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*Washington University in St. Louis*

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Measuring and Predicting Total Energy Expenditure Among Highly Active  
Humans in Natural Environments

by

Cara Ocobock

A dissertation presented to the  
Graduate School of Arts and Sciences  
of Washington University in  
partial fulfillment of the  
requirements for the degree  
of Doctor of Philosophy

May 2014

St. Louis, MO



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## **ABSTRACT OF DISSERTATION**

### **Measuring and predicting total energy expenditure among highly active humans in natural environments**

by

Cara Ocobock

Doctor of Philosophy in Anthropology

Washington University in St. Louis, 2014

Professor Erik Trinkaus, Chair

Assistant Professor Herman Pontzer, Co-Chair

The current model for predicting human total energy expenditure (TEE), the Factorial Method, significantly underestimates actual TEE, particularly among highly active populations. In this study, the Allocation Model is presented for predicting TEE. Unlike the Factorial Method, the Allocation Model includes metabolic cost terms for both thermoregulation and the thermic effect of food, as well as using more accurate basal metabolic rate and activity cost estimations. The Allocation Model was tested using doubly labeled water and flex-heart rate measured TEEs of healthy, highly active adults (N=56) participating in National Outdoor Leadership School semester long courses. Two of the semester-long courses took place in both hot and temperate climates and the other two in both temperate and cold climates.

The Allocation Model produces TEE predictions that are not significantly different from measured TEE values. Overall, the Allocation Model comes within 12% of measured TEE values. The Allocation Model also comes within 10% of measured TEEs greater than 3500 kCal day<sup>-1</sup> compared to a 30.2% underestimation by the factorial method. This analysis demonstrates that the Allocation Model is more accurate at TEE prediction than the Factorial Method across a

range of activity levels and in different climates. Furthermore, the Allocation Model succeeds where the Factorial Method has failed – at high levels of energy expenditure. The Allocation Model can also be used to better understand how energy is allocated under different climatic and activity level conditions. From this, it was found that in cold conditions, the heat produced from activity helps to mitigate potentially high costs of thermoregulation. I was also able to analyze the relationship between the surface area/mass ratio and energy expenditure in the different climates. This allowed me to determine whether an energetic advantage of Bergmann's and Allen's rules was present among the NOLS population. In this study it was found that a greater surface area/mass ratio provided an energetic advantage in hot climates. However, there is also evidence that a greater surface area/mass ratio is advantageous for heat dissipation in cold environments in individuals wearing heavily insulated clothing.

The results presented here suggest the Allocation Model is a powerful new tool that should be used in place of the Factorial Method for estimating human TEE, and can be used to analyze adaptations, life history strategies and differential energy allocation among highly active humans in natural environments.

## **CHAPTER 1: Introduction**

Energetics have played a key role in shaping human ecology and evolution (Leonard and Ulijaszek 2002). This realization, along with improved technology, have led anthropologists to take a greater interest in, and conduct more research on, the study of human total energy expenditure, i.e., the total number of calories used per day. Research on energetics gives insight into how humans interact with their environment and how differences in body shape and size can impact that interaction. A number of studies have assessed how humans allocate energy, for example by examining subsistence strategies, growth and repair, reproductive output, thermoregulatory demands, mobility patterns, and human brain-size evolution (Durnin 1990, Roberts et al. 1991, Haggarty et al. 1994, Leonard and Robertson 1994, Aiello and Wheeler 1995, Leonard et al. 1995, 1997, Panter-Brick 1996a, b, Spurr et al. 1996, Tikuisis et al. 2000, Leonard and Ulijaszek 2002). Furthermore, body shape and size have been implicated as factors impacting the cost of both thermoregulation and activity (Ruff 1991, 1994, Tikuisis et al. 2000, Steudel-Numbers 2006, Tilkens et al. 2007, Holliday and Hilton 2010). This large body of work has examined the impact of individual environmental and morphological factors on human energy expenditure both in the laboratory and with indigenous populations. But little research has been conducted on the comprehensive impact that environmental and morphological factors have on total energy expenditure among human populations living in a variety of natural environments.

This burgeoning interest in measuring human energetics has led to the need for an easy and inexpensive way to estimate human total energy expenditure. The current method for such estimations is the Factorial Method created by the FAO/WHO/UNU (1985), and it is used to estimate calorie requirements. This method has a number of practical applications, such as

optimizing athletic training programs and in determining optimal diets for food aid, and military and research expeditions. This research has been used to not only better understand modern human energy expenditure patterns, but the energy patterns of past hominins as well (Froehle and Churchill 2009). However, the Factorial Method has been shown to produce large underestimations, particularly at high levels of energy expenditure (Leonard et al. 1997). Given the practical applications, this underestimation could have grave implications particularly when providing food aid, as well as giving an inaccurate portrayal of past hominin energy expenditure.

My work here evaluates human total energy expenditure as the result of the interactions between body proportions, physiology and the environment among highly active humans living in a variety of natural environments. Students taking part in National Outdoor Leadership School semester long courses were the study population in this research. These students took part in rigorous activities such as hiking, climbing and cross-country skiing on a daily basis while living in the wilderness with limited resources for three months. These courses took place in temperate, hot, and cold environments of the Western United States. Data on total energy expenditure, activity levels, caloric intake, anthropometrics and environmental variables were collected. Total energy expenditure was measured using both the doubly labeled water method and the flex-heart rate method. A new model for better predicting total energy expenditure, the Allocation Model, was developed and is presented and tested here.

The data collected for this research can be used to answer a number of questions; however, the scope here has been limited to just three.

***1) Will an anthropometric model treating basal metabolic rate, activity, thermoregulation and the thermic effect of food as interacting variables produce more accurate total energy expenditure estimates than current methods?***

Current models are unable to accurately predict total energy expenditure and do not account for inherent variation in body size, climate, and activity level. The most frequently used model, the Factorial Method (FAO/WHO/UNU 1985), estimates total energy expenditure by summing the energetic cost of basal metabolic rate and activity throughout the day. Activity costs are estimated as a multiple of basal metabolic rate based on the intensity of each activity (FAO/WHO/UNU 1985). This method has been applied to industrialized populations (Borel 1984, Geissler et al. 1986, Warwick et al. 1988, Roberts et al. 1991, Haggarty et al. 1994, Spurr et al. 1996, Leonard et al. 1997, Warwick 2006) and non-industrialized populations (Leonard et al. 1995, Katzmarzyk et al. 1996, Dufour and Piperata 2008). Work done by Leonard et al. (1995) on highland and coastal Ecuadorian populations revealed increased activity levels and energy expenditures associated with more traditional agricultural practices observed in the highlands compared to coastal commercial agricultural practices. This study was also one of the earliest studies to show that the Factorial Method underestimated total energy expenditure.

A number of researchers have also attempted to estimate total energy expenditure among extinct hominins (Leonard and Robertson 1992, Leonard and Robertson 1997, Sorenson and Leonard 2001, Steegman et al. 2002, Aiello and Wheeler 2003, Steudel-Numbers and Tilkens 2004, Churchill 2006, Froehle and Churchill 2009). These studies are often based on multiple steps of estimation, such as estimates of body size, activity levels, and climate for extinct hominin populations. For example, work by Froehle and Churchill (2009) calculated basal metabolic rate and total energy expenditure estimates for Neanderthals based on body mass and physical activity level estimations. For cold climate inhabiting Neanderthals, they estimated female total energy expenditure to range from 3180-3190 kcal day<sup>-1</sup>, and a male Neanderthal estimated range of 4469-4877 kcal day<sup>-1</sup> (Froehle and Churchill 2009). Interestingly, Froehle and

Churchill (2009) found similar values for anatomically modern humans concurrently inhabiting cold climates with females having an energy expenditure range of 1351-1509 kcal day<sup>-1</sup> and males 2972-3320 kcal day<sup>-1</sup>. The authors contend that Neanderthals on average had higher total energy expenditures, but that this was due to Neanderthals having larger estimated body masses. Neanderthals males and females were an average of 9.1 kg and 7.2 kg respectively heavier than anatomically modern humans. These results are suspect because they do not take into account differences in body shape and possibly metabolically cost saving technology, or possible tradeoffs between activity and thermoregulation. For example, Neanderthals have been characterized as having reduced distal limb length, which has been implicated as a cold climate adaptation whereas anatomically modern humans first entering these northern climes have been characterized by relatively longer distal limbs (Trinkaus 1981, Ruff 1991, 1994). Froehle and Churchill (2009) admittedly concede that differences in body shape as well as technology were not taken into account when calculating their estimates. Furthermore, they did not take into account possible tradeoffs between thermoregulation and activity. For example, it has been shown in laboratory studies that heat produced through activity can help mitigate the cost of thermoregulation in cold conditions (Toner et al. 1986, Tikuisis et al. 2000), such that perhaps the high activity cost estimates of Neanderthals (Studel-Numbers and Tilkens 2004, Churchill 2006) would confer a thermoregulatory advantage. The issues presented here are also likely the cause for the low TEE estimates they calculated for Neanderthals and modern humans.

All of these studies provide a useful framework for comparing total energy expenditure, activity levels, and their variation, but they are limited by the inaccuracy and underestimation of total energy expenditure inherent in current detection methods like the Factorial Method commonly used (Leonard et al. 1997). Studies comparing measured total energy expenditure

with Factorial Method predictions have shown that the Factorial Method consistently underestimates total energy expenditure (Durnin 1990, Roberts et al. 1991, Haggarty et al. 1994, Leonard et al. 1995, 1997, Spurr et al. 1996). Underestimation of total energy expenditure appears to be greatest among active populations and can be as high as 30% (Leonard et al. 1997).

It has been proposed that the Factorial Method fails to accurately estimate total energy expenditure due to poor basal metabolic rate estimations, poor activity cost estimations, the lack of cost terms for thermoregulation, and the thermic effect of food (Leonard et al. 1997). The limitations and poor accuracy of the Factorial Method suggest the view of total energy expenditure based solely on basal metabolic rate and activity is simplistic, and a new, more comprehensive, and more accurate predictive model is needed. To that end, I have developed a new model, the Allocation Model, for predicting total energy expenditure, which treats basal metabolic rate, activity costs, thermoregulatory costs, and the cost due to the thermic effect of food, as interacting variables. It will be shown that the Allocation Model outperforms the Factorial Method in any given climate over a wide range of activity levels.

***2) Will total energy expenditure in hot and cold climates be greater than that in temperate climates? And how does energy allocation differ between the climates?***

The energetic demands of indigenous populations living in extreme climates have been a topic of interest for over 85 years (Heinbecker 1928). In cold conditions peripheral vasoconstriction, non-shivering thermogenesis, behavioral responses and increased basal metabolic rate have been identified as physiological responses that help maintain core body temperature despite low environmental temperatures (Stocks et al. 2004, Moran 2008). The cost due to thermoregulation is lower during exercise under cold conditions. Sweating, vasodilation and changes in basal metabolic rate (both increases and decreases) help to maintain core body

temperature in hot conditions (Osiba 1957, Yurugi et al. 1972, Ogata and Sasaki 1975, Shapiro et al., 1980; Hori, 1995; Chinevere et al., 2008).

These studies have elucidated a number of metabolic responses to extreme hot and cold temperatures. But few have researched the same population in more than one climatic condition and analyzed the accompanying changes in metabolic cost. Furthermore, the importance of physical activity in reducing the cost of thermoregulation in natural cold conditions among a highly active population has not been analyzed. In the work presented here, total energy expenditure is measured and compared in temperate, hot and cold climates. The Allocation Model is then used to analyze energy allocation differences between the climates to better understand how much energy is distributed among basal metabolic rate, thermoregulation, activity, and the thermic effect of food.

***3) Will total energy expenditure in hot and cold climates be influenced by body shape and size, surface area/mass ratio, as predicted by Bergmann's and Allen's rules for thermoregulation?***

Bergmann's rule describes a pattern in which animals living in higher latitudes have greater body mass than more equatorial animals (Bergmann 1947). Allen's rule for thermoregulation describes an ecogeographical pattern in which animals living in higher latitudes exhibit shorter appendages than those living closer to the equator (Allen 1877). These rules have been tested in a wide variety of animals from insects (Bidau and Marti 2008) to birds (Chui and Doucet 2009) to mammals (Frafjord 2008). Anthropologists and human biologists have tested these rules within humans through both laboratory studies (Shapiro et al. 1980, McArdle et al. 1984a, b, Tikuisis et al. 2000, Tilkens et al. 2007) and comparisons of indigenous and past populations (Trinkaus 1981, Holliday and Trinkaus 1991, Ruff 1994, Holliday 1997a, b, 1999, Holliday and Hilton 2010). These studies have determined that shorter limbs, broader bi-iliac breadth, larger body mass, and a lower surface area/mass ratio confer an energetic

advantage in cold temperatures (Ruff 1991, 1994, Tikuisis et al. 2000, Tilkens et al. 2007, Holliday and Hilton 2010), since low surface area reduces the amount of area through which body heat can dissipate to the environment. This, in turn, reduces the amount of heat the body needs to produce to maintain body temperature within acceptable limits (Tilkens et al. 2007). The reverse is true for hot climates; longer limbs and lower body mass increase body surface area enabling greater heat dissipation, thereby reducing the body's need to eliminate excess heat (Shapiro et al. 1980).

These studies have provided an excellent source of information on how humans react to extreme temperatures in laboratory conditions, as well as a possible explanation for the latitudinal variation seen in body proportions today. At present, there are no studies linking possible differences in energy expenditure in different climatic extremes to variations in body shape among humans. The research presented here aims to determine if human body shape and size impact total energy expenditure and if they are important to climatic adaptation, or if there are other biological and behavioral processes at work to mitigate environmental stressors.

Better understanding human energetics is not only important for its practical applications of food aid, expedition logistics, and athletic training, but also for providing a useful lens through which to view human ecology and life history. The differential timing of, and energy allocation to, growth, maturity and maintenance, reproduction, and mortality determine life history strategies. Adjustments in energy budgets can impact the timing of any, or all, of these different life stages (Ellison 2003). For example, a decreased energy budget would lead to slower growth and later sexual maturation. Such an adjustment would be beneficial in resource-limited environments, but has the possible consequence of reduced reproductive output, which could negatively impact population level success (Worthman 2003). Exploring energy allocation

differences between climates will aid our understanding of not only morphological and physiological adaptations to those climates, but also differences in life history strategies. For example, indigenous Canadian Cree populations have a much higher rate of infant macrosomia, defined here as greater than the 90<sup>th</sup> percentile for gestational age, compared to non-indigenous Canadian populations, 34.3% and 11.1% respectively (Rodrigues et al. 2000). High maternal weight in the obese range and gestational diabetes are known to increase the chance of infant macrosomia. However, once these factors were controlled for, indigenous Canadian populations still presented a higher rate of macrosomia and reduced rate of low birth rates compared to non-indigenous populations (Rodrigues et al. 2000). Increased growth and fat deposition during the fetal stage could represent a shift in life history strategy, selecting for larger infants better fit to withstand the harsh climate once outside of the womb.

My research presented here attempts to address some of the gaps in our current understanding of human total energy expenditure and explore the importance of the interaction among human morphology, physiology, and the environment. A clearer picture of this interaction could produce more accurate estimates for total energy expenditure to be used for numerous practical applications. But, it could also provide useful insight into the subtle, and possibly adaptive, differences in life history strategies adopted by humans.

## **Chapter 2: Human Energy Expenditure**

### ***Introduction***

Total Energy Expenditure (TEE), the total number of calories used per day, is comprised of a number of different components, such as basal metabolic rate, thermoregulation, physical activity, and growth and reproduction (Leonard and Ulijaszek, 2002). Other factors such as immune and digestive costs play a smaller role in energy output (Leonard and Ulijaszek, 2002). The relative contribution of these different TEE components depends on body size, age, health status, reproductive status, and level of physical activity (Benedict 1915, Keys et al. 1973, Peters 1983, Schmidt-Nielsen 1984, Holliday 1986, Flynn et al. 1989, Leonard and Robertson 1997a, Piers et al. 1998, Wang et al. 2000, Bogin 2001, West et al. 2002, Henry 2005).

Humans are unique among primates in having the largest and most expensive brains, as well as large body size, slow maturation rates, high activity levels, and high reproductive outputs (Leonard and Robertson 1992, 1994, Ulijaszek 1995, Leonard and Robertson 1997a). Studies examining human energy expenditure have explored how humans interact with their environment to meet their high-energy demands and how that energy is subsequently allocated. Allocations include, but are not limited to, body maintenance, subsistence strategies, growth and maintenance, reproductive output, thermoregulatory demands, mobility patterns, and brain growth and maintenance (Durnin 1990, Roberts et al. 1991, Haggarty et al. 1994, Leonard and Robertson 1994, Aiello and Wheeler 1995, Leonard et al. 1995, 1997a, Panter-Brick 1996a, b, Spurr et al. 1996, Tikuisis et al. 2000, Leonard and Ulijaszek 2002, Pontzer et al. 2012). How human ancestors allocated their available energy likely had an immense impact on our evolutionary trajectory.

This chapter broadly presents the history and background of our current knowledge of human energetics and the different components that comprise human TEE. When applicable, this chapter will also highlight the ways in which humans are energetically unique among apes.

### ***Interspecific Variation in Basal Metabolic Rate***

Basal metabolic rate has been the focus of centuries of research, and for good reason: it comprises roughly 30% of the total amount of energy organisms spend daily, although this is highly variable across species (Ricklefs et al. 1996, Raichlen et al. 2010, Westerterp and Speakman 2010). As far back as the mid-late 1700s, Lavoisier, the “father of basal metabolism,” made the connection between oxygen and food consumption with the production of heat and muscular work (Hulbert and Else 2004). Lavoisier, along with his wife, determined that animal respiration consisted of oxygen from the environment and carbon dioxide and hydrogen produced by the animal. They also demonstrated that the rate of oxygen consumption changed with food consumption, activity and environmental temperature (Hulbert and Else 2004). Since then, great strides have been made in the study of basal metabolism including the definition we currently use: Basal metabolic rate (BMR) is the minimum amount of energy required to sustain the life of a non-moving, non-growing, non-reproducing and non-digesting organism (Hulbert and Else 2004, Henry 2005). A lively debate on how to best model BMR has been ongoing since the 19<sup>th</sup> century (Hulbert and Else 2004).

A number of physical characteristics have been suggested to best predict the BMR of endothermic, homeothermic animals. For example, Sarrus and Rameaux (1839) argued that heat loss and production, and thereby BMR, were better determined by body surface area, from which heat is dissipated, than by body mass, proposing that BMR was proportional to  $2/3$  body mass. This was later supported by studies from Rubner (1883) and Schmidt-Nielson (1972). The  $2/3$  rule became known as Rubner’s Law. However, during this time two independent studies came

to the opposite conclusion, namely, that body mass rather than surface area better predicted BMR. Brody and Proctor (1932) and Kleiber (1932) both found that BMR was proportional to the 0.73 power of body mass for animals of different sizes. Over time and continued study, this exponent was adjusted to 0.75 and become known as Kleiber's Law, and is widely used today to predict the BMR of endothermic mammals and birds (Benedict 1938, Hemmingsen 1960, Kleiber 1961, Hulbert and Else 2004). Despite the almost ubiquitous use of Kleiber's Law, animated discussion still continues over the proper body characteristic that best predicts BMR across homeothermic endotherms.

West et al. (2002) investigated Kleiber's Law and developed a hypothesis that the 0.75-power scaling of energy use was the result of the "fractal-like character of biological networks" (West et al. 2002, p. 2473). In this study, West et al. (2002) included mammals as small as 2.5g (shrews from the Order Soricidae) to ones as large as  $4 \times 10^6$ g (elephants from the Order Proboscidae). They found that Kleiber's Law of a 0.75 scaling exponent for BMR held across a large range of body size and 27 mammalian orders. Furthermore, this relationship was empirically extended to the microscopic level demonstrating that BMR was proportional to 0.75 body mass for unicellular organisms and even isolated mammalian cells (West et al. 2002). The fractal-like pattern for energy transfer through biological networks proposed in West et al. (2002) models the body as a hierarchy of fractally branching supply networks. This is easily visualized as the circulatory system that begins with the heart and large arteries that become successively smaller until termination at capillaries connected to cells. Of course, the termination point can be carried out to the molecular level of energy transfer. In the larger vessels, there is a pulsing flow that continues through the network. As the vessels become narrower near the termination site, resistance increases and the pulsing is dampened to almost zero in the capillaries and the

pulsatile energy is dissipated. This dampening of pulsatile flow and large energy dissipation, through the kinetic energy loss of flowing blood with ever-smaller vessels explains why larger animals expend less energy per kilogram than smaller animals (West et al. 2002).

In response to this, White and Seymour (2002) contended that basal metabolic rate was proportional to body mass to the  $2/3$  power, Rubner's Law. They argued that studies supporting Kleiber's Law did not take into account differences in internal body temperature among different Orders of mammals. Furthermore, they stated that Kleiber's Law was achieved through inclusion of inappropriate data, arguing that domestic animals, and, more importantly, members of the Order Artiodactyla, should not have been included. They contended that artiodactyls skewed Kleiber's Law towards a higher BMR-mass proportion. Artiodactyls digest food through slow, microbial fermentation making it difficult to confidently determine if and when the animal has reached a post-absorptive state, one of the requirements of BMR measurement. Once White and Seymour removed artiodactyls from previous analyses, Kleiber's Law still held true with an exponent not significantly different from 0.75. Given these results, White and Seymour contended that the high metabolic rates of humans and carnivores skewed the results towards a higher BMR-body mass relationship. White and Seymour conducted an analysis that excluded the Orders Artiodactyla, Lagomorpha, Macropodidae, Soricidae, Cetacea and Proboscidae, roughly 14% of Mammalia and the majority of large bodied mammals (White and Seymour, 2002). Their different analyses excluding various orders resulted in exponents relating body mass to BMR ranging from 0.65-0.71. From this, they argued that BMR was proportional to body mass to the  $2/3$  power and that BMR is primarily driven by heat loss from the body.

Though there is a strong relationship between body mass and basal metabolic rate across several magnitudes of body size, there are significant differences in interspecific basal metabolic

rate. These differences may have had far reaching evolutionary consequences on ranging, subsistence strategies, and life history patterns as well as group social structure and reproductive output (Raichlen et al. 2010).

### ***Factors Affecting BMR within Species***

Age is a determining factor in how BMR varies within humans. Human metabolic rates are high at a given mass during infancy and childhood due to the cost of growth. Once corrected for size, the mass-specific basal metabolic rate for newborns, infants, and a growing child are almost twice that of an adult (Butte 2000, Butte and King 2005, Leonard et al. 2012). Mass-specific BMR gradually slows until growth is complete and full adult size is reached at roughly 18 years (Holliday 1986, Bogin 2001, Leonard et al. 2012). The basal metabolic rate will then remains constant in healthy, non-reproducing individuals until the age of 45, when a slow decline in BMR begins (Piers et al. 1998). This decline in BMR has been attributed to changes in body composition that occur with age – increased fat mass and decreased fat-free mass (Keys et al. 1973, Flynn et al. 1989, Piers et al. 1998).

Other factors thought to contribute to the age related decline in body systems such as BMR are a decrease in liver volume and function, low whole-body protein turnover, a decrease in thyroid hormone production, and a decrease in tissue sensitivity to thyroid hormone (Piers et al. 1998). Change in body water content (Shock et al. 1963) and levels of total body potassium ions (Calloway and Zanni 1980) have also been implicated; however, there has not been much empirical support for these hypotheses (Piers et al. 1998).

Changes in fat-free mass (FFM) explain much of the decrease in BMR with age for older adults. Tzankoff and Norris (1977) demonstrated that the decrease in skeletal muscle mass observed in older individuals accounted for all of the BMR reduction observed; this was confirmed by a later study (Zurlo et al. 1990). However, FFM is not comprised solely of skeletal

muscle – it is also composed of the internal organs, the skeleton and the blood. When a person is at rest, skeletal muscle contributes relatively little to BMR, whereas the internal organs will maintain a relatively high metabolic rate (Piers et al. 1998). This would suggest that older individuals, with decreased muscle mass, would have a higher BMR for their FFM, since the energetically demanding internal organs would make up a greater proportion of the FFM. This is not the case, which suggests that loss of FFM is not the lone variable leading to a BMR decline with increasing age. Piers et al. (1998) took an in depth look at the relationship between the different types of FFM and how they varied in young and old subjects. They found that appendicular lean tissue mass (skeletal muscle) was significantly lower in older adults, but that non-appendicular lean tissue mass (visceral mass) was not significantly different between the young and old subjects. However, in this study, they found that the differences in lean tissue mass were not enough to fully account for the BMR decline with increasing age. Piers et al. (1998) also found that older individuals who maintained an active lifestyle did not experience a significant BMR decline.

Though the majority of the variation in BMR is captured by body mass, it was found that BMR varies with sex and age enough that researchers had to, and still do, use different equations to accurately reflect the sex and age of their target population (Cunningham 1980, Ravussin et al. 1982, Owen et al. 1986, Ravussin et al. 1986, McNeill et al. 1987, Owen et al. 1987, Jensen et al. 1988, Kashiwazaki et al 1988, Owen 1988, Ravussin and Bodardus 1989, Heshka et al. 1990, Mifflin et al. 1990, Elia 1992b, Couture and Hulbert 1995, Wang et al. 2000, Froehle 2008).

### ***Human Responses to Altitude and Cold***

Basal metabolic rate studies have taken place across the globe examining the subtle differences in BMR across indigenous populations from a wide variety of geographical locations and climates. One topic of interest was, and still is, the impact of high altitude on human

physiology. Such environments are intriguing because in order to survive and thrive at high altitudes, humans must cope with low oxygen pressure, which reduces the amount of oxygen available to body tissues inducing hypoxia (Frisancho 1993, Moran 2008). High altitude also presents other stresses such as cold, malnutrition, high winds and limited food resources (Frisancho 1993, Moran 2008). Over the years, a suite of physiological adaptations for increasing the supply of oxygen to the body in hypoxic conditions have been identified. These adaptations vary according to whether the population studied is indigenous to high altitudes or native to low altitudes and has since moved to a higher altitudes. For example, indigenous high-altitude populations exhibit significantly larger lung volumes, whereas indigenous low-land populations increase ventilation rate to increase the amount of oxygen brought into the body (Frisancho 1993, Moran 2008). Though there can be differences in physiological adaptations among high-altitude populations.

Both indigenous high-altitude populations, and indigenous low-altitude populations temporarily at high altitudes, exhibit a higher concentration of hemoglobin, the oxygen-carrying molecule of red blood cells. Hemoglobin concentration increases to improve the oxygen carrying capacity of blood (Beall 2001, Beall 2006, Moran 2008). Both types of populations also exhibit greater capillarization to increase the amount of blood delivered to tissues (Hurtado 1964, Moore 2000, Moran 2008). Low-landers who venture to high altitudes experience an increase in basal metabolic rate due to the increased ventilation rate, increased red blood cell production and increased capillarization (Moran 2008). The metabolic rate will eventually return to the previous low-land levels once acclimatization to high altitude occurs, usually within two weeks (Shvartz et al. 1974). However, there is no inherent increase in metabolic rate among native high-altitude populations (Moran 2008). This is perhaps due to high-altitude physiological adaptations that

occur during growth and development; however, this remains unresolved. Any increase in BMR observed among these populations is thought to be the adaptive result of exposure to cold conditions, an environmental factor concurrent with high altitude (Moran 2008).

Indigenous circumpolar populations have been of physiological interest for over a century (Krogh and Krogh 1915). This early interest was originally focused on these populations' unusual, protein heavy diet. Heinbecker (1928) looked at the frequency and severity of ketosis among the Polar and Baffin Island Eskimos believing that their high-protein, high-fat and low-carbohydrate diet would lead to extreme ketosis. However, Heinbecker found that this group had a low susceptibility to ketosis compared with non-indigenous subjects. Furthermore, he observed that the Polar and Baffin Island Eskimos had a basal metabolic rate 33% higher than basal rates among temperate populations (Heinbecker 1928). Heinbecker (1931) took a second set of measurements and found that the Baffin Island Eskimos had a similar BMR to temperate subjects subsisting on a similar diet. (Heinbecker 1931). He attributed the high metabolic rates to a protein rich diet.

Since these early studies, methodology and detail of study have greatly improved. There are now a number of more recent studies of indigenous circumpolar populations revealing that basal metabolic rates increase with decreasing ambient temperature (Hammel 1964, Folk 1966, Hanna 1968, Little and Hochner 1973, Leonard et al., 2002; Snodgrass et al., 2005, Moran 2008). Among indigenous populations, BMRs among the Inuit were 20-40% higher than that of control groups (Hammel 1964, Moran 2008). An increased BMR has also been observed among the Yakut of Siberia (Leonard et al. 2002, Snodgrass et al. 2005, 2006, 2008).

Much like indigenous high-altitude populations, circumpolar populations possess a suite of physiological responses that help maintain core body temperature despite extreme cold

temperatures. These include increased peripheral vasoconstriction, non-shivering thermogenesis, behavioral responses and increased basal metabolic rate (Stocks et al. 2004, Moran 2008).

Increased peripheral vasoconstriction, known as the “hunting response”, is thought to reduce the skin temperature, which reduces the amount of heat lost to the environment. This reduces the heat flow to the extremities, and, therefore, the heat lost to the environment. However, it has been noted that in more extreme conditions, cold-induced vasodilation occurs to protect parts of the body that are vulnerable to over exposure such as the hands and feet (Stocks et al. 2004, Moran 2008). Shivering is a common response to cold exposure, but does not increase the total body heat production to a significant degree (Folk 1966). Therefore, shivering is not a long-term solution to cold exposure.

Non-shivering thermogenesis refers to an increase in cellular metabolism without the increased muscle movement seen in shivering. This process is associated with brown adipose tissue (BAT), which is extremely dense in mitochondria. Within this tissue, the mitochondria interrupt the electron transport chain that typically produces adenosine triphosphate (ATP), the basic unit of energy utilized by the body for all functions. The short-circuiting acts to release heat rather than ATP, contributing to the overall heat content of the body (Cannon and Nedergaard 2012). Non-shivering thermogenesis, and, therefore, BAT are present in infants and indigenous cold climate populations (Moran 2008). Furthermore, increased BAT activity leads to a 40% increase in basal metabolic rate (Cannon and Nedergaard 2012, Ouellet et al. 2012). This has been documented among temperate men exposed to acute cold conditions, suggesting that BAT is not limited solely to infants and indigenous populations (Cannon and Nedergaard 2012, Ouellet et al. 2012).

### ***Predicting BMR Response to Cold***

Work on indigenous populations, though insightful, is also difficult, expensive and troubled by numerous confounding variables. In light of that, a number of laboratory studies have been done to explore the effect of controlled cold conditions on un-acclimatized humans. However, first it is useful to discuss the basic physics behind heat loss. The basic heat loss equation is:

$$\text{Heat Transferred} = \frac{\text{Surface Area (Temperature 1 - Temperature 2)}}{\text{Resistance of Insulating Material}}$$

where Temperature 1 would be the environmental temperature and Temperature 2 would be the skin temperature. To apply this to an organism, particularly humans, the heat transferred is the heat lost to the environment. The Surface Area is the surface area of the human; however, when clothing is worn variable amounts of surface area are more exposed to the environment than others. The insulating material in the case of humans would be fat, muscle and skin. Clothing, when worn, would also be included in this term. These basic concepts are important to keep in mind when reviewing the metabolic response to cold climates (Frisancho 1993, Walker 2008)

Several studies have focused on the relationship between body composition and cold response (Tilkens et al. 2007). Hatfield and Pugh (1951) found that adipose tissue has almost twice the thermal resistance of muscle tissue. This suggests that, at rest, individuals with greater adiposity would lose less body heat in cold conditions, conferring an energetic advantage. An early study on this topic found that individuals with greater fat thickness on both the trunk and limbs experienced a reduced drop in body temperature when swimming in cold water (Sloan and Keatinge 1973). This study also found that subcutaneous fat was a better insulator against the cold than fat deep to that layer (Sloan and Keatinge 1973). Kollias et al. (1974) studied the thermal responses of women exposed to cool water. They found that lean women experienced a

greater drop in core temperature and greater increase in metabolic rate than obese women. This added further evidence that greater adiposity confers a thermoregulatory advantage in cold temperatures, confirming Sloan and Keatinge's findings (1973). Smith and Hanna (1975) explored the difference in heat loss between cold air and cold water conditions. They found that among their male subjects, there was greater heat loss in the cold water than in the cold air condition. However, they found that greater adiposity conferred a greater resistance to body cooling regardless of the cold medium used (Smith and Hanna 1975).

Two studies done in the 1980s took a comprehensive look at body composition, core body temperature and metabolic rate in cold-water exposure both during rest and activity among men and women (McArdle et al. 1984a, McArdle et al., 1984b). The study at rest determined that lean men and women experienced a greater increase in metabolic rate and a greater decrease in core body temperature when resting in cold water when compared to men and women of average and above average adiposity. Subjects with the greatest adiposity also had the greatest resistance to changes in metabolic rate and core body temperature (McArdle et al. 1984a). The study that focused on cold temperature responses during exercise, conducted on the same subjects from the at-rest study, found that exercise conferred a thermoregulatory advantage.

An early study looked at metabolic rate responses, both resting and during exercise, to cold exposure in subjects who worked in cold environments and compared it with students who experienced little long duration cold exposure (Strømme et al. 1963). Their findings support others discussed here in that resting metabolic rate rose, and body temperature declined, when subjects were exposed to cold temperatures. Furthermore, they found a relationship between intensity of exercise and body temperature during cold exposure. At high levels of exercise, there was no drop in body temperature when exposed to cold. However, at low exercise levels,

subjects exposed to cold had a higher metabolic rate than during their temperate exposure (Strømme et al. 1963). Active muscle, whether through physical activity or shivering, can add to heat production helping to combat cold conditions (McArdle et al. 1984a, McArdle et al., 1984b). Also, subjects whose daily lives regularly exposed them to cold temperatures experienced slower body cooling than the students who were not regularly exposed to cold. The authors suggested that acclimatization to cold exposure leads to a lower thermosensitivity. It takes a lower temperature to induce physiological reactions to cold exposure than is seen among non-acclimatized subjects (Strømme et al. 1963).

A more recent study by Tikuisis et al. (2000) also exposed men and women to cold-water immersion. This study mirrored the others in that subjects with greater adiposity had a greater resistance to body cooling. They also found a three-fold increase in metabolic rate in response to cold-water immersion. As expected from basic principles of heat loss, they, along with others, found that there is increased heat loss with an increased surface area to volume ratio. The increased loss in body heat was found to diminish when subjects exercise (Toner et al. 1986, Tikuisis et al. 2000). Furthermore, Tikuisis et al. (2000) found that there is no need for sex-specific adjustments when predicting cold exposure responses when adiposity and surface area-to-body mass ratio are taken into account.

The increased BMR in response to cold conditions is thought to be the result of a short-term acclimatization among people temporarily exposed to cold conditions and long-term physiological adaptations among indigenous circumpolar populations. The result of these physiological responses (increased metabolic rate, vasoconstriction, shivering and non-shivering thermogenesis) is a reduced risk for hypothermia as well as a reduction in the pain and discomfort associated with extremely cold conditions (Stocks et al. 2004, Moran 2008).

### ***BMR Responses to Heat***

Like many other mammals, humans also exhibit short- and long-term physiological responses to heat. The primary concern in a hot environment, whether dry or humid, is hyperthermia. As a result, the physiological response to hot climates is to increase body heat dissipation to maintain a normal body temperature (Hori 1995). Metabolic studies exploring the impact of heat exposure on humans are not quite as clear as the studies examining metabolism in cold climates. However, there are a number of physiological responses to hot climates, and, interestingly, they do not differ between indigenous and non-indigenous populations (Moran 2008). In hot, dry environments humans experience lower pulse rates and body temperatures among acclimatized individuals (Wyndham et al. 1964, Wyndham 1966, Moran 2008). Among non-acclimatized individuals there is increased sweating (Moran, 2008). The degree of sweating decreases with acclimatization to hot environments (Wyndham et al. 1964, Hori 1995). Men appear to have a greater advantage in hot, dry environments because their sweat production capacity is greater than that of women (Shapiro et al. 1980). However, it was noted that despite a lower sweat capacity, women were able to maintain a core temperature similar to men during exercise (Avellini et al. 1980a, Avellini et al. 1980b, Keatisuwan et al. 1996, Gagnon et al. 2008). Gagnon et al. (2008) suggested that this was due to greater internal heat production by men, forcing the need for greater sweat production to maintain core body temperature within normal levels.

Physiological responses to humid heat are poorly understood. Given the high water content of the air in hot, humid environments sweating does little to cool the body. Women are considered to have an advantage over men in this case. In a study done by Shapiro et al. (1980) the women in his sample had a higher surface area to body mass ratio, which enabled greater heat loss through radiation and convection to maintain a low body core temperature.

Another documented response is increased vasodilation for more efficient heat dissipation (Ladell 1964, Hori 1995, Moran 2008). Vasodilation increased the cutaneous blood flow to enable greater heat dissipation (Hori, 1995). It has been noted that among acclimatized individuals, body temperature is greater in the limbs than it is at the core. This is thought to combat a rise in core temperature and encourage heat dissipation from high surface area limbs (Hori, 1995). The limited number of laboratory studies done on this topic suggested that an increase in metabolic rate accompanies an increase in ambient temperature with high relative humidity. In contrast, basal metabolic rate does not appear to increase with increasing ambient temperature and low relative humidity (Shapiro et al., 1980; Hori, 1995; Chinevere et al., 2008). Studies done with Japanese men found that with an increase in monthly ambient temperature there was a decrease in basal metabolic rate (Osiba 1957, Yurugi et al. 1972, Ogata and Sasaki 1975, Hori 1995). The risk of hyperthermia in hot climates becomes especially challenging during physical activity when the body is not only contending with environmental heat, but also heat produced by the active body.

### ***The Cost of Physical Activity***

A number of studies have estimated the total energy expenditure among industrialized populations (Borel 1984, Geissler et al. 1986, Stein et al. 1988, Warwick et al. 1988, Roberts et al. 1991, Haggarty et al. 1994, Spurr et al. 1996, Leonard et al. 1997, Plasqui and Westerterp 2004, Warwick 2006). For example, Spurr et al. (1996) studied urban Columbian women using both the Flex-heart rate method and the Factorial Method and compared the total energy expenditure of women who worked in the home with those who were employed outside of the home. This study found that metabolic rate and activity level did not significantly differ between the two groups when body mass was taken into account. The women had an average BMR of  $1601 \pm 223$  kcal day<sup>-1</sup> with a TEE of  $2249 \pm 460$  kcal day<sup>-1</sup> using the Flex-HR method and

1858±252 kcal day<sup>-1</sup> using the Factorial Method. Washing clothes, sweeping floors and walking took the lion's share of the activity cost accrued throughout the day (Spurr et al. 1996).

Another study measured the TEE among active, adult males from the United Kingdom in both the summer and winter using the doubly labeled water method (Haggarty et al. 1994). This study found that their subjects had an average BMR measured through respirometry of 1717±141 kcal day<sup>-1</sup> in the summer and 1707±198 kcal day<sup>-1</sup> in the winter. Haggarty et al. (1994) also found that their subjects were more active, though not significantly so, in the summer spending an average of 3435±643 kcal day<sup>-1</sup> compared to 3415±1.020 kcal day<sup>-1</sup> in the winter. High levels of moderate-vigorous leisure activities accounted for roughly 1,700 kcal day<sup>-1</sup>. Close to 50% of these subjects took part in moderate physical activity at least three times a week, whereas only 17% took part in no exercise activity (Haggarty et al. 1994). The most common activities were sitting, walking, running or jogging, housework and laboratory work (Haggarty et al. 1994).

Black et al. (1996) performed a meta-analysis of TEE and BMR among affluent populations. They used TEE values from doubly labeled water studies, 574 measurements, and physical activity levels (PAL), the ratio of TEE/BMR, to assess how closely true PAL comes to recommendations from the FAO/WHO/ UNU (1985). Their subjects totaled 1156 males and females across a range of ages, heights, weights and health statuses. They found that TEE, BMR and activity energy expenditure increased with body size and declined with age. Men were found to have a greater mass adjusted TEE, roughly 11%, than women. Unsurprisingly, Black et al. (1996) found that physical activity level depended on occupation, preference for sport and leisure activities, age and health status. They found physical activity levels among these affluent people to be consistent with FAO/WHO/UNU (1985) recommendations; but to be underestimated by the UK Department of Health (Black et al. 1996)

Studies have also measured TEE among non-industrialized and indigenous populations (Stein et al. 1988, Durnin, 1990, Minghelli 1990, Leonard et al. 1995, Katzmarzyk et al. 1996, Panter-Brick 1996a, b, Butte et al. 1997, Aleman-Mateo et al. 2006, Snodgrass et al. 2006, Dufour and Piperata 2008, Kashiwazaki et al. 2009, Pontzer et al. 2012). A sample of studies that involve the use of DLW, the Flex-HR method, and the Factorial Method are presented for their relevance to the methodology used in this project.

Leonard et al. (1995) studied the total energy expenditure among coastal and highland Ecuadoreans. The coastal Ecuadoreans took part in commercial agriculture and lived at elevations less than 200 m above sea level. The highland group utilized small-scale agriculture and dairy farming (Leonard et al. 1995, p. 1147). They lived at elevations 3000-3400 m above sea level. Measurements classified the highland group at a very high physical activity level. Men within this group had a BMR, measured using Douglas-bag indirect calorimetry, of  $1600 \pm 112$  kcal day<sup>-1</sup> and  $1251 \pm 79$  kcal day<sup>-1</sup> for women. Their TEEs were  $3762 \pm 760$  kcal day<sup>-1</sup> and  $2459 \pm 707$  kcal day<sup>-1</sup> measured by the Flex-HR method for men and women respectively. The Factorial Method estimated  $3128 \pm 492$  kcal day<sup>-1</sup> for men and  $2146 \pm 244$  kcal day<sup>-1</sup> for women. The coastal men and women were classified at a light PAL with BMRs similar to their highland counterparts, but TEEs as calculated by the Flex-HR method, of  $2416 \pm 349$  kcal day<sup>-1</sup> for men and  $1970 \pm 139$  kcal day<sup>-1</sup> for women. The Factorial Method estimated  $2213 \pm 318$  kcal day<sup>-1</sup> for men and  $1919 \pm 213$  kcal day<sup>-1</sup> for women (Leonard et al. 1995). This suggested a greater metabolic cost of highland Ecuadoreans was incurred from more strenuous activity during daily work and possibly from living at higher elevations. This also demonstrates that TEE is underestimated by the Factorial Method.

Dugas et al. (2011) also performed a meta-analysis of TEE measured by doubly labeled water doubly labeled water to test the assumption that people from developing countries have higher TEEs and PALs than those from industrialized countries. They obtained data from 98 studies on DLW measured TEE, age, weight, body mass index and physical activity level and then assessed the human development index for a total of 4972 individuals from 118 different cohorts. There was no significant difference in PAL between industrialized and developing countries, and there was no significant difference in TEE once controlled for age, weight, and PAL (Dugas et al. 2011).

Recent work by Pontzer et al. (2012) mirrors the study by Dugas et al. (2011). Pontzer et al. (2012) measured the TEE among the Hadza hunter-gatherers using the doubly labeled water method. In this study they found that the Hadza have a high PAL, but their TEE was not greater than that of Westerners once body size is taken into account (Pontzer et al 2012). This suggests that activity may not impact TEE as much as previously thought, and that energy allocation among different physiological activities may differ not just between species but also between populations within a species. Furthermore, TEE may be evolutionarily constrained within a species and not significantly impacted by cultural differences (Pontzer et al. 2012).

### ***Modeling BMR and TEE in Fossil Hominins***

The large body of work measuring TEE among living populations has led a number of researchers to estimate activity levels and TEE among extinct hominins (Leonard and Robertson 1992, Leonard and Robertson 1997, Sorenson and Leonard 2001, Steegman et al. 2002, Aiello and Wheeler 2003, Steudel-Numbers and Tilkens 2004, Churchill 2006, Froehle and Churchill 2009). These studies are often based on multiple steps of estimation, given estimates in body size, activity levels, and climate for extinct human populations. It has been estimated that *Homo erectus* had a TEE 40-45% greater than their australopithecine predecessors, assuming they had

similar activity levels. If *H. erectus* had activity levels more similar to the rest of genus *Homo*, it was predicted their TEE would be 80-85% greater than australopithecines. These higher costs are associated with greater body size, brain size and ranging (Leonard and Robertson 1997). It has been predicted that Neanderthal males and females had higher TEE averages of 7.3% and 4.9% respectively, than anatomically modern humans, respectively (Froehle and Churchill 2009). However, corrected figures from Trinkaus (2013) suggest that there is actually little difference in TEE between Neanderthals and modern humans.

Studies of industrialized and non-industrialized populations, like those discussed above, are important for defining the range of variation in physical activity levels. Understanding how much energy individuals and populations expend on basal metabolic rate, thermoregulation and physical activity helps elucidate how much energy is still left unaccounted for in a total energetic budget. These studies have also provided the basis for making metabolic rate estimates for past populations. However, there are several other expensive metabolic processes besides BMR, thermoregulation and activity levels that account for the rest of TEE, some better and more easily studied than others.

### ***Other Costs Adding to Total Energy Expenditure***

The following topics are a few of the metabolic processes, outside of the main components discussed above, that contribute to total energy expenditure. However, since these processes are not the focus of the project at hand, they will only be touched upon.

### **Reproduction and Lactation**

Human metabolic cost of reproduction is currently an active area of research. Whereas little is known about reproductive cost among males, a fair amount is known about the metabolic costs of pregnancy and lactation among females. Most of these studies have measured and predicted metabolic rates of pregnancy and lactation in order to make energy intake

recommendations for optimal pregnancy outcomes and adequate milk production (Butte and King 2005). The daily metabolic cost of pregnancy is not constant throughout a full term pregnancy. There are significant differences between the trimesters. Estimates suggest that the first trimester is the most metabolically inexpensive with only an additional  $103 \text{ kcal day}^{-1}$  needed. A pregnant female's metabolic rate increases by  $328 \text{ kcal day}^{-1}$  during the second trimester and  $536 \text{ kcal day}^{-1}$  during the third trimester (Butte and King 2005). Much of this metabolic cost is due to protein and fat deposition on the fetus (Butte and King 2005). There are, however, significant differences between well-nourished and undernourished women. Well-nourished women will experience a rise in metabolic rate quickly after conception. Undernourished women experience a suppressed basal metabolism that will last into the third trimester, as observed among Gambian women (Lawrence et al. 1987, Butte and King 2005). This suppressed basal metabolic rate was also found among British and Scottish women of lower body weights (Spaaij 1993, Prentice et al. 1996, Butte and King 2005).

Though pregnancy, particularly during the third trimester, may seem energetically costly, lactation is actually the most metabolically expensive part of the female reproductive cycle (Butte and King 2005). Energetic efficiency of lactation is far greater than that of the placenta during pregnancy. Roughly 80-95% of the metabolic energy a mother puts into lactation is transferred to the child through energy dense milk (Butte and King 2005). In contrast, the placenta, which essentially feeds the fetus, consumes at least 20-30% of the energy provided by the mother intended for the fetus (Carter 2000). This means there is a far greater return, from the perspective of the offspring, from lactation. Regardless of this energetic efficiency, lactation places a high absolute metabolic burden on the mother. Women breastfeeding their child exclusively incur an estimated additional  $626 \text{ kcal day}^{-1}$  metabolic cost. This cost is of course

lower,  $461 \text{ kcal day}^{-1}$ , among women who only partially breastfeed. Furthermore, well-nourished women who can rely on mobilizing existing tissue for energy experience a lower metabolic cost of lactation,  $453 \text{ kcal day}^{-1}$  (Butte and King 2005). It is clear from these studies that the metabolic cost of pregnancy and lactation are substantial, particularly in energy sparse environments.

### Growth

The main reason behind the high cost of pregnancy and lactation is that a new person and associated fetal structures are being built. This building, or growth, is metabolically expensive. During growth and development a child will go through different phases, some more energetically costly than others. The most energetically costly phase of growth is during the first two years of life. During this time growth accounts for 37-38% of the total energy expenditure of an infant less than two years old (Holliday 1986, Butte 2000). This rate drops dramatically at age two. Energetically, this translates to TEE averages of  $334 \text{ kcal day}^{-1}$  for a one month old and  $955 \text{ kcal day}^{-1}$  for a two year old. The downshift in growth rate translates to  $92.8 \text{ kcal kg}^{-1} \text{ day}^{-1}$  at one month of age and  $84.2 \text{ kcal kg}^{-1} \text{ day}^{-1}$  at two years of age (Butte 2000). This demonstrates the decrease in the metabolic cost of growth rate in the first two years of life. After this period of high growth rate, the rate and cost of growth sharply declines and accounts for only 2% of TEE (Holliday 1986, Butte 2000). Boys experience a higher growth rate and cost than girls. At two years old, girls expend an average of  $955 \text{ kcal day}^{-1}$  and boys  $1,194 \text{ kcal day}^{-1}$ . This difference between the sexes continues throughout adolescence and puberty. After two years of age, the growth rate remains roughly constant, varying between 1-4% of TEE, with minor rate increases during puberty that only minimally affect TEE (Holliday 1986, Butte 2000). Females expend  $2627 \text{ kcal day}^{-1}$  at 18 years old and males at the same age expend  $3583 \text{ kcal day}^{-1}$  (Butte 2000).

This large difference is due to both greater overall body size among males and greater muscle deposition during puberty (Bogin 2012).

### Brain Growth and Maintenance

A large component of the high growth rate and cost during the first two years of life is due to the high cost of brain growth. The brain grows rapidly during the first twelve months of infancy and then the growth rate declines (Holliday 1986, Leonard et al. 2012). 90-95% of full brain size is reached by five years of age when body weight is only one-third of final adult size. At one month, brain growth costs roughly  $140 \text{ kcal day}^{-1}$ , which is over 42% of the infant's total energy expenditure (Holliday 1986). The cost of brain growth declines to  $311 \text{ kcal day}^{-1}$ , 32% of TEE, at two years of age. When the brain is nearly adult size at 5 years of age, the metabolic cost of the brain is  $365 \text{ kcal day}^{-1}$ , 27% of TEE (Holliday 1986, Leonard et al. 2012)). Even at adult size, the brain requires a large proportion of total energy expenditure. The brain accounts for 20-25% of the energy required during rest among humans. Human brains are much larger relative to body size than other primates. Brain metabolism only accounts for 8-10% of resting metabolic rate among primates and 3-5% among other mammals (Leonard et al. 2012). In order to meet the high-energy demands of large brains, humans have improved their diet quality, consuming energy dense foods often rich in fat (Leonard et al. 2012).

### Digestive Metabolic Costs

There are a number of studies that examine the thermic effect of food, or the metabolic cost associate with digesting food. Work by Kinabao and Durnin (1990) estimated the thermic effect of food (TEF) to be roughly 10% of the caloric intake. For example, if a person were to consume 500 calories of food, it would cost roughly 50 calories to digest that food. Kinaboa and Durnin also found that meal composition, i.e., the amount carbohydrates, protein and fat, do not have an impact on digestive costs. However, the amount of calories consumed does impact the

TEF (Kinaboa and Durnin 1990, Tai et al. 1991). Through the thermic effect of food, a 600 kcal meal increased BMR by 21% and a 1200 kcal meal increased BMR by 33%. Studies also show the long-term effect of TEF. An increase in metabolic rate after a meal can last over five hours, and likely the TEF of one meal runs into the TEF of the next meal (Kinaboa and Durnin, 1990). This study, among others (Segal et al 1987, Tai et al. 1991, Belleisle et al. 1997, Farshchi et al. 2004, Halton and Hu 2004) has demonstrated that TEF is a significant contributor to total energy expenditure.

### Immune System Costs

The metabolic costs associated with immune function are still poorly understood. A recent study was conducted on the metabolic cost of non-febrile respiratory illness among young adult men (Muehlenbein et al. 2010). This study documented a significant increase, 8-14%, in resting metabolic rate when compared to non-ill levels. Another study found that among subjects with a febrile illness, resting metabolic rate increased 7-15% for every 1°C increase in body temperature (Elia 1992a). Study of immune metabolic costs has far reaching implications from proper nutrition for ill patients to better understanding the impact illness has on growth and development (Muehlenbein et al. 2010).

### **Summary**

Human energy budgets are highly complex and highly adaptable. TEE is comprised of a number of different energetic factors such basal metabolic rate, physical activity, thermoregulation, growth, maintenance, immune function, and reproduction, to name just a few. The cost of each of these varies within and between species. In humans, as in many other species, the metabolic costs of these different components are correlated with age, sex, health status, and morphological variables such as body mass and height. However, individual characteristics are not the only variables that affect metabolic costs. TEE and its associate

components are also sensitive to environmental factors such as altitude and temperature. A shift to environmental extremes often leads to an associated change in metabolic costs. Cold climates and high altitudes lead to increases in basal metabolic rate as well as thermoregulation.

Metabolic costs in hot climates are not as well understood due to the confounding humidity variable, and have been associated with both decreases and increases in basal metabolic rate and thermoregulation. However, it is important to note that TEE components do not stand alone, but interact with one another. One example presented here was a decrease in thermoregulatory cost associated with high activity levels. This suggests that the body relies on the interaction between morphology, physiology, behavior and the environment to more efficiently perform energetic endeavors. Furthermore, it allows for internal tradeoffs to occur when differing energetic demands, pregnancy for example, present themselves. Better understanding and estimates of these costs, how they interact, and how they are differentially allocated could be used for numerous practical applications. It could also provide useful insight into life history strategies adopted by humans.

### **Chapter 3: The Importance of Energetics in Bergmann's and Allen's Rules**

#### ***Introduction***

Bergmann's rule describes an ecogeographical pattern in which homeothermic animals living in higher latitudes and colder climates tend to have greater body mass than homeothermic animals inhabiting more equatorial, hotter climates (Bergmann 1947). Allen's rule for thermoregulation describes a similar pattern in which homeothermic animals living in higher latitudes tend to exhibit shorter appendages than those living closer to the equator (Allen 1877). Both of these rules summarize a more general ecogeographic relationship between body surface area and body mass and climate (Mayr 1956, 1963), namely such the ratio of surface area to body mass (or volume) is minimized in cold climates and maximized in hot climates to reduce or increase heat dissipation respectively (Ruff 1994). Bergmann and Allen contended that this variation was an evolutionary adaptation to the thermal environment (Bergmann 1847, Allen 1877). These rules have been tested using a wide variety of animals from insects (Bidau and Marti 2008) to birds (Chui and Doucet 2009) to mammals (Frafjord 2008). This chapter discusses the history of Bergmann's and Allen's rules, their application to fossil hominins and modern humans, and current work on the adaptive advantage of these ecogeographic rules to humans.

#### ***Bergmann's and Allen's Rule for Thermoregulation: The Occasionally Sordid Early History***

The early intent of Bergmann's and Allen's ecogeographical rules was to use thermal or ecogeographical clines to explain body shape and size variation among animals. Larger bodied, shorter limbed animals were seen in colder climates and smaller bodied, longer limbed animals in hot climates. Anthropologists and human biologists have tested these rules in humans through both laboratory studies (Shapiro et al. 1980, McArdle et al. 1984a, b, Tikuisis et al. 2000, Tilkens et al. 2007) and by comparisons of body proportions in indigenous and past populations

(Trinkaus 1981, Holliday and Trinkaus 1991, Ruff 1994, Holliday 1997a, b, 1999, Holliday and Hilton 2010). William Ridgeway made the earliest attempt at applying Allen's and Bergmann's rules to humans, rules, by then well established among other animals, in 1908 (Ridgeway 1908, Ruff 1994). He argued against the idea that physical similarity was the result of racial identity and instead emphasized the importance of environmental constraints on human body shape and size (Ridgeway 1908, Ruff 1994). Unfortunately, Ridgeway did not stop there. He extended his argument to encourage control over interracial marriage, stating that it would produce inferior children unfit for any environment (Ridgeway 1908, Ruff 1994).

Other studies looking at the impact of these rules on human variation were sparse during the first half of the 20<sup>th</sup> century (Hooton 1946, Ruff 1994). Studies that did look at the importance of climate on human variation focused mainly on nasal and cranial morphology because of the abundance of data on these features from a wide variety of human populations originally used for racial classifications (Ruff 1994). Thomsen was the first to relate variation in nasal morphology to climate (1913, 1923). His work concluded that more narrow, projecting nasal morphology was associated with cold, dry climates, reasoning that this shape better warmed and moistened the air before it passed to the lungs. Thomsen's work also identified humidity as an important climatic variable affecting nasal morphology (Ruff 1994, Thomsen 1913, 1923). Furthermore, he was one of the first to extend his observations of modern humans to fossil hominins suggesting that they too possessed nasal morphologies directed by the environment (Thomsen 1913).

In the second half of the 20<sup>th</sup> century, there was a renewed interest in Bergmann's and Allen's ecogeographical rules. This interest was initiated by Coon et al.'s volume (1950) and driven by the desire to better understand the physiological demands of different climates on

humans following the World War II effort (Ruff 1994). Because of this, more data were gathered on whole body variation rather than just nasal and cranial variation. As seen with Ridgeway, much of this work looked to climate driven variation and adaptation as a new method of racial classification (Ruff 1994). The most geographically comprehensive of these early studies, covering all continents except Antarctica, were performed by Roberts (1953). He concluded that there was indeed an inverse relationship between body mass and temperature. Higher body masses were observed in cold climates, lower body masses in hot climates, and medium body masses in temperate climates (Roberts 1953). However, he did not find a significant relationship between climate and stature. Later, Roberts went on to look at relative limb lengths and body breadths (Roberts 1978) concluding that data from both studies supported Bergmann's rule (Roberts 1953, 1978).

Work done by Schreider (1950, 1951) looked at the relationship of body mass to surface area and how it varied with climate. He found that the surface area-to-body mass ratio increased in populations from temperate to hot climates and decreased from temperate to cold climates (Schreider 1950). This suggested greater surface area for a given mass in hot climates and reduced surface area among cold climate populations adding support to the application of Bergmann's and Allen's rules among humans. Schreider also documented a different relationship of body mass to surface area between men and women, but did not have sufficient data at the time to fully explore this difference (Schreider 1950). Schreider furthered his work on Bergmann's and Allen's rules by suggesting that heat regulation was related to these anatomical ecogeographical patterns (Schreider 1951). He performed two experiments relating sweat production, body temperature and body shape among young men during heat exposure. He found that men with a low body surface area for a given mass sweat more profusely and had a greater

increase in body temperature than men with a high body surface area (Schreider 1951).

Schreider's work is some of the earliest to look at the physiological implications of Bergmann's and Allen's rules among humans (Ruff 1994). Carleton Coon's book *The Origin of Races* (1963), as well as his earlier volume (1950), focused on the use of anatomical ecogeographical patterns as one of the most important features for racial classification. Coon was also the first to suggest that low mean crural (tibio-femoral) indices reflected cold adaptation. Furthermore, these works cast doubt on the possibility of ecogeographical patterns being extended to fossil hominins. The focus on anthropological racism and negativism towards including fossil analysis drew heavy criticism and ended the newfound anthropological interest in Bergmann's and Allen's rules (Dobzhansky 1963, Montagu 1963, Washburn 1963).

### ***A Shift Away From Racial Focus***

The next two decades were noted by sharp rebuke of the studies done during the 1950's and further statements of the improbability of applying ecogeographical patterns to the fossil record (Washburn 1963). Fortunately, this took the focus away from racial categorization and placed it on the need for more empirical evidence of the presence of Bergmann's and Allen's rules among humans. There were several critiques of the applicability of these rules to humans. First, features associated with particular climates were often found across a wide variety of climatic regimes and did not seem to apply to all species. Second, other factors such as nutrition could also impact body shape and size. Third, other morphological features such as fur, vasoconstriction, and vasodilation were more efficient physiological mechanisms for maintaining heat balance (Scholander 1955). Fourth, human's use of culture to buffer environmental impact negates the need for morphological and physiological adaptations to some extreme environments. Fifth, physiological explanations behind the anatomical ecogeographical patterns were too simplistic and applied too broadly (Washburn 1963, Ruff 1994). This fifth claim led to

a rigorous debate during the late 1950s and early 1960s as to the applicability of ecogeographical patterns to human populations (Scholander 1955, Mayr 1956, Newman 1956, Scholander 1956, Irving 1957, Wilber 1957, Garn 1958).

Scholander was the first and strongest opponent of the idea that changes in the relationship of surface area to volume better conserve heat. He believed this paled in comparison to the efficiency of other heat saving properties among mammals such as fur or vascular heat exchange (Scholander 1955). Scholander was also responsible for early work on physiological adaptations to different climates among mammals and birds, studying the balance between heat loss and heat production (Scholander et al. 1950). His research empirically discredited the idea that cold adapted animals have lower body temperatures to reduce the body-to-air temperature differential and thereby body heat loss (Scholander et al. 1950). He argued that heat loss was mitigated by insulation (fur, fat, clothing etc.), but that heat production was unaffected by climate (Scholander et al. 1950). However, Scholander and others later went on to demonstrate greater heat production (increased basal metabolic rate) was present among cold adapted humans, small mammals, and birds and was an observable adaptation during cold exposure (Scholander 1955, Hart et al. 1956, Irving et al. 1956, Scholander et al. 1958a, 1958b).

Scholander's early views on the importance of heat insulation rather than heat production were expanded upon by Newman in the mid-1950s. Newman, though he largely agreed with Scholander, disagreed with the contention that humans' only adaptations to cold climates were clothing and behavior citing numerous studies on the physiological ability of Eskimos and other cold adapted populations to maintain higher extremity temperatures than non-cold adapted populations (Newman 1956). Furthermore, Newman contended that Bergmann's rule did function in humans, citing Robert's (1953) and Schreider's (1950, 1951) work discussed above

(Newman 1956, 1960, 1961). He, did not however, bolster the argument for Allen's rule among humans, but admitted more evidence was needed to make a case either way (Newman 1956). The most definitive and cogent argument for the presence of Bergmann's and Allen's ecogeographical rules came from Ernst Mayr.

In Mayr's book *Animal Species and Evolution* (1963), he discussed at length humans and their susceptibility to natural selection like all other mammals. He contended that human variation was not merely an accident but the result of natural selection better adapting each population to its particular surroundings (Mayr 1963). Mayr also addressed the criticisms laid out above. First, he pointed out that the majority of species with a wide geographic range do follow anatomical ecogeographic patterns, and exceptions to the rules can be explained by different migratory patterns. Second, he argued that different adaptations to the environment (morphological, physiological, behavioral etc.) are additive and one does not take away from another. The use of vasoconstriction does not negate the advantage of a smaller surface area; they both work to reduce heat loss in cold climates. Finally, Mayr addressed the impact of other factors on ecogeographical clines such as nutrition, distribution of resources, and culture buffering and expressed that despite these confounding factors, a strong and regular relationship still exists between body shape and size and climate. He later contended that human variation, like variation among all other widely distributed animals, was not merely an accident but the result of natural selection better adapting each population to its particular surroundings (Mayr 1963).

The late 1960s and early 1970s saw a massive collaborative effort aimed at collecting worldwide anthropometric data (Ruff 1994). Hiernaux spearheaded work among African populations in his monograph (1968) and several accompanying papers (Hiernaux 1975,

Hiernaux et al. 1975, Hiernaux and Froment 1976). In 1964, Schreider took an in depth look at weight-to-surface area ratios among humans across the globe as they related to Bergmann's and Allen's ecogeographical rules. In this work, Schreider reiterated that cultural buffering alone could account for human survival in climatic extremes. He turned to analysis of the body weight-to-surface area ratio and found evidence for ecogeographical gradients in this ratio. People from colder climates had a higher ratio, suggesting a low surface area, and those from hot climates tended to have lower ratios, suggesting a high body surface area (Schreider 1964). He contended that this lent credence to the applicability of Bergmann's rule among human populations. To test Allen's rule, Schreider analyzed limb lengths with respect to body weight. He found that limbs tended to be longer in populations from hot climates than compared to cold climate populations (Schreider 1964).

Finally, Schreider aimed to discredit the popular example commonly used to explain Bergmann's and Allen's rules among humans: the comparison, "...the Eskimo, with its bulk shape..." to "...the tall, thin Nilotic" (Schreider 1964, pp 5). Schreider argued that this was a gross oversimplification that suggested there was only one way in which to increase or decrease the body weight-to-body surface area ratio. In fact, the same result could be achieved through any number of different combinations of anatomical variation giving rise to populations such as the Pygmies or Otomi exhibiting overall diminished stature yet maintaining a weight-to-surface area ratio expected for their tropical climates (Schreider 1964).

In Roberts' book, *Climate and Human Variability* (1978), he comprehensively discussed many of the fine details related to human climatic adaptation. This included the importance of different anthropometrics in the body weight-to-surface area ratio and the physiological mechanisms involved in managing heat or cold stress. Roberts reiterated much of what had been

said previously about the overall latitudinal/thermal cline of body weight-to-surface area supporting Bergmann's rule. However, he also addressed individual anthropometric measurements and how variation in trunk height, trunk breadth, limb length and limb circumference impact body surface area and ultimately morphological climatic adaptation (Roberts 1978). He examined relative sitting height (summed height of the head, neck and trunk) and, by proxy, lower limb length across populations. He found that relative sitting height increased and lower limb length decreased with decreasing annual temperature (Roberts 1978). Furthermore, he found that body proportions, rather than body weight, were more closely related to mean annual temperature. Roberts also attempted to examine arm length. However, at the time, most anthropometric measurements of the upper limb were limited to arm span, which is a poor measure for this purpose because it combines the transverse measure of shoulder breadth along with linear arm length. These two components have opposing relationships with annual temperature (Roberts 1978). Despite this complication, Roberts found that arm length increased and arms became more slender with increasing annual temperature.

Finally, Roberts looked at chest breadth and found that populations from colder climes had greater chest breadth than those from hot climates (Roberts 1978). His analysis of the different anthropometric measurements supported Allen's rule. However, Roberts, like Schreider (1964), cautioned against an overgeneralized view of Bergmann's and Allen's ecogeographical rules. He suggested redefining them to include the different aspects of morphological variation and not just gross body shape and size. His goal was "...to separate 'relative size' into its components of linearity and bulk, to envisage intrasubspecific variation, and to provide for the fact that the development of one region or of one characteristic may obviate modifications of any other" (Roberts 1978, pp. 32). He too cited the example of Pygmies maintaining a similar body

weight-to-surface area ratio as other African populations despite their overall diminution in body size. With this book, research on Bergmann's and Allen's rules moved into a new decade and a new interest in applying these ecogeographical rules to the fossil record.

### ***The Applicability of Bergmann's and Allen's Rules Among Fossil Hominins***

The resurgence of interest in ecogeographical rules as they apply to fossil hominins began in the early 1980s. These studies, and the majority of fossil work done on this topic, focused on Neanderthals and the possibility of morphological adaptation to cold climates. For example, Trinkaus (1981) explored recent human and Neanderthal limb proportions as they related to cold adaptation and established the relationship between mean annual temperature and brachial and crural indices. He found that low brachial and crural indices were associated with low mean annual temperature and that Neanderthals have relatively short distal limbs relative to the proximal limbs. He concluded that while Neanderthal brachial indices do in fact fall within the recent human range. However, they do so at the low end of the range overlapping with Eskimo, Lapp and Europeans, which also tend toward the lower end of the recent human range (Trinkaus 1981). For the crural index, Neanderthals fell below the recent human range; only Lapp and Eskimo populations were close to the Neanderthal range (Trinkaus 1981). Trinkaus provided two possible interpretations for these results. First, the abbreviated distal limbs would act to reduce body surface area and thereby heat loss providing Neanderthals with a morphological adaptation to the cold climates they inhabited. The link between distal limb length and heat dissipation was already well established (Robinson 1968). Trinkaus argued that the shortened distal limbs could also provide a biomechanical advantage that would favor greater force production but limit speed. However, Trinkaus stated that this second interpretation is in disagreement with the "robusticity and limb proportions present in the European and Near Eastern early 'anatomically modern' samples" (Trinkaus 1981, pp. 219). Given this, Trinkaus

accepted his first interpretation that Neanderthal shortened distal limbs were an adaptation to cold climates.

Work on this topic did not just focus on limb proportions, but also cranial morphology. Beals et al. (1984) looked at the relationship of brain size and cranial morphology to climate. They found that in recent populations crania tended to be larger and more rounded (an increase in both cranial length and breadth) in cold climates than in hotter ones. When they looked to the fossil record, they found this pattern still held, particularly among Neanderthals. Though they found an ecogeographical pattern in cranial size and shape, they did not argue that climate was the cause, and even conceded that the proximal cause is still unknown (Beals et al. 1984).

In a detailed and highly comprehensive article, Ruff (1994) explored morphological adaptations to climate among modern humans and fossil hominins. He concluded that body shape and size vary according to the predictions of Bergmann's and Allen's ecogeographical rules such that surface area relative to body mass will increase in hot climates and decrease in cold climates (Ruff 1994). Using a cylindrical model of the body based on absolute pelvic breadth he argued that predictions could be made about trunk and limb shape. For example, regardless of stature, trunk and bi-iliac breadth should increase, and limb length should decrease in cold climates while the converse is true in hot climates. The data from both living humans and fossil hominins seem to support this supposition (Ruff 1994). Ruff (1994) established that there is a relationship between bi-iliac breadth and mean annual temperature among recent humans, such that bi-iliac breadth increases as mean annual temperature decreases (Ruff 1994). Others, for example Holliday (1997a) have also found similar results. Holliday described the relationship between mean annual temperature and the ratio of long bone length to trunk length. He found that with decreasing mean annual temperature the long bones are short relative to trunk length

(Holliday 1997a). “European Neandertals are characterized by an overall postcranial morphology that can be described as ‘hyperpolar’; their limb and body proportions are extremely cold adapted, and seem to follow expectations derived from Bergmann’s and Allen’s rules” (Holliday 1997a, pp. 256). Ruff’s work, along with those of many others (Katzmarzyk and Leonard 1998, Ruff 2002, Steegmann 2002, 2007, Gustafsson and Lindenfors 2009) have well established the applicability of Bergmann’s and Allen’s rules to both fossil and modern humans.

Much recent work on the tradeoff between climatic adaptation and mobility efficiency among Neanderthals (Holliday and Falsetti 1995, Steudel-Numbers and Tilkens 2004, Weaver and Steudel-Numbers 2005, Maki and Pontzer 2008, Froehle and Churchill 2009, Higgins and Ruff 2011). It has been suggested that while Neanderthal shortened distal limbs confer a thermoregulatory advantage in cold climates they also confer a locomotor disadvantage (Steudel-Numbers and Tilkens 2004). It is established that lower limb length affects the cost of locomotion: shorter limbs lead to more expensive locomotion and longer limbs lead to metabolically cheaper locomotion as discussed here in the second chapter (Kram and Taylor 1990). The cold adapted shortened distal limbs of Neanderthals meant they experienced as much as a 30% higher cost of locomotion than modern humans. (Steudel-Numbers and Tilkens 2004). Others have built upon this work to estimate Neanderthal energy expenditure given the high metabolic demand of living in a cold climate and increased locomotor costs). For example, Froehle and Churchill (2009) estimated that Neanderthal males and females had total energy expenditures on average 7.3% and 4.9% higher than anatomically modern humans, respectively (Froehle and Churchill 2009). However, recent work (Trinkaus 2013) suggests that there may actually be very little difference in TEE between Neanderthals and modern humans. The higher estimates of a Neanderthal TEE from Froehle and Churchill (2009) are likely due to inconsistent

results when the fossil samples are properly assessed (Trinkaus 2013). However, if Neanderthals or modern cold adapted populations did not have shortened distal limbs, would their total energy expenditures be even greater to accommodate potentially higher thermoregulatory costs? This leads to the central question concerning Bergmann's and Allen's rules: What is the energetic advantage to these morphological adaptations to climate?

### ***Experimentally Quantifying the Energetic Benefits of Climatic Adaptions***

It has been well established that Bergmann's and Allen's ecogeographical rules apply to humans and that thermal clines in human morphological variation exist. However, why this pattern exists, and persists, is still unclear. For an adaptation to evolve in parallel among different species, it presumably has to confer some form of advantage. If these morphological adaptations to climate did not grant an energetic advantage, especially in the face of a trade off with poor locomotor performance, they would not be maintained. As discussed in Chapter 2, a vast amount of research has been conducted to quantify the metabolic cost of thermoregulation particularly is it relates to the metabolic advantage of Bergmann's and Allen's rules.

A fair amount of early laboratory work, mostly with mice, has been done on experimentally eliciting a morphological response to different climatic conditions. Consistent results came from trying to replicate the predictions of Allen's rule. Relative to control mice, mice raised in colder temperatures developed shorter limbs, and mice raised in hot temperatures developed longer limbs (Sumner 1909, Ogle 1934, Emery et al 1940 Harrison et al. 1959, Harrison 1960, 1963, Chevillard et al. 1963, Steegmann and Platner 1968, Riesenfeld 1973). However, researchers were not able to produce consistent results when testing Bergmann's rule. Mice exposed to extreme temperatures, high or low, gained weight slowly (Barnett and Scott 1963, Riesenfeld 1973). However, when mice were raised at more moderate hot or cold temperatures, the mice exposed to cold gained weight more quickly than mice raised at hot

temperatures (Sumner 1909, Sundstroem 1922, Ogle 1934, Harrison 1960). These studies indicated a clear association between limb length and the climate in which the animal is raised. Given these data it is reasonable to infer that shortened limbs are cold adapted and longer limbs are hot adapted (Trinkaus 1981). However, it is the energetic consequences of these adaptations, particularly among humans, that are of chief interest.

Work on the energetic advantages conferred from the morphological adaptations described by Bergmann and Allen are sparse. The majority of experiments looking at metabolic responses to extreme temperature were done on adults often using cold exposure conditions through water emersion. A number of these studies were discussed in Chapter 2; however, much of that research focused mainly on the absolute metabolic response to cold exposure and not how it varied with different body shapes and sizes. Sloan and Keatinge (1973) examined the cooling rate of young people while swimming in cold water. They found that younger individuals cooled faster than older ones and boys cooled faster than girls. The important finding was that body surface area and surface fat thickness were the best correlates with heat loss. Individuals with a lower body surface area and lower surface fat thickness experienced greater rates of cooling (Sloan and Keatinge 1973).

Sloan and Keatinge (1973) did not measure metabolic changes during their experiment. However, metabolic rate was examined in a study done by Kollias et al. (1974). They looked at the metabolic response of women exposed to cold water. They found two different anatomical correlates with body cooling. The first was body fat and the second the surface area-to-mass ratio. Women with a greater body fat percentage (28.9 – 40.9%) also had a relatively lower surface area-to-mass ratio and experienced reduced rates of cooling when exposed to cold water. Whereas women with an average percent body fat (21.0 – 24.0%) and high surface area

experienced a higher rate of cooling with an accompanying increase in metabolic rate to counteract the heat loss (Kollias et al. 1974). The importance of body surface area and body fat thickness to cold adaptation was reiterated later in a study done by Tikuisis et al. (2000). In this study too men and women were experimentally exposed to cold temperatures. They found that during cold water immersion, metabolic rate increased to three times resting levels in both men and women. However, body temperature cooling rates were lower in men than in women. Here too, Tikuisis et al. (2000) found that body surface area was the strongest correlate to body cooling and metabolic heat production with lower body surface area-to-mass ratios experiencing reduced cooling and metabolic response.

In a recent study, Tilkens et al. (2007) looked at the relationship between resting metabolic rate and lower limb length. They examined if there was a difference in this relationship when only the length of the distal lower limb segment, or only the proximal lower limb segment was used (Tilkens et al. 2007). They found that lower limb length is related to resting metabolic rate such that as lower limb length increases, resting metabolic rate increases. They then specified that it appears to be the proximal limb segment length, i.e., the thigh, that is driving this relationship.

These studies, among others, have determined that shorter limbs, broader bi-iliac breadth, and large body mass confer an energetic advantage in cold temperatures (Tikuisis et al. 2000, Tilkens et al. 2007, Holliday and Hilton 2010), as these reduce the amount of body surface area exposed to the environment and reduce the amount of area through which body heat can dissipate. This, in turn, reduces the amount of heat the body needs to produce to maintain body temperature within acceptable limits (Tilkens et al. 2007). The reverse is true for hot

temperatures; longer limbs and lower body mass increase body surface area enabling greater heat dissipation, thereby reducing the body's need to eliminate excess heat (Shapiro et al. 1980).

### ***Summary***

The studies discussed here provide an excellent source of information on how humans react to extreme temperatures in laboratory conditions, and provide explanations for the latitudinal variation seen in body proportions today. However, there are currently no studies looking at the possible energetic advantage conferred by morphological variables among highly active humans living in a variety of natural environments. At present, there are no studies measuring energy expenditure among humans linking possible differences in energy expenditure in different climates to variation in body shape. This type of analysis would help determine if there is a true energetic advantage to Bergmann's and Allen's rules among humans, or if there are other biological and behavioral processes at work to mitigate environmental stressors.

## **Chapter 4: Measuring and Predicting Human Energy Expenditure**

### ***Introduction***

Human energetics has profited from both greater research interest by anthropologists and human biologists in the past several years and with the increased ease of being able to measure and estimate human TEE (Leonard and Ulijaszek 2002). Humans are unique in having relatively high activity levels and energetic demands, and yet we maintain higher reproductive rates than other primates in spite of these greater energetic needs (Leonard and Robertson 1997).

Understanding human energy expenditure provides insight into how humans interact with their environment to meet their high energy demands and how that energy is subsequently allocated.

Work examining energy allocation has explored subsistence strategies, growth and repair, reproductive output, thermoregulatory demands, mobility patterns, and human brain-size evolution (Durnin 1990, Roberts et al. 1991, Haggarty et al. 1994, Leonard and Robertson 1994, Aiello and Wheeler 1995, Leonard et al. 1995, 1997, Panter-Brick 1996a, b, Spurr et al. 1996, Tikuisis et al. 2000, Leonard and Ulijaszek 2002). This chapter discusses the different methods utilized by researchers to measure and predict human energy expenditure.

### ***Measuring Human Energy Expenditure***

Anthropological work on human energy expenditure dates back to the mid-20<sup>th</sup> century with Lee's (1965) and Rappaport's (1968) work, which examined the flow of energy between the study populations and their environments. Though rudimentary by today's standards, Lee and Rappaport provided the impetus for improving our methodology for measuring and understanding human energy balance (Ulijaszek 1995). Today there are several methods for measuring TEE through direct calorimetry, indirect calorimetry, and estimations based on physiological variables.

### Direct Calorimetry Methodology

Direct calorimetry measures the rate of heat loss (convective, radiation, and conductive) from a subject. Atwater and Benedict (1903) devised the first direct calorimeter during a series of experiments on direct calorimetry and respiratory gas exchange (Webb et al. 1980, Kaiyala and Ramsay 2011). There are numerous types of calorimeters, but no matter the type, all are extremely expensive and require highly specialized knowledge for proper operation (Close et al. 1980, Levine 2005). Furthermore, the necessary chambers involved in direct calorimetry restrict the movement and activity level of the subject being measured. There have been great advances since Atwater and Benedict, and there are now direct calorimetry chambers the size of large rooms for human studies allowing a greater range of movement (Kaiyala and Ramsay 2011). However, movement is still restricted and this limits the scope of research that can be conducted using direct calorimetry (Close et al. 1980). Because of this, direct calorimetry is rarely used by the majority of researchers, and is limited to only the most specialized laboratories. Despite the drawbacks to using direct calorimetry, it is worth discussing because of the contributions this method has made to our knowledge of energy expenditure and because of its high degree of accuracy. When properly used, direct calorimetry can provide results with an accuracy of 2% or better (Webster et al. 1986). This high degree of accuracy has led to a number of researchers using direct calorimetry to validate other methods for measuring energy expenditure (Close and Mount 1975, Dauncey et al 1978, Close et al. 1980, Snellen 2000). There are four types of direct calorimetry systems: isothermal, heat sink, convection, and direct differential (Levine 2005, Kaiyala and Ramsay 2011). All four types consist of a chamber that can be built and arranged in a variety of configurations, and the systems require careful calibration to ensure accurate results (Close and Mount 1975, Dauncey et al. 1978, Close et al. 1980, Webster et al. 1986).

### Isothermal Direct Calorimetry

An isothermal (heat-flow or heat conduction) system is comprised of a chamber with an insulated lining. The inner side of the lining is in thermal equilibrium with the inside of the chamber where the subject is positioned. The outside of the lining is in thermal equilibrium with the chamber wall and is kept at a constant temperature with circulating fluid, generally water, using a jacket or bath (Levin 2005, Kaiyala and Ramsay 2011). The heat released by the subject flows through the lining of the chamber and reaches the constant temperature outer lining. An integrated thermopile, consisting of numerous thermocouples, transforms the temperature gradient created by the flow of heat from the subject into voltages. The total voltage generated by this temperature gradient represents the heat loss by radiation, conduction, and convection, of the subject from which metabolic rate can be calculated (Kaiyala and Ramsay 2011).

### Heat Sink Direct Calorimetry

Heat sink, or adiabatic, systems are also comprised of a chamber. However, in this case, heat loss from the subject is removed via a liquid-cooled heat exchanger (Levine 2005). The inner and outer portions of this chamber are kept at equal temperatures to regulate the rate of heat extraction by the heat exchanger (Levine 2005). The specific heat of the cooling liquid, flow rate, and temperature increase must be known in order to calculate the dry heat loss of the subject (Kaiyala and Ramsay 2011). One of the advantages of using an enclosed chamber is that the internal environment of the chamber can be adjusted to create different experimental conditions to test any number of research questions (Dauncey et al. 1978). Interestingly, a suit heat sink calorimeter has been designed for use with humans during exercise. (Webb 1995, 1997, Kaiyala and Ramsay 2011). Cooling liquid, the temperature of which can be closely controlled and monitored, flows through the suit through a series of small tubing. The benefit to the suit is that it

allows for energy expenditure measurements to be taken during any number of activities in any number of locations. It also enables longer measurement durations (Kaiyala and Ramsay 2011).

#### Convection Direct Calorimetry

The convection system, like the previous two, also consists of a chamber. However, unlike the flow of liquid in the isothermal and heat sink systems, a convection system relies on a known rate of airflow. Heat loss can be calculated by using flow rate, the specific heat capacity of air and the change in the temperature of the air leaving the chamber (Levine 2005). Simply put, it relies on the temperature difference between the air entering and exiting the chamber (Kaiyala and Ramsay 2011).

#### Differential Direct Calorimetry

Differential direct calorimetry consists of two identical chambers; the subject is in one and an electric heater in the other. The electric heater is adapted to produce identical temperatures in both chambers. The heat delivered to the heater equals the heat produced by the subject and therefore the subject's metabolic rate (Kaiyala and Ramsay 2011).

#### Indirect Calorimetry Methodology – Respirometry

Indirect calorimetry requires measurement of oxygen consumption and carbon dioxide production using either a respiratory chamber, or mask-based systems run from a desktop system or portable/wearable units (Jequier and Shutz 1983, Gayda et al. 2010). This method requires subjects to be in a respiratory chamber or wear a mask continuously for energy expenditure measurements. Indirect calorimetry estimates metabolic rate from established relationships between energy transfer and CO<sub>2</sub> production given the amount of fuel and oxygen consumed (Kaiyala and Ramsay 2011). The amount of energy produced for a given amount of oxygen consumed or carbon dioxide produced depends on the fuel (fat, carbohydrate or protein) being oxidized. Substrate oxidation estimates depend on the respiratory quotient (RQ) – the ratio of

CO<sub>2</sub> produced to O<sub>2</sub> consumed. RQs of 1.0, 0.85 and 0.7 can indicate that carbohydrate, protein or fat respectively are being catabolized; however, it is not always this clear. An RQ of 0.85 could also indicate a mix of macronutrient catabolism (Kaiyala and Ramsay 2011).

There are several assumptions made when estimating metabolic rate using respirometry. First, it must be assumed that test subjects exhibit the same pattern of fuel catabolism as the subjects from the original experiments that established the relationship between metabolic rate, fuel utilization and respirometry (Walsberg and Hoffman 2005, Kaiyala and Ramsay 2011). Second, the cost of fuel conversion within the body, such as gluconeogenesis, is negligible (Kaiyala and Ramsay 2011). Third, the carbon dioxide pool within the body remains constant. This can be violated by a number of different metabolic disorders (Kaiyala and Ramsay 2011). Fourth, there is no contribution of anaerobic metabolism during measurement (Kaiyala and Ramsay 2011). Fifth, it is assumed that subjects are post-prandial since measurements using respirometry greatly differ from that of direct calorimetry while metabolic rates are measured after a meal is consumed (Garby 1989, 1991, Kaiyala and Ramsay 2011). There are four types of indirect calorimetry systems with which to measure energy expenditure: total collection, confinement, closed-circuit and open-circuit (Levine 2005).

#### Total Collection Indirect Calorimetry

Total collection indirect calorimetry systems rely on an airtight rigid container or flexible bag to collect expired air. An example of a rigid container is the Tissot Gasometer, which is a glass bell suspended over water and contains an internal circulation fan. Air is removed from the bell, and the subject breathes through a mouthpiece fitted with a one-way valve. The bell fills with the expired air and the bell slowly rises above the water seal. The height of the bell and the composition of the expired air are measured to determine O<sub>2</sub> consumption and CO<sub>2</sub> production (Levine 2005). An example of a flexible bag for total collection indirect calorimetry is the

Douglas bag. The Douglas bag is made of a flexible, leak-proof material and is often very large. The top of the bag is connected to a three-way valve by tubing. This valve has three configurations: open to atmospheric air, open to expired air or to completely seal the bag. To collect expired air, the valve is first opened to atmospheric air and then rolled to remove all the air from the bag. The valve is then set to allow in only expired air from the subject who is connected to the bag via a mouthpiece. The subject breathes into the bag for the duration of the measurement, roughly 10-20 minutes, and then the valve is set to seal the bag. The air collected in the bag is then analyzed for O<sub>2</sub> and CO<sub>2</sub> concentrations (Yoshida et al. 1981, deGroot et al. 1983, Levine 2005). A modified, portable version of the Douglas bag was devised to allow for a greater range of mobility and exercise to be researched (Daniels 1971). However, this portable unit required the use of a car, with the top down, equipment in the back seat, a patient driver and a researcher on the hood to hold hoses close to the exercising subject as he ran around a track (Daniels 1971). Whether it is portable within a car or stationary within a laboratory, the Douglas bag system is still used today to validate new indirect calorimetry methods (McLaughlin et al. 2001, Rietjens et al. 2001).

### Confinement System

The confinement system consists of an airtight chamber of known volume in which the subject is sealed. Changes in the concentration of O<sub>2</sub> and CO<sub>2</sub> are measured over time to estimate oxygen consumption and carbon dioxide production (Levine 2005). Use of confinement systems is uncommon.

### Closed-Circuit System

Closed-circuit systems measure changes in gas concentrations that take place in a sealed respiratory gas circuit (Levine 2005). This form of indirect calorimetry was used in the early days of energy expenditure measurements, but is highly uncommon today. In this system,

expired air is drawn into some sealed container, and the amount of carbon dioxide and water vapor absorbed are measured. Oxygen is re-introduced into the system and energy expenditure is calculated using the amount carbon dioxide absorbed and oxygen introduced (Levine 2005). A smaller version of this is known as a spirometer.

#### Open-Circuit Indirection Calorimetry

Open-circuit indirect calorimetry systems can be used for measurements of greater durations, from hours to days depending on the experimental demands. There are two types of open-circuit systems. The first is a ventilated open-circuit in which subjects breathe into a container through which air is drawn from the environment (Levine 2005). There are different ways to collect and subsequently analyze expired air. A mouthpiece, mask, transparent hood, canopy or even a chamber can be used for this purpose (Sorkin et al. 1980). A pump draws out expired air, the flow rate of which is measured. This air is then mixed and sampled for analysis (Levine 2005). In such an open-flow system, the flow into the system must equal the flow out of the system. Expired air is passed through two different filters: one to remove water and the other to remove carbon dioxide (Fedak et al. 1981). Once the expired air has passed through these filters, it passes through an oxygen analyzer, which measures the fraction of oxygen in the expired air. The amount of oxygen consumed by the subject is calculated from the measured fraction of oxygen and the flow rate (Fedak et al. 1981). This type of system requires calibration of both the oxygen analyzer and the flowmeter by injecting the system with a known flow rate of nitrogen. Measuring the displacement of oxygen by nitrogen is used to calibrate the oxygen displacement, or consumption, by the subject (Fedak et al. 1981)

The second type is an expiratory collection open-circuit system. This system has the benefit of being modified for portable use making energy expenditure measurements of free-living individuals possible. This type of system consists of a facemask or mouthpiece that is

connected to a device. Cosmed K4 b2 is an example of a portable open circuit system and is discussed at length here since it was the unit used for the data collection presented here. This unit is light-weight, battery powered and self-contained (McLaughlin et al. 2001). The Cosmed K4 b2 unit measures oxygen consumption and carbon dioxide production as well as the ventilation fraction of both gases on a breath-by-breath basis (McLaughlin et al. 2001). This unit also measures heart rate and calculates RQ. The data can be directly transmitted to a PC through a hard wire connection or through telemetry. The data can also be stored in the memory of the portable unit to be downloaded at a later time (McLaughlin et al. 2001).

The Cosmed unit sits in a chest harness strapped to the subject who also wears a mask which covers the mouth and nose for collecting expired air. Attached to the mask is a flowmeter, which contains a turbine and an opto-electric reader with a linear response in the 0-300 L min<sup>-1</sup> ventilation range (McLaughlin et al. 2001). The flow rate of expired air is measured and a proportion of it is analyzed at the end of each measurement period (Levine 2005). “The K4 b2 uses a Cosmed patented oxygen analyzer (range 7-24%) and an infrared non-dispersive thermostated carbon dioxide analyzer (range 0-8%), and proprietary software” (McLaughlin et al. 2001, pp. 281). The Cosmed software is also used for numerous calculations including that of metabolic rate. Portable open-circuit units have become a popular system for collecting energy expenditure data because of the freedom of mobility allowing a greater range of research questions.

#### Non-Calorimetric Methodology

Non-calorimetric methods for estimating energy expenditure are often used due to their ease of use and relative economy. These methods estimate energy expenditure through physiological variables that are related to energy expenditure such as heart rate and muscle activity. These methods have been standardized and validated using calorimetric methods

(Levine 2005). Five different methods are discussed here: integrated electromyography, pulmonary ventilation volume, thermal imaging, flex-heart rate method and the doubly labeled water method.

### Integrated Electromyography

This form of non-calorimetric measurement measures muscular activity to estimate energy expenditure. Electrical activity from muscle fibers is measured throughout the duration of the measurement period. Work on the relationship between muscle activation measured by EMG and metabolic rate dates back to 1943 with measurements of muscle activity of calf muscles while lying down and while standing (Jacobson 1943, deVries et al. 1976). It was found that there was EMG activity among resting muscles and it eventually concluded that the low-level potentials had to be more than typical background noise expected during EMG measurements (Joseph et al. 1955, Nightingale 1958, deVries et al. 1976). DeVries et al. (1976) simultaneously collected resting EMG and oxygen consumption data on human subjects to determine the relationship between resting muscle electrical activity and resting metabolic rate. They found a significant correlation; however, their work was highly contested (deVries et al. 1976). Carrier et al. (2011) found that during walking and running, muscle activity was minimized at given speeds, but that different muscles are not tuned to different speeds. The reason metabolic rate estimation from EMG measurements is not commonly used is that multiple muscle groups need to be measured since the strength/force relationship is different for different muscle groups. This makes integrated electromyography an impractical technique for whole-body activity (Levine 2005). However, EMG in conjunction with either direct or indirect calorimetry has been used to understand the relationship between muscle work and metabolic rate (Seliger et al. 1980, Sun and Hill 1993).

### Pulmonary Ventilation Volume

For a very short measurement period, directly measuring the volume of gas exchanged, the pulmonary ventilation volume, can be used to estimate energy expenditure (Levine 2005). However, this is only practical for very short measurement durations and is not used in natural settings for measurements among free-living populations.

### Thermal Imaging

Early studies using thermal imaging to measure heat lost to the environment suffered from poor accuracy and precision. However, recent technology has made this a more viable technology to measure energy expenditure (Levine 2005). Work has been done to adapt infrared thermal imaging to measure heat loss in humans (Shuran and Nelson 1991). Convection, radiation and evaporation can be calculated from data collected from digitized infrared thermal images of body surface temperature. Shuran and Nelson (1991) estimated metabolic rates from thermal imaging and from open-circuit indirect calorimetry among humans while fasting and then at different postprandial intervals. They found no significant difference in the metabolic rate results between thermal imaging and indirect calorimetry. Studies such as this promote the use of thermal imaging as a non-invasive method for estimating metabolic rate.

### Flex-Heart Rate Method

The flex-heart rate method uses a known linear relationship between heart rate and metabolic rate to measure energy use based on data collected from small, portable heart rate monitors worn by subjects (Leonard 2003). This method allows for more flexibility than indirect calorimetry; however, it does require subjects to wear both a small heart rate monitor and a beeper-sized heart rate data logger that are not water-proof. Furthermore, the linear relationship between heart rate and metabolic rate is different from one individual to the next. Therefore, it is necessary to calibrate each individual through simultaneously measuring heart rate and metabolic

rate, often through indirect calorimetry. Measurements must be taken while the subject is at rest and then while the subject exercises at progressively greater intensities to gather data on a wide range of activity levels (Ulijaszek 1992).

The relationship between heart rate and metabolic rate at low levels of activity is curvilinear. At higher levels of activity the relationship is linear. The point at which the relationship changes from curvilinear to linear is known as the Flex Point. The calculation of metabolic rate from heart rate depends on the relationship of a given heart rate to that individual's Flex Point. If the heart rate is below the Flex Point, metabolic rate is estimated to be the average metabolic rate at resting levels calculated from the calibration. If the heart rate is above the Flex Point, the equation derived from the linear relationship of metabolic rate to heart rate determined during calibration is used to estimate the metabolic rate (Ulijaszek 1992, Leonard 2003).

Validation studies have found that the flex-heart rate method is accurate, the average error falls within  $\pm 6\%$  (Ceesay et al. 1989, Leonard et al. 1995, Kashiwazaki 1999). However, there can be a fair amount of variation in flex-heart rate measurements, particularly if care is not taken during individual calibrations (Dauncey and James 1979, Close et al. 1980, Kashiwazaki 1999, Hiilloskorpi et al. 2003). Flex-HR discrepancies have been reported to range from -22.2% - 52.1% at the individual level (Livingstone et al. 1990, Leonard 2003). It has also been noted that because of the variability, the flex-heart rate method gives better estimates for group energy expenditure rather than on the individual level (Kalkwarf et al. 1989, Kashiwazaki 1999). However, the flex-heart rate method has the benefit of being highly portable with the use of small heart rate monitors. Furthermore, it enables long-term data collection, 1-2 weeks, on total energy expenditure given the current data logging capabilities of modern heart rate monitors. It is

also more affordable than indirect calorimetry systems, and measurements can be taken on multiple people in any location at the same time once calibrations are complete. These benefits have made the flex-heart rate method the tool of choice for free-living energy expenditure measurements (Leonard et al. 1995, Wareham et al. 1997).

#### Doubly Labeled Water Method

Doubly labeled water is a highly accurate method that uses the differential rates of oxygen and hydrogen elimination to determine average daily metabolic rates over a 1-3 week period (Schoeller et al. 1986, Ulijaszek 1992, Levine 2005). This method requires expensive doses of doubly labeled water, bodily fluid sample collections, and subsequent sample analysis. In a doubly labeled water dose, both the hydrogen and oxygen of water are labeled using stable, non-radioactive isotopes of deuterium ( $^2\text{H}$ ) and oxygen-18 ( $^{18}\text{O}$ ) (Schoeller et al. 1986, Schoeller 1988, Schoeller et al. 1995, Schoeller and Luke 1997, Levine 2005). A general formula for doubly labeled water is  $^2\text{H}_2^{18}\text{O}$ , though in a dose some of the water is of the form  $^2\text{H}_2\text{O}$  and  $\text{H}_2^{18}\text{O}$ . Once the dose is administered  $^{18}\text{O}$  will distribute throughout the body into body water, expired  $\text{CO}_2$ , and  $\text{H}_2\text{CO}_3$ . The concentration of labeled oxygen will slowly decrease over time through expired  $\text{CO}_2$  and water elimination through urine, perspiration and respiration. The deuterium will distribute throughout the body in body water and  $\text{H}_2\text{CO}_3$ , and the concentration will decrease at a rate different from  $^{18}\text{O}$  as water is eliminated. With both oxygen and hydrogen labeled and known amounts of each in the body, the difference in elimination rates of deuterium and  $^{18}\text{O}$  can be determined which will then characterize the  $\text{CO}_2$  elimination rate (Schoeller et al. 1986, Schoeller 1988, Schoeller et al. 1995, Schoeller and Luke 1997, Levine 2005).

Baseline samples of urine, saliva, or blood are taken from subjects before the doubly labeled water dose is administered. The subject is then given an accurately weighed dose orally and given time for the isotopes to evenly distribute throughout the body water pool – called the

deuterium dilution space (IAEA 2009). Then samples of urine, saliva, or blood are collected regularly for 1-3 weeks during which time the isotope concentration is slowly decreasing. Another form of this method only requires two samples to be taken, one after the dose is administered and one at the end of the measurement period. The concentration, and, therefore, elimination rates of  $^2\text{H}$  and  $^{18}\text{O}$  are determined through mass spectroscopy of the serial samples (Schoeller et al. 1986, Schoeller 1988, Schoeller et al. 1995, Schoeller and Luke 1997, Ulijaszek 1992, Levine 2005). The elimination rates are then used to calculate an average total energy expenditure using well-established equations (Schoeller et al. 1986, Schoeller 1988, Schoeller et al. 1995, Schoeller and Luke 1997, Levine 2005, IAEA 2009).

The doubly labeled water method has been validated to within 2-5% of whole body calorimetry measurements making it a highly accurate method for estimating total energy expenditure (Ulijaszek 1992). This method is also desirable because of the ease of data collection in the field, leaving all of the difficult analysis work for the laboratory. The dose administration is a one-time event and the periodic, but regular bodily fluid collections, take only moments. This allows subjects the freedom to go about their daily activities with very little disruption. The one drawback to this method is the expense. Doubly labeled water doses and the means to analyze collected samples are expensive, limiting the scope with which it can be used (Ulijaszek 1992).

### ***Estimating and Predicting Human Energy Expenditure***

Though these methods are highly accurate, they are also expensive and logistically difficult, especially when used among non-industrialized populations with limited access to electricity and possible cultural aversions. Also, these methods cannot be used to measure energy expenditure among past populations. Therefore, using predictive models is an attractive method for estimating TEE, and a fair amount of work has gone into their development (Passmore and

Durnin 1955, Durnin and Passmore 1967, Thomas 1973, Smith 1981, Hawkes et al. 1982, Dufour 1983, FAO/WHO/UNU 1985, Galvin 1985, James and Schofield 1990, Froehle and Churchill 2009).

### Activity Logs

A low tech and highly affordable method of estimating energy expenditure is through the use of activity logs. This requires that the research subjects, or someone observing them, keep a daily diary of the types and duration of activities. These can be more detailed by including such information as the time of day the activity takes place or distance and elevation traveled (Kalkwarf et al. 1989). The activities recorded are then converted into energy expenditures using either published tables relating specific activities to their metabolic cost or individual measurements on the subjects completing the activity logs (Kalkwarf et al. 1989, Ulijaszek 1992). The costs of the individual activities are summed for each day to give TEE. Though this method is economically convenient, it is well known for underestimating energy expenditure. Poor recording practices by subjects and poor activity cost estimates produce the error in energy expenditure estimates from activity logs (Kalkwarf et al. 1989).

### Kinematic Measurements

Kinematics can be used to estimate energy expenditure by the quantification of a subject's movements in conjunction with a measure of energy expenditure during that activity (Levine 2005). Pedometers and accelerometers are the two most commonly used instruments to estimate energy expenditure based on kinematic measurements. Both pedometers and accelerometers can be personalized for each subject with information such as height, weight, and age. Pedometers lack the sophistication of accelerometers, because they only measure each stride the subject performs and does not take into account stride length nor total body displacement. Accelerometers on the other hand electronically measure total body displacement, and some

types do so using three axes (Levine 2005). Accelerometers detect body accelerations and decelerations as a way of measuring physical activity with details of frequency and intensity (Bouten et al. 1994). The relationship between body acceleration and metabolic rate is used to estimate energy expenditure, though individual calibrations similar to that for the flex-heart rate method improve accuracy (Bouten et al. 1994). Because of the lack of sensitivity, during static exercise for example, these instruments are more useful for comparing activity levels between groups rather strictly measuring total physical activity (Bouten et al. 1994, Bassett et al. 2000, Levine 2005). Recent work has found the relationship between accelerometer data and TEE is not consistent, and that the addition of accelerometer data does not help to explain additional variation seen in TEE (Butte et al. 2012, Westerterp 2013)

#### *The Factorial Method*

The currently recommended and most frequently used model for predicting energy expenditure without physiological measurements is the Factorial Method (FAO/WHO/UNU 1985) The Factorial Method estimates total energy expenditure by summing the energetic cost of BMR and activity throughout the day. Activity costs are estimated as a multiple of BMR based on the intensity of each activity (FAO/WHO/UNU 1985). This method has been applied to industrialized populations (Borel 1984, Geissler et al. 1986, Warwick et al. 1988, Roberts et al. 1991, Haggarty et al. 1994, Spurr et al. 1996, Leonard et al. 1997, Warwick 2006). For example, Spurr et al. (1996) studied urban Columbian women and compared the total energy expenditure of women who worked in the home with those who were employed outside of the home. Non-industrialized populations have also been the subject of Factorial TEE studies (Leonard et al. 1995, Katzmarzyk et al. 1996, Dufour and Piperata 2008). For example, Leonard et al. (1995) examined the differences in the energetic demands of coastal and highland Ecuadorean agriculturalists. Finally, a number of researchers have estimated TEE among extinct hominins

(Leonard and Robertson 1992, Leonard and Robertson 1997, Sorenson and Leonard 2001, Steegman et al. 2002, Aiello and Wheeler 2003, Steudel-Numbers and Tilkens 2004, Churchill 2006, Froehle and Churchill 2009). These studies are based on multiple steps of estimation: estimates in body size, activity level, and climate for extinct hominin populations. All of these studies provide a useful framework for comparing TEE, activity levels, and variation, but are limited by the inaccuracy and underestimation inherent in the factorial method (Leonard et al. 1997).

Studies comparing directly measured TEE with Factorial Method predictions have shown that the Factorial Method consistently underestimates true TEE (Durnin 1990, Roberts et al. 1991, Haggarty et al. 1994, Leonard et al. 1995, 1997, Spurr et al. 1996). Underestimation of TEE appears to be greatest among highly active populations. Roberts et al. (1991) measured energy expenditure, using indirect calorimetry, the doubly labeled water method, and the Factorial Method among young adult British men with sedentary occupations but strenuous leisure activities. This study found that the Factorial Method underestimated TEE measured using doubly labeled water by 16-22%. Roberts et al. (1991) suggested that inappropriate values assigned to individual activity costs may account for the bias seen in the Factorial Method. In a similar study of young British men, Haggarty et al. (1994) also found that the Factorial Method underestimated doubly labeled water measured TEE by 23%, though predictive costs for leisurely activities were not significantly different from the measured costs.

Because of the limitations of factorial modeling, several researchers have measured TEE directly through the flex-heart rate and doubly labeled water methods. These studies have examined both industrialized (Roberts et al. 1991, Haggarty et al. 1994, Leonard et al. 1995, Spurr et al. 1996, Butte 2003, Plasqui and Westerterp 2004, Snodgrass et al. 2006) and non-

industrialized populations (Durnin, 1990, Minghelli 1990, Katzmarzyk et al. 1996, Panter-Brick 1996a, b, Butte et al. 1997, Aleman-Mateo et al. 2006, Kashiwazaki et al. 2009, Pontzer et al. 2013). Leonard et al. (1995, 1997) measured TEE using the flex-heart rate and doubly labeled methods among highland and coastal Ecuadoreans and among indigenous and non-indigenous peoples of Central Siberia. They compared their TEE measurements to predictions formulated from the Factorial Method. These findings mirror those above; the Factorial Method consistently underestimates TEE by an average of 15% and that the underestimation was greatest among those subjects who were highly active. Furthermore, Leonard et al. (1995) pointed out that measured BMRs were 19% higher than predicted values based on body mass within their subject pool. When plotting measured TEE vs. predicted TEE, Leonard et al. (1997) found the regression slope ( $b = 0.24$ ) was significantly less than identity, and  $r = 0.50$ , with poorer predictions at higher activity levels. Leonard et al. (1997) suggested that discrepancies in BMR predictions, activity cost estimations, and the absence of thermoregulatory costs in predictive models lead to the observed underestimations.

### ***Summary***

These different methodologies have provided human biologists and anthropologists alike a large tool kit with which to measure total energy expenditure. However, not all methods are created equal. As discussed above, some methods such as direct calorimetry are highly accurate, but limit the type of energetic data collection to measurements of sedentary or low activity subjects. Indirect calorimetry, though not as highly accurate as direct calorimetry, is portable and enables researchers to collect energetic data for a wide range of activities in any number of environments. Both types of calorimetry are accurate and used to validate other methods of measuring energy expenditure; however, they both require expensive equipment, have a limited data collection period per measurement session, and can be cumbersome for measurements

among free-living humans. Other methods such as the flex-heart rate and doubly labeled water methods have been developed to more easily measure total energy expenditure and have proved invaluable for measurements in the field on free-living populations. However, not all researchers have the resources to utilize these methods for their work, and in such cases must necessarily turn to predictive models for estimating energy expenditure. Though the Factorial Method is useful in many cases, its lack of accuracy particularly at high activity levels, leaves something to be desired. Rectifying the absence of an accurate predictive model is the chief goal of the work presented here.

## **Chapter 5: Materials and Methods**

### ***Introduction***

This chapter describes the participants and the methods used to measure anthropometrics and total energy expenditure among 59 individuals participating in semester-long National Outdoor Leadership School (NOLS) courses. The new model for predicting human total energy expenditure presented here is explained in detail as are the statistical that have been utilized. This study was approved by the Human Research Protection Office of Washington University in St. Louis (IRB: 201104106). NOLS is a US-based, not-for profit outdoor education program that was founded in 1965. NOLS offers students the chance to live in the wilderness for an extended period of time, anywhere from two weeks to four months, with only what they can carry in their backpacks. The NOLS core curriculum is taught on every expedition, including outdoor skills, leadership, risk management, and environmental studies. Their ultimate goal is to train students to become independent wilderness travelers and leaders.

### ***Participants***

The 59 subjects (40 males, 19 females, ages 18-30 years, *Appendix 1*), participating in this study took part in four semester-long courses. Two of the courses (n=25) were in the Spring/Summer semester that lasted for three months and the other two (n=28) were in the Fall/Winter semester that lasted four months. The pilot study (n=6) that was conducted during the summer of 2010 (**Table 5.1**).

**Table 5. 1.** The NOLS courses that took part in this study with their corresponding dates and climates.

<i>Course</i>	<i>Semester</i>	<i>Climates</i>	<i>Course Duration</i>
WSS 1	Spring/Summer	Temperate and Hot	6/2/11 – 8/10/11
WSS 2	Spring/Summer	Temperate and Hot	6/4/11 – 8/12/11
FSR 5	Fall/Winter	Temperate and Cold	9/4/11 – 12/3/11
FSR 8	Fall/Winter	Temperate and Cold	9/8/11 – 12/10/11
Pilot	Summer	Temperate	7/1/10 – 8/4/10

This subject pool was advantageous for two reasons. First, NOLS students were highly active and highly motivated to participate. This made them ideal for both representing physically active populations and managing the logistics and time commitment necessary for this study. Second, the semester-long courses allowed for two different seasonal temperatures to be tested within one group of subjects. Subjects taking part in the Spring/Summer semester were exposed to temperate conditions and hot conditions for a month each. Subjects taking part in the Fall/Winter semester were exposed to temperate and cold conditions for a month each. This means that each student acted as his/her own control, the temperate condition, and an extreme temperature, either hot or cold depending on the course in which they participated. During the pilot study, subjects only took part in a month long course in the Rocky Mountains and were exposed to temperate conditions.

Before subjects took part, the study was fully explained and consent forms were read and signed. Subjects received no official compensation for participation; however, as a gesture of gratitude subjects received a NOLS t-shirt, a selection of three NOLS books, and were brought candy bars and fresh fruit while on their course in the wilderness.

Subjects took part in two different types of data collection bouts. The first bout consisted of resting metabolic rate, heart rate calibration, anthropometric and bioelectrical impedance measurements. These data were collected three times throughout the semester long course:

before the course began (Pre-Course Battery), in between the different climate regimes (Mid-Course Battery) and at the end of the course (Post-Course Battery). The second type of data collection consisted of heart rate monitor, doubly labeled water, food diary, activity diary, and daily temperature data collection. These data were collected twice during each semester course, once during the temperate regime and once during the extreme, either hot or cold, climate regime; this data collection is referred to as the Energy and Activity Assessment Battery. Because the Pilot study took place in only one climate, there was only a Pre- and Post-Course battery. Please refer to **Fig. 5.1** for the general schedule of data collection.

Pre-Course Battery	Temperate Acclimation	Temperate Battery	Subjects Finish Section	Mid-Course Battery	Cold or Hot Acclimation	Cold or Hot Battery	Subjects Finish Section	Post-Course Battery
RMR, HR Calibration, Anthropometrics	2 weeks	Energy and Activity Assessment	1-2 weeks	RMR, HR Calibration, Anthropometrics	2 weeks	Energy and Activity Assessment	1-2 weeks	RMR, HR Calibration, Anthropometrics

**Figure 5. 1.** The general schedule of data collection for the semester courses. The Pre-, Mid- and Post-Course Battery collections consisted of RMR, HR calibration and anthropometric data collection. The Energy and Activity Assessment Batteries consisted of HR monitor, DLW, temperature, activity log and food log data collection.

**Data Collection Locations**

Data collection took place in several different locations across the Western United States (**Table 5.2**). Pre-, Mid- and Post-Course Batteries took place in two locations: at the NOLS headquarters in Lander, Wyoming and at the NOLS River Base in Vernal, Utah. Data collected in the temperate regime for the Spring/Summer semester courses took place in the Absaroka Mountain Range of Wyoming. Data in the hot regime for the Spring/Summer semester courses took place in Devil’s Tower, Wyoming and City of Rocks, Idaho. Data in the temperate regime for the Fall/Winter semester courses took place in the Wind River Mountain Range, Wyoming and in the Absaroka Mountain Range, Wyoming for the cold regime.

**Table 5. 2.** Locations of the different data collection batteries for each course.

<i>Course</i>	<i>Pre-Course Battery</i>	<i>Temperate Climate</i>	<i>Mid-Course Battery</i>	<i>Hot Climate</i>	<i>Cold Climate</i>	<i>Post-Course Battery</i>
WSS 1	Lander, WY	Absaroka Range, WY	Lander, WY	City of Rocks, ID	–	Vernal, UT
WSS 2	Vernal, UT	Absaroka Range, WY	Lander, WY	Devil’s Tower, ID	–	Lander, WY
FSR 5	Lander, WY	Wind River Range, WY	Lander, WY	–	Absaroka Range, WY	Lander, WY
FSR 8	Lander, WY	Wind River Range, WY	Lander, WY	–	Absaroka Range, WY	Lander, WY
Pilot	Lander, WY	Wind River Range, WY	–	–	–	Lander, WY

### ***Anthropometrics and Body Composition***

Several external anatomical measurements were collected following Lohman et al. (1988) (Table 5.3, Appendix 1). These measurements were collected using a standard cloth measuring tape in millimeters and large calipers. Body mass, percent body fat and muscle mass were collected using a bioelectrical impedance scale, Tanita BC-558 Ironman Segmental Body Composition Monitor (Tanita Corporation, Arlington Heights, IL, USA).

### ***Resting Metabolic Rate and Heart Rate Calibrations***

Resting metabolic rates were collected from each subject using a portable respirometry unit (Costmed K4b2, Chicago, IL, USA) following Gayda et al. (2010). This system measures oxygen consumption and carbon dioxide production using a breath-by-breath analysis. RMR measurements were taken early in the morning before subjects had their first meal. Subjects were in a supine position on foam pads placed on the floor, in a temperature controlled room, and rested 15-20 minutes before measurements were taken. Measurements were then taken for 6-8 minutes with the last four minutes of the measurement averaged to determine RMR.

**Table 5. 3.** Anthropometric measurements collected.

<i>Measurement</i>	<i>Definition</i>
Neck + Head length	Taken from the C-7 spinous process to the skull apex
Head circumference	Taken from glabella to opisthocranium
Neck length	Taken from the junction of the neck and shoulder to the mastoid process
Neck circumference	Taken from the length mid-point of the neck
Total arm length	Acromion to dactylion
Upper arm length	Acromion to olecranon
Lower arm length	Radion to stylium
Hand length	Stylium to dactylion
Upper arm circumference	Taken at the length mid-point of the upper arm
Forearm circumference	Taken at the length mid-point of the forearm
Wrist circumference	Taken just distal to the styloid process
Chest breadth	Males – nipple/fourth rib level, females – just below the bust
Chest depth	Males – nipple/fourth rib level, females – just below the bust
Chest circumference	Males – nipple/fourth rib level, females – just below the bust
Bi-iliac	Taken from the most lateral distance between the left and right tubercles
Bi-asis	Distance between the left and right anterior superior iliac spines
Total leg length	Greater trochanter to floor
Upper leg length	The lateral cord from the greater trochanter to tibia
Low leg length	Tibia to the tip of lateral malleolus
Foot length	Heel to toe
Proximal thigh circumference	Taken at the junction of the thigh and pelvis
Mid-thigh circumference	Taken at the length mid-point thigh
Distal thigh circumference	Taken just above the knee
Calf circumference	Taken at the maximal circumference of the calf
Ankle circumference	Taken just above the lateral malleolus

Heart rate calibrations, used to calculate TEE from heart rate using the Flex-HR Method, were also performed using a portable respirometry unit (Costmed K4b2, Chicago, IL, USA) following Gayda et al. (2010). Subjects wore both the portable respirometry unit and a heart rate strap during calibrations so that metabolic rate and heart rate were collected simultaneously. This provided the data to determine the relationship between heart rate and metabolic rate ( $\text{kcal day}^{-1}$ ) at a variety of exercise intensities. The HR calibrations for all but one session of two courses took place at the NOLS headquarters in Lander, WY (**Table 5.2**). These subjects were asked to stand, walk ( $1\text{m s}^{-1}$ ,  $1.5\text{m s}^{-1}$ ,  $2\text{m s}^{-1}$ ), and run ( $2\text{m s}^{-1}$ ,  $2.5\text{m s}^{-1}$ ,  $3\text{m s}^{-1}$ ) for five minutes at each speed on a treadmill while heart rate (bpm) and respirometry ( $\text{kcal min}^{-1}$ ) data were simultaneously recorded (Cosmed K4B2, Chicago, IL, USA).

One session each of two courses performed their HR calibrations at the NOLS River Base in Vernal, UT. There was no treadmill available at this location. Subjects were asked to stand, walk at three different self-determined speeds (slow, normal and fast walk) and run at three different self-determined speeds (slow, normal and fast run). A well-worn ovoid track-way was measured (57.6m) and used for the walking and running calibrations. Speeds were determined by using a stopwatch to time subjects as they completed each lap of the track-way. This also served to help subjects maintain a constant speed. Subjects were asked to maintain these speeds for five minutes. Data collected for resting metabolic rates were averaged ( $\text{kcal day}^{-1}$ ) for the last four minutes of the RMR measurement. This was done for the Pre-Course, Mid-Course and Post-Course resting metabolic rate measurements (*Appendix 2*).

To execute the Flex-HR method, the flex-point and the linear relationship, calibration equation, between energy expenditure and heart rate at different exercise intensity levels were first determined. The flex-point was determined to be the mean of the highest heart rate at rest and the lowest heart rate during exercise. To determine the calibration equation for heart rates above the flex-point, the heart rates were plotted against their corresponding energy expenditure and the linear relationship determined. Please refer to *Appendix 4* for the flex-points and calibration equations for each subject.

### ***In Field Energy Expenditure and Activity Measurements***

#### ***Flex-Heart Rate Method***

ActiTrainer heart rate monitors (ActiGraph, Pensacola, FL, USA) were used to collect heart rate data (Crouter et al. 2006). The ActiTrainer collected a minute-by-minute heart rate and those data were stored in the unit's internal memory and later downloaded for analysis and TEE calculations. This device also collected the number of steps, 3-axis accelerometry data, date and

time. Subjects wore a combination ActiTrainer data recorder and heart rate strap for 6-11 days depending on the course (**Table 5.4**).

<i>Course</i>	<i>Temperate</i>	<i>Hot</i>	<i>Cold</i>
WSS 1	6/24/11 – 7/4/11	7/20/11 – 7/25/11	–
WSS 2	8/1/11 – 8/10/11	7/10/11 – 7/15/11	–
FSR 5	9/14/11 – 9/20/11	–	11/23/11 – 11/29/11
FSR 8	9/25/11 – 10/2/11	–	12/1/11 – 12/7/11
Pilot	7/25/10 – 7/30/10	–	–

**Table 5. 4.** Dates during which subjects took part in the Energy and Activity Assessment data collection battery which included the subjects wearing the ActiTrainer heart rate monitors, doubly labeled water sample collection, temperature data collection and the subjects filling out the activity and food logs.

Subjects wore the data recorder either on an elastic belt around the waist or attached to the heart rate monitor chest strap. Subjects were asked to wear the ActiTrainer during all waking hours, and, if they felt comfortable, to wear the unit while sleeping. Subjects were also asked to remove the heart rate monitor unit when submerged in water.

Heart rate data were downloaded from the ActiTrainers and then converted to .csv files using the ActiGraph software (ActiGraph, Pensacola, FL, USA) for each Energy and Activity Assessment Battery of each subject. Missing data or erroneous heart rates (any heart rates above 200 or below 40) and their corresponding times were deleted. For those subjects who did not wear heart rate monitors while sleeping, resting heart rate, and, therefore, resting metabolic rate was inserted during sleeping hours. Daily metabolic rates were calculated for the remaining data, a mean of 16.4 hours day<sup>-1</sup> for temperate climates, 17.3 hours day<sup>-1</sup> for hot climates and 15.0 hours day<sup>-1</sup> for cold climates. The mean days of data collection were 8.75, 6 and 6.5 days for temperate, hot and cold climates respectively. The calibration equations and RMRs from the data collection battery after the Energy and Activity Assessment Battery of each climate were used (**Table 5.5**). Heart rates below the flex-point were assigned the resting metabolic rate. All heart

rates above the flex-point, indicating activity, were run through the calibration equations to calculate TEE. These metabolic rates were then used to extrapolate a full 24-hour total metabolic rate. Daily energy expenditures were calculated for each subject within each climate regime.

**Table 5. 5.** Heart rate calibration and RMR battery used to calculate total energy expenditure for the Energy and Activity Assessment Battery of each climate.

<i>Course</i>	<i>Temperate</i>	<i>Hot</i>	<i>Cold</i>
WSS 1	Mid-Course Battery	Post-Course Battery	–
WSS 2	Post-Course Battery	Mid-Course Battery	–
FSR 5	Mid-Course Battery	–	Post-Course Battery
FSR 8	Mid-Course Battery	–	Post-Course Battery
Pilot	Post Course Battery	–	–

#### *Doubly Labeled Water Method*

Total TEE (kcal day<sup>-1</sup>) was measured using the doubly labeled water (DLW) method.

Eight subjects took part in a DLW validation portion of this study. Three of these subjects were measured twice, once in the temperate environment and once in the extreme environment. Two subjects were measured once, one in the temperate environment and the other in a cold environment. The other three subjects took part in the pilot study, which took place in a temperate environment. Subjects were given an oral dose of DLW (116.08-122.62g; 10% H<sub>2</sub><sup>18</sup>O, 6% <sup>2</sup>H<sub>2</sub>O). Dose bottles were rinsed with bottled water twice which was also consumed by subjects to ensure the full dose was administered. Urine samples were collected prior to the DLW dose, 6-8 hours after the dose and then every other day for the duration of the Energy and Activity Assessment Battery. Urine samples were collected in clean, dry wax coated paper cups. Four 2ml cryovials (Sarstedt) were filled at each urine sample collection. Vials were labeled with the date, time and subject specific information. Vials were then placed in two waterproof plastic bags and kept cold in a small soft-pack cooler using either pack snow or mountain river water during the temperate sessions. In the hot sessions, bagged vials were kept in a large cooler filled

with ice. During the cold sessions, bagged vials were kept in a waterproof bag left exposed to the adequate freezing ambient temperatures (average -9.4°C). Once samples were taken out of the field, they were placed in -80°C freezer at Washington University in St. Louis for long-term storage.

Doubly labeled water samples from 5 subjects were analyzed using the Picarro Cavity Ring-Down Spectroscopy system (Sunnyvale, CA, USA) at Hunter College in New York. DLW samples from the three pilot study subjects were analyzed with gas-isotope mass spectroscopy at the Baylor College of Medicine, under the direction of Dr. William Wong. Prior to analysis, urine samples were filtered through carbon and placed in clean, glass vials for injection into the spectroscopy unit. This unit is equipped with an auto injector and a flash evaporator, and the sample introduction sequence from Brand et al. (2009) was used (Thorsen et al. 2011). Samples (4-5.2µL) were drawn into the syringe and into the evaporator in the presence of dry nitrogen (Thorsen et al. 2011). Isotope abundances were measured using the ring-down method described in the previous chapter. Each series of urine sample analyses was begun and ended using a non-enriched lab standard. Each vial, both lab-standard and urine sample, was sampled eight times. Only the last three samples of each vial were used in order to reduce the impact of sample memory from the previous sample. Dose dilutions of the DLW doses administered to subjects were also generated and analyzed in the same manner as described above.

Daily energy expenditure was calculated from the isotope concentrations determined from the Cavity Ring-Down Spectroscopy system using the following equations from IAEA (2009).

$$TEE = 22.4 rCO_2 \left( 1.10 + \frac{3.90}{R} \right) \quad (5.1)$$

Where TEE ( $\text{kcal day}^{-1}$ ) is total energy expenditure,  $r\text{CO}_2$  is carbon dioxide production and  $R$  is the respiration quotient.

$$r\text{CO}_2 = 0.455 \text{ TBW} (1.007k_O - 1.041k_D) \quad (5.2)$$

Where  $\text{TBW}$  is total body water,  $k_O$  is the  $^{18}\text{O}$  elimination rate and  $k_D$  is the  $^2\text{H}$  elimination rate.

$$\text{TBW} = \frac{\text{TBW}_O + \text{TBW}_D}{2} \quad (5.3)$$

$$\text{TBW}_O = \frac{N_O}{1.007} \quad (5.4)$$

$$\text{TBW}_D = \frac{N_D}{1.041} \quad (5.5)$$

Where  $\text{TBW}_O$  is the  $^{18}\text{O}$  body water enrichment,  $\text{TBW}_D$  is the  $^2\text{H}$  body water enrichment,  $N_O$  is the  $^{18}\text{O}$  dilution space and  $N_D$  is the  $^2\text{H}$  dilution space. TEE was calculated for each of the climates.

#### Activity, Food and Clothing Diaries

Subjects were asked to keep self-reported activity and food diaries for the duration of the Energy and Activity Assessment Battery. Subjects reported activity type (hiking, walking, climbing, cross country skiing, digging snow etc.), distance or duration of activity and backpack weight during reported activity. Subjects reported type and quantity of food. Collapsible measuring cups were provided to aid measuring accuracy, though many subjects opted not to use these and instead estimated food amounts. Subjects also documented all of the clothing they took with them while in the field. There were also asked to document the brand and garment name.

Activity diaries kept by subjects were transcribed into a database. Each day was entered separately to include the activity and its corresponding distance and duration. All distances and elevations were converted to meters. Data from the food logs were also transcribed into a database in a day-by-day basis. Calories were calculated and assigned to each food entry using the *NOLS Cookery* (Pearson 2004), *NOLS Backcountry Cooking* (Pearson and Kuntz 2008),

*NOLS Backcountry Nutrition* (Howley Ryan 2008) and the official USDA National Nutrient Database for Standard Reference (USDA 2012). Calories were summed for each day along with total carbohydrates, dietary fiber, sugar, protein, total fat, trans fat and saturated fat. The average for each subject was calculated for the Energy and Activity Assessment Battery of each climate.

Temperature Data

Temperature was measured using the Extech RHT10 Humidity and Temperature USB Data-logger (Extech Industries, Nashua, NH, USA). Two subjects each carried one data-logger in an outside pocket of their backpacks for the duration of the Energy and Activity Assessment Battery. This device measured and recorded temperature and humidity on a minute-by-minute basis, which was later downloaded for analysis.

Temperature data was downloaded using the Extech software (Extech Industries, Nashua, NH, USA) and then exported to a .csv file. Hi, lo and mean temperatures were calculated for each day as well as averaged across the Energy and Activity Assessment Battery of each climate (**Table 5.6, Appendix 5**). Temperature data was estimated from published values for the Pilot Study.

**Table 5. 6.** The minimum, maximum and mean temperatures (°C) for the Energy and Activity Assessment Data Battery for each climate.

<i>Course</i>	<i>Temperate</i>			<i>Hot</i>		
	<i>Minimum</i>	<i>Maximum</i>	<i>Mean</i>	<i>Minimum</i>	<i>Maximum</i>	<i>Mean</i>
WSS 1	1.2	42.1	15.6	15.1	45.1	23.3
WSS 2	0.3	39.2	13.5	15.4	46.7	23.5
	<i>Temperate</i>			<i>Cold</i>		
	<i>Minimum</i>	<i>Maximum</i>	<i>Mean</i>	<i>Minimum</i>	<i>Maximum</i>	<i>Mean</i>
FSR 5	-2.1	30.3	6.2	-17.45	17.0	-4.9
FSR 8	0	41.4	14.0	-26.8	14.8	-9.4
<i>Pilot</i>	<i>Temperate</i>					
	<i>Minimum</i>	<i>Maximum</i>	<i>Mean</i>			
Pilot	-3.3	25	12.8			

### ***Predictive Models for Daily Energy Expenditure***

Daily energy expenditure was estimated using both the factorial method and the new method presented in this work.

#### ***Factorial Method***

TEE was predicted for each subject in each climate using the Factorial Method following FAO/WHO/UNU (1985). The general form of the Factorial Method is:

$$TEE = BMR + Activity \quad (5.6)$$

BMR was calculated using existing equations from Henry (2005), which estimate BMR using age, sex and body mass. Activity costs were calculated as a multiple of BMR based on the intensity of the activity (FAO/WHO/UNU 1985). BMR multiples were assigned to the different activities according to FAO/WHO/UNU (1985), and using subjects' activity logs to determine type and duration of activities (**Table 5.7**).

**Table 5.7.** Factorial method multiples of basal metabolic rate for determining activity costs (FAO/WHO/UNU 1985).

<i>Activity</i>	<i>Multiple of BMR</i>
Sleeping	1.0
Resting	1.4
Light activity (socializing, cooking etc.)	2.1
Moderate Activity (yoga, push-ups etc.)	2.8
Heavy Activity (hiking w/ light load, swimming, downhill skiing, etc.)	3.8
Very Heavy Activity (hiking w/ heavy load, climbing, cross country skiing, etc.)	5.1

#### ***Allocation Model for Predicting TEE***

TEE was also predicted for each subject in each climate using the new model presented here. This model takes the general form of:

$$TEE = BMR + E_{activity} + E_{therm} + TEF \quad (5.7)$$

Where *BMR* is basal metabolic rate, *E<sub>activity</sub>* is the metabolic cost of activity, *E<sub>therm</sub>* is the metabolic cost of thermoregulation and *TEF* is the thermic effect of food.

Basal Metabolic Rate, BMR

For BMR age, sex and mass specific equations from Henry (2005) were used. All subjects were in the same age bracket of 18-30 years old. The following are the BMR (kcal day<sup>-1</sup>) equations for males (3) and for females (4):

$$\text{BMR} = 16.0M + 545 \tag{5.8}$$

$$\text{BMR} = 13.1M + 558$$

(5.9)

Where  $M$  is body mass (kg).

Metabolic Cost of Activity,  $E_{\text{activity}}$

$E_{\text{activity}}$  was determined by activity specific cost equations (**Table 5.8**).

**Table 5. 8.** Activity specific equations for determining the total metabolic cost of activity.

<i>Activity</i>	<i>Equation</i>	<i>Unit</i>	<i>Source</i>
Walking	$17.25M^{0.449}$	J m <sup>-1</sup> kg <sup>-1</sup>	Rubenson et al. 2007 (5.10)
Running	$6.11+0.319(M) - 0.18(L_L)$	LO <sub>2</sub> km <sup>-1</sup>	Steudel-Numbers et al. 2004 (5.11)
Climbing	$0.1352M + 1.7853$	kcal min <sup>-1</sup>	Booth et al. 1999 (5.12)
Hiking	$1.5M + (2.0(M+ B)(BM^1)^2 + \eta(M + B)[1.5v^2 + 0.35vg]$	Watts	Pandolf et al. 1977 (5.13)
Cross Country Skiing	$0.274Mt$	kcal	McArdle et al. 2001 (5.14)
Downhill Skiing	$32.4Mt$	mL O <sub>2</sub>	Audet 1994 (5.15)
Digging Snow	$6.0Mt$	kcal	Ainsworth et al. 2000 (5.16)
Swimming	$0.1Mt$	kcal	Capelli et al. 1998 (5.17)
Push-Ups & Sit-Ups	$0.08Mt$	kcal	McArdle et al. 2001 (5.18)
Yoga	$0.1Mt$	kcal	McArdle et al. 2001 (5.19)

The variables are as follows:  $M$  is body mass (kg),  $L_L$  is lower limb length,  $B$  is backpack weight (kg),  $\eta$  is the terrain factor estimated to be 1.20 (Pandolf et al. 1977),  $v$  is speed (m s<sup>-1</sup>),  $g$  is the percent grade of terrain, and  $t$  is the time (hrs.). Climbing speed was estimated to be 3.2 m min<sup>-1</sup> (Booth et al. 1999). Percent grade of the terrain was determined using distance and elevation travelled documented in the activity logs. Hiking speed (m s<sup>-1</sup>) was determined using the following equation from Pandolf et al. (1977):

$$-0.0083B + 1.5092 \quad (5.20)$$

Where  $B$  is the backpack weight (kg). As backpack weight increases, speed decreases. All activity metabolic costs were converted into calories and then summed for each day.

#### The Metabolic Cost of Thermoregulation, $E_{\text{therm}}$

$E_{\text{therm}}$  was calculated following the COMFA outdoor thermal comfort model (Kenny et al. 2009). This model is based on first principles of metabolic heat production, convection, radiation and evaporation. All equations come from Kenny et al. (2009). The general form of this model is:

$$E_{\text{therm}} = M + R_{RT} - C - E - L \quad (5.21)$$

Where  $M$  is the metabolic heat generated by a person ( $\text{W m}^{-2}$ ),  $R_{RT}$  is radiation absorbed by a person ( $\text{W m}^{-2}$ ),  $C$  is the convective heat loss ( $\text{W m}^{-2}$ ),  $E$  is the evaporative heat loss ( $\text{W m}^{-2}$ ), and  $L$  is the long-wave radiation heat loss ( $\text{W m}^{-2}$ ). In temperate climates an estimate of 25% exposed skin surface area was used, 10% for cold climates, and 60% for hot climates following ISO (2007) guidelines.

#### *Generated Metabolic Heat*

The metabolic heat generated by a person was calculated using the following equations, which come from Kenny et al. (2009):

$$M = (1 - f)M_a \quad (5.22)$$

$$f = 0.150 - (0.0173e) - (0.0014T_a) \quad (5.23)$$

Where  $M_a$  is the “metabolic intensity” of the person, ( $\text{W m}^{-2}$ ) is the metabolic cost of activity,  $f$  is the correction for heat loss consumed through breathing,  $T_a$  is the ambient temperature ( $^{\circ}\text{C}$ ) and  $e$  is the ambient vapor pressure (kPa) calculated as follows:

$$e = 610.7 \left( 10^{\frac{7.5T_a}{237.3 + T_a}} \right) \quad (5.24)$$

### Heat Loss Through Convection

The metabolic heat lost by a person through convection,  $C$  ( $\text{W m}^{-2}$ ), was calculated using the following equations from Kenny et al. (2009):

$$C = \rho C_p \left( \frac{T_{sk} - T_a}{r_c + r_a} \right) \quad (5.25)$$

where  $\rho C_p$  is the volumetric heat capacity of air ( $\sim 1212 \text{ J m}^{-3} \text{ K}^{-1}$ ),  $T_{sk}$  is the skin surface temperature ( $^{\circ}\text{C}$ ),  $T_a$  is the ambient temperature ( $^{\circ}\text{C}$ ),  $r_c$  is the clothing resistance ( $\text{s m}^{-1}$ ,  $s$  is seconds) and  $r_a$  is the boundary air resistance ( $\text{s m}^{-1}$ ). Within eq. 5.25,

$$r_a = \frac{0.17}{ARe^n Pr^{0.33} k} \quad (5.26)$$

$$T_{sk} = T_c - \left( \frac{Mr_t}{\rho C_p} \right) \quad (5.27)$$

where  $T_c$  is the individual's core temperature ( $^{\circ}\text{C}$ ), and  $r_t$  is the body tissue resistance. Within eq. 5.27,

$$T_c = 36.5 + 0.0043M \quad (5.28)$$

$$r_t = -0.1M_a + 65 \quad (5.29)$$

Where  $A$  and  $n$  are the empirically derived constants 0.193 and 0.618 respectively, and  $k$  is the thermal diffusivity of air ( $\sim 22 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$ ).  $Re$  is Reynolds number:

$$Re = \frac{0.17V}{v_i} \quad (5.30)$$

Where  $V$  is the free stream air velocity and  $v_i$  is the kinematic viscosity of air ( $\sim 1.5 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$ ).

$$r_c = r_{co}(1 - 0.05(0.196P)^{0.4}V^{0.5}) \quad (5.31)$$

Where  $P$  is the air permeability of clothing fabric ( $\text{L m}^2 \text{ s}^{-1}$ ) and  $r_{co}$  is the insulation value of clothing ( $\text{s m}^{-1}$ ). These values were obtained from ISO (2007). A value of  $228 \text{ s m}^{-1}$ ,  $138 \text{ s m}^{-1}$  and  $474 \text{ s m}^{-1}$  were used for temperate, hot and cold climates respectively.

### *Long-wave Radiation*

The metabolic heat lost through long wave radiation was determined with the following equations from Kenny et al. (2009):

$$L = A_{eff} \varepsilon \sigma (T_{sf} + 273.15)^4 \quad (5.32)$$

Where  $A_{eff}$  is the reduction factor based on the radiative area of a standing human with an applied value of 0.78 (Kenny et al. 2009),  $\varepsilon$  is the emissivity of human skin and clothing which has a value of 0.95 and  $\sigma$  is the Stefan-Boltzmann constant ( $5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$ ).  $T_{sf}$  is the surface temperature of an individual, which is determined as follows:

$$T_{sf} = \left( \frac{T_{sk} - T_a}{r_c + r_a} \right) r_a + T_a \quad (5.33)$$

### *Evaporative Heat Loss*

The metabolic heat lost through evaporation was determined with the following equations from Kenny et al. (2009):

$$E = E_s + E_i \quad (5.34)$$

Where  $E_s$  is the evaporative heat loss through perspiration ( $\text{W m}^{-2}$ ) and  $E_i$  is the evaporative heat loss through skin diffusion ( $\text{W m}^{-2}$ ).

$$E_s = 0.42(M - 58) \quad (5.35)$$

$$E_i = \rho L_v \left( \frac{q_s - q_a}{r_{cv} + r_{ac} + r_{tv}} \right) \quad (5.36)$$

Where  $\rho$  is the density of air ( $\sim 1.16 \text{ kg m}^{-3}$ ),  $L_v$  is the latent heat of vaporization ( $2,442 \text{ J g}^{-1}$ ) and  $r_{tv}$  is the deep skin tissue resistance to vapor transfer estimated to be  $7.7 \times 10^3 \text{ (s m}^{-1}\text{)}$ . The variable,  $q_s$ , is the specific humidity at skin temperature and  $q_a$  is the specific humidity at the ambient air temperature. The boundary air layer resistance to vapor transfer is represented by  $r_{av}$  and  $r_{cv}$  is the clothing vapor resistance. These variables were determined as follows:

$$q_s = 0.622 \left( \frac{e}{p_a - e} \right) \quad (5.37)$$

Where  $e$  is calculated using  $T_{sk}$ .

$$q_a = 0.622 \left( \frac{e}{p_a - e} \right) \quad (5.38)$$

Where  $e$  is calculated using  $T_a$ .

$$r_{av} = 0.92r_a \quad (5.39)$$

$$r_{cv} = r_c \quad (5.40)$$

### *Metabolic Heat Gained Through Radiation*

The metabolic heat gained through absorbed radiation was calculated using the following equation from Kenny et al. (2008):

$$R_{RT} = A_{eff} \left( \varepsilon \sigma (T_{sf} + 273.15)^4 + \rho C p \left( \frac{T_c - T_a}{r_a} \right) \right) \quad (5.41)$$

The final result for  $E_{Therm}$  was converted into kcal spent each day.

### The Thermic Effect of Food, *TEF*

The thermic effect of food, or the metabolic cost incurred from digesting food, was estimated to be 10% the caloric intake (Kinabo and Durnin 1990). Daily caloric intakes were calculated from the daily food logs kept by each subject as described above; 10% of each subject's daily intake was taken to be that subject's metabolic cost of digesting food.

### *Statistical Analysis*

Plots were generated using Microsoft© Excel© for Mac 2010 and RStudio, ©RStudio, INC. 2009-2012. All statistical analyses including linear regressions, multiple regressions, Tukey's pairwise comparisons were performed using IBM© SPSS© Version 21, and results were considered significant at  $p < 0.05$ . Individual details on statistical analyses are provided in the results chapters where relevant.

## **Chapter 6: Testing the Allocation Model for predicting human total energy expenditure in natural environments**

### ***Introduction***

Extensive work has been done to produce models that accurately predict total human energy expenditure. These models have been used to develop energy and nutrition standards across populations and have even been applied to produce energy expenditure estimates for past populations (Borel 1984, Geissler et al. 1986, Warwick et al. 1988, Roberts et al. 1991, Haggarty et al. 1994, Spurr et al. 1996, Leonard et al. 1997, FAO/WHO/UNU 2001, Churchill 2006, Warwick 2006, Froehle and Churchill 2009). The most popular model in use, the Factorial Method, tends to underestimate human TEE by as much as 30% at high levels of energy expenditure (Leonard et al. 1997). The Factorial Method does not include estimates for the cost of thermoregulation nor the thermic effect of food. Though this is a well-established concern, little effort has gone into producing a new model that better captures TEE and its multiple, interacting components.

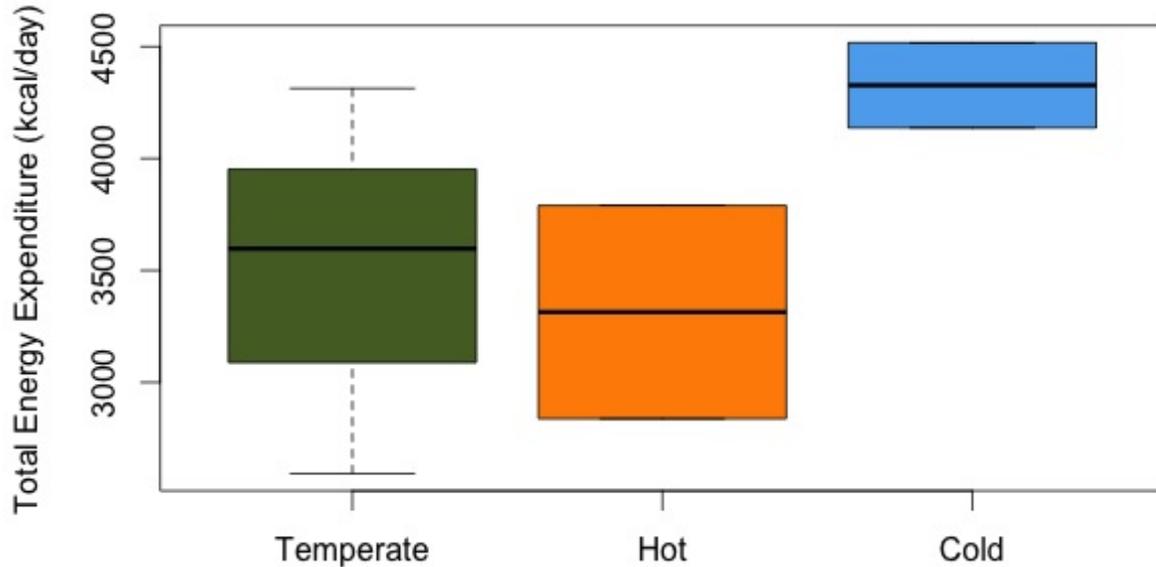
This chapter presents the Allocation Model for predicting TEE among highly active populations living in natural environments. Results from doubly labeled water and Flex-Heart Rate TEE measurements are presented first. Comparisons between the results of these two methods are then made. The results for the Allocation Model for predicting TEE are then presented detailing the metabolic costs for each of the components included in this model. This is followed by the TEE results from using the Factorial Method. Comparisons of TEE estimates from the doubly labeled water method, Flex-Heart Rate method, Factorial Method and the new Allocation Model are made and analyzed to determine the most effective model for predicting human TEE. Differences between climates, when present, are discussed in the following chapter.

## Results

### Total energy expenditure measurements from the doubly labeled water method

Total energy expenditure was measured by the doubly labeled water method (DLW) among a subset (N=11) of National Outdoor Leadership School semester students (N=59) partaking in vigorous physical activity while living in a variety of different climates. Mean daily TEE measurements in temperate climates (N=7) range from 2593-4313 kCal day<sup>-1</sup> and has a mean of 3512±654 kCal day<sup>-1</sup>. In hot climates (N=2), TEE ranges from 2838-4517 kCal day<sup>-1</sup> and has a mean of 3314±269 kCal day<sup>-1</sup>, and in cold climates (N=2), TEE ranges from 4137-3790 kCal day<sup>-1</sup> and has a mean 4327±673 kCal day<sup>-1</sup>. A full summary of TEE measurements by the DLW method can be found in **Fig. 6.1** and **Table 6.1**.

**Figure 6. 1.** Mean total energy expenditure (kCal day<sup>-1</sup>) for each subject in temperate, hot and cold climates as measured by the doubly labeled water method. Temperate climate TEEs range from 2593 – 4313 kCal day<sup>-1</sup>. Hot climates range from 2838 – 3790 kCal day<sup>-1</sup> and cold climates range from 4137 – 4517 kCal day<sup>-1</sup>.

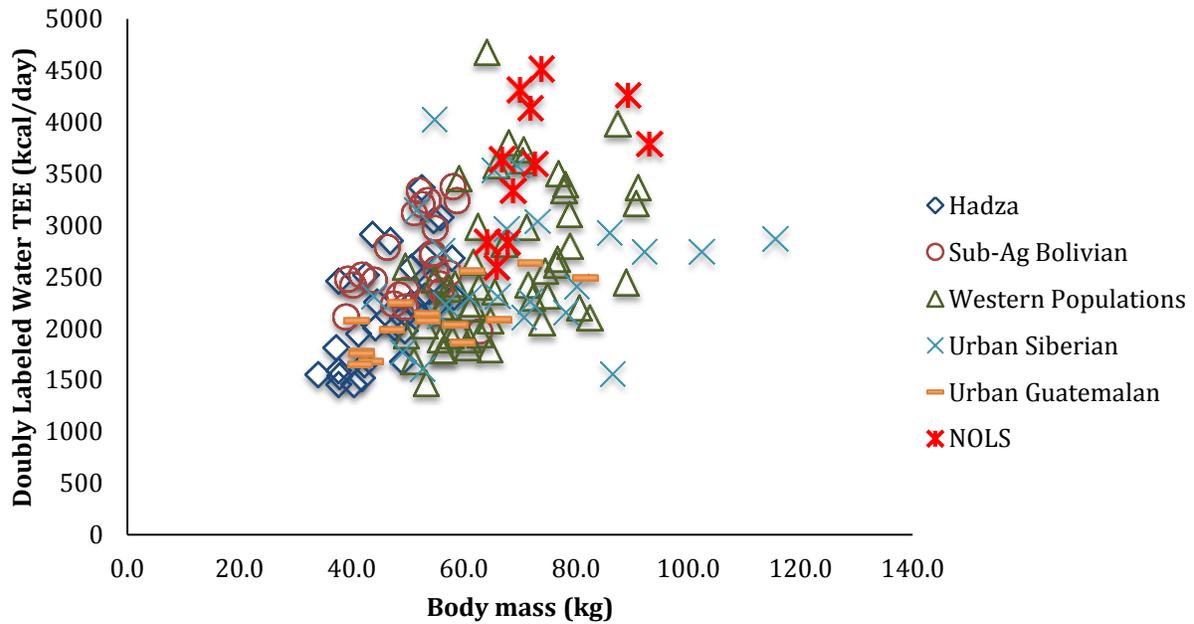


**Table 6. 1.** Summary of the total energy expenditure for each subject in temperate, hot and cold climates as measured by the doubly labeled water method, Flex-HR method, the Allocation Model and the Factorial Method. The latter three methods are described below.

<i>Climate</i>	<i>Subject</i>	<i>Sex</i>	<i>Mass (kg)</i>	<i>Fat %</i>	<i>DLW TEE (kCal day<sup>-1</sup>)</i>	<i>Flex-HR TEE (kCal day<sup>-1</sup>)</i>	<i>Allocation Model TEE (kCal day<sup>-1</sup>)</i>	<i>Factorial Method TEE (kCal day<sup>-1</sup>)</i>
Temperate	NS1-12	M	89.9	12.5	4264	5427	3280	3156
	NS2-1	F	64.5	23.7	2837	2814	3217	2591
	FS5-12	F	65.8	27.1	2593	3949	2595	2196
	FS8-10	M	72.7	11	3597	3138	3118	2839
	Pilot 1	F	68.7	23.5	3340	3729	3675	2286
	Pilot 3	M	70.0	7.9	3641	4031	3537	2644
	Pilot 4	M	69.7	5.0	4313	4889	4276	2839
Hot	NS1-12	M	95.0	14.4	3790	5668	3629	3093
	NS2-1	F	65.5	21.2	2838	3651	2154	2027
Cold	FS5-1	M	73.8	5.8	4517	9155	5090	3031
	FS8-10	M	71.9	11.9	4137	4678	5687	3261

The NOLS sample used in this study has a high TEE, and was compared to TEE data from DLW measurements from traditional Hadza hunter-gatherers (N=30), subsistence-agricultural Bolivians (N=24), Western populations (N=51), urban Siberians (N=27) and urban Guatemalans (N=14) (**Fig. 6.2**). A linear regressions controlling for age, sex, fat free mass and height followed by a Tukey’s pair-wise comparison (F=11.036, p<0.001) reveals that the NOLS sample has a significantly higher TEE than each of the aforementioned populations (p < 0.001 for all cases). **Table 6.2** summarizes the means for each of the populations as well as the difference observed from NOLS. The high TEE observed among the NOLS sample makes it an ideal population for testing the efficacy of TEE prediction by the Allocation Model at high levels of energy expenditure.

**Figure 6. 2.** The relationship between body mass and total energy expenditure as measured through the doubly labeled water method for the Hadza, sub-agrarian Bolivians, Western populations, urban Siberians, urban Guatemalans, and the NOLS population. The NOLS population has a significantly higher total energy expenditure than the other populations.



**Table 6. 2.** Summary of the mean daily energy expenditure for Hadza, sub-agricultural Bolivians, Western, urban Siberian and urban Guatemalan populations. The difference in TEE between these populations and NOLS is also presented. NOLS TEE was significantly higher in each case. Sources: <sup>1</sup>Pontzer et al. 2012, <sup>2</sup>Kashiwazaki et al. 2009, <sup>3</sup>Prentice et al. 1986, <sup>4</sup>Welle et al. 1992, <sup>5</sup>Davidson et al. 1997, <sup>6</sup>Schulz et al. 1989, <sup>7</sup>Seale et al. 1990, <sup>8</sup>Snodgrass et al. 2006, <sup>9</sup>Stein et al. 1988.

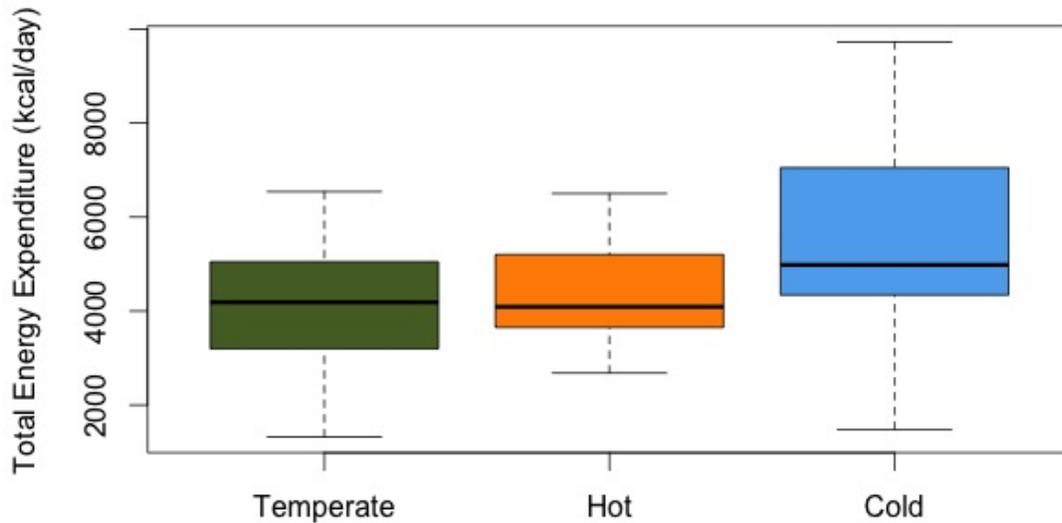
<i>Population</i>	<i>N</i>	<i>Body Mass</i>	<i>TEE (kCal day<sup>-1</sup>)</i>	<i>TEE Difference from NOLS (kCal day<sup>-1</sup>)</i>
Hadza <sup>1</sup>	30	46.6±6.9	2212±537	-1318
Sub-agrarian Bolivian <sup>2</sup>	24	51.0±6.2	2639±413	-891
Western <sup>3,4,5,6,7</sup>	51	66.9±10.9	2582±701	-948
Urban Siberian <sup>8</sup>	27	68.7±16.9	2701±725	-829
Urban Guatemalan <sup>9</sup>	14	54.1±12.0	2070±308	-1460

Total energy expenditure measurements from the Flex-Heart Rate method

Total energy expenditure was measured using the Flex-Heart Rate method simultaneously with the DLW measurements in temperate, hot and cold climates. Flex-Heart Rate measurements were taken from all subjects participating in this study (N=52). Flex-Heart Rate equations and flex points can be found in *Appendix 4*. TEE from the Flex-Heart Rate method was calculated in three main ways for each course and climate: on a daily basis for each individual, daily mean over the entire data collection period for each individual, and a group mean for the entire data collection period. For individual daily TEE values please refer to *Appendix 6*. From this point, analyses are performed on the mean daily TEE for the entire data collection period for each individual.

Mean daily TEE calculated for the entire data collection period as measured by the Flex-HR method is  $4197 \pm 1084$  kCal day<sup>-1</sup> for temperate climates (N=52),  $4301 \pm 595$  kCal day<sup>-1</sup> for hot climates (N=21) and  $5739 \pm 1923$  kCal day<sup>-1</sup> for cold climates (N=22) (**Fig. 6.3**). A summary of the daily TEEs for the entire collection period for each course can be found in Table **6.3**. For a full report of mean daily TEE values for the entire collection period for each course please refer to *Appendix 7*.

**Figure 6. 3.** Summary of daily TEE throughout the data collection period for temperate, hot and cold climates as measured by the Flex-HR method. Temperate climate TEEs range from 2150 – 6541 kCal day<sup>-1</sup>. Hot climates range from 2680 – 6501 kCal day<sup>-1</sup> and cold climates range from 2266 – 9730 kCal day<sup>-1</sup>.



**Table 6. 3.** A summary of mean daily total energy expenditure as measured by the Flex-Heart Rate method. The range and mean values are provided for the climates experienced by each course.

<i>Course</i>	<i>Climate</i>	<i>N</i>	<i>Mean Body Mass (kg)</i>	<i>Mean Temp. (°C)</i>	<i>TEE Range (kCal day<sup>-1</sup>)</i>	<i>Mean TEE +/- std dev (kCal day<sup>-1</sup>)</i>
WSS1	Temperate	13	74.0±10.3	15.9±2.8	3509-6141	4928±893
WSS1	Hot	11	79.5±9.0	23.6±2.2	3654-5668	4653±863
WSS2	Temperate	11	68.9±7.67	13.6±1.5	2814-6541	4430±1161
WSS2	Hot	11	72.1±8.4	23.7±1.5	2680-6501	4557±1908
FSR5	Temperate	12	73.2±9.6	6.5±1.1	2150-5050	3482±813
FSR5	Cold	10	75.2±8.8	-4.4±3.0	1483-9730	5379±2235
FSR8	Temperate	14	73.3±14.7	12.6±2.3	1322-5807	3911±1298
FSR8	Cold	13	72.0±11.4	-10.8±5.4	2266-9270	5745±2045
Pilot	Temperate	6	67.5±5.2	12.8±1.2	3603-4889	4105±457

TEE values vary greatly within each course. Typical NOLS courses consist of a flexible schedule such that the students alternate between days of rigorous activity, such as hiking for 5-7 miles at altitudes of 13,000 feet or greater, immediately followed by a more relaxed day during which students will take part in lighter activities, such as fishing or ecology and wildlife lessons

taught by course leaders. This pattern of a rigorous day followed by a light day was typical for all courses and climates.

Furthermore, there is a significant difference between courses taking place in similar climates, temperate climates in particular (**Table 6.4**). This can be attributed to a number of different factors. Each course is tailored to the skill level of the students participating. If a course is particularly struggling with the high level of activity and adjustment to living in the wilderness, course instructors will slow down the course, requiring less physical activity each day. The activity level of a course is also determined by the overall health of each of the course participants. If a number of students are injured (blisters, Achilles' tendonitis and twisted ankles are common injuries) then course instructors adjust the course goals and slow down their movement through the backcountry. A special case in this study is the FSR5 course. This course had a particularly difficult time adjusting to living in the wilderness, and therefore, covered less ground. Furthermore, during the cold section, roughly half of this course contracted giardia, an intestinal parasite that causes violent diarrhea, stomach cramps and nausea. Until medicine was dropped into the course's location, FSR5 covered little to no ground. Also, during this time, it should be noted that the ill members of FSR5 consumed very little food due to their unpleasant symptoms. However, since there was no significant difference in TEE between the course that was ill and its sister course, there was no need to remove it from the study

**Table 6. 4.** P-values for differences, between the mean daily Flex-HR TEE for the data collection period for all courses. Unless otherwise indicated, temperate portions of all courses are compared. Significant differences are bold and highlighted in red (independent samples T-Test). The FSR courses had significantly lower TEEs than the WSS courses.

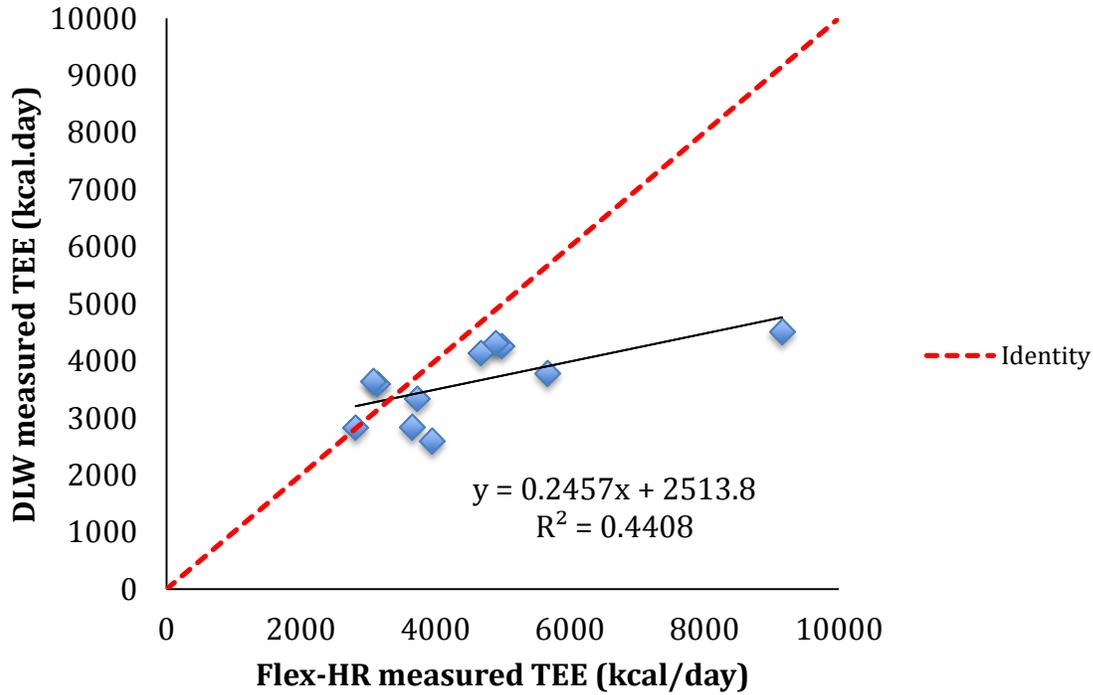
	<i>WSS1</i>	<i>WSS2</i>	<i>FSR5</i>	<i>FSR8</i>	<i>Pilot</i>
<i>WSS1</i>	-				
<i>WSS2</i>	0.29	-			
<i>FSR5</i>	<b>0.001</b>	<b>0.035</b>	-		
<i>FSR8</i>	<b>0.047</b>	0.338	0.342	-	
<i>Pilot</i>	0.09	0.58	0.147	0.65	-
	<i>WSS2 Hot</i>	<i>FSR8 Cold</i>			
<i>WSS1 Hot</i>	0.118	-			
<i>FSR5 Cold</i>	-	0.692			

*Doubly labeled water TEE vs. Flex-Heart Rate TEE*

Comparisons between the TEE results of the DLW method and the Flex-Heart Rate method need to be made to ensure that the Flex-HR results accurately measure TEE particularly on the individual level. The DLW method is considered the “gold standard” for measuring TEE, such that if Flex-HR measurements are significantly different from DLW results then a correction factor should to be applied to Flex-HR measurements. This will enable a more accurate representation of TEE and make for a better comparison with models predicting TEE.

**Figure 6.4** shows the relationship between DLW measured TEE and Flex-HR TEE. The percent difference between Flex-HR TEE and DLW TEE ranges from -15.6% – 102.7% with a mean of 24±34.1% (**Table 6.5**). There is no significant difference in this sample when the subject’s DLW-measured TEE is compared to that subject’s mean daily Flex-HR TEE for the data collection period (Bonferroni adjusted  $\alpha=0.008$ ,  $p=0.026$  paired t-test). A Bonferroni adjustment was used since three of the subjects were measured twice for the DLW analysis, once in the temperate portion of their course and once in the extreme temperature portion of their course.

**Figure 6. 4.** The relationship between DLW measured TEE and Flex-HR measured TEE. There is a greater discrepancy between DLW and Flex-HR TEEs at higher TEE measurements.



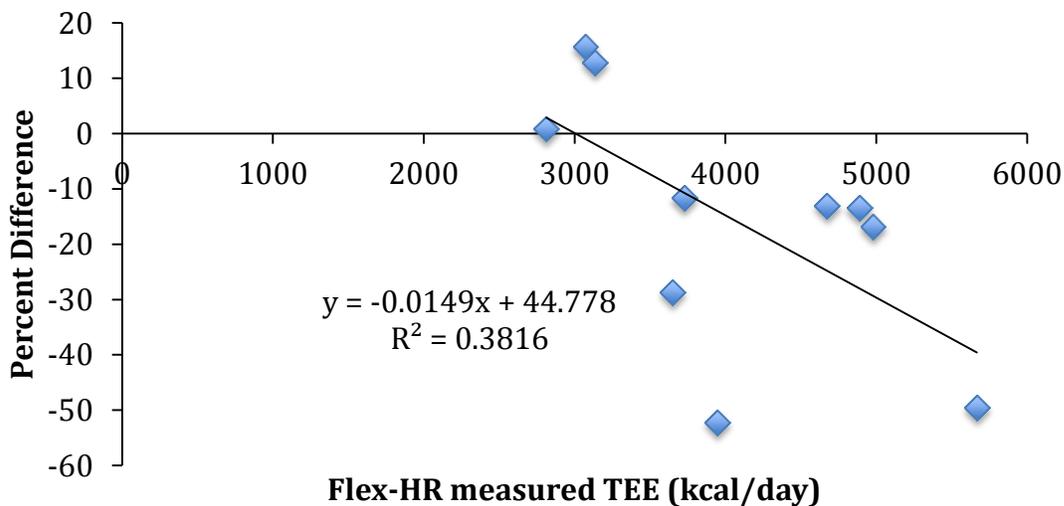
**Table 6. 5.** A summary of the DLW measurements compared to the Flex-HR TEE measurements.

<i>Subject</i>	<i>Climate</i>	<i>DLW TEE</i>	<i>Mean Individual Flex-HR TEE</i>	<i>Percent Difference</i>
NS1-12	Temperate	4264	4981	16.8
NS1-12	Hot	3790	5668	49.6
NS2-1	Temperate	2837	2813	-0.8
NS2-1	Hot	2838	3651	28.6
FS5-12	Temperate	2593	3948	52.3
FS5-1	Cold	4517	9155	102.7
FS8-10	Temperate	3597	3137	-12.8
FS8-10	Cold	4137	4677	13.1
Pilot 1	Temperate	3340	3729	11.6
Pilot 3	Temperate	3641	3073	-15.6
Pilot 4	Temperate	4313	4889	13.4
<b>Mean</b>				<b>23.5%</b>

Though there is no significant difference between the DLW and Flex-HR TEE measurements, there are greater discrepancies between Flex-HR and DLW measurements at

higher levels of TEE. Subject FS5-1 has an exceptionally large discrepancy between Flex-HR and DLW measurements. This measurement is greater than 9000 kcal day<sup>-1</sup>, which is substantially higher than the highest human doubly labeled water TEE measurement of roughly 7000 kcal day<sup>-1</sup> among Tour de France cyclists (Hammond and Diamond 1997). When subject FS5-1 is removed from the analysis (**Figure 6.5**) it is evident that Flex-HR discrepancies are greatest above 3000 kcal day<sup>-1</sup>, and after this point, Flex-HR overestimates DLW measured TEEs by 17%. This suggests that when using the Flex-HR TEE measurements for comparisons with modeled TEE within the NOLS population, that a 17% correction factor should be applied to all Flex-HR measurements greater than 3000 kcal day<sup>-1</sup>. This correction leads to a range of 2150-5429 kcal day<sup>-1</sup> and a mean of 3563±804 kcal day<sup>-1</sup> for the temperate climate, 2680-5396 kcal day<sup>-1</sup> and a mean of 3633±765 for the hot climate, and 2266-8076 kcal day<sup>-1</sup> and a mean of 4780±1647 kcal day<sup>-1</sup> for the cold climate.

**Figure 6. 5.** The Flex-HR TEE measurements compared to their percent difference from DLW measurements. There are greater discrepancies at higher TEEs.



*The Allocation Model for predicting human total energy expenditure*

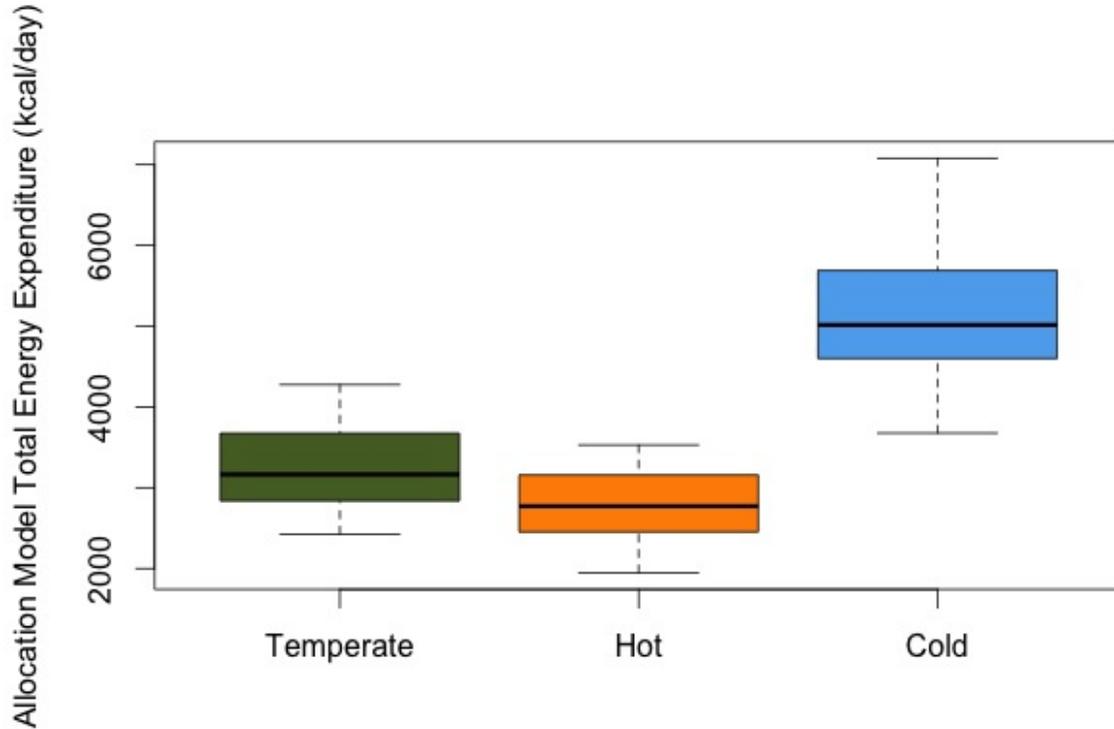
The Allocation Model is designed to better predict human total energy expenditure over a range of physical activity levels and in any given climate. This model consists of metabolic cost terms for basal metabolic rate (BMR), activity, thermoregulation and the thermic effect of food (TEF).

$$TEE = BMR + Activity + Thermoregulation + TEF$$

This section reports the metabolic cost as determined by the Allocation Model for TEE as well as the different components mentioned above for the different courses and climates. Any differences that exist between climates will be discussed in detail in the next chapter. The Allocation Model was used to calculate metabolic costs on a day-by-day basis as well as a daily mean for the entire data collection period; please refer to *Appendices 6 and 7* for the full set of values for each individual in each course and climate.

The Allocation Model produced daily TEEs with a mean of  $3242 \pm 517$  kcal day<sup>-1</sup> for the temperate climate (N=52),  $2704 \pm 396$  kcal day<sup>-1</sup> for the hot climate (N=21) and  $5200 \pm 802$  kcal day<sup>-1</sup> for the cold climate (N=22) (**Fig. 6.6**). A full summary of the Allocation Model calculated mean daily TEEs for each course is found in **Table 6.6**.

**Figure 6. 6.** Summary of daily TEEs for the entire data collection period as calculated from the Allocation Model for temperate, hot and cold climates. TEEs range from 2439-4276 kCal day<sup>-1</sup> for the temperate climate, 1947-3629 kCal day<sup>-1</sup> for the hot climate and 3965-7080 kcal day<sup>-1</sup> for the cold climate.



**Table 6. 6.** A summary of the mean daily TEE values over the entire data collection period as calculated by the Allocation Model. The range and mean values are provided for the climates experienced by each course.

<i>Course</i>	<i>Climate</i>	<i>TEE Range (kCal day<sup>-1</sup>)</i>	<i>Mean TEE (kCal day<sup>-1</sup>)</i>
WSS1	Temperate	2483-3530	3031±302
WSS1	Hot	2397-3629	2928±339
WSS2	Temperate	3208-4219	3789±266
WSS2	Hot	1947-2965	2480±314
FSR5	Temperate	2439-3497	2817±272
FSR5	Cold	3965-5407	4595±449
FSR8	Temperate	2469-3951	3063±431
FSR8	Cold	4405-7080	5678±754
Pilot	Temperate	3537-4276	3908±283

The following figures (**Fig. 6.7 A-C**) show the range of the daily breakdown of energy expenditure between BMR, activity, thermoregulation and TEF for the different climates during the entire data collection period. **Table 6.7** summarizes the percentage each cost comprises of the

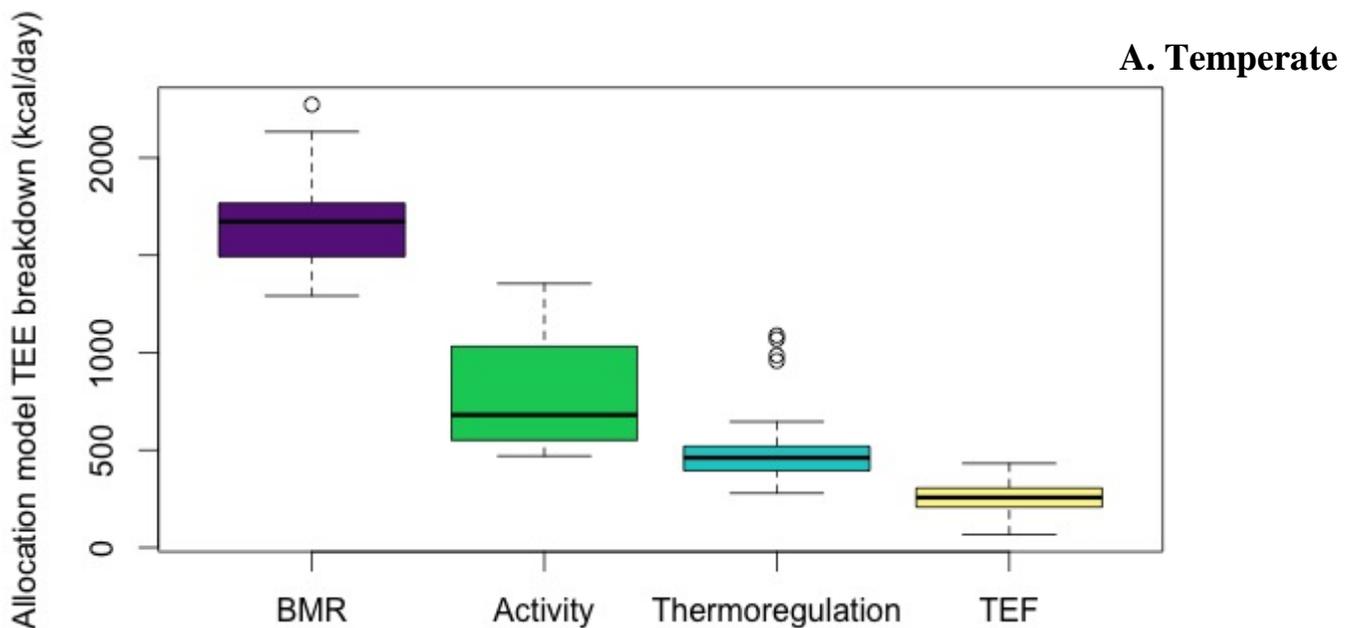
TEE budget for the three different climates and **Table 6.8** summarizes the minimum, maximum and mean metabolic cost of each component. Please refer to *Appendix 8* for the full set of

Allocation Model cost breakdown values for each individual in each course and climate.

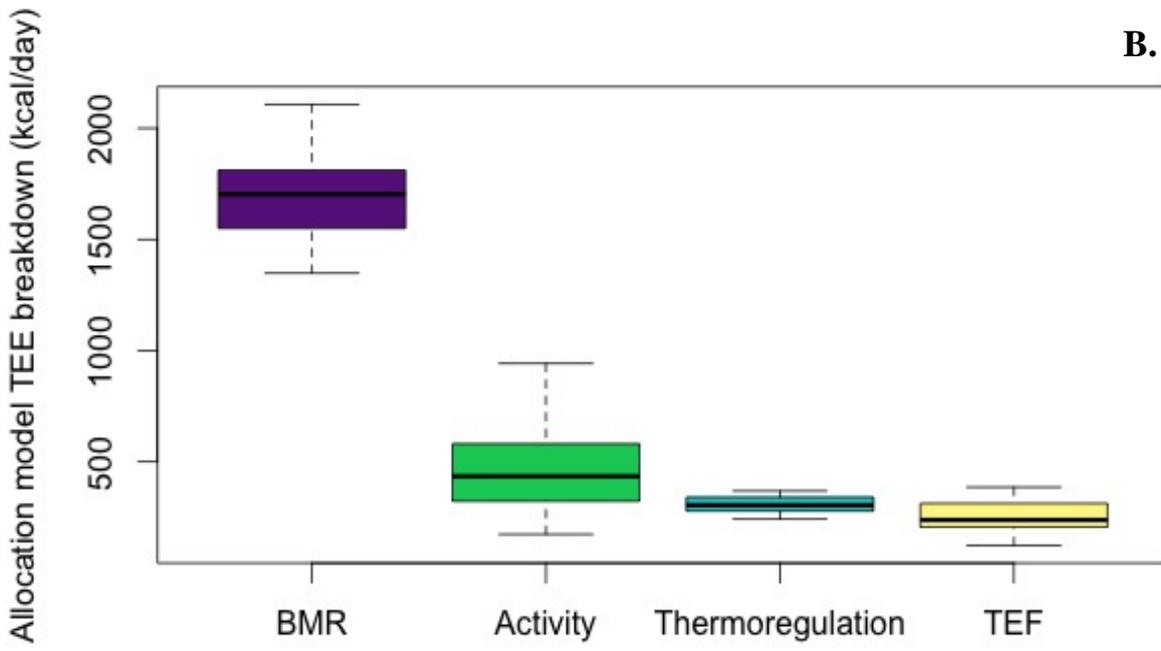
**Table 6. 7.** Summary of the Allocation Model metabolic cost breakdown for each TEE component: BMR, activity, thermoregulation and TEF for temperate, hot and cold climates. The percentage of TEE each component makes up and its corresponding mean cost (kcal day<sup>-1</sup>) are reported.

<i>Climate</i>	<i>BMR</i>	<i>Activity</i>	<i>Thermoregulation</i>	<i>TEF</i>
<i>Temperate</i>	52.1% (1662)	24.4% (780)	15.5% (494)	8.0% (254)
<i>Hot</i>	62.3% (1690)	17.2% (465)	11.3% (306)	9.2% (250)
<i>Cold</i>	31.7% (1680)	43.7% (2316)	19.2% (1018)	5.3% (282)

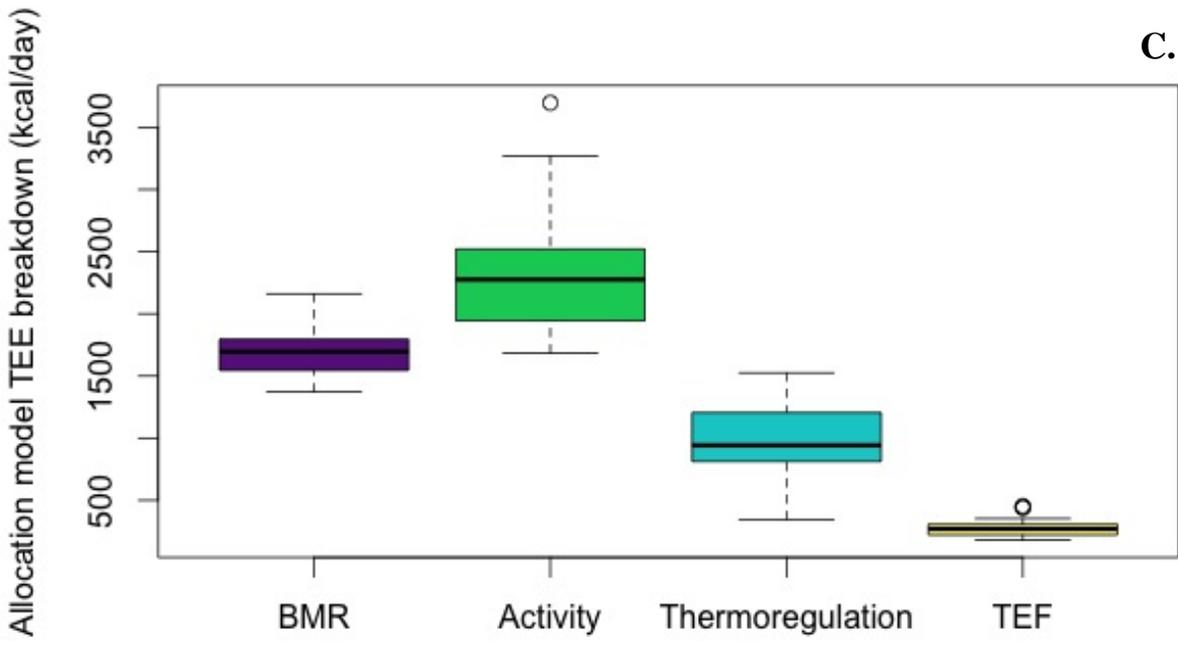
**Figure 6. 7.** A summary of the breakdown of TEE for **A)** Temperate, **B)** Hot and **C)** Cold climates as determined by the Allocation Model. For temperate and hot climates, BMR accounts for the majority of the TEE budget followed by activity, thermoregulation and then TEF. For the cold climate, activity accounts for the greatest proportion of the TEE budget followed by BMR, then thermoregulation and lastly by TEF.



**B. Hot**



**C. Cold**



**Table 6. 8.** Summary of the Allocation Model metabolic cost breakdown for each TEE component: BMR, activity, thermoregulation and TEF for each course. The minimum, maximum and mean cost ( $\text{kCal day}^{-1}$ ) for each component is presented.

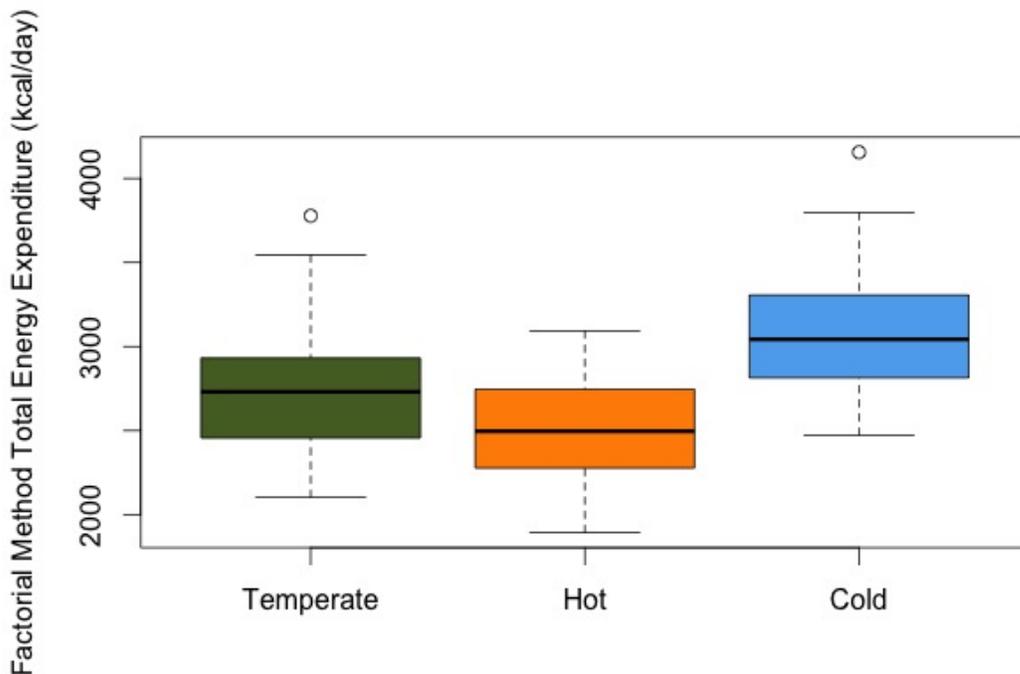
<i>Climate</i>		<i>BMR</i> ( $\text{kCal day}^{-1}$ )	<i>Activity</i> ( $\text{kCal day}^{-1}$ )	<i>Thermoregulation</i> ( $\text{kCal day}^{-1}$ )	<i>TEF</i> ( $\text{kCal day}^{-1}$ )
<i>WSS1</i>					
<i>Temperate</i>	<i>Minimum</i>	1292	534	402	183
	<i>Maximum</i>	2115	733	563	314
	<i>Mean</i>	1731	609	480	252
<i>WSS1 Hot</i>					
	<i>Minimum</i>	1427	394	272	131
	<i>Maximum</i>	2108	942	353	386
	<i>Mean</i>	1768	569	318	282
<i>WSS2</i>					
<i>Temperate</i>	<i>Minimum</i>	1339	958	331	147
	<i>Maximum</i>	1887	1355	640	338
	<i>Mean</i>	1633	1122	461	262
<i>WSS2 Hot</i>					
	<i>Minimum</i>	1348	174	242	124
	<i>Maximum</i>	1844	674	369	346
	<i>Mean</i>	1612	361	293	218
<i>FSR5</i>					
<i>Temperate</i>	<i>Minimum</i>	1386	470	310	67
	<i>Maximum</i>	2134	666	562	353
	<i>Mean</i>	1665	527	423	240
<i>FSR5 Cold</i>					
	<i>Minimum</i>	1408	1686	346	181
	<i>Maximum</i>	2030	2407	1448	444
	<i>Mean</i>	1700	1953	920	290
<i>FSR8</i>					
<i>Temperate</i>	<i>Minimum</i>	1345	625	279	86
	<i>Maximum</i>	2273	1020	525	432
	<i>Mean</i>	1687	747	425	236
<i>FSR8 Cold</i>					
	<i>Minimum</i>	1372	2196	562	195
	<i>Maximum</i>	2161	3697	1525	453
	<i>Mean</i>	1660	2678	1117	274
<i>Pilot</i>					
	<i>Minimum</i>	1334	903	646	272
	<i>Maximum</i>	1695	1258	1089	389
	<i>Mean</i>	1500	1143	950	323

The Factorial Method for predicting human total energy expenditure

The Factorial Method uses multiples of BMR to calculate TEE. Each activity is assigned a multiple of BMR, activity duration is recorded, and costs accrued throughout the day are summed to estimate TEE. The Factorial Method does not include metabolic cost terms for thermoregulation nor the cost due to thermic effect of food. The Factorial Method was used to calculate metabolic costs on a day-by-day basis as well as a daily mean for the entire data collection period; please refer to *Appendices 6 and 7* for the full set of values for each course and climate.

The Factorial Method produced daily TEE mean of  $2741 \pm 371$  kCal day<sup>-1</sup> for the temperate climate (N=52),  $2490 \pm 308$  kCal day<sup>-1</sup> for the hot climate (N=21) and  $3093 \pm 394$  kCal day<sup>-1</sup> for the cold climate (N=22) (**Fig. 6.8**). A full summary of the Allocation Model calculated mean daily TEEs for each course is found in **Table 6.9**.

**Figure 6. 8.** Summary of mean daily TEEs for the entire data collection period as calculated from the Factorial Method for temperate, hot and cold climates. Temperate climate TEEs range from 2103 – 3778 kCal day<sup>-1</sup>, hot climates range from 1894 – 3093 kCal day<sup>-1</sup> and cold climates range from 2473 – 4156 kCal day<sup>-1</sup>.



**Table 6. 9.** A summary of the mean TEE values over the entire data collection period as calculated by the Factorial Method. Mean and range values are provided for the climates experienced by each course.

<i>Course</i>	<i>Climate</i>	<i>TEE Range (kCal day<sup>-1</sup>)</i>	<i>Mean TEE (kCal day<sup>-1</sup>)</i>
WSS1	Temperate	2103-3383	2778 <sub>±</sub> 346
WSS1	Hot	2117-3093	2624 <sub>±</sub> 295
WSS2	Temperate	2399-3356	2923 <sub>±</sub> 266
WSS2	Hot	1894-2746	2342 <sub>±</sub> 249
FSR5	Temperate	2143-330	2576 <sub>±</sub> 302
FSR5	Cold	2473-3565	2985 <sub>±</sub> 299
FSR8	Temperate	2236-3778	2804 <sub>±</sub> 462
FSR8	Cold	2638-4156	3202 <sub>±</sub> 445
Pilot	Temperate	2277-2839	2527 <sub>±</sub> 217

Allocation Model vs. Factorial Method

This section details the effectiveness of the Allocation Model and Factorial Method to predict TEE using the DLW and corrected and uncorrected Flex-HR observed TEE values for comparison. The effectiveness of both methods is examined using the mean daily TEE for all courses and in each climate. **Table 6.10** summarizes the mean daily TEE for each climate using both predictive models and both the corrected and uncorrected Flex-HR values. **Table 6.11** summarizes the mean daily TEEs for each course using both predictive models and both the corrected and uncorrected Flex-HR values.

**Table 6. 10.** Summary of the mean daily TEE values using the uncorrected Flex-HR values, corrected Flex-HR values, Allocation Model and Factorial Method for temperate, hot and cold climates.

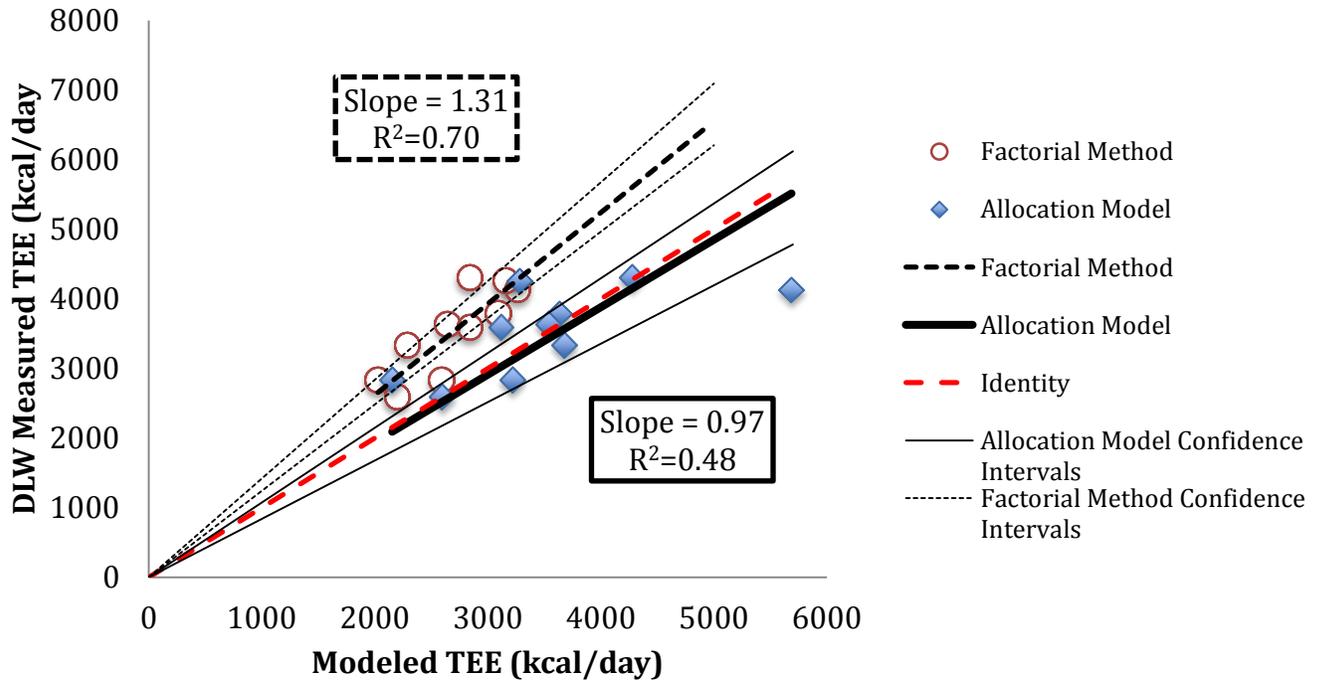
<i>Climate</i>	<i>Uncorrected Flex-HR (kCal day<sup>-1</sup>)</i>	<i>Corrected Flex-HR (kCal day<sup>-1</sup>)</i>	<i>Allocation Model (kCal day<sup>-1</sup>)</i>	<i>Factorial Method (kCal day<sup>-1</sup>)</i>
<i>Temperate</i>	4197 <sub>±</sub> 1084	3563 <sub>±</sub> 804	3242 <sub>±</sub> 517	2745 <sub>±</sub> 374
<i>Hot</i>	4301 <sub>±</sub> 595	3633 <sub>±</sub> 765	2704 <sub>±</sub> 396	2490 <sub>±</sub> 308
<i>Cold</i>	5739 <sub>±</sub> 1923	4780 <sub>±</sub> 1647	5200 <sub>±</sub> 802	3105 <sub>±</sub> 399

**Table 6. 11.** Summary of the mean daily TEE values using the uncorrected Flex-HR values, corrected Flex-HR values, Allocation Model and Factorial Method for each course and climate.

<i>Course</i>	<i>Climate</i>	<i>Uncorrected Flex-HR (kCal day<sup>-1</sup>)</i>	<i>Corrected Flex-HR (kCal day<sup>-1</sup>)</i>	<i>Allocation Model (kCal day<sup>-1</sup>)</i>	<i>Factorial Method (kCal day<sup>-1</sup>)</i>
WSS1	Temperate	4928±893	4090±778	3031±302	2778±346
WSS1	Hot	4653±863	3862±588	2928±339	2624±295
WSS2	Temperate	4430±1161	3720±956	3789±266	2923±266
WSS2	Hot	3949±1185	3404±910	2480±314	2342±249
FSR5	Temperate	3482±813	3068±562	2817±272	2576±302
FSR5	Cold	5733±1986	4758±1728	4678±449	2999±309
FSR8	Temperate	4127±1105	3536±812	3116±431	2826±474
FSR8	Cold	5745±2045	4800±1718	5678±754	3202±445
Pilot	Temperate	4105±457	3407±424	3908±283	2527±217

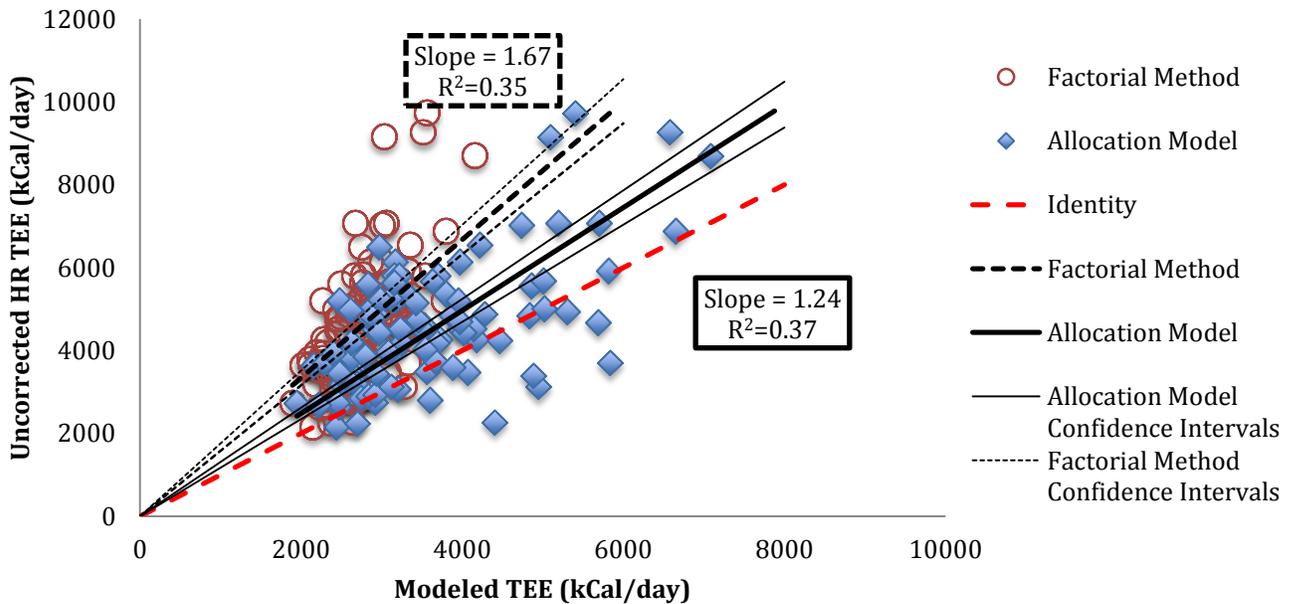
There are two goals when comparing a predictive model to the observed data. The first goal is to achieve a one-to-one relationship; to obtain a slope of 1.0 when performing linear regressions of the predictive values against the observed values. A second goal is for the model to account for a high degree of variance, or a high r-squared value. A linear regression drawn through the origin of the Allocation Model with the DLW measured TEEs produces a slope of 0.97,  $R^2=0.48$ . A linear regression drawn through the origin of the Factorial Method with the DLW TEE values for daily TEE produces a slope of 1.31,  $R^2=0.70$ . The slope from the Factorial Method is significantly different from a slope of one, but the slope from the Allocation Model is not (**Fig. 6.9**). The slopes of the two predictive methods are significantly different from one another: confidence interval of 0.839 – 1.074 at  $\alpha=0.05$  for the Allocation Model and confidence interval of 1.242 – 1.419 at  $\alpha=0.05$  for the Factorial Method (Allocation Model:  $F=328.98$ ,  $p<0.001$ ; Factorial Method:  $F=1126.688$ ,  $p<0.001$ ).

**Figure 6. 9.** Linear regression of the Allocation Model and the Factorial Method TEE data against the observed DLW TEE data. The slopes of both predictive models are significantly different from each other. The Factorial Method slope is significantly different than a slope of one, but the slope from the Allocation Model is not significantly different from identity.



A linear regression drawn through the origin for predicted TEE from the Allocation Model plotted against the uncorrected Flex-HR TEE values for mean daily TEE produces a slope of 1.24,  $R^2=0.37$ . A linear regression drawn through the origin of the Factorial Method with the uncorrected Flex-HR TEE values for daily TEE produces a slope of 1.67,  $R^2=0.35$ . Linear regressions were performed (Allocation Model:  $F=1270.365$ ,  $p<0.001$ ; Factorial Method:  $F=1409.046$ ,  $p<0.001$ ). These slopes are significantly different from one another and from a slope of one (**Fig. 6.10**): confidence interval of 1.173 – 1.311 at  $\alpha=0.05$  for the Allocation Model and confidence interval of 1.581 – 1.758 at  $\alpha=0.05$  for the Factorial Method.

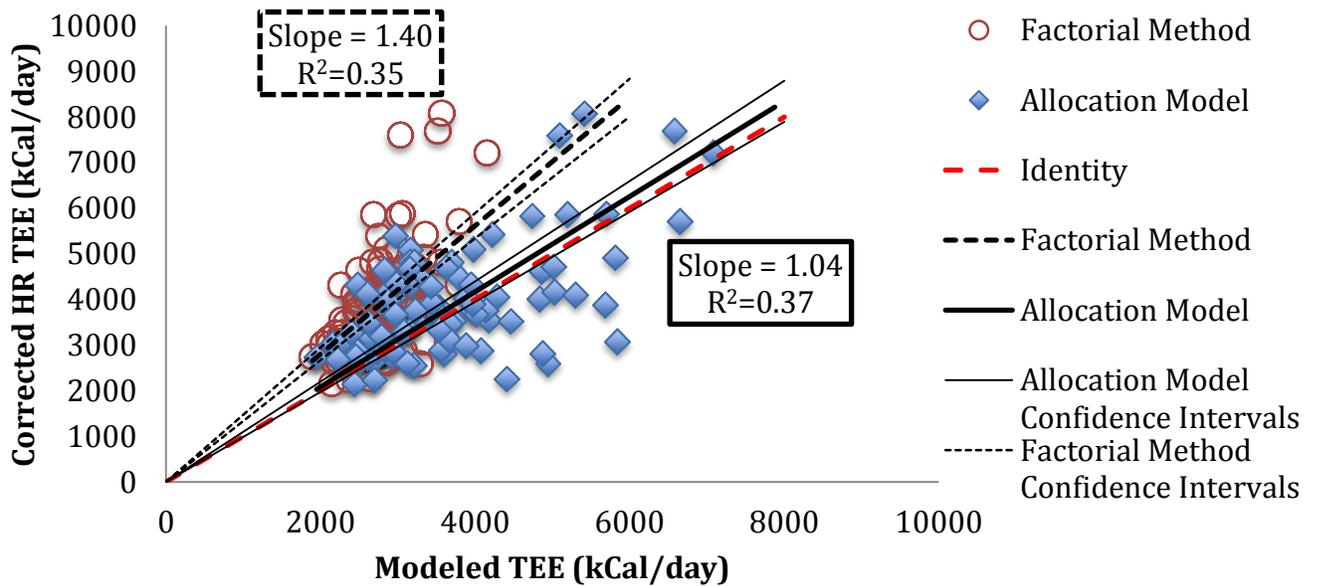
**Figure 6. 10.** Linear regression of the Allocation Model and the Factorial Method TEE data against the observed, uncorrected Flex-HR TEE data. The slopes of both predictive models are significantly different from each other as well as from the goal of identity.



However, as noted above, the Flex-HR TEE data deviated from the doubly labeled water TEE data. Doubly labeled water is the “gold standard” for TEE indirect measurement. Given this, it is a reasonable assumption that the Flex-HR method overestimates TEE in this population and a 17% correction factor at TEEs greater than 3000 kcal day<sup>-1</sup> is in order for proper comparison with modeled TEE estimates, as discussed above. A linear regression drawn through the origin of the plot of the Allocation Model with the corrected Flex-HR TEE values for mean daily TEE produces a slope of 1.04, R<sup>2</sup>=0.37. A linear regression drawn through the origin of the Factorial Method with the corrected Flex-HR TEE values for mean daily TEE produces a slope of 1.40, R<sup>2</sup>=0.35 (**Fig. 6.11**). These slopes are significantly different from one another and the Factorial Method is significantly different from a slope of one (F=1626.834, p<0.001):

confidence interval of 1.334 – 1.472 at  $\alpha=0.05$ . However, the slope of the Allocation Model closes in on identity and is not significantly different from a slope of one: confidence interval of 0.987 – 1.099 at  $\alpha=0.05$  ( $F=1364.5$ ,  $p<0.001$ ).

**Figure 6. 11.** Linear regression of the Allocation Model and the Factorial Method TEE data against the corrected Flex-HR TEE data. The slopes of both predictive models are significantly different from each other. The Factorial Method slope is significantly different than a slope of one, but the slope from the Allocation Model is not significantly different from identity.

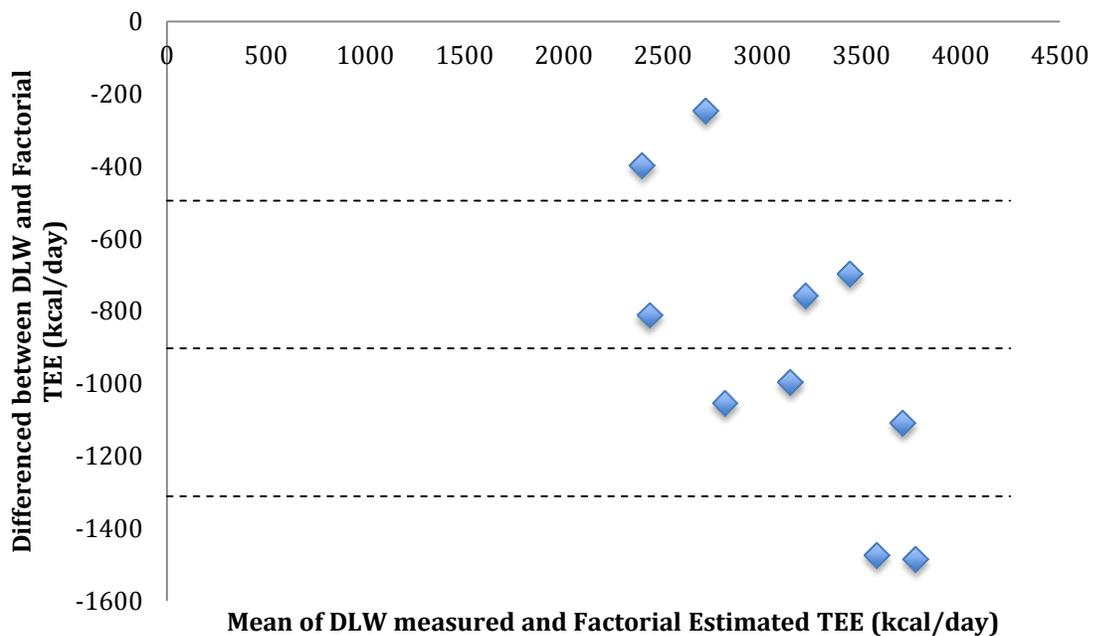


The Factorial Method is known for underestimating measured TEE, particularly at high activity levels. Leonard et al. (1997) found this underestimation to be as high as 30%. For the entire TEE sample in this study, the Allocation Model overestimates TEE by mean of 4.1% and the Factorial Method underestimates TEE by 25.3%. The percent differences are significantly different from one another (paired samples T-test,  $p<0.001$ ). At TEEs  $>3000$  kCal day<sup>-1</sup>, the Factorial Method underestimates TEE by 31.6% and the Allocation Model underestimates TEE by only 10.7%. The percent differences are significantly different (paired samples T-test,

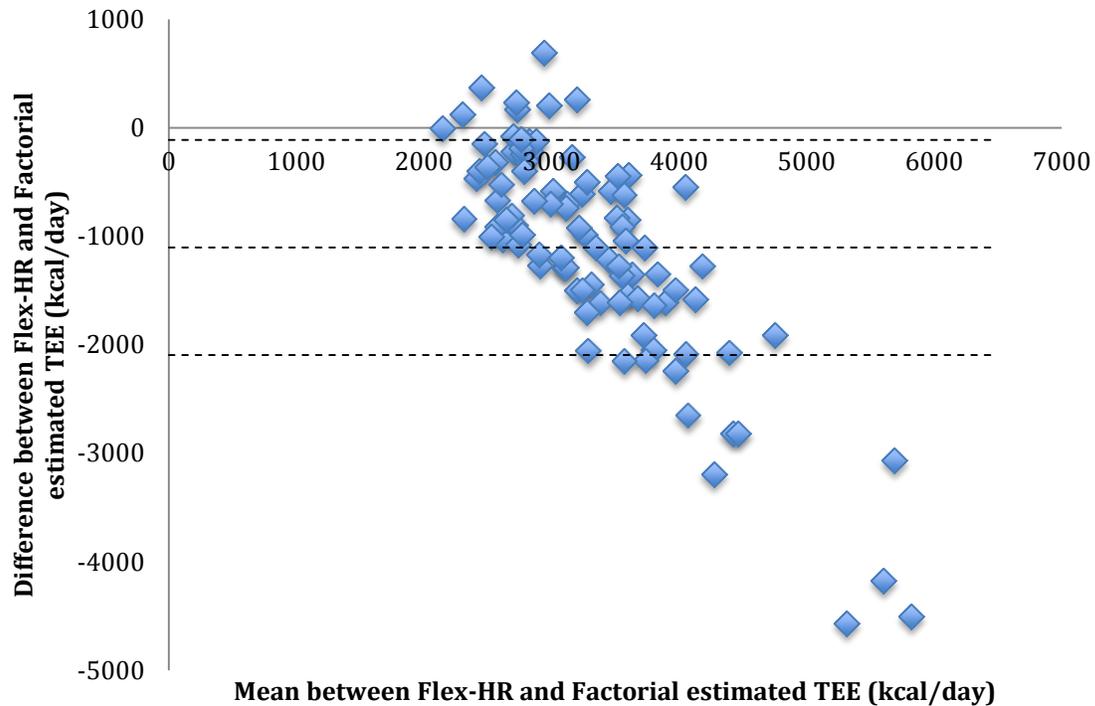
$p < 0.001$ ). It should be noted from **Fig. 6.11** that the Factorial Method is unable to make TEE predictions greater than 4000 kcal day<sup>-1</sup>.

The Bland-Altman method was applied to the data to determine if there was any bias in the Factorial Method and Allocation Model. **Figure 6.12** shows the Bland-Altman plot for the Factorial Method compared to the double labeled water measurements for TEE. This analysis revealed that the Factorial Method tends to underestimate TEE at greater levels of energy expenditure. **Figure 6.13** shows the Bland-Altman plot for the Factorial Method compared to the corrected Flex-HR method. Here too, the Factorial Method underestimates TEE at high levels of energy expenditure.

**Figure 6. 12.** Bland-Altman analysis of the Factorial Method compared to doubly labeled water measured TEE. The Factorial Method underestimates TEE at high levels of energy expenditure.

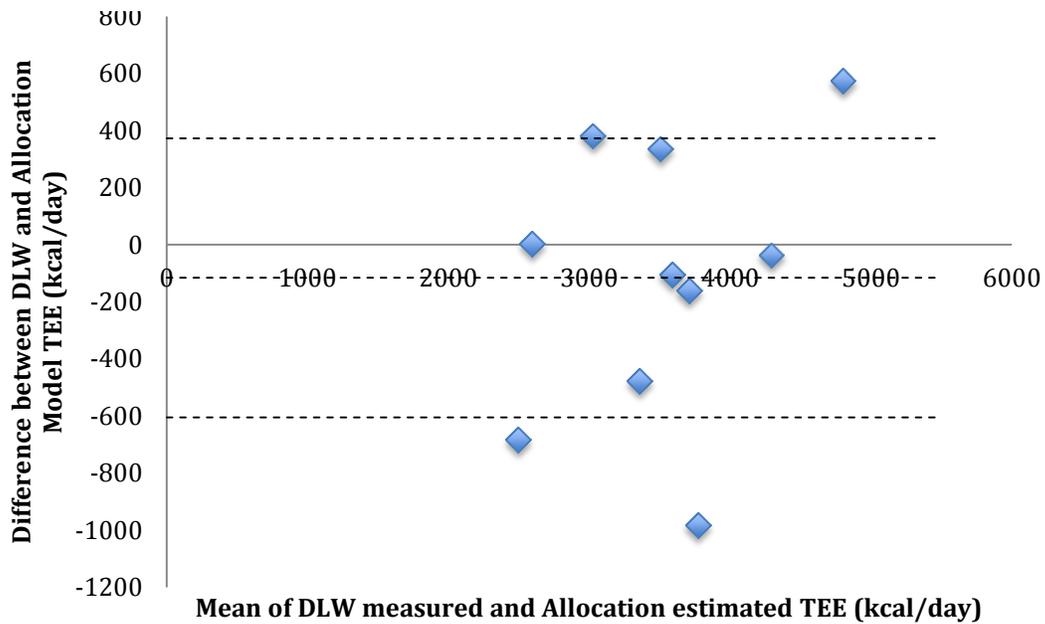


**Figure 6. 13.** Bland-Altman analysis of the Factorial Method compared to Flex-HR measured TEE. The Factorial Method underestimates TEE at high levels of energy expenditure.

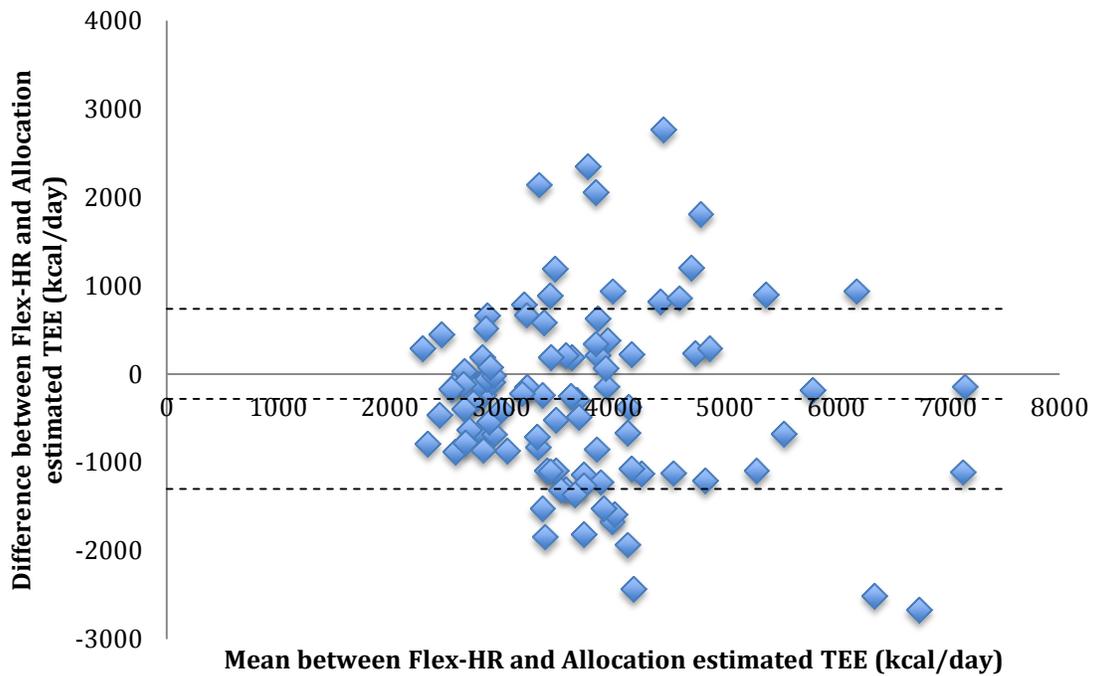


It can be seen from the Bland-Altman plot (**Fig. 6.14**) that the Allocation Model does not present a consistent bias as the Factorial Method does when compared to doubly labeled water measured TEE. The Allocation Model has the tendency to produce worse predictions at higher levels of TEE; however, the inaccuracy does not bias towards overestimate nor underestimation. The same pattern hold true for the Bland-Altman plot comparing the Allocation Model to the Flex-HR measured TEE (**Fig. 6.15**).

**Figure 6. 14.** Bland-Altman analysis of the Allocation Model compared to doubly labeled water measured TEE. The Allocation Model does not present the bias seen with the Factorial Method.

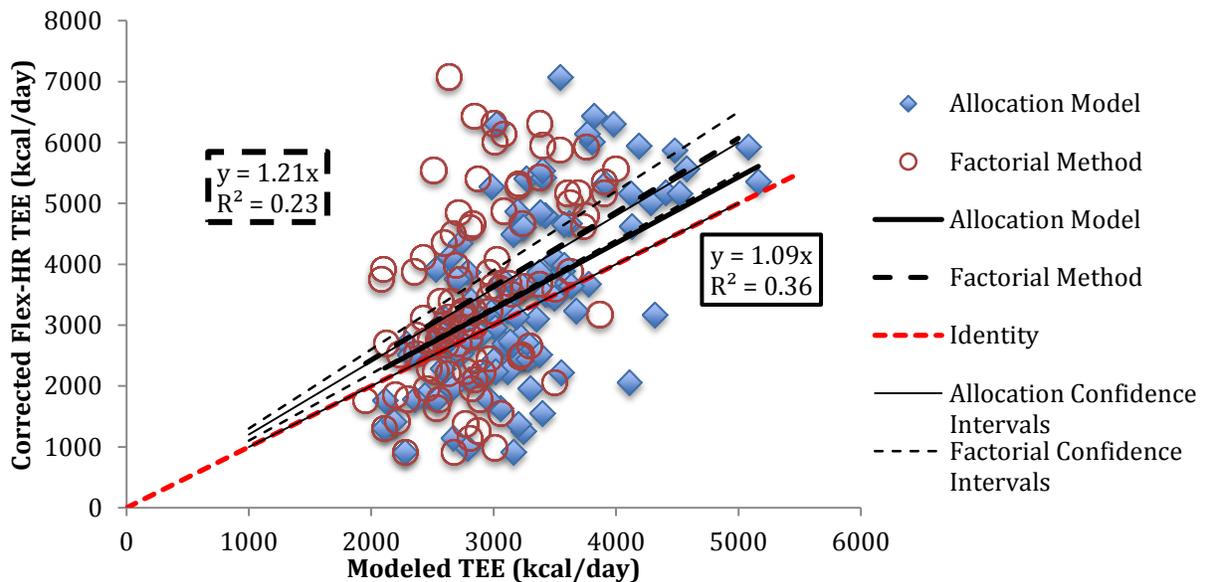


**Figure 6. 15.** Bland-Altman analysis of the Allocation Model compared to Flex-HR measured TEE. The Allocation Model does not present the bias seen with the Factorial Method.



There is a high level of variation from subject to subject making these comparisons difficult. However, to get past this inherent variation, the Allocation Model and Factorial Method predictions were compared to Flex-HR measurements for a sub-sample of 12 subjects who had high quality Flex-HR calibrations and in-field data collection. The predictions and measurements were compared for each day during the temperate climate data collection rather than a weekly average of TEE as was used for previous analyses (**Fig. 6.16**). Even on a day-to-day basis, the Allocation Model outperforms the Factorial both with a slope not significantly different from a slope of one, and explaining 36% of the observed variation seen in TEE. The confidence intervals for the Allocation Model is 1.0-1.2,  $\alpha=0.05$  ( $F=936.3$ ,  $p<0.001$ ). The Factorial Method is significantly different from a slope of one and explains 23% of the observed variation. The confidence interval for the Factorial Method is 1.1-1.3,  $\alpha=0.05$  ( $F=762.8$ ,  $p<0.001$ ).

**Figure 6. 16.** The Allocation Model outperforms the Factorial Method when predicting TEE on a day-to-day basis for a subset of NOLS subjects when compared to corrected Flex-HR TEE values.



Some differences do appear when linear regressions of TEE are compared for each climate individually (Allocation Model: Temperate-F=1216.121,  $p<0.001$ ; Hot-F=802.987,  $p<0.001$ ; Cold-F=273.758,  $p<0.001$ . Factorial Method: Temperate-F=1545.618,  $p<0.001$ ; Hot-F=668.018,  $p<0.001$ ; Cold-F=257.719,  $p<0.001$ ) Slopes for the Allocation Model do not significantly differ from identity in cold climates, but the Factorial Method slopes do differ significantly from identity. In temperate climates, the Allocation Model slope is significantly different from identity and from the Factorial Method slope. In the hot climate, the Allocation Model is significantly different than identity and not significantly different from the Factorial Method. In all three climates, the Factorial Method slopes significantly differ from identity. **Table 6.12** provides a summary of the confidence intervals, relationship between the models and relationship to identity for the Allocation Model. **Table 6.13** provides a summary of the confidence intervals, relationship between the models and relationship to identity for the Factorial Method. **Figure 6.17 A-C** illustrates the differences between the Allocation Model and Factorial Method for the different climates.

**Table 6. 12.** Summary of the slopes, confidence intervals and difference from the Factorial Method and identity for the Allocation Model. The Allocation Model is not significantly different from identity for cold climates, but is significantly different from identity in temperate and hot climates. The hot climate is the only case in which the allocation mode is not significantly different than the Factorial Method.

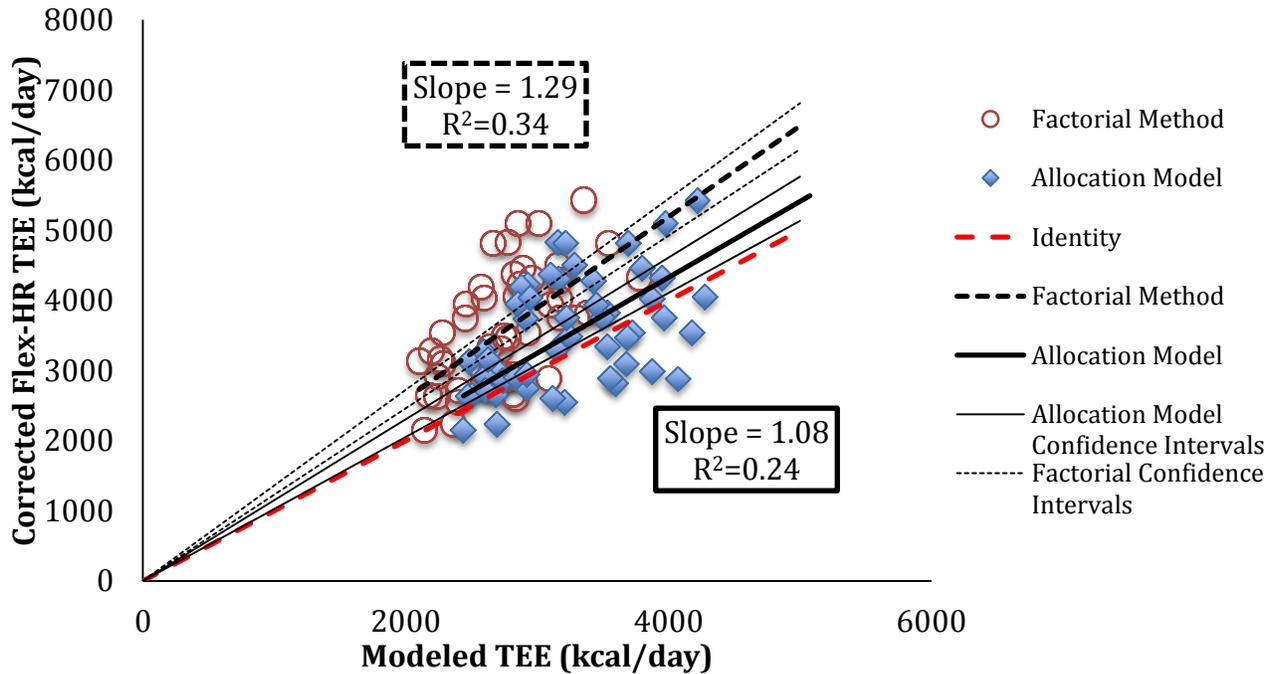
<i>Climate</i>	<i>Allocation Model slope</i>	<i>Allocation Model CI, <math>\alpha=0.05</math></i>	<i>Significant difference from Factorial Method</i>	<i>Significant difference from identity</i>
<i>Temperate</i>	1.08	1.027-1.153	Yes	Yes
<i>Hot</i>	1.34	1.243-1.440	No	Yes
<i>Cold</i>	0.92	0.809-1.040	Yes	No

**Table 6. 13.** Summary of the slopes, confidence intervals and difference from the Allocation Model and identity for the Factorial Method. The Factorial Method is significantly different from identity for all three climates. The hot climate is the only one in which the Factorial Method is not significantly different than the Allocation Model.

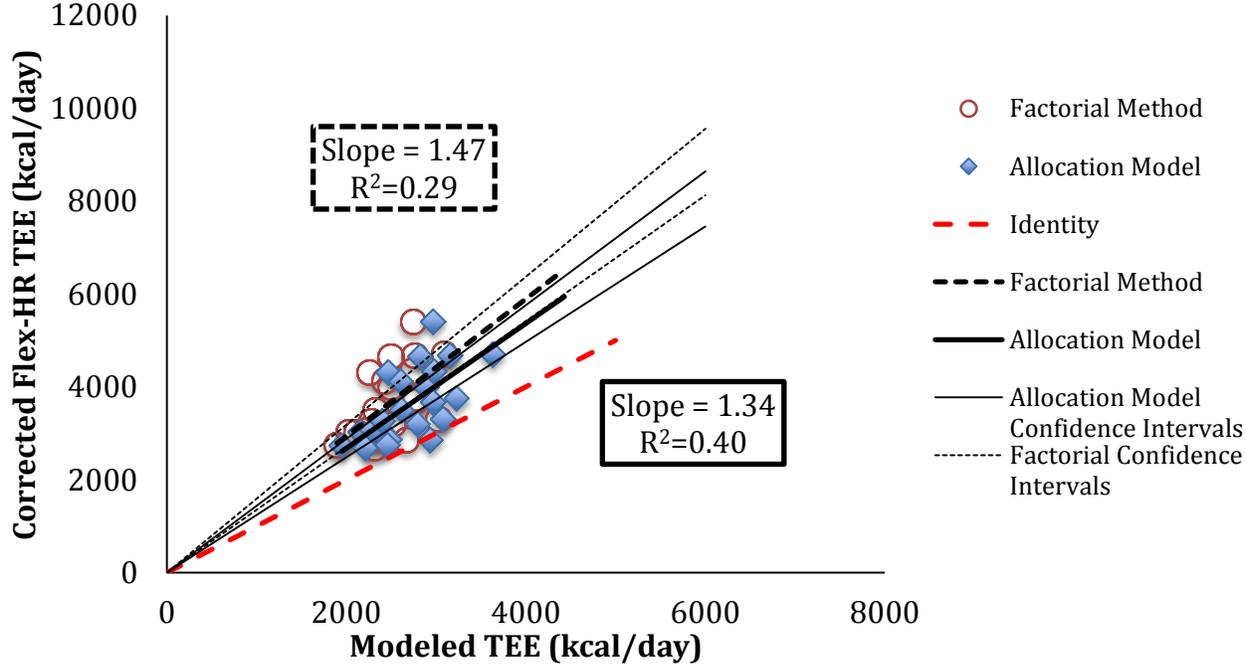
<i>Climate</i>	<i>Factorial Method slope</i>	<i>Factorial Method CI, <math>\alpha=0.05</math></i>	<i>Significant difference from Allocation Model</i>	<i>Significant difference from identity</i>
<i>Temperate</i>	1.29	1.231-1.363	Yes	Yes
<i>Hot</i>	1.47	1.355-1.593	No	Yes
<i>Cold</i>	1.55	1.350-1.751	Yes	Yes

**Figure 6. 17.** A summary of the difference in the mean daily TEE predictive ability of the Allocation Model and Factorial Method for A) Temperate, B) Hot and C) Cold climates. For the cold climate, the Allocation Model is not significantly different from identity, but is significantly different from the Factorial Method. For the hot climate, the Allocation Model and Factorial Method are not significantly different from one another, but are both significantly different from identity.

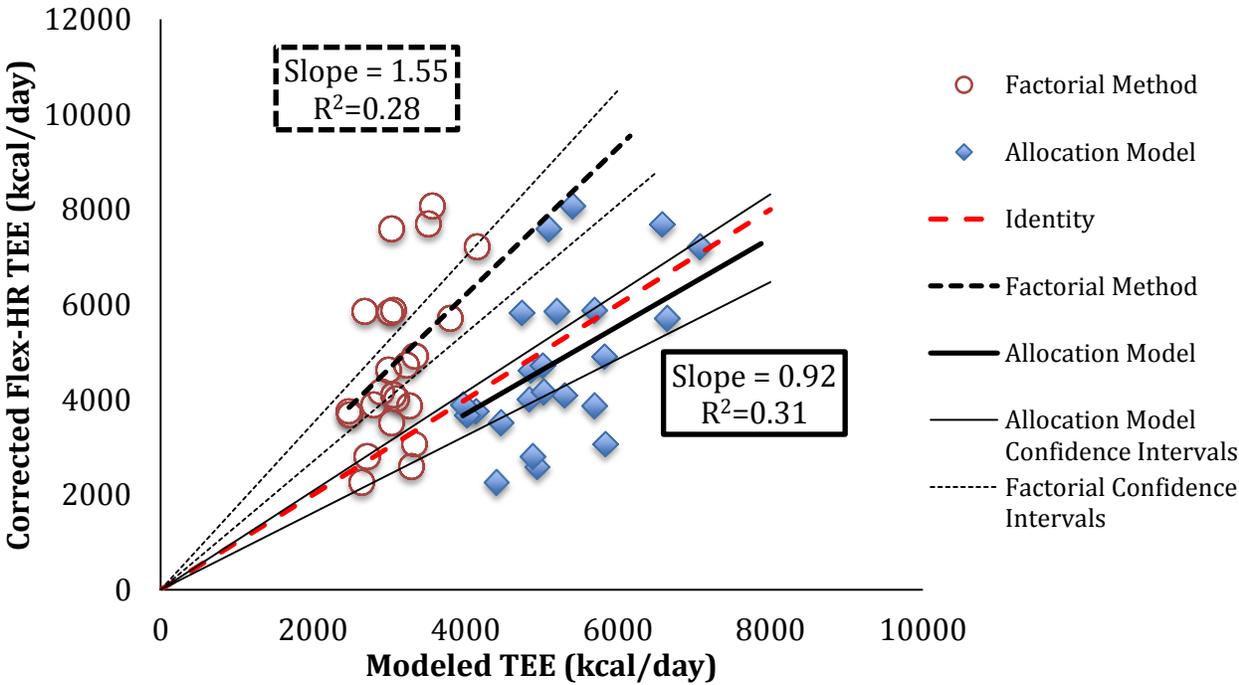
### A. Temperate



**B. Hot**

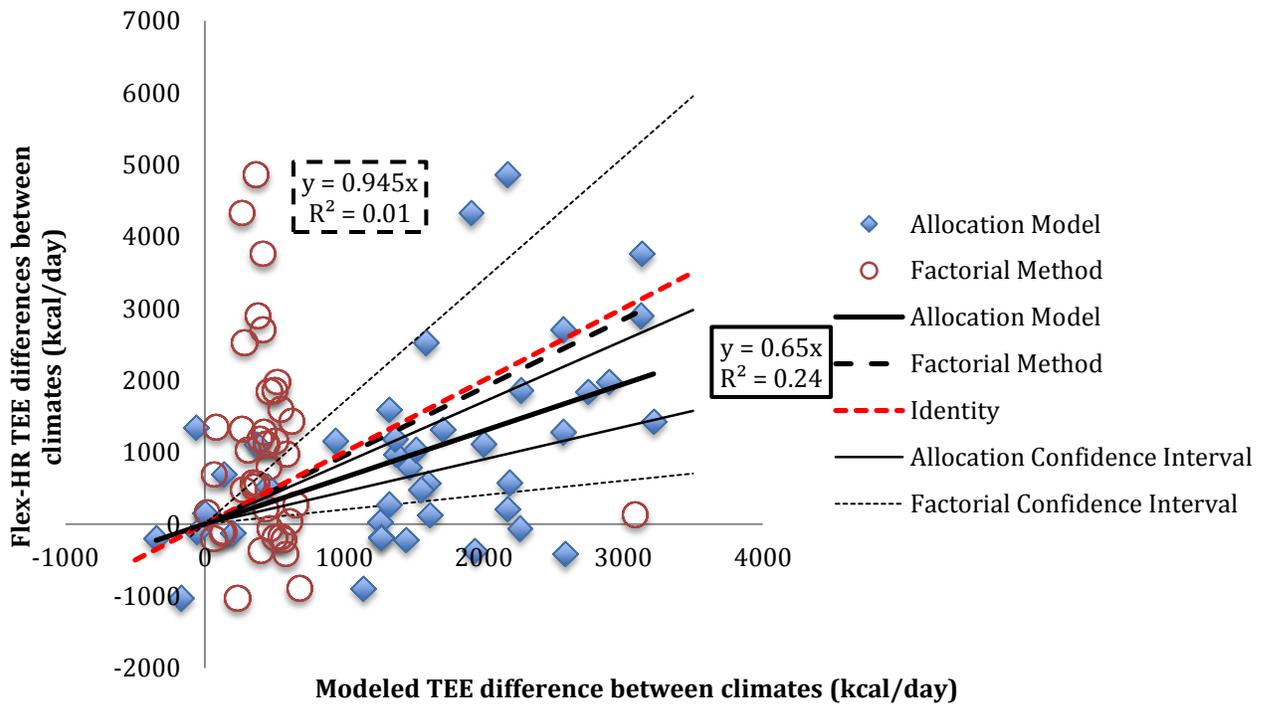


**C. Cold**



The change in energy expenditure in different climates predicted by the Allocation Model and the Factorial Method were plotted against the Flex-HR measured changes between the climates (**Fig. 6.18**). This was done for each subject such that each subject is their own control to account for inherent individual variation in metabolic rates. As with analysis, the goal is to achieve a slope of one. Both the Factorial Method and the Allocation Model do a poor job of predicting energy expenditure changes between the climates. The Factorial Method is only able to account for 1% of the variance; however, the Allocation Model accounts for 24% of the variance seen in the differences in energy expenditure between climates. The Factorial Method is not significantly different from identity; however, this is only true because of the large confidence interval of 0.2 – 1.7,  $\alpha=0.05$  ( $F=6.55$ ,  $p = 0.014$ ). The Allocation Model is significantly different from identity with a confidence interval of 0.45-0.85

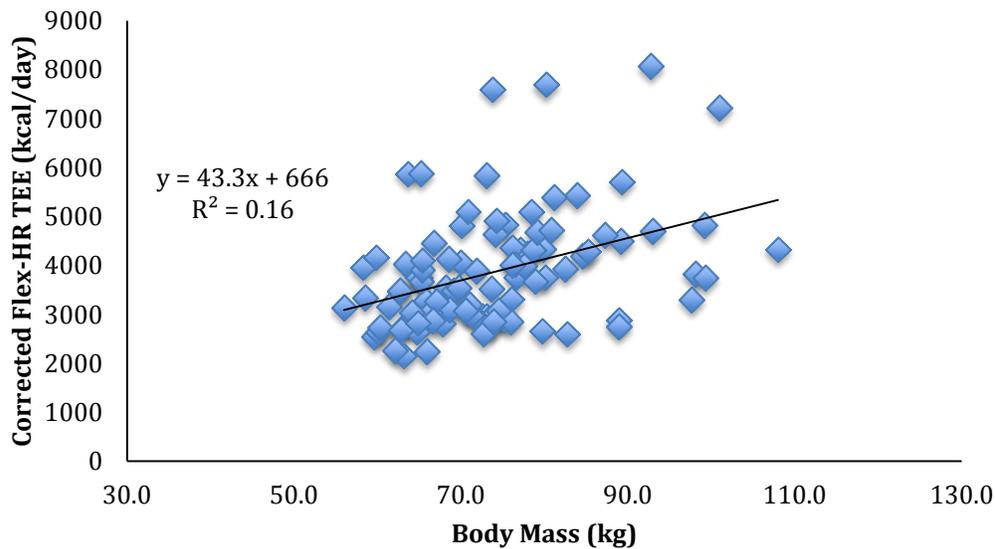
**Figure 6. 18.** The relationship between modeled and measured changes in total energy expenditure between climates.



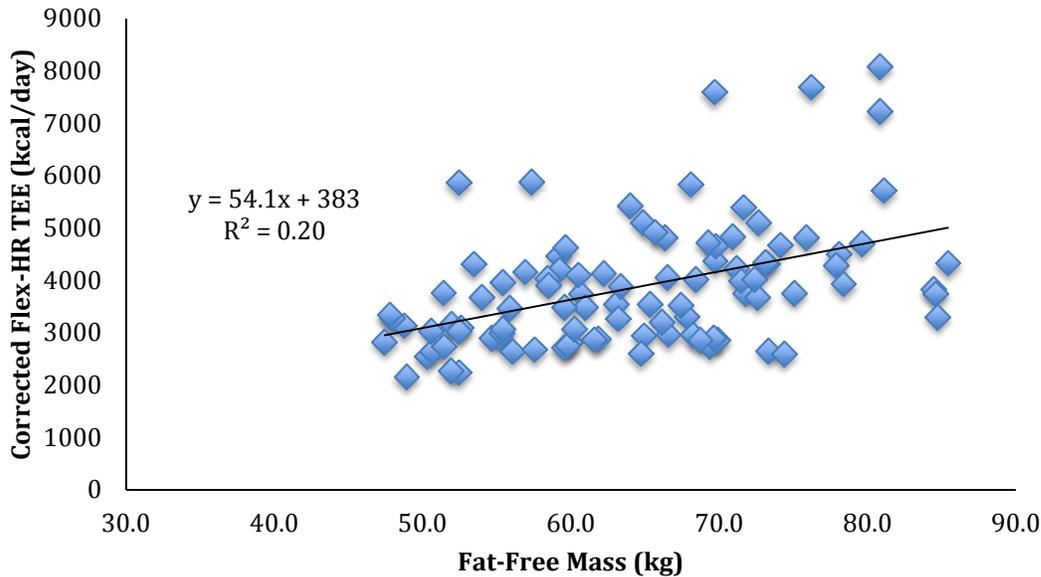
Allocation Model vs. anthropometric driven predictions

To determine if the Allocation Model accounts for more variation than simple anthropometric predictors, both body mass and fat-free mass were plotted for each subject against their TEE. **Figure 6.19** shows that body mass only accounts for 16% of the variation seen in TEE among the NOLS population compared to 35% and 37% by the Factorial Method and Allocation Model respectively. Fat-free mass accounts for 20% of the variation seen in TEE among the NOLS population (**Fig. 6.20**). This suggests that models such as the Factorial Method and the Allocation Model are able to account for more variation than simple anthropometric predictors.

**Figure 6. 19.** The relationship between body mass and TEE among the NOLS population across all courses and climates. Body mass explains 16% of the observed variation.



**Figure 6. 20.** The relationship between fat-free mass and TEE among the NOLS population across all courses and climates. Fat-free mass explains 20% of the observed variation



Subjects experienced changes in their body mass during courses. As a test to see if this change in body mass related to a change in TEE, body mass differences between climates were compared to TEE differences between climates (**Fig. 6.20**). The changes in body mass are a poor predictor of changes in TEE, explaining only 3% of the observed variation compared to 24% by the Allocation Model. This too suggests that simple anthropometric predictors are unable to account for most of the variation seen in TEE.

### ***Discussion***

The NOLS population used in this study has a higher level of total energy expenditure compared to that of Western populations and traditional, non-industrialized populations. This makes the NOLS population ideal for testing the new Allocation Model that aims to predict TEE at high activity levels better than the Factorial Method. Total energy expenditure was measured through the doubly labeled water method and the Flex-Heart Rate method. The Flex-HR method

produced TEEs that were 24% higher than the doubly labeled water results; however, this is not uncommon. Flex-HR discrepancies have been reported to range from -22.2% - 52.1% at the individual level (Livingstone et al. 1990, Leonard 2003). At the group level, Flex-HR measurements come within 2-3% of DLW measured TEE values, but more frequently within 10% of DLW measurements (Leonard 2003).

There are a number of possible reasons for the divergence between DLW and Flex-HR among the NOLS sample. The ActiTrainer devices used to collect HR data were used for extended periods of time without recharging, used for eight different 6-11 days long data collection bouts over seven months, exposed to the elements in the backcountry and exposed to possible interference from satellite phones and avalanche beacons. Since there is currently no documentation of ActiTrainer data degradation over repeated use and abuse or interference from other devices, it is difficult to confirm that any of the above reasons are possible causes for the large difference between the DLW and Flex-HR results.

However, this does bring to light a possible cause for concern when using heart rate monitors and the Flex-HR method for estimating TEE. The Flex-HR method produces TEE overestimates that become greater with higher levels of energy expenditure. The Flex-HR method has been in use since 1988 (Spurr et al. 1988), and has been put into wide spread use for measuring TEE among free-living humans (Leonard 2003). A number of validation studies have been conducted finding that the Flex-HR method accurately estimates TEE among adults within  $\pm 6\%$  of DLW measurements (Spurr et al. 1988, Ceesay et al. 1989, Livingstone et al. 1990, Livingstone et al. 1992, Lovelady et al. 1993, Leonard 2003). Flex-HR validation has been extended to children, the obese, the disabled, and the elderly. Even in these cases, Flex-HR comes within  $\pm 10\%$  of DLW measurements (Leonard 2003). However, little has been done to

validate the Flex-HR method at TEEs greater than 3000 kcal day<sup>-1</sup>. This study presented Flex-HR measurements consistently greater than 3000 kcal day<sup>-1</sup>. It even presented Flex-HR values greater than 9000 kcal day<sup>-1</sup>, which is more than 2000 kcal day<sup>-1</sup> greater than the highest DLW measured TEE among humans – Tour de France cyclists. This clear overestimation suggests that work needs to be done to better evaluate the accuracy of the Flex-HR method among highly active humans. Furthermore, the overestimation by the Flex-HR method would suggest the need to reassess already completed studies that have used the Flex-HR method to estimate TEE particularly among highly active people.

Given the overestimation of Flex HR TEE above 3000 kcal/day and the well-documented accuracy of the DLW method, Flex-HR results were corrected for comparison with predictive models on the individual level. These corrected Flex-HR TEEs were used to evaluate the predictive ability of the new Allocation Model as well as assess the Factorial Method. The Allocation Model includes metabolic cost terms for thermoregulation and thermic effect of food as well as basal metabolic rate and activity. The Allocation Model was developed to better predict TEE in any climate across a wide range of activity levels, and in particular improve upon TEE estimates at high activity levels where the Factorial Method falls short. Linear regressions revealed that the Allocation Model, unlike the Factorial Method, produces a slope that is not significantly different from identity. This suggests that the Allocation Model outperforms the Factorial Method when predicting mean daily TEE. The Allocation Model performs particularly well at high TEEs. The Factorial Method and even the Flex-HR method both falter at high TEEs, the former underestimates and the latter overestimates. This suggests that these two methods are unable to account for possible internal tradeoffs when energy expenditures are high. The Allocation Model appears to avoid this issue. However, both models have low r-squared values.

Given the high level of individual variation in metabolic rate this is not wholly unexpected. The Allocation Model does better than the Factorial Method when explaining variance. This is likely due to the ability of the Allocation Model to produce TEE estimates greater than 4000 kcal day<sup>-1</sup>, a common level of energy expenditure among the highly active NOLS subjects. Furthermore, the Allocation Model is able to explain more variation than TEE predictions based on simple anthropometric measurements such as body mass and fat-free mass.

This analysis demonstrates that the new Allocation Model for predicting human total energy expenditure is more accurate than the Factorial Method, and possibly even the Flex-HR method, across a range of activity levels and in different climates. Furthermore, the Allocation Model succeeds where the Factorial Method has failed – at high levels of energy expenditure. The results presented here suggest that particularly at high levels of activity, the Allocation Model should be used in place of the Factorial Method for estimating human TEE, and that more work is necessary to validate the Flex-Heart Rate method.

## **Chapter 7: Comparison of human total energy expenditure and energy allocation in different climates**

### ***Introduction***

A number of studies have been done both in laboratory and natural settings exploring metabolic cost differences associated with a range of temperatures. There is a well-established metabolic cost increase with decreasing temperatures (Sloan and Keatinge 1973, Kollias et al. 1974, McArdle et al. 1984a, McArdle et al., 1984b) and cold climates (Krogh and Krogh 1915, Heinbecker 1928, Heinbecker 1931, Strømme et al. 1963, Hammel 1964, Folk 1966, Hanna 1968, Little and Hochner 1973, Leonard et al., 2002, Leonard et al. 2005, Snodgrass et al. 2005, 2006, 2008, Moran 2008). Laboratory studies have also demonstrated that the increased loss of body heat associated with cold temperatures diminishes when subjects exercise (Toner et al. 1986, Tikuisis et al. 2000). The metabolic response to hot climates is not as clearly understood as that of cold climates, and it seems to depend on the relative humidity of the environment. Metabolic rate has been documented to increase in hot, humid environments, but decrease in hot, dry environments (Osiba 1957, Yurugi et al. 1972, Ogata and Sasaki 1975, Shapiro et al., 1980; Hori, 1995; Chinevere et al., 2008).

Though these studies have illuminated many of the details of the different metabolic costs associated with various temperatures and climates, few have been able to study the same population in more than one climatic condition and analyze the accompanying changes in metabolic cost. Furthermore, few have analyzed the importance of activity in reducing the cost of thermoregulation in natural cold conditions among a highly active population. This chapter presents the measured TEE values and estimated metabolic costs of its components from the Allocation Model. These results are then used to analyze the differences in TEE and energy

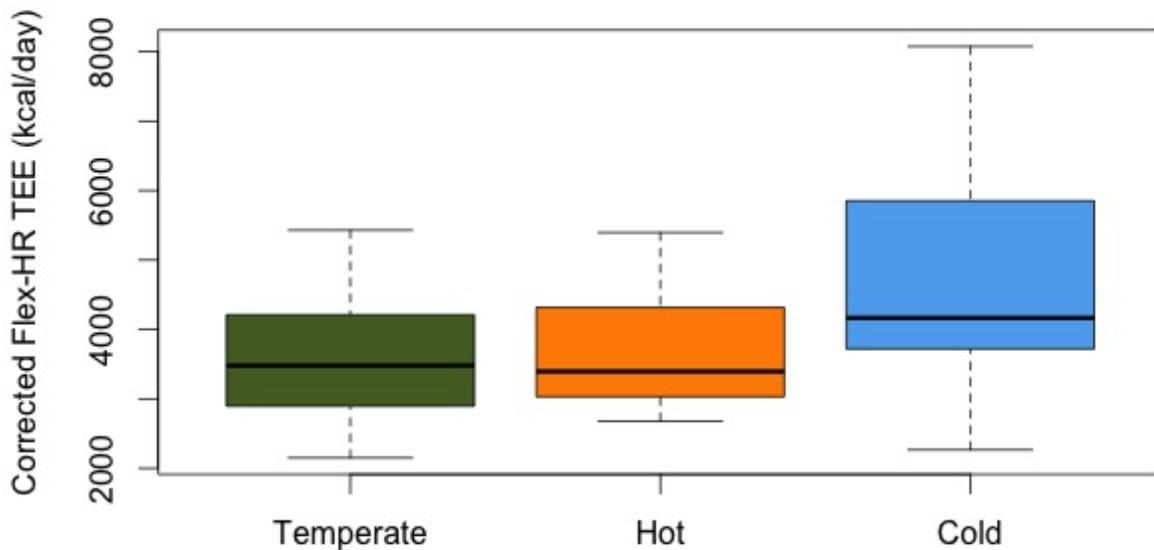
allocation associated with temperate, hot and cold climates. Finally, the importance of activity level in reducing increased thermoregulatory costs in cold climates is discussed.

## Results

### Total energy expenditure measurements from the flex-heart rate method

As discussed in the previous chapter, the flex-HR method produced TEE values that were 24% higher than TEE values measured by the doubly labeled water method. Only the corrected flex-HR TEE values, 17% correction factor for TEEs  $>3000$  kcal day<sup>-1</sup>, will be used for analysis in this chapter. Mean daily TEE was  $3563 \pm 804$  kcal day<sup>-1</sup> for temperate climates,  $3633 \pm 765$  kcal day<sup>-1</sup> for hot climates and  $4780 \pm 1647$  kcal day<sup>-1</sup> for cold climates. **Fig. 7.1** shows the range of TEE values for temperate, hot and cold climates.

**Figure 7. 1.** Corrected flex-HR measured mean total energy expenditure (kCal day<sup>-1</sup>) for each subject in temperate, hot and cold climates during the data collection period. Temperate climate TEEs ranged from 2150 – 5429 kcal day<sup>-1</sup>. Hot climates ranged from 2680 – 5396 kcal day<sup>-1</sup> and cold climates ranged from 2266 – 8076 kcal day<sup>-1</sup>.

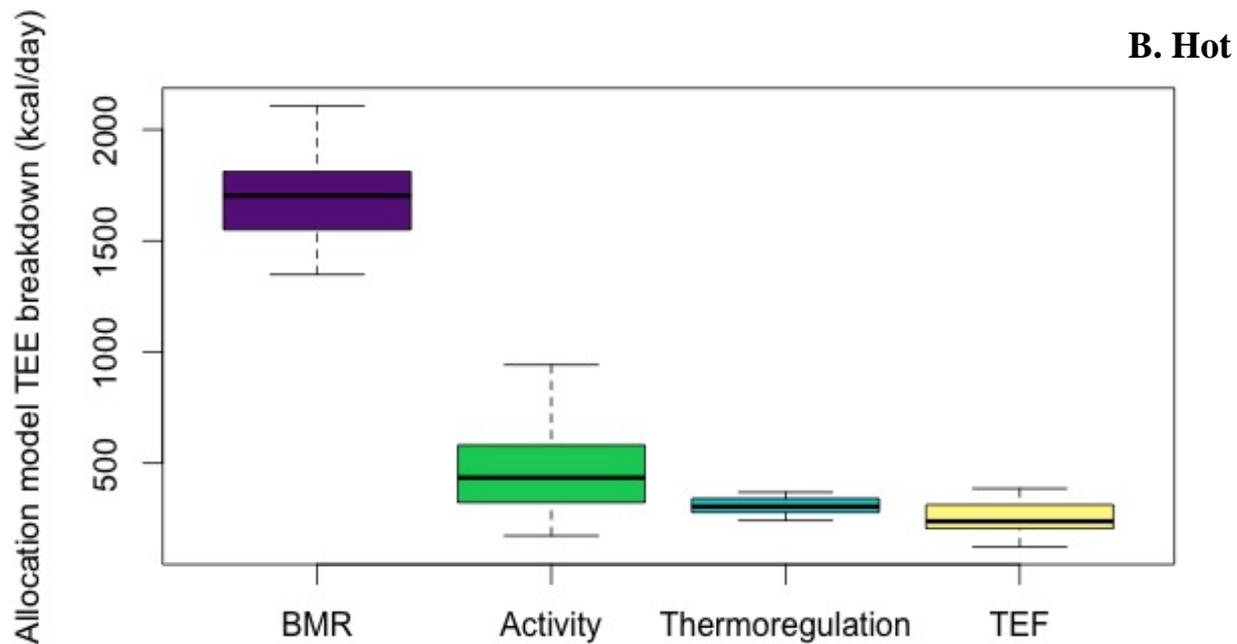
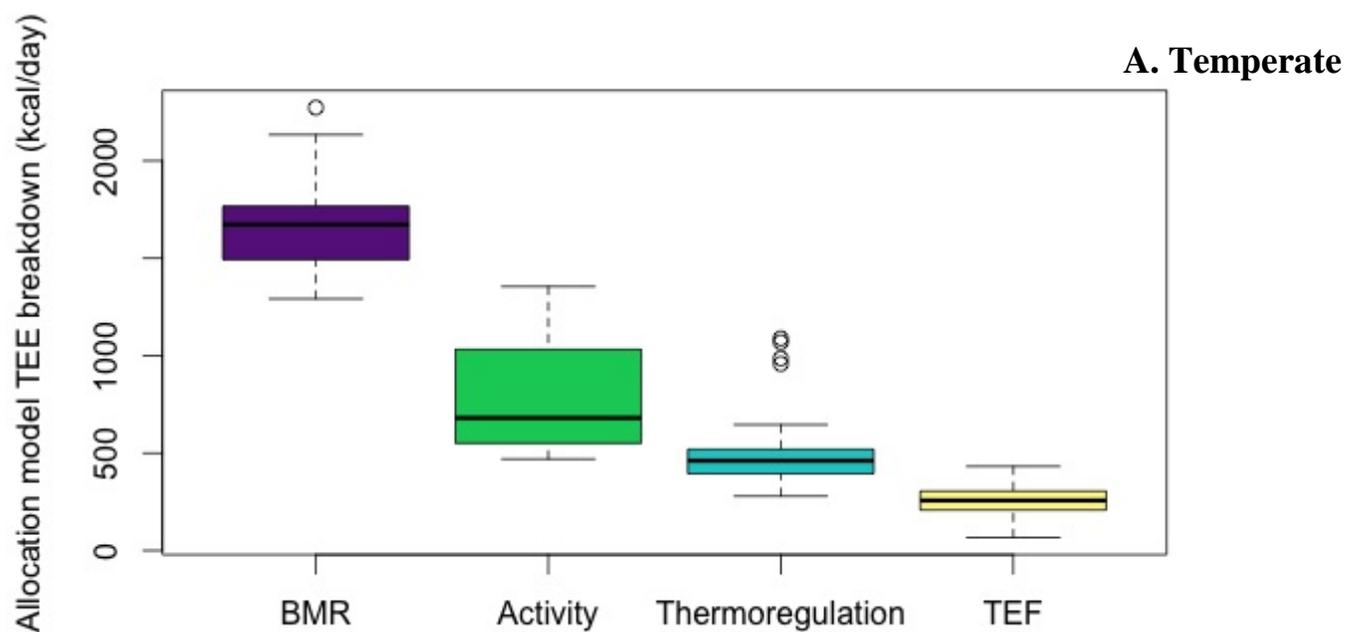


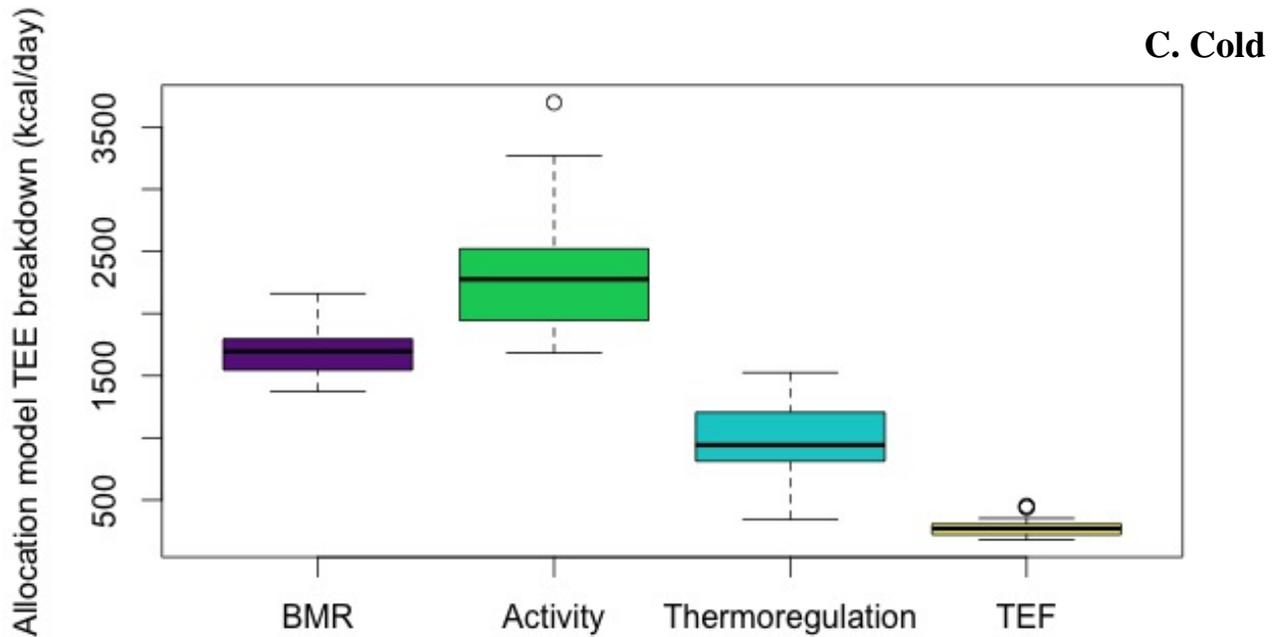
A multiple regression controlling for age, sex, mass, and height, for the corrected flex-HR TEE values was performed with Tukey's pair-wise comparisons ( $F=10.882$ ,  $p<0.001$ ). There was no significant difference between TEEs in temperate and hot climates ( $p=0.97$ ), but subjects experienced significantly higher TEEs in cold climates than in temperate or hot climates ( $p<0.01$  for both temperate and hot climates, Bonferroni corrected  $\alpha=0.017$ ). Since subjects acted as their own controls in the temperate climate and then took part in either a hot or cold climate portion of the course, paired t-tests were also performed; this difference approached significance ( $p=0.08$ , paired-samples T-test). Subjects taking part in temperate and cold climates experienced significantly higher TEEs, expending an additional  $1550 \text{ kcal day}^{-1}$  in cold climates ( $p<0.0001$ , paired-samples T-test, Bonferroni corrected  $\alpha=0.025$ ). 70% of subjects expended more energy in temperate climates than in hot, and 83% expended more in cold climates than in temperate climates.

#### Total energy expenditure breakdown by the Allocation Model

The Allocation Model was used to estimate the costs of basal metabolic rate, activity, thermoregulation and the thermic effect of food. **Fig. 7.2** shows the summary of the allocation breakdown for temperate, hot and cold climates. Each component estimated by the Allocation Model is then analyzed separately. Please refer to *Appendix 8* for the full set of values of the Allocation Model cost breakdown for each individual in each course and climate.

**Figure 7. 2.** A summary of the breakdown of TEE for **A)** Temperate, **B)** Hot and **C)** Cold climates as determined by the Allocation Model.



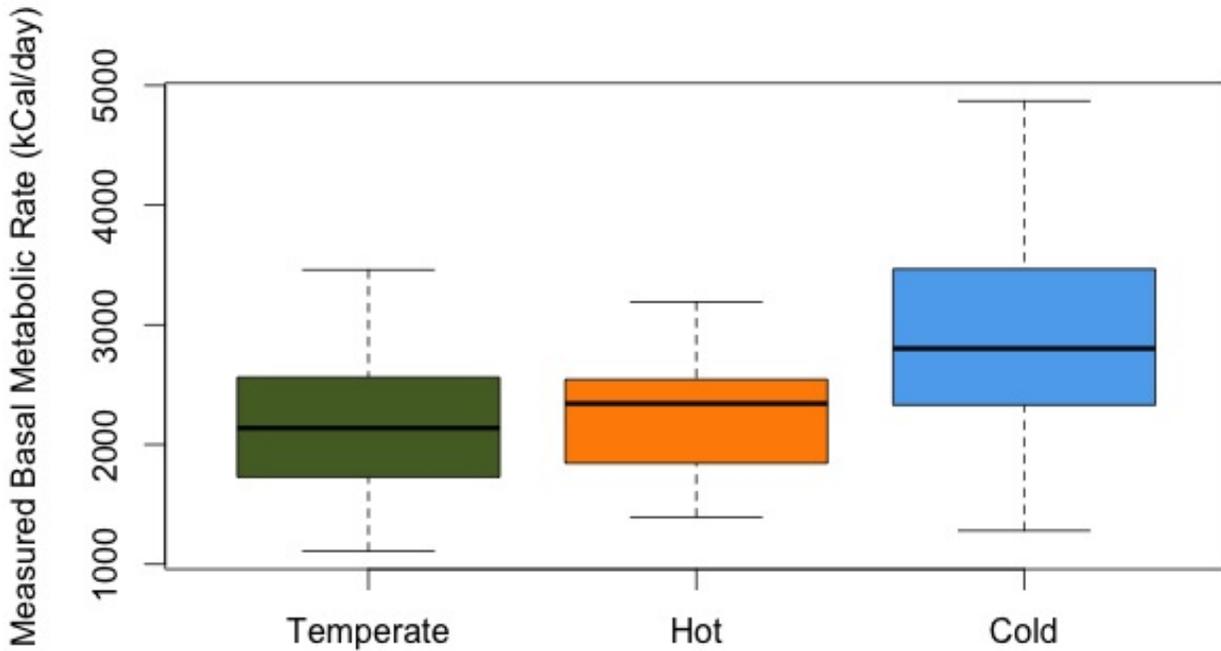


### Basal Metabolic Rate

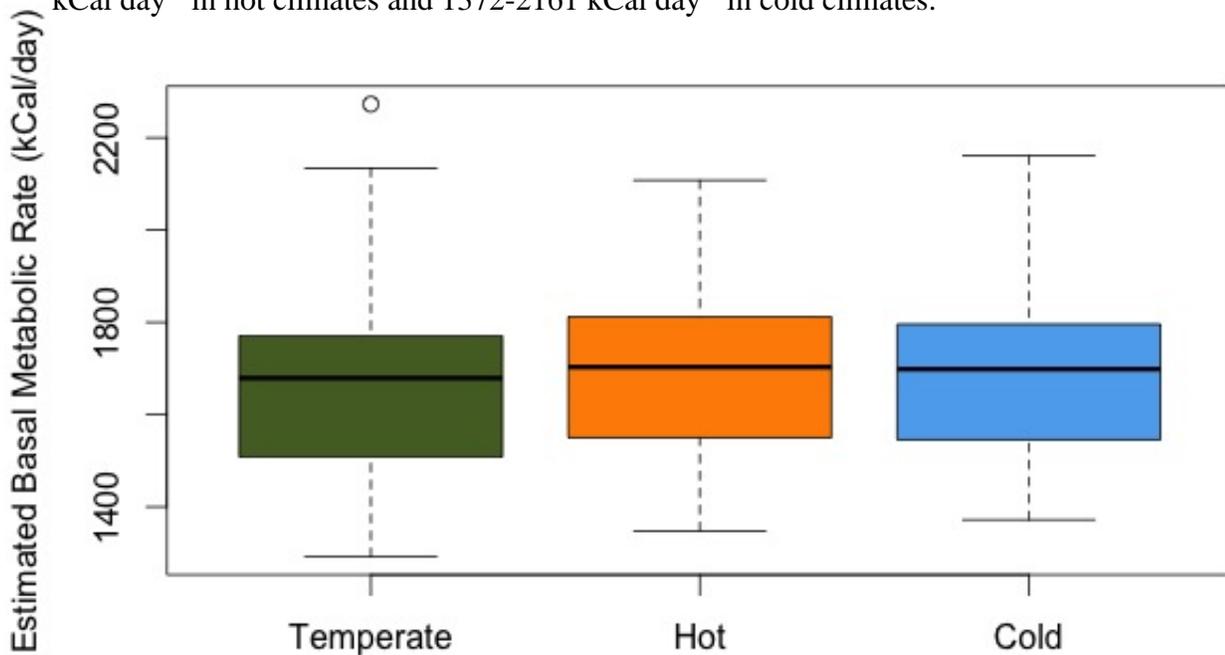
A concern when modeling energy expenditure is accurately estimating basal metabolic rate, which becomes increasingly difficult outside of thermoneutral temperatures. Measured basal metabolic rates have a mean of  $2176 \pm 550$  kCal day<sup>-1</sup> for temperate climates,  $2251 \pm 460$  kCal day<sup>-1</sup> for hot climates, and  $2898 \pm 855$  kCal day<sup>-1</sup> for cold climates (**Fig. 7.3**). Estimated basal metabolic rate, calculated using equations from Henry (2005) based on body mass, has a mean of  $1662 \pm 220$  kCal day<sup>-1</sup> for temperate climates,  $1690 \pm 185$  kCal day<sup>-1</sup> for hot climates, and  $1680 \pm 204$  kCal day<sup>-1</sup> for cold climates (**Fig. 7.4**). Estimated BMR values are significantly lower than measured BMR values across all climates as well as within each climate ( $p < 0.0001$  for all, paired-samples t-tests, Bonferroni corrected  $\alpha = 0.017$ ). Estimated BMR was 24% lower than measured BMR for temperate climates, 25% lower in hot climates, and 43% lower in cold climates. All BMRs were measured in a climate controlled room kept at the same temperature of

22.8°C throughout the entire data collection. For comparisons between climates, only measured BMR was used.

**Figure 7. 4.** Measured basal metabolic rate (kCal day<sup>-1</sup>) for temperate, hot and cold climates. Measured BMR values in temperate climates ranged from 1109-3490 kCal day<sup>-1</sup>, 1393-3191 kCal day<sup>-1</sup> in hot climates and 1280-4870 kCal day<sup>-1</sup> in cold climates.



**Figure 7. 3.** Estimated basal metabolic rate (kCal day<sup>-1</sup>) for temperate, hot and cold climates. Estimated BMR values in temperate climates ranged from 1292-2273 kCal day<sup>-1</sup>, 1348-2108 kCal day<sup>-1</sup> in hot climates and 1372-2161 kCal day<sup>-1</sup> in cold climates.

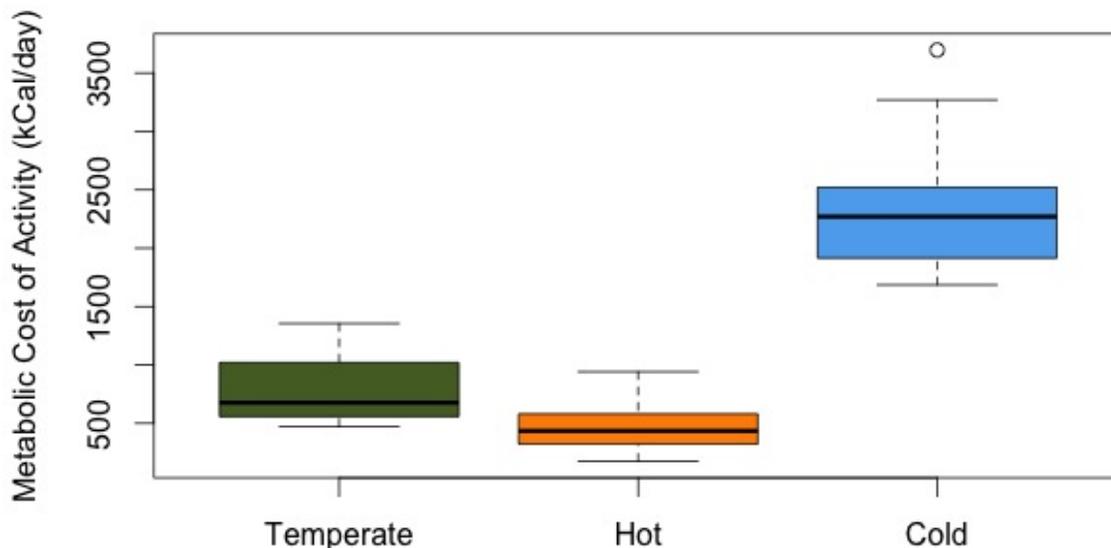


Multiple regressions analysis controlling for age, sex, mass, and height for measured BMRs with Tukey's pair-wise comparisons was performed ( $F=11.570$   $p<0.001$ ). This revealed that there was no significant difference between BMR in temperate climates and hot climates ( $p=0.790$ ). However, measured BMRs were significantly higher in cold climates than in temperate climates ( $p<0.001$ , Bonferroni corrected  $\alpha=0.017$ ) and hot climates ( $p<0.001$ , Bonferroni corrected  $\alpha=0.017$ ). Cold climate BMR was 26% higher than temperate climate BMR and 24% higher than hot climate BMR. Comparisons within each subject for the different climates revealed similar findings. There was no significant difference between measured BMR in temperate climates and hot climates ( $p=0.1$ , paired-samples t-test). However, BMR in cold climates was significantly higher than in temperate climates ( $p<0.001$ , paired-samples t-test).

### Activity

Activity costs were estimated using the Allocation Model described earlier in Chapter 5. Activity costs averaged  $780\pm 261$   $\text{kCal day}^{-1}$  for temperate climates,  $465\pm 176$   $\text{kCal day}^{-1}$  for hot climates, and  $2316\pm 502$   $\text{kCal day}^{-1}$  for cold climates (**Fig. 7.5**).

**Figure 7. 5.** Estimated activity costs ( $\text{kCal day}^{-1}$ ) using the Allocation Model for temperate, hot and cold climates. Estimated activity costs in temperate climates ranged from 470-1355  $\text{kCal day}^{-1}$ , 174-942  $\text{kCal day}^{-1}$  in hot climates and 1686-3697  $\text{kCal day}^{-1}$  in cold climates.

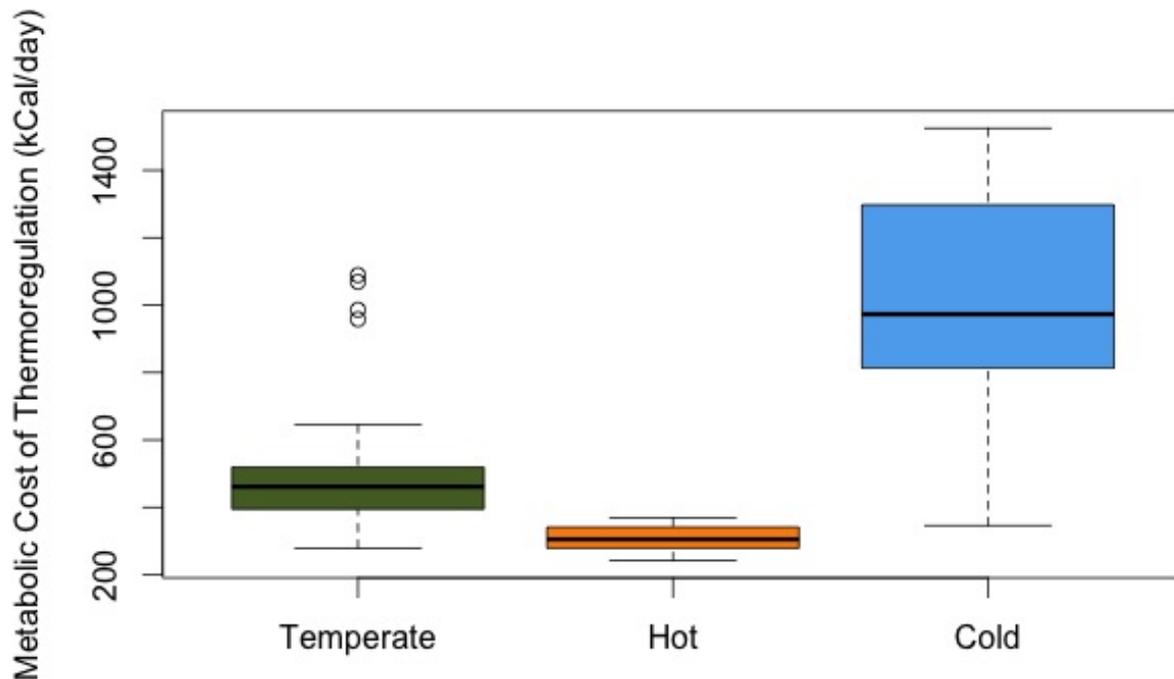


Multiple regressions analysis controlling for age, sex, mass and height for measured BMRs with Tukey's pair-wise comparisons was performed ( $F=233.255$ ,  $p<0.001$ , Bonferroni corrected  $\alpha=0.017$ ). Estimated activity costs for each climate were significantly different from one another. Temperate activity costs were significantly higher than hot climate activity costs ( $p<0.001$ , Bonferroni corrected  $\alpha=0.017$ ) and cold climate activity costs were significantly higher than both temperate and hot climate activity costs ( $p<0.001$  for both, Bonferroni corrected  $\alpha=0.017$ ). Cold activity levels were 67% and 80% higher than temperate and hot climates respectively. Temperate activity levels were 40% higher than in hot climates. Comparisons within each subject for the different climates revealed the same pattern: temperate climate activity levels were significantly higher than hot climate activity levels and cold climate activity levels were significantly higher than temperate climate activity levels ( $p<0.001$  for both, paired-samples t-test, Bonferroni corrected  $\alpha=0.017$ ).

### Thermoregulation

Thermoregulatory costs were estimated using the Allocation Model described earlier. Thermoregulatory costs averaged  $494\pm 173$  kCal day<sup>-1</sup> for temperate climates,  $306\pm 38$  kCal day<sup>-1</sup> for hot climates, and  $1018\pm 310$  kCal day<sup>-1</sup> for cold climates (**Fig. 7.6**).

**Figure 7. 6.** Estimated thermoregulatory costs (kCal day<sup>-1</sup>) using the Allocation Model for temperate, hot and cold climates. Estimated thermoregulatory costs in temperate climates ranged from 279-1089 kCal day<sup>-1</sup>, 242-369 kCal day<sup>-1</sup> in hot climates and 346-1525 kCal day<sup>-1</sup> in cold climates.



Multiple regressions analysis controlling for age, sex, mass and height for activity costs with Tukey's pair-wise comparisons was performed ( $F=92.45$ ,  $p<0.001$ , Bonferroni corrected  $\alpha=0.017$ ). Estimated thermoregulatory costs for each climate were significantly different from one another. Temperate thermoregulatory costs were significantly higher than hot climate thermoregulatory costs ( $p<0.001$ ) and cold climate thermoregulatory cost were significantly higher than both temperate and hot climate thermoregulatory costs ( $p<0.001$  for both). Cold thermoregulatory costs were 53% and 71% higher than temperate and hot climates respectively. Temperate activity levels were 38% higher than in hot climates. Comparisons within each subject for the different climates revealed the same pattern: temperate climate thermoregulatory costs were significantly higher than hot climate thermoregulatory costs, and cold climate

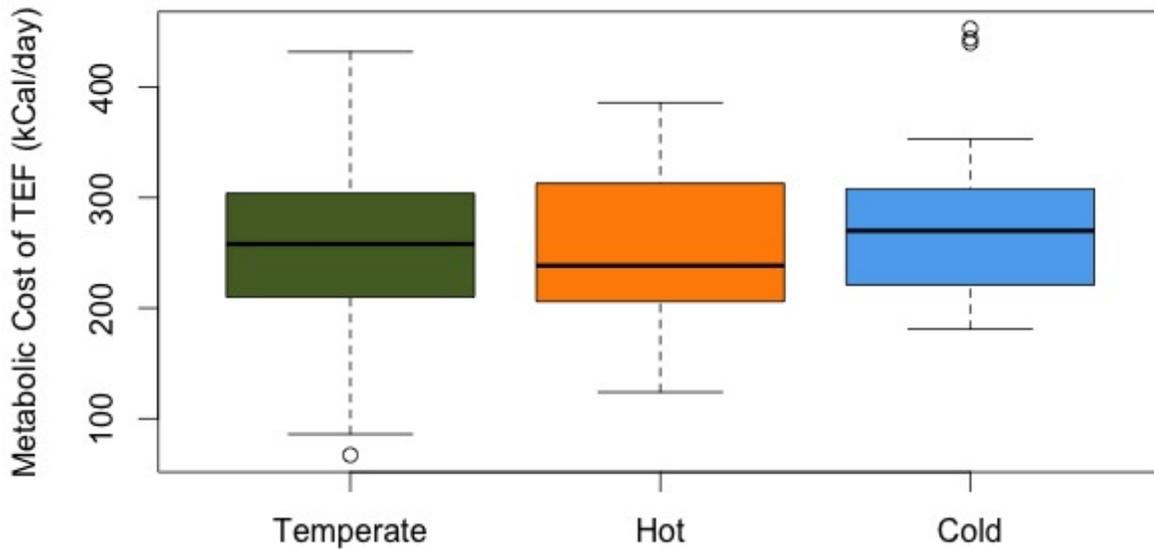
thermoregulatory costs were significantly higher than that of temperate climates ( $p < 0.001$  for both, paired-samples t-test).

#### Thermic Effect of Food

Thermic effect of food (TEF) costs was estimated using the Allocation Model described earlier. TEF costs averaged  $254 \pm 70$  kCal day<sup>-1</sup> for temperate climates,  $250 \pm 75$  kCal day<sup>-1</sup> for hot climates, and  $282 \pm 77$  kCal day<sup>-1</sup> for cold climates (**Fig. 7.7**).

Multiple regressions analysis controlling for age, sex, mass and height for TEF with Tukey's pair-wise comparisons was performed ( $F=1.294$ ,  $p=0.279$ ). There was no significant difference between any of the climates ( $p=0.945$  for temperate and hot climates,  $p=0.340$  for temperate and cold climates, and  $p=0.315$  for hot and cold climates). Comparisons within each subject for the different climates revealed that temperate and hot climates did not have a significantly different TEF ( $p=0.850$ , paired-samples t-test). However, cold climate TEF was significantly higher than temperate climate TEF ( $p < 0.01$ , paired-samples t-test, Bonferroni corrected  $\alpha=0.017$ ).

**Figure 7. 7.** Estimated TEF costs (kCal day<sup>-1</sup>) using the Allocation Model for temperate, hot and cold climates. Estimated TEF costs in temperate climates ranged from 67-432 kCal day<sup>-1</sup>, 124-386 kCal day<sup>-1</sup> in hot climates and 181-282 kCal day<sup>-1</sup> in cold climates.



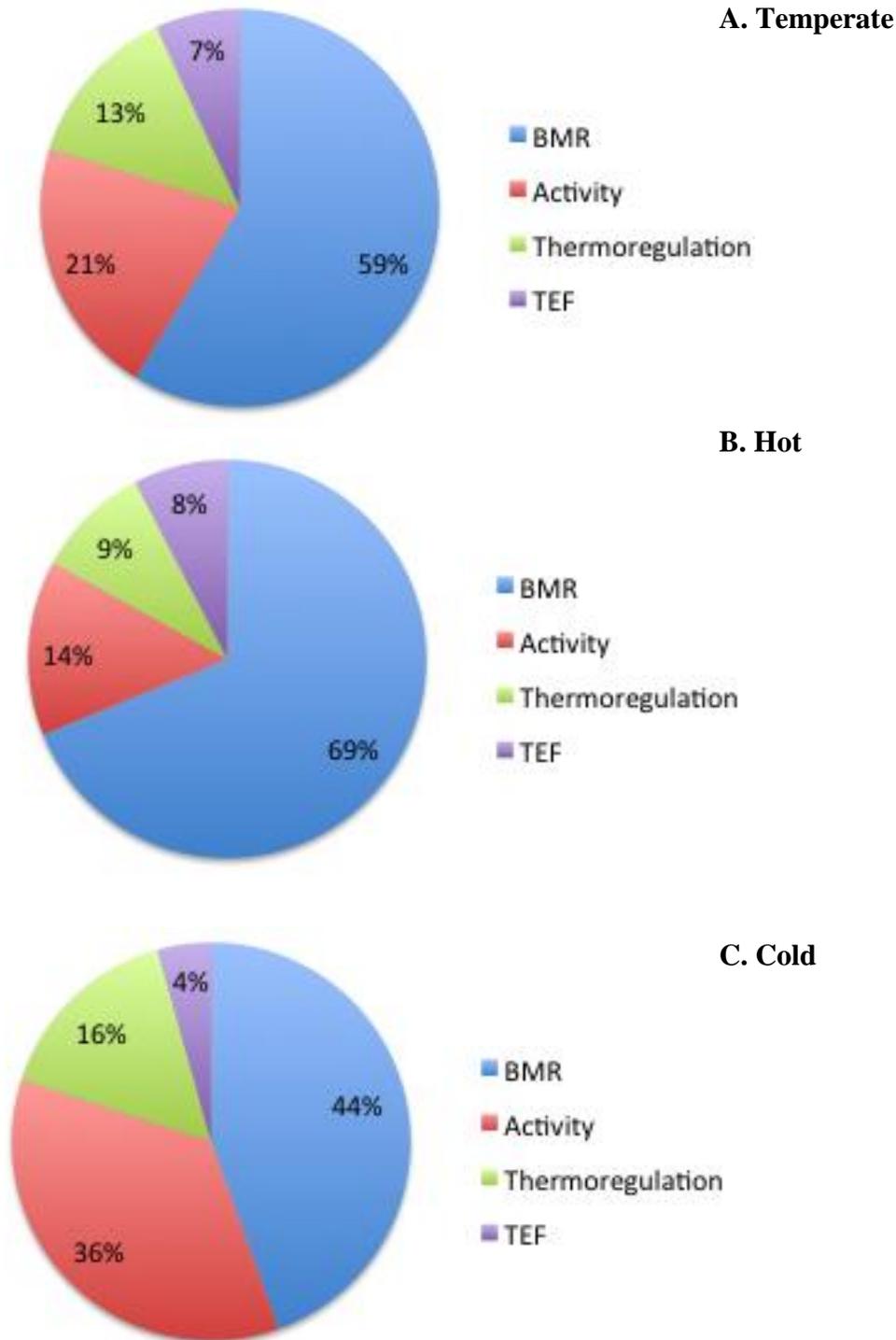
Allocation breakdown between climates

The following figures (**Fig. 7.8A-C**) show the range of the average daily breakdown of energy expenditure between BMR, activity, thermoregulation, and TEF for the different climates during the entire data collection period. Measured BMR values and allocation estimated values for activity, thermoregulation, and TEF were used. **Table 7.1** summarizes the mean metabolic cost (kCal day<sup>-1</sup>) each for each component of the TEE budget for the three different climates.

**Table 7. 1.** Summary of the mean temperature, body mass and metabolic cost (kCal day<sup>-1</sup>) breakdown for each TEE component: measured BMR and Allocation Model estimated activity ( $E_{Act}$ ), thermoregulation ( $E_{Therm}$ ) and TEF costs for temperate, hot and cold climates.

<i>Climate</i>	<i>Temp °C</i>	<i>N</i>	<i>Mass</i>	<i>BMR</i>	<i>E<sub>Act</sub></i>	<i>E<sub>Therm</sub></i>	<i>TEF</i>
<i>Temperate</i>	12.3	56	71.4	2176	780	494	254
<i>Hot</i>	23.7	22	75.8	2251	465	306	250
<i>Cold</i>	-7.6	23	73.6	2898	2316	1018	282

**Figure 7. 8.** The percentage that BMR, activity, thermoregulation and TEF comprise of TEE for the different climates **A) Temperate**, **B) Hot** and **C) Cold** during the entire data collection period. Basal metabolic rate makes up over half of the total energy expenditure budget in both temperate and hot climates. In cold climates, activity takes up a larger proportion of the energy expenditure budget compared to temperate and hot climates



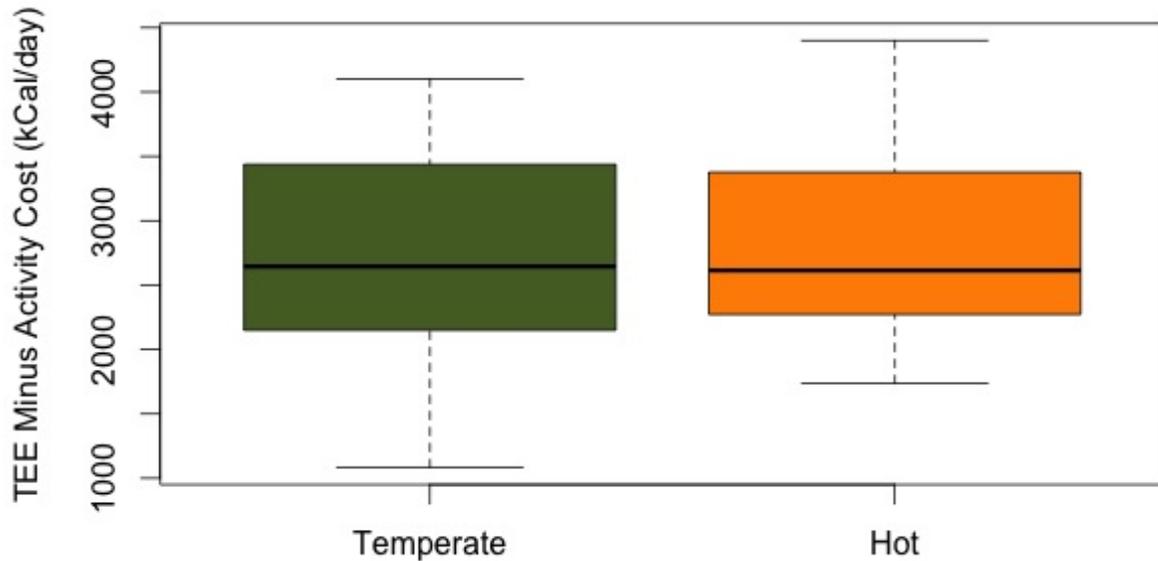
The most notable difference in allocation breakdown between the climates is the proportion of TEE that is made up by activity cost. Activity comprises  $36 \pm 3.6\%$  of TEE for cold climates compared to  $21 \pm 4.7\%$  and  $14 \pm 4.3\%$  in temperate and hot climates respectively. Surprisingly, the percentage that thermoregulation comprises of the total energy budget is similar between the climates:  $13 \pm 4.4\%$ ,  $9 \pm 1.3\%$  and  $16 \pm 4.8\%$  for temperate, hot and cold climates respectively. Though the analyses presented earlier demonstrated that there is an increased cost associated with cold climates for each component of the total energy budget, it is worth examining what the impact of high activity levels in cold climates has on the energy budget.

*The impact of high activity levels on the cost of thermoregulation*

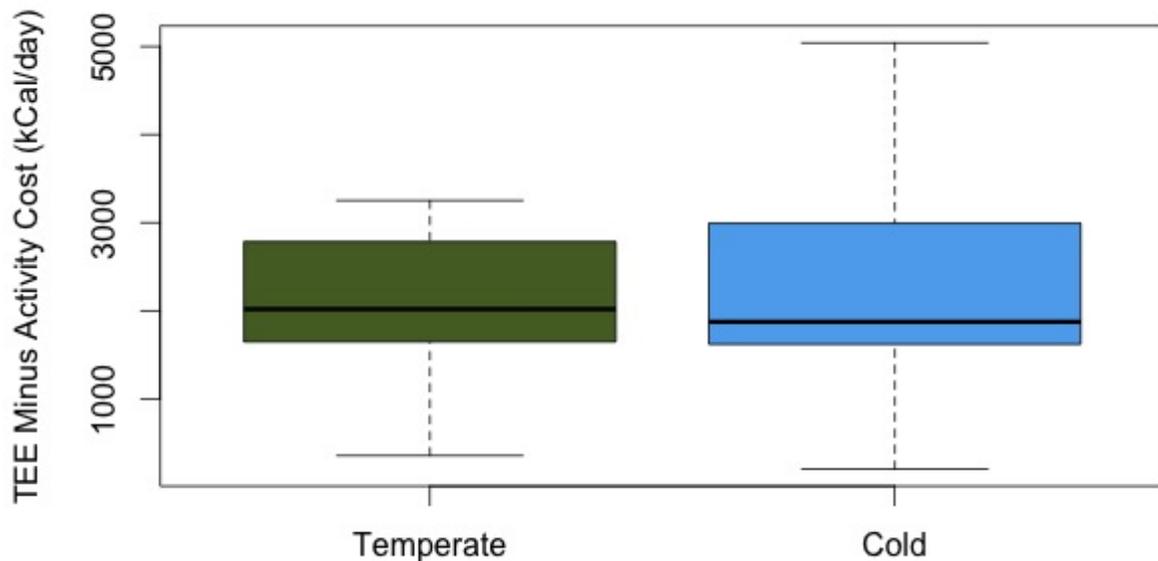
In order to analyze the impact activity had on the total energy expenditure budget, activity cost was subtracted from TEE for the two different course types. If core body temperature was maintained only through the physiological mechanisms for thermoregulation, then a significant difference between climates, once activity costs were removed from TEE, would be expected. However, if a combination of thermoregulation and heat produced through physical activity maintained core body temperature, as suggested by Tikuisis et al. (2000), then no significant difference would be expected between climates once activity costs were removed from TEE.

The temperate-hot climate courses were analyzed separately from the temperate-cold climate courses. When activity costs are removed from TEE, there is no significant difference in the remainder of the energy budget between the temperate and hot climates ( $p=0.535$ , paired-samples t-test) (**Fig. 7.9**). Furthermore, there is no significant difference between temperate and cold climates once activity is removed from the total energy budget ( $p=0.428$ , paired-samples t-test) (**Fig. 7.10**).

**Figure 7. 9.** The remainder of the energy budget once activity costs are removed for the temperate-hot climate courses. The remainder of the energy budget averaged 2657 kCal day<sup>-1</sup> for the temperate climate and 2770 kCal day<sup>-1</sup> for the hot climate. There was no significant difference between the two budgets once activity costs were removed (p=0.535).



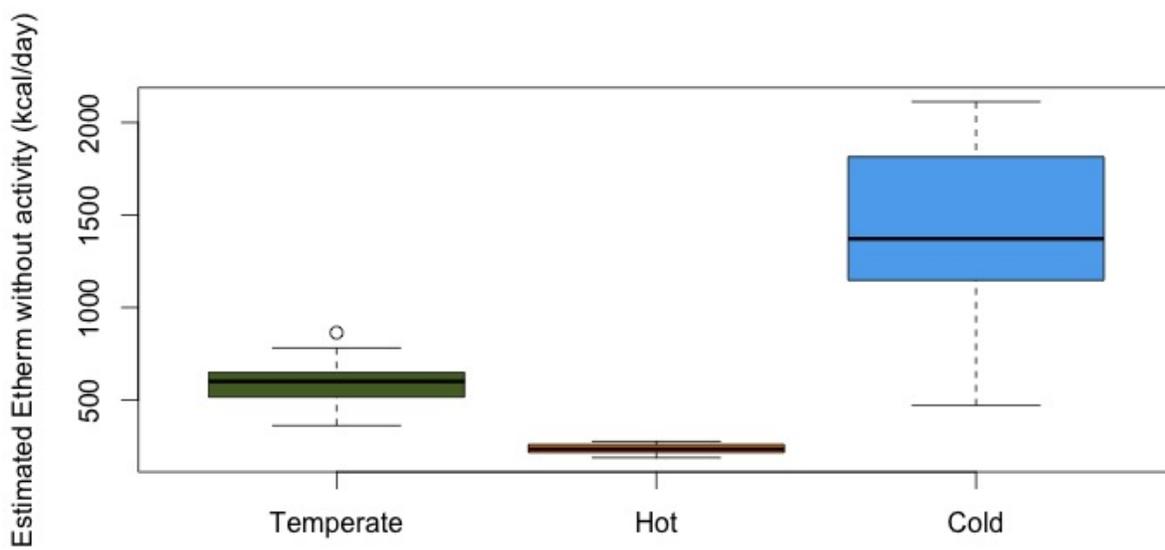
**Figure 7. 10.** The remainder of the energy budget once activity costs are removed for the temperate-cold climate courses. The remainder of the energy budget averaged 2146 kCal day<sup>-1</sup> for the temperate climate and 2244 kCal day<sup>-1</sup> for the cold climate. There was no significant difference between the two budgets once activity costs were removed (p=0.428).



There is no significant difference between metabolic costs of the different climates once activity costs are removed. This suggests, particularly for cold climates, that high levels of activity can mitigate the expected increased metabolic cost due to thermoregulation in cold climates.

To determine how much thermoregulation would cost without heat produced through activity, thermoregulatory costs were estimated using the Allocation Model with zero activity assumed. When zero activity is used in the Allocation Model, thermoregulatory costs range from 362-864 kcal day<sup>-1</sup>, with a mean of 585±106 kcal day<sup>-1</sup> in temperate climates (**Fig. 7.11**). Thermoregulatory costs range from 188-277 kcal day<sup>-1</sup>, with a mean of 237±27 kcal day<sup>-1</sup> in hot climates. Thermoregulatory costs range from 470-2112 kcal day<sup>-1</sup>, with a mean of 1428±432 kcal day<sup>-1</sup> in cold climates. Thermoregulatory costs in temperate climates were significantly higher than in hot climates ( $p<0.001$ ,  $F=20.3$ , Bonferroni corrected  $\alpha=0.017$ ). Thermoregulatory costs in cold climates were significantly higher than in temperate and hot climates (temperate:  $p<0.001$ ,  $F=50.8$ ; hot:  $p<0.001$ ,  $F=40.04$ , Bonferroni corrected  $\alpha=0.017$ ).

**Figure 7. 11.** Thermoregulatory costs estimated using the Allocation Model when zero activity is assumed. Temperate climates had a mean thermoregulatory cost of 585±106 kcal day<sup>-1</sup>, 237±27 kcal day<sup>-1</sup> in hot climates, and 1428±432 kcal day<sup>-1</sup> in cold climates.



Estimated thermoregulatory costs without activity costs included were significantly higher than thermoregulatory costs with activity in the temperate and cold climates, 23% and 29% higher respectively ( $p < 0.0001$ , for both temperate and cold, Student's paired t-test, Bonferroni corrected  $\alpha = 0.0085$ ). This suggests that activity helps to lower thermoregulatory costs in the face of cold conditions. However, in hot climates thermoregulatory costs without activity were significantly lower, 30% lower, than thermoregulatory costs with activity included ( $p < 0.0001$ , Student's paired t-test, Bonferroni corrected  $\alpha = 0.0085$ ). This suggests that activity in hot climates increases the thermoregulatory burden. The extra heat produced through activity is heat that needs to be dissipated through physiological mechanisms such as sweating. Overall, however, the hot climate condition was not energetically stressful compared to the temperate and cold climates. The temperate climate was energetically demanding in a thermoregulatory standpoint because the days were warm with temperatures at or above 30°C, but during the nights the temperature would drop below freezing. The cold climate was the most energetically demanding with constant cold temperatures with which the subjects had to contend.

### ***Discussion***

The NOLS population was used for this study for many reasons, but one of the most compelling was that subjects were able to act as their own control by taking part in a course in a temperate climate and then in a course in either a hot or cold climate. Analysis of the flex-HR TEE results revealed that there was no significant difference between temperate and hot climate TEE. However, subjects taking part in cold climates experienced significantly higher TEEs than what they experienced in temperate climates. This mirrors studies done on indigenous populations that found increased metabolic rates associated with cold climates (Leonard et al., 2002, 2005, Snodgrass et al. 2005, 2006, 2008).

Comparing measured BMR values to estimated BMR values, estimated values were significantly lower than measured values among the NOLS population. The NOLS population had their BMR measured first thing in the morning in a climate controlled room kept at the same temperature of 22.8°C before consuming the first meal of the day and after having rested for at least 15 minutes before a 6-8 minute measurement was taken. It is possible the high observed BMRs were due to short measurement durations or subject noncompliance concerning food intake. Altitude could also be a factor in the high measured BMRs. All measurements were taken at roughly the same altitude, ~1500m, which was a good deal higher than sea level, and there is a known increase in BMR with increasing altitude (Frisancho 1993, Moran 2008). Despite, these possible issues, these data suggest that estimates for BMR are not accurately representing observed BMR, and that any models based solely on BMR and multiples of BMR should be used with caution.

Measured BMRs were not significantly different between the hot and temperate climates; however, BMRs from the cold climates were significantly higher than those of the temperate climates. These results, too, mirror studies done on circumpolar populations and in experimentally induced cold conditions (Krogh and Krogh 1915, Heinbecker 1928, Heinbecker 1931, Strømme et al. 1963, Hammel 1964, Folk 1966, Hanna 1968, Little and Hochner 1973, Sloan and Keatinge 1973, Kollias et al. 1974, McArdle et al. 1984a, McArdle et al., 1984b, Toner et al. 1986, Tikuisus et al. 2000, Leonard et al., 2002, 2005, Snodgrass et al. 2005, 2006, 2008, Moran 2008).

The costs due to activity and thermoregulation were each significantly higher in cold climates than in both temperate and hot climates. And the costs due to activity and thermoregulation in temperate climates were significantly higher than in hot climates. There was

no significant difference between temperate and hot climates in the cost due to the thermic effect of food. However, in cold climates, the cost due to TEF was significantly higher, though marginally higher, than in temperate climates, but not in hot climates. The lack of difference between hot and cold climates may be due to the fact that during hot climate courses, subjects had access to coolers filled with ice much like the cold climates had free access to abundant snow. This ability to keep food cool allowed subjects to increase the quality of their diet by including more perishable items such as fresh meat, eggs, fruits and vegetables. Subjects were able to consume more similar foods during hot and cold climates than during temperate climates, leading to more similar thermic effects of food costs.

The various components of TEE differed proportionally between the climates. BMR took up over half of the TEE budget in temperate and hot climates. Temperate climates had a greater percentage of activity and thermoregulation comprising the TEE than in hot climates. Activity took up a far greater proportion of TEE in cold climates than in either temperate or hot climates. High levels of activity under cold conditions have been implicated in laboratory studies as a mechanism for reducing thermoregulatory heat production (Toner et al. 1986, Tikuisus et al. 2000). In this study it was found that, once activity costs were removed from TEE, there was not a significant difference between hot and temperate climates or between cold and temperate climates. Furthermore, when zero activity is assumed, thermoregulatory costs were exceptionally large in cold climates, greater than 2000 kcal day<sup>-1</sup> in some instances, and there was a significant difference in cost between climates. Like the laboratory studies, this suggests that heat produced through activity can be an effective means of maintaining core body temperature and reducing the potential metabolic cost of thermoregulation, particularly in cold conditions.

The results presented here demonstrate the differences in TEE and its components between temperate, hot, and cold climates. Furthermore, this analysis presents the importance of physical activity level in mitigating thermoregulatory costs incurred by populations inhabiting a cold climate, which has only previously been demonstrated under laboratory conditions.

## **Chapter 8: Testing the importance of body surface area in the cost of thermoregulation in natural environments**

### ***Introduction***

Bergmann's and Allen's rules summarize a general ecogeographic relationship between body surface area and body mass that varies with climate (Mayr 1956, 1963), such that the ratio of surface area-to-body mass (or volume) is minimized in cold climates and maximized in hot climates to reduce or increase heat dissipation respectively (Ruff 1994). It has been well established that these ecogeographical rules apply to humans, and that thermal clines in human morphological variation exist (Ruff 1994). Researchers have attempted to define the energetic benefit to morphological adaptations to climate (Sloan and Keatinge 1973, Kollias et al. 1974, Tikuisis et al. 2000, Tilkens et al. 2007, Holliday and Hilton 2010). However, at present, there are no studies measuring energy expenditure among humans in natural environments linking possible differences in energy expenditure in different climates to variation in body shape and size. This type of analysis would help determine if there is a true energetic advantage to Bergmann's and Allen's rules among humans, or if there are other biological and behavioral processes at work to mitigate environmental stressors.

This chapter presents a summary of the surface area of the highly active NOLS population and compares the surface area/mass ratio of this study population to that of native populations from temperate, hot and cold climates. Then the relationship between the surface area/mass ratio and energy expenditure is examined to determine if an energetic advantage of Bergmann's and Allen's rules is present among the NOLS population. The implications of an energetic advantage of particular morphologies and the importance of cultural buffering in extreme climates are then discussed.

## Results

### Descriptions of surface area and surface area/mass

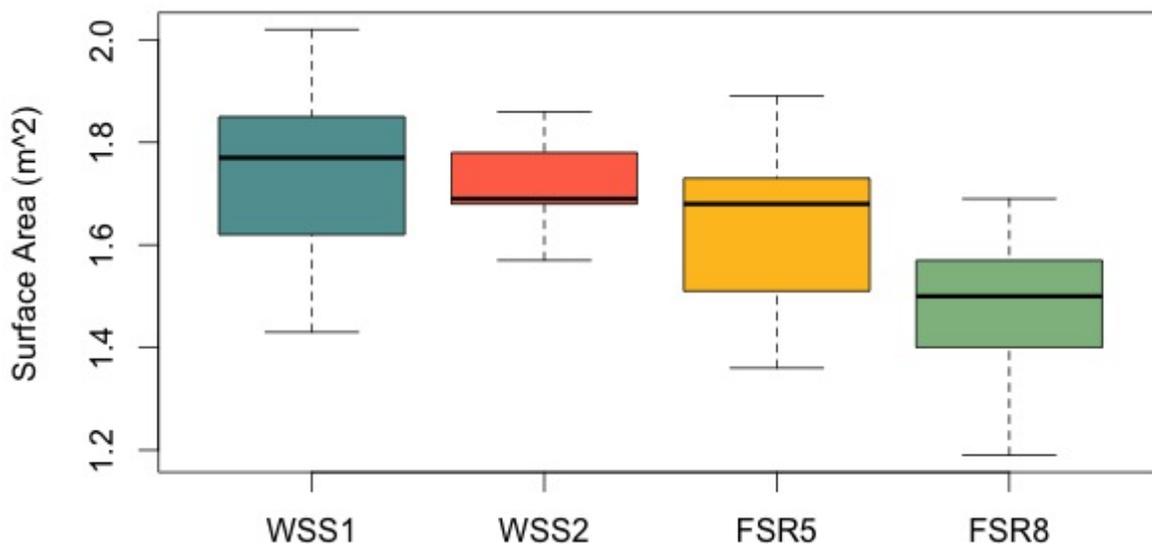
Surface area was calculated for the NOLS population using the cylindrical model developed by Ruff (1991, 1994). This model uses subject height and bi-iliac breadth to determine surface area and has shown to be an effective estimation (Ruff 1991, 1994). Heights ranged from 1.61-1.97 m and bi-iliac breadth ranged from 22.0-34.5 cm. Surface areas ranged from 1.19-2.02 m<sup>2</sup>. **Table 8.1** summarizes the mean height, bi-iliac breadth, and surface area for each course.

**Fig. 8.1** represents the surface areas for each course. For individual morphological values, please refer to *Appendix 1*.

**Table 8. 1.** Summary of mean mass, height and bi-iliac breadth for each course. The mean height for the entire sample was  $1.79 \pm 0.08$  m and the mean bi-iliac breadth was  $29.0 \pm 2.5$  cm. The mean surface area for the entire sample was  $1.63 \pm 0.18$  m<sup>2</sup>.

Course	N	Mass (kg)	Height (m)	Bi-iliac Breadth (cm)	Surface Area (m <sup>2</sup> )
WSS1	13	74.0 $\pm$ 10.3	1.81 $\pm$ 0.10	30.6 $\pm$ 1.6	1.73 $\pm$ 0.17
WSS2	11	68.9 $\pm$ 7.67	1.78 $\pm$ 0.06	30.9 $\pm$ 1.2	1.72 $\pm$ 0.08
FSR5	12	73.2 $\pm$ 9.6	1.79 $\pm$ 0.07	28.6 $\pm$ 2.0	1.62 $\pm$ 0.16
FSR8	14	73.3 $\pm$ 14.7	1.77 $\pm$ 0.08	26.3 $\pm$ 1.9	1.47 $\pm$ 0.14

**Figure 8. 1.** The range, maximum and minimum, of surface areas for each course. WSS1 ranged from 1.55-2.02m<sup>2</sup>, WSS2 ranged from 1.57-1.86m<sup>2</sup>, FSR5 ranged from 1.36-1.89m<sup>2</sup> and FSR8 ranged from 1.19-1.69m<sup>2</sup>.



As described in chapter two, the surface area/mass ratio is the important characteristic that confers an advantage in extreme climates. A high surface area/mass ratio confers an advantage in hot climates allowing more heat to be dissipated. A low ratio confers an advantage in cold climates reducing the amount of heat dissipated from the body. Since NOLS students have the tendency to lose weight during their courses, the surface area/mass ratio is different for the different climates. For individual changes in morphological characteristics experienced during the NOLS course, please refer to *Appendix 2*. **Table 8.2** provides a summary of mean mass and mean surface area/mass for each course and climate. For temperate climates, mass ranged from 56.0-108.0 kg with a mean of  $73.6 \pm 11.4$ kg and surface area/mass ranged from 0.016-0.030 kg m<sup>-2</sup> with a mean of  $0.022 \pm 0.003$  kg m<sup>-2</sup>. For hot climates, mass ranged from 59.6-97.7 kg with a mean of  $75.6 \pm 9.6$ kg and surface area/mass ranged from 0.020-0.030 kg m<sup>-2</sup> with a mean of  $0.023 \pm 0.003$  kg m<sup>-2</sup>. For cold climates, mass ranged from 59.9-101.0 kg with a mean of  $73.8 \pm 10.5$ kg and surface area/mass ranged from 0.016-0.026 kg m<sup>-2</sup> with a mean of  $0.021 \pm 0.002$  kg m<sup>-2</sup>. There was no significant difference between climates for each course (p>0.05, paired t-test).

**Table 8. 2.** Summary of the mean mass and surface area/mass ratio for each course and climate. Both mass and surface area/mass ratio change with climate due to mass changed experienced during NOLS courses.

<i>Course</i>	<i>Climate</i>	<i>Mass (kg)</i>	<i>Surface area/mass (kg m<sup>-2</sup>)</i>
WSS1	Temperate	$76.0 \pm 10.7$	$0.023 \pm 0.002$
WSS1	Hot	$78.7 \pm 9.7$	$0.023 \pm 0.002$
WSS2	Temperate	$70.8 \pm 7.5$	$0.025 \pm 0.002$
WSS2	Hot	$72.5 \pm 8.4$	$0.024 \pm 0.003$
FSR5	Temperate	$73.7 \pm 9.9$	$0.022 \pm 0.003$
FSR5	Cold	$76.1 \pm 8.8$	$0.023 \pm 0.003$
FSR8	Temperate	$73.8 \pm 15.1$	$0.020 \pm 0.002$
FSR8	Cold	$72.4 \pm 11.8$	$0.020 \pm 0.002$

The NOLS population was compared to temperate (N=16), hot (N=32) and cold (N=7) climate peoples whose morphological measurements were obtained from the literature. Temperate in this case is defined as 30°-50° absolute latitude; hot climates are defined as 0°-30° latitude; and cold climates are above 50° absolute latitude. Linear regressions followed by Tukey's pair-wise comparisons of height, weight, and bi-iliac breadth reveal that the NOLS population is significantly ( $p < 0.001$ ) taller and heavier ( $p < 0.02$ ) than the populations in the three other climates ( $F=35.967$ ,  $p < 0.001$  for height;  $F=28.113$ ,  $p < 0.001$  for weight). The bi-iliac breadth for the NOLS population was not significantly different from cold and temperate climates, but was significantly higher ( $p < 0.001$ ) than bi-iliac breadths in hot climates ( $F=23.666$ ,  $p < 0.001$ ). Please refer to **Table 8.3** for a summary of the differences and statistical significances of height, weight and bi-iliac breadth.

**Table 8.3.** Summary of the differences in height, weight and bi-iliac breadth between the NOLS population and the cold, hot and temperate peoples, calculated as (NOLS – indigenous population). Differences highlighted in red and bolded are statistically significant.

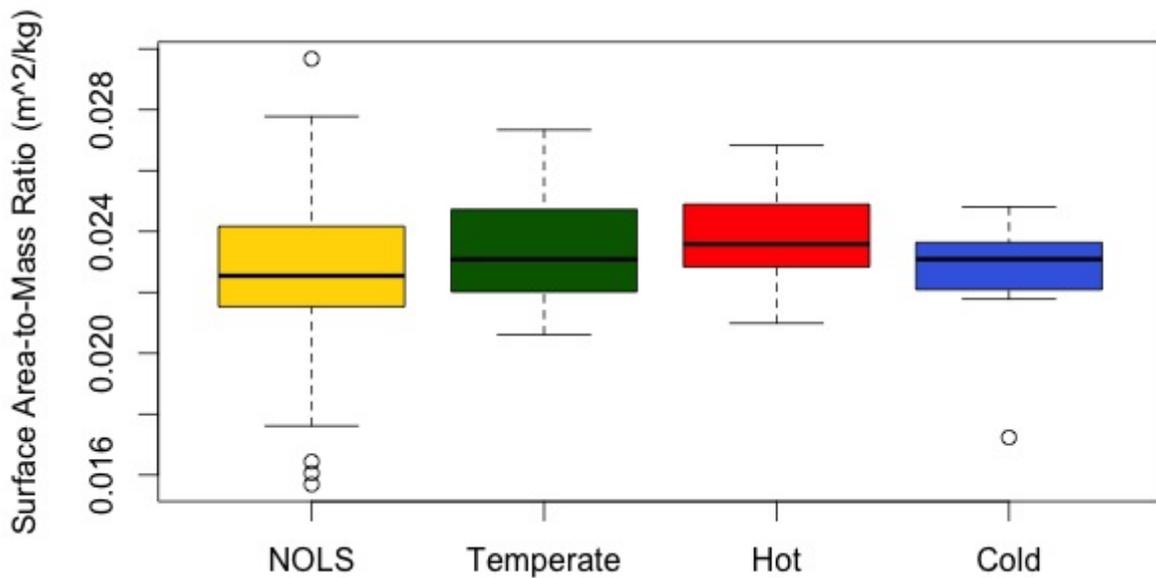
	<i>Height (cm)</i>	<i>Weight (kg)</i>	<i>Bi-Iliac Breadth (cm)</i>
<i>NOLS – Temperate</i>	<b>16</b>	<b>6.95</b>	0.03
<i>NOLS – Hot</i>	<b>18</b>	<b>19.6</b>	<b>3.70</b>
<i>NOLS – Cold</i>	<b>16</b>	<b>13.02</b>	1.31

The cylindrical method was used to calculate surface area of the temperate, hot, and cold climate peoples (Ruff 1991). The mean temperate NOLS surface area/mass ratio is  $0.022 \pm 0.003$   $\text{kg m}^{-2}$ ,  $0.024 \pm 0.002$   $\text{kg m}^{-2}$  for people from temperate climates,  $0.024 \pm 0.002$   $\text{kg m}^{-2}$  for people from hot climates and  $0.022 \pm 0.002$   $\text{kg m}^{-2}$  for people from cold climates. **Table 8.4** provides a summary of the temperate, hot and cold populations. **Fig. 8.2** shows the distribution of surface area/mass ratio for the temperate NOLS, temperate, hot, and cold climates.

A linear regression of surface area/mass and climate followed by Tukey's pair-wise comparisons of the surface area/mass ratio reveals that the temperate NOLS surface area/mass

ratio is not significantly different from that of people from temperate and cold climates, but is significantly lower ( $p < 0.03$ ) than that of people from hot climates ( $F = 22.280$ ,  $p < 0.001$ ). **Table 8.5** describes the results of the linear regression in detail. Individual details of mass, height, bi-iliac breadth, surface areas, and surface area/mass ratio values collected from the literature for temperate, hot, and cold climates can be found in *Appendix 9*.

**Figure 8. 2.** Summary of the distribution of the surface area/mass ratio for the temperate NOLS population as well as for people from different climates collected from the literature. Temperate NOLS surface area/mass ratio ranged from 0.016-0.030  $\text{kg m}^{-2}$ . Temperate climate surface area/mass ratio ranged from 0.021-0.027  $\text{kg m}^{-2}$ . Hot climate surface area/mass ratio ranged from 0.021-0.027  $\text{kg m}^{-2}$ . Cold climate surface area/mass ratio ranged from 0.017-0.025  $\text{kg m}^{-2}$ .



**Table 8. 4.** Surface area and surface area/mass summary for the temperate, hot and cold populations gathered from the literature. <sup>1</sup>Eveleth and Tanner 1976, <sup>2</sup>Laughlin 1951, <sup>3</sup>Vincent et al. 1962, <sup>4</sup>Ruff 1994, <sup>5</sup>Froment and Hiernaux 1984, <sup>6</sup>Cavalli-Sforza 1986, <sup>7</sup>Abbie 1956-1957, <sup>8</sup>Ghesquiere and Karvonen 1981.

<i>Population</i>	<i>Individuals</i>	<i>Climate</i>	<i>Surface Area (m<sup>2</sup>)</i>	<i>Surface Area/Mass Ratio (m<sup>2</sup> kg<sup>-1</sup>)</i>
Eskimo <sup>1</sup>	19 (M=10, F=9)	Cold	1.55 ± 0.13	0.027 ± 0.002
Aleut <sup>2</sup>	2 (M=1, F=1)	Cold	1.50 ± 0.08	0.022 ± 0.001
Belgian <sup>1</sup>	2 (M=1, F=1)	Cold	1.48 ± 0.12	0.024 ± 0.001
Irish <sup>1</sup>	1 (F)	Cold	1.47	0.024
Sara <sup>1</sup>	2 (M=1, F=1)	Hot	1.39 ± 0.08	0.022 ± 0.001
Tutsi <sup>1</sup>	2 (M=1, F=1)	Hot	1.32 ± 0.15	0.024 ± 0.002
Hutu <sup>1</sup>	1 (F)	Hot	1.15	0.022
Mbuti Pygmy <sup>3,4</sup>	2 (M=1, F=1)	Hot	1.07 ± 0.12	0.026 ± 0.0004
Bayenga <sup>3</sup>	1 (F)	Hot	1.22	0.022
Sahalian <sup>5</sup>	2 (M=1, F=1)	Hot	1.32 ± 0.08	0.024 ± 0.001
Sudanian <sup>5</sup>	2 (M=1, F=1)	Hot	1.31 ± 0.05	0.024 ± 0.001
W. Aka Pygmy <sup>6</sup>	2 (M=1, F=1)	Hot	1.14 ± 0.05	0.025 ± 0.001
Bagandu/Issongo <sup>6</sup>	2 (M=1, F=1)	Hot	1.22 ± 0.05	0.023 ± 0.0004
Karkar <sup>1</sup>	2 (M=1, F=1)	Hot	1.28 ± 0.08	0.025 ± 0.002
Lufa <sup>1</sup>	2 (M=1, F=1)	Hot	1.28 ± 0.09	0.024 ± 0.001
Australian Aborigine <sup>7</sup>	2 (M=1, F=1)	Hot	1.30 ± 0.12	0.026 ± 0.002
Fulero <sup>1</sup>	1 (M)	Hot	1.19	0.025
Venda <sup>1</sup>	1 (M)	Hot	1.35	0.022
Kivu Twa Pygmy <sup>8</sup>	1 (M)	Hot	1.16	0.025
Shi&Havu <sup>8</sup>	1 (M)	Hot	1.29	0.023
Katanga <sup>1</sup>	1 (M)	Hot	1.27	0.022
Kasai <sup>1</sup>	1 (M)	Hot	1.32	0.022
Algerian <sup>1</sup>	1 (M)	Hot	1.50	0.023
Ethiopian <sup>1</sup>	2 (M)	Hot	1.36 ± 0.05	0.025 ± 0.00001
Indian <sup>1</sup>	1 (M)	Hot	1.32	0.027
Lau <sup>1</sup>	1 (M)	Hot	1.60	0.021
Bulgarian <sup>1</sup>	4 (M=2, F=2)	Temperate	1.44 ± 0.07	0.023 ± 0.0001
Czech <sup>1</sup>	1 (F)	Temperate	1.42	0.021
French <sup>1</sup>	1 (F)	Temperate	1.50	0.027
Sardinian <sup>1</sup>	1 (F)	Temperate	1.34	0.026
Rumanian <sup>1</sup>	2 (M=1, F=1)	Temperate	1.44 ± 0.09	0.025 ± 0.001
Japanese <sup>1</sup>	2 (M=1, F=1)	Temperate	1.39 ± 0.08	0.026 ± 0.001
Kurdish Jew <sup>1</sup>	2 (M=1, F=1)	Temperate	1.39 ± 0.09	0.022 ± 0.0001
Yeminite Jew <sup>1</sup>	2 (M=1, F=1)	Temperate	1.26 ± 0.05	0.023 ± 0.002
Danish <sup>1</sup>	1 (M)	Temperate	1.54 m <sup>2</sup>	0.021 m <sup>2</sup> kg <sup>-1</sup>
Algerian <sup>1</sup>	1 (M)	Temperate	1.50 m <sup>2</sup>	0.023 m <sup>2</sup> kg <sup>-1</sup>

**Table 8. 5.** Summary of the linear regression pair-wise results for surface area/mass ratios of NOLS, temperate, hot and cold climates. All significant results are in bold and red. The NOLS population surface area/mass ratio was significantly lower than hot climates, but not significantly different from the temperate and cold climates.

	<i>Temperate</i>	<i>Hot</i>	<i>Cold</i>
<i>NOLS</i>	p=0.313	<b>p=0.031</b>	p=0.99
<i>Temperate</i>		p=0.963	p=0.667
<i>Hot</i>			p=0.398

The NOLS population has a surface area/mass range that includes the ranges of temperate, hot and cold climates. This makes the NOLS population a reasonable sample with which to analyze the potential impact body shape and size have on thermoregulatory cost in a variety of environments.

*Surface area/mass ratio and thermoregulatory costs in hot and cold climates*

This section aims to determine if there is a relationship between the surface area/mass ratio and thermoregulatory costs in hot and cold climates among the NOLS population as implied by Bergmann’s and Allen’s rules. If these ecogeographical rules confer an energetic advantage, it is expected that subjects with low surface area/mass ratios would expend less energy in cold climates and more in hot climates compared to subjects with high surface area/mass ratios. The inverse would be true for subjects with high surface area/mass ratios.

The components of energy expenditure that are affected by environmental temperature are basal metabolic rate and thermoregulatory costs as discussed in chapters two and three. Activity and thermic effect of food (TEF) costs were subtracted from TEE to leave only BMR and thermoregulation costs (TEE-(Activity+TEF)). For further analysis this term is referred to as thermoregulatory costs. The sum of BMR and thermoregulation was not used because surface area was one of the variables used in estimating the cost of thermoregulation. Using this sum

would create an artificial relationship between thermoregulatory costs and the surface area/mass ratio.

In temperate climates, thermoregulatory costs ranged from 1609-2748 kcal day<sup>-1</sup> with a mean of 2167±297 kcal day<sup>-1</sup>. In hot climates, thermoregulatory costs ranged from 1591-2380 kcal day<sup>-1</sup> with a mean of 1988±211 kcal day<sup>-1</sup>. In cold climates, thermoregulatory costs ranged from 1671-3353 kcal day<sup>-1</sup> with a mean of 25517±422 kcal day<sup>-1</sup>. Table 8.6 provides a thermoregulatory cost summary for each course and climate.

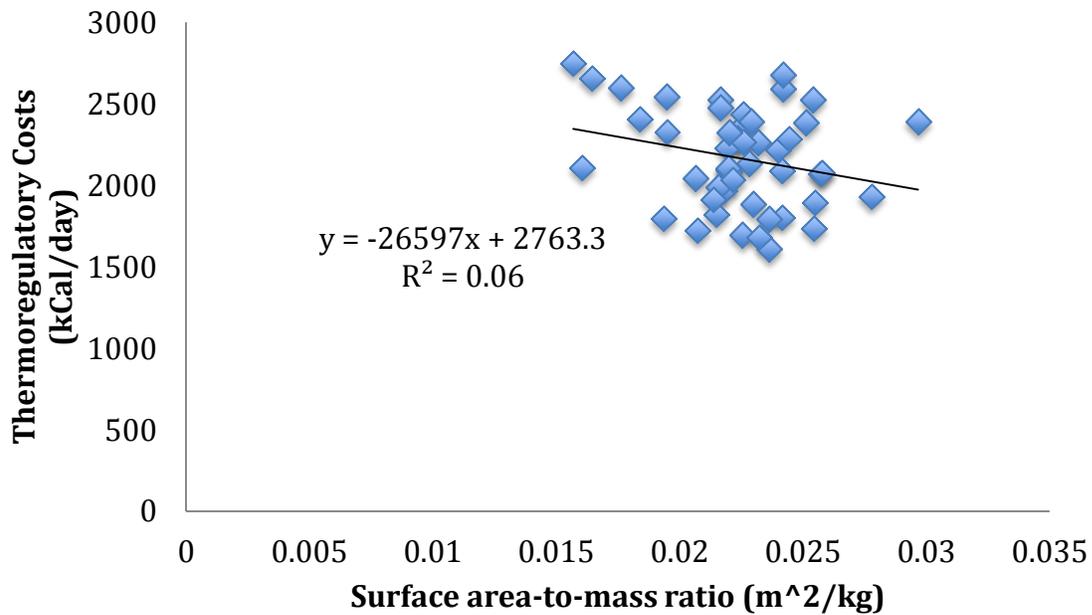
**Table 8. 6.** Summary of mean thermoregulatory costs (kcal day<sup>-1</sup>) for each course and climate.

<i>Course</i>	<i>Climate</i>	<i>N</i>	<i>Mass (kg)</i>	<i>Thermoregulatory Costs</i>
WSS1	Temperate	13	74.0±10.3	2170±249
WSS1	Hot	11	79.5±9.0	2077±210
WSS2	Temperate	11	68.9±7.67	2405±192
WSS2	Hot	11	72.1±8.4	1900±171
FSR5	Temperate	12	73.2±9.6	2050±226
FSR5	Cold	10	75.2±8.8	2376±371
FSR8	Temperate	14	73.3±14.7	2079±348
FSR8	Cold	13	72.0±11.4	2725±396

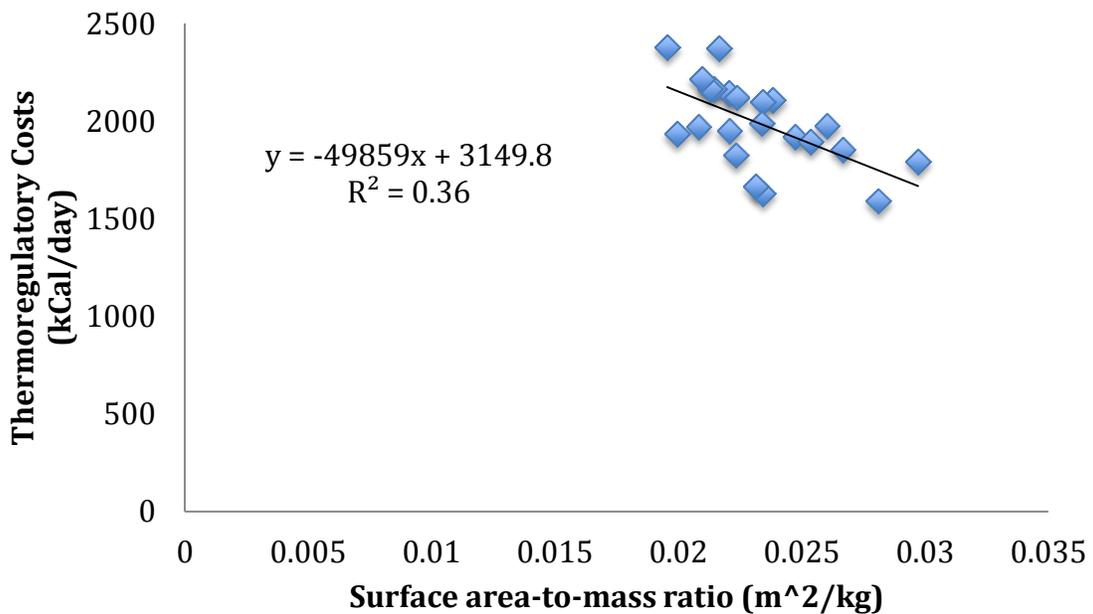
A linear regression was performed to determine the relationship between the surface area/mass ratio and thermoregulatory costs in temperate, hot and cold climates. Surface area/mass was not significantly related to thermoregulatory costs in temperate climates (p=0.09, F=2.956), though there was the tendency for thermoregulatory costs to decrease with increasing surface area (**Fig. 8.3**). Surface area/mass was significantly related to thermoregulatory costs in hot climates (p=0.003, F=11.245, Bonferroni corrected  $\alpha=0.017$ ). **Figure 8.4** depicts this relationship where thermoregulatory costs decrease with increasing surface area/mass ratio. This correlation was not significant in cold climates (p=0.09, F=3.107) (**Fig. 8.5**). The results are similar when regressing surface area/mass against estimated thermoregulatory costs when zero activity is assumed. There was no significant relationship between surface area/mass in

temperate ( $p=0.08$ ,  $F=5.782$ ) or cold climates ( $p=0.07$ ,  $F=3.427$ ), but there was a significant relationship in hot climates ( $p<0.01$ ,  $F=12.638$ , Bonferroni corrected  $\alpha=0.017$ ).

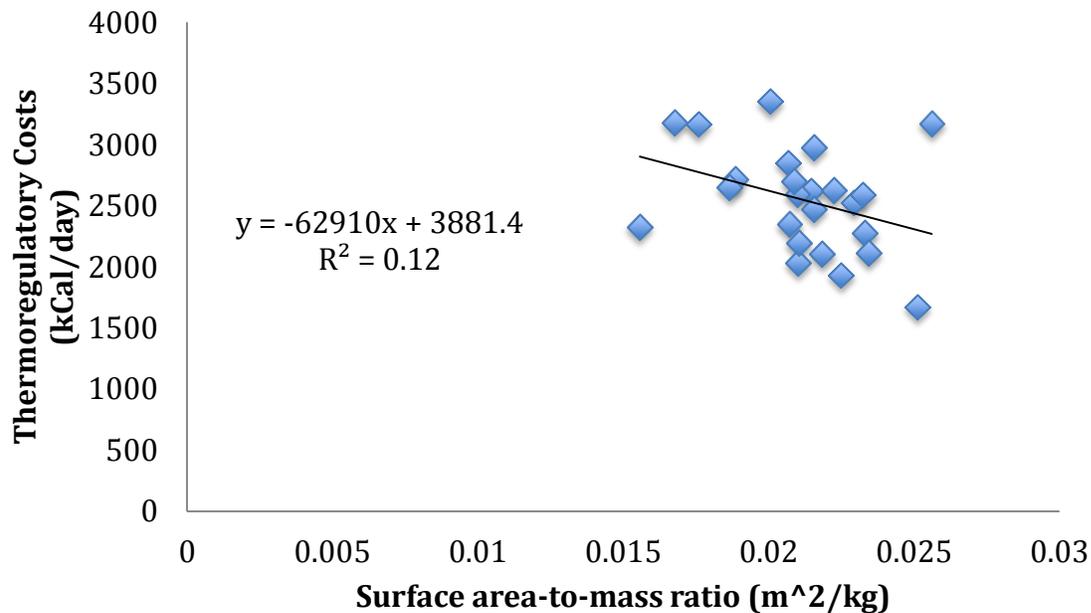
**Figure 8. 3.** There is no relationship between thermoregulatory costs and surface area/mass ratios in temperate climates ( $p=0.09$ ).



**Figure 8. 4.** Thermoregulatory costs decrease with increase surface area/mass ratios in hot climates ( $p=0.003$ ).

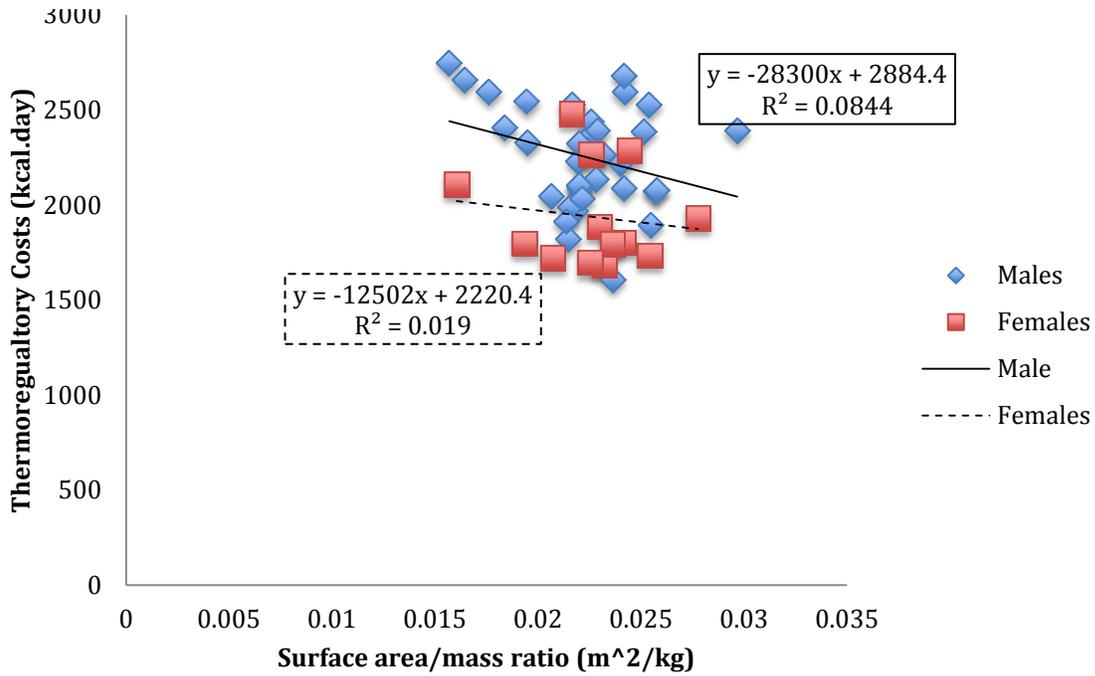


**Figure 8. 5.** There is no relationship between thermoregulatory costs and surface area/mass ratios in cold climates ( $p=0.09$ ).

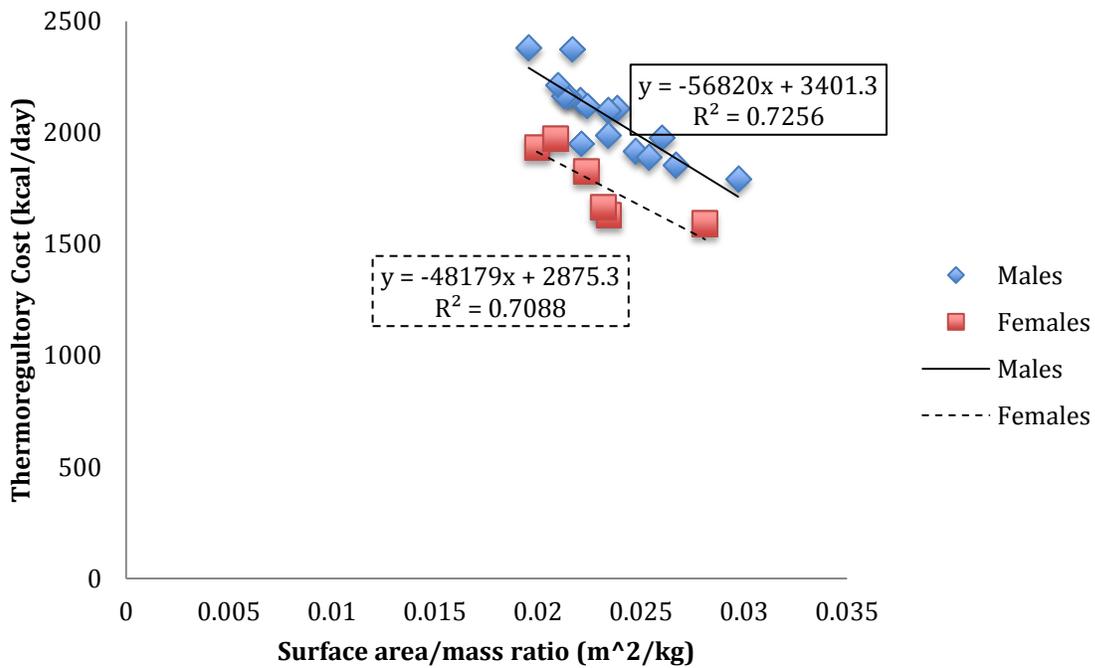


When looking at the sexes separately, we see some similarities to the pattern from the group as a whole. There was no significant relationship between thermoregulatory costs and surface area/mass in men or women in temperate climates (**Fig. 8.6**) ( $p=0.09$ ,  $F=3.042$ ,  $p=0.653$ ,  $F=0.214$  respectively). In hot climates, there was a significant relationship between thermoregulatory costs and surface area/mass ratios in men, but not in women (**Fig. 8.7**) ( $p<0.001$ ,  $F=36.996$ ,  $p=0.036$ ,  $F=9.678$  respectively, Bonferroni corrected  $\alpha=0.017$ ). Thermoregulatory costs decreased with increasing surface area. In the cold climate, there was no significant relationship between thermoregulatory costs and surface area/mass ratios in men, but there was a significant relationship in women (**Fig. 8.8**) ( $p=0.069$ ,  $F=3.801$ ,  $p=0.009$ ,  $F=1.886$  respectively, Bonferroni corrected  $\alpha=0.017$ ). Thermoregulatory costs decreased with increasing surface area.

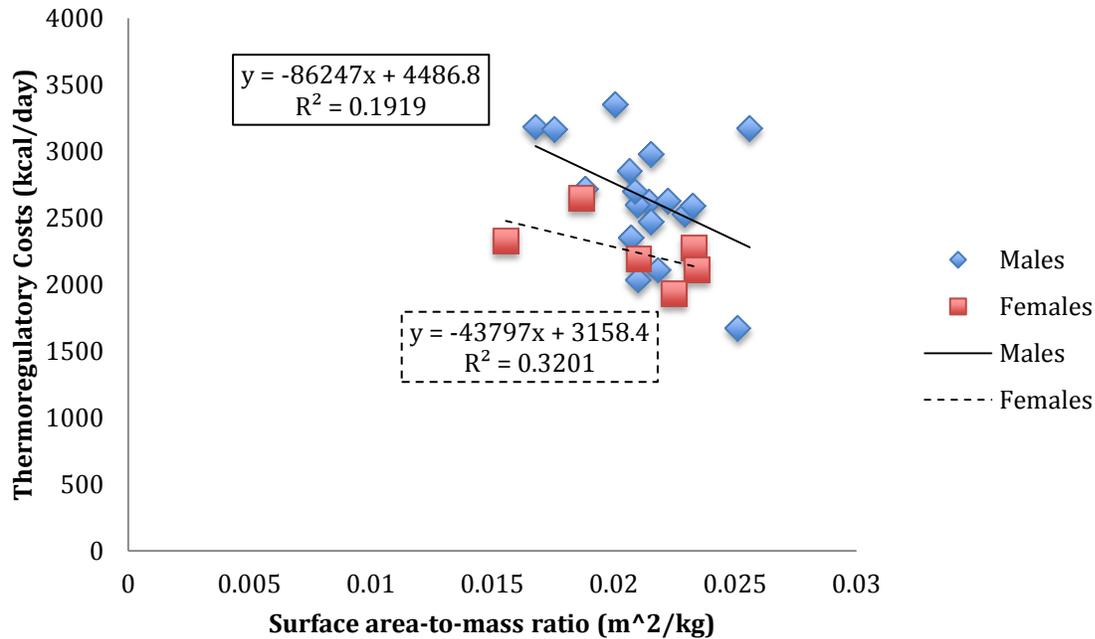
**Figure 8. 6.** There is no relationship between thermoregulatory costs and surface area/mass ratios in temperate climates among males or females. ( $p=0.09$ ,  $F=3.042$ ,  $p=0.653$ ,  $F=0.214$  respectively)



**Figure 8. 7.** Thermoregulatory costs decrease with increase surface area/mass ratios in hot climates for males but not females ( $p<0.001$ ,  $F=36.996$ ,  $p=0.036$ ,  $F=9.678$  respectively, Bonferroni corrected  $\alpha=0.017$ ).



**Figure 8. 8.** Thermoregulatory costs decrease with increase surface area/mass ratios in cold climates for females but not males ( $p < 0.009$ ,  $F = 1.886$ ,  $p = 0.069$ ,  $F = 3.801$  respectively, Bonferroni corrected  $\alpha = 0.017$ ).



### Discussion

The NOLS population has a surface area/mass ratio that is not significantly different than comparative samples from temperate and cold climates, but is significantly lower than that of people from hot climates. However, the range of surface area/mass within the NOLS population is large, and includes the ranges of native populations from temperate, hot, and cold climates. This makes NOLS a reasonable population with which to test the possible energetic implications of Bergmann's and Allen's Rules. It is expected that if the ecogeographical rules conferred an energetic advantage, NOLS subjects with a low surface area/mass ratio would expend less energy in the cold portion of their course than students with a higher surface area/mass ratio. Subjects with a high surface area/mass ratio would expend less energy in hot climates than their low surface area/mass ratio course-mates. Only one of these two expectations held to be true. In hot climates, thermoregulatory costs decreased with increasing surface area/mass ratios. There

was no significant relationship between thermoregulatory costs and surface area/mass ratios in either temperate or cold climates. However, counter to expectation, both the temperate and cold climates showed a trend of decreasing thermoregulatory costs with increasing surface area/mass ratios similar to what is seen in the hot climate. These results are suggestive of the importance of cultural and technological buffering against the elements.

Humans have been described as a tropical animal, such that human physiology is better suited for warm and moderate climates with limited ability to physiologically cope with cold climates (Havenith 1999, 2002). As such, humans have been able to occupy cold environments only through the inclusion of cultural and technological buffering. The use of clothing, shelter, and heating technologies have made just about any part of the planet habitable for humans (Havenith 2002). The NOLS population studied here had limited access to climate buffering technology. This is particularly true for the hot climate portion of their courses. Students were living outside with only trees and tents for shelter. They had no available cooling devices except for shade, when available, and plenty of drinking water. The hot climate part of the course, with respect to climate buffering technology, was the closest to conditions found in non-industrialized, hot climate regions. Subjects in the hot climates were fully exposed to the elements, daily temperatures of which could and did top 45°C. Without modern day technology, subjects relied almost solely on physiological mechanisms for maintaining body temperature. Because of this, it is of little surprise that there was a significant relationship between surface area/mass ratios and thermoregulatory costs in the hot climate as would be expected from the predictions of ecogeographical rules. The lack of significance seen among females may be due to the small sample size of women in this study.

The cold climate portion of the NOLS courses did not have access to heating technologies; however, they did have wind-proof tents as well as many, many layers of clothing specifically designed to withstand the elements of cold climates. Because of this, subjects in the cold climate did not have to rely so heavily upon their limited physiological mechanisms for mitigating cold stress. Furthermore, the fact that subjects wore so many layers during the cold climates brings to light the topic of microclimates. The thick, insulating layers of clothing not only protect against heat loss to the environment but also create a microclimate between the body and the clothing (Havinth 2002, Gavin 2003).

The goal of clothing is to maintain a comfortable body temperature (Gavin 2003). Changes in clothing insulation or body temperature will lead to changes in the microclimate temperature, possibly outside of the range of comfortable temperatures (Gavin 2003). For example, activity increases internal body temperature, and in the presence of heavy insulating clothing, the body cannot dissipate the excess body heat, which can lead to sweating and discomfort. This is particularly important in the NOLS population since activity levels were so high, greater than 36% of TEE, in the cold climates (please refer the previous chapter for further details). The high levels of activity and clothing insulation likely created a microclimate similar to the hot climates experienced by other NOLS subjects such that temperatures above the thermal comfort zone were experienced despite average environmental temperatures of  $-9^{\circ}\text{C}$ . Subjects dealt with this artificial ambient temperature much like those in the hot environments – through physiological mechanisms of heat dissipation. This explains the trend of decreasing thermoregulatory costs with increasing surface area/mass ratios, and the significant relationship found in women. However, this brings to light an issue with the Allocation Model. It does not differentiate between thermoregulatory costs designated for keep the body warm or cooling it

down. With the use of highly specialized clothing in combination with activity it is likely that during the cold portion of the course subjects experienced heat stress. Including skin and core body temperature measurements during data collection would help to differentiate between thermoregulatory costs associated with either raising or lowering body temperature.

The relationship of body shape and size is particularly important when humans encounter hot environments whether natural or artificially produced. Humans, in this study, with a greater surface area/mass ratio are energetically thrifty in hot climates. Furthermore, there is evidence that a greater surface area/mass ratio is advantageous for heat dissipation while heavily insulated from cold environments. A comparison of thermoregulatory costs in hot, humid climates and hot, dry climates would aid our poor understanding of the metabolic response to different levels of humidity. Though there is not a significant relationship, in this case, between cold climates and body shape and size, it cannot be wholly disregarded. Further study with humans with more limited cultural buffering and lower activity levels, compared to the NOLS sample, would better elucidate the possible advantage a low surface area/mass ratio would confer in cold climates. This study suggests that there is a physiological aspect to Bergmann's and Allen's rules and requires further study.

## **CHAPTER 9: CONCLUSION**

My research presented here aims to better understand how, and by how much, humans expend energy. From this work, several conclusions can be drawn about how to best measure and predict human energy expenditure as well as the differential energy demands encountered in a variety of environments. This chapter discusses the results of each analysis and their implications separately, and also attempts to integrate them into a broader context.

### ***Better total energy expenditure prediction through the Allocation Model***

One of the chief goals of this research was to produce a new model, the Allocation Model,

$$TEE = BMR + Activity + Thermoregulation + Thermic Effect of Food$$

that better predicted human energy expenditure than the current model used, the Factorial Method. Over different levels of activity and across environments, the Allocation Model produces a slope that is not significantly different from the ideal slope of 1.0, or identity. However, when the climates are analyzed separately, only for the cold climate is the slope not significantly different from identity. The Factorial Method was significantly different in all cases. The Allocation Model underestimates TEE by only 4.1% compared to the Factorial Method, which underestimates TEE by more than 25%. The Allocation Model also more accurately estimates TEE at high levels of energy expenditure where the Factorial Method has failed historically. For TEEs greater than 3000 kcal day<sup>-1</sup>, the Allocation Model produces a mean underestimate of less than 11% whereas the Factorial Method produces a mean underestimate greater than 31%. Furthermore, the Factorial Method does not produce TEE estimates greater than 4000 kcal day<sup>-1</sup>, but the Allocation Model is not bound by such a constraint.

This analysis has shown that the Allocation Model outperforms the Factorial Method for predicting human total energy expenditure in a variety of natural environments over a range of

activity levels. This suggests that the Allocation Model should be used in place of the Factorial Method for predicting total energy expenditure among humans, particularly if the study population is highly active. Since the Allocation Model is more explicit, including terms for basal metabolic rate, detailed activity costs, thermoregulation, and the thermic effect of food, it can be used to analyze how energy is allocated both within and between populations as well as whole energy budgets. Like the Factorial Method, the Allocation Model is mutable: new energetic terms, for example immune and reproductive costs, can be added or changed to improve accuracy and even tailored to a particular population or circumstance. The Allocation Model can also be used to more accurately estimate recommended caloric intakes for food aid and research, recreational, and military expeditions.

The Allocation Model enables us to view human evolution more accurately through an energetic lens. If the independent variables of body mass, body shape, and activity levels are accurately assessed, and with better paleo-environment and diet reconstructions, it is now possible to use the Allocation Model to more accurately estimate TEE and differential energy allocation of past hominins. The Allocation Model can be used to help analyze past hominin demographics and answer such questions as: What population size could the environment sustain given individual energy budgets? Given hominin energetic demand and environmental supply, what would we expect the maximum reproductive output to be? What level would hunting efficiency, i.e., energy spent hunting prey compared to energy consumed from captured prey, have to reach in order to sustain a certain population size? The Allocation Model can also be used to examine thermoregulatory stress, and perhaps gain insight into when cultural buffering would have been necessary for survival in certain climates.

As a whole, the Allocation Model helps to further our understanding of anatomical, physiological, and environmental interactions of modern humans as well as those experienced by past hominins. The Allocation Model, developed and tested here, has provided a new, inexpensive method for estimating total energy expenditure for humans. Though further validation is needed, it is a powerful new tool that will aid the study of humans and their ancestors.

### ***The need for further Flex-Heart Rate Method validation***

One unexpected result to come from this research is the poor TEE estimation by the Flex-Heart Rate method at high levels of energy expenditure. The Flex-HR method produced physiologically impossible TEEs ( $9000 \text{ kcal day}^{-1}$ ) for humans, which are  $2000 \text{ kcal day}^{-1}$  higher than the highest doubly labeled water measured TEE among humans (Hammond and Diamond 1997). Flex-HR has been validated among a number of different human populations, both healthy and unhealthy (Spurr et al. 1988, Ceesay et al. 1989, Livingstone et al. 1990, Livingstone et al. 1992, Lovelady et al. 1993, Leonard 2003). However, it has not been thoroughly evaluated at high levels of energy expenditure. Perhaps the Flex-HR method is unable to account for internal tradeoffs at high levels of energy expenditure, which is an issue that the Allocation Model seems to avoid. Data degradation and heart rate monitor interference along with TEE overestimations by the Flex-HR method warrant further research and validation. Also, previous studies that used the Flex-HR method need to be reassessed to determine if the calculated TEEs are overestimated as suggested by the work here. A reevaluation of these studies could bring to light not only different data and analysis, but possibly different conclusions.

### *Energy expenditure in different climates*

This research demonstrated it is metabolically expensive to live in cold climates, and that there is little to no difference between the energy budgets in hot and temperate climates. Both basal metabolic rate and thermoregulatory costs were significantly higher in the cold climates than in either the temperate or hot climates. It was found that predictive equations for basal metabolic rate underestimate measured values among the NOLS population. This underestimation could be due to an inability to take into account increased fitness (Speakman and Selman 2003), altitude and climatic conditions in which this population was living – variables all known to increase resting metabolic rate (Moran 2008). This further emphasizes the need for caution when using energy budget predictive equations that rely solely upon basal metabolic rate to produce predictions.

An unexpected result from this work was the amount of energy spent on activity in the cold climates compared to the other conditions. Activity costs comprised 36% of the total energy budget in cold climates compared to 21% and 14% in temperate and hot climates respectively. When the cost of activity was removed from the energy budget, there was no difference in the total energy expenditure of temperate, hot, and cold climates. In laboratory studies, the heat produced through activity has been implicated as potentially reducing thermoregulatory costs. To my knowledge, the study presented here is the first to demonstrate the importance of activity mitigating thermoregulatory costs for humans living in natural environments. Furthermore, this shows the utility of the Allocation Model to dissect total energy expenditure into its component parts in a way the doubly labeled water method, flex-heart rate method, or Factorial Method cannot. We can also have confidence in the results of the Allocation Model, as opposed to the

Factorial Method; because of its total energy expenditure estimates closely match those of the doubly labeled water method.

This has important implications for understanding mechanisms with which past hominins managed thermoregulatory stress. In the absence of cultural buffering such as thermally effective clothing to protect against the inherent dangers of cold climates, behavioral changes to increase activity levels may have been employed to maintain body core temperatures. Neanderthals, in particular, have been a focus of a number of studies regarding total energy expenditure estimation. Neanderthals have been estimated to have high activity costs relative to concurrent anatomically modern humans by as much as 30% (Steudel-Numbers and Tilkens 2004, Churchill 2006). These higher activity costs are associated with the large body mass and reduced lower limb lengths observed in Neanderthals suggested to be a cold climate adaptations for reducing body surface area (Trinkaus 1981). But, these cold adaptations also resulted in increased walking and running costs. (Steudel-Numbers and Tilkens 2004). The results I present here suggest that in cold climates, the high level and cost of Neanderthal activity could have effectively negated additional costs due to thermoregulation and perhaps even reduced any selective pressures for greater locomotor efficiency.

Understanding the importance of activity for survival in extreme cold conditions could allow for a post hoc analysis of the survivors and victims of failed Arctic, Antarctic, and mountaineering expeditions. Were the survivors the ones that kept moving even in the face of starvation and inclement weather? Were the victims the ones who decided to stay put and wait for help? These questions can be analyzed using the detailed correspondence, journals, and personal accounts of such expeditions. With further study and validation among indigenous populations and laboratory research, quantifying the importance of activity in extreme conditions

could allow for greater education prior to such expeditions, providing more detailed recommendations should the worst-case scenario come to pass.

This theory can also be applied to modern humans and past hominins in hot climates. Neanderthals were cold adapted with their short limbs which decreased heat loss and increased activity costs and thereby heat production. Modern humans and past hominin populations, *Homo ergaster* in particular, living in hot climates, are characterized by long limbs. These long limbs serve a two-fold purpose. First, they increased body surface area, which increases the ability to dissipate heat; second, they are adaptations for more efficient locomotor, walking and running, costs. More efficient locomotion would reduce the calories used and the heat produced during activity. This would effectively reduce the heat load burden during activity and the possibility of experiencing the negative and even fatal effects of hyperthermia (Shapiro et al. 1980, Moran 2008). This would have provided selective pressure for long limbs not only from an efficiency standpoint but also from a thermoregulatory one. The interaction between heat produced by activity and thermoregulatory costs adds an additional layer of complexity to Bergmann's and Allen's rules.

### ***An energetic advantage to Bergmann's and Allen's ecogeographical rules***

Bergmann's and Allen's rules define the types of body shape and size that are expected in different climates. Latitudinal clines in surface area/mass ratio have been well documented in humans, and it is suggested that a low ratio confers an advantage in cold climates, and a high ratio an advantage in hot climates. However, few studies have attempted to determine if there is an energetic advantage conferred by this potentially adaptive surface area/mass ratio. In the work presented here, I looked at whether differences in surface area/mass altered the energy budget of the NOLS study population living in hot and cold climates. The NOLS population had a wide

range of surface area/mass ratios allowing for this analysis to be conducted. As predicted by Bergmann's and Allen's rules, individuals with a higher surface area/mass ratio expended less energy in hot climates than those individuals with a low surface area/mass ratio. Counter to Bergmann's and Allen's rules, there was no significant relationship between surface area/mass in cold climates. Though there wasn't a significant relationship, there was a trend similar to what was seen in the hot climates, reduced total energy expenditure with increased surface area/mass.

These results highlight the theory that humans are a tropical animal with more physiological and anatomical mechanisms to cope with heat than with cold. In the absence of modern technology in hot climates, similar to the NOLS population, humans rely on their ability to dissipate heat through sweating and heat transfer, which are aided by increased body surface area. With limited physiological ability to maintain body temperature in cold climates, humans rely on cultural and behavioral mechanisms to survive in cold climates. The NOLS population utilized both highly advanced clothing designed for cold climates and high levels of activity to stay warm in the face of cold conditions. Interestingly, the combination of highly effective insulating clothing and heat produced through activity created a tropical-like microclimate between the subjects and their clothing. It is likely due to this warm microclimate that a trend for decreased energy expenditure with increased surface area/mass was observed. However, this study does not dispute the existence of even the adaptive need for lower surface area/mass ratios observed among indigenous cold-living populations.

The NOLS population is not the result of many generations born and raised in a cold climate; thus they would not have the adaptive morphology seen in indigenous cold populations today. There are a number of possibilities why lower surface area/mass persists among arctic populations despite climate buffering technology. First, developmental requirements should be

considered. Infants and small children cannot benefit from the heat produced through high levels of activity and rely on cultural buffering as well as their own anatomical and physiological mechanisms to reduce heat dissipation and produce heat. An example of this is the increased rate of macrosomia among indigenous Canadian infants described at the beginning of this thesis, this small change in fetal growth could provide a selective advantage. Second, this surface area/mass adaptation may exist to buffer against climatic extremes, such as a particularly inclement winter or severe storm, in which cultural and technological buffering can go only so far. Third, the daily lives of indigenous cold populations can drastically differ from that of the NOLS population. Hunting among these populations often requires staying still in one position for an extended period of time. This of course negates the possible heat producing benefits of activity, increasing the physiological demand to reduce heat dissipation and increase heat production.

Given the mixed results produced by this analysis, further research needs to be done looking into the impact of the surface area/mass ratio among less culturally buffered people in cold climates. Similar research needs to be done among indigenous populations of hot and cold climates with the possibility of conducting laboratory work with members of these populations under conditions opposite of that in which they live. Furthermore, work needs to be done to examine a possible relationship between total energy expenditure in different climates and distal limb segment lengths. A greater understanding of the relationships between energy expenditure, body shape and size and the environment will help us to better understand the morphological variation we see among fossil hominins across the globe.

### ***Life history strategies***

The Allocation Model can be used to assess human energy allocation differences between populations and between climates. Better understanding how humans and their ancestors

allocated energy can help us explore the subtle, and possibly adaptive, differences in life history strategies observed today. Environmental constraints lead to necessary energy tradeoffs. Limited resources could simultaneously demand increased activity levels to gather resources while also reducing reproductive output. Cold climates produce both resource limitation and increased energy demand for both metabolically and behaviorally mitigating the harsh environment, which can be assessed using the Allocation Model. Such constraints on Neanderthals and anatomically modern humans could have led to lower reproductive rates and offspring investment, leading to small population sizes which is supported by genetic evidence (Green et al. 2006, Eller et al. 2009). The Allocation Model can be used to assess the differential energy allocation necessary to survive in harsh climates and produce estimates for how much energy would have been available for reproduction. This would be a new way with which to examine Neanderthal and anatomically modern human ecology and demography.

The Allocation Model could also be used to assess the life history shift seen in human evolution. The human life history strategy differs from apes by having a longer life span; longer, dependent juvenile period; reproductive support by non-reproductive individuals; and male reproductive support through provisioning (Kaplan et al. 2000). It is argued that these life history shifts are the result of genus *Homo* focusing on large, calorie dense food items that require a high level of both skill and knowledge. Kaplan et al. (2000) suggest that this exploitation of high quality plant and animal resources produced selective pressures for both increased intelligence and an increased juvenile period with support of non-reproductive adults during which time juveniles learn the knowledge and skills required to survive. The specialized skills and knowledge associated with this type of food acquisition in a complex environment would have aided the development of social intelligence and the development of complex social relations

(Kaplan et al. 2000). At the heart of such developments is an increased brain size, which is well documented through the evolution of genus *Homo* (Aiello and Wheeler 1995). Work by Aiello and Wheeler (1995) has suggested that larger brain size and more complex development would have required both a higher number and quality of calories. This larger brain would also require an expanded juvenile period for brain growth to occur, and for juveniles to learn the knowledge and skills required to survive (Kaplan et al. 2000). The Allocation Model could be used to assess this life history strategy shift by allowing the dissection (cost of large brains and increased cost of high skilled food acquisition for example) and analysis of genus *Homo* and early modern human energy budgets. This enables a more detailed and energetics focused analysis of life history strategies.

### ***Summary***

The Allocation Model is a powerful new tool with the ability to better, and more easily assess the energy budgets of modern humans and their ancestors. It has been used here to examine the energy allocation details of highly active people living in temperate, hot and cold climates. From this analysis, the importance of activity for keeping warm in cold climates was revealed. The Allocation Model was also used here to examine the potential energetic advantage of Bergmann's and Allen's rules. The results described an energetic advantage of a high surface area/mass ratio in hot climates, but no clear relationship between body proportions and energy expenditure in cold climates. The entirety of the research conducted here and the future questions it poses and directions it leads aid our understanding of how interactions between the environment, physiology, anatomy and culture has helped drive human evolution and continues to shape the way we live today.

## APPENDICES

*Appendix 1A.* Morphological data for all NOLS subjects collected during the Pre-Course Battery data collection.

<i>Subject</i>	<i>Sex</i>	<i>Age (yrs)</i>	<i>Height (m)</i>	<i>Leg Length (cm)</i>	<i>Weight (kg)</i>	<i>Fat %</i>	<i>Muscle Mass (kg)</i>	<i>Surface Area (m<sup>2</sup>)</i>
NS1-1	M	29	1.93	0.97	104.70	20.5	79.2	2.35
NS1-2	M	25	1.75	0.84	71.90	7.7	63.1	1.87
NS1-3	F	19	1.70	0.85	69.10	23.0	50.5	1.80
NS1-4	F	25	1.62	0.84	58.60	15.5	47.0	1.62
NS1-5	M	36	1.88	0.95	81.10	11.4	68.3	2.07
NS1-6	M	19	1.87	1.01	68.80	5.9	61.6	1.92
NS1-7	M	18	1.89	0.93	83.70	6.4	74.5	2.10
NS1-8	F	19	1.64	0.87	67.00	23.7	48.5	1.73
NS1-9	M	20	1.82	0.94	83.30	8.6	72.4	2.05
NS1-10	F	20	1.55	0.83	81.90	32.1	52.8	1.81
NS1-11	M	19	1.78	0.95	64.20	9.1	55.1	1.80
NS1-12	M	21	1.86	0.93	90.70	15.9	72.6	2.16
NS1-13	M	19	1.85	0.87	76.70	6.7	68.1	2.00
NS1-14	M	20	1.80	0.89	78.30	10.7	66.5	1.98
NS2-1	F	20	1.68	0.84	64.8	23.0	47.4	1.74
NS2-2	M	29	1.85	0.97	85.3	15.7	68.4	2.09
NS2-3	F	21	1.7	0.90	74.1	26.1	50.6	1.85
NS2-4	F	20	1.72	0.90	56.4	14.6	45.7	1.66
NS2-5	M	24	1.79	0.90	67.1	10.0	57.4	1.85
NS2-6	M	20	1.875	0.95	74.1	5.0	67.0	1.99
NS2-7	M	18	1.74	0.91	63.8	10.8	54.1	1.77
NS2-8	F	19	1.76	0.89	88.6	33.2	56.2	2.05
NS2-9	M	21	1.825	0.98	62.1	10.6	52.7	1.81

NS2-10	M	18	1.795	0.93	73.2	5.6	63.6	1.92
NS2-11	M	19	1.79	0.92	65.3	5.8	58.4	1.82
FS5-1	M	29	1.88	0.97	74.8	8.7	64.9	2.00
FS5-2	M	19	1.78	0.90	68.5	14.7	55.5	1.85
FS5-3	M	20	1.82	0.89	84	10.3	71.7	2.05
FS5-4	M	20	1.83	0.96	75.8	12.8	62.8	1.97
FS5-5	F	20	1.68	0.82	61.7	22.5	45.4	1.70
FS5-6	F	18	1.68	0.85	70.2	28.3	47.8	1.80
FS5-7	M	21	1.72	0.87	78.1	15.9	62.4	1.91
FS5-9	F	20	1.73	0.88	86.3	31.7	56.0	2.00
FS5-10	M	20	1.84	0.98	77.6	12.2	64.8	2.00
FS5-11	M	22	1.88	0.93	73.6	5.0	66.4	1.99
FS5-12	F	18	1.69	0.87	65.8	23.0	48.1	1.76
FS5-13	F	22	1.74	0.98	65.5	21.2	49.0	1.79
FS5-15	M	21	1.92	0.94	100.8	16.8	79.8	2.31
FS5-16	M	18	1.75	0.91	63.5	6.0	56.8	1.77
FS8-1	M	31	1.73	0.87	69.6	12.0	58.3	1.83
FS8-2	M	18	1.74	0.90	55.9	5.0	50.4	1.67
FS8-3	M	18	1.79	0.87	107.8	27.4	74.5	2.26
FS8-4	M	18	1.86	0.95	113.1	24.7	81.1	2.37
FS8-5	M	18	1.75	0.87	68.4	6.4	60.8	1.83
FS8-6	M	18	1.97	1.01	82.4	6.9	72.9	2.16
FS8-7	F	18	1.72	0.87	59.9	14.6	48.6	1.71
FS8-8	M	19	1.78	0.92	60.5	5.0	54.6	1.76
FS8-9	M	19	1.81	0.93	71.3	13.1	58.9	1.91
FS8-10	M	18	1.77	0.91	74.4	13.9	60.8	1.91
FS8-11	F	18	1.71	0.89	62.7	19.3	48.0	1.73
FS8-12	M	19	1.85	0.93	89.6	13.5	73.7	2.14
FS8-13	M	18	1.72	0.88	64.6	13.5	53.1	1.76
FS8-14	F	18	1.61	0.83	64.4	28.8	43.5	1.68

Pilot 1	F	31	1.65	0.83	71.6	29.4	48.1	1.78
Pilot 2	F	29	1.55	0.78	60.0	27.3	41.4	1.59
Pilot 3	M	25	1.66	0.88	70.2	9.5	60.4	1.78
Pilot 4	M	21	1.79	0.90	73.7	7.1	65.1	1.92
Pilot 5	M	44	1.72	0.89	75.1	12.0	62.8	1.88
Pilot 6	F	23	1.80	0.96	73.6	26.8	52.2	1.93

**Appendix 1B.** Morphological data for all NOLS subjects collected during the Mid-Course Battery data collection.

<i>Subject</i>	<i>Sex</i>	<i>Age (yrs)</i>	<i>Height (m)</i>	<i>Leg Length (cm)</i>	<i>Weight (kg)</i>	<i>Fat %</i>	<i>Muscle Mass (kg)</i>	<i>Surface Area (m<sup>2</sup>)</i>
NS1-1	M	29	1.93	0.97	96.1	13.9	78.7	2.27
NS1-2	M	25	1.75	0.84	67.8	5.4	60.9	1.82
NS1-4	F	25	1.62	0.84	56.2	12.9	46.5	1.59
NS1-5	M	36	1.88	0.95	76.4	7.3	67.3	2.02
NS1-6	M	19	1.87	1.01	71.5	8.3	62.3	1.96
NS1-7	M	18	1.89	0.93	72.3	5.0	65.3	1.98
NS1-8	F	19	1.64	0.87	64.7	14.2	52.7	1.70
NS1-9	M	20	1.82	0.94	77.0	8.8	66.7	1.98
NS1-10	F	20	1.55	0.83	81.9	32.1	52.8	1.81
NS1-11	M	19	1.78	0.95	61.5	6.5	54.6	1.77
NS1-12	M	21	1.86	0.93	89.9	12.5	74.8	2.15
NS1-13	M	19	1.85	0.87	76.2	6.0	68.1	1.99
NS1-14	M	20	1.80	0.89	74.5	8.5	64.8	1.94
NS2-1	F	20	1.68	0.84	65.5	21.2	49	1.74
NS2-2	M	29	1.85	0.97	84.5	11.8	70.9	2.08
NS2-3	F	21	1.70	0.90	73.5	25.6	51.9	1.85
NS2-4	F	20	1.72	0.90	60.2	14.7	48.7	1.71
NS2-5	M	24	1.79	0.90	69.3	5.8	62.1	1.87
NS2-6	M	20	1.88	0.95	74.4	6.0	66.4	1.99
NS2-7	M	18	1.74	0.91	67.8	7.7	59.5	1.82

NS2-8	F	19	1.76	0.89	89.0	32.8	56.8	2.06
NS2-9	M	21	1.83	0.98	61.7	8.4	53.7	1.81
NS2-10	M	18	1.80	0.93	75.7	7.0	66.9	1.95
NS2-11	M	19	1.79	0.92	71.1	9.3	61.3	1.89
FS5-1	M	29	1.88	0.97	73.5	5.6	66	1.99
FS5-2	M	19	1.78	0.90	65.1	6.8	57.6	1.81
FS5-3	M	20	1.82	0.89	79.8	8.1	69.7	2.01
FS5-4	M	20	1.83	0.96	73.1	6.7	64.8	1.94
FS5-5	F	20	1.68	0.82	63.2	22.6	46.5	1.72
FS5-6	F	18	1.68	0.85	67.4	24.1	48.6	1.77
FS5-7	M	21	1.72	0.87	76.1	10.9	64.4	1.89
FS5-9	F	20	1.73	0.88	84.6	30.0	56.2	1.99
FS5-10	M	20	1.84	0.98	76.0	8.0	66.5	1.98
FS5-11	M	22	1.88	0.93	73.3	5.0	66.2	1.99
FS5-12	F	18	1.69	0.87	65.8	27.1	45.5	1.76
FS5-13	F	22	1.74	0.98	64.8	13.5	53.3	1.78
FS5-15	M	21	1.92	0.94	99.3	14.8	80.5	2.29
FS5-16	M	18	1.75	0.91	63.0	5.5	56.5	1.77
FS8-1	M	31	1.73	0.87	69.2	11.9	58	1.82
FS8-2	M	18	1.74	0.90	58.3	5.0	52.6	1.70
FS8-3	M	18	1.79	0.87	99.2	23.5	72.2	2.18
FS8-4	M	18	1.86	0.95	108.0	20.9	81.3	2.32
FS8-5	M	18	1.75	0.87	66.2	5.0	59.7	1.80
FS8-6	M	18	1.97	1.01	82.5	5.0	74.6	2.16
FS8-7	F	18	1.72	0.87	61.4	15.4	49.4	1.73
FS8-8	M	19	1.78	0.92	61.5	5.0	55.5	1.77
FS8-9	M	19	1.81	0.93	71.8	9.6	61.6	1.91
FS8-10	M	18	1.77	0.91	72.7	11.0	61.4	1.89
FS8-11	F	18	1.71	0.89	60.1	15.8	48.1	1.70
FS8-12	M	19	1.85	0.93	85.3	8.7	74	2.09
FS8-13	M	18	1.72	0.88	63.4	7.9	55.4	1.75

FS8-14	F	18	1.61	0.83	65.9	20.4	49.8	1.70
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**Appendix 1C.** Morphological data for all NOLS subjects collected during the Post-Course Battery data collection.

<i>Subject</i>	<i>Sex</i>	<i>Age (yrs)</i>	<i>Height (m)</i>	<i>Leg Length (cm)</i>	<i>Weight (kg)</i>	<i>Fat %</i>	<i>Muscle Mass (kg)</i>	<i>Surface Area (m<sup>2</sup>)</i>
NS1-1	M	29	1.93	0.97	95.0	13.3	78.4	2.26
NS1-5	M	36	1.88	0.95	80.3	6.3	71.5	2.06
NS1-6	M	19	1.87	1.01	77.0	7.9	67.4	2.02
NS1-7	M	18	1.89	0.93	79.1	7.0	69.9	2.05
NS1-8	F	19	1.64	0.87	66.8	20.9	50.2	1.72
NS1-9	M	20	1.82	0.94	80.5	8.5	70.0	2.02
NS1-10	F	20	1.55	0.83	75.7	32.1	48.8	1.75
NS1-11	M	19	1.78	0.95	64.3	5.0	58.1	1.80
NS1-12	M	21	1.86	0.93	95.0	14.4	77.3	2.20
NS1-13	M	19	1.85	0.87	80.6	6.4	71.7	2.04
NS1-14	M	20	1.80	0.89	79.6	8.1	69.6	1.99
NS2-1	F	20	1.68	0.84	64.5	23.7	46.7	1.73
NS2-2	M	29	1.85	0.97	79.8	11.6	67.1	2.03
NS2-3	F	21	1.7	0.90	72.2	27.4	49.8	1.83
NS2-4	F	20	1.72	0.90	58.0	15.6	46.5	1.68
NS2-5	M	24	1.79	0.90	64.5	7.6	56.7	1.81
NS2-6	M	20	1.875	0.95	71.1	6.4	63.3	1.96
NS2-7	M	18	1.74	0.91	63.8	11.4	53.7	1.77
NS2-8	F	19	1.76	0.89	84.8	30.4	56.1	2.01
NS2-9	M	21	1.825	0.98	61.0	10.9	51.6	1.80
NS2-10	M	18	1.795	0.93	71.5	10.7	60.7	1.90
NS2-11	M	19	1.79	0.92	66.2	8.5	57.5	1.83
FS5-1	M	29	1.88	0.97	73.8	5.6	66.2	1.99
FS5-2	M	19	1.78	0.90	66.8	6.1	59.6	1.83
FS5-3	M	20	1.82	0.89	82.8	10.2	70.7	2.04
FS5-4	M	20	1.83	0.96	73.7	8.5	64.1	1.95

FS5-7	M	21	1.72	0.87	73.1	6.9	64.7	1.86
FS5-9	F	20	1.73	0.88	87.3	31.7	56.6	2.01
FS5-10	M	20	1.84	0.98	80.8	14.3	65.9	2.04
FS5-11	M	22	1.88	0.93	76.2	5.0	68.8	2.02
FS5-12	F	18	1.69	0.87	64.9	20.8	48.8	1.74
FS5-13	F	22	1.74	0.98	65.3	17.3	51.3	1.79
FS5-15	M	21	1.92	0.94	92.8	12.9	76.9	2.23
FS5-16	M	18	1.75	0.91	65.4	10.6	55.6	1.80
FS8-1	M	31	1.73	0.87	70.6	14.7	57.2	1.84
FS8-2	M	18	1.74	0.90	59.9	5.0	54.0	1.72
FS8-4	M	18	1.86	0.95	101.0	20.0	76.8	2.26
FS8-5	M	18	1.75	0.87	67.2	6.1	60.0	1.82
FS8-6	M	18	1.97	1.01	80.2	5.0	72.4	2.13
FS8-7	F	18	1.72	0.87	63.7	17.7	49.8	1.75
FS8-8	M	19	1.78	0.92	65.4	7.5	57.4	1.82
FS8-9	M	19	1.81	0.93	74.3	11.6	62.4	1.94
FS8-10	M	18	1.77	0.91	71.9	11.9	60.2	1.88
FS8-11	F	18	1.71	0.89	62.1	16.4	49.3	1.73
FS8-12	M	19	1.85	0.93	89.3	9.2	77.1	2.13
FS8-13	M	18	1.72	0.88	65.2	12.1	54.4	1.77
FS8-14	F	18	1.61	0.83	64.9	26.9	45.7	1.68
Pilot 1	F	31	1.645	0.83	68.7	23.5	49.8	1.75
Pilot 2	F	29	1.55	0.78	58.5	18.4	45.4	1.57
Pilot 3	M	25	1.66	0.88	66.8	7.9	58.5	1.74
Pilot 4	M	21	1.785	0.90	70.0	5.0	63.2	1.87
Pilot 5	M	44	1.72	0.89	69.7	6.3	62.1	1.82
Pilot 6	F	23	1.8	0.96	71.4	22.5	52.5	1.90

**Appendix 2.** Basal metabolic rate measurements and estimates ( $\text{kcal day}^{-1}$ ) for all NOLS subjects for temperate, hot and cold climates. Missing data indicates subjects who either were ill or sustained an injury and could not take part in measurements except in the case of subject from the Pilot study in which they only took part in one climate.

<i>Subject</i>	<i>Climate</i>	<i>mBMR</i>	<i>eBMR</i>	<i>Climate</i>	<i>mBMR</i>	<i>eBMR</i>
NS1-5	Temperate	2902	1799	Hot	2490	1827
NS1-1	Temperate	2368	2115	Hot	2404	2108
NS1-6	Temperate	2967	1707	Hot	1766	1787
NS1-7	Temperate	2441	1779	Hot	2721	1683
NS1-8	Temperate	1604	1400	Hot	1510	1427
NS1-9	Temperate	2562	1793	Hot	2445	1823
NS1-12	Temperate	3460	1972	Hot	2300	2033
NS1-13	Temperate	3329	1751	Hot	2874	1812
NS1-14	Temperate	3430	1764	Hot	2781	1809
NS1-2	Temperate	2770	1667			
NS1-4	Temperate	1651	1292			
NS2-2	Temperate	1787	1887	Hot	2313	1844
NS2-1	Temperate	1577	1446	Hot	1688	1399
NS2-3	Temperate	2209	1544	Hot	1844	1534
NS2-4	Temperate	1109	1339	Hot	1393	1348
NS2-5	Temperate	1675	1636	Hot	2544	1619
NS2-6	Temperate	2219	1772	Hot	2619	1732
NS2-7	Temperate	2211	1614	Hot	2234	1612
NS2-8	Temperate	1881	1723	Hot	2466	1723
NS2-9	Temperate	2026	1548	Hot	1869	1550
NS2-10	Temperate	2285	1771	Hot	2372	1727
NS2-11	Temperate	1686	1679	Hot	3193	1643
FS5-1	Temperate	1803	1721	Cold	4070	1726
FS5-2	Temperate	2587	1587	Cold	1280	1614
FS5-3	Temperate	2181	1822	Cold	2564	1870
FS5-4	Temperate	2164	1715	Cold	3906	1724
FS5-5	Temperate	1173	1386			
FS5-7	Temperate	2509	1763	Cold	3834	1715
FS5-9	Temperate	1499	1666	Cold	3185	1702
FS5-10	Temperate	2682	1761	Cold	3312	1838
FS5-11	Temperate	2189	1718	Cold	4870	1764
FS5-12	Temperate	1570	1420	Cold	2305	1408
FS5-13	Temperate	1994	1407	Cold	2784	1413
FS5-15	Temperate	2811	2134	Cold	4319	2030
FS5-16	Temperate	2096	1553	Cold	2820	1591
FS8-1	Temperate	2213	1652	Cold	2272	1675
FS8-2	Temperate	2097	1478	Cold	2515	1503

FS8-3	Temperate	2936	2132			
FS8-4	Temperate	2491	2273	Cold	3178	2161
FS8-6	Temperate	2704	1865	Cold	2887	1828
FS8-7	Temperate	1614	1362	Cold	2126	1392
FS8-8	Temperate	1946	1529	Cold	2522	1591
FS8-9	Temperate	1876	1694	Cold	2828	1734
FS8-10	Temperate	1985	1708	Cold	2354	1695
FS8-11	Temperate	1209	1345	Cold	2114	1372
FS8-12	Temperate	2873	1910	Cold	3622	1974
FS8-13	Temperate	1677	1559	Cold	2405	1588
FS8-14	Temperate	1636	1421	Cold	1493	1408
Pilot 1	Temperate	1728	1378			
Pilot 2	Temperate	2075	1334			
Pilot 4	Temperate	2675	1695			
Pilot 5	Temperate	2137	1583			
Pilot 6	Temperate	2061	1508			

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**Appendix 3.** Changes in body mass (kg), fat percentage and muscle mass (kg) for each subject after temperate, hot and cold climate portions of the courses.

<i>Subject</i>	<i>Climate</i>	<i>Sex</i>	<i>Age (yrs)</i>	<i>Height (m)</i>	<i>Weight (kg)</i>	<i>Fat %</i>	<i>Muscle Mass (kg)</i>
NS1-1	Temperate	M	29	1.93	-8.6	-6.6	-0.5
NS1-2	Temperate	M	25	1.75	-4.1	-2.3	-2.2
NS1-4	Temperate	F	25	1.62	-2.4	-2.6	-0.5
NS1-5	Temperate	M	36	1.88	-4.7	-4.1	-1
NS1-6	Temperate	M	19	1.87	2.7	2.4	0.7
NS1-7	Temperate	M	18	1.89	-11.4	-1.4	-9.2
NS1-8	Temperate	F	19	1.64	-2.3	-9.5	4.2
NS1-9	Temperate	M	20	1.82	-6.3	0.2	-5.7
NS1-10	Temperate	F	20	1.55	-4.2	3.4	-5.2
NS1-11	Temperate	M	19	1.78	-2.7	-2.6	-0.5
NS1-12	Temperate	M	21	1.86	-0.8	-3.4	2.2
NS1-13	Temperate	M	19	1.85	-0.5	-0.7	0
NS1-14	Temperate	M	20	1.80	-3.8	-2.2	-1.7
NS2-1	Temperate	F	20	1.68	-1.0	2.5	-2.3
NS2-2	Temperate	M	29	1.85	-4.7	-0.2	-3.8
NS2-3	Temperate	F	21	1.70	-1.3	1.8	-2.1
NS2-4	Temperate	F	20	1.72	-2.2	0.9	-2.2
NS2-5	Temperate	M	24	1.79	-4.8	1.8	-5.4
NS2-6	Temperate	M	20	1.88	-3.3	0.4	-3.1
NS2-7	Temperate	M	18	1.74	-4.0	3.7	-5.8
NS2-8	Temperate	F	19	1.76	-4.2	-2.4	-0.7
NS2-9	Temperate	M	21	1.83	-0.7	2.5	-2.1
NS2-10	Temperate	M	18	1.80	-4.2	3.7	-6.2
NS2-11	Temperate	M	19	1.79	-4.9	-0.8	-3.8
FS5-1	Temperate	M	29	1.88	-1.3	-3.1	1.1
FS5-2	Temperate	M	19	1.78	-3.4	-7.9	2.1
FS5-3	Temperate	M	20	1.82	-4.2	-2.2	-2

FS5-4	Temperate	M	20	1.83	-2.7	-6.1	2
FS5-5	Temperate	F	20	1.68	1.5	0.1	1.1
FS5-6	Temperate	F	18	1.68	-2.8	-4.2	0.8
FS5-7	Temperate	M	21	1.72	-2.0	-5	2
FS5-9	Temperate	F	20	1.73	-1.7	-1.7	0.2
FS5-10	Temperate	M	20	1.84	-1.6	-4.2	1.7
FS5-11	Temperate	M	22	1.88	-0.3	0	-0.2
FS5-12	Temperate	F	18	1.69	0.0	4.1	-2.6
FS5-13	Temperate	F	22	1.74	-0.7	-7.7	4.3
FS5-15	Temperate	M	21	1.92	-1.5	-2	0.7
FS5-16	Temperate	M	18	1.75	-0.5	-0.5	-0.3
FS8-1	Temperate	M	31	1.73	-0.4	-0.1	-0.3
FS8-2	Temperate	M	18	1.74	2.4	0	2.2
FS8-3	Temperate	M	18	1.79	-8.6	-3.9	-2.30
FS8-4	Temperate	M	18	1.86	-5.1	-3.8	0.20
FS8-5	Temperate	M	18	1.75	-2.2	-1.4	-1.10
FS8-6	Temperate	M	18	1.97	0.1	-1.9	1.70
FS8-7	Temperate	F	18	1.72	1.5	0.8	0.80
FS8-8	Temperate	M	19	1.78	1.0	0	0.90
FS8-9	Temperate	M	19	1.81	0.5	-3.5	2.70
FS8-10	Temperate	M	18	1.77	-1.7	-2.9	0.60
FS8-11	Temperate	F	18	1.71	-2.6	-3.5	0.10
FS8-12	Temperate	M	19	1.85	-4.3	-4.8	0.30
FS8-13	Temperate	M	18	1.72	-1.2	-5.6	2.30
FS8-14	Temperate	F	18	1.61	1.5	-8.4	6.30
Pilot 1	Temperate	F	31	1.65	-2.9	-5.9	3.8
Pilot 2	Temperate	F	29	1.55	-1.5	-8.9	8.8
Pilot 3	Temperate	M	25	1.66	-3.4	-1.6	-4.2
Pilot 4	Temperate	M	21	1.79	-3.7	-2.1	-4.2
Pilot 5	Temperate	M	44	1.72	-5.4	-5.7	-1.6
Pilot 6	Temperate	F	23	1.80	-2.3	-4.3	0.8

NS1-1	Hot	M	29	1.93	-1.1	-0.6	-0.3
NS1-5	Hot	M	36	1.88	3.9	-1	4.2
NS1-6	Hot	M	19	1.87	5.5	-0.4	5.1
NS1-7	Hot	M	18	1.89	6.8	2	4.6
NS1-8	Hot	F	19	1.64	2.1	6.7	-2.5
NS1-9	Hot	M	20	1.82	3.5	-0.3	3.3
NS1-10	Hot	F	20	1.55	-2.0	-3.4	1.2
NS1-11	Hot	M	19	1.78	2.8	-1.5	3.5
NS1-12	Hot	M	21	1.86	5.1	1.9	2.5
NS1-13	Hot	M	19	1.85	4.4	0.4	3.6
NS1-14	Hot	M	20	1.80	5.1	-0.4	4.8
NS2-1	Hot	F	20	1.68	0.7	-1.8	1.6
NS2-2	Hot	M	29	1.85	-0.8	-3.9	2.5
NS2-3	Hot	F	21	1.70	-0.6	-0.5	1.3
NS2-4	Hot	F	20	1.72	3.8	0.1	3
NS2-5	Hot	M	24	1.79	2.2	-4.2	4.7
NS2-6	Hot	M	20	1.88	0.3	1	-0.6
NS2-7	Hot	M	18	1.74	4.0	-3.1	5.4
NS2-8	Hot	F	19	1.76	0.4	-0.4	0.6
NS2-9	Hot	M	21	1.83	-0.4	-2.2	1
NS2-10	Hot	M	18	1.80	2.5	1.4	3.3
NS2-11	Hot	M	19	1.79	5.8	3.5	2.9
FS5-1	Cold	M	29	1.88	-2.1	-1.7	-0.7
FS5-2	Cold	M	19	1.78	-1.4	-2.8	0.6
FS5-3	Cold	M	20	1.82	-1.8	-1.1	-0.6
FS5-4	Cold	M	20	1.83	-2.2	-0.8	-1.3
FS5-7	Cold	M	21	1.72	-2.5	-5.8	1.9
FS5-9	Cold	F	20	1.73	1.3	-1.8	2.3
FS5-10	Cold	M	20	1.84	-1.4	6	-5.8
FS5-11	Cold	M	22	1.88	-1.6	-0.4	-1.2
FS5-12	Cold	F	18	1.69	-2.6	-7.4	2.8

FS5-13	Cold	F	22	1.74	-1.2	-2.9	0.9
FS5-15	Cold	M	21	1.92	-3.1	-1.2	-1.5
FS5-16	Cold	M	18	1.75	-2.1	2.1	-3.1
FS8-1	Cold	M	31	1.73	-1.4	1.3	-2.10
FS8-2	Cold	M	18	1.74	-1.3	-0.7	-0.90
FS8-4	Cold	M	18	1.86	-5.8	-1.1	-3.40
FS8-5	Cold	M	18	1.75	-3.2	0.2	-2.90
FS8-6	Cold	M	18	1.97	-3.3	-1.9	-1.50
FS8-7	Cold	F	18	1.72	-2.9	-4.1	0.40
FS8-8	Cold	M	19	1.78	-2.7	0.6	-2.90
FS8-9	Cold	M	19	1.81	-3.1	0.4	-3.00
FS8-10	Cold	M	18	1.77	-2.7	-4	0.70
FS8-11	Cold	F	18	1.71	-3.9	-2	-1.80
FS8-12	Cold	M	19	1.85	-1.6	-3	1.10
FS8-13	Cold	M	18	1.72	-1.0	0.1	-0.90
FS8-14	Cold	F	18	1.61	-3.2	-0.6	-1.20

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**Appendix 4.** Flex-Heart Rate calibration equations and flex-points (bpm) for each subject collected during the Pre- (PrC), Mid- (MC) and Post-Course (PoC) Battery data collections. Missing data indicate subjects with poor calibrations, were ill or sustained an injury and could not take part in measurements except in the case of subject from the Pilot study in which they only took part in one climate.

<i>Subject</i>	<i>PrC Equation</i>	<i>PrC Flex Point</i>	<i>MC Equation</i>	<i>MC Flex Point</i>	<i>PoC Equation</i>	<i>PoC Flex Point</i>
NS1-1	$y = 0.15x - 11.29$	96	$y = 0.17x - 12.33$	100	$y = 0.18x - 13.67$	100
NS1-2	$y = 0.11x - 5.50$	90	$y = 0.12x - 8.72$	95		
NS1-3	$y = 0.02x + 5.44$	110				
NS1-4	$y = 0.08x - 2.92$	102	$y = 0.12x - 7.85$	94		
NS1-5	$y = 0.14x - 5.97$	100	$y = 0.12x - 4.74$	90		
NS1-6	$y = 0.10x - 5.91$	97	$y = 0.13x - 7.39$	114	$y = 0.16x - 12.42$	104
NS1-7	$y = 0.05x + 5.06$	112			$y = 0.15x - 9.97$	90
NS1-8	$y = 0.07x - 2.65$	109	$y = 0.08x - 3.55$	89	$y = 0.10x - 7.25$	104
NS1-9	$y = 0.11x - 4.41$	95	$y = 0.06x + 3.07$	107	$y = 0.15x - 9.62$	103
NS1-10	$y = 0.05x + 2.03$	123			$y = 0.12x - 8.07$	98
NS1-11	$y = 0.08x + 0.55$	93	$y = 0.10x - 3.74$	78	$y = 0.06x + 2.90$	90
NS1-12	$y = 0.17x - 11.55$	99	$y = 0.18x - 12.20$	104	$y = 0.20x - 13.56$	100
NS1-13	$y = 0.03x + 5.88$	96	$y = 0.04x + 5.95$	98	$y = 0.17x - 10.88$	98
NS1-14	$y = 0.12x - 5.98$	89	$y = 0.01x + 10.75$		$y = 0.15x - 10.16$	102
NS2-1	$y = 0.06x - 0.71$	92	$y = 0.09x - 3.71$	104	$y = 0.11x - 7.44$	103
NS2-2	$y = 0.14x - 5.70$	78	$y = 0.17x - 8.32$	72	$y = 0.12x - 3.04$	71
NS2-3	$y = 0.05x + 2.77$	95	$y = 0.15x - 10.93$	103	$y = 0.11x - 7.08$	101
NS2-4	$y = 0.07x - 3.81$	98	$y = 0.08x - 4.45$	87	$y = 0.08x - 4.14$	95
NS2-5	$y = 0.13x - 9.14$	105	$y = 0.16x - 10.56$	98	$y = 0.11x - 5.24$	96
NS2-6	$y = 0.15x - 8.21$	80	$y = 0.16x - 8.62$	83	$y = 0.12x - 4.77$	83
NS2-7	$y = 0.09x - 2.88$	96	$y = 0.14x - 8.83$	91	$y = 0.11x - 5.25$	90
NS2-8	$y = 0.11x - 8.50$	108	$y = 0.18x - 19.34$	125	$y = 0.17x - 15.93$	117
NS2-9	$y = 0.12x - 8.04$	95	$y = 0.11x - 5.21$	87	$y = 0.09x - 3.52$	91
NS2-10	$y = 0.13x - 7.95$	101	$y = 0.16x - 9.23$	91	$y = 0.07x + 1.32$	101
NS2-11	$y = 0.13x - 8.16$	96	$y = 0.16x - 8.88$	92	$y = 0.10x - 1.97$	80
FS5-1	$y = 0.01x + 11.06$	98	$y = 0.12x - 4.22$	94	$y = 0.21x - 7.75$	93

FS5-2	$y = 0.03x + 6.49$	95	$y = 0.11x - 7.59$	113	$y = 0.24x - 21.80$	123
FS5-3	$y = 0.10x - 2.97$	98	$y = 0.11x - 3.81$	107	$y = 0.13x - 8.51$	108
FS5-4	$y = 0.09x - 1.01$	109	$y = 0.11x - 4.16$	105	$y = 0.24x - 19.49$	98
FS5-5	$y = 0.08x - 3.28$	112	$y = 0.07x - 1.36$	113		
FS5-7	$y = 0.10x - 1.55$	111	$y = 0.08x + 0.94$	92	$y = 0.23x - 10.39$	93
FS5-9	$y = 0.08x - 3.10$	100	$y = 0.11x - 6.49$	101	$y = 0.21x - 17.99$	116
FS5-10	$y = 0.03x + 8.57$	95	$y = 0.13x - 8.90$	102	$y = 0.22x - 15.20$	102
FS5-11	$y = 0.12x - 6.04$	106	$y = 0.15x - 11.65$	110	$y = 0.14x - 8.57$	100
FS5-12	$y = 0.13x - 11.95$	125	$y = 0.08x - 4.90$	100	$y = 0.15x - 8.78$	110
FS5-13	$y = 0.12x - 10.53$	113	$y = 0.11x - 7.23$	125	$y = 0.09x - 4.98$	108
FS5-15	$y = 0.15x - 9.08$	100	$y = 0.15x - 9.17$	108	$y = 0.35x - 28.61$	92
FS5-16	$y = 0.07x - 0.56$	80	$y = 0.08x - 2.52$	90	$y = 0.14x - 5.67$	90
FS8-1	$y = 0.10x - 4.06$	86	$y = 0.10x - 3.85$	88	$y = 0.13x - 7.28$	97
FS8-2	$y = 0.10x - 5.43$	110	$y = 0.18x - 13.0$	96	$y = 0.11x - 3.55$	104
FS8-3	$y = 0.13x - 6.14$	85	$y = 0.17x - 11.49$	105		
FS8-4	$y = 0.12x - 5.03$	88	$y = 0.11x - 2.80$	97	$y = 0.22x - 13.22$	97
FS8-6	$y = 0.04x + 6.17$	90	$y = 0.10x + 0.34$	101	$y = 0.39x - 27.99$	104
FS8-7	$y = 0.07x - 0.92$	89	$y = 0.08x - 3.14$	95	$y = 0.07x + 1.45$	94
FS8-8	$y = 0.09x - 4.70$	112	$y = 0.12x - 7.82$	115	$y = 0.19x - 11.00$	100
FS8-9	$y = 0.12x - 4.54$	90	$y = 0.11x - 5.11$	89	$y = 0.09x + 3.17$	93
FS8-10	$y = 0.06x + 0.05$	96	$y = 0.07x + 0.47$	94	$y = 0.07x + 2.05$	94
FS8-11	$y = 0.06x - 4.57$	120	$y = 0.06x - 1.08$	134	$y = 0.21x - 19.79$	130
FS8-12	$y = 0.14x - 6.21$	111	$y = 0.12x - 3.65$	104	$y = 0.22x - 11.98$	109
FS8-13	$y = 0.07x + 0.97$	89	$y = 0.08x - 0.96$	90	$y = 0.11x - 3.08$	96
FS8-14	$y = 0.07x - 3.82$	110	$y = 0.08x - 4.53$	111	$y = 0.17x - 13.03$	107
Pilot 1	$y = 0.0764x - 3.1629$	90			$y = 0.08x - 2.84$	100
Pilot 2	$y = 0.0877x - 5.3104$	108			$y = 0.08x - 3.982$	107
Pilot 3	$y = 0.1139x - 7.0871$	100				
Pilot 4	$y = 0.0914x - 5.1708$	90			$y = 0.17x - 10.803$	90
Pilot 5					$y = 0.006x + 5.36$	94
Pilot 6	$y = 0.1054x - 7.3481$	110			$y = 0.06x - 0.89$	104

**Appendix 5.** Temperature data (minimum, maximum and mean in C°) for each course in temperate, hot and cold climates.

<i>Course</i>		<i>Dates</i>										
		6/24/11	6/25/11	6/26/11	6/27/11	6/28/11	6/29/11	6/30/11	7/1/11	7/2/11	7/3/11	7/4/11
NS1	Min	12.8	2.0	3.0	1.4	3.9	5.6	9.8	2.7	4.2	7.8	11.0
Temperate	Max	29.3	30.7	20.8	29.1	28.0	38.7	28.3	36.1	22.7	32.4	24.8
	Mean	20.6	16.8	13.1	11.0	13.6	17.3	15.7	16.3	13.0	19.8	17.4
		7/20/11	7/21/11	7/22/11	7/23/11	7/24/11	7/25/11					
NS1 Hot	Min	17.2	16.0	16.9	15.2	17.6	21.9					
	Max	44.4	34.7	29.3	29.8	37.0	35.2					
	Mean	26.5	22.0	21.1	21.3	24.4	26.2					
		8/1/11	8/2/11	8/3/11	8/4/11	8/5/11	8/6/11	8/7/11	8/8/11	8/9/11	8/10/11	
NS2	Min	7.6	4.8	7.1	2.5	6.8	3.3	1.7	3.9	1.5	0.4	
	Max	20.7	38.4	28.2	36.4	30.5	32.7	33.2	36.1	32.9	32.1	
	Mean	12.3	15.4	11.8	14.4	16.2	13.6	12.1	14.7	12.4	12.9	
		7/10/11	7/11/11	7/12/11	7/13/11	7/14/11	7/15/11					
NS2 Hot	Min	19.3	16.5	15.6	19.9	17.2	15.9					
	Max	33.0	36.0	32.7	35.3	37.2	46.7					
	Mean	23.6	21.6	22.5	23.3	25.0	26.1					
		9/14/11	9/15/11	9/16/11	9/17/11	9/18/11	9/19/11	9/20/11				
FS5	Min	2.9	2.4	2.5	0.3	-1.5	-0.9	0.1				
	Max	11.0	15.3	23.2	14.2	20.1	19.4	23.7				
	Mean	5.9	7.6	8.2	4.6	6.3	6.1	6.9				
		11/23/11	11/24/11	11/25/11	11/26/11	11/27/11	11/28/11	11/29/11				
FS5 Cold	Min	-5.8	-8.4	-14.4	-17.5	-13.4	-8.9	-10.3				
	Max	17.0	7.6	-1.7	10.9	11.3	2.8	6.4				

	Mean	1.5	-3.4	-6.5	-8.9	-4.4	-4.1	-4.9	
		9/25/11	9/26/11	9/27/11	9/28/11	9/29/11	9/30/11	10/1/11	10/2/11
FS8	Min	3.6	5.0	0.0	5.2	2.3	3.3	4.6	7.5
Temperate	Max	39.3	31.2	26.7	28.1	31.3	24.6	29.9	25.2
	Mean	14.0	11.3	9.6	12.1	12.0	11.2	12.9	17.9
		12/1/11	12/2/11	12/3/11	12/4/11	12/5/11	12/6/11	12/7/11	
FS8 Cold	Min	-18.0	-17.8	-20.0	-20.0	-26.8	-14.4	-11.0	
	Max	13.7	-4.5	-5.8	-9.1	6.1	-1.6	-2.0	
	Mean	0.5	-11.8	-15.2	-15.1	-16.1	-10.4	-7.5	

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**Appendix 6.** Daily total energy expenditure values for each subject in temperate, hot and cold climates as measured by the Flex-Heart Rate, Corrected Flex-Heart Rate, Allocation Model and Factorial methods (kcal day<sup>-1</sup>). Missing data indicate subjects who either were ill or sustained an injury and could not take part in measurements.

<i>Subject</i>	<i>Climate</i>	<i>Date</i>	<i>Flex-HR</i>	<i>Corrected Flex-HR</i>	<i>Allocation Model</i>	<i>Factorial Method</i>
NS1-5	Temperate	6/24/11	3834	3183	2832	2564
NS1-1	Temperate	6/24/11	1298	1298	2792	3013
NS1-6	Temperate	6/24/11	1709	1709	2664	2431
NS1-7	Temperate	6/24/11	1692	1692	2422	2534
NS1-8	Temperate	6/24/11	1512	1512	2096	1995
NS1-9	Temperate	6/24/11	1439	1439	2510	2555
NS1-12	Temperate	6/24/11	1500	1500	2672	2810
NS1-13	Temperate	6/24/11	2617	2617	2690	2495
NS1-14	Temperate	6/24/11	1658	1658	2561	2513
NS1-2	Temperate	6/24/11	2966	2966	2658	2374
NS1-4	Temperate	6/24/11	1676	1676	1873	1840
NS1-5	Temperate	6/25/11	5728	4754	2728	2597
NS1-1	Temperate	6/25/11	4737	3932	3113	3052
NS1-6	Temperate	6/25/11	3766	3125	2707	2463
NS1-7	Temperate	6/25/11	4281	3553	2649	2567
NS1-8	Temperate	6/25/11	3295	2735	2305	2021
NS1-9	Temperate	6/25/11	3965	3291	2704	2588
NS1-12	Temperate	6/25/11	3926	3259	2729	2846
NS1-13	Temperate	6/25/11	4289	3560	2782	2528
NS1-14	Temperate	6/25/11	4383	3638	2763	2546
NS1-2	Temperate	6/25/11	6420	5329	2784	2405
NS1-4	Temperate	6/25/11	3532	2932	2017	1864
NS1-5	Temperate	6/26/11	7113	5904	3268	2874
NS1-1	Temperate	6/26/11	4838	4015	3776	3378
NS1-6	Temperate	6/26/11	4348	3609	3049	2726
NS1-7	Temperate	6/26/11	6995	5806	3242	2841

NS1-8	Temperate	6/26/11	4823	4003	2805	2237
NS1-9	Temperate	6/26/11	5248	4356	3198	2864
NS1-12	Temperate	6/26/11	4621	3835	3424	3150
NS1-13	Temperate	6/26/11	7540	6259	3397	2798
NS1-14	Temperate	6/26/11	6339	5262	3108	2818
NS1-2	Temperate	6/26/11	7205	5980	3393	2662
NS1-4	Temperate	6/26/11	5773	4792	2858	2063
NS1-5	Temperate	6/27/11	4093	3397	2606	2424
NS1-1	Temperate	6/27/11	4222	3504	2982	2848
NS1-7	Temperate	6/27/11	3113	2584	2514	2396
NS1-8	Temperate	6/27/11	2606	2606	2027	1886
NS1-9	Temperate	6/27/11	3399	2821	2575	2415
NS1-12	Temperate	6/27/11	4476	3715	2816	2656
NS1-13	Temperate	6/27/11	5668	4704	2714	2359
NS1-14	Temperate	6/27/11	4742	3936	2618	2376
NS1-2	Temperate	6/27/11	5183	4302	2678	2245
NS1-4	Temperate	6/27/11	2314	2314	1998	1740
NS1-5	Temperate	6/28/11	7910	6565	3806	3013
NS1-1	Temperate	6/28/11	4179	3469	4315	3867
NS1-7	Temperate	6/28/11	7053	5854	4615	3801
NS1-8	Temperate	6/28/11	4276	3549	3181	2561
NS1-9	Temperate	6/28/11	9084	7540	3914	3279
NS1-12	Temperate	6/28/11	6800	5644	4124	3606
NS1-13	Temperate	6/28/11	6229	5170	3669	2933
NS1-14	Temperate	6/28/11	6950	5769	3845	3226
NS1-2	Temperate	6/28/11	7438	6173	4359	3048
NS1-4	Temperate	6/28/11	4661	3869	2804	2760
NS1-5	Temperate	6/29/11	5415	4495	2644	2423
NS1-1	Temperate	6/29/11	2776	2776	2801	2848
NS1-7	Temperate	6/29/11	5020	4167	3157	3081
NS1-8	Temperate	6/29/11	2383	2383	2048	1886

NS1-9	Temperate	6/29/11	3900	3237	2412	2415
NS1-12	Temperate	6/29/11	3826	3176	2554	2656
NS1-13	Temperate	6/29/11	4482	3720	2468	2359
NS1-14	Temperate	6/29/11	3711	3080	2422	2376
NS1-2	Temperate	6/29/11	5924	4917	3194	2245
NS1-4	Temperate	6/29/11	3495	2901	2555	1740
NS1-5	Temperate	6/30/11	8081	6707	3766	3082
NS1-1	Temperate	6/30/11	6595	5474	4286	3622
NS1-7	Temperate	6/30/11	6633	5506	3680	3047
NS1-8	Temperate	6/30/11	5185	4303	3285	2399
NS1-9	Temperate	6/30/11	8645	7175	3794	3071
NS1-12	Temperate	6/30/11	8306	6894	3980	3378
NS1-13	Temperate	6/30/11	4700	3901	3708	3000
NS1-14	Temperate	6/30/11	7262	6027	3800	3022
NS1-2	Temperate	6/30/11	7259	6025	3586	2855
NS1-4	Temperate	6/30/11	5141	4267	2864	2213
NS1-5	Temperate	7/1/11	6414	5324	3195	3082
NS1-1	Temperate	7/1/11	5111	4242	3559	3622
NS1-7	Temperate	7/1/11	5104	4236	3262	3047
NS1-8	Temperate	7/1/11	3343	2774	2560	2399
NS1-12	Temperate	7/1/11	7142	5927	3411	3378
NS1-13	Temperate	7/1/11	6028	5003	3177	3000
NS1-14	Temperate	7/1/11	4975	4129	2986	3022
NS1-2	Temperate	7/1/11	5047	4189	3140	2855
NS1-4	Temperate	7/1/11	3993	3314	2639	2213
NS1-5	Temperate	7/2/11	7831	6499	4184	3403
NS1-1	Temperate	7/2/11	7329	6083	4576	3999
NS1-7	Temperate	7/2/11	7125	5914	3816	3364
NS1-8	Temperate	7/2/11	4147	3442	3416	2648
NS1-12	Temperate	7/2/11	6074	5041	4133	3730
NS1-13	Temperate	7/2/11	10057	8347	4126	3312

NS1-14	Temperate	7/2/11	7684	6378	4170	3336
NS1-2	Temperate	7/2/11	7017	5824	3960	3152
NS1-4	Temperate	7/2/11	5336	4429	3410	2443
NS1-5	Temperate	7/3/11	6947	5766	2980	3195
NS1-1	Temperate	7/3/11	6325	5250	3421	3754
NS1-6	Temperate	7/3/11	4429	3676	2853	3030
NS1-7	Temperate	7/3/11	5856	4860	2807	3158
NS1-8	Temperate	7/3/11	4146	3441	2537	2486
NS1-12	Temperate	7/3/11	4718	3916	3212	3502
NS1-13	Temperate	7/3/11	7640	6341	3181	3110
NS1-14	Temperate	7/3/11	6006	4985	3052	3132
NS1-2	Temperate	7/3/11	5040	4183	2851	2959
NS1-4	Temperate	7/3/11	3070	2548	2229	2293
NS1-5	Temperate	7/4/11	4188	3476	2789	2736
NS1-1	Temperate	7/4/11	3268	2712	3210	3215
NS1-6	Temperate	7/4/11	3581	2972	2676	2595
NS1-7	Temperate	7/4/11	4270	3544	2655	2704
NS1-8	Temperate	7/4/11	2881	2881	2332	2129
NS1-12	Temperate	7/4/11	8306	6894	3028	2998
NS1-13	Temperate	7/4/11	4775	3963	2820	2663
NS1-14	Temperate	7/4/11	4188	3476	2806	2682
NS1-2	Temperate	7/4/11	4291	3561	2791	2534
NS1-4	Temperate	7/4/11	2581	2581	2065	1964
NS2-2	Temperate	8/1/11	2714	2714	4111	3497
NS2-1	Temperate	8/1/11	1197	1197	3160	2679
NS2-3	Temperate	8/1/11	1893	1893	3421	2861
NS2-4	Temperate	8/1/11	1638	1638	3093	2480
NS2-5	Temperate	8/1/11	2504	2504	3592	3031
NS2-6	Temperate	8/1/11	1467	1467	3637	3283
NS2-7	Temperate	8/1/11	1821	1821	3500	2990
NS2-8	Temperate	8/1/11	1825	1825	3670	3191

NS2-9	Temperate	8/1/11	1661	1661	3244	2868
NS2-11	Temperate	8/1/11	2093	2093	3529	3111
NS2-2	Temperate	8/2/11	6994	5805	3914	3206
NS2-1	Temperate	8/2/11	4469	3710	3094	2568
NS2-3	Temperate	8/2/11	3189	2646	3060	2742
NS2-4	Temperate	8/2/11	4491	3728	2977	2377
NS2-5	Temperate	8/2/11	4257	3533	3189	2905
NS2-6	Temperate	8/2/11	4803	3986	3464	3147
NS2-7	Temperate	8/2/11	5807	4820	3503	2865
NS2-8	Temperate	8/2/11	4316	3582	3689	3058
NS2-9	Temperate	8/2/11	4260	3536	3113	2749
NS2-10	Temperate	8/2/11	4920	4083	3610	3144
NS2-11	Temperate	8/2/11	6589	5468	3392	2982
NS2-2	Temperate	8/3/11	8461	7022	3820	2842
NS2-1	Temperate	8/3/11	2889	2889	2918	2623
NS2-3	Temperate	8/3/11	2575	2575	2993	2802
NS2-4	Temperate	8/3/11	3795	3150	3145	2429
NS2-5	Temperate	8/3/11	5276	4379	3348	2968
NS2-6	Temperate	8/3/11	3820	3171	3372	3215
NS2-7	Temperate	8/3/11	5826	4836	3361	2928
NS2-8	Temperate	8/3/11	4277	3550	3674	3125
NS2-9	Temperate	8/3/11	3688	3061	3220	2808
NS2-10	Temperate	8/3/11	4642	3853	3428	3212
NS2-11	Temperate	8/3/11	5817	4828	3405	3047
NS2-2	Temperate	8/4/11	7049	5851	5162	3906
NS2-1	Temperate	8/4/11	2434	2434	2441	2199
NS2-3	Temperate	8/4/11	4933	4095	2674	2348
NS2-4	Temperate	8/4/11	2909	2909	2422	2035
NS2-5	Temperate	8/4/11	4204	3489	2790	2488
NS2-6	Temperate	8/4/11	6662	5529	3087	2694
NS2-7	Temperate	8/4/11	8284	6876	3075	2453

NS2-8	Temperate	8/4/11	2163	2163	2863	2619
NS2-9	Temperate	8/4/11	5101	4234	2791	2354
NS2-10	Temperate	8/4/11	3641	3022	2980	2692
NS2-11	Temperate	8/4/11	6482	5380	2949	2553
NS2-2	Temperate	8/5/11	4926	4089	3075	2724
NS2-1	Temperate	8/5/11	2953	2953	3116	2770
NS2-3	Temperate	8/5/11	2405	2405	3184	2958
NS2-5	Temperate	8/5/11	3099	2573	3392	3133
NS2-6	Temperate	8/5/11	4625	3839	3675	3394
NS2-7	Temperate	8/5/11	3654	3032	3420	3091
NS2-8	Temperate	8/5/11	2588	2588	3881	3299
NS2-9	Temperate	8/5/11	3212	2666	3284	2965
NS2-10	Temperate	8/5/11	3431	2848	3788	3391
NS2-11	Temperate	8/5/11	6050	5022	3729	3216
NS2-2	Temperate	8/6/11	6807	5650	4409	3687
NS2-1	Temperate	8/6/11	1812	1812	3201	2770
NS2-3	Temperate	8/6/11	3388	2812	3393	2958
NS2-5	Temperate	8/6/11	5158	4281	3623	3133
NS2-6	Temperate	8/6/11	5162	4284	3852	3394
NS2-7	Temperate	8/6/11	5477	4546	3441	3091
NS2-8	Temperate	8/6/11	4282	3554	3763	3299
NS2-9	Temperate	8/6/11	4259	3535	3679	2965
NS2-10	Temperate	8/6/11	5999	4979	3931	3391
NS2-11	Temperate	8/6/11	7937	6588	3929	3216
NS2-2	Temperate	8/7/11	7727	6413	4481	3542
NS2-1	Temperate	8/7/11	4086	3391	3350	2770
NS2-3	Temperate	8/7/11	4202	3488	3537	2958
NS2-5	Temperate	8/7/11	5304	4402	3685	3133
NS2-6	Temperate	8/7/11	5324	4419	3944	3394
NS2-7	Temperate	8/7/11	6102	5064	3663	3091
NS2-8	Temperate	8/7/11	4386	3641	4037	3299

NS2-9	Temperate	8/7/11	4540	3768	3496	2965
NS2-11	Temperate	8/7/11	7353	6103	3818	3216
NS2-2	Temperate	8/8/11	6144	5099	3619	3233
NS2-1	Temperate	8/8/11	2158	2158	3058	2533
NS2-3	Temperate	8/8/11	3000	3000	3041	2705
NS2-4	Temperate	8/8/11	1933	1933	2728	2345
NS2-5	Temperate	8/8/11	3602	2990	3410	2866
NS2-6	Temperate	8/8/11	3032	2517	3420	3104
NS2-7	Temperate	8/8/11	4326	3591	3230	2827
NS2-8	Temperate	8/8/11	3299	2738	3786	3017
NS2-9	Temperate	8/8/11	3539	2938	3088	2712
NS2-11	Temperate	8/8/11	6250	5188	3501	2942
NS2-2	Temperate	8/9/11	7795	6469	5080	3760
NS2-1	Temperate	8/9/11	3558	2953	8329	2770
NS2-3	Temperate	8/9/11	4844	4020	6809	2958
NS2-4	Temperate	8/9/11	3732	3097	6482	2564
NS2-5	Temperate	8/9/11	4299	3568	6629	3133
NS2-6	Temperate	8/9/11	5115	4245	7491	3394
NS2-7	Temperate	8/9/11	6715	5573	7380	3091
NS2-8	Temperate	8/9/11	4116	3416	7557	3299
NS2-9	Temperate	8/9/11	6213	5157	7411	2965
NS2-10	Temperate	8/9/11	6426	5334	7624	3391
NS2-11	Temperate	8/9/11	7263	6029	7931	3216
NS2-2	Temperate	8/10/11	6798	5642	4521	3906
NS2-1	Temperate	8/10/11	2580	2580	3297	2825
NS2-3	Temperate	8/10/11	4423	3671	3471	3017
NS2-4	Temperate	8/10/11	2999	2999	2765	2615
NS2-5	Temperate	8/10/11	4973	4127	3586	3197
NS2-6	Temperate	8/10/11	5229	4340	3726	3462
NS2-7	Temperate	8/10/11	5781	4798	3403	3153
NS2-8	Temperate	8/10/11	3485	2893	3768	3365

NS2-9	Temperate	8/10/11	5375	4461	3505	3025
NS2-11	Temperate	8/10/11	5605	4652	3581	3281
FS5-1	Temperate	9/14/11	1014	1014	2318	2285
FS5-2	Temperate	9/14/11	1715	1715	2111	2106
FS5-3	Temperate	9/14/11	1637	1637	2000	2419
FS5-4	Temperate	9/14/11	1201	1201	2276	2276
FS5-5	Temperate	9/14/11	672	672	1794	1840
FS5-7	Temperate	9/14/11	2160	2160	2595	2340
FS5-9	Temperate	9/14/11	1858	1858	2190	2212
FS5-10	Temperate	9/14/11	1497	1497	2166	2338
FS5-11	Temperate	9/14/11	1633	1633	2280	2281
FS5-12	Temperate	9/14/11	2346	2346	2154	1885
FS5-13	Temperate	9/14/11	973	973	1871	1868
FS5-15	Temperate	9/14/11	1694	1694	2766	2833
FS5-16	Temperate	9/14/11	2244	2244	2198	2062
FS5-1	Temperate	9/15/11	2086	2086	2333	2302
FS5-2	Temperate	9/15/11	3550	2947	2289	2122
FS5-3	Temperate	9/15/11	2235	2235	2163	2437
FS5-4	Temperate	9/15/11	2350	2350	2359	2293
FS5-5	Temperate	9/15/11	1263	1263	1922	1854
FS5-7	Temperate	9/15/11	3031	2516	2508	2357
FS5-9	Temperate	9/15/11	3320	2755	2317	2229
FS5-10	Temperate	9/15/11	2892	2892	2164	2355
FS5-11	Temperate	9/15/11	2700	2700	2433	2298
FS5-12	Temperate	9/15/11	3277	2720	2051	1899
FS5-13	Temperate	9/15/11	2030	2030	2086	1882
FS5-15	Temperate	9/15/11	2866	2866	2885	2854
FS5-16	Temperate	9/15/11	2578	2578	2095	2077
FS5-1	Temperate	9/16/11	7656	6354	3559	2723
FS5-2	Temperate	9/16/11	7293	6053	3399	2510
FS5-3	Temperate	9/16/11	5161	4284	2986	2882

FS5-4	Temperate	9/16/11	6386	5300	3385	2712
FS5-5	Temperate	9/16/11	4409	3659	2857	2192
FS5-7	Temperate	9/16/11	2160	2160	3744	2788
FS5-9	Temperate	9/16/11	9315	7731	3543	2636
FS5-10	Temperate	9/16/11	3995	3316	3044	2786
FS5-11	Temperate	9/16/11	3704	3075	3162	2717
FS5-12	Temperate	9/16/11	5726	4753	2996	2246
FS5-13	Temperate	9/16/11	7320	6076	3083	2226
FS5-15	Temperate	9/16/11	6596	5475	3926	3376
FS5-16	Temperate	9/16/11	3691	3064	2858	2457
FS5-1	Temperate	9/17/11	1889	1889	3151	2895
FS5-2	Temperate	9/17/11	5917	4911	3161	2669
FS5-3	Temperate	9/17/11	3250	2698	2837	3065
FS5-4	Temperate	9/17/11	2347	2347	2962	2884
FS5-5	Temperate	9/17/11	1710	1710	2686	2331
FS5-7	Temperate	9/17/11	8171	6782	3507	2965
FS5-9	Temperate	9/17/11	6054	5025	3243	2803
FS5-10	Temperate	9/17/11	2807	2807	2874	2962
FS5-11	Temperate	9/17/11	3099	2572	3036	2890
FS5-12	Temperate	9/17/11	4233	3513	2816	2389
FS5-13	Temperate	9/17/11	2786	2786	2696	2367
FS5-15	Temperate	9/17/11	4649	3859	3685	3589
FS5-16	Temperate	9/17/11	3595	2984	2783	2612
FS5-1	Temperate	9/18/11	2850	2850	3519	2922
FS5-2	Temperate	9/18/11	5246	4354	3577	2693
FS5-3	Temperate	9/18/11	3865	3208	3285	3093
FS5-4	Temperate	9/18/11	2929	2929	3550	2911
FS5-5	Temperate	9/18/11	3416	2835	3023	2353
FS5-7	Temperate	9/18/11	7321	6076	3623	2992
FS5-9	Temperate	9/18/11	6129	5087	3581	2829
FS5-10	Temperate	9/18/11	3383	2808	3357	2989

FS5-11	Temperate	9/18/11	3801	3155	3352	2916
FS5-12	Temperate	9/18/11	4949	4108	3155	2411
FS5-13	Temperate	9/18/11	4782	3969	3075	2388
FS5-15	Temperate	9/18/11	6212	5156	4317	3622
FS5-16	Temperate	9/18/11	2750	2750	3012	2636
FS5-1	Temperate	9/19/11	1852	1852	2580	2563
FS5-2	Temperate	9/19/11	3726	3093	2656	2363
FS5-3	Temperate	9/19/11	2365	2365	2529	2713
FS5-4	Temperate	9/19/11	2338	2338	2538	2554
FS5-5	Temperate	9/19/11	1550	1550	2211	2064
FS5-7	Temperate	9/19/11	2874	2874	2722	2625
FS5-9	Temperate	9/19/11	3623	3007	2620	2482
FS5-10	Temperate	9/19/11	2969	2969	2597	2623
FS5-11	Temperate	9/19/11	2526	2526	2581	2559
FS5-12	Temperate	9/19/11	2926	2926	2225	2115
FS5-13	Temperate	9/19/11	2000	2000	2208	2095
FS5-15	Temperate	9/19/11	5125	4253	3132	3178
FS5-16	Temperate	9/19/11	5368	4455	2598	2313
FS5-1	Temperate	9/20/11	1826	1826	2995	2855
FS5-2	Temperate	9/20/11	4120	3419	3186	2632
FS5-3	Temperate	9/20/11	3861	3205	2981	3022
FS5-4	Temperate	9/20/11	3189	2647	2998	2845
FS5-5	Temperate	9/20/11	2030	2030	2580	2299
FS5-7	Temperate	9/20/11	2160	2160	3357	2924
FS5-10	Temperate	9/20/11	2481	2481	2987	2922
FS5-11	Temperate	9/20/11	2829	2829	3012	2850
FS5-12	Temperate	9/20/11	4186	3474	2765	2356
FS5-13	Temperate	9/20/11	2411	2411	2510	2334
FS5-15	Temperate	9/20/11	4456	3699	3765	3540
FS5-16	Temperate	9/20/11	2690	2690	2670	2576
FS8-1	Temperate	9/25/11	4799	3983	3238	3238

FS8-2	Temperate	9/25/11	5939	4930	3187	3187
FS8-3	Temperate	9/25/11	5251	4358	3811	3811
FS8-4	Temperate	9/25/11	5789	4805	4104	4104
FS8-6	Temperate	9/25/11	5394	4477	3530	3530
FS8-7	Temperate	9/25/11	3918	3252	2744	2744
FS8-8	Temperate	9/25/11	1560	1560	2737	2737
FS8-9	Temperate	9/25/11	4342	3604	3363	3363
FS8-10	Temperate	9/25/11	3498	2903	3295	3295
FS8-11	Temperate	9/25/11	2511	2511	2581	2581
FS8-12	Temperate	9/25/11	5745	4768	3633	3633
FS8-13	Temperate	9/25/11	8428	6995	3154	3154
FS8-14	Temperate	9/25/11	1773	1773	2727	2727
FS8-1	Temperate	9/26/11	2956	2956	3016	2525
FS8-2	Temperate	9/26/11	4526	3756	3011	2258
FS8-3	Temperate	9/26/11	6532	5422	3595	3258
FS8-4	Temperate	9/26/11	6843	5680	4232	3473
FS8-6	Temperate	9/26/11	4150	3445	3365	2850
FS8-7	Temperate	9/26/11	4941	4101	2702	2082
FS8-8	Temperate	9/26/11	1085	1085	2559	2336
FS8-9	Temperate	9/26/11	3460	2872	3090	2588
FS8-10	Temperate	9/26/11	3514	2917	3157	2610
FS8-11	Temperate	9/26/11	3164	2626	2483	2056
FS8-12	Temperate	9/26/11	5253	4360	3450	2918
FS8-13	Temperate	9/26/11	4185	3474	2927	2383
FS8-14	Temperate	9/26/11	2994	2994	2724	2172
FS8-1	Temperate	9/27/11	3599	2987	3134	2544
FS8-2	Temperate	9/27/11	5143	4268	2775	2275
FS8-3	Temperate	9/27/11	6880	5710	3524	3283
FS8-4	Temperate	9/27/11	6211	5155	3833	3499
FS8-6	Temperate	9/27/11	4394	3647	3224	2871
FS8-7	Temperate	9/27/11	5156	4279	2530	2097

FS8-9	Temperate	9/27/11	2741	2741	2927	2608
FS8-10	Temperate	9/27/11	3895	3233	3012	2630
FS8-11	Temperate	9/27/11	3521	2922	2485	2071
FS8-12	Temperate	9/27/11	6352	5272	3389	2940
FS8-13	Temperate	9/27/11	4180	3470	2794	2401
FS8-14	Temperate	9/27/11	2671	2671	2539	2188
FS8-1	Temperate	9/28/11	3322	2758	2734	2372
FS8-2	Temperate	9/28/11	2829	2829	2286	2121
FS8-3	Temperate	9/28/11	4065	3374	3097	3061
FS8-4	Temperate	9/28/11	3161	2624	3227	3263
FS8-6	Temperate	9/28/11	5162	4284	3064	2677
FS8-7	Temperate	9/28/11	2317	2317	2118	1956
FS8-9	Temperate	9/28/11	1230	1230	2464	2431
FS8-10	Temperate	9/28/11	2579	2579	2661	2452
FS8-11	Temperate	9/28/11	1240	1240	1949	1931
FS8-12	Temperate	9/28/11	4320	3585	2908	2742
FS8-13	Temperate	9/28/11	5182	4301	2666	2239
FS8-14	Temperate	9/28/11	1729	1729	2258	2040
FS8-1	Temperate	9/29/11	4855	4030	3598	3125
FS8-2	Temperate	9/29/11	5822	4833	2973	2795
FS8-3	Temperate	9/29/11	5629	4672	4052	4032
FS8-4	Temperate	9/29/11	4046	3358	4107	4299
FS8-6	Temperate	9/29/11	6295	5225	3721	3527
FS8-7	Temperate	9/29/11	3727	3094	2898	2576
FS8-10	Temperate	9/29/11	3302	2740	3372	3230
FS8-11	Temperate	9/29/11	3112	2583	2666	2544
FS8-12	Temperate	9/29/11	4874	4046	3634	3612
FS8-13	Temperate	9/29/11	4494	3730	3096	2949
FS8-14	Temperate	9/29/11	2550	2550	2975	2688
FS8-1	Temperate	9/30/11	5088	4223	3376	2959
FS8-2	Temperate	9/30/11	4566	3790	2946	2647

FS8-3	Temperate	9/30/11	6421	5329	4012	3819
FS8-4	Temperate	9/30/11	5789	4805	4279	4071
FS8-6	Temperate	9/30/11	3397	2819	3483	3340
FS8-7	Temperate	9/30/11	3616	3002	2803	2440
FS8-10	Temperate	9/30/11	2039	2039	3399	3059
FS8-11	Temperate	9/30/11	2694	2694	2641	2409
FS8-12	Temperate	9/30/11	5126	4255	3658	3420
FS8-13	Temperate	9/30/11	4583	3804	3193	2793
FS8-14	Temperate	9/30/11	2017	2017	2853	2545
FS8-1	Temperate	10/1/11	4799	3983	3634	2997
FS8-2	Temperate	10/1/11	4526	3756	2811	2681
FS8-3	Temperate	10/1/11	5874	4876	3755	3868
FS8-4	Temperate	10/1/11	4637	3848	3871	4123
FS8-6	Temperate	10/1/11	4372	3629	3746	3383
FS8-7	Temperate	10/1/11	3015	2502	2585	2471
FS8-11	Temperate	10/1/11	2223	2223	2476	2440
FS8-12	Temperate	10/1/11	4457	3699	3337	3464
FS8-13	Temperate	10/1/11	2984	2984	2791	2829
FS8-14	Temperate	10/1/11	1966	1966	2773	2578
Pilot 1	Temperate	7/25/10	2441	2441	2318	1512
Pilot 2	Temperate	7/25/10	2727	2727	2162	1771
Pilot 4	Temperate	7/25/10	2727	2727	2620	1869
Pilot 5	Temperate	7/25/10	2540	2540	2534	1403
Pilot 6	Temperate	7/25/10	2758	2758	2468	1953
Pilot 1	Temperate	7/26/10	4671	3877	4242	2745
Pilot 2	Temperate	7/26/10	4493	3729	4034	3023
Pilot 4	Temperate	7/26/10	5590	4640	4757	3201
Pilot 5	Temperate	7/26/10	4550	3776	4415	2441
Pilot 6	Temperate	7/26/10	4577	3799	4457	3283
Pilot 1	Temperate	7/27/10	3921	3255	3913	2418
Pilot 2	Temperate	7/27/10	3649	3028	3542	2448

Pilot 4	Temperate	7/27/10	4818	3999	4193	2732
Pilot 5	Temperate	7/27/10	4096	3400	4150	2286
Pilot 1	Temperate	7/28/10	4351	3611	3722	2588
Pilot 2	Temperate	7/28/10	4478	3717	4266	2973
Pilot 4	Temperate	7/28/10	6364	5282	6232	3660
Pilot 5	Temperate	7/28/10	3861	3204	4132	2154
Pilot 6	Temperate	7/28/10	3598	2986	3964	2659
Pilot 1	Temperate	7/29/10	3159	2622	3684	2019
Pilot 2	Temperate	7/29/10	4462	3703	3756	2884
Pilot 4	Temperate	7/29/10	5232	4342	3927	2981
Pilot 5	Temperate	7/29/10	4276	3549	4255	2217
Pilot 6	Temperate	7/29/10	3647	3027	4421	2517
Pilot 1	Temperate	7/30/10	3830	3179	4173	2434
Pilot 2	Temperate	7/30/10	4375	3631	3461	2763
Pilot 4	Temperate	7/30/10	4603	3820	3927	2594
Pilot 5	Temperate	7/30/10	6310	5237	5568	3161
Pilot 6	Temperate	7/30/10	3433	2850	4079	2521
NS1-5	Hot	6/20/11	2507	2507	2507	2443
NS1-1	Hot	6/20/11	1981	1981	2596	2820
NS1-6	Hot	6/20/11	1804	1804	2626	2413
NS1-7	Hot	6/20/11	2959	2959	2717	2649
NS1-8	Hot	6/20/11	3053	2534	2754	2202
NS1-9	Hot	6/20/11	2109	2109	2440	2449
NS1-10	Hot	6/20/11	2342	2342	1974	2109
NS1-11	Hot	6/20/11	2504	2504	2223	2084
NS1-12	Hot	6/20/11	8716	7235	3225	2725
NS1-13	Hot	6/20/11	2061	2061	2312	2480
NS1-14	Hot	6/20/11	2090	2090	2472	2420
NS1-5	Hot	6/21/11	5410	4490	3351	2791
NS1-1	Hot	6/21/11	5252	4359	3496	3189
NS1-6	Hot	6/21/11	6287	5219	3266	2702

NS1-7	Hot	6/21/11	4470	3710	3073	2581
NS1-8	Hot	6/21/11	4169	3460	2643	2224
NS1-9	Hot	6/21/11	6471	5371	4052	3309
NS1-10	Hot	6/21/11	7394	6137	3029	2446
NS1-11	Hot	6/21/11	4910	4076	2659	2264
NS1-12	Hot	6/21/11	5418	4497	3960	3263
NS1-13	Hot	6/21/11	7235	6005	3558	2895
NS1-14	Hot	6/21/11	4876	4047	3194	2924
NS1-5	Hot	6/22/11	2969	2969	3751	3087
NS1-6	Hot	6/22/11	4710	3909	3069	2551
NS1-7	Hot	6/22/11	4261	3536	2810	2428
NS1-8	Hot	6/22/11	3783	3140	2140	2004
NS1-9	Hot	6/22/11	4581	3803	2599	2561
NS1-10	Hot	6/22/11	5037	4181	2569	2354
NS1-11	Hot	6/22/11	3722	3089	2441	2413
NS1-12	Hot	6/22/11	4392	3645	3139	3012
NS1-13	Hot	6/22/11	5826	4835	2924	2825
NS1-14	Hot	6/22/11	4404	3655	2844	2820
NS1-5	Hot	6/23/11	5785	4801	3506	2918
NS1-1	Hot	6/23/11	2591	2591	3043	3000
NS1-6	Hot	6/23/11	7143	5929	2901	2448
NS1-7	Hot	6/23/11	3626	3010	2562	2452
NS1-8	Hot	6/23/11	3610	2996	2402	2108
NS1-9	Hot	6/23/11	5638	4680	2840	2722
NS1-10	Hot	6/23/11	5337	4430	2378	2226
NS1-11	Hot	6/23/11	4544	3772	2460	2170
NS1-12	Hot	6/23/11	6284	5216	4265	3530
NS1-13	Hot	6/23/11	4891	4059	3167	2727
NS1-14	Hot	6/23/11	4523	3754	2944	2722
NS1-5	Hot	6/24/11	5147	4272	3236	2756
NS1-1	Hot	6/24/11	6970	5785	3298	3023

NS1-6	Hot	6/24/11	4460	3702	2764	2434
NS1-7	Hot	6/24/11	4243	3522	2863	2675
NS1-9	Hot	6/24/11	7192	5969	2915	2615
NS1-10	Hot	6/24/11	6464	5365	2638	2256
NS1-11	Hot	6/24/11	4331	3595	3323	2724
NS1-12	Hot	6/24/11	4635	3847	3759	3122
NS1-13	Hot	6/24/11	6523	5414	3600	2895
NS1-14	Hot	6/24/11	6021	4998	3332	2890
NS1-5	Hot	6/25/11	5317	4414	3007	2622
NS1-1	Hot	6/25/11	3081	2558	3288	3186
NS1-6	Hot	6/25/11	4449	3693	2704	2427
NS1-7	Hot	6/25/11	3567	2960	2734	2358
NS1-9	Hot	6/25/11	5396	4479	3036	2755
NS1-10	Hot	6/25/11	4630	3843	2252	2183
NS1-11	Hot	6/25/11	5220	4333	2607	2292
NS1-12	Hot	6/25/11	4563	3788	3427	2903
NS1-13	Hot	6/25/11	7273	6036	3360	2755
NS1-14	Hot	6/25/11	4658	3866	3017	2750
NS2-2	Hot	7/11/11	5421	4499	2792	2610
NS2-1	Hot	7/11/11	5521	4583	2523	2019
NS2-3	Hot	7/11/11	2631	2631	2311	2169
NS2-4	Hot	7/11/11	5170	4291	2472	1949
NS2-5	Hot	7/11/11	3717	3085	2447	2291
NS2-6	Hot	7/11/11	3844	3191	2818	2515
NS2-7	Hot	7/11/11	3390	2813	2676	2314
NS2-9	Hot	7/11/11	2396	2396	2279	2207
NS2-10	Hot	7/11/11	3771	3130	3320	2623
NS2-11	Hot	7/11/11	5072	4210	2563	2395
NS2-2	Hot	7/12/11	8132	6750	3587	2832
NS2-1	Hot	7/12/11	3031	2515	2224	1992
NS2-3	Hot	7/12/11	2008	2008	2481	2312

NS2-4	Hot	7/12/11	2043	2043	1777	1997
NS2-5	Hot	7/12/11	7473	6203	2759	2351
NS2-6	Hot	7/12/11	5925	4918	2878	2400
NS2-7	Hot	7/12/11	2232	2232	2578	2240
NS2-9	Hot	7/12/11	2184	2184	1877	2296
NS2-10	Hot	7/12/11	3169	2630	2808	2495
NS2-11	Hot	7/12/11	6840	5677	3012	2510
NS2-2	Hot	7/13/11	5533	4593	3032	2917
NS2-1	Hot	7/13/11	2902	2902	2156	2084
NS2-3	Hot	7/13/11	4192	3479	2380	2311
NS2-4	Hot	7/13/11	2399	2399	1918	1789
NS2-5	Hot	7/13/11	2789	2789	2243	2212
NS2-6	Hot	7/13/11	5188	4306	2778	2603
NS2-7	Hot	7/13/11	4638	3850	2535	2531
NS2-9	Hot	7/13/11	2567	2567	2725	2476
NS2-11	Hot	7/13/11	5562	4616	2866	2477
NS2-2	Hot	7/14/11	5269	4373	2905	2781
NS2-1	Hot	7/14/11	1887	1887	1999	2073
NS2-3	Hot	7/14/11	7663	6360	2255	2167
NS2-4	Hot	7/14/11	2008	2008	1774	1841
NS2-5	Hot	7/14/11	3135	2602	2276	2259
NS2-6	Hot	7/14/11	9632	7995	3234	2527
NS2-7	Hot	7/14/11	4370	3627	2435	2394
NS2-9	Hot	7/14/11	2566	2566	2207	2416
NS2-10	Hot	7/14/11	3761	3122	3090	2927
NS2-11	Hot	7/14/11	4023	3339	2423	2434
NS2-2	Hot	7/15/11	8150	6764	2508	2591
NS2-1	Hot	7/15/11	4914	4079	1865	1966
NS2-3	Hot	7/15/11	5135	4262	2036	2156
NS2-4	Hot	7/15/11	4051	3363	1795	1894
NS2-5	Hot	7/15/11	5743	4767	2285	2274

NS2-6	Hot	7/15/11	7687	6380	2431	2434
NS2-7	Hot	7/15/11	5293	4393	2146	2265
NS2-9	Hot	7/15/11	5754	4776	1999	2178
NS2-10	Hot	7/15/11	5245	4353	2544	2427
NS2-11	Hot	7/15/11	7250	6017	2163	2308
FS5-1	Cold	11/24/11	9098	7551	4736	3204
FS5-3	Cold	11/24/11	2703	2703	4589	3472
FS5-9	Cold	11/24/11	5198	4314	4731	3159
FS5-10	Cold	11/24/11	4627	3840	4594	3412
FS5-11	Cold	11/24/11	4969	4124	4390	3276
FS5-12	Cold	11/24/11	2544	2544	3527	2615
FS5-13	Cold	11/24/11	5318	4414	3934	2624
FS5-1	Cold	11/25/11	8252	6849	7055	3711
FS5-3	Cold	11/25/11	2615	2615	7298	4021
FS5-10	Cold	11/25/11	3485	2893	7156	3952
FS5-11	Cold	11/25/11	4127	3426	6979	3794
FS5-12	Cold	11/25/11	2420	2420	5632	3028
FS5-13	Cold	11/25/11	3400	2822	5847	3039
FS5-1	Cold	11/26/11	9150	7594	4707	2631
FS5-3	Cold	11/26/11	2708	2708	4689	2850
FS5-7	Cold	11/26/11	6874	5705	4818	2614
FS5-9	Cold	11/26/11	5771	4790	4605	2594
FS5-10	Cold	11/26/11	3482	2890	4453	2801
FS5-11	Cold	11/26/11	4293	3563	4475	2689
FS5-12	Cold	11/26/11	4751	3943	3894	2147
FS5-13	Cold	11/26/11	3708	3078	3772	2155
FS5-1	Cold	11/27/11	12025	9981	4782	2564
FS5-2	Cold	11/27/11	1483	1483	3206	2398
FS5-3	Cold	11/27/11	4130	3428	4593	2778
FS5-4	Cold	11/27/11	4407	3657	4156	2562
FS5-7	Cold	11/27/11	9883	8203	4813	2548

FS5-9	Cold	11/27/11	5632	4675	4440	2528
FS5-10	Cold	11/27/11	10068	8357	4995	2731
FS5-11	Cold	11/27/11	6935	5756	4395	2621
FS5-12	Cold	11/27/11	9854	8179	4355	2092
FS5-13	Cold	11/27/11	4867	4040	3566	2100
FS5-15	Cold	11/27/11	12688	10531	5750	3016
FS5-16	Cold	11/27/11	6346	5267	4014	2365
FS5-1	Cold	11/28/11	5181	4300	4849	3578
FS5-4	Cold	11/28/11	3993	3314	5079	3575
FS5-7	Cold	11/28/11	6788	5634	5550	3555
FS5-10	Cold	11/28/11	6791	5637	5672	3810
FS5-11	Cold	11/28/11	3570	2963	4931	3658
FS5-12	Cold	11/28/11	5197	4314	4539	2920
FS5-15	Cold	11/28/11	4794	3979	5868	4208
FS5-16	Cold	11/28/11	3440	2856	4443	3300
FS5-1	Cold	11/29/11	11500	9545	4411	2498
FS5-3	Cold	11/29/11	3494	2900	3834	2706
FS5-4	Cold	11/29/11	4352	3612	3900	2495
FS5-7	Cold	11/29/11	4566	3790	3837	2482
FS5-9	Cold	11/29/11	5687	4721	4028	2463
FS5-11	Cold	11/29/11	5139	4265	3851	2553
FS5-12	Cold	11/29/11	2429	2429	2911	2038
FS5-13	Cold	11/29/11	4867	4040	3373	2046
FS5-15	Cold	11/29/11	11709	9718	5102	2938
FS5-16	Cold	11/29/11	4315	3582	3541	2303
FS8-1	Cold	12/1/11	4064	3373	4702	2682
FS8-2	Cold	12/1/11	5567	4621	4782	2408
FS8-4	Cold	12/1/11	8320	6906	6287	3461
FS8-6	Cold	12/1/11	8351	6931	5878	2928
FS8-7	Cold	12/1/11	5358	4447	4540	2230
FS8-8	Cold	12/1/11	5766	4786	5002	2549

FS8-9	Cold	12/1/11	4849	4025	4883	2777
FS8-10	Cold	12/1/11	4680	3884	4727	2715
FS8-11	Cold	12/1/11	2521	2521	3662	2196
FS8-12	Cold	12/1/11	6020	4997	5533	3161
FS8-13	Cold	12/1/11	6406	5317	5193	2543
FS8-14	Cold	12/1/11	3458	2870	4246	2255
FS8-1	Cold	12/2/11	4407	3658	4383	2916
FS8-2	Cold	12/2/11	4225	3507	3756	2617
FS8-4	Cold	12/2/11	9944	8254	5710	3762
FS8-6	Cold	12/2/11	11356	9426	5387	3183
FS8-7	Cold	12/2/11	7916	6570	4185	2424
FS8-8	Cold	12/2/11	7301	6060	4436	2771
FS8-9	Cold	12/2/11	6891	5719	4591	3019
FS8-10	Cold	12/2/11	5946	4936	4515	2952
FS8-11	Cold	12/2/11	2329	2329	3254	2388
FS8-12	Cold	12/2/11	5164	4286	4745	3436
FS8-13	Cold	12/2/11	8349	6930	4588	2765
FS8-14	Cold	12/2/11	3960	3287	3782	2452
FS8-1	Cold	12/3/11	3760	3121	4285	3109
FS8-2	Cold	12/3/11	2909	2909	3638	2791
FS8-4	Cold	12/3/11	6499	5394	5520	4012
FS8-6	Cold	12/3/11	6213	5157	4702	3394
FS8-7	Cold	12/3/11	6824	5664	4250	2585
FS8-8	Cold	12/3/11	5086	4221	4075	2955
FS8-9	Cold	12/3/11	4201	3487	4305	3219
FS8-10	Cold	12/3/11	4680	3884	4916	3148
FS8-11	Cold	12/3/11	2134	2134	3472	2546
FS8-12	Cold	12/3/11	3939	3270	4856	3665
FS8-13	Cold	12/3/11	6990	5801	4426	2949
FS8-14	Cold	12/3/11	2027	2027	3566	2615
FS8-1	Cold	12/4/11	2275	2275	6427	3601

FS8-2	Cold	12/4/11	6780	5627	6218	3233
FS8-4	Cold	12/4/11	9432	7828	9167	4647
FS8-6	Cold	12/4/11	10788	8954	8041	3931
FS8-7	Cold	12/4/11	7919	6573	6462	2994
FS8-8	Cold	12/4/11	3645	3025	6128	3422
FS8-9	Cold	12/4/11	6269	5204	7021	3728
FS8-10	Cold	12/4/11	5694	4726	6947	3646
FS8-11	Cold	12/4/11	2170	2170	5431	2949
FS8-12	Cold	12/4/11	9970	8275	8487	4244
FS8-13	Cold	12/4/11	8441	7006	6959	3415
FS8-14	Cold	12/4/11	3670	3046	5915	3028
FS8-1	Cold	12/5/11	6614	5489	9434	4351
FS8-2	Cold	12/5/11	3118	2588	5646	3233
FS8-4	Cold	12/5/11	9328	7742	9197	4647
FS8-6	Cold	12/5/11	10231	8492	7991	3931
FS8-7	Cold	12/5/11	7919	6573	6489	2994
FS8-8	Cold	12/5/11	3660	3038	6131	3422
FS8-9	Cold	12/5/11	6014	4992	7127	3728
FS8-10	Cold	12/5/11	2465	2465	6396	3646
FS8-11	Cold	12/5/11	2128	2128	5400	2949
FS8-12	Cold	12/5/11	8258	6854	8296	4244
FS8-13	Cold	12/5/11	6431	5338	6494	3415
FS8-14	Cold	12/5/11	3402	2823	5820	3028
FS8-1	Cold	12/6/11	2275	2275	5857	3318
FS8-2	Cold	12/6/11	6522	5413	5562	2979
FS8-6	Cold	12/6/11	6594	5473	6694	3623
FS8-7	Cold	12/6/11	6504	5398	6086	2759
FS8-8	Cold	12/6/11	5644	4684	5740	3154
FS8-9	Cold	12/6/11	6925	5748	6450	3436
FS8-10	Cold	12/6/11	4602	3819	6144	3360
FS8-11	Cold	12/6/11	2145	2145	4799	2718

FS8-12	Cold	12/6/11	8798	7302	7442	3911
FS8-13	Cold	12/6/11	6391	5304	6152	3147
FS8-14	Cold	12/6/11	3794	3149	5406	2791
FS8-1	Cold	12/7/11	2504	2504	5730	3318
FS8-2	Cold	12/7/11	6018	4995	5558	2979
FS8-6	Cold	12/7/11	11356	9426	7369	3623
FS8-8	Cold	12/7/11	3485	2893	5584	3154
FS8-9	Cold	12/7/11	6343	5264	6336	3436
FS8-10	Cold	12/7/11	4680	3884	6161	3360
FS8-11	Cold	12/7/11	2433	2433	4819	2718
FS8-12	Cold	12/7/11	6020	4997	7172	3911
FS8-13	Cold	12/7/11	6571	5454	6041	3147
FS8-14	Cold	12/7/11	3458	2870	5415	2791

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**Appendix 7.** Mean total energy expenditure values for each subject in temperate, hot and cold climates as measured by the Flex-Heart Rate, Corrected Flex-Heart Rate, Allocation Model and Factorial methods (kcal day<sup>-1</sup>). Missing data indicate subjects who either were ill or sustained an injury and could not take part in measurements.

<i>Subject</i>	<i>Climate</i>	<i>Flex-HR</i>	<i>Corrected Flex-HR</i>	<i>Allocation Model</i>	<i>Factorial Method</i>
NS1-5	Temperate	6141	5097	3164	2854
NS1-1	Temperate	4607	3824	3530	3383
NS1-6	Temperate	3567	2960	2715	2731
NS1-7	Temperate	5195	4312	3165	2958
NS1-8	Temperate	3509	2912	2599	2241
NS1-9	Temperate	5097	4231	2925	2869
NS1-12	Temperate	5427	4504	3280	3156
NS1-13	Temperate	5820	4831	3158	2778
NS1-14	Temperate	5263	4369	3103	2823
NS1-2	Temperate	5799	4813	3217	2667
NS1-4	Temperate	3779	3137	2483	2103
NS2-2	Temperate	6541	5429	4219	3356
NS2-1	Temperate	2814	2814	3596	2591
NS2-3	Temperate	3485	2893	3558	2767
NS2-4	Temperate	3071	2549	3208	2399
NS2-5	Temperate	4268	3542	3724	2932
NS2-6	Temperate	4524	3755	3967	3176
NS2-7	Temperate	5379	4465	3798	2892
NS2-8	Temperate	3474	2883	4069	3087
NS2-9	Temperate	4185	3473	3683	2774
NS2-10	Temperate	4843	4020	3875	3173
NS2-11	Temperate	6144	5099	3976	3009
FS5-1	Temperate	2739	2739	2922	2662
FS5-2	Temperate	4510	3743	2911	2454
FS5-3	Temperate	3196	2653	2683	2818
FS5-4	Temperate	2963	2963	2867	2652

FS5-5	Temperate	2150	2150	2439	2143
FS5-7	Temperate	3982	3305	3151	2726
FS5-9	Temperate	5050	4191	2878	2577
FS5-10	Temperate	2861	2861	2741	2724
FS5-11	Temperate	2899	2899	2837	2657
FS5-12	Temperate	3949	3278	2595	2196
FS5-13	Temperate	3186	2644	2504	2176
FS5-15	Temperate	4514	3747	3497	3300
FS5-16	Temperate	3274	2717	2602	2402
FS8-1	Temperate	4203	3488	3247	2746
FS8-2	Temperate	4764	3954	2856	2456
FS8-3	Temperate	5807	4820	3692	3544
FS8-4	Temperate	5211	4325	3951	3778
FS8-6	Temperate	4738	3932	3448	3100
FS8-7	Temperate	3813	3165	2626	2264
FS8-9	Temperate	2943	2943	2920	2815
FS8-10	Temperate	3138	2604	3118	2839
FS8-11	Temperate	2638	2638	2469	2236
FS8-12	Temperate	5161	4284	3430	3174
FS8-13	Temperate	4862	4036	2946	2592
FS8-14	Temperate	2243	2243	2693	2362
Pilot 1	Temperate	3729	3095	3675	2286
Pilot 2	Temperate	4031	3345	3537	2644
Pilot 4	Temperate	4889	4058	4276	2839
Pilot 5	Temperate	4272	3546	4176	2277
Pilot 6	Temperate	3603	2990	3878	2587
NS1-5	Hot	4522	3754	3226	2769
NS1-1	Hot	3975	3299	3077	3030
NS1-6	Hot	4809	3991	2888	2496
NS1-7	Hot	3854	3199	2793	2524
NS1-8	Hot	3654	3032	2397	2117

NS1-9	Hot	5231	4342	2980	2735
NS1-10	Hot	5201	4317	2473	2263
NS1-11	Hot	4205	3490	2619	2325
NS1-12	Hot	5668	4705	3629	3093
NS1-13	Hot	5635	4677	3153	2763
NS1-14	Hot	4429	3676	2967	2754
NS2-2	Hot	6501	5396	2965	2746
NS2-1	Hot	3651	3030	2154	2027
NS2-3	Hot	3700	3071	2293	2223
NS2-4	Hot	2737	2737	1947	1894
NS2-5	Hot	3936	3267	2402	2277
NS2-6	Hot	5599	4647	2828	2496
NS2-7	Hot	3460	2872	2474	2349
NS2-8	Hot	2754	2754	2453	
NS2-9	Hot	2680	2680	2217	2315
NS2-10	Hot	3444	2858	2938	2666
NS2-11	Hot	4974	4129	2605	2425
FS5-1	Cold	9155	7599	5090	3031
FS5-3	Cold	3130	2598	4942	3284
FS5-4	Cold	4250	3528	4464	3028
FS5-7	Cold	7028	5833	4735	3011
FS5-9	Cold	5572	4625	4856	2989
FS5-10	Cold	5691	4723	5007	3228
FS5-11	Cold	4839	4016	4837	3098
FS5-12	Cold	4533	3762	4143	2473
FS5-13	Cold	4432	3679	4017	2482
FS5-15	Cold	9730	8076	5407	3565
FS5-16	Cold	4701	3902	3965	2795
FS8-1	Cold	3700	3071	5831	3328
FS8-2	Cold	5020	4166	5023	2892
FS8-4	Cold	8704	7225	7080	4156

FS8-6	Cold	9270	7694	6580	3516
FS8-7	Cold	7073	5871	5195	2678
FS8-8	Cold	4941	4101	5299	3061
FS8-9	Cold	5928	4920	5816	3335
FS8-10	Cold	4678	3883	5687	3261
FS8-11	Cold	2266	2266	4405	2638
FS8-12	Cold	6881	5711	6647	3796
FS8-13	Cold	7083	5879	5693	3055
FS8-14	Cold	3396	2818	4878	2708

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**Appendix 8.** The mean daily energy allocation breakdown as calculated by the Allocation Model for each subject in temperate, hot and cold climates. The components of the total energy expenditure (TEE) are basal metabolic rate (BMR), activity, thermoregulation and the thermic effect of food (TEF). All components are reported in kcal day<sup>-1</sup>.

<i>Subject</i>	<i>Sex</i>	<i>Age (yrs)</i>	<i>Height (m)</i>	<i>Weight (kg)</i>	<i>Climate</i>	<i>BMR</i>	<i>Activity</i>	<i>Thermoregulation</i>	<i>TEF</i>	<i>TEE</i>
NS1-5	M	36	1.88	78.4	Temperate	1799	565	563	236	3164
NS1-1	M	29	1.93	98.1	Temperate	2115	733	430	253	3530
NS1-6	M	19	1.87	72.6	Temperate	1707	544	413	277	2715
NS1-7	M	18	1.89	77.1	Temperate	1779	685	488	262	3165
NS1-8	F	19	1.64	64.3	Temperate	1400	534	402	263	2599
NS1-9	M	20	1.82	78.0	Temperate	1793	613	476	216	2925
NS1-12	M	21	1.86	89.2	Temperate	1972	660	466	183	3280
NS1-13	M	19	1.85	75.4	Temperate	1751	557	539	310	3158
NS1-14	M	20	1.80	76.2	Temperate	1764	590	500	249	3103
NS1-2	M	25	1.75	70.1	Temperate	1667	676	561	314	3217
NS1-4	F	25	1.62	56.0	Temperate	1292	542	444	205	2483
NS2-2	M	36	1.88	80.1	Temperate	1887	1355	640	338	4219
NS2-1	M	29	1.93	97.7	Temperate	1446	1056	331	256	3596
NS2-3	M	19	1.87	77.6	Temperate	1544	1146	397	147	3558
NS2-4	M	18	1.89	71.1	Temperate	1339	958	383	319	3208
NS2-5	F	19	1.64	66.3	Temperate	1636	1060	459	277	3724
NS2-6	M	20	1.82	79.9	Temperate	1772	1162	451	210	3967
NS2-7	F	20	1.55	78.7	Temperate	1614	1044	534	228	3798
NS2-8	M	19	1.78	62.7	Temperate	1723	1310	396	281	4069
NS2-9	M	21	1.86	93.0	Temperate	1548	995	447	297	3683
NS2-10	M	19	1.85	79.2	Temperate	1771	1161	457	324	3875
NS2-11	M	20	1.80	79.0	Temperate	1679	1093	581	206	3976
FS5-1	M	29	1.85	83.9	Temperate	1721	526	351	325	2922
FS5-2	F	20	1.68	67.8	Temperate	1587	481	491	353	2911
FS5-3	F	21	1.70	75.3	Temperate	1822	560		302	2683
FS5-4	F	20	1.72	59.6	Temperate	1715	523	371	258	2867

FS5-5	M	24	1.79	68.2	Temperate	1386	471	310	272	2439
FS5-7	M	20	1.88	76.7	Temperate	1763	540	562	287	3151
FS5-9	M	18	1.74	66.8	Temperate	1666	586	514	186	2878
FS5-10	F	19	1.76	88.9	Temperate	1761	539	374	67	2741
FS5-11	M	21	1.83	62.7	Temperate	1718	525	372	222	2837
FS5-12	M	18	1.80	76.6	Temperate	1420	484	465	225	2595
FS5-13	M	19	1.79	70.9	Temperate	1407	479	388	230	2504
FS5-15	M	29	1.85	81.2	Temperate	2134	666	463	234	3497
FS5-16	F	20	1.68	64.2	Temperate	1553	470	413	166	2602
FS8-1	F	21	1.70	74.5	Temperate	1652	710	452	432	3247
FS8-2	F	20	1.72	60.3	Temperate	1478	625	512	241	2856
FS8-3	M	24	1.79	67.1	Temperate	2132	949	525	86	3692
FS8-4	M	20	1.88	74.2	Temperate	2273	1020	475	182	3951
FS8-6	M	18	1.74	66.7	Temperate	1865	816	463	304	3448
FS8-7	F	19	1.76	88.9	Temperate	1362	649	435	179	2626
FS8-8	M	21	1.83	62.8	Temperate	1529	650	279	168	2427
FS8-9	M	18	1.80	73.9	Temperate	1694	731	383	277	2920
FS8-10	M	19	1.79	68.6	Temperate	1708	738	393	335	3118
FS8-11	M	29	1.88	73.5	Temperate	1345	639	336	149	2469
FS8-12	M	19	1.78	65.1	Temperate	1910	838	496	186	3430
FS8-13	M	20	1.82	79.8	Temperate	1559	665	473	248	2946
FS8-14	M	20	1.83	73.1	Temperate	1421	685	301	286	2693
Pilot 1	F	20	1.68	63.2	Temperate	1378	903	1089	306	3675
Pilot 2	M	21	1.72	76.1	Temperate	1334	1227	646	329	3537
Pilot 4	F	20	1.73	84.6	Temperate	1695	1214	1069	316	4276
Pilot 5	M	20	1.84	76.0	Temperate	1583	1258	958	389	4176
Pilot 6	M	22	1.88	73.3	Temperate	1508	1112	986	272	3878
NS1-5	F	18	1.69	65.8	Hot	1827	739	316	345	3226
NS1-1	F	22	1.74	64.8	Hot	2108	491	272	206	3077
NS1-6	M	21	1.92	99.3	Hot	1787	394	321	386	2888
NS1-7	M	18	1.75	63.0	Hot	1683	516	294	300	2793

NS1-8	M	29	1.88	73.8	Hot	1427	528	304	240	2397
NS1-9	M	19	1.78	66.8	Hot	1823	581	339	237	2980
NS1-10	M	20	1.82	82.8	Hot	1589	410	343	131	2473
NS1-11	M	20	1.83	73.7	Hot	1548	460	306	305	2619
NS1-12	M	21	1.72	73.1	Hot	2033	942	341	313	3629
NS1-13	F	20	1.73	87.3	Hot	1812	618	353	370	3153
NS1-14	M	20	1.84	80.8	Hot	1809	584	310	263	2967
NS2-2	M	22	1.88	76.2	Hot	1844	541	369	211	2965
NS2-1	F	18	1.69	64.9	Hot	1399	315	264	175	2154
NS2-3	F	22	1.74	65.3	Hot	1534	323	290	146	2293
NS2-4	M	21	1.92	92.8	Hot	1348	174	243	182	1947
NS2-5	M	18	1.75	65.4	Hot	1619	265	300	219	2402
NS2-6	M	31	1.73	69.2	Hot	1732	383	367	346	2828
NS2-7	M	18	1.74	58.3	Hot	1612	334	279	249	2474
NS2-8	M	18	1.79	99.2	Hot	1723	274	249	206	2453
NS2-9	M	18	1.86	108.0	Hot	1550	301	242	124	2217
NS2-10	M	18	1.97	82.5	Hot	1727	674	279	314	2938
NS2-11	F	18	1.72	61.4	Hot	1643	393	345	224	2605
FS5-1	M	19	1.78	61.5	Cold	1726	1916	1448		5090
FS5-2	M	19	1.81	71.8	Cold	1614	1735	346	270	3676
FS5-3	M	18	1.77	72.7	Cold	1870	2148	580	440	4942
FS5-4	F	18	1.71	60.1	Cold	1724	1913	766	444	4464
FS5-7	M	19	1.85	85.3	Cold	1715	1898	1217	311	4735
FS5-9	M	18	1.72	63.4	Cold	1702	2265	941	262	4856
FS5-10	F	18	1.61	65.9	Cold	1838	2097	942	288	5007
FS5-11	M	31	1.73	70.6	Cold	1764	1978	826	269	4837
FS5-12	M	18	1.74	59.9	Cold	1408	1686	868	181	4143
FS5-13	M	18	1.86	101.0	Cold	1413	1696	840	207	4017
FS5-15	M	18	1.97	80.2	Cold	2030	2407	1378	281	5407
FS5-16	F	18	1.72	63.7	Cold	1591	1699	886	232	3965
FS8-1	M	19	1.78	65.4	Cold	1675	2903	800	453	5831

FS8-2	M	19	1.81	74.3	Cold	1503	2196	1091	233	5023
FS8-4	M	18	1.77	71.9	Cold	2161	3697	1430	201	7080
FS8-6	F	18	1.71	62.1	Cold	1828	2938	1525	289	6580
FS8-7	M	19	1.85	89.3	Cold	1392	2335	1467	210	5195
FS8-8	M	18	1.72	65.2	Cold	1591	2397	1036	275	5299
FS8-9	F	18	1.61	64.9	Cold	1734	2722	1117	243	5816
FS8-10	F	31	1.65	68.7	Cold	1695	2634	1004	353	5687
FS8-11	F	29	1.55	58.5	Cold	1372	2276	562	195	4405
FS8-12	M	21	1.79	70.0	Cold	1974	3270	1194	210	6647
FS8-13	M	44	1.72	69.7	Cold	1588	2390	1389	326	5693
FS8-14	F	23	1.80	71.4	Cold	1408	2379	786	305	4878

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**Appendix 9.** Individual details of height, mass, surface areas ( $m^2$ ) and surface area/mass ratio ( $m^2 kg^{-1}$ ) values collected from the literature for temperate, hot and cold climates.

<i>Population</i>	<i>Height (m)</i>	<i>Weight (kg)</i>	<i>Sex</i>	<i>Surface Area</i>	<i>SA/M</i>	<i>Source</i>
Yakut	1.67	102.4	M	2.10	0.0205	Snodgrass et al. 2006
Yakut	1.75	85.9	M	2.02	0.0235	Snodgrass et al. 2007
Yakut	1.67	78.1	M	1.87	0.0239	Snodgrass et al. 2008
Yakut	1.71	73.1	M	1.85	0.0253	Snodgrass et al. 2009
Yakut	1.65	54.7	M	1.59	0.0291	Snodgrass et al. 2010
Yakut	1.67	65.8	M	1.74	0.0264	Snodgrass et al. 2011
Yakut	1.77	65.4	M	1.81	0.0277	Snodgrass et al. 2012
Yakut	1.79	67.6	M	1.85	0.0274	Snodgrass et al. 2013
Yakut	1.70	69.4	M	1.81	0.0260	Snodgrass et al. 2014
Yakut	1.58	61.0	M	1.62	0.0266	Snodgrass et al. 2015
Yakut	1.66	66.0	M	1.74	0.0263	Snodgrass et al. 2016
Yakut	1.79	80.1	M	1.99	0.0249	Snodgrass et al. 2017
Yakut	1.68	92.1	M	2.02	0.0219	Snodgrass et al. 2018
Yakut	1.64	49.0	M	1.51	0.0309	Snodgrass et al. 2019
Yakut	1.60	70.7	F	1.74	0.0246	Snodgrass et al. 2020
Yakut	1.53	56.7	F	1.53	0.0271	Snodgrass et al. 2021
Yakut	1.59	86.4	F	1.89	0.0219	Snodgrass et al. 2022
Yakut	1.54	56.1	F	1.53	0.0273	Snodgrass et al. 2023
Yakut	1.51	55.7	F	1.51	0.0271	Snodgrass et al. 2024
Yakut	1.54	51.5	F	1.48	0.0287	Snodgrass et al. 2025
Yakut	1.66	43.9	F	1.46	0.0332	Snodgrass et al. 2026
Yakut	1.49	71.8	F	1.66	0.0232	Snodgrass et al. 2027
Yakut	1.52	52.6	F	1.47	0.0280	Snodgrass et al. 2028
Yakut	1.63	115.5	F	2.17	0.0188	Snodgrass et al. 2029
Yakut	1.53	74.7	F	1.72	0.0231	Snodgrass et al. 2030
Yakut	1.55	66.0	F	1.65	0.0250	Snodgrass et al. 2031
Yakut	1.51	39.0	F	1.29	0.0332	Snodgrass et al. 2032

Yakut	1.56	72.1	F	1.72	0.0239	Snodgrass et al. 2033
Eskimo	1.53	60.0	F	1.57	0.0262	Heinbecker 1928
Eskimo	1.59	63.0	F	1.65	0.0262	Heinbecker 1928
Eskimo	1.60	72.0	M	1.75	0.0243	Heinbecker 1928
Eskimo	1.46	45.1	F	1.34	0.0298	Heinbecker 1931
Eskimo	1.55	62.5	F	1.61	0.0258	Heinbecker 1931
Eskimo	1.43	62.0	F	1.52	0.0245	Heinbecker 1931
Eskimo	1.48	52.2	F	1.44	0.0277	Heinbecker 1931
Eskimo	1.73	67.0	M	1.80	0.0269	Heinbecker 1931
Eskimo	1.55	49.9	M	1.47	0.0294	Rabinowitch and Smith 1936
Eskimo	1.60	59.9	M	1.62	0.0271	Rabinowitch and Smith 1936
Eskimo	1.59	63.5	M	1.65	0.0260	Rabinowitch and Smith 1936
Eskimo	1.52	45.4	F	1.39	0.0307	Rabinowitch and Smith 1936
Eskimo	1.45	50.8	F	1.41	0.0277	Rabinowitch and Smith 1936
Eskimo	1.63	61.7	M	1.66	0.0269	Rabinowitch and Smith 1936
Eskimo	1.55	53.5	M	1.51	0.0282	Rabinowitch and Smith 1936
Eskimo	1.61	50.3	F	1.51	0.0301	Rabinowitch and Smith 1936
Eskimo	1.57	47.2	M	1.45	0.0307	Rabinowitch and Smith 1936
Eskimo	1.65	67.1	M	1.74	0.0259	Rabinowitch and Smith 1936
Arctic	1.56	66.3	F	1.44	0.0218	Eveleth and Tanner 1976
Arctic	1.53	80.5	F	1.39	0.0172	Laughlin 1951
Arctic	1.66	67.2	M	1.55	0.0231	Eveleth and Tanner 1976
Arctic	1.64	67.7	M	1.52	0.0224	Laughlin 1951
SS Africa	1.64	58.3	F	1.32	0.0227	Eveleth and Tanner 1976
SS Africa	1.62	52.8	F	1.21	0.0230	Eveleth and Tanner 1976
SS Africa	1.56	52.1	F	1.15	0.0221	Eveleth and Tanner 1977
SS Africa	1.37	38.2	F	0.99	0.0259	Vincent et al. 1962; Ruff 1994
SS Africa	1.54	54.2	F	1.22	0.0225	Vincent et al. 1962
SS Africa	1.59	52.5	F	1.26	0.0241	Froment and Hiernaux 1984
SS Africa	1.60	51.4	F	1.28	0.0248	Froment and Hiernaux 1984
SS Africa	1.45	42.7	F	1.10	0.0257	Cavalli-Sforza 1986

SS Africa	1.54	50.4	F	1.18	0.0235	Cavalli-Sforza 1986
Pacific	1.52	47.0	F	1.22	0.0261	Eveleth and Tanner 1976
Pacific	1.52	49.2	F	1.22	0.0248	Eveleth and Tanner 1976
SS Africa	1.57	45.4	F	1.21	0.0267	Abbie 1956-1957
SS Africa	1.74	66.8	M	1.43	0.0215	Eveleth and Tanner 1976
SS Africa	1.59	47.8	M	1.19	0.0249	Eveleth and Tanner 1976
SS Africa	1.75	56.6	M	1.43	0.0253	Eveleth and Tanner 1976
SS Africa	1.67	60.4	M	1.35	0.0224	Eveleth and Tanner 1976
SS Africa	1.70	59.3	M	1.37	0.0232	Froment and Hiernaux 1984
SS Africa	1.70	58.4	M	1.35	0.0231	Froment and Hiernaux 1984
SS Africa	1.54	45.8	M	1.16	0.0253	Ghesquiere and Karvonen 1981
SS Africa	1.45	43.4	M	1.06	0.0245	Ruff 1994: Ghesquiere and Karvonen 1981
SS Africa	1.64	56.6	M	1.29	0.0228	Ghesquiere and Karvonen 1981
SS Africa	1.64	56.6	M	1.27	0.0225	Eveleth and Tanner, 1976
SS Africa	1.67	60.0	M	1.32	0.0220	Eveleth and Tanner 1976
SS Africa	1.53	48.3	M	1.18	0.0243	Cavalli-Sforza 1986
SS Africa	1.61	54.6	M	1.25	0.0229	Cavalli-Sforza 1986
Indo-Mediterranean	1.73	64.8	M	1.50	0.0231	Eveleth and Tanner 1976
Indo-Mediterranean	1.67	56.8	M	1.41	0.0249	Eveleth and Tanner 1976
Indo-Mediterranean	1.69	53.6	M	1.34	0.0249	Eveleth and Tanner 1976
Indo-Mediterranean	1.64	49.2	M	1.32	0.0268	Eveleth and Tanner 1976
Pacific	1.73	76.1	M	1.60	0.0210	Eveleth and Tanner 1976
Pacific	1.61	56.4	M	1.33	0.0236	Eveleth and Tanner 1976
Pacific	1.60	58.5	M	1.34	0.0230	Eveleth and Tanner 1976
Pacific	1.70	56.7	M	1.38	0.0244	Abbie 1956, 1957
Hadza	1.54	49.0	F	1.45	0.0296	Pontzer et al. 2012
Hadza	1.45	42.2	F	1.30	0.0307	Pontzer et al. 2012
Hadza	1.45	41.8	F	1.30	0.0310	Pontzer et al. 2012
Hadza	1.43	40.4	F	1.26	0.0312	Pontzer et al. 2012
Hadza	1.49	49.0	F	1.41	0.0288	Pontzer et al. 2012
Hadza	1.41	37.6	F	1.21	0.0322	Pontzer et al. 2012

Hadza	1.64	55.0	F	1.59	0.0289	Pontzer et al. 2012
Hadza	1.51	50.6	F	1.44	0.0286	Pontzer et al. 2012
Hadza	1.37	37.6	F	1.19	0.0317	Pontzer et al. 2012
Hadza	1.41	34.0	F	1.16	0.0342	Pontzer et al. 2012
Hadza	1.49	53.0	F	1.46	0.0276	Pontzer et al. 2012
Hadza	1.38	41.2	F	1.24	0.0302	Pontzer et al. 2012
Hadza	1.53	44.2	F	1.38	0.0312	Pontzer et al. 2012
Hadza	1.42	37.2	F	1.22	0.0327	Pontzer et al. 2012
Hadza	1.43	37.6	F	1.22	0.0326	Pontzer et al. 2012
Hadza	1.35	37.8	F	1.18	0.0312	Pontzer et al. 2012
Hadza	1.71	55.8	M	1.65	0.0295	Pontzer et al. 2012
Hadza	1.54	46.8	M	1.42	0.0304	Pontzer et al. 2012
Hadza	1.66	52.8	M	1.57	0.0298	Pontzer et al. 2012
Hadza	1.50	43.6	M	1.35	0.0309	Pontzer et al. 2012
Hadza	1.58	52.4	M	1.52	0.0290	Pontzer et al. 2012
Hadza	1.54	47.6	M	1.43	0.0301	Pontzer et al. 2012
Hadza	1.45	42.5	M	1.30	0.0306	Pontzer et al. 2012
Hadza	1.62	50.6	M	1.52	0.0300	Pontzer et al. 2012
Hadza	1.58	58.2	M	1.58	0.0272	Pontzer et al. 2012
Hadza	1.65	54.6	M	1.59	0.0292	Pontzer et al. 2012
Hadza	1.67	54.0	M	1.60	0.0297	Pontzer et al. 2012
Hadza	1.61	57.8	M	1.60	0.0277	Pontzer et al. 2012
Hadza	1.53	44.5	M	1.38	0.0310	Pontzer et al. 2012

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