Chapter 12

Thermoregulation in *Homo erectus* and the Neanderthals: A Reassessment Using a Segmented Model

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Abstract Thermoregulation is widely believed to have influenced body size and shape in the two best-known extinct members of genus *Homo*, *Homo erectus* and *Homo neanderthalensis*, and to have done so in contrasting ways. *H. erectus* is thought to have been warm adapted, while *H. neanderthalensis* is widely held to have been cold adapted. However, the methods that have been used to arrive at these conclusions ignore differences among body segments in a number of thermoregulation-related variables. We carried out a study designed to determine whether the current consensus regarding the thermoregulatory implications of the size and shape of the bodies of *H. erectus* and *H. neanderthalensis* is supported when body segment differences in surface area, skin temperature, and rate of movement are taken into account.

The study involved estimating heat loss for a number of Holocene modern human skeletal samples and several fossil hominin specimens, including five Pleistocene *H. sapiens*, the well-known *H. erectus* partial skeleton KNM-WT 15000, a *H. erectus* specimen from Dmanisi, Georgia, and three Neanderthals. The resulting heat loss estimates were then used in two sets of comparative analyses. In the first, we focused on whole-body heat loss and tested predictions concerning heat loss in KNM-WT 15000 and European Neanderthals relative to modern humans, and within *H. erectus* and *H. neanderthalensis*. In the second set of analyses we again tested predictions concerning heat loss in *H. erectus* and *H. neanderthalensis* relative to modern humans, and within *H. erectus* and *H. neanderthalensis*, but this time we focused on the contribution of their limbs to heat loss.

The results of the study do not fully support the current consensus regarding the thermoregulatory adaptations of *Homo erectus* and *Homo neanderthalensis*. The whole-body heat loss estimates were consistent with the idea that KNM-WT 15000 was warm adapted and that European Neanderthals were cold adapted, and with the notion that there are thermoregulation-related differences in body size and shape within *H erectus* and *H. neanderthalensis*. The whole-limb estimates told a similar story. In contrast, the results of our analysis of limb segment-specific heat loss were not consistent with the current consensus regarding the thermoregulatory significance of distal limb length in *H. erectus* and *H. neanderthalensis*. Contrary to expectation, differences between the proximal and distal limb segments did not follow any particular trend.

The obvious implication of these results is that, while we can be more confident about the basic idea that thermoregulation influenced the evolution of body size and shape in *H. erectus* and *H. neanderthalensis*, we need to be more cautious in attributing differences in limb segment size to thermoregulation. Based on our results, it is possible that other factors influenced limb segment size in these species more than thermoregulation. Identifying these factors will require further research.

Keywords Body size • Hominin evolution • Thermoregulation • *Homo neanderthalensis* • Limb proportions

Introduction

Thermoregulation is widely believed to have influenced body size and shape in the two best-known extinct members of genus *Homo*, *Homo erectus* and *Homo neanderthalensis*, and to have done so in contrasting ways. KNM-WT 15000, the famous nearly-complete juvenile male *H. erectus*

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skeleton from 1.5 million year old deposits in West Turkana, Kenya, is reconstructed as relatively narrow bodied and long limbed, and these characteristics are usually interpreted as adaptations to hot conditions (Ruff and Walker 1993; Ruff 1994). In contrast, the Neanderthals are reconstructed as having stocky bodies and relatively short forearms and lower legs. These traits are generally accepted to be adaptations to cold conditions—so much so that the shape of the Neanderthal body is often described as "hyperpolar" (Holliday 1997; Weaver 2003; Tilkens et al. 2007).

The rationale for both these hypotheses is that altering the breadth of the trunk and the length of the distal limb segments affects the ratio of surface area to body mass (SA:BM), and this in turn affects heat loss (Trinkaus 1981; Ruff 1991). The reason for this is that more heat is lost when SA:BM is large than when SA:BM is small (Trinkaus 1981; Ruff 1991). Reducing trunk breadth and lengthening the distal limb segments should increase SA:BM and therefore increase heat loss, whereas broadening the trunk and shortening the distal limb segments should decrease SA:BM and therefore decrease heat loss (Trinkaus 1981; Holliday and Ruff 2001). Thus, the relatively narrow trunk and relatively long distal limb segments of KNM-WT 15000 would have given him an advantage in high ambient temperatures, while the broad trunks and relatively short distal limb segments of the Neanderthals would have given them an advantage in low ambient temperatures.

While changing the ratio of surface area to body mass undoubtedly has the potential to impact heat loss, there are reasons for questioning the consensus that KNM-WT 15000 was hot climate adapted and the Neanderthals were cold climate adapted. One is that the hypotheses do not take into account the fact that the segments of the body move at different speeds during locomotion and therefore experience different wind speeds. Because wind speed influences heat loss, it is possible that the relationship between trunk breadth and limb length on the one hand and heat loss on the other is more complicated than the thermoregulatory interpretation of body size and shape in KNM-WT 15000 and the Neanderthals assumes. Another reason for questioning the consensus view of these hominins is that in living humans skin temperature varies among body segments (e.g., Houdas and Ring 1982). This too suggests SA:BM may be too simple to adequately represent the thermoregulatory abilities of KNM-WT 15000 and the Neanderthals. Lastly, while the impact of differences in whole-body SA:BM on thermoregulation have been quantified in various ways (e.g., Wheeler 1993; Ruff 1993, 1994), no study has attempted to quantify the specific contribution of the limbs to thermoregulation in fossil hominins. Consequently, it has not been demonstrated that the limb proportion differences between KNM-WT 15000 and modern humans, or between the latter and Neanderthals, actually translate into significant heat loss differences.

With the foregoing in mind, we carried out a study designed to determine whether the current consensus regarding the thermoregulatory implications of the size and shape of the bodies of *H. erectus* and *H. neanderthalensis* is supported when body segment differences in surface area, skin temperature, and rate of movement are considered. The study involved estimating heat loss for a number of modern human skeletal samples, and for fossil specimens that have been assigned to *H. erectus* and *H. neanderthalensis*. The resulting heat loss estimates were then used in two sets of comparative analyses. In the first, we focused on whole-body heat loss and tested predictions concerning heat loss in KNM-WT 15000 and European Neanderthals relative to modern humans. We also tested predictions concerning heat loss within *H. erectus* and *H. neanderthalensis*. In the second set of analyses, we again tested predictions concerning heat loss in *H. erectus* and *H. neanderthalensis* relative to modern humans, and within *H. erectus* and *H. neanderthalensis*, but this time we focused on the contribution of their limbs to heat loss. The results of the study suggest that the current consensus requires some modification.

Materials and Methods

The limb bone data used in the study are presented in Table 12.1. The humerus, femur, and tibia data for the Holocene modern human samples are the male means provided by Trinkaus (1981). The ulna values for the Holocene samples were estimated by adding 5% to the length of the radius values given by Trinkaus (1981), as per Haeusler and McHenry (2004). The humerus, femur, and tibia data for the five Pleistocene human specimens (Skhul IV, Skhul V, Predmosti 3, Predmosti 14, Caviglione 1) and the three Neanderthal specimens (La Ferrassie 1, La Chapelle 1, and Shanidar 4) are also from Trinkaus (1981). As with the Holocene modern human samples, the ulna values for these specimens were estimated by adding 5% to the length of the radius. The long bone lengths for the Dmanisi individual are for the large adult from the site. They were taken from Lordkipanidze et al. (2007), with the exception of ulna length, which was estimated from the length of the humerus using the equation provided by Haeuseler (2001). The lengths of KNM-WT 15000's long bones were taken from Ruff and Walker (1993). They are the lengths at the time of death rather than the lengths that have been estimated for KNM-WT 15000 as an adult.

Table 12.2 lists the stature and body mass estimates used in the study. Some estimates were taken directly from the

Table 12.1 Limb bone lengths (mm) for the samples used in this study. Values in square brackets are estimates

Sample	Taxon	Humerus	Ulna	Femur	Tibia	Notes
Inuit	Holocene *H. sapiens*	30.4	[24.0]	40.8	33.1	Data from Trinkaus (1981). Eskimo male mean. Ulna value estimated by adding 5% to the length of radius, as per Haeusler and McHenry (2004).
Yugoslavians	Holocene *H. sapiens*	33.0	[25.8]	45.5	38.1	Data from Trinkaus (1981). Male mean. Ulna value estimated by adding 5% to the length of radius, as per Haeusler and McHenry (2004).
Lapps	Holocene *H. sapiens*	30.6	[23.8]	41.0	32.5	Data from Trinkaus (1981). Male mean. Ulna value estimated by adding 5% to the length of radius, as per Haeusler and McHenry (2004).
Amerinds	Holocene *H. sapiens*	30.8	[25.1]	42.3	35.9	Data from Trinkaus (1981). New Mexico Amerindian male mean. Ulna value estimated by adding 5% to the length of radius, as per Haeusler and McHenry (2004).
Melanesians	Holocene *H. sapiens*	31.7	[26.0]	43.6	37.1	Data from Trinkaus (1981). Male mean. Ulna value estimated by adding 5% to the length of radius, as per Haeusler and McHenry (2004).
Egyptians	Holocene *H. sapiens*	32.5	[26.8]	45.3	38.7	Data from Trinkaus (1981). Male mean. Ulna value estimated by adding 5% to the length of radius, as per Haeusler and McHenry (2004).
Skhul IV	Pleistocene *H. sapiens*	33.7	[28.8]	49.0	43.4	Data from Trinkaus (1981). Ulna value estimated by adding 5% to the length of radius, as per Haeusler and McHenry (2004).
Skhul V	Pleistocene *H. sapiens*	38.0	[28.1]	51.5	41.2	Data from Trinkaus (1981). Ulna value estimated by adding 5% to the length of radius, as per Haeusler and McHenry (2004).
Predmosti 3	Pleistocene *H. sapiens*	35.7	[29.3]	48.7	42.1	Data from Trinkaus (1981). Ulna value estimated by adding 5% to the length of radius, as per Haeusler and McHenry (2004).
Predmosti 14	Pleistocene *H. sapiens*	33.6	[27.8]	45.2	39.5	Data from Trinkaus (1981). Ulna value estimated by adding 5% to the length of radius, as per Haeusler and McHenry (2004).
Caviglione 1	Pleistocene *H. sapiens*	34.2	[27.6]	47.0	41.2	Data from Trinkaus (1981). Ulna value estimated by adding 5% to the length of radius, as per Haeusler and McHenry (2004).
Shanidar 4	*H. neanderthalensis*	30.5	[24.7]	42.2	33.4	Data from Trinkaus (1981). Ulna value estimated by adding 5% to the length of radius, as per Haeusler and McHenry (2004).
La Chapelle 1	*H. neanderthalensis*	31.2	[23.8]	43.0	34.0	Data from Trinkaus (1981). Ulna value estimated by adding 5% to the length of radius, as per Haeusler and McHenry (2004).
La Ferrassie 1	*H. neanderthalensis*	33.7	[25.6]	45.8	37.0	Data from Trinkaus (1981). Ulna value estimated by adding 5% to the length of radius, as per Haeusler and McHenry (2004).
Dmanisi	*H. erectus*	29.5	[24.3]	38.6	30.6	Data from Lordkipandze et al. (2007). Ulna length estimated from humerus length using the equation provided by Haeusler (2001).
KNM-WT 15000	*H. erectus*	31.9	27.0	42.9	38.0	Ruff and Walker (1993); juvenile values.

literature; others were obtained with the aid of published equations for estimating body mass and stature. In the latter cases, equations derived from geographically appropriate reference samples were employed as far as possible.

All the statures and body masses of the Holocene human samples were estimated with published equations. The stature estimate for the Inuit sample was obtained from femur length with Feldesman and Fountain's (1996) equation; encouragingly, it is the same as the Eskimo/Inuit estimate used by Ruff (1994). Raxter et al.'s (2008) femur-based stature equation was used for the Egyptian sample because it is specific to Egyptians. Yugoslav, Lapp, and Amerindian statures were calculated from femur length using Trotter and Gleser's (1958) equation for whites, while the stature of the Melanesian sample was estimated from femur length using Trotter and Gleser's (1958) equation for blacks. The body masses of most of the samples were estimated from stature with Ruff and Walker's (1993) male equation. While this

Table 12.2 Stature (cm) and body mass (kg) estimates used in this study. See Materials and Methods section for details

Sample	Taxon	Stature	Body mass
Inuit	Holocene *H. sapiens*	159	67
Yugoslavians	Holocene *H. sapiens*	171	65
Egyptians	Holocene *H. sapiens*	167	61
Lapps	Holocene *H. sapiens*	161	56
Amerinds	Holocene *H. sapiens*	164	59
Melanesians	Holocene *H. sapiens*	164	59
Skhul IV	Pleistocene *H. sapiens*	179	66
Skhul V	Pleistocene *H. sapiens*	185	70
Predmosti 3	Pleistocene *H. sapiens*	179	71
Predmosti 14	Pleistocene *H. sapiens*	170	66
Caviglione 1	Pleistocene *H. sapiens*	175	65
Shanidar 4	*H. neanderthalensis*	162	71
La Chapelle 1	*H. neanderthalensis*	164	76
La Ferrassie 1	*H. neanderthalensis*	171	85
Dmanisi	*H. erectus*	153	50
KNM-WT 15000	*H. erectus*	160	48

equation does not account for variation in body breadth, the latter variable was not available for the samples in question. We considered using body breadths from other sources but decided that the additional error introduced by this procedure outweighed the benefits. The only human sample for which we used both stature and body breadth to estimate body mass was the Inuit one. The difference between a stature-based estimate for this sample and published estimates (e.g., Ruff 1994) was sufficiently large that using stature and body breadth method seemed warranted. The Inuit sample's body mass was estimated from stature and bi-iliac breadth with Ruff et al.'s (2005) equation for males; we used the mean bi-iliac breath for Eskimo/Inuit presented in Ruff (1994).

Turning now to the fossil specimens, the stature and body mass estimates for La Ferrassie 1 and KNM-WT 15000 were obtained directly from the literature (Ruff et al. 1997, 2005; Ruff and Walker 1993). Ruff et al. (2005) give a stature estimate of 162 cm for La Chappelle 1. Using the same femur length and formula (Trotter and Gleser' (1952) equation for whites) we obtained an estimated stature of 164 cm. We opted to use the latter value. The stature estimate for the Dmanisi individual was taken from Ruff (2010). We used Lordkipanidze et al. (2007)'s femoral head-derived body mass estimate for the Dmanisi specimen rather than their average value because the latter involves variables whose connection with body mass is unclear. The stature estimates for Skhul IV, Skhul V, Predmosti 3, Predmosti 14, Caviglione 1, and Shanidar 4 were obtained using Trotter and Gleser's (1958) femur-length based equation for whites. It has been argued that this equation is less accurate for early modern humans than Trotter and Gleser's (1958) formula for blacks or taking an average of the estimates yielded by the two formulae (Holliday 1997; Ruff et al. 1997). However, we found that the latter course of action produced estimates that fell within the standard error for the white formula (SE = 3.94). The body mass estimates for Skhul IV, Skhul V, Predmosti 3, Predmosti 14, Caviglione 1, and Shanidar 4 were taken from Froehle and Churchill (2009).

Having compiled the limb, stature, and body mass data, we estimated the surface areas of each taxon's body segments. The approach we used is rooted in the segmented method of estimating surface area employed by Haycock et al. (1978), Cross et al. (2008), and Cross and Collard (2011). For the limb segments, long bone lengths were combined with surface area per unit of length values derived from Cross et al.'s (2008) data. Cross et al. (2008) estimated that approximately 27% of the femur is situated within the trunk segment. They based this value on the observation that crotch height marks the lower boundary of the trunk segment and that palpation of the greater trochanter indicated that 27% of the femur was above the crotch. In an analysis of Cross et al.'s (2008) segment displacement data, we observed no difference between the displacement of markers placed on the greater trochanters and markers placed on the trunk, which supports the inclusion of the upper portion of the femur in the trunk segment. Accordingly, 27% was subtracted from the femora before the surface area of the upper leg was estimated. The surface areas of the non-limb segments were estimated by summing the limb segment surface areas, dividing the resulting figure by the percentage of total body surface area that the limbs represent in Cross et al.'s (2008) sample, and then multiplying the quotient by the percentage of surface area that the non-limb segments represent in Cross et al.'s (2008) sample. Total surface area is the sum of all segment surface areas. For comparative purposes, the total surface area for each sample/specimen was also estimated using the standard Du Bois and Du Bois (1916) equation: Surface area (cm^2) = 0.007184 * H$^{0.725}$ * W$^{0.425}$. Segment and total surface area estimates are listed in Table 12.3.

After obtaining the surface areas, we estimated displacement distances for the segments and walking cycle durations (Table 12.4). We accomplished this with the aid of Cross et al.'s (2008) 3D motion capture data. First, we estimated total arm length. This was necessary because the skeletal samples and fossil hominin specimens lacked data on hand length. We found that, on average, hand length was 75% of lower arm length in Cross et al.'s (2008) dataset, and we assumed this to be the case for our sample. Next, we estimated displacement distances for the trunk and head/neck from total arm length. We used this approach because we found that the displacement distances of the trunk and head/neck were most strongly correlated with total arm length in Cross et al.'s (2008) data (r^{2}s > 0.96). Subsequently, we estimated upper arm displacement distances

Table 12.3 Segment surface area estimates (cm^2) for the samples used in this study. UA = upper arms; LA = lower arms; UL = upper legs; LL = lower legs; HN = head and neck; Total = sum of segment surface areas; Standard = Estimate of total surface area obtained with the standard, Dubois and Dubois method

Sample	UA	LA	UL	LL	HN	Trunk	Hands	Feet	Total	Standard
Inuit	1782.0	1032.5	2897.4	2152.2	1077.7	5395.0	648.6	1269.5	16255	15440
Yugoslavians	1934.5	1109.9	3231.2	2477.3	1199.5	6004.7	721.9	1413.0	18092	17495
Egyptians	1905.2	1152.9	3217.0	2516.3	1204.8	6031.1	725.0	1419.2	18171	16850
Lapps	1858.3	1118.5	3096.2	2412.2	1162.8	5821.1	699.8	1369.8	17539	15823
Amerinds	1805.5	1079.8	3003.9	2334.2	1126.9	5641.5	678.2	1327.5	16998	16396
Melanesian	1793.8	1023.9	2911.6	2113.2	1074.7	5380.1	646.8	1266.0	16210	16396
Skhul IV	1975.5	1239.0	3479.7	2821.9	1304.1	6528.3	784.8	1536.2	19669	18323
Skhul V	2227.6	1208.9	3657.2	2678.8	1339.2	6704.2	806.0	1577.6	20199	19241
Predmosti 3	2092.7	1260.5	3458.4	2737.3	1308.6	6550.8	787.5	1541.5	19737	18900
Predmosti 14	1969.6	1196.0	3209.9	2568.3	1225.6	6135.6	737.6	1443.8	18486	17650
Caviglione 1	2004.8	1187.4	3337.7	2678.8	1262.0	6317.4	759.5	1486.6	19034	17908
La Ferrassie 1	1975.5	1101.3	3252.5	2405.7	1197.0	5992.5	720.4	1410.1	18055	19737
La Chapelle 1	1828.9	1023.9	3053.6	2210.7	1112.4	5568.6	669.4	1310.3	16778	18259
Shanidar 4	1787.9	1062.6	2996.8	2171.7	1098.9	5501.2	661.3	1294.5	16575	17581
Dmanisi	1729.3	1045.4	2741.2	1989.6	1028.5	5148.9	619.0	1211.6	15514	14532
KNM-WT 15000	1870.0	1161.5	3067.8	2470.8	1174.4	5879.3	706.8	1383.5	17670	14753

Table 12.4 Segment displacement estimates (per cycle) for the samples used in this study. UA = upper arm; LA = lower arm; UL = upper leg; LL = lower leg. HN = head and neck. Cycle duration = heel strike to the next heel strike of the same foot

Sample	UA	LA	UL	LL	HN	Trunk	Hand	Foot	Cycle duration
Inuit	145.33	173.64	158.26	157.01	136.04	138.50	207.34	155.22	1.05
Yugoslavians	160.81	192.14	164.44	163.14	148.01	149.36	229.43	161.28	1.10
Egyptians	164.18	196.16	164.77	163.47	150.61	151.73	234.24	161.61	1.10
Lapps	158.26	189.08	162.69	161.40	146.03	147.57	225.78	159.57	1.08
Amerinds	151.59	181.12	161.11	159.84	140.88	142.89	216.28	158.02	1.07
Melanesians	144.93	173.16	157.93	156.68	135.73	138.21	206.77	154.89	1.05
Skhul IV	176.84	211.29	170.20	168.85	160.40	160.61	252.30	166.93	1.14
Skhul V	185.12	221.18	169.92	168.58	166.80	166.42	264.11	166.66	1.13
Predmosti 3	184.58	220.54	169.08	167.75	166.38	166.04	263.34	165.84	1.13
Predmosti 14	171.86	205.33	165.30	164.00	156.55	157.11	245.19	162.13	1.10
Caviglione 1	172.53	206.14	167.51	166.19	157.07	157.59	246.15	164.30	1.12
La Ferrassie 1	161.76	193.27	163.79	162.50	148.74	150.03	230.78	160.65	1.09
La Chapelle 1	146.54	175.09	160.10	158.83	136.98	139.35	209.07	157.02	1.07
Shanidar 4	148.90	177.90	159.23	157.97	138.80	141.00	212.43	156.17	1.06
Dmanisi	144.32	172.43	155.25	154.02	135.26	137.79	205.90	152.27	1.03
KNM-WT 15000	163.51	195.36	162.97	161.69	150.09	151.25	233.28	159.85	1.09

from total arm length with a regression equation developed on the basis of Cross et al.'s (2008) data. Estimating displacement distances for the lower arm and hand is complicated by the fact that the strength of the correlation between segment length and displacement varies within limbs, because the displacement of a segment is related not only to its length but also to the properties of the segments with which it articulates. As a consequence, simply summing segment displacement distances for segments without taking into account their interactions produces an unrealistic arm-swing pattern. We dealt with this problem by calculating the percentage of upper arm displacement that lower arm and hand displacement represent in Cross et al.'s (2008) sample. Lower arm displacement was found to be 119.48% of upper arm displacement, and hand displacement was found to be 142.67% of upper arm displacement. These values were then used to estimate lower arm and hand displacement in the skeletal samples and fossil hominin specimens. Thereafter, we estimated displacement distances for the legs. The approach we used was similar to the one we employed for the arms: The displacement distance of the upper leg was estimated from total leg length, and the displacement distances of the lower leg and foot were calculated from upper leg displacement using percentages derived from Cross et al.'s (2008) data (+99.21% and +98.08%, respectively). Lastly, we estimated walking cycle duration. To do so, we used Cross et al.'s (2008) data to generate a regression equation that allowed walking cycle duration to be estimated from upper leg displacement.

Having estimated the surface areas and displacement rates of the body segments, we then modeled each sample as walking bipedally at 1.2 m/s and used Cross et al.'s (2008) methods to calculate individual heat production (Table 12.5), convective heat loss, radiant heat loss, and heat balance. One-point-two meters per second is widely accepted to be the average human walking speed (Hinrichs and Cavanagh 1981; Langlois et al. 1997; Orendurff et al. 2004; Neptune et al. 2008), and has been used in many studies of this type (e.g., Hinrichs and Cavanagh 1981; Orendurff et al. 2004; Neptune et al. 2008). In addition, it is employed in such tasks as setting crossing signals (Langlois et al. 1997). Cross et al.'s (2008) method involves three steps. First, the target individual's heat production is calculated with the following equation:

$$\text{Heat production} = w * v * a \tag{1}$$

where w the individual's total body weight in kilograms, v is their walking speed (1.2 m/s), and a is a constant pertaining to the production of heat by metabolism and work and is equal to 2. Convective and radiant heat loss are then estimated for each body segment with the following equations:

$$\begin{aligned}&\text{Convective heat loss (in Watts)}\\&\quad = (STsk - Ta) * \sqrt{c} * SSA * 8.3\end{aligned} \tag{2}$$

$$\text{Radiant heat loss (in Watts)} = (STsk - Tr) * SSA * 5.2 \tag{3}$$

where Ta is ambient temperature in degrees centigrade, $STsk$ is segment-specific skin temperature in degrees centigrade in Ta, c is the segment-specific displacement rate in meters per second (i.e., the square root of total displacement divided by cycle duration), SAA is segment-specific surface areas, Tr is radiant temperature, and 8.3 and 5.2 are heat transfer coefficients. The last step of Cross et al.'s (2008) method is to sum the segment-specific estimates for convective and radiant heat loss, and then divide this value by the estimate for heat production. The resulting values represent the individuals' whole-body relative heat loss. We made estimates for each sample/specimen in ambient temperatures of 20°C, 25°C, 30°C, and 35°C (Table 12.6).

Relative heat loss for each limb segment was estimated by summing the segment-specific convective and radiant heat loss values and dividing the resulting figure by the estimate for total body heat production. Estimates were again made for each sample/specimen in ambient temperatures of 20°C, 25°C, 30°C, and 35°C (Table 12.7). Whole-limb values (i.e., the sum of heat loss estimates for the proximal and distal segments of each limb) were also calculated to assess the responses of entire limbs.

The task of estimating the thermal responses of extinct, culture-using hominins has the potential to be extremely complex. The model employed in this study was kept simple

Table 12.5 Heat production estimates in Watts for the samples used in this study. See main text for details of how heat production was estimated

Sample	Heat production
Inuit	160.8
Yugoslavians	156.0
Egyptians	146.4
Lapps	134.4
Amerinds	141.6
Melanesians	141.6
Skhul IV	158.4
Skhul V	168.0
Predmosti 3	170.4
Predmosti 14	158.4
Caviglione 1	156.0
Shanidar 4	170.4
La Chapelle 1	182.4
La Ferrassie 1	204.0
Dmanisi	120.0
KNM-WT 15000	115.2

in order to establish, all else being equal, what the thermal implications of observed proportional differences would have been. No attempt was made to account for possible inter-population variability in adipose characteristics, vasoconstriction or vasodilation, sweat gland distribution and production, the amount or density of body hair, or the thermal properties of clothing. Individuals were modeled as if they were hairless, naked bipeds employing a modern human striding bipedal gait. The same segment skin temperatures were used for both modern and fossil individuals. Skin temperatures were taken from Houdas and Ring (1982). These values were derived from motionless adult humans in each of the ambient temperatures considered in this study. Following Cross et al. (2008), *Tr* was treated as equal to *Ta*. Research employing thermal mannequins has shown that convective and radiant heat transfer coefficients vary somewhat from one segment to the next (e.g., Quintela et al. 2004; Oliveira et al. 2011). However, attempts to use mannequins to model the thermal properties of body segments during walking (e.g., Oliveira et al. 2011) have not yet included sufficiently realistic segment kinematics to believe that their segment-specific heat transfer coefficients would provide more accurate estimates of thermal response during locomotion than the coefficients employed here.

Once the relative heat loss values had been calculated, we carried out two sets of analyses. The first focused on whole-body heat loss. Initially, we compared the whole-body heat loss estimates for KNM-WT 15000 and the two European Neanderthals, La Ferrassie 1 and La Chapelle 1, with the whole-body heat loss estimates for the modern human samples. Because arguments in the literature have focused on the relationship between total body surface area, limb proportions, and mean annual temperature or latitude (the assumption being that total body surface area and limb proportions reflect adaptation to thermal stress) we used comparable ratios that incorporate the contributions of segment-specific data. The first ratio we employed is the ratio of the sum of segment heat loss to heat production (SSHL:HP). In this ratio, SSHL represents the variable for which SA is assumed to be a proxy, and HP represents the amount of heat generated by a walking hominin of a given weight. We predicted that, if the current consensus regarding the thermoregulatory adaptations of KNM-WT 15000 and the Neanderthals is correct, then KNM-WT 15000 should consistently have a higher SSHL:HP (i.e., dissipate relatively more heat) than the modern humans in our sample, and that the European Neanderthals should consistently have lower SSHL:HP (i.e., retain relatively more heat) than our modern human sample.

Having compared whole-body heat loss across the species, we examined whole-body heat loss within the *H. erectus* and *H. neanderthalensis* samples. There is reason to think that the mean annual temperature at Dmanisi would have been cooler at 1.7 Ma than the mean annual temperature at West Turkana at 1.6 Ma (Lordkipanidze et al. 2007), and that the mean annual temperature at La Ferrassie and La Chapelle at the time they were occupied by Neanderthals would have been cooler than the mean annual temperature at Shanidar when it was occupied by Neanderthals (Froehle and Churchill 2009). Thus, the prediction we tested was that the Dmanisi specimen should exhibit lower SSHL:HP than KNM-WT 15000, and that the two European Neanderthals should exhibit lower SSHL:HP than the Neanderthal from Shanidar.

Table 12.6 Segmented (SEG) and conventional (CON) method estimates of whole-body relative heat loss (Total Heat Loss in Watts/Heat Production in Watts), in ambient temperatures of 20°C, 25°C, 30°C, and 35°C

Sample	20°C		25°C		30°C		35°C	
	SEG	CON	SEG	CON	SEG	CON	SEG	CON
Inuit	1.280	1.266	1.018	0.884	0.589	0.538	0.089	0.087
Yugoslavians	1.506	1.371	1.205	0.957	0.692	0.583	0.105	0.094
Egyptians	1.592	1.385	1.273	0.967	0.732	0.589	0.111	0.095
Lapps	1.528	1.417	1.215	0.989	0.703	0.602	0.106	0.098
Amerinds	1.524	1.393	1.216	0.973	0.701	0.592	0.106	0.096
Melanesians	1.582	1.393	1.263	0.973	0.728	0.592	0.110	0.096
La Ferrassie 1	1.135	1.164	0.907	0.813	0.522	0.495	0.079	0.080
La Chapelle 1	1.149	1.195	0.917	0.835	0.529	0.508	0.080	0.082
Shanidar 4	1.219	1.231	0.970	0.860	0.561	0.524	0.085	0.085
Dmanisi	1.645	1.457	1.300	1.018	0.757	0.620	0.115	0.100
KNM-WT 15000	1.973	1.983	1.572	1.076	0.907	0.655	0.138	0.106
Skhul IV	1.601	1.392	1.289	0.972	0.736	0.592	0.111	0.096
Skhul V	1.570	1.378	1.261	0.962	0.720	0.586	0.110	0.095
Predmosti 3	1.511	1.335	1.211	0.932	0.694	0.568	0.106	0.092
Predmosti 14	1.509	1.341	1.205	0.936	0.694	0.570	0.106	0.092
Caviglione 1	1.573	1.382	1.261	0.965	0.723	0.587	0.110	0.095

Table 12.7 Segment-specific relative heat loss (Segment Heat Loss in Watts/Total Body Heat Production in Watts) in ambient temperatures of 20°C, 25°C, 30°C, and 35°C

Sample	20°C				25°C			
	UA	LA	UL	LL	UA	LA	UL	LL
Inuit	0.132	0.078	0.219	0.119	0.096	0.054	0.185	0.080
Yugoslavians	0.154	0.090	0.255	0.143	0.111	0.062	0.219	0.096
Egyptians	0.160	0.099	0.267	0.153	0.116	0.068	0.229	0.103
Lapps	0.160	0.093	0.263	0.140	0.116	0.064	0.222	0.094
Amerinds	0.154	0.094	0.257	0.147	0.111	0.065	0.219	0.099
Melanesians	0.160	0.098	0.265	0.151	0.116	0.068	0.227	0.102
La Ferrassie 1	0.119	0.068	0.194	0.105	0.086	0.046	0.166	0.070
La Chapelle 1	0.118	0.068	0.201	0.106	0.086	0.046	0.170	0.071
Shanidar 4	0.124	0.076	0.211	0.112	0.090	0.052	0.179	0.075
Dmanisi	0.173	0.107	0.277	0.147	0.125	0.073	0.233	0.099
KNM-WT 15000	0.200	0.127	0.321	0.191	0.145	0.087	0.275	0.128
Skhul IV	0.155	0.099	0.267	0.158	0.113	0.068	0.232	0.106
Skhul V	0.168	0.093	0.264	0.142	0.122	0.064	0.230	0.095
Predmosti 3	0.155	0.096	0.246	0.143	0.113	0.066	0.214	0.096
Predmosti 14	0.155	0.096	0.246	0.144	0.112	0.066	0.212	0.097
Caviglione 1	0.159	0.097	0.260	0.153	0.116	0.066	0.224	0.103
Sample	30°C				35°C			
	UA	LA	UL	LL	UA	LA	UL	LL
Inuit	0.056	0.037	0.094	0.055	0.018	0.008	0.003	0.008
Yugoslavians	0.065	0.042	0.110	0.067	0.021	0.009	0.003	0.010
Egyptians	0.068	0.046	0.115	0.071	0.022	0.010	0.003	0.011
Lapps	0.068	0.043	0.113	0.065	0.022	0.010	0.003	0.010
Amerinds	0.065	0.044	0.111	0.068	0.021	0.010	0.003	0.010
Melanesians	0.068	0.046	0.114	0.070	0.022	0.010	0.003	0.010
La Ferrassie 1	0.050	0.032	0.083	0.049	0.016	0.007	0.002	0.007
La Chapelle 1	0.050	0.032	0.086	0.049	0.016	0.007	0.003	0.007
Shanidar 4	0.053	0.035	0.091	0.052	0.017	0.008	0.003	0.008
Dmanisi	0.074	0.050	0.119	0.069	0.024	0.011	0.004	0.010
KNM-WT 15000	0.085	0.059	0.138	0.089	0.027	0.013	0.004	0.013
Skhul IV	0.066	0.047	0.115	0.074	0.021	0.010	0.003	0.011
Skhul V	0.071	0.043	0.114	0.066	0.023	0.010	0.003	0.010
Predmosti 3	0.066	0.045	0.106	0.066	0.021	0.010	0.003	0.010
Predmosti 14	0.066	0.045	0.106	0.067	0.021	0.010	0.003	0.010

In the second set of analyses, we examined the contribution of the limbs and limb segments to heat loss. In these analyses we focused on limb-specific and limb segment-specific ratios of HL to HP. Here HL represents the amount of convective and radiant heat lost by a given pair of limbs (e.g., both arms) or limb segments (e.g., both forearms), and HP represents the amount of heat generated by the body as a whole for a walking hominin of a given weight. We began by testing the prediction that the limbs of European Neanderthals should have lower segment HL:HP values than those of modern humans, while the limbs of KNM-WT 15000 should have higher segment HL:HP values than those of modern humans. Next, we tested the prediction that that the limbs of KNM-WT 15000 should lose more heat than those of the Dmanisi specimen, while the limbs of the European Neanderthals should lose less heat than those of the Middle Eastern Neanderthal. Subsequently, we investigated the contribution of the upper and lower limb segments to heat loss. Based on the argument of Trinkaus (1981) and Holliday and Ruff (2001) that the distal segments of the limbs are particularly evolutionarily labile with respect to thermoregulation, we predicted that differences in segment-specific relative heat loss between Neanderthals and *H. erectus* should be more pronounced in the distal segments of each limb than in their proximal segments.

Results

The pattern of relative whole-body heat loss (Table 12.6) in our sample is consistent with the current consensus concerning the thermoregulatory implications of the size and shape of the bodies of *H. erectus* and *H. neanderthalensis*. As predicted, KNM-WT 15000 is estimated to have lost more heat than the modern human samples, and the two European Neanderthals are estimated to have lost less heat than the modern human samples.

Table 12.8 lists the mean SSHL:HP for our modern human sample as well as the number of standard deviations above or below these means that the estimates for each of the fossil hominins depart. Of the modern humans samples, the Inuit were estimated to have the lowest SSHL:HP and the Egyptians were estimated to have the highest HL:HP in all four ambient temperatures. The Inuit departed from the human mean by −1.8 to −2.0SD while the Egyptians departed from the human mean by +0.8 to +1.8SD. Results for the European Neanderthals were consistent with the arguments for polar adaptation. The Neanderthals displayed the lowest HL:HP of all the samples including the Eskimo. The two European Neanderthals differed from the human mean by −3.0SD or greater in each ambient temperature, while Shanidar 4 differed from the human mean by −2.4 or greater. Also consistent with the arguments for thermal adaptation, KNM-WT 15000 consistently had the highest SSHL:HP of all of the specimens, departing from the human mean by +4.0–6.7SD.

The results of the intra-species comparisons were also consistent with the current consensus regarding the thermoregulatory implications of the size and shape of the bodies of *H. erectus* and *H. neanderthalensis* (Tables 12.6 and 12.8). As predicted, the European Neanderthals had lower HL:HP values than the Near Eastern Neanderthal from Shanidar, and KNM-WT 15000 had a higher HL:HP value than the Dmanisi *H. erectus* specimen.

Our assessment of the thermal responses of hominin limbs indicated that whole-limb relative heat loss estimates (i.e., the sum of heat loss estimates for the proximal and distal segments of each limb) followed a similar pattern to that for whole-body heat loss (Table 12.8). As with overall SSHL:HP, the relative ranking of specimens and populations remained constant across the four ambient temperatures. Of the modern humans samples, the Inuit were estimated to have the lowest segment HL:HP values, differing from the modern human mean by −0.8 to −2.8SD depending on the limb segment and ambient temperature. The Egyptians were estimated to have the highest segment HL:HP values, differing from the modern human mean by less than +1.3SD for all four limb segments regardless of ambient temperature. As predicted, and consistent with the arguments for polar adaptation, the limbs of the Neanderthals consistently had the lowest segment HL:HP of the other samples including the Inuit. The limbs of KNM-WT 15000 consistently had the highest segment HL:HP of the other hominins, typically losing between +3.6 and +6.0SD more heat than the modern human mean. Also as predicted, the two European Neanderthal specimens were found to lose relatively less heat from their limbs than the Middle Eastern Neanderthal. The limbs of the two European Neanderthals lost approximately −3SD (−1.5SD to −3.4SD) less heat than the modern human mean while the Shanidar Neanderthal lost around −2SD (−1.1SD to −2.6SD) less heat than the modern human mean. The predicted pattern was also identified in our *H. erectus* sample. The *H. erectus* specimen from Dmanisi lost relatively less heat from its limbs than did the African *H. erectus*, KNM-WT 15000. Thus, the pattern of relative heat loss for the limbs of *H. erectus* and *H. neanderthalensis* is also consistent with the current consensus regarding the thermoregulatory implications of the size and shape of the bodies of *H. erectus* and *H. neanderthalensis*.

In contrast, our findings regarding the contribution of the proximal and distal segments of each limb to heat loss were not consistent with the predictions of the hypothesis that the distal segments of the limbs are particularly evolutionarily labile in relation to thermoregulation. The differences in the number of standard deviations by which the upper and lower limb segments depart from the modern human means were often small in both *H. neanderthalensis* and *H. erectus* (Table 12.8). More importantly, there was no obvious pattern in the differences between average heat loss estimates for the upper and lower limb segments (Table 12.9). At 20° C, for example, there is no difference between the average heat loss for the Neanderthals' upper and lower arm segments. The same holds for the average heat loss values for their upper and lower leg segments. At 35°C, in contrast, the lower arm loses more heat than the upper arm, while the lower leg loses less heat than upper leg. The estimates for *H. erectus* are also not consistent with the predictions of the hypothesis. At 20°C, the lower arm loses more heat than the upper arm, which is the predicted pattern. But the lower leg loses less heat than the upper leg, which is not the predicted pattern. At 35°C, neither set of segments is consistent with the predictions of the hypothesis. The lower arm loses less heat than upper arm, and the lower leg loses less heat than the upper leg.

The change in differences between the upper and lower segments as we move from colder to warmer ambient temperature does not conform to expectation either. Given that Neanderthal arms and legs are supposed to be adapted to cold conditions, we should see a closer fit with the predictions of the hypothesis as temperature declines, yet the differences between the upper and lower segments actually disappear at the lowest temperature, 20°C. The same holds

Table 12.8 Relative heat loss in Watts in TA = 20°C, 25°C, 30°C, and 35°C. Holocene mean and standard deviation (SD) are for the Holocene human skeletal sample (i.e., excluding the fossil modern human samples). Values for other samples represent the number of standard deviations to which they depart from the modern human mean. WB = whole-body heat loss/total heat production; UA = upper arm heat loss/total heat production; LA = lower arm heat loss/total heat production; UL = upper leg heat loss/total heat production; LL = lower leg heat loss/total heat production

Sample	20ºC					25ºC				
	WB	UA	LA	UL	LL	WB	UA	LA	UL	LL
Inuit	−1.94	−1.91	−2.00	−1.94	−1.92	−1.94	−1.87	−1.81	−1.99	−2.00
Yugoslavians	0.03	0.09	−0.29	0.06	0.08	0.08	0.05	−0.20	0.13	0.05
Egyptians	0.79	0.64	1.00	0.72	0.92	0.81	0.60	1.00	0.76	0.84
Lapps	0.11	0.42	0.13	0.50	−0.19	0.04	0.41	−0.54	0.34	−0.25
Amerinds	0.07	−0.12	0.25	0.19	0.38	0.04	−0.13	−0.46	0.15	0.31
Melanesians	0.01	0.41	0.86	0.58	0.75	−0.47	0.44	0.15	−2.05	0.61
Holocene human mean (SD)	1.502 (0.114)	0.153 (0.011)	0.092 (0.007)	0.254 (0.018)	0.142 (0.012)	1.198 (0.093)	0.111 (0.008)	0.063 (0.005)	0.217 (0.016)	0.096 (0.008)
La Ferrassie 1	−3.2	−3.1	−3.4	−3.3	−3.1	−3.1	−3.1	−3.3	−3.2	−3.2
La Chapelle 1	−3.1	−3.2	−3.4	−2.9	−3.0	−3.0	−3.2	−3.3	−2.9	−3.1
Shanidar 4	−2.5	−2.6	−2.3	−2.4	−2.5	−2.4	−2.6	−2.2	−2.4	−2.6
Dmanisi	1.3	1.8	2.1	1.3	0.4	1.1	1.8	2.1	1.0	0.4
KNM-WT 15000	4.1	4.3	5.0	3.8	4.1	4.0	4.2	4.8	3.6	4.0
Skhul IV	0.9	0.2	1.0	0.7	1.3	1.0	0.2	1.1	0.9	1.3
Skhul V	0.6	1.4	0.1	0.6	0.0	0.7	1.3	0.2	0.8	−0.1
Predmosti 3	0.1	0.2	0.6	−0.4	0.1	0.1	0.2	0.6	−0.2	0.0
Predmosti 14	0.1	0.2	0.6	−0.4	0.2	0.1	0.2	0.6	−0.3	0.1
Caviglione 1	0.6	0.5	0.7	0.3	0.9	0.7	0.6	0.7	0.5	0.8

Sample	30ºC					35ºC				
	WB	UA	LA	UL	LL	WB	UA	LA	UL	LL
Inuit	−2.0	−2.2	−2.1	−2.0	−1.8	−1.8	−2.8	−0.9	−0.8	−1.8
Yugoslavians	0.0	0.1	−0.3	0.0	0.1	0.8	0.1	0.4	0.8	−0.1
Egyptians	0.8	0.7	1.1	0.6	0.9	1.8	1.0	1.3	1.3	0.5
Lapps	0.1	0.5	−0.7	0.4	−0.2	0.8	0.7	0.1	1.1	−0.4
Amerinds	0.0	−0.1	−0.6	0.1	0.4	0.7	−0.1	0.2	0.9	0.1
Melanesians	−0.5	0.5	0.1	−2.2	0.6	0.6	0.7	0.6	−0.9	0.4
Holocene human mean (SD)	0.691 (0.052)	0.065 (0.004)	0.043 (0.003)	0.110 (0.008)	0.066 (0.006)	0.100 (0.006)	0.021 (0.001)	0.009 (0.001)	0.003 (0.0003)	0.010 (0.001)
La Ferrassie 1	−3.3	−3.7	−3.8	−3.3	−2.9	−3.5	−4.7	−2.0	−1.8	−2.8
La Chapelle 1	−3.1	−3.7	−3.8	−3.0	−2.8	−3.4	−4.8	−2.0	−1.5	−2.7
Shanidar 4	−2.5	−3.0	−2.6	−2.4	−2.3	−2.6	−3.9	−1.2	−1.1	−2.3
Dmanisi	1.3	2.1	2.3	1.2	0.4	2.5	2.8	2.1	1.7	0.2
KNM-WT 15000	4.2	5.0	5.3	3.5	3.8	6.7	6.0	4.0	3.3	3.0
Skhul IV	0.9	0.2	1.2	0.6	1.3	1.9	0.3	1.3	1.2	0.9
Skhul V	0.6	1.6	0.2	0.5	0.0	1.6	2.1	0.7	1.1	−0.2
Predmosti 3	0.1	0.3	0.6	−0.5	0.1	1.0	0.4	0.9	0.4	−0.2
Predmosti 14	0.0	0.2	0.6	−0.5	0.2	0.9	0.3	1.0	0.4	−0.1
Caviglione 1	0.6	0.7	0.7	0.2	0.8	1.6	0.9	1.0	1.0	0.5

Table 12.9 Comparison of average heat loss estimates for Neanderthals and *H. erectus* upper and lower limb segments. UA = upper arm. LA = lower arm. UL = upper leg. LL = lower leg

		20°C	25°C	30°C	35°C
Neanderthals	UA	−3.0	−3.0	−3.5	−4.5
	LA	−3.0	−2.9	−3.4	−1.7
		No difference	LA loses more heat	LA loses more heat	LA loses more heat
	UL	−2.9	−2.8	−2.9	−1.5
	LL	−2.9	−3.0	−2.7	−2.6
		No difference	LL loses less heat	LL loses more heat	LL loses less heat
H. erectus	UA	3.1	3.0	3.6	4.4
	LA	3.6	3.5	3.8	3.1
		LA loses more heat	LA loses more heat	LA loses more heat	LA loses less heat
	UL	2.6	2.3	2.4	2.5
	LL	2.3	2.2	2.1	1.6
		LL loses less heat	LL loses less heat	LL loses less heat	LL loses less heat

for *H. erectus*. Given that its arms and legs are supposed to be adapted to warmer temperatures, we might expect to see a closer fit with the predictions of the hypothesis as temperature increases, but the differences between heat loss estimates for the arm segments at 35°C are the reverse of what the hypothesis predicts, whereas those at 20°C, 25°C, and 30°C are consistent with the hypothesis.

Looking at the amount of change in limb segment heat loss across the four ambient temperatures does not alter the picture. As we move from 20°C to 35°C, we see that the upper arms of Neanderthals change by 1.5SD while their lower arms change by 1.3SD, which means that the lower arms respond to the change in ambient temperature less than the upper arms. The same is true for the Neanderthals' leg segments: the upper leg segments change by 1.4SD from 20°C to 35°C while the lower leg segments change by 0.3SD. Both of these findings are inconsistent with the predictions of the hypothesis. It is a similar story for *H. erectus*. Moving from 20°C to 35°C, the upper arms change by 1.3SD while the lower arms change by 0.5SD, which means that the lower arms of *H. erectus* also respond to the change in ambient temperature less than its upper arms. Turning to the leg segments of *H. erectus*, the amount of change is greater in the lower leg than in the upper leg as we move from 20°C to 35°C. The upper leg changes by only 0.1SD while the lower leg changes by 0.7SD. But the change in the lower leg is in the opposite direction to the one predicted by the hypothesis.

In sum, then, the limb segments' heat loss estimates do not support the hypothesis that the distal limb segments of *H. erectus* and *H. neanderthalensis* were more affected by heat loss-related selection than their proximal limb segments.

Discussion

The results of the study were mixed. The whole-body heat loss estimates we obtained follow the pattern predicted by the thermoregulation hypothesis. They suggest that the African *H. erectus* specimen in our sample, KNM-WT 15000, would have lost more heat than the humans in our sample, and that the European Neanderthal specimens in our sample would have conserved more heat than the humans in our sample. They also suggest that the hot-climate-dwelling KNM-WT 15000 would have lost less heat than the colder-climate *H. erectus* specimen from Dmanisi, and that the two cold-climate Neanderthal specimens, La Ferrassie 1 and La Chapelle 1, would have conserved more heat than the warmer-climate Middle Eastern Neanderthal specimen, Shanidar 4. The whole-limb heat loss estimates we obtained follow the pattern predicted by the thermoregulation hypothesis too. They suggest that the limbs of KNM-WT 15000 would have lost more heat than those of the humans in our sample, while the limbs of the European Neanderthal specimens in our sample would have conserved more heat than those of the humans in our sample. The whole-limb heat loss estimates also suggest that, as predicted, the limbs of KNM-WT 15000 would have lost less heat than those of the Dmanisi specimen, and that the limbs of La Ferrassie 1 and La Chapelle 1 would have lost less heat than those of Shanidar 4. In contrast, the limb segment heat loss estimates we obtained are not consistent with the predictions of the hypothesis that the distal limb segments of *H. erectus* and *H. neanderthalensis* were more affected by heat loss-related selection than their proximal limb segments. The heat loss differences between the proximal and distal limb segments did not exhibit any obvious pattern. Thus, our results generally support the current consensus regarding the thermoregulatory implications of the size and shape of the bodies of *H. erectus* and *H. neanderthalensis*, but they are not entirety consistent with it.

Because the methods used in this study differ from those employed in previous studies it is important that we ensure that our data are as reliable as if we had used the conventional methods. The equation used in this study for estimating heat production is the same as the one used in other studies (e.g., Dennis and Noakes 1999; Marino et al. 2004), so the variables of interest in this regard are the estimates of total skin surface area and relative heat loss. To assess the reliability of the former, we estimated total skin surface area with both our segmented method and the conventional Du Bois and Du Bois (1916) method. Consistent with the findings of Cross et al. (2008) and Cross and Collard (2011), a paired t-test found these two sets of estimates (N = 16) to be statistically indistinguishable (p = 0.118). We also tested the reliability of our proxy for relative heat loss, HL:HP, to ensure that the additional heat loss variables included in our method (i.e., segment specific skin temperatures, segment specific wind speeds derived from 3D kinematic data, and segment specific surface areas) were tracking the patterns identified with the conventional proxy for relative heat loss, SA:BM. When this analysis was performed SA:BM consistently and significantly correlated with HL:HP in each of the four ambient temperatures with r-values ranging from 0.980 to 0.992. This suggests that the additional variables used to establish the ratios of HL to HP produce a thermoregulatory proxy that is consistent with the SA:BM ratio. As a further check on the reliability of our proxy for relative heat loss, we calculated HL:HP ratios for each of our samples using conventional methods. To do this we estimated skin surface area using the Du Bois and Du Bois (1916) equation and then used these along with a weighted mean skin temperature and a wind speed equal to walking speed to estimate convective and radiant heat loss following the method outlined by Dennis and Noakes (1999). When these conventional method HL:HP values were compared to those derived from our segmented approach, we found the two sets of estimates to be strongly and significantly correlated at all four ambient temperatures (r = 0.950 to 0.965, p = 0.000). Given these results, there is reason to believe that our method is as reliable as the conventional method of estimating heat loss in humans and other hominins.

Another “quality control” issue that needs to be addressed is whether the segment-specific data we employed had any effect on the results. Cross and Collard (2011) found that variation in limb proportions explained most of the difference between the results yielded by the conventional approach to estimating skin surface area and a segmented approach similar to the one we have used here. With this finding in mind, we revisited the HL:HP estimates that we generated with the segmented and conventional methods, and performed regression analyses in which we investigated how much of the difference between the estimates yielded by the two methods could be explained by the brachial, crural, and intermembral indices. The results indicated that limb segment length differences explained more than 70% of the variation in the differences between methods. When limb segment relative heat loss (i.e., segment HL:HP) values were used as the independent variables in the regression analyses we found that they explained over 98% of the difference between the two sets of HL:HP estimates (r = 0.982–0.998, p = 0.000). It is clear from these results that the segment-specific data did have an effect on the results, as intended.

The main implication of our study is that the current consensus regarding the thermoregulatory implications of the size and shape of the bodies of *H. erectus* and *H. neanderthalensis* may need some revision. The fact that the results of our whole-body and whole-limb analyses suggest that KNM-WT 15000 was warm-adapted and that the European Neanderthals were cold-adapted suggests that the basic idea that thermoregulation affected the evolution of body size and shape in *H. erectus* and *H. neanderthalensis* is correct. The same holds for fact that our whole-body and whole-limb analyses suggest that the Dmanisi *H. erectus* specimen was more cold adapted than KNM-WT 15000, and that the Middle Eastern Neanderthal in our sample was more warm adapted than the two European Neanderthals in our sample. However, the failure of our limb segment analyses to identify consistent differences between the proximal and distal limb segments in terms of heat loss raises the possibility that the idea that selection altered the lengths of the distal limb segments in *H. erectus* and *H. neanderthalensis* to improve thermoregulation is incorrect.

With regard to future research, the most obvious task concerns the hypothesis that selection altered the lengths of the distal limb segments in *H. erectus* and *H. neanderthalensis* to improve thermoregulation. Given the kinematics of walking, and especially the fact that the distal segments of limbs experience greater displacement than the upper segments of limbs, it is somewhat surprising that the distal limb segments do not demonstrate a greater sensitivity to thermoregulation-related selection. The results of modeling exercises like the one reported here are heavily assumption-dependent. So, one possibility is that the hypothesis is correct and that our results did not support its predictions because some of the assumptions we made are wrong. Repeating the exercise with a different set of assumptions will indicate whether such is the case. Unfortunately, this is currently impossible for one important assumption – that the impact of evaporative heat loss (i.e., sweating) can be safely ignored. We know that there are differences among body segments in both the number of sweat glands and their recruitment pattern (e.g., Buono 2000), so it is feasible that taking evaporative heat loss into account would have reduced the number of results that do not fit the predictions of the hypothesis. However, as far as we are aware, segment-specific data for the dynamics of evaporative heat loss during walking do not exist at this time. Collecting such data would be a useful undertaking, needless to say.

While "assumption error" may be the most obvious explanation for the failure of the analyses to support the hypothesis, it is worth considering the possibility that the hypothesis is incorrect and that some other factor or set of factors had a stronger influence on the variation in distal limb segment length within and between *H. erectus* and *H. neanderthalensis* than did temperature. The obvious candidate for the factor affecting the lower legs is locomotion. Is it possible that the lengths of the distal segments of the legs of *H. erectus* and *H. neanderthalensis* have been selected in relation to a locomotion-related variable, such as terrain (e.g., Higgins and Ruff 2011)? As far as the forearms are concerned, one possibility worth investigating is that the within and between species differences are connected with differences in weapon use. Perhaps, for example, long forearms are useful for throwing objects, while short forearms are beneficial when using a thrusting spear. A less obvious factor that could have affected both the lower leg and the forearm is genetic drift. In recent years it has become increasingly clear that drift, in the form of the iterative founder effect, has played an important role in structuring modern human genetic and phenotypic variation (e.g., Weaver et al. 2007). There seems to be no reason why it might not have also played an important role in structuring genetic and phenotypic variation in other fossil hominin species such as *H. erectus* and *H. neanderthalensis*. Lastly, it is also worth considering the possibility that clothing may have reduced the impact of thermoregulation-related selection. To the best of our knowledge, nobody has suggested that *H. erectus* used clothing, but it has been argued that Neanderthals utilized clothing (e.g., Sørenson 2009; Collard et al. in press). If Neanderthals did in fact use clothing, then the nature of thermoregulation-related selection on the limbs could well have been reduced to the extent that other factors became more important influences on the size of the proximal and distal limb segments.

Conclusions

In the study presented here, we employed a novel way of assessing hominin thermoregulatory responses to ambient thermal stress during normal walking. The method we used differs from the conventional approach in that it takes into account the fact that different parts of the body differ in surface area, skin temperature, and 3D kinematics rather than treating the body as an undifferentiated mass. Importantly, this allows for the estimation of differences in thermal response due to differences in both body size *and* proportions.

In the study we used the segmented method to determine whether the current consensus regarding the thermoregulatory implications of the size and shape of the bodies of *H. erectus* and *H. neanderthalensis* is supported when body segment differences in surface area, skin temperature, and rate of movement are taken into account. Based on comparisons with modern humans, we tested the hypothesis that the well known African *H. erectus* specimen KNM-WT 15000 was adapted for warm conditions. We also tested the hypothesis that the European Neanderthals were adapted for cold conditions. In addition, by comparing specimens of conspecifics from locations with markedly different ambient temperatures, we investigated whether there is evidence of adaptation to thermal conditions within *H erectus* and within *H. neanderthalensis*.

The results of our study only partly supported the current consensus. The whole-body heat loss estimates were consistent with the idea that KNM-WT 15000 was warm adapted, and that European Neanderthals were cold adapted. The whole-body heat loss estimates were also consistent with the notion that there are thermoregulation-related differences in body size and shape within *H erectus* and *H. neanderthalensis*. The whole-limb estimates told a similar story. They too followed the predicted pattern. However, the results of our analysis of limb segment-specific heat loss were not consistent with the current consensus regarding the thermoregulatory implications of the size and shape of the bodies of *H. erectus* and *H. neanderthalensis*. Contrary to expectation, differences between the proximal and distal limb segments did not follow any particular trend.

The obvious implication of these results is that, while we can be more confident about the idea that thermoregulation influenced the evolution of body size and shape in *H. erectus* and *H. neanderthalensis*, we need to be more cautious in attributing differences in limb segment size to thermoregulation. Based on our results, the possibility that other factors influenced limb segment size in these species more than thermoregulation should be given serious consideration. Identifying these factors will require further research.

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