The effect of bi-iliac breadth on core body temperature in runners

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Abstract

Thermoregulation is argued to be an important factor influencing body breadth in hominins based on the relationship of surface area to body mass first proposed by Bergmann. Selection for a narrow thorax, and thus a narrow pelvis, increases body surface area relative to body mass, which could be beneficial in hot climates if it leads to a decrease in core body temperature. However, the relationship between pelvic breadth and thermoregulation in humans has not been established. Although previous work has shown that bi-iliac breadth is significantly positively associated with latitude in humans, we lack an understanding of whether this association is due to climate-related selection, neutral evolutionary processes, or other selective pressures. A missing piece of the puzzle is whether body breadth at the iliac blades is an important factor in thermoregulation. Here, we examine this in a mixed-sex sample of 28 adult runners who ran for one hour at 3.14 m s^{-1} in a variety of climatic conditions while their core body temperatures were measured using internal temperature sensors. The association of maximum core temperature with anthropometric and demographic variables such as age, sex, mass, body fat percentage, and bi-iliac breadth was analyzed using a linear mixed effect model. Due to the small sample size, the model was also bootstrapped. We found that an increase in absolute bi-iliac breadth was significantly associated with an increase in maximum core temperature. Overall, this preliminary analysis suggests a link between variation in bi-iliac breadth and maximum core body temperature during running, but further investigation is needed.

Keywords: Thermoregulation; Pelvis; Bergmann's rule; Allen's rule; Body breadth; Pelvic breadth

1. Introduction

Thermoregulation is thought to have played an important role in body shape and size in the hominin lineage (Trinkaus, 1981; Ruff, 1991, 1993, 1994, 1995; Holliday, 1997; Tilkens et al., 2007; Weaver and Hublin, 2009; Roseman and Auerbach, 2015; Hora et al., 2020; Hora et al., 2022). For example, the wide thorax characteristic of Neandertals is considered to be an adaptation to a cold climate, while the narrow thorax of *Homo erectus*, as typified by KNM-WT 15000, is generally interpreted as an adaptation to a hot climate (Ruff and Walker, 1993; Collard and Cross, 2017). In the case of Neandertals, the association between thorax width, body surface area to mass ratio, and heat retention is frequently invoked in the literature as an explanation of Neandertal body proportions compared to those of modern humans, although other explanations such as genetic drift, primitive retentions, and energetic requirements are also posited (e.g., Holliday, 1997; Gómez-Olivencia et al., 2009; Weaver, 2009). One reason that the link between thorax width and thermoregulation in hominins is uncertain is that there is no empirical evidence that the former is directly associated with core body temperature.

The hypothesis that thorax width affects core body temperature derives from the relationship between body mass and surface area, consistent with Bergmann's (1847) rule. Metabolic heat is a by-product of active tissue metabolism produced through cellular respiration (Kenny and Flouris, 2014). An increase in body mass, locomotor velocity, and/or work (i.e., the transfer of energy by the application of force over a distance; Winter and MacLaren, 2001) leads to an increase in heat production (Nielsen, 1996; Gleeson, 1998; Cross et al., 2008). Heat is dissipated via radiative, convective, evaporative, and conductive heat loss through the skin.

Although the skin can both absorb and dissipate heat, skin surface area in large part determines the body's heat dissipation potential (Kenny and Jay, 2013). For people with similar body mass, an individual with a narrower thorax will have greater surface area than an individual with a wider thorax. All other factors being equal, in the same climatic conditions both individuals should produce similar amounts of body heat due to their similar body mass, but the individual with greater surface area should dissipate that heat more readily and thus have a lower core body temperature.

Ruff's (1991, 1994) cylindrical thermoregulatory model is based on the relationship of surface area to mass. The model shows that if the human body is treated as a cylinder, bi-iliac breadth (the widest diameter of the pelvis) determines the diameter of the cylinder and thus thorax width. For this reason, bi-iliac breadth is a major determinant of the cylinder's (i.e., the body's) surface area. It is therefore reasonable to use bi-iliac breadth as a measurement of thorax width.

If high body surface area relative to body mass is favored in an environment, selection would be expected to decrease bi-iliac breadth, while if low body surface area relative to body mass is favored, selection might increase bi-iliac breadth (Ruff, 1991, 1994). In concert with other thermoregulatory strategies, a population evolving in a hot climate would likely be under selection to maximize surface area to body mass ratio for thermoregulatory benefits such as exercising at a higher intensity or for longer duration in hot ambient conditions before risking negative outcomes such as hyperthermia. Conversely, a population evolving in a cold climate should be under selection to minimize surface area to body mass ratio and retain heat to avoid hypothermia. Consequently, the former population should evolve narrower pelves than the latter population. In support of this argument in relation to modern humans, there is a strong and

significant positive correlation between skeletal bi-iliac breadth and latitude (used as a proxy for climate; Ruff, 1991; Holliday and Hilton, 2010; Cowgill et al., 2012), suggesting that as human populations began to adapt to colder climates further from the equator, thermoregulatory selection led to increased bi-iliac breadth (Ruff, 1991; Weaver, 2002; Auerbach, 2012). Furthermore, several studies found that body size is strongly negatively correlated with climatic temperature (Roberts, 1953; Katzmarzyk and Leonard, 1998; Taylor, 2006) and the ratio of surface area to body mass is negatively correlated with body temperature in experimental trials, consistent with the predictions of Bergmann's rule (Robinson, 1942; Wyndham et al., 1964; Bar-Or et al., 1969; Sloan and Keatinge, 1973; Wyndham, 1973; Kollias et al., 1974; Smith and Hanna, 1975; Epstein et al., 1983; McArdle et al., 1984; Austin and Lansing, 1986; Ruff, 1994). However, in contrast with these findings, a number of studies failed to find a consistent correlation between surface area to body mass ratio and core body temperature(Burse, 1979; Havenith et al., 1995; Anderson et al., 1995; Anderson, 1999; del Coso et al., 2011; Cramer and Jay, 2016), casting doubt on the extent to which Bergmann's proposed thermoregulatory mechanism applies to humans.

Although the ratio of surface area to body mass is important, thermoregulation is complicated and influenced by many factors. Thermoregulatory responses to climatic conditions and exercise may be affected by factors such as aerobic fitness (Pandolf et al., 1977; Aoyagi et al., 1998; Mora-Rodriguez, 2012), acclimatization (Avellini et al., 1980; Havenith and van Middendorp, 1990; Aoyagi et al., 1998; Epstein et al., 2012), sex (Fox et al., 1969; Cunningham et al., 1978; Paolone et al., 1978; Frye and Kamon, 1981; Horstman and Christensen, 1982; Gagnon and Kenny, 2012a; Armed Forces Health Surveillance Bureau, 2017; Iyoho et al., 2017; Wardle, 2017; Corbett et al., 2020), age (Wagner and Horvath, 1985; Bar-Or, 1998), body

composition (Friedl, 1992; Havenith et al., 1995; Dennis and Noakes, 1999; Marino et al., 2000), limb length (Allen, 1877; Tilkens et al., 2007; Cross et al., 2008), attire (Henane et al., 1979; McLellan, 1993; Montain et al., 1994; McLellan et al., 1996; O'Brien et al., 2011), and menstrual cycle phase (Pivarnik et al., 1992; Glickman-Weiss et al., 2000; Kuwahara et al., 2005; Janse de Jonge et al., 2012). All of these factors must be taken into account when designing a study aimed to parse out the possible effect of bi-iliac breadth on core body temperature, whether in humans or extinct hominins. For example, based on Allen's (1877) rule, if two individuals have the same body mass, but one has longer limb segments, the longer-limbed individual will have a higher surface area to mass ratio and thus the potential to dissipate more heat. In terms of hominin evolution, accurate estimates of limb segment lengths have been shown as a critical part of thermoregulatory models because studies of humans have found that proximal and distal limb segments have differing skin surface temperatures and experience different wind speeds during locomotion (Cross et al., 2008; Cross and Collard, 2011; Collard and Cross, 2017).

This study is concerned with testing whether bi-iliac breadth has a significant effect on core temperature. To address this question, the relationship between bi-iliac breadth and core temperature was tested in a mixed-sex group of 28 physically fit adult runners who ran under a variety of climatic conditions. Telemetric temperature sensors were used to measure the core temperature of the runners. A linear mixed effects model was bootstrapped to determine if bi-iliac breadth affects maximum core body temperature, controlling for other possible contributing factors. Ascertaining the role of bi-iliac breadth in core body temperature will enable the determination of whether the thermoregulation hypothesis has a valid basis in human physiology

and can be invoked as a potential factor influencing thorax breadth and bi-iliac breadth in humans and other hominins.

2. Materials and methods

2.1. Study participants

Seven runs (trials) were conducted in total. Fifty-five adults volunteered for the study, but only 39 participated in at least one trial. Of those 39, seven (five women and two men) were unable to maintain the required pace. Two participants' temperature sensors gave unrealistically low temperature readings throughout (<36 °C). Upon investigation, it was determined that they swallowed the temperature sensor less than four hours before the start of the run, so their data were excluded from the analysis. An additional two individuals had starting core temperature readings of over 40 °C after sitting in the shade for 30 minutes before the start of the trial. These very high readings were thought to be erroneous (Moran and Mendal, 2002), and thus their data were excluded as well. The final number of participants thus consisted of 28 individuals—10 females and 18 males—ranging from 18–44 years of age. All participants stated that they were healthy and injury free. Females were asked to take part only if they stated they were not taking birth control pills. Approval for the experimental protocol was obtained from the Institutional Review Boards of the City University of New York and New York University (IRB protocols 2015–1517 and IRB–FY2016–189, respectively).

2.2. Experimental design

Each of the 28 subjects participated in a minimum of one, one-hour trial at a pace of 3.14 m s^{-1}, while their core temperature was recorded. It was decided that subjects should run for one hour due to thermal inertia, where the onset of cooling mechanisms lags behind the onset of exercise. Metabolic heat production generally reaches a steady state after five minutes, but whole-body heat loss may not reach a steady state until after 30 minutes or more (Kenny and Jay, 2013). When exercise occurs in compensable climatic conditions in which core temperature can plateau, an hour allows sufficient time for this to occur after the initial thermal inertia is overcome (Davies, 1979; Kenny and Jay, 2013). The physical fitness of the participants was not tested other than to exclude data from anyone who could not maintain the pace of 3.14 m s^{-1} for the entirety of the hour. All individuals were permanent residents of New York City and regularly ran outside and were thus considered to be acclimatized to the same conditions.

Seven experimental trials took place between December, 2016 and July, 2017. Participants ran on a flat, circular, 0.8-km outdoor paved track in Central Park, New York. All subjects wore a tank top, shorts, and running shoes, and in females a sports bra. They were instructed to drink plenty of water prior to the run, but they were prohibited from drinking anything during the run. Participants were asked not to consume caffeine or alcohol within 24 hours of the start of the run. They were not instructed regarding food consumption before the run, although they were prohibited from eating during the run. All experiments occurred between 10:00 am and 2:00 pm except for Trial 6 which ended at 7:25 pm. All participants were instructed to arrive 30 minutes before the start of the run so that they could sit and rest in the shade before the start of the run.

Temperature readings were recorded every 0.8 km. Internal core temperature was measured using FDA approved single-use HQ Inc. CorTemp® ingestible temperature sensors

and an HQ Inc. CorTemp® external monitor, which have been shown to provide an accurate measure of internal core temperature (McKenzie and Osgood, 2004; Byrne et al., 2006; Gant et al., 2006; Osinchuk et al., 2014; Sagui et al., 2017).

Wet bulb global temperature, ambient temperature, and relative humidity were measured every 30 minutes during each trial using an Extech HT30 Heat Stress wet bulb global temperature meter. Wet bulb global temperature includes the variables of ambient temperature, humidity, wind speed, and sunlight. Although in this study the effects of climatic conditions on thermoregulation were not explicitly tested, it is important to note that trials took place in a variety of climatic conditions, although they were cancelled if it rained. Additionally, it is important to note that the number of subjects who participated in each trial varied and so some trials are represented by more data than others.

2.3. Rationale for study design

Debate exists about the optimum design for studies that seek to determine factors that significantly influence core body temperature during exercise. Individuals with a higher maximum volumetric oxygen consumption (VO_{2max}, i.e., greater physical fitness) have been shown to have a lower resting core temperature and thus potentially a lower maximum core temperature during exercise (Fritzsche and Coyle, 2000). Early studies tried to control for variation in physical fitness between subjects by determining VO_{2max} for each individual and having all subjects exercise at the same relative exercise intensity (i.e., the same percentage of their VO_{2max}; Åstrand, 1960; Saltin and Hermansen, 1966). However, as VO_{2max} varies among individuals, this meant that subjects were exercising at different absolute intensities, with fitter individuals exercising at higher intensities than less fit individuals and thus producing more heat

due to their higher workloads (Mora-Rodriguez et al., 2010; Wardle, 2017). More recent studies have favored a fixed absolute workload rather than a relative workload. In these studies, VO_{2max} is not correlated with the heat gain during exercise because all subjects exercise at the same absolute intensity, regardless of their VO_{2max} (Jay et al., 2011). However, this has the opposite problem to relative exercise intensity in that less fit individuals will be working relatively harder than fitter individuals. For this experiment the latter method was chosen because VO_{2max} was not measured in this study and therefore relative workloads could not be calculated.

As with the consideration of VO_{2max}, it is reasonable to consider controlling for differences in lower limb length. Effective limb length has an inverse relationship with cost of transport (J kg^{-1} m^{-1}) in terrestrial animals (Pontzer, 2007), and lower limb length has been found to have a significant negative effect on energetic expenditure (VO_2) in humans during walking and running (Steudel-Numbers and Tilkens, 2004; Steudel-Numbers et al., 2007). Therefore, humans with shorter lower limbs will most likely expend more energy and thus produce more heat at a given locomotor speed than humans with longer lower limbs.

One method employed in previous studies is Froude number (Fr), V^2 g^{-1} l^{-1}, where V is velocity, g is the gravitational constant, and l is a 'characteristic length', i.e., lower limb length. Froude number has been widely used to estimate optimal walking speed within and between species (Vaughan and O'Malley, 2005) because animals moving at equal Fr are thought to be traveling at equivalent velocities (Kramer and Sarton-Miller, 2008). To employ Fr in the current study would mean calculating Fr for each subject and adjusting their individual velocity when running so that Fr was the same for each subject. However, this would again involve individuals running at different velocities and working at different absolute intensities compared to one another. As the intention of including Fr in the analysis would be to compensate for variation in

lower limb length and its effects on energetic expenditure and thus heat production, including lower limb length in the models should achieve the same goal. Although this necessarily means that individuals will be exercising at different Fr, the question being asked is whether variation in bi-iliac breadth affects heat production at a specific velocity. This is a reasonable question to ask because requiring all individuals to run at the same velocity is more likely to mimic actual conditions during human evolution. For example, if a group were hunting together, it seems reasonable to expect that they would all run at a similar speed. Furthermore, it would be impossible to monitor and enforce different individual velocities when the participants in the study ran together in groups.

2.4. Measurement of anthropometric and demographic variables

Subjects reported their age and all self-identified as either female or male. Anthropometric measurements were taken by J.E. while the subjects wore shorts and a tank top. Measurement error was not assessed.

Bi-iliac breadth (also sometimes defined in the anthropometric literature as bi-iliocristale breadth, e.g., Landers et al. 2013) was measured using sliding anthropometric calipers which were placed horizontally on the subject's hips while they were standing. Placement of the calipers was determined by palpating the subject's hips bilaterally to determine the location of the anterior superior iliac spines, then following the iliac crests from the anterior superior iliac spines posteriorly to the most lateral points on the trunk in the midaxillary plane. The sliding calipers were tightened the maximum amount that was comfortable for the subject. This measurement follows the methodology used by previous researchers (Jamison and Zegura, 1970; Eveleth and Tanner, 1976; National Center for Health Statistics, 1988; Rani et al., 2021).

In addition to bi-iliac breadth, several anthropometric and demographic variables are hypothesized to affect thermoregulatory ability. These are sex, age, body mass (hereafter referred to as 'mass'), body fat percentage, and lower limb length. Stature, body surface area, and the ratio of body surface area to mass may also be important factors in thermoregulation, but these variables were not included in the model (see Supplementary Online Material [SOM] S1).

Mass was measured using a standard digital scale with an accuracy of ± 0.1 kg which was calibrated monthly. Body fat percentage was measured using skinfold calipers with an accuracy of ± 0.01 cm. Four skinfold measurements were taken: biceps, triceps, subscapular, and supra-iliac. Body fat percentage was calculated based on these skinfold measurements using equations from Durnin and Womersely (1974), which are based on Siri (1956). First, body density was calculated using the $\log_{10}$ of the summed value of the four skinfolds, adjusting the equation for sex and age. Second, density was used in the following equation to calculate body fat percentage:

$$\text{body fat percentage} = (4.95/d - 4.50) \times 100,$$

where d is density, 4.95 is a term that accounts for the proportional difference of an individual from the density of a reference body, and 4.50 is the standard deviation (Siri, 1956).

Limb length is hypothesized to affect thermoregulation based on Allen's (1877) rule. Because upper and lower limb length are highly correlated with one another in humans ($r = 0.84$, $p < 0.01$ in our sample) and lower limb length affects locomotor economy and thus heat production (Steudel-Numbers et al., 2007), lower limb length was used in this study. The measurement of the lower limb was taken on the right side from the greater trochanter of the femur to the distal fibula.

The response variable of interest in this study was maximum core temperature, which was defined as the maximum recorded temperature a subject reached during a trial.

2.5. Statistical analyses

All statistical analyses, creation of the linear mixed effects model, and bootstrapping were performed in R v. 4.3.3 (R Core Team, 2024). The explanatory variables for the model were bi-iliac breadth, sex, age, mass, body fat percentage, lower limb length, and wet bulb global temperature. The response variable was maximum core temperature.

For the purposes of modeling the data, all continuous explanatory variables were standardized by first centering the data for each variable to a mean of zero and then scaling the data to a standard deviation of one to facilitate interpretation of model estimates (Schielzeth, 2010). Sex, a categorical variable, was coded as 0 = female and 1 = male. Each trial was also coded as one of seven different levels to allow analysis of trial as a categorical variable. Outliers were identified as any data points that fell 1.5 × the interquartile distance from the 1st or 3rd quartile.

To test for significant differences in maximum core temperature between the seven trials, first the distribution of the data was tested for normality using a Shapiro-Wilk normality test where $p \leq 0.05$ was considered a significant departure from a normal distribution. If normally distributed (as in the case of maximum core temperature), a one-way analysis of variance (ANOVA) was used to test for differences between trials. If the results indicated significant differences between trials, a Tukey's HSD test was used to determine which trials differed significantly from one another. When conducting multiple post hoc pairwise analyses, the chances of finding a significant but erroneous association increase (i.e., Type I error increases;

Bender and Lange, 2001). Therefore, due to the multiple comparisons, the determination of significance was based on the Bonferroni-Holm method (Aickin and Gensler, 1996) of adjusting the *p*-value by reducing it based on the number of post hoc pairwise tests, which yielded an adjusted α value of 0.0024.

Correlation between explanatory variables was assessed by performing Pearson correlation tests in the R stats package (R Core Team, 2024) on each pair of explanatory variables.

A linear mixed effects model was chosen for this study because each trial consisted of a different combination of subjects. Although all subjects were asked to participate in all seven trials, trial composition varied, with some subjects participating multiple times while others chose not to. A linear mixed effects model accounts for the nonindependence of the subjects' data by incorporating random effects (Harrison et al., 2018). Here, the fixed effects of the linear mixed effects model were bi-iliac breadth, sex, age, mass, body fat percentage, lower limb length, and wet bulb global temperature, while the random effects were subject and trial. The random effect of subject is partially crossed with trial as some subjects appeared in more than one trial. Maximum core temperature was the response variable of interest. The package lme4 version 1.1-35.5 (Bates et al., 2014) was used to create the linear mixed effects model. The model allowed random intercepts, but not random slopes, meaning that the assumption was made that the participants had the same relationship between the response variable and the fixed effects, but each may have started at a different body temperature.

Once the model was fitted, the residuals were plotted in R using the car package version 3.1-2 (Fox and Weisberg, 2019) to check for deviation from the assumptions of normally distributed and homogenous residuals.

Due to the small number of observations and the large number of variables in the model, bootstrapping was performed to obtain more robust model parameters and more reasonable confidence intervals (Thai et al., 2013). The model was bootstrapped 3000 times. A fixed effect was considered significant if the 95% confidence interval for the estimate did not include zero.

3. Results

3.1 Summary data

Tables 1–3 and Figures 1–2 summarize the anthropometric, climatic, and core temperature data. Figure 3 and SOM Figure S3 show the linear relationship between bi-iliac breadth and maximum core temperature for each subject and the fitted versus residual values, respectively.

The largest number of participants took part in Trial 2. As a result, the greatest variation in most variables can be found in Trial 2. The majority of subjects (18) participated in only one trial, but ten participated in more than one.

Subjects were of disparate body types and ages. For example, mass ranged from 49.8 kg to almost double that at 94.4 kg. Body fat was also highly variable, ranging from 13.1% to 31.6%, but the majority of subjects (21 out of 28) had a percentage body fat of 25% or lower. Mass and body fat percentage were both highly and significantly correlated with sex. Males were associated with greater mass and lower body fat than females (SOM Table S1).

Bi-iliac breadth ranged from 25.5 cm to 37.5 cm, with the sample skewing toward the higher end of the modern human distribution. The subjects ranged in age from 18 to 44, with

about half (12) in their 20's. Lower limb length ranged from 0.71 m to 0.94 m, with two females having the shortest and longest lower limbs.

3.2. Correlation of climatic variables

Trial and wet bulb global temperature were highly and significantly correlated (SOM Table S1), raising the question as to whether both variables should be included in the model. The main source of variation among trials was climatic conditions such as wet bulb global temperature, which explains the near perfect correlation between the two variables. However, trial could encompass non-climatic variation as well. For example, the fact that trials took place on different days and at different times of day. Trial was therefore retained in the linear mixed effects model to avoid pseudoreplication.

Ambient temperature was highly and significantly correlated with wet bulb global temperature and with trial (SOM Table S1). Although wet bulb global temperature was not significantly correlated with relative humidity (SOM Table S1), wet bulb global temperature encompasses both ambient temperature and relative humidity and therefore only wet bulb global temperature was included in the model to avoid overfitting.

3.3. The relationship between trial and core temperature

A one–way ANOVA indicated there were significant differences between trials for maximum core temperature (SOM Table S2). However, a Tukey HSD multiple-comparison test with the Bonferroni adjusted *p*-value indicated that there were no significant differences in maximum core temperature between any two pairs of trials (SOM Table S3). The mean and standard deviation in core temperature per lap for each trial is presented in SOM Figure S1.

3.4. Linear mixed effects model

There were no outliers for maximum core temperature and the Shapiro-Wilk test indicated it was normally distributed (W = 0.96, p = 0.10). The summary statistics for the linear mixed effects model can be found in Table 4 and the variance-covariance matrix in SOM Table S4. The plots of the residuals are presented in SOM Figure S2. None of the fixed effects reached significance, but bi-iliac breadth approached significance. In addition, the model was singular (see SOM S2).

3.5. Bootstrapping

The bootstrapping results are presented in Table 5. Bi-iliac breadth, mass, body fat percentage, and wet bulb global temperature were all associated with increased maximum core temperature; when these variables increase, maximum core temperature is estimated to increase. Age, sex, and lower limb length were associated with decreased maximum core temperature such that as these variables increase, maximum core temperature is expected to decrease. For sex, this means that being female is associated with a higher maximum core temperature than being male. However, the associations with maximum core temperature were only considered significant if the 95% confidence interval for the estimate did not include zero, which was the case for bi-iliac breadth, sex, and mass.

4. Discussion

4.1. Model results

For a given mass, during running, this study found that bi-iliac breadth approached significance in the linear mixed effects model for maximum core temperature, and the bootstrapped model estimate was significant. The bootstrapped model estimate for mass was also significant, in line with the expectations of thermoregulatory theory which predicts that greater mass will produce more heat. As mass and bi-iliac breadth were strongly and significantly correlated (SOM Table S1) due to larger individuals tending to have larger pelves, some of the variation explained by bi-iliac breadth may be due to its link with mass, despite mass being included in the models. However, the two variables were not perfectly correlated and if bi-iliac breadth is removed from the linear mixed effects model, mass does not reach significance. This suggests that bi-iliac breadth has an effect independent of mass, which may be due to its hypothesized close relationship to surface area. As surface area increases relative to mass, heat dissipation potential should increase, and bi-iliac breadth may be functioning in the same way. Indeed, surface area to mass ratio was strongly negatively correlated with bi-iliac breadth in the sample, in keeping with Ruff's cylindrical model; as bi-iliac breadth increases, surface area to mass ratio decreases, meaning individuals with larger bi-iliac breadth in the sample should reach higher maximum core temperatures than those with smaller bi-iliac breadths, and this is indeed what was found.

This result has potential implications for hominin evolution because hominin body proportions are hypothesized to be, at least in part, adaptations to climatic conditions. If bi-iliac breadth does indeed influence maximum core body temperature, as was found in this study, then this would support arguments that the wide pelvis and thorax of *Homo neanderthalensis* and the potentially relatively narrow pelvis and thorax of *H. erectus* would be beneficial in cold and hot climates, respectively.

The estimate for sex was also significant in the bootstrapped model, with males being associated with lower maximum core temperature than females. Physical characteristics can confound the detection of differences in the autonomic thermoeffector functions between sexes that are due to cutaneous vasomotion (the dilation of blood vessels in the skin) and sudomotion (the stimulation of the sweat glands; Gagnon and Kenny, 2012a,b). There is evidence that females have reduced sudomotor activity (i.e., a decreased sweat gland output) and lower thermosensitivity (i.e., their thermoregulatory mechanisms initiate at a higher temperature) compared with males (Shapiro et al., 1980; Inoue et al., 2005; Ichinose–Kuwahara et al., 2010; Gagnon and Kenny, 2012a,b). However, other researchers argue that these differences are in fact due to physical characteristics and not due to differences in autonomic–driven pathways for heat loss (Burse, 1979; Avellini et al., 1980; Havenith and van Middendorp, 1990; McLellan, 1998; Notley et al., 2017).

It is therefore subject to discussion whether sex has an independent effect on thermoregulation outside of its correlation with attributes such as mass and body fat percentage. The reason why body fat percentage was not significant in this study is perhaps because sex was highly and significantly correlated with body fat percentage in the sample (SOM Table S1). Body fat percentage and body fat distribution are sexually dimorphic, with females having a higher total body fat percentage that is distributed more peripherally on the body than in males (Kissebah and Krakower, 1994; Taylor et al., 2010). In other words, sex and body fat percentage are not fully independent variables and it could be that the difference in core temperature between females and males in the study is, in part, due to differences in body fat percentage.

The fact that increasing age negatively affected maximum core body temperature is a curious result, although age was not a significant predictor in the model. Previous research

indicates that older individuals have delayed onset of sweating and decreased skin blood flow, suggesting that maximum core body temperature should increase with age, not decrease (Armstrong and Kenney, 1993; Dufour and Candas, 2007). However, individuals generally lose physical fitness and muscle mass as they age, which could explain deteriorating thermoregulatory mechanisms such as the onset of sweating and decreased skin blood flow (Armstrong and Kenney, 1993; Dufour and Candas, 2007). It's possible that the older individuals in the study were still too young for their thermoregulatory mechanisms to have deteriorated, or that their practice of running regularly outdoors strengthened their thermoregulatory mechanisms compared to non-runners of a similar age.

4.2. Climatic Data

The core temperature data were collected in a variety of climatic conditions (Table 2), which may be expected to influence maximum core temperature. For example, it would be predicted that maximum core temperature would be significantly higher on a hotter compared to a colder day. However, what the results of this study revealed was that wet bulb global temperature, which includes the variables of ambient temperature, humidity, wind speed, and sunlight, was not a significant predictor of maximum core temperature, and the Tukey HSD test indicated that maximum core temperature did not differ significantly between trials. These results suggests that core temperature data are comparable among trials, despite differences in climatic conditions. Potentially, the differences in climatic variables among the trials were not large enough to cause a significant difference in maximum core temperature, or the sample sizes of the trials were possibly too small to detect it.

4.3. Comparative bi-iliac breadth

The most surprising anthropometric result was the range and values for bi-iliac breadth. Mean bi-iliac breadth in the sample was 30.5 ± 2.9 cm, with a range from 25.5 cm to 37.5 cm (Table 1). The mean value and, indeed, all values over 29.0 cm, are high, even for living Artic populations (Ruff, 1991). For example, reported means for samples from Inuit groups are 29.7 cm in Ruff (1991) and 28.6 ± 0.2 cm for females and 29.1 ± 0.3 cm for males in Ruff et al. (2005). Jamison and Zegura (1970) reported a mean of 29.6 ± 1.9 cm for a sample of adult females Inuit. For a sample of tall, wide-bodied Finns, Ruff et al. (2005) found an average of 27.9 ± 0.2 cm for females and 29.9 ± 0.3 cm for males. Ruff (1991) also reported a worldwide range for bi-iliac breadth of 22.9–29.7 cm (although values in Ruff et al., 2005 exceed this range). It is clear, therefore, that the bi-iliac breadth values in this study are in the upper end of, and mostly supersede, values found by other researchers.

There are several possible explanations for this finding. The first is that although the same method was used to measure bi-iliac breadth in this study as the studies cited above, potentially J.E. did not tighten the sliding calipers to the same extent, thus including more soft tissue in the measurements.

The second is that, through chance, the study includes a highly skewed sample of individuals with large bi-iliac breadth. To test this hypothesis, the anthropometric data were examined for all 55 subjects who originally volunteered. Of these 55, 47 have a recorded bi-iliac breadth. The mean for this group (which includes an additional 19 individuals who were not ultimately included in the study) is 29.4 ± 3.0 cm with a range of 25.4 cm to 37.5 cm. If only the 19 individuals who were not included in the study are examined, the range in bi-iliac breadth is 25.4 cm to 30.2 cm, with a mean of 27.8 ± 1.9 cm. This would be more in keeping with the

results of other studies. Additionally, all individuals with a bi-iliac breadth over 30.2 cm (17 in total) in the sample of 47 individuals were also in the study sample of 28 individuals, which is suggestive that the 28 subjects represent, in fact, a skewed sample.

The third possibility is that skeletal bi-iliac breadth in the sample is not larger than average, but the subjects have significantly more body fat at the hips than in previous studies. This is quite possible as seven individuals (i.e., 25%) in this study had body fat percentages of 25% or greater, which is considered overweight (Gallagher et al., 2000). This sample may therefore not have an unusually wide bi-iliac breadth, but instead have increased levels of body fat compared to samples studied by other researchers. The only way to determine if this is true would be to obtain magnetic resonance images of the participants and measure their skeletal bi-iliac breadth, but this is not feasible.

A fourth possibility is that outliers are skewing the bi-iliac breadth data. None of the high values for bi-iliac breadth are outliers as calculated by 1.5 * IQR + Q3, where IQR is the interquartile distance between quartile 1 and quartile 3 (Q3), which would be any value above 38.1 cm for the data. However, this threshold is essentially meaningless because of anatomical and functional constraints on skeletal bi-iliac breadth (although living bi-iliac does not have the same constraints due to body fat). In other words, it would be extremely unlikely to find an individual capable of completing this study with a bi-iliac breadth above 38.1 cm. Using the traditional method for calculating outliers, therefore, is not useful in this situation, making it difficult to ascertain if outliers are skewing the data.

Lastly, it is possible that the highest values of bi-iliac breadth (e.g., 37.5 cm and 36.2 cm) in the sample are erroneous. However, this possibility is countered by the fact that these individuals were of greater mass and shorter height, indicating a heavyset and wide body type.

4.4. Limitations of the study

There are multiple caveats to this study. As is often the case with this kind of study, the sample size is small. Because of the reduced power of any model with a small dataset, it is exceedingly difficult to parse out the effect of any one explanatory variable on a response variable (in this case, bi-iliac breadth on maximum core temperature). The fact that a significant effect of bi-iliac breadth on maximum core temperature was detected despite the small sample size, and especially considering the sample skewed towards individuals with larger bi-iliac breadths relative to world-wide samplings (Hiernaux, 1985; Ruff, 1994; Ruff et al., 2005), perhaps indicates that further investigation into the role of bi-iliac breadth in core temperature variation might be fruitful.

This study was designed to answer a specific question: does bi-iliac breadth have a significant effect on core body temperature in a sample of habitual runners in New York City who ran at a specific velocity? Therefore, whether the same results would be obtained in other populations and using differing study designs is unknown and requires further testing, especially as the sample was skewed toward individuals with larger bi-iliac breadth. We fully acknowledge that this study is only a first step in determining the effect of bi-iliac breadth on core body temperature, and that other study designs could be equally informative. For example, utilizing velocities determined by Fr. The participants in this study did not exercise at velocities determined by Fr in part because the link between cost of transport and lower limb length at 'equivalent' velocities determined by Fr may be weak (Steudel-Numbers and Weaver, 2006; Kramer and Sarton-Miller, 2008; but see Riesenfeld, 1981 and Ruff, 1994), which could be due to lower limb length not scaling isometrically to mass in humans. It also would have been

impractical to try to ensure individual participants ran at different velocities relative to each other when they completed the trials simultaneously. Additionally, given the option, humans will choose to run at an optimal speed that minimizes energy expenditure and thus heat production (Rathkey and Wall-Scheffler, 2017). As subjects in this study ran at a set velocity, those running faster than their optimal speed would be expected to have produced more body heat as they were expending a greater amount of energy than those running at, or close to, their optimal speed.

Another caveat is that the participants ran in groups of various sizes, and this may have affected their gait and energy usage, and potentially their core temperature, compared to running alone. Future studies may want to test core temperature in individuals running alone rather than in groups, but we would argue that any differences in core temperature that result from running individually or in groups are likely to be small, and also that running in groups may more accurately mimic practical conditions during human evolution and amongst living humans, such as group persistence hunting (e.g., Liebenberg, 2006; Lieberman et al., 2020).

Additionally, core temperature fluctuates during the menstrual cycle (Grucza et al., 1993). It was assumed that all female participants were in follicular phase based on their self-reporting of their last period, but this assumption was not directly tested, which may have influenced the results.

Furthermore, certain subjects appeared more than once in the data, climatic conditions varied between trials, and subjects were not matched for anthropometric or demographic variables. All these caveats mean that the results should be interpreted cautiously, but this study still provides important preliminary data.

5. Conclusions

This initial study provides promising data in support of the hypothesis that bi-iliac breadth evolved as a thermoregulatory adaptation in hominins. This is an important addition to the literature and to the understanding of the applicability of Bergmann's rule to humans. It also provides a test of Ruff's (1991, 1994) cylindrical thermoregulatory model. The results indicate that increases or decreases in bi-iliac breadth in a population over time could be beneficial from a thermoregulatory perspective because bi-iliac breadth has a significant effect on maximum core temperature.

Thermoregulation involves the interaction of autonomic pathways, behavior, and climatic conditions, making parsing the effects of specific variables difficult. Thus, further investigation into the role of bi-iliac breadth in thermoregulation is needed, especially if we wish to better understand the role of bi-iliac breadth in hominin evolution.

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Competing Interests

The authors declare no competing interests.

Data Sharing Plans

All of our data are included in this paper. The R code used in this study is included in SOM.

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Figures

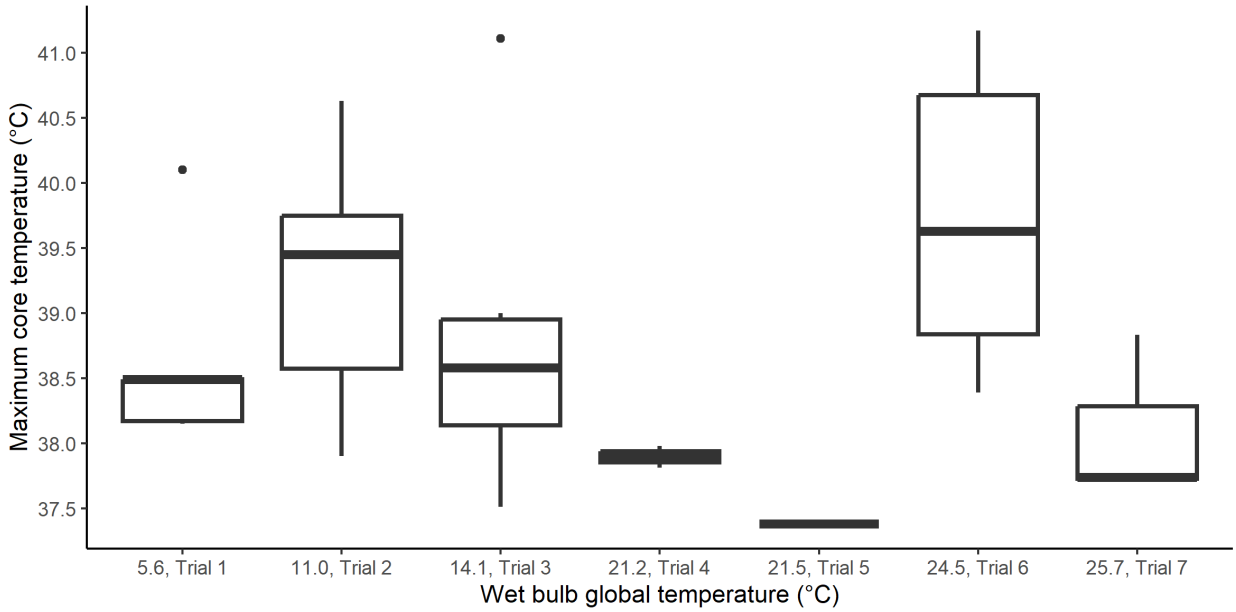


Figure 1. Boxplots of maximum core temperature for the 28 individuals whose data were used to fit the linear mixed effects model. The temperature boxes for each trial extend from the first to the third quantiles (Q1 to Q3, i.e., the interquartile range or IQR), while the whiskers extend to Q1 minus 1.5 multiplied by IQR, and Q3 plus 1.5 multiplied by IQR. Values falling above or below the whiskers are outliers for that particular trial.

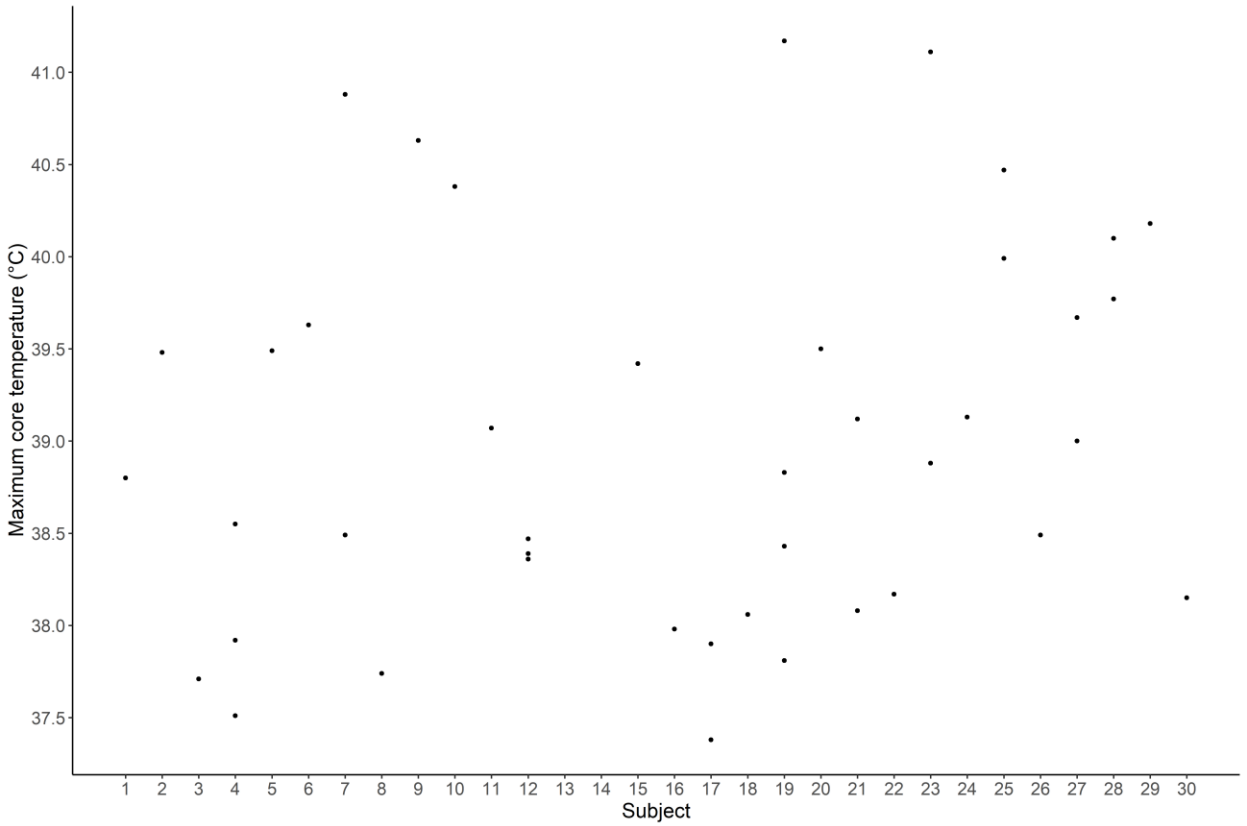


Figure 2. Maximum core temperature for each individual subject. If a subject participated more than once (in more than one trial), they will be represented by more than one point.

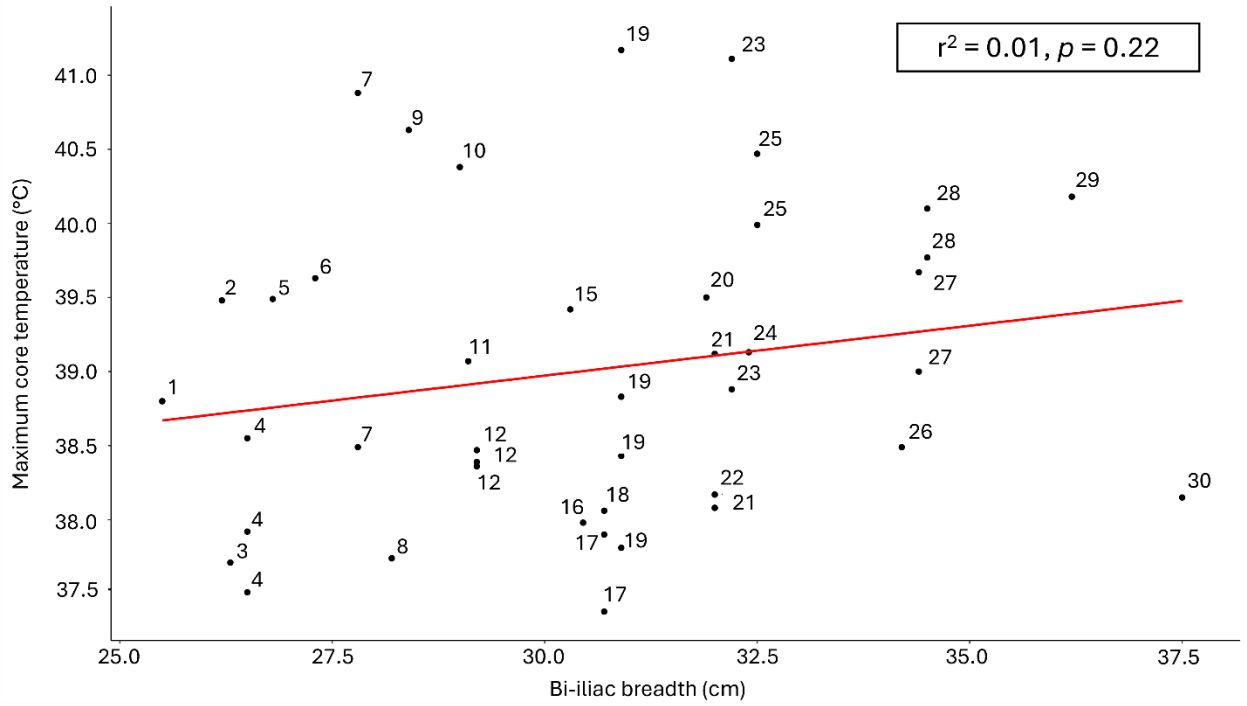


Figure 3. The regression of maximum core temperature on bi-iliac breadth for each of the 28 subjects. The r^2 and *p*-values are given for the regression line.

Table 1

Anthropometric and demographic data for the participants in the seven trials, as well as information about which trial(s) they participated in. The mean (±SD) is given for both the combined sample and for females and males separately.

			Age	Bi-iliac breadth (cm)	Body mass (kg)	Lower limb length (cm)	Body fat percentage
Combined sample			27.9 ± 6.9	30.5 ± 2.9	69.9 ± 11.5	83.4 ± 5.9	20.4 ± 4.7
Females			28.3 ± 6.8	28.5 ± 2.4	58.1 ± 5.7	82.5 ± 7.0	25.4 ± 3.5
Males			29.6 ± 7.4	31.7 ± 2.9	74.6 ± 9.6	84.4 ± 5.7	18.5 ± 4.0
Subject	Trial	Sex					
1	3	F	20	25.5	65.5	86.0	25.3
2	2	F	30	26.2	49.8	79.5	21.7
3	7	F	24	26.3	58.2	81.3	21.0
4	2, 3, 6	M	22	26.5	65.7	77.0	20.0
5	2	F	22	26.8	50.9	83.0	20.5
6	6	F	22	27.3	56.5	72.0	30.3
7	1, 6	F	28	27.8	54.2	82.0	25.7
8	7	M	35	28.2	70.4	87.6	16.2
9	2	M	23	28.4	67.1	74.5	13.5
10	2	F	38	29.0	61.2	80.0	31.6
11	2	F	33	29.1	54.8	71.0	29.3
12	2, 3, 6	M	19	29.2	69.5	81.0	13.1
15	2	M	18	30.3	70.8	93.0	14.2
16	4	M	26	30.5	66.9	84.5	15.2
17	2, 5	M	32	30.7	63.3	78.0	14.7
18	3	M	35	30.7	64.0	88.0	14.7
19	2, 4, 6, 7	M	22	30.9	84.9	88.0	20.0
20	2	M	34	31.9	87.1	91.0	21.1
21	2, 6	M	38	32.0	72.1	82.0	18.9
22	1	F	43	32.0	55.1	85.0	24.0
23	2, 3	F	26	32.2	68.5	94.0	24.7
24	2	M	44	32.4	74.9	77.5	23.6
25	2, 6	M	28	32.5	74.8	78.0	17.9
26	1	M	40	34.2	92.3	84.0	25.6
27	2, 3	M	31	34.4	67.0	86.0	21.8
28	1, 2	M	24	34.5	94.4	91.0	20.7
29	2	M	32	36.2	80.6	86.0	25.0

30	1	M	30	37.5	76.3	92.0	16.8

Table 2

Summary temperature, anthropometric, and demographic data for each of the seven trials. Wet bulb global temperature, ambient temperature, and relative humidity are means of measurements taken at 30-minute intervals during the trials and mean core temperature values are given for the combined sample for each trial ±SD.

	Trial 1 *n* = 5		**Trial 2** *n* = 18		**Trial 3** *n* = 6		**Trial 4** *n* = 2		**Trial 5** *n* = 1		**Trial 6** *n* = 7		**Trial 7** *n* = 3	
Sex	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Participants	2	3	5	13	2	4	0	2	0	1	2	5	1	2
Wet bulb global temperature (°C)	5.6		11.0		14.1		21.2		21.5		24.5		25.7	
Ambient temperature (°C)	9.6		14.7		20.2		28.0		27.5		31.7		29.6	
Percentage relative humidity	38.6		50.6		28.5		32.7		42.5		41.5		58.5	
Mean starting core temperature ± SD (°C)	38.4 ± 0.6		38.1 ± 0.7		38.0 ± 0.4		37.1 ± 1.0		37.1		37.9 ± 1.0		37.0 ± 0.6	

Mean heat gain ± SD (°C)	1.1 ± 0.3	1.4 ± 0.7	1.3 ± 1.0	1.1 ± 0.5	0.8	2.3 ± 1.0	1.6 ± 0.1
Mean maximum core temperature ± SD (°C)	38.7 ± 0.9	39.2 ± 0.8	38.8 ± 1.2	37.9 ± 0.1	37.4	39.9 ± 1.1	38.1 ± 0.6
Mean age ± SD	33.0 ± 8.1	28.7 ± 7.2	25.5 ± 6.4	24.0 ± 2.8	32	25.6 ± 6.4	27.0 ± 7.0
Mean bi-iliac breadth ± SD	33.2 ± 3.6	30.7 ± 2.8	29.7 ± 3.4	30.1 ± 0.3	30.7	29.5 ± 1.4	28.5 ± 2.3
Mean body mass ± SD	74.5 ± 19.4	69.8 ± 12.0	66.7 ± 2.1	75.9 ± 12.8	63.3	68.2 ± 10.6	71.2 ± 13.3
Mean lower limb length ± SD	86.8 ± 0.0	82.8 ± 0.1	85.3 ± 0.0	86.2 ± 0.0	78.0	80.0 ± 0.0	85.6 ± 0.0
Mean body fat% ± SD	22.6 ± 3.8	20.7 ± 5.1	19.9 ± 5.1	17.6 ± 3.4	14.7	20.8 ± 5.6	19.1 ± 2.5

Table 3

Core temperature data for each subject for each trial.

Trial	Subject	Starting core temperature (°C)	Heat gain (°C)	Maximum core temperature (°C)
1	7	38.3	1.0	38.49
1	22	37.7	0.9	38.17
1	26	39.0	1.0	38.49
1	28	39.0	1.6	40.1
1	30	37.8	0.9	38.15
2	2	38.4	1.6	39.48
2	4	37.4	1.0	37.92
2	5	38.6	1.4	39.49
2	9	37.8	1.7	40.63
2	10	37.8	3.1	40.38
2	11	37.4	0.4	39.07
2	12	38.1	0.8	38.47
2	15	37.0	3.0	39.42
2	17	38.5	0.8	37.9
2	19	38.0	0.9	38.43
2	20	38.5	1.5	39.5
2	21	37.4	1.2	38.08
2	23	37.8	1.6	38.88
2	24	37.6	2.1	39.13
2	25	39.5	1.0	39.99
2	27	38.7	1.5	39.67
2	28	38.8	1.5	39.77
2	29	39.6	1.1	40.18
3	1	37.8	1.5	38.8
3	4	37.3	0.8	37.51
3	12	38.0	0.9	38.36
3	18	38.2	0.3	38.06
3	23	38.4	3.2	41.11
3	27	38.3	1.2	39
4	16	37.7	0.7	37.98
4	19	36.4	1.4	37.81
5	17	37.1	0.8	37.38
6	4	37.7	1.4	38.55
6	6	37.5	2.6	39.63
6	7	39.5	1.9	40.88
6	12	37.3	1.6	38.39
6	19	39.2	2.5	41.17
6	21	37.7	2.0	39.12

6	25	36.8	4.2	40.47
7	3	36.8	1.5	37.71
7	8	36.6	1.6	37.74
7	19	37.7	1.7	38.83

Table 4

Summary statistics for the maximum core temperature linear mixed effects model.

	Estimate	**Standard error**	**Degrees of freedom**	**t-statistic**	***p*-value**
(Intercept)	39.65	0.61	28.01	64.57	<0.01
Bi-iliac breadth	0.45	0.23	31.19	1.96	0.06
Age	-0.19	0.17	31.31	-1.08	0.29
Sex	-1.29	0.75	30.92	-1.71	0.10
Mass	0.34	0.29	31.02	1.19	0.24
Body fat percentage	0.07	0.25	30.89	0.27	0.79
Lower limb length	-0.09	0.2	31.77	-0.42	0.68

Wet bulb global temperature	0.09	0.29	4.65	0.33	0.76

Table 5

The results of the bootstrap method. The data for the linear mixed effects model were randomly resampled with replacement 3000 times. The table provides the metrics for each model predictor. A predictor is considered significant if the 95% confidence interval for the estimate does not include zero.

	Estimate	**Standard error**	**Upper 95% CI**	**Lower 95% CI**
Intercept	39.64	0.66	38.92	41.7
Bi-iliac breadth	0.45	0.28	0.37	0.99
Age	-0.19	0.21	-0.82	0.03
Sex	-1.29	0.91	-3.26	-0.74
Mass	0.34	0.34	0.01	1.10
Body fat percentage	0.07	0.31	-0.48	0.72
Lower limb length	-0.08	0.24	-0.62	0.31
Wet bulb global temperature	0.09	0.19	-0.18	0.56

Abbreviations: CI = confidence interval.

Supplementary Online Material (SOM):

SOM S1

Stature, surface area, and surface area to mass ratio

Stature was excluded as an explanatory variable because Ruff's (1991, 1994) cylindrical thermoregulatory model specifically asserts that variation in stature will have no effect on variation in surface area or surface area to mass ratio and thus no effect on thermoregulation.

Surface area and the ratio of surface area to mass were excluded as variables in this study for several reasons. The first is that we needed to carefully select which variables to include in our model as we only collected a small dataset of 42 observations and overfitting a model by using too many explanatory variables relative to the amount of data collected reduces the power of the model. Second, the most common way to calculate surface area is the Du Bois and Du Bois (1916) equation while relies on mass and stature:

$$\text{body surface area} = 0.007184 \times \text{stature}^{0.725} \times \text{mass}^{0.425}$$

Therefore, including mass, surface area, and the ratio of surface area to mass increases the problems of collinearity as surface area and mass are almost perfectly correlated ($r = 0.95$ in our study sample) as are surface area to mass ratio and mass ($r = –0.90$ in our study sample). This is almost certainly because mass is used to estimate surface area and surface area to mass ratio. Third, the reason bi-iliac breadth is being investigated in relation to thermoregulation in this study is because of its hypothesized causal relationship with surface area. Therefore, the

effects of bi-iliac breadth should be equivalent to those of surface area if the cylindrical thermoregulatory model (Ruff, 1991, 1994) is correct.

However, to ensure that we were not excluding important factors from our models, the Pearson correlation was calculated for stature, surface area, and surface area to mass ratio and maximum core temperature. Stature was measured to the nearest 0.1 cm using a standard tape measure. Surface area was calculated using the Du Bois and Du Bois (1916) equation (see above). Surface area to mass ratio was calculated by using the surface area value from the Du Bois and Du Bois (1916) equation and dividing it by mass.

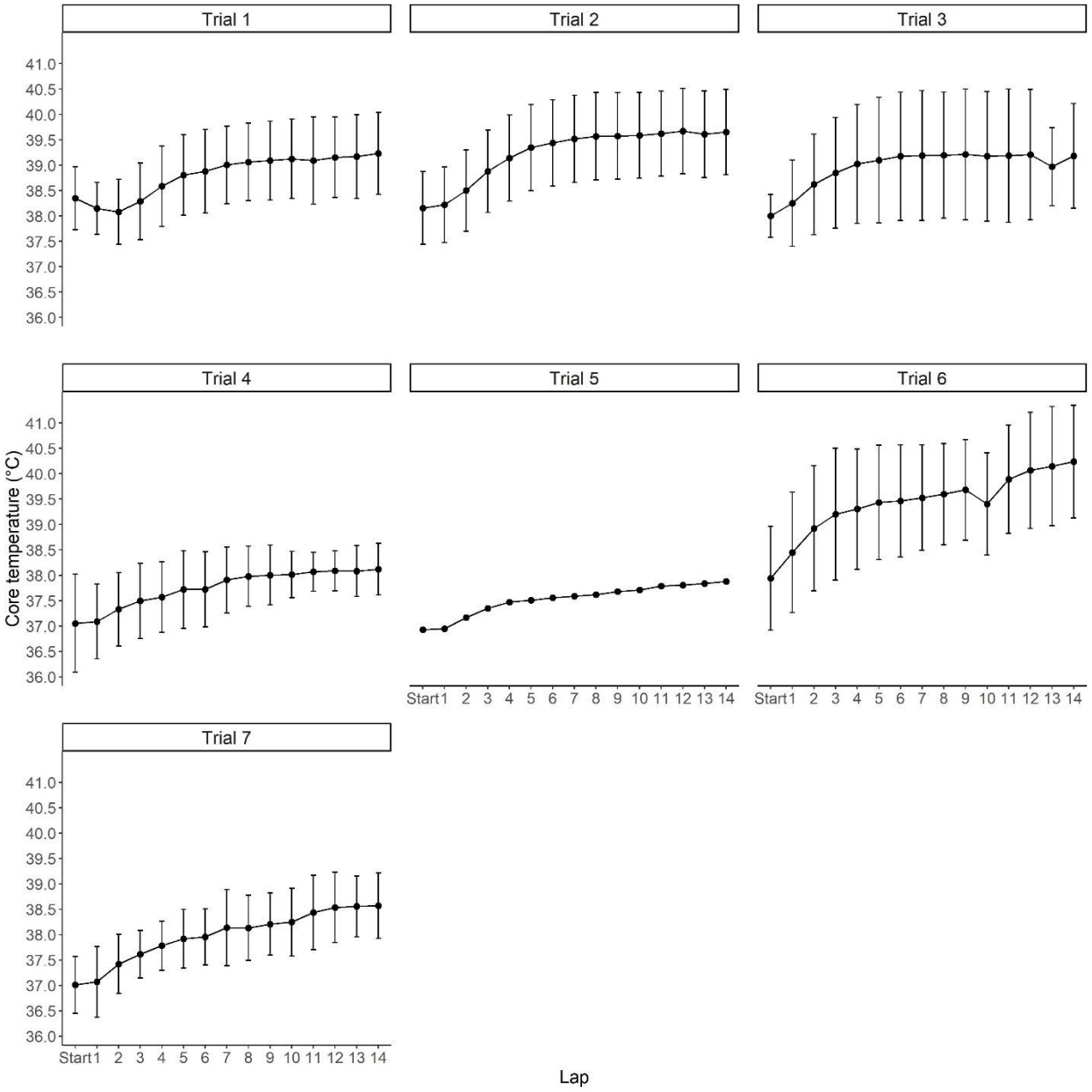
None of the three variables were strongly or significantly correlated with maximum core temperature ($p > 0.20$ in all three cases).

All three variables were also included in turn in the linear mixed effects model to ascertain if they were being erroneously excluded, but none of them reached or approached significance.

SOM S2

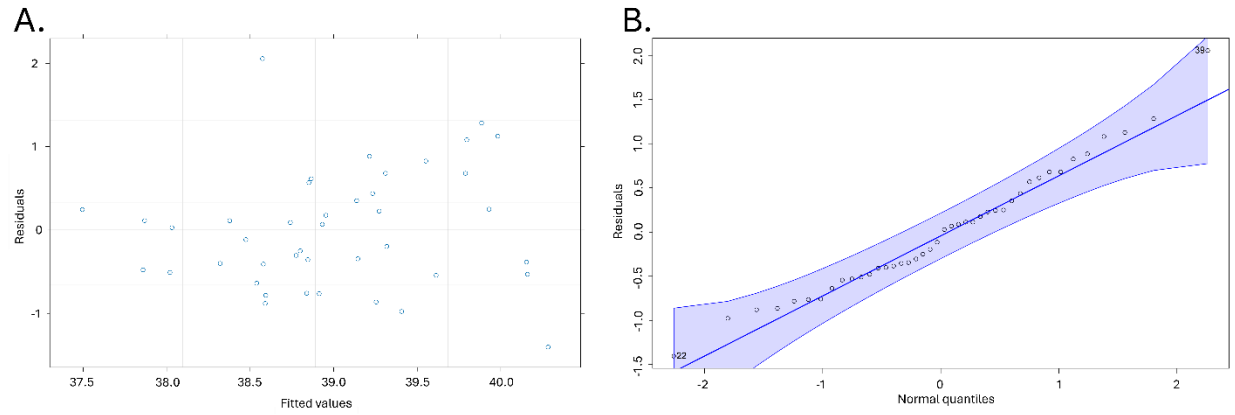
Singularity

The linear mixed effects model for maximum core temperature was singular, indicating the model was over-fitted and lacked power, and thus these results should be interpreted with caution. Upon further investigation, the singular fit of the model was found to be due to a lack of variance in the random effects, with boundary estimates approaching (or equaling) zero. No combination of fixed effects enabled the model to converge, but if subject was removed, it converged. However, we could not remove the random effects of subject or trial without encountering the problem of pseudoreplication, so they remained in the model.

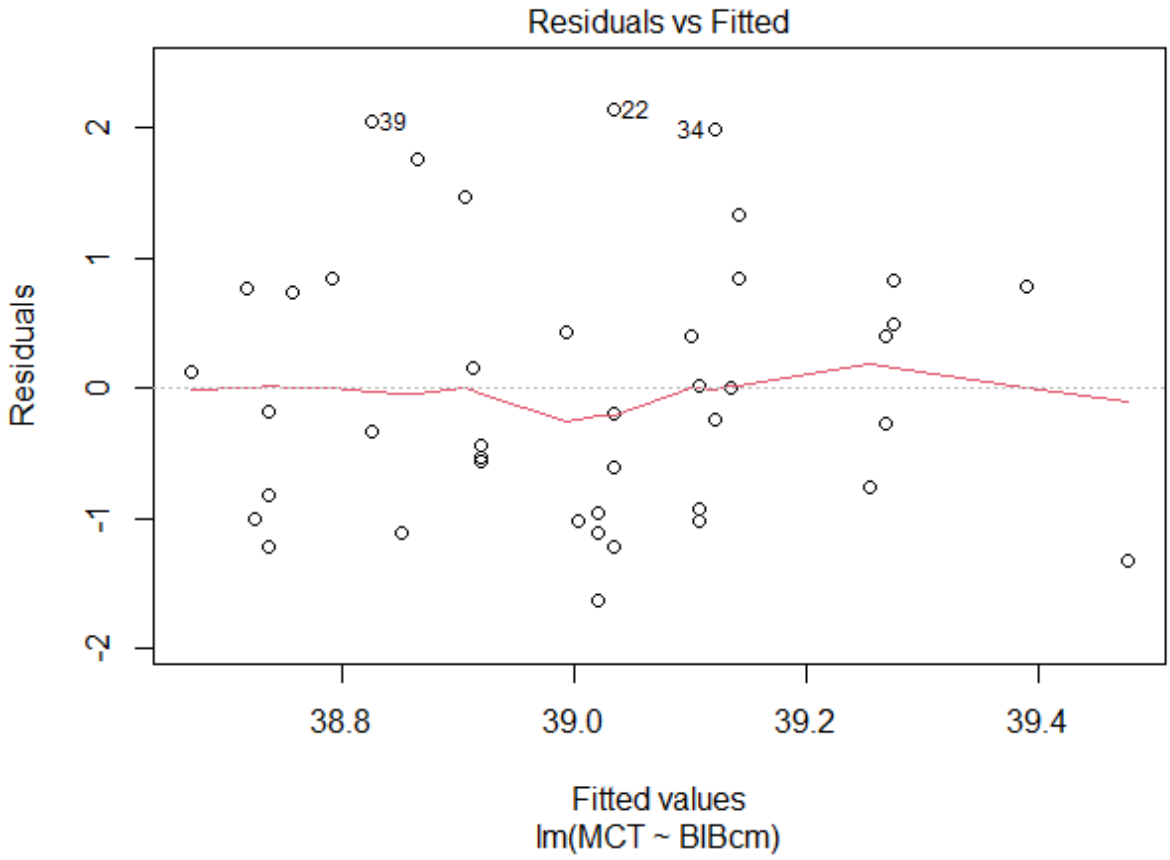


SOM Figure S1. The black circles indicate the mean core temperature for each lap , including the starting temperature before the trial began. The vertical lines indicate ± 1 SD above and below the mean. Lap is plotted on the x axis and mean core temperature for the sample on the y

axis. Note that in Trial 5 there was only one participant so there are no lines for standard deviation.



SOM Figure S2. The residuals, which are the discrepancy between the observed values and the predicted values (i.e., a measurement of the goodness of fit of the model to the data; Cox and Snell, 1968), of the linear mixed effects model were evaluated using a Residuals vs. Fitted plot (A) and a Quantile-Quantile (Q-Q) plot (B). (A) compares the residual values to the predicted values and helps identify nonlinear relationships (James et al., 2013). In linear relationships, the residuals should be randomly distributed around zero with constant variance (Wright and London, 2009). (B) helps determine if the residuals are nonnormally distributed (James et al., 2013). When normally distributed, the residuals fall along a straight line; the presence of outliers or a nonnormal distribution can cause the residuals to deviate from the line (Wright and London, 2009).



SOM Figure S3. The residuals and the fitted values for the linear relationship between maximum core temperature and bi-iliac breadth (main text Figure 3).

SOM Table S1

Results of the Pearson correlation test between each pair of explanatory variables.[a]

	BIB		Age		Sex		Mass		Body fat %		LLL		WBGT		Trial		AT		RH		Stature		SA	
	r^2	*p*																						
BIB																								
Age	0.39	**0.01**																						
Sex	0.44	<**0.01**	-0.03	0.82																				
Mass	0.62	<**0.01**	-0.05	0.77	0.65	<**0.01**																		
Body fat %	-0.04	0.81	0.30	**0.05**	-0.67	<**0.01**	-0.17	0.28																
LLL	0.50	<**0.01**	-0.07	0.66	0.10	0.52	0.50	<**0.01**	-0.08	0.61														
WBGT	-0.34	**0.03**	-0.26	0.10	0.07	0.65	-0.07	0.64	-0.16	0.32	-0.17	0.27												
Trial	-0.33	**0.03**	-0.23	0.15	0.04	0.79	-0.07	0.65	-0.14	0.39	-0.16	0.32	0.98	<**0.01**										
AT	-0.33	**0.04**	-0.27	0.09	0.07	0.64	-0.08	0.62	-0.16	0.32	-0.17	0.27	0.99	<**0.01**	0.97	<**0.01**								
RH	-0.05	0.77	-0.10	0.52	-0.01	0.98	-0.03	0.85	-0.01	0.93	-0.11	0.48	0.01	0.99	-0.04	0.78	-0.12	0.45						
Stature	0.55	<**0.01**	-0.06	0.72	0.44	<**0.01**	0.68	<**0.01**	-0.38	**0.01**	0.79	<**0.01**	-0.12	0.46	-0.10	0.52	-0.12	0.45	-0.11	0.51				
SA	0.65	<**0.01**	-0.06	0.71	0.64	<**0.01**	0.96	<**0.01**	-0.27	0.08	0.65	<**0.01**	-0.09	0.56	-0.09	0.59	-0.10	0.54	-0.02	0.90	0.85	<**0.01**		
SA:M	-0.49	<**0.01**	-0.10	0.53	-0.63	<**0.01**	-0.90	<**0.01**	-0.04	0.80	-0.22	0.16	<0.01	0.96	-0.02	0.90	-0.01	0.94	-0.06	0.72	-0.32	**0.04**	-0.32	**0.041**

Abbreviations: BIB = bi-iliac breadth, LLL = lower limb length, WBGT = wet bulb global temperature, AT = ambient temperature, RH = relative humidity, SA = surface area, SAM = surface area to mass ratio.

[a] Bolded values indicate $p \leq 0.05$.

SOM Table S2

The results of the one-way analysis of variance (ANOVA) to test if there were significant differences between trials in maximum core temperature. As $p \leq 0.05$, the ANOVA indicates that there were significant differences.

	Degrees of freedom	**Sum of squares**	**Mean square**	**F-value**	***p*-value**
Trial	6	13.21	2.20	2.53	0.04
Residuals	35	30.42	0.87	-	-

SOM Table S3

Results of the Tukey HSD tests for significant differences in maximum core temperature between each pair of trials. In all cases $p \geq 0.05$, indicating there were no significant differences. The column headings 'Lower bound' and 'Upper bound' signify the lower and upper extents of the 95% confidence intervals for the difference in means between the two trials being compared.

Trials	Difference of means	Lower bound	Upper bound	Adjusted *p*-value
1-2	0.56	-0.91	2.04	0.89
1-3	0.13	-1.64	1.89	1.00
1-4	-0.79	-3.22	1.65	0.95
1-5	-1.30	-4.49	1.89	0.86
1-6	1.06	-0.64	2.77	0.46
1-7	-0.59	-2.71	1.54	0.98
2-3	-0.44	-1.81	0.94	0.95
2-4	-1.35	-3.52	0.82	0.47
2-5	-1.86	-4.86	1.13	0.47
2-6	0.50	-0.80	1.80	0.89
2-7	-1.15	-2.97	0.67	0.45
3-4	-0.91	-3.29	1.47	0.89
3-5	-1.43	-4.57	1.72	0.79
3-6	0.94	-0.68	2.56	0.55
3-7	-0.71	-2.77	1.35	0.93
4-5	-0.51	-4.08	3.05	1.00
4-6	1.85	-0.49	4.19	0.20
4-7	0.20	-2.46	2.86	1.00
5-6	2.36	-0.75	5.48	0.24
5-7	0.71	-2.65	4.08	0.99
6-7	-1.65	-3.66	0.36	0.17

SOM Table S4

Variance-covariance matrix for the linear mixed effects model.

	(Intercept)	**Bi-iliac breadth**	**Age**	**Sex**	**Mass**	**Body fat percentage**	**Lower limb length**	**Wet bulb global temperature**
(Intercept)	0.38							
Bi-iliac breadth	0.03	0.05						
Age	0.02	-0.02	0.03					
Sex	-0.40	-0.04	-0.03	0.56				
Mass	0.12	-0.01	0.02	-0.16	0.08			
Body fat percentage	-0.11	-0.01	-0.02	0.16	-0.04	0.06		
Lower limb length	-0.06	-0.02	0.00	0.08	-0.03	0.02	0.04	

Wet bulb global temperature	-0.02	0.01	0.00	-0.01	0.00	0.00	0.00	0.08

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