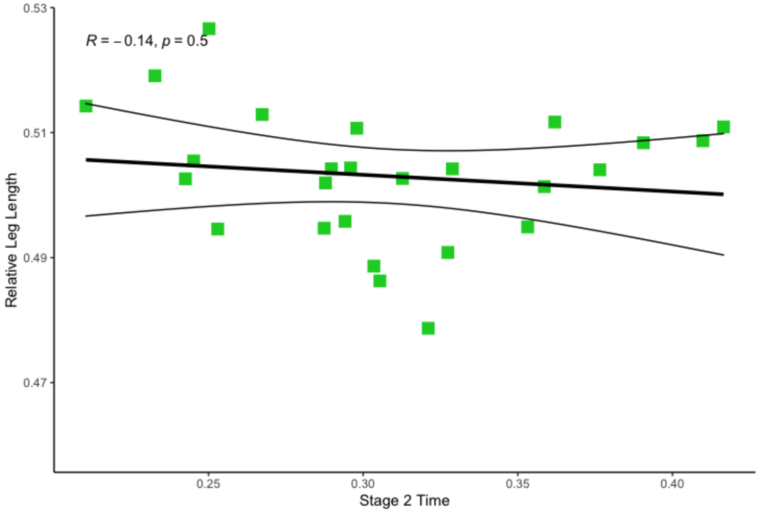

R = 0.23, p = 0.4
Estimated Lean Mass (kg)
50
45
40
0.200
0.225
0.250
0.275
Stage 1 Time

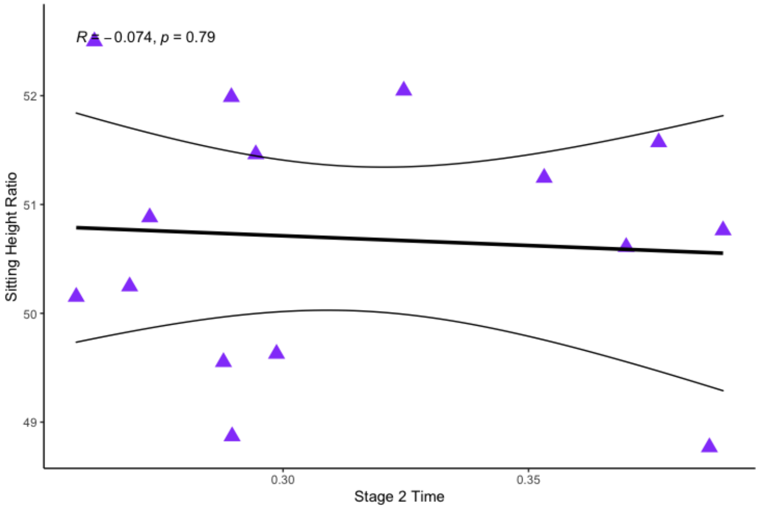

R = −0.11, p = 0.57
EstimatedLeanMass
70
60
50
0.15
0.20
0.25
0.30
Stage 1 Time

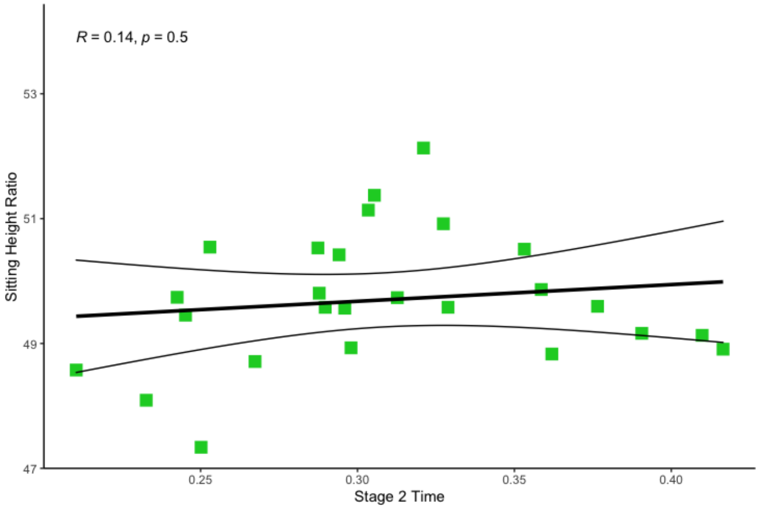
Stage 2 Times

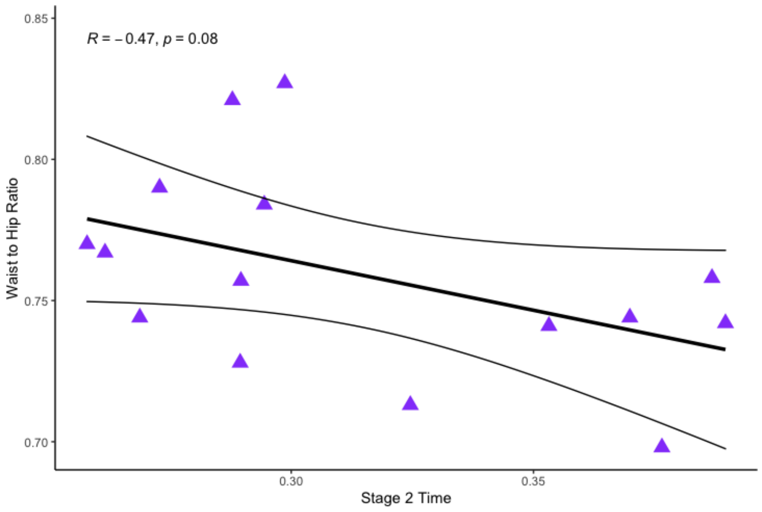
Females	Males

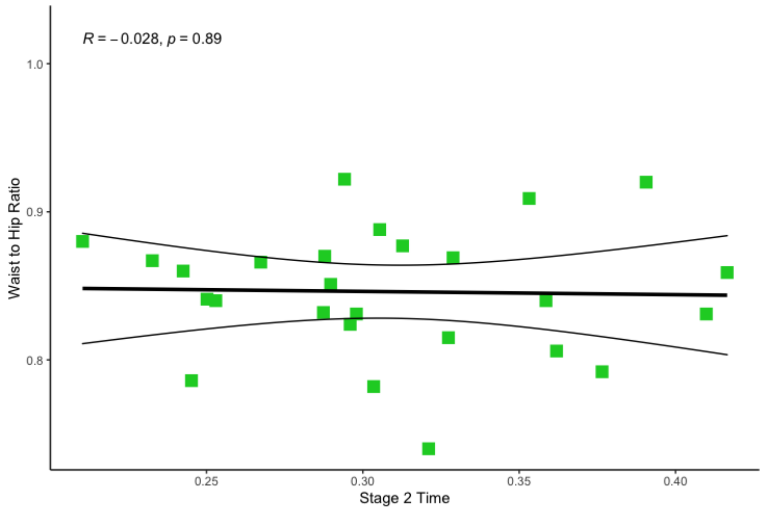


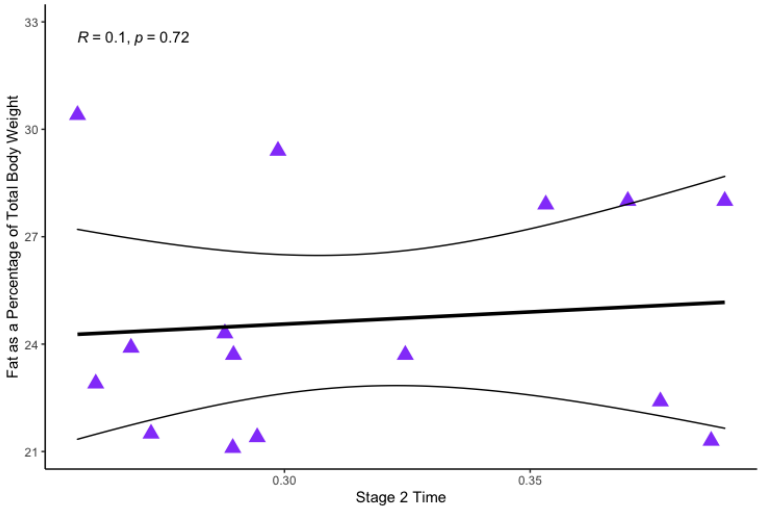


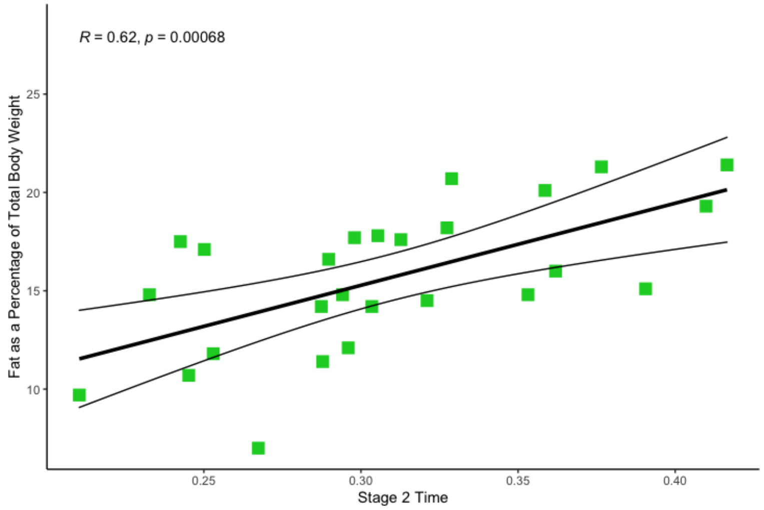


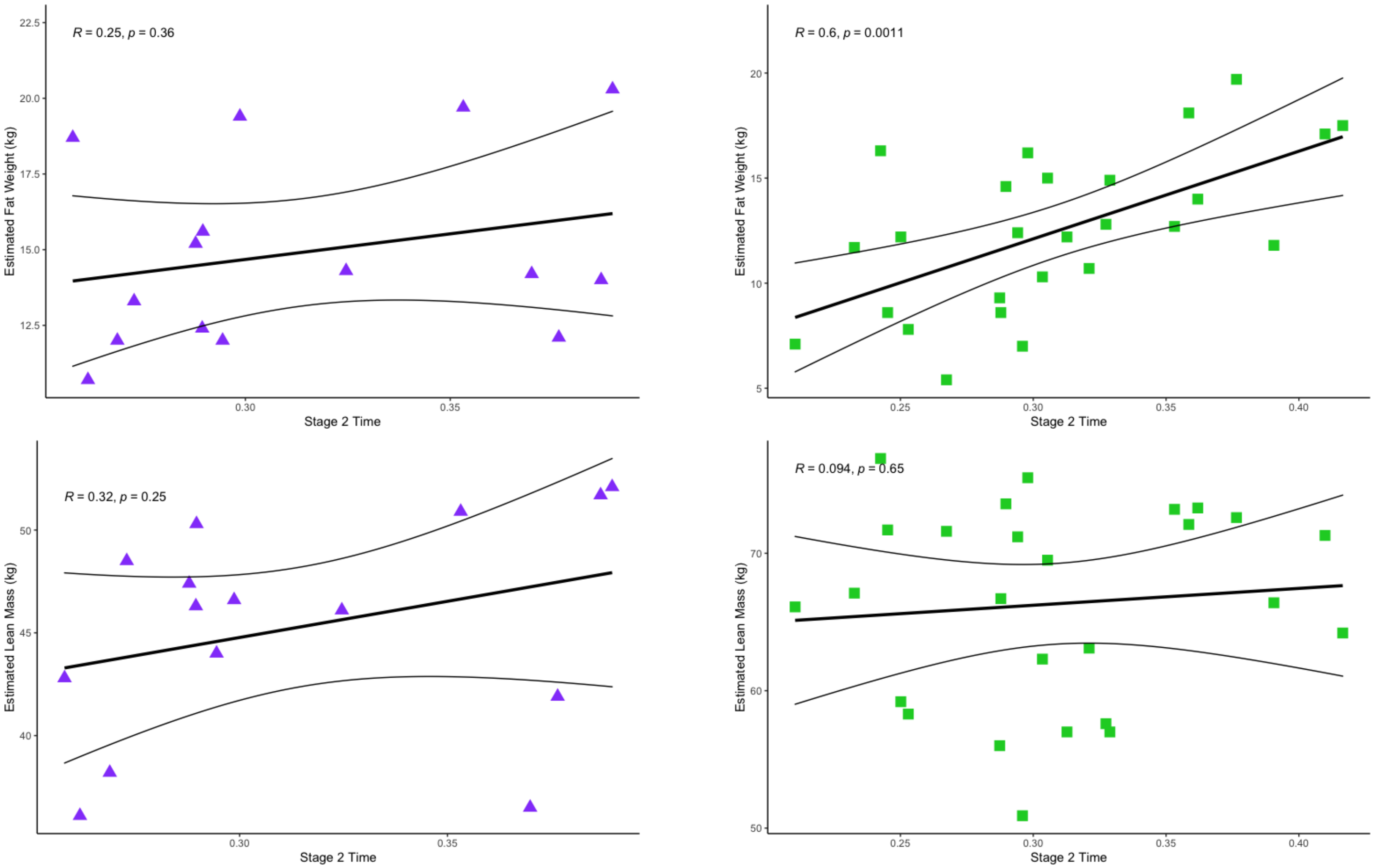



R = –0.47, p = 0.08
Waist to Hip Ratio
0.85
0.80
0.75
0.70
0.30
0.35
Stage 2 Time


R = –0.028, p = 0.89
Waist to Hip Ratio
1.0
0.9
0.8
0.25
0.30
0.35
0.40
Stage 2 Time

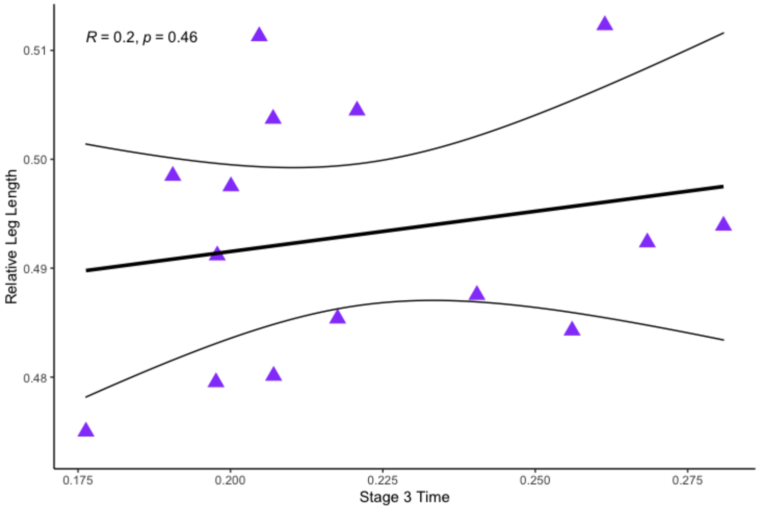

R = 0.1, p = 0.72
Fat as a Percentage of Total Body Weight
33
30
27
24
21
0.30
0.35
Stage 2 Time

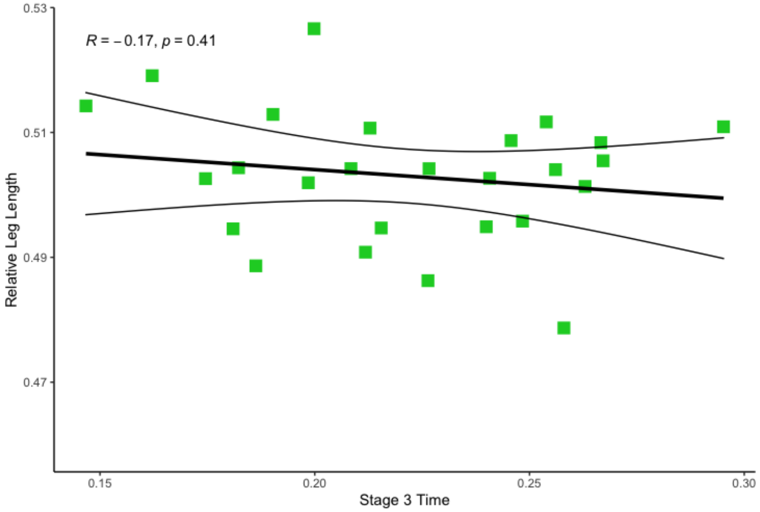

R = 0.62, p = 0.00068
Fat as a Percentage of Total Body Weight
25
20
15
10
0.25
0.30
0.35
0.40
Stage 2 Time

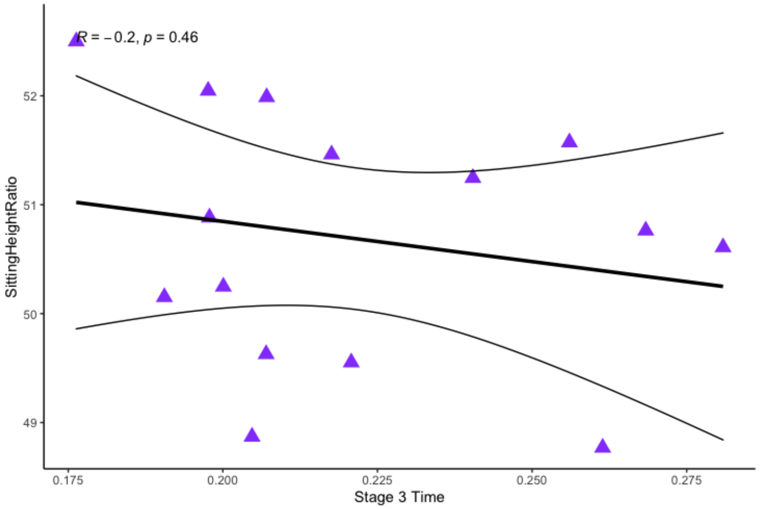

R = 0.25, p = 0.36
Estimated Fat Weight (kg)
22.5
20.0
17.5
15.0
12.5
0.30
0.35
Stage 2 Time
R = 0.6, p = 0.0011
Estimated Fat Weight (kg)
20
15
10
5
0.25
0.30
0.35
0.40
Stage 2 Time
R = 0.32, p = 0.25
Estimated Lean Mass (kg)
50
45
40
0.30
0.35
Stage 2 Time
R = 0.094, p = 0.65
Estimated Lean Mass (kg)
70
60
50
0.25
0.30
0.35
0.40
Stage 2 Time

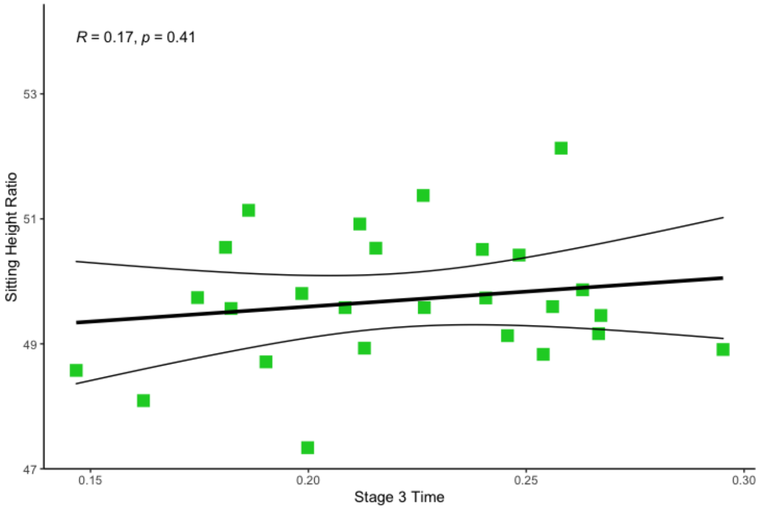
Stage 3 Times

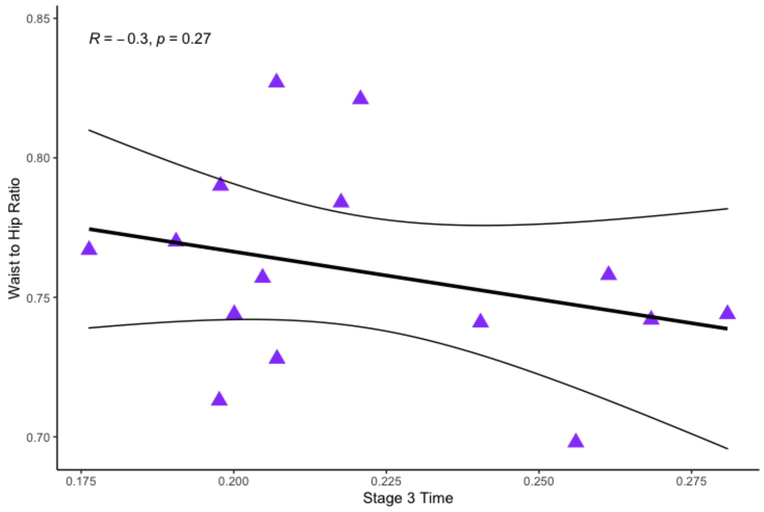
Females	Males

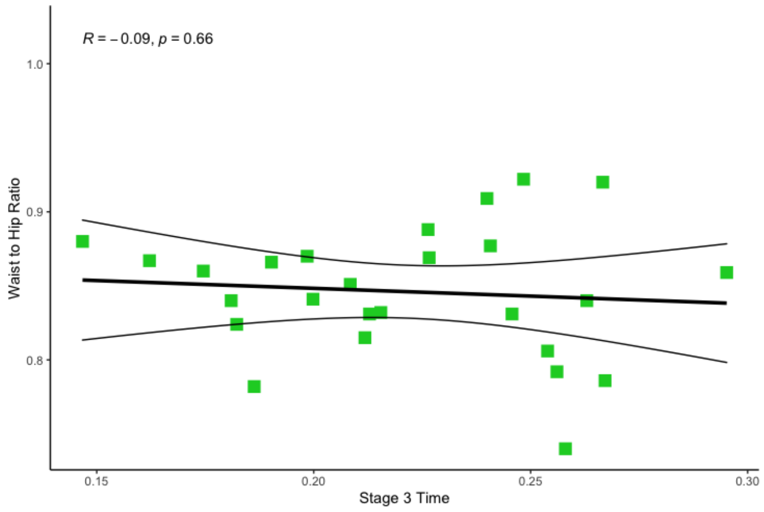


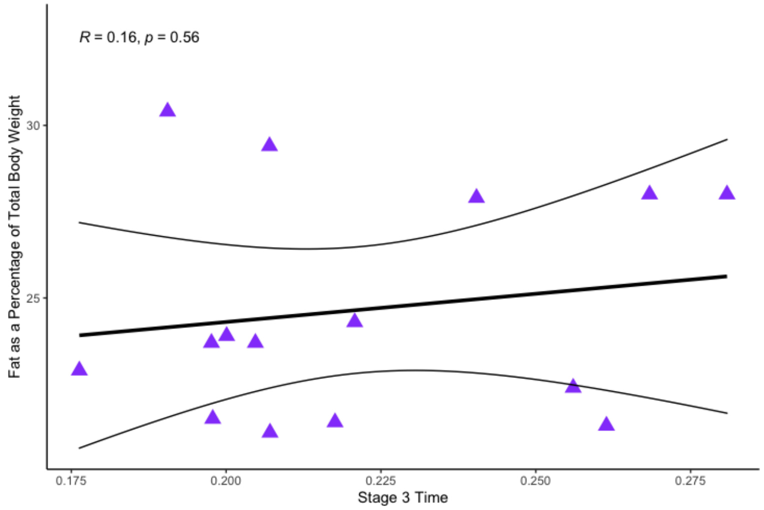


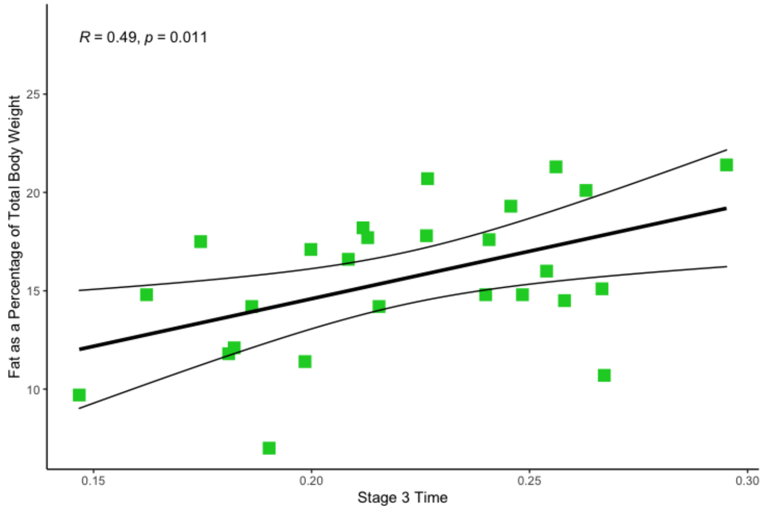


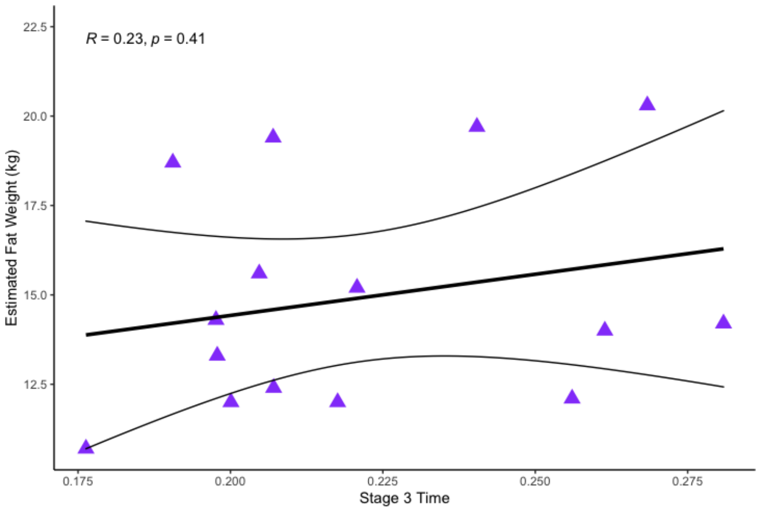


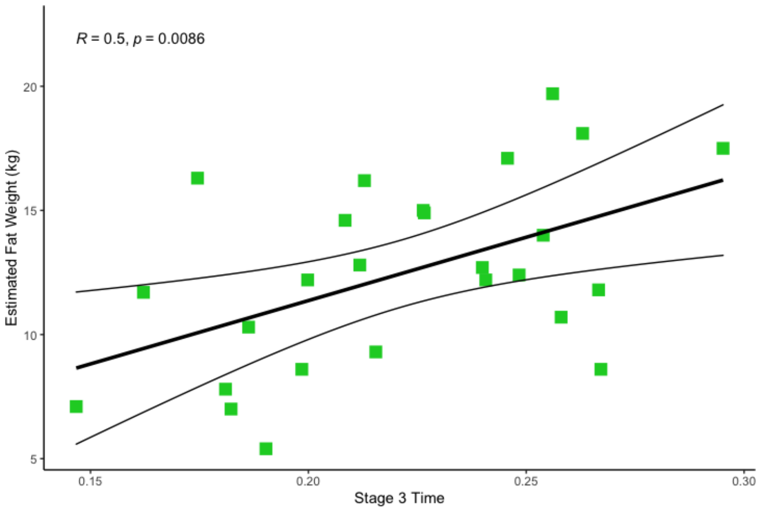

R = −0.3, p = 0.27
Waist to Hip Ratio
0.85
0.80
0.75
0.70
0.175
0.200
0.225
0.250
0.275
Stage 3 Time

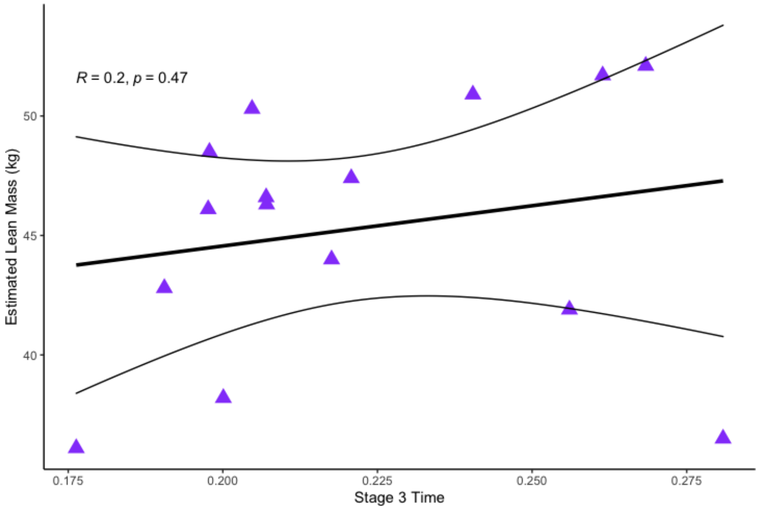

R = −0.09, p = 0.66
Waist to Hip Ratio
1.0
0.9
0.8
0.15
0.20
0.25
0.30
Stage 3 Time

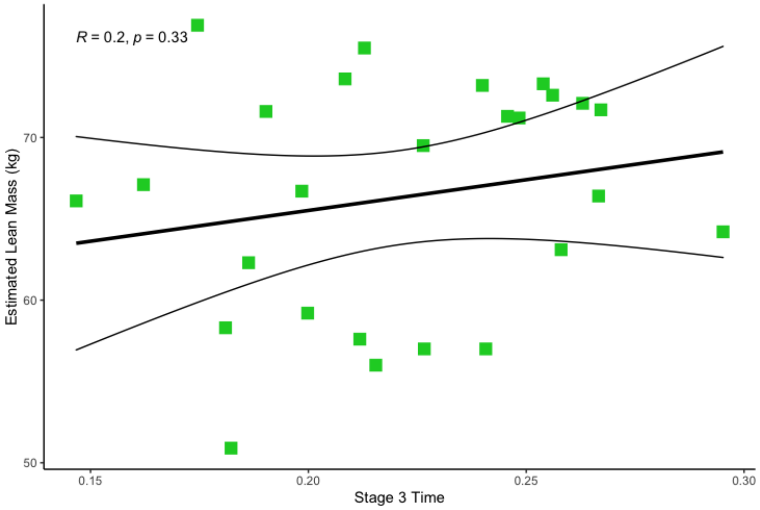

R = 0.16, p = 0.56
Fat as a Percentage of Total Body Weight
30
25
0.175
0.200
0.225
0.250
0.275
Stage 3 Time


R = 0.49, p = 0.011
Fat as a Percentage of Total Body Weight
25
20
15
10
0.15
0.20
0.25
0.30
Stage 3 Time


R = 0.23, p = 0.41
Estimated Fat Weight (kg)
22.5
20.0
17.5
15.0
12.5
0.175
0.200
0.225
0.250
0.275
Stage 3 Time

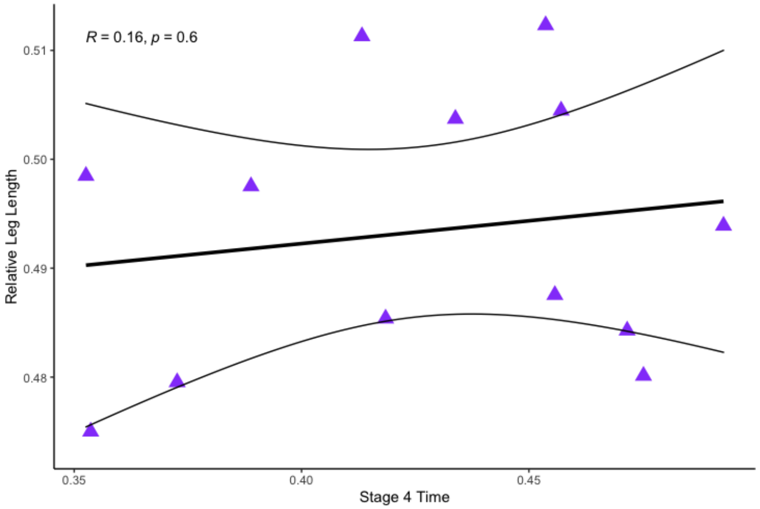

R = 0.5, p = 0.0086
Estimated Fat Weight (kg)
20
15
10
5
0.15
0.20
0.25
0.30
Stage 3 Time

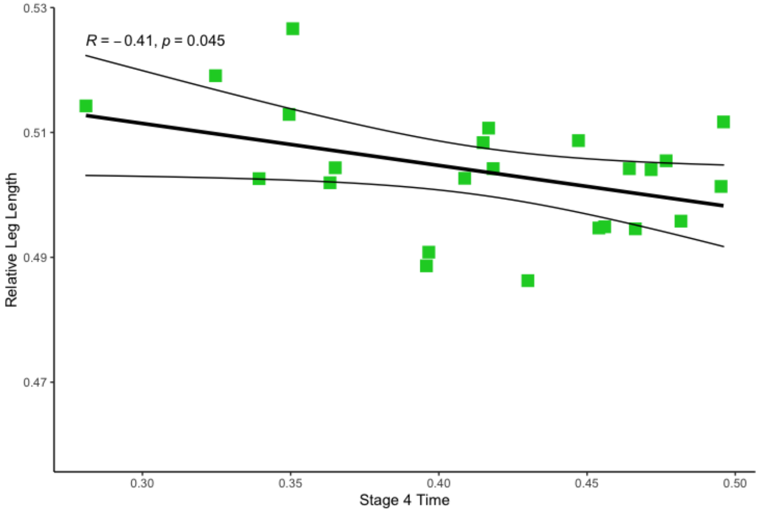

R = 0.2, p = 0.47
Estimated Lean Mass (kg)
50
45
40
0.175
0.200
0.225
0.250
0.275
Stage 3 Time

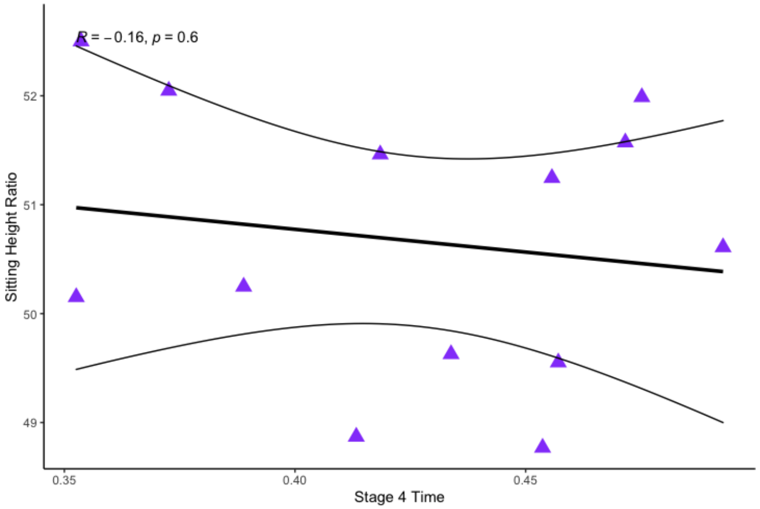

R = 0.2, p = 0.33
Estimated Lean Mass (kg)
70
60
50
0.15
0.20
0.25
0.30
Stage 3 Time

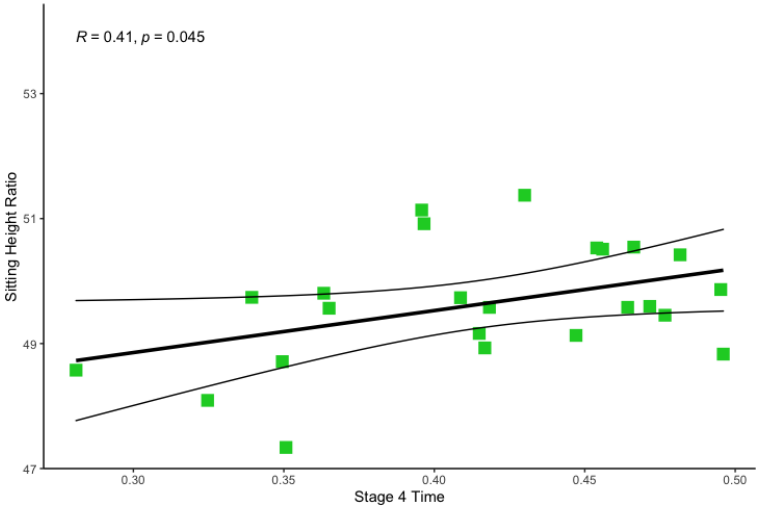
Stage 4 Times

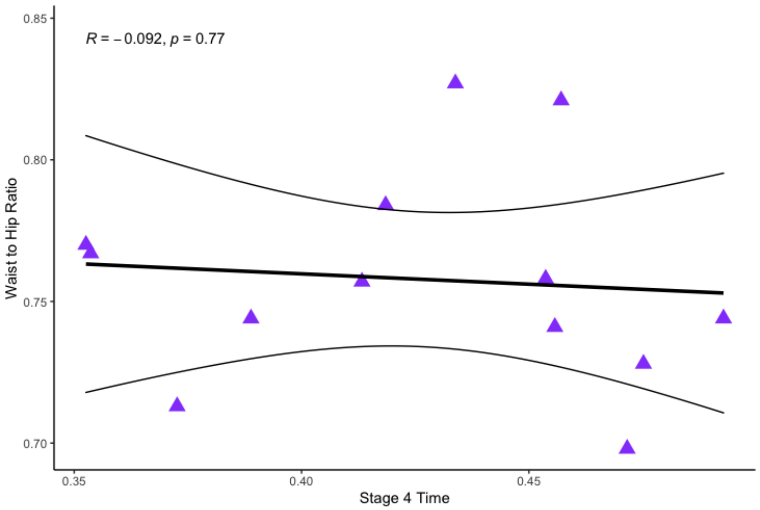
Females	Males

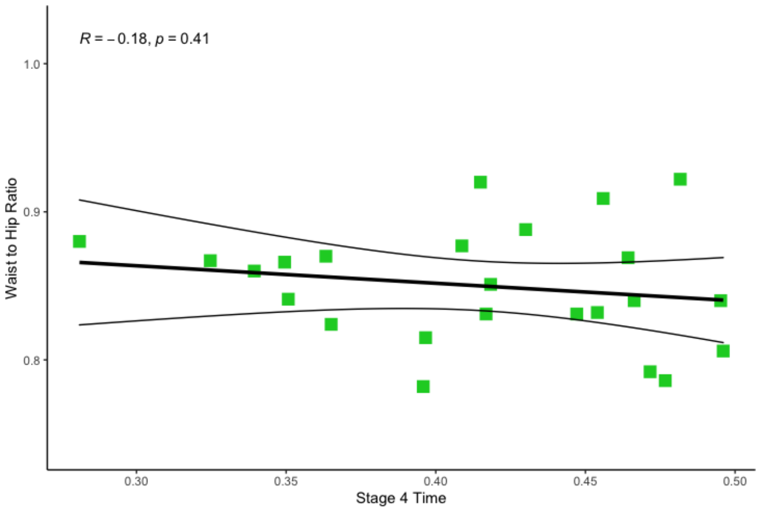


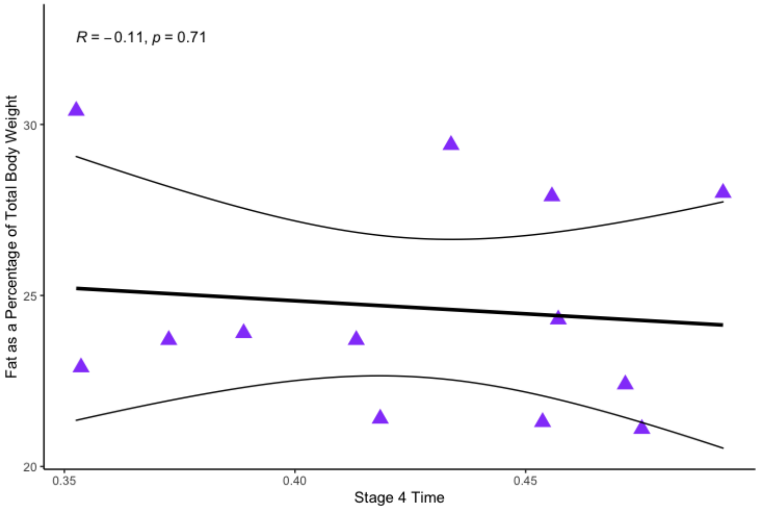


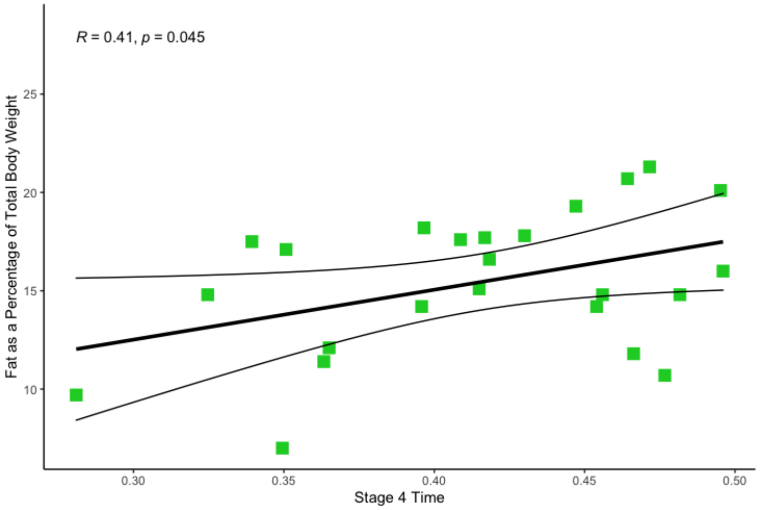


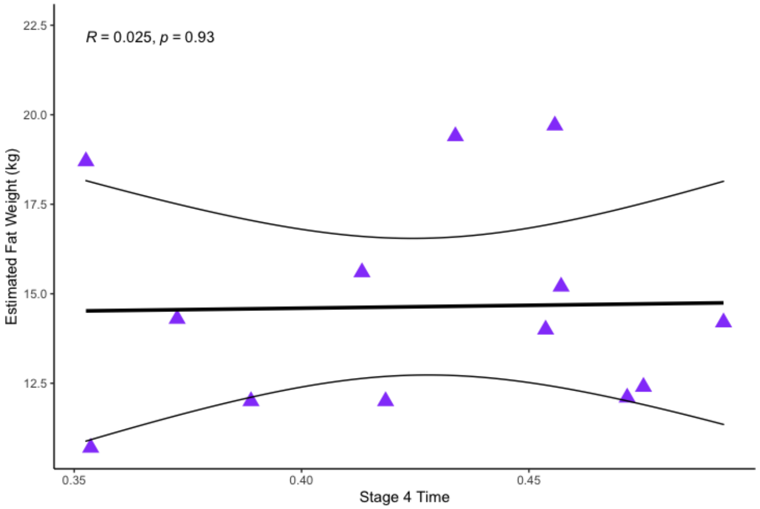


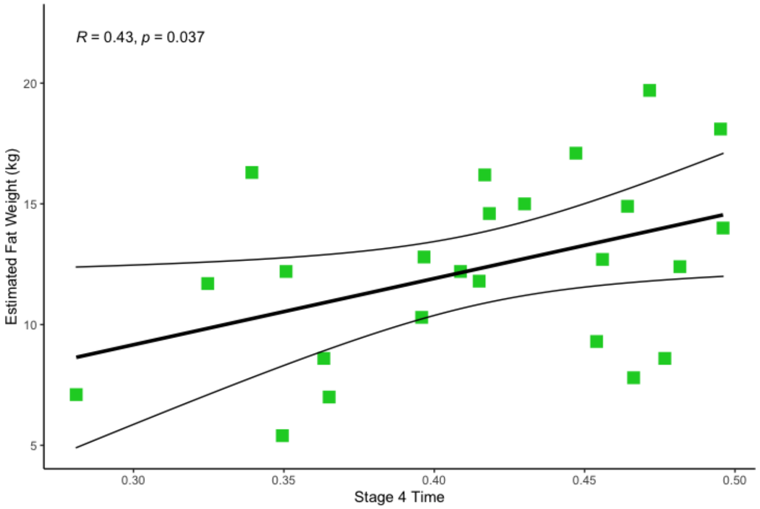

R = −0.092, p = 0.77
Waist to Hip Ratio
0.85
0.80
0.75
0.70
0.35
0.40
0.45
Stage 4 Time

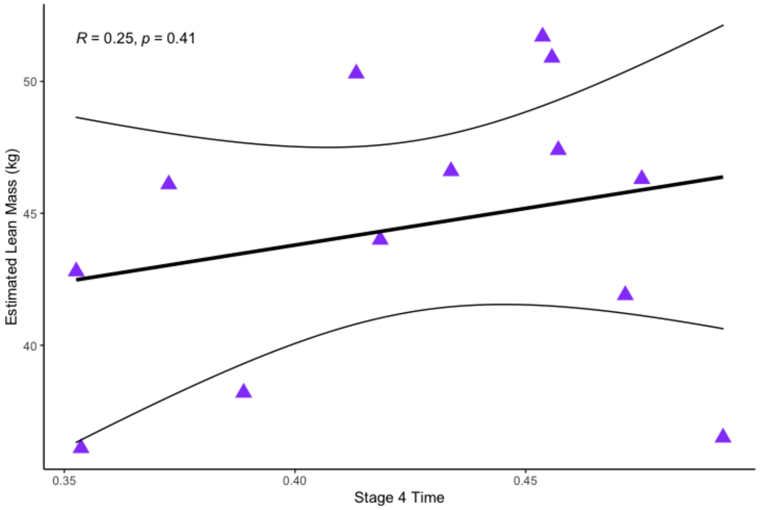

R = −0.18, p = 0.41
Waist to Hip Ratio
1.0
0.9
0.8
0.30
0.35
0.40
0.45
0.50
Stage 4 Time

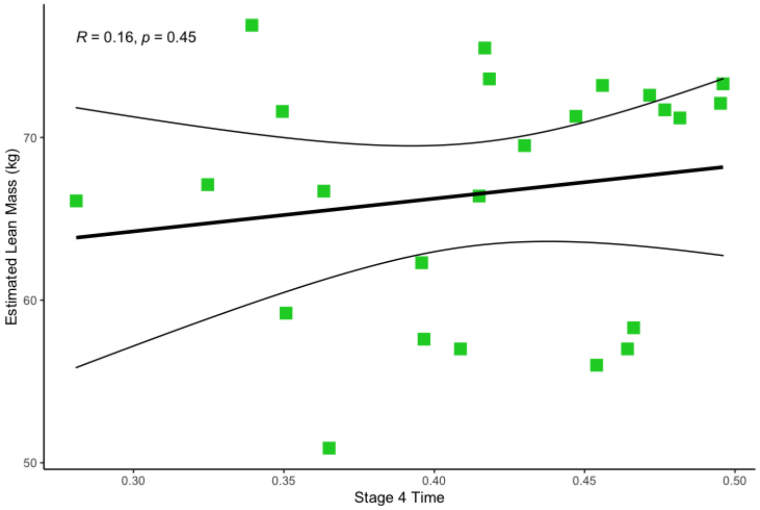

R = −0.11, p = 0.71
Fat as a Percentage of Total Body Weight
30
25
20
0.35
0.40
0.45
Stage 4 Time


R = 0.41, p = 0.045
Fat as a Percentage of Total Body Weight
25
20
15
10
0.30
0.35
0.40
0.45
0.50
Stage 4 Time


R = 0.025, p = 0.93
Estimated Fat Weight (kg)
22.5
20.0
17.5
15.0
12.5
0.35
0.40
0.45
Stage 4 Time

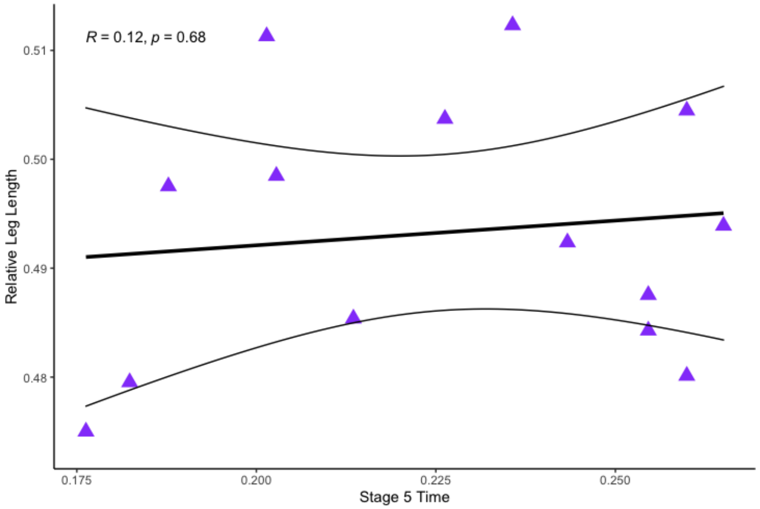

R = 0.43, p = 0.037
Estimated Fat Weight (kg)
20
15
10
5
0.30
0.35
0.40
0.45
0.50
Stage 4 Time

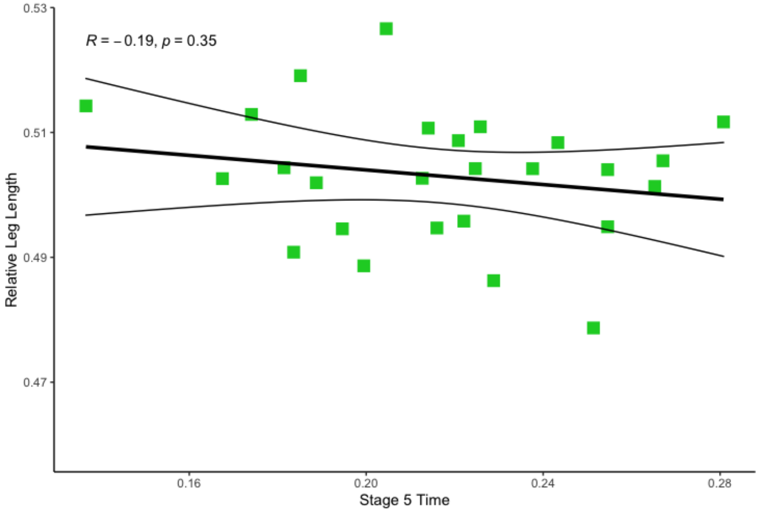

R = 0.25, p = 0.41
Estimated Lean Mass (kg)
50
45
40
0.35
0.40
0.45
Stage 4 Time

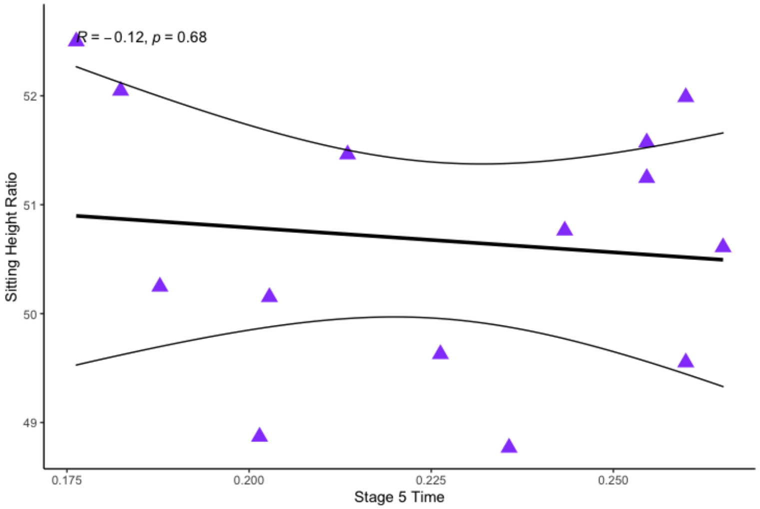

R = 0.16, p = 0.45
Estimated Lean Mass (kg)
70
60
50
0.30
0.35
0.40
0.45
0.50
Stage 4 Time

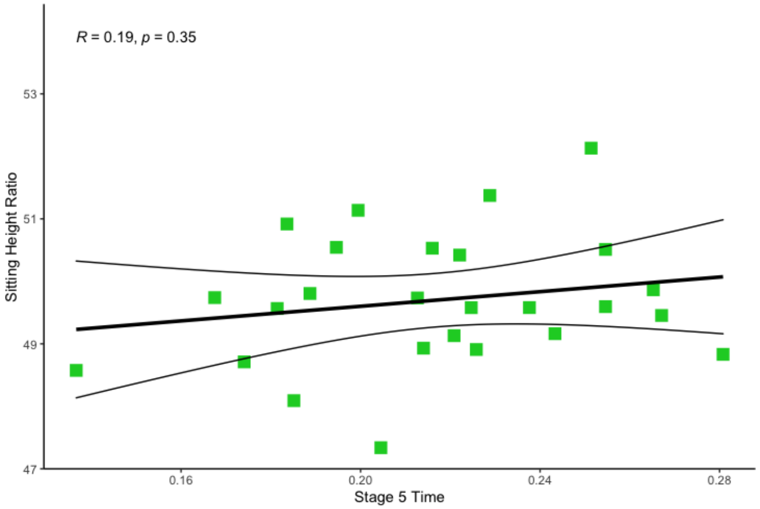
Stage 5 Times

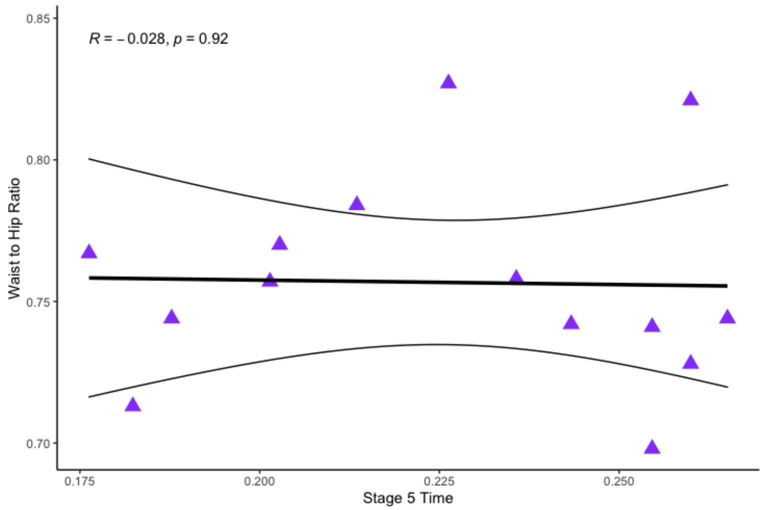
Females	Males

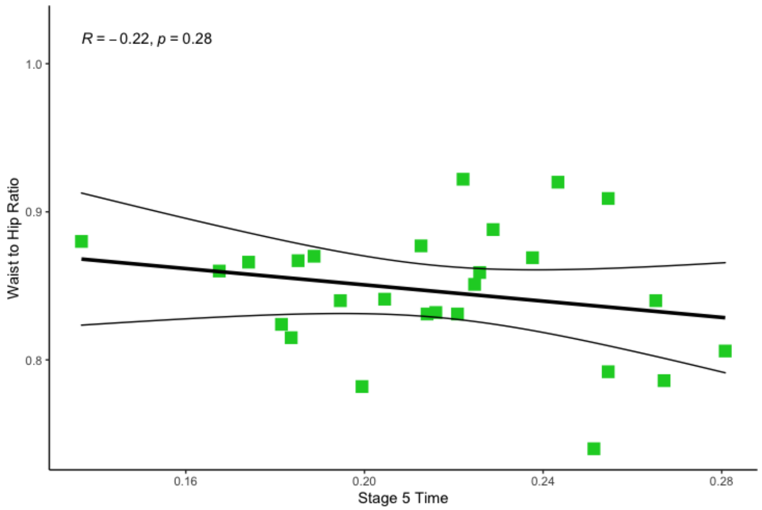


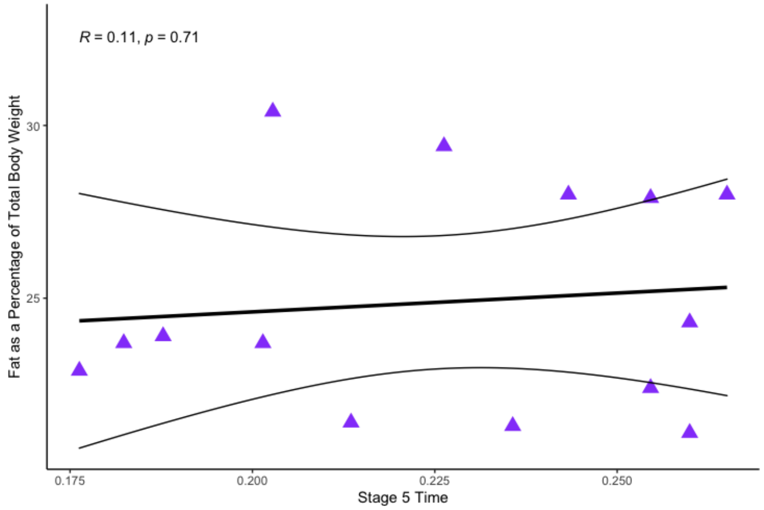


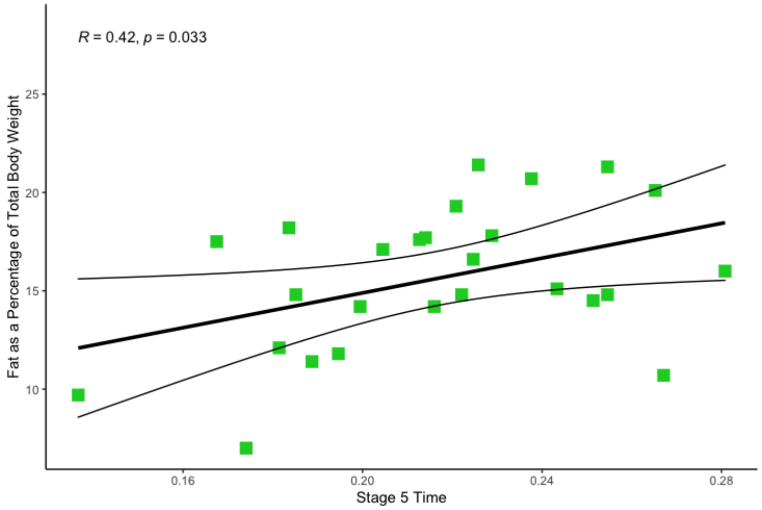


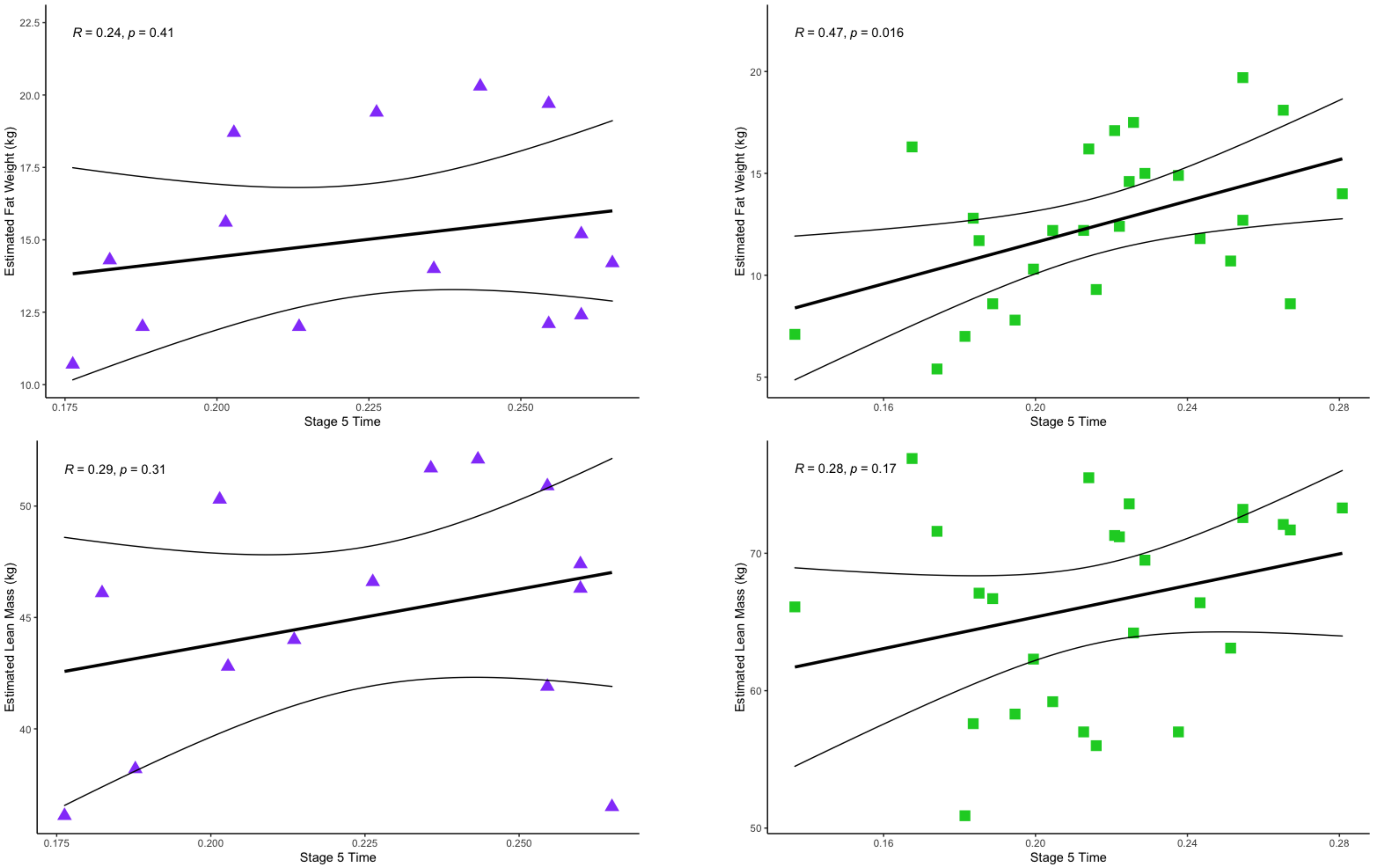



R = −0.028, p = 0.92
Waist to Hip Ratio
0.85
0.80
0.75
0.70
0.175
0.200
0.225
0.250
Stage 5 Time


R = −0.22, p = 0.28
Waist to Hip Ratio
1.0
0.9
0.8
0.16
0.20
0.24
0.28
Stage 5 Time

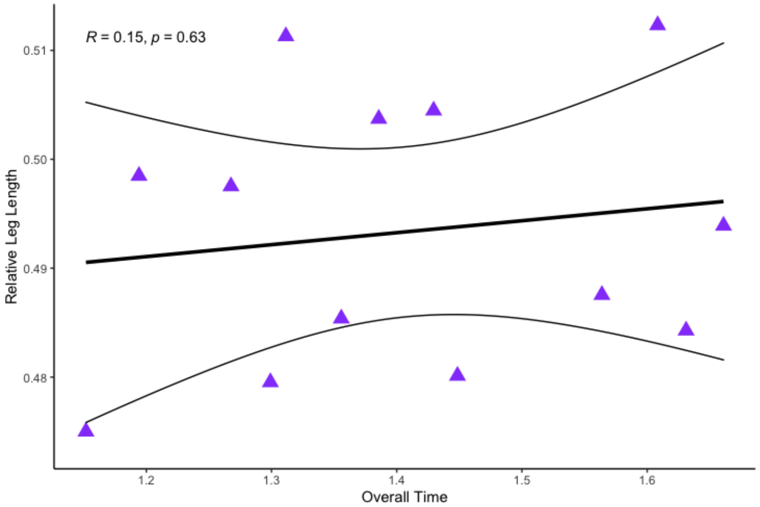

R = 0.11, p = 0.71
Fat as a Percentage of Total Body Weight
30
25
0.175
0.200
0.225
0.250
Stage 5 Time

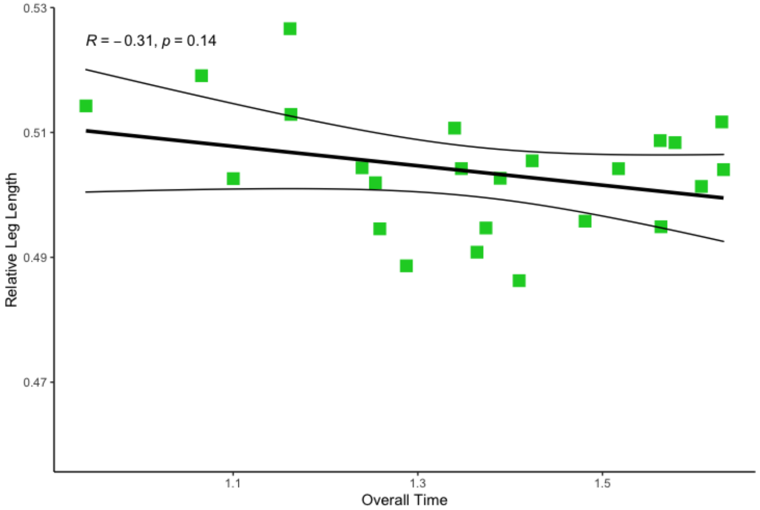

R = 0.42, p = 0.033
Fat as a Percentage of Total Body Weight
25
20
15
10
0.16
0.20
0.24
0.28
Stage 5 Time

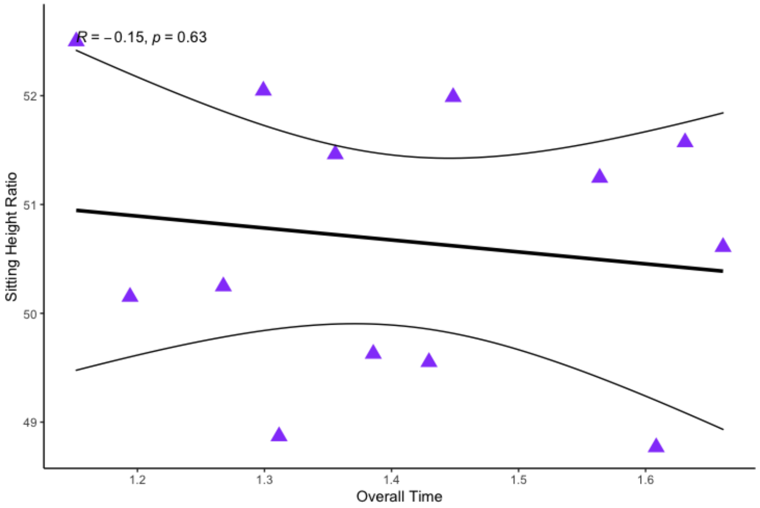

R = 0.24, p = 0.41
Estimated Fat Weight (kg)
22.5
20.0
17.5
15.0
12.5
10.0
0.175
0.200
0.225
0.250
Stage 5 Time
R = 0.47, p = 0.016
Estimated Fat Weight (kg)
20
15
10
5
0.16
0.20
0.24
0.28
Stage 5 Time
R = 0.29, p = 0.31
Estimated Lean Mass (kg)
50
45
40
0.175
0.200
0.225
0.250
Stage 5 Time
R = 0.28, p = 0.17
Estimated Lean Mass (kg)
70
60
50
0.16
0.20
0.24
0.28
Stage 5 Time

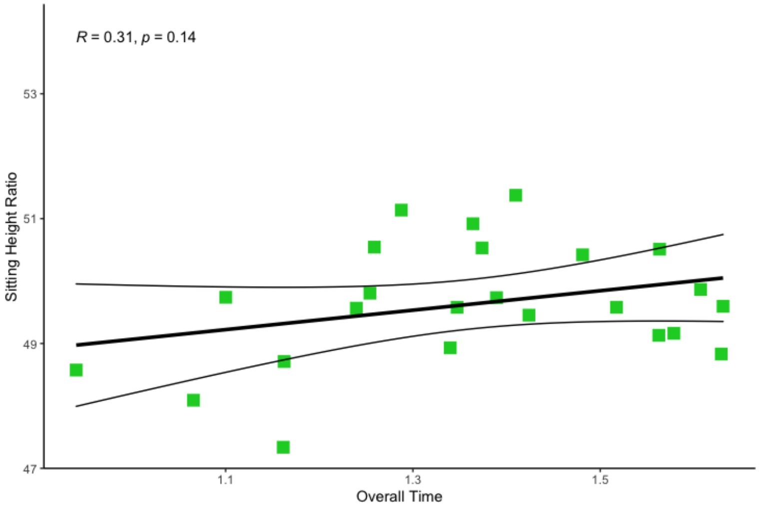
Overall Times

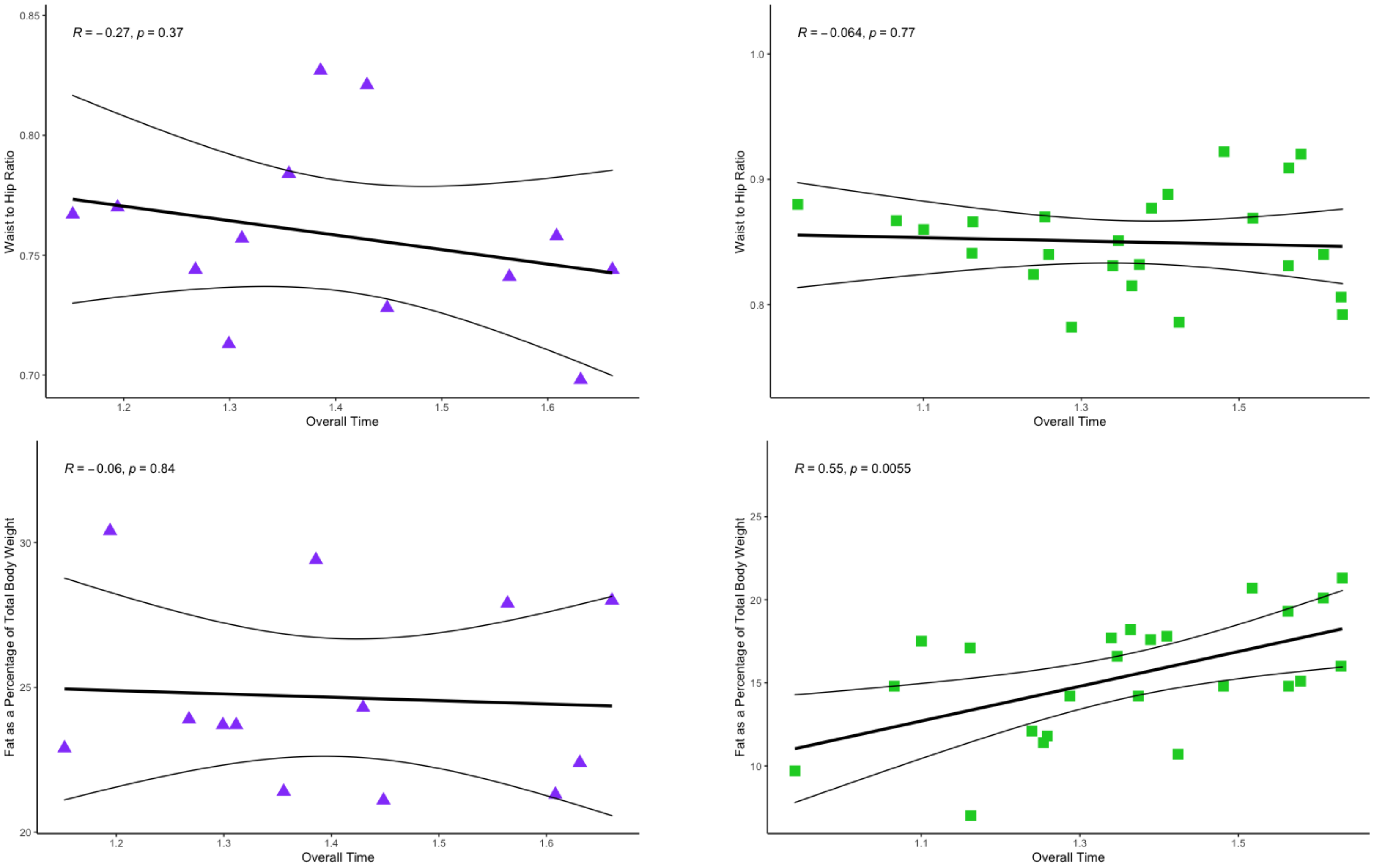
Females	Males

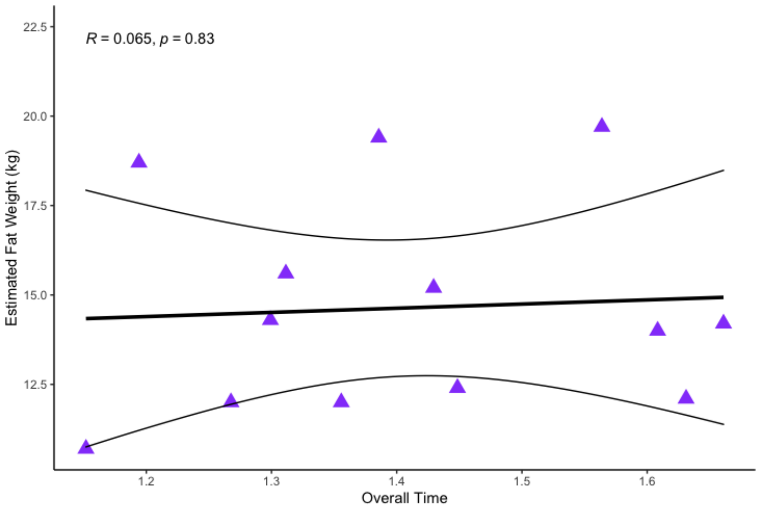


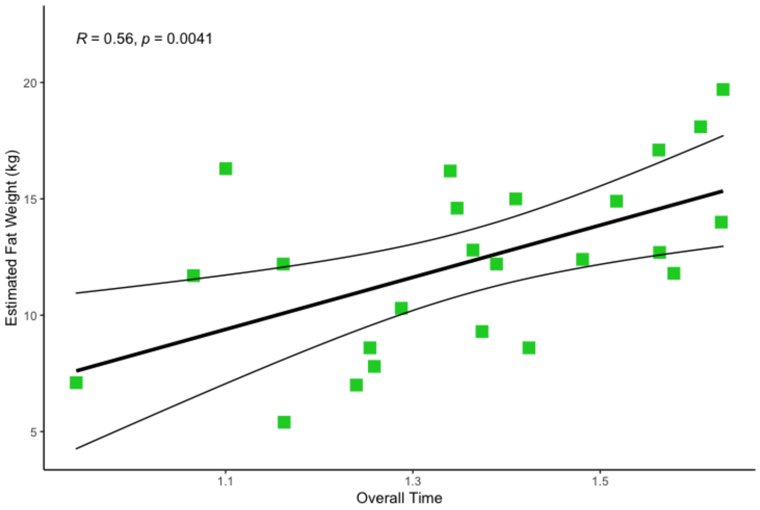


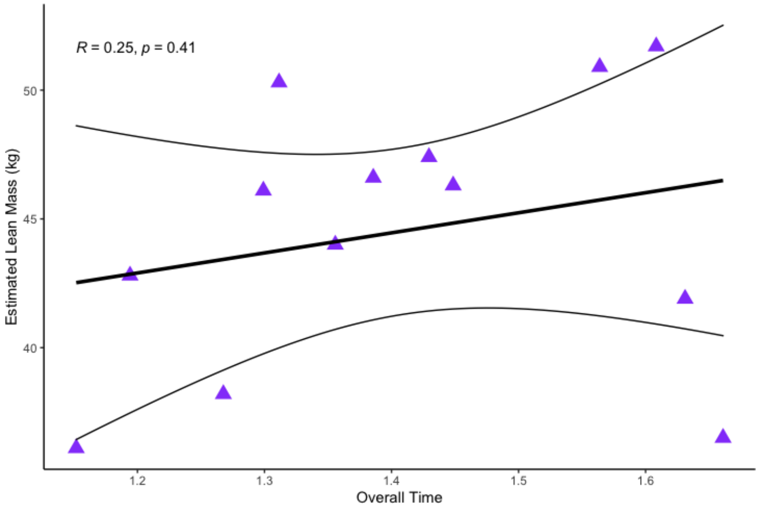


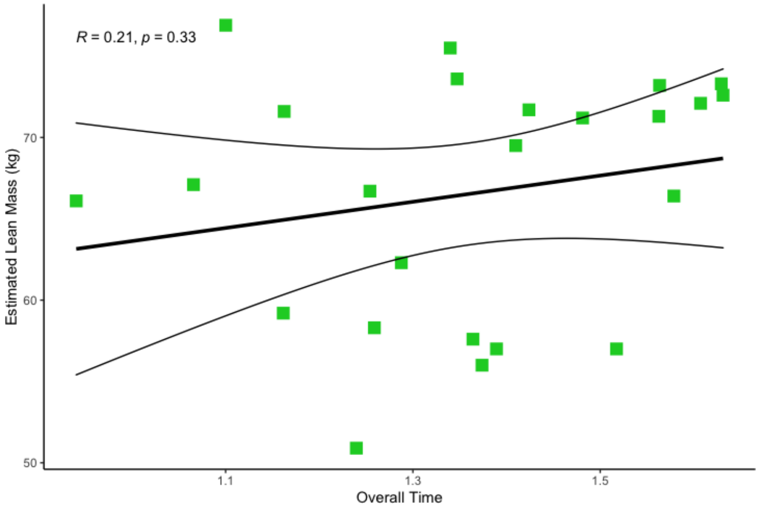



R = −0.27, p = 0.37
Waist to Hip Ratio
0.85
0.80
0.75
0.70
1.2
1.3
1.4
1.5
1.6
Overall Time
R = −0.064, p = 0.77
Waist to Hip Ratio
1.0
0.9
0.8
1.1
1.3
1.5
Overall Time
R = −0.06, p = 0.84
Fat as a Percentage of Total Body Weight
30
25
20
1.2
1.3
1.4
1.5
1.6
Overall Time
R = 0.55, p = 0.0055
Fat as a Percentage of Total Body Weight
25
20
15
10
1.1
1.3
1.5
Overall Time


R = 0.065, p = 0.83
Estimated Fat Weight (kg)
22.5
20.0
17.5
15.0
12.5
1.2
1.3
1.4
1.5
1.6
Overall Time


R = 0.56, p = 0.0041
Estimated Fat Weight (kg)
20
15
10
5
1.1
1.3
1.5
Overall Time


R = 0.25, p = 0.41
Estimated Lean Mass (kg)
50
45
40
1.2
1.3
1.4
1.5
1.6
Overall Time


R = 0.21, p = 0.33
Estimated Lean Mass (kg)
70
60
50
1.1
1.3
1.5
Overall Time