



## Influence of lower limb configuration on walking cost in Late Pleistocene humans



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### ABSTRACT

It has been proposed that Neandertals had about 30% higher gross cost of transport than anatomically modern humans (AMH) and that such difference implies higher daily energy demands and reduced foraging ranges in Neandertals. Thus, reduced walking economy could be among the factors contributing to the Neandertals' loss in competition with their anatomically modern successors. Previously, Neandertal walking cost had been estimated from just two parameters and based upon a pooled-sex sample. In the present study, we estimate sex-specific walking cost of Neandertals using a model accounting for body mass, lower limb length, lower limb proportions, and other features of lower limb configuration. Our results suggest that Neandertals needed more energy to walk a given distance than did AMH but the difference was less than half of that previously estimated in males and even far less pronounced in females. In contrast, comparison of the estimated walking cost adjusted to body mass indicates that Neandertals spent less energy per kilogram of body mass than AMH thanks to their lower limb configuration, males having 1–5% lower and females 1–3% lower mass-specific net cost of transport than AMH of the same sex. The primary cause of high cost of transport in Neandertal males is thus their great body mass, possibly a consequence of adaptation to cold, which was not fully offset by their cost-moderating lower limb configuration. The estimated differences in absolute energy spent for locomotion between Neandertal and AMH males would account for about 1% of previously estimated daily energy expenditure of Neandertal or AMH males.

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### Introduction

It has been proposed that Neandertals had 30% greater gross cost of transport than did contemporary anatomically modern humans (AMH) (Stuedel-Numbers and Tilkens, 2004). That would imply greater energy cost of foraging (Weaver and Stuedel-

Numbers, 2005), reduced effective foraging radius (Verpoorte, 2006; Anwar et al., 2007; MacDonald et al., 2009), and greater daily energy expenditure or at least higher proportion of energy spent on locomotion relative to other activities (MacDonald et al., 2009). These proposed consequences of such high walking cost would have disadvantaged Neandertals in their struggle for survival and in possible competition with AMH (Churchill, 2007; MacDonald et al., 2009). Estimation of Neandertal walking cost is thus important for understanding the life and extinction of Neandertals and the expansion of AMH to Eurasia during the Late Pleistocene.

While previous estimation of Neandertal gross cost of transport (Stuedel-Numbers and Tilkens, 2004) was based on a pooled-sex sample, sex-specific estimation of walking cost would be beneficial for drawing inferences about sexual division of labor in this taxon. Furthermore sex-specific analysis avoids biases related to potential differences in male to female proportion in the compared samples. Stuedel-Number and Tilkens (2004) estimated gross cost of transport for Neandertals from just two morphological features: body mass and lower limb length; but other features of lower limb configuration also affect walking cost (Pontzer et al., 2009).

*Abbreviations:* a, ankle; AMH, anatomically modern humans; BMR, basal metabolic rate;  $COM_{trunk}$ , trunk's center of mass; COP, center of pressure; EMA, effective mechanical advantage; EUP, early Upper Paleolithic Europeans; g, gravitational acceleration; GRF, ground reaction force; grossCOT, gross or total cost of transport (cost to travel a given distance including basal metabolic cost and postural cost); h, hip; k, knee; l, muscle fascicle length;  $L_{step}$ , step length; mass-specific netCOT, mass-specific net cost of transport; MIS, marine isotope stage; MPMH, Middle Paleolithic modern humans; netCOT, net cost of transport (cost to travel a given distance excluding basal metabolic cost and postural cost, energy used exclusively for locomotion); PAR, physical activity ratio; r, muscle moment arm; R, moment arm of the ground reaction force; v, walking speed;  $V_{muscle}$ , mass-specific volume of muscles activated per distance traveled;  $\sigma$ , constant relating tension to muscle cross-sectional area.

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Although most features of lower limb configuration are very likely intercorrelated in homogenous populations or species and could thus usually be effectively omitted from models linking walking cost to general anatomical variables in such populations (e.g., Steudel-Numbers and Tilkens, 2004), caution should be maintained when extrapolating results of such models to specimens deviating from the lower limb configuration of an initial sample (Kramer and Sylvester, 2009; Pontzer et al., 2009).

Neandertal postcranial morphology is characterized by a wide and relatively high trunk, which results in a great body mass, and by short limbs (Ruff, 1994; Ruff et al., 1997; Holliday, 1997a, 1999). Both the wide voluminous trunk and short limbs have been proposed to reflect structural adaptation to cold environment, as anticipated by Bergmann's and Allen's ecogeographic rules (Ruff, 1994; Holliday, 1997b, 1999). However, the same characteristics (with the exception of upper limb length in humans) also affect walking cost (e.g., Taylor et al., 1982; Pontzer, 2005). The great body mass resulting from a voluminous trunk would impose a heavy load onto Neandertals' lower limbs, which would need to be withstood by bones and overcome by muscles during locomotion. Since most of the energy spent for locomotion is consumed by muscles that oppose gravity (i.e., body weight Griffin et al., 2003), it is reasonable to expect that Neandertals, with their great body mass, would have had high walking cost (at least when expressed as non-adjusted to body mass). In addition, short lower limbs of Neandertals would correspond to short steps. As a result, more steps would be required to cover a given distance and thus Neandertal would expend even more energy for locomotion.

In addition to body mass and lower limb length, however, walking cost is influenced also by other features of the lower limb configuration, among the most important being effective mechanical advantage (EMA) of the limb joints (defined as the ratio of muscle moment arm to moment arm of the ground reaction force) and muscle fascicle length of limb extensors (Biewener, 1989; Roberts et al., 1998; Sockol et al., 2007; Pontzer et al., 2009). Neandertals are reported to have differed considerably from AMH in parameters determining EMA at the knee and ankle (Trinkaus, 1975, 1983; Miller and Gross, 1998; Schmitt, 1998; Trinkaus and Rhoads, 1999). At the knee, Neandertals are expected to have had both parameters determining EMA modified in a direction to maximize knee EMA. The moment arm of the knee extensor, quadriceps femoris, is long due to posteriorly displaced tibial condyles and a thick patella (Trinkaus, 1983, 1986). The moment arm of the ground reaction force at the knee is expected to be short in Neandertals as a consequence of their lower limb proportions (i.e., short tibia relatively to femur) or due to absolutely short lower limbs (Polk, 2004; Gruss, 2007). At the ankle, Neandertals are expected to have had a prolonged muscle moment arm due to a long calcaneus (particularly from the midtalar trochlea to the posterior margin of the calcaneal tuberosity; Trinkaus, 1981, 1983, 1986). A longer calcaneus would have increased the mechanical advantage of ankle plantar flexors through power arm enlargement (Trinkaus, 1983, 1986). It is also to be expected that Neandertals differed from AMH in muscle fascicle lengths, as these seem to reflect the longitudinal characteristics of the limb segments (Griffin et al., 2003) in which Neandertals and AMH clearly differed (Trinkaus, 1981; Holliday, 1999). As a whole, the characteristic lower limb configuration of Neandertals could constitute an effective cost-saving mechanism selected to moderate the impact of their great body mass upon their walking cost. Thus, walking cost estimation accounting for lower limb configuration is desirable for evaluating the possible walking cost differences between Neandertals and AMH.

The goal of this study is to estimate the sex-specific walking cost of Neandertals while accounting for their lower limb configuration in comparison with that of other Late Pleistocene humans. Further,

we aim to evaluate the influence of particular features of the Neandertal lower limb configuration on walking cost. We also evaluate the possible influence of the walking cost difference between Neandertals and AMH upon their daily energy expenditure for walking.

## Materials and methods

### Sample

The compared Late Pleistocene sample consists of 50 individuals (35 males; 15 females; see [Supplementary Online Material \[SOM\] Table S1](#) for specimens and data sources) divided into three groups: Neandertals (MIS [marine isotope stage] 5–3), Middle Paleolithic modern humans (MPMH; MIS 5), and early Upper Paleolithic Europeans (EUP; MIS 3–2 with an upper limit of 18,000 years BP [before present]). The comparative Holocene sample consists of 21 individuals (15 males; six females) from the Opava-Pivovar burial site, Czech Republic (sixteenth to eighteenth century). The MPMH, EUP and Holocene samples we also refer to as anatomically modern humans (AMH). Due to fragmentation of the Pleistocene material, a single average sex-specific representative of each comparative group was computed from the individual data and further processed in our analyses.

### Measurements

We used six measurements defined by Martin (Bräuer, 1988): bi-pelvic breadth (Pel 2), femoral bicondylar length (Fe 2), femoral head superoinferior diameter (Fe 18), tibial maximum length (Ti 1a), talar articular height (Tal 3b), and calcaneal height (Cal 4). An additional four measurements were also used: skeletal trunk height (Franciscus and Holliday, 1992), tibial condylar displacement (anteroposterior distance, perpendicular to the diaphyseal axis, from the anterior surface of the tibial tuberosity to the line between the anteroposterior centers of the tibial condyles; Trinkaus, 1983; Trinkaus and Rhoads, 1999), subtalar length (distance between the posterior edge of calcaneal tuberosity and the anterior edge of first metatarsal head measured parallel to the basal plane of the subtalar skeleton on the articulated pedal skeleton; Trinkaus, 1975), and posterior pedal moment arm (distance between the posterior edge of the calcaneal tuberosity and the middle of the medial talar trochlear arc measured parallel to the basal plane of the subtalar skeleton on the articulated pedal skeleton; Trinkaus, 1975).

### Walking cost estimates

Walking cost can be expressed in various ways, and researchers are far from a consensus about terminology. In the present study, we follow the definitions of Steudel-Numbers et al. (2007) for terms used to discuss the absolute amount of energy spent on walking not adjusted to body mass. In addition, an estimate of cost adjusted to body mass is used here. Thus, we will use three estimates of walking cost: 1) gross cost of transport (grossCOT), which is the cost to travel a given distance and including the costs of keeping a vertical body position and of general metabolism during locomotion; 2) net cost of transport (netCOT), which is the cost to travel a given distance but excluding basal metabolic cost and postural cost, thus representing energy used exclusively for locomotion; and 3) mass-specific net cost of transport (mass-specific netCOT), which is netCOT adjusted by body mass and is ordinarily used for inter-species comparisons.

**GrossCOT estimation** The gross cost of transport (grossCOT;  $\text{ml O}_2 \text{ m}^{-1}$ ) was calculated as:

$$\text{grossCOT} = \frac{\text{BMR} \times \text{PAR}}{v} + \text{netCOT}, \quad (1)$$

where BMR is basal metabolic rate ( $\text{ml O}_2 \text{ s}^{-1}$ ), PAR is the physical activity ratio for standing, and  $v$  is walking speed ( $\text{m s}^{-1}$ ).  $\text{BMR} \times \text{PAR}$  represents the cost per second of general metabolism and maintaining upright body position during locomotion, and thus it is divided by walking speed to give the cost per distance traveled. The NetCOT is the actual cost of moving the body through space, and we will address that below.

Basal metabolic rate was estimated from body mass and mean annual temperature using sex-specific equations for individuals between 18 and 50 years of age from Froehle (2008: Table 3, set B). Basal metabolic rate values were converted from  $\text{kcal day}^{-1}$  to  $\text{ml O}_2 \text{ s}^{-1}$  ( $1 \text{ ml O}_2 = 0.00483 \text{ kcal}$ ; Brown and Brengelmann, 1965). Values of BMR are given in Table 1. Body mass was taken from the literature for specimens from Late Pleistocene samples (SOM Table S1). In the Holocene sample, body mass was estimated using a morphometric method based on stature and bi-pelvic breadth (Ruff et al., 2005) whenever bi-pelvic breadth was measurable ( $n = 15$ ). We estimated stature from maximum femoral length plus maximum tibial length using sex-specific equations of Ruff et al. (2012). Living bi-iliac breadth was estimated from skeletal bi-iliac breadth prior to body mass estimation (Ruff et al., 1997). In nine specimens, the morphometric method could not be used and thus a mechanical method of body mass estimation using femoral head superoinferior diameter (Ruff et al., 2012) was used instead. Body mass values are given in Table 1. Mean annual temperatures for the Late Pleistocene specimens were taken from Froehle and Churchill (2009) ( $n = 45$ ) or estimated using the same approach ( $n = 5$ ). In the Holocene sample, a mean annual temperature of  $7.3^\circ\text{C}$  was used.

The PAR for standing was used as an approximation for cost of maintaining an upright body position during locomotion as recommended by Schmidt-Nielsen (1972). A constant of 1.5 was used as the male PAR, and a constant of 1.4 was used as the female PAR (FAO/WHO/UNU, 1985).

Equivalent walking speed (Froude number = 0.2) was calculated from a specimen's hip height (sum of femoral length, tibial length, talar height and calcaneal height; Alexander and Jayes, 1983). Froude number 0.2 was used previously for walking cost comparisons (Sockol et al., 2007). Furthermore, we empirically determined that Froude number 0.2 is a good proxy for individual preferred walking speed in a sample of 32 human adults (hip height 0.75–1.08 m; mean  $\text{Fr} = 0.198$  with no significant differences between males and females and no significant correlation between Froude number and hip height) walking on a treadmill. Each participant signed a consent form approved by the Institutional Review Board of Charles University, Faculty of Science, prior to examination. Preferred walking speed was established on a treadmill by

**Table 1**

Predicted body mass, basal metabolic rate (BMR), and walking speed of average sex-specific representatives of Neandertal (Nea), Middle Paleolithic modern humans (MPMH), and early Upper Paleolithic Europeans (EUP). The comparative Holocene sample is characterized by sex-specific sample size, mean, and standard deviation (in parentheses).

	Sex	Body mass (kg)	BMR ( $\text{kcal d}^{-1}$ )	Walking speed ( $\text{m s}^{-1}$ )
Nea	M	79.4	1840	1.31
	F	62.3	1386	1.23
MPMH	M	70.0	1652	1.39
	F	60.3	1331	1.32
EUP	M	69.8	1739	1.37
	F	62.3	1410	1.29
Holocene	M ( $n = 15$ )	68.7 (6.0)	1704 (88)	1.33 (0.02)
	F ( $n = 6$ )	59.7 (4.9)	1374 (45)	1.28 (0.02)

increasing the speed in  $0.1 \text{ km h}^{-1}$  increments from a relatively slow speed until the participant reported to walk at his preferred speed. The speed was then increased by  $1.5 \text{ km h}^{-1}$  and then decremented by  $0.1 \text{ km h}^{-1}$  until the preferred speed was re-established. The mean of the two established speeds was then designated as the individual preferred speed. Walking speed values are given in Table 1.

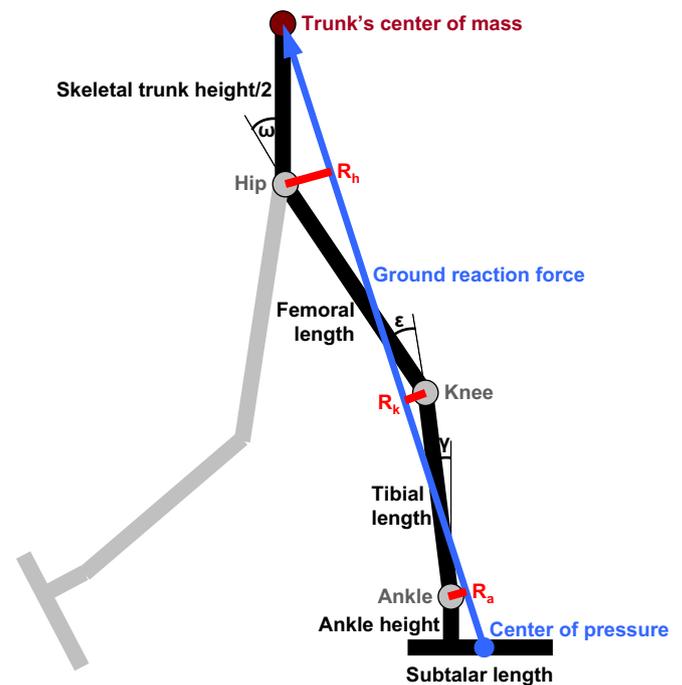
**NetCOT and mass-specific netCOT estimation** The NetCOT ( $\text{ml O}_2 \text{ m}^{-1}$ ) was calculated by multiplying body mass by mass-specific netCOT. Body mass sources and methods of estimation are described above, and values are given in Table 1.

Mass-specific netCOT ( $\text{ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ ) was estimated using the equation of Pontzer et al. (2009: Figure 2): mass-specific netCOT =  $0.0030 \times V_{\text{musc}} + 0.0547$ , where  $V_{\text{musc}}$  is mass-specific volume of muscles activated per distance traveled that is calculated using a rewritten Equation (3) from Pontzer et al. (2009):

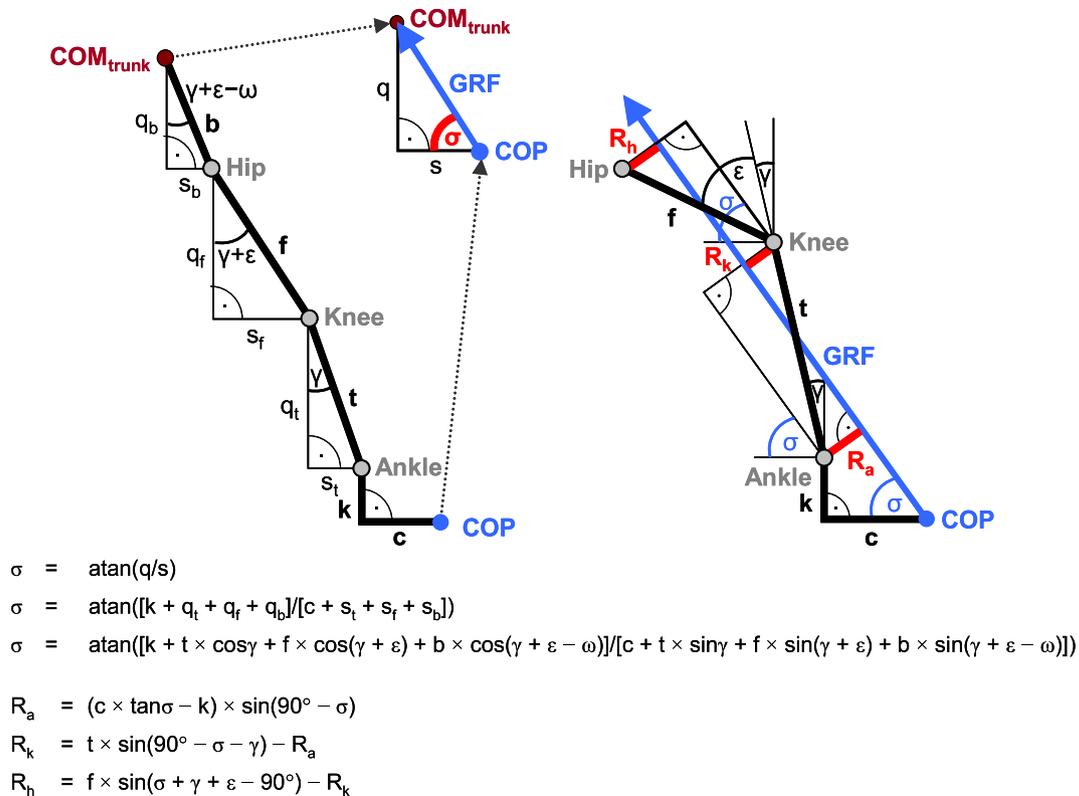
$$V_{\text{musc}} = \left( \frac{R_h \times l_h}{r_h} + \frac{R_k \times l_k}{r_k} + \frac{R_a \times l_a}{r_a} \right) \times \frac{g}{\sigma \times L_{\text{step}}} \quad (2)$$

where  $R_i$  is the moment arm of the ground reaction force,  $l_i$  is muscle fascicle length,  $r_i$  is muscle moment arm ( $[R_i \times l_i]/r_i$  was calculated for each limb joint:  $h$ , hip;  $k$ , knee;  $a$ , ankle),  $g$  is gravitational acceleration,  $\sigma$  is a constant relating tension to muscle cross-sectional area (usually  $20 \text{ N cm}^2$ ; Biewener, 1989), and  $L_{\text{step}}$  is step length. We did not take into account inertial and gravitational moments at each joint and effects of bi-articular muscles, but these should not affect our results significantly (Pontzer et al., 2009).

The moment arm of the ground reaction force ( $R_i$ ) at each joint was estimated using the 2D sagittal model of locomotor posture (Figs. 1–2). The model consists of four articulated segments: trunk, thigh, shank and foot. Lower limb posture at each 1/1000 of stance phase was simulated using the lengths of the subjects' limb segments and joint angles (same for each subject; Fig. 3) derived from



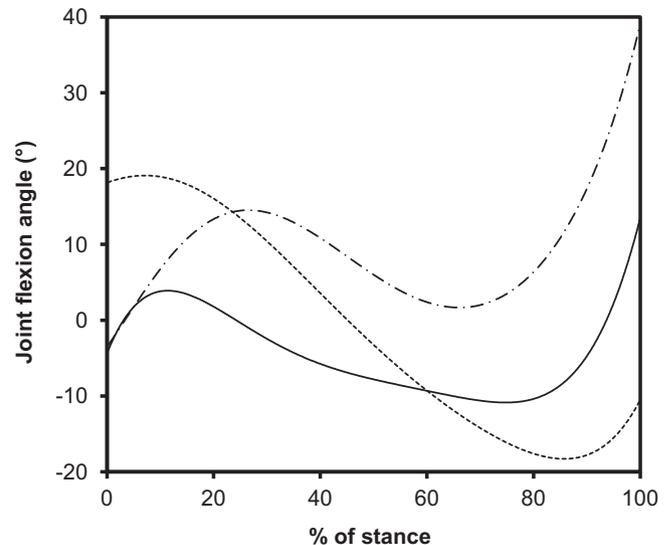
**Figure 1.** Model for computation of moment arms of the ground reaction force at the hip ( $R_h$ ), knee ( $R_k$ ) and ankle ( $R_a$ ) at each fraction of stance phase using skeletal trunk height, femoral length, tibial length, ankle height, subtalar length, posterior pedal moment arm, relative location of center of pressure, and flexion angles at hip ( $\omega$ ), knee ( $\epsilon$ ) and ankle ( $\gamma$ ) joints (for details see Fig. 2).



**Figure 2.** Calculation of the angle ( $\sigma$ ) between the vector of the ground reaction force (GRF) and the sole of the foot and calculation of the moment arms of the GRF at the hip ( $R_h$ ), knee ( $R_k$ ) and ankle ( $R_a$ ) at each 1/1000 of stance phase, where  $b$  is distance between the trunk's center of mass ( $\text{COM}_{\text{trunk}}$ ) and hip joint center (= skeletal trunk height/2; mm),  $f$  is femoral length (= femoral bicondylar length; mm),  $t$  is tibial length (= tibial maximum length; mm),  $k$  is ankle height (= talar articular height + calcaneal height; mm),  $c$  is horizontal distance between ankle joint center and center of pressure (COP; = proportion of subtalar length; mm),  $\gamma$  is ankle joint angle ( $^\circ$ ),  $\epsilon$  is knee joint angle ( $^\circ$ ), and  $\omega$  is hip joint angle ( $^\circ$ ).

previously acquired values of the 26 non-obese young adults (14 males, 12 females; body mass 45.3–97.1 kg; lower limb length 695–977 mm) walking at their preferred speed (mean  $1.31 \text{ m s}^{-1}$ ; range  $0.97\text{--}1.67 \text{ m s}^{-1}$ ) on a treadmill (Hora et al., 2012). Orientation of the ground reaction force (GRF) vector is given by the location of the instant center of pressure (COP) and the trunk's center of mass ( $\text{COM}_{\text{trunk}}$ ), which is actually a simplification of the findings by Maus et al. (2010). This approximation seems suitable for the entire stance phase except for the very beginning (heel strike and immediately thereafter) and the very end (just before toe off), so we omitted 0–10% and 90–100% of stance phase from our analyses. Since GRF is low at the very beginning and very end of the stance phase, we considered this approach appropriate for our model. The location of the instant COP was determined by scaling published values (Hutton and Stokes, 1991) to each subject's subtalar length. Specifically, we digitized the data from Hutton and Stokes's Figure 2.5 and we expressed the COP–heel distances at published percentages of stance as percentages of subtalar length. We developed a 6th order polynomial regression model relating the COP–heel distance evaluated as a percentage of subtalar length to percentage of stance. Finally, we used this regression model to estimate individual COP position at each 1/1000 of stance phase from the individual subtalar length. Based on the results of Gruss (2007), we assumed that COP position at each time point as a percentage of subtalar length is independent of body size. The  $\text{COM}_{\text{trunk}}$  was assumed to lie at half of the skeletal trunk height vertically above the hip joint, which seems to be a reasonable approximation of the  $\text{COM}_{\text{trunk}}$  position defined in Winter (2009) as 50% of the distance between the greater trochanter and glenohumeral joint. The  $R_i$  at each 1/1000 of stance phase was determined as a perpendicular distance between the GRF vector and the center of

rotation for the particular joint. We averaged the  $R$  values obtained for each 1/1000 of stance phase when  $R$  values were  $>25\%$  of the maximum for the step (Biewener et al., 2004), and the resulting value was then used for the  $V_{\text{muscle}}$  estimation. Values of variables required for  $R_i$  estimations are given in Table 2. The values of estimated  $R_i$  for recent humans (Table 3) accord well with those previously reported



**Figure 3.** Joint flexion angles at the hip (dotted line), knee (dot-and-dashed line) and ankle (solid line) during stance phase of walking used in the model of locomotor posture for estimating moment arms of the ground reaction force and step length.

**Table 2**

Dimensions used for estimating moment arms of the ground reaction force and step length of average sex-specific representatives of Neandertal (Nea), Middle Paleolithic modern humans (MPMH), and early Upper Paleolithic Europeans (EUP). The comparative Holocene sample is characterized by sex-specific sample size, mean, and standard deviation (in parentheses).

	Sex	Skeletal trunk height <sup>a</sup> (mm)	Femoral bicondylar length (mm)	Tibial maximum length (mm)	Ankle height (mm)	Subtalar length (mm)	Posterior pedal moment arm (mm)
Nea	M	493.7	445.1	352.9	71.5	182.0	57.2
	F	458.7	398.1	308.5	59.8	154.5	46.0
MPMH	M	489.2	492.7	420.8	73.3	179.0	59.0
	F	449.1	452.3	365.0	65.6	165.0	45.0
EUP	M	504.6	480.7	403.5	69.6	177.4	51.7
	F	468.9	428.2	362.3	61.9	165.0	49.0
Holocene	M (n = 15)	501.1 (19.6)	464.9 (15.5)	375.1 (15.3)	66.4 (4.6)	187.6 (7.1)	58.0 (3.0)
	F (n = 6)	480.4 (20.6)	427.0 (13.8)	345.5 (6.6)	59.1 (3.7)	169.8 (7.5)	51.3 (2.0)

<sup>a</sup> Skeletal trunk height (STH) of Neandertal female estimated using formula:  $STH_{\text{Nea female}} = 0.929 \times STH_{\text{Nea male}}$  (0.929 is the ratio of female STH to male STH of EUP; we assumed that STH sexual dimorphism is the same in Neandertals as in EUP). STH of MPMH male was estimated from femoral length and ratio of recent sub-Saharan femoral length to STH (0.993; [Holliday, 1997a](#)). STH of MPMH female was estimated using formula:  $STH_{\text{MPMH female}} = 0.929 \times STH_{\text{MPMH male}}$ .

by [Griffin et al. \(2003\)](#) and [Pontzer et al. \(2009\)](#). Similarly, the orientation of  $R_i$  during the stance phase, which reflects the orientation of joint centers relative to the GRF vector, fits well the description given by [Perry and Burnfield \(2010\)](#). The average Neandertal has shorter  $R_i$  than does the AMH of the same sex.

Mean muscle fascicle length ( $l_i$ ) of extensors at each joint was determined by scaling published values to each subject's length of the corresponding lower limb bone ([Pontzer et al., 2009](#)). We used the ratios of fascicle length to lower limb length based on cadaver measurements published by [Griffin et al. \(2003\)](#) as a base for evaluating ratios of fascicle length to segment length for each muscle group (femur length for hip and knee extensors and tibia length for ankle extensors). Since only mean overall limb length and no demographic data on cadavers were given in [Griffin et al. \(2003\)](#), we used mean femur and tibia length of Euroamericans ([Trinkaus and Rhoads, 1999](#)) as a proxy for mean segment lengths of cadavers and we assumed that ankle height of Euroamericans is 68 mm. Values of  $l_i$  are given in [Table 3](#). The average Neandertal has shorter  $l_i$  than does the AMH of the same sex.

The mean muscle moment arm ( $r_i$ ) of extensors at each joint was determined as follows:  $r_h$  was calculated as the arithmetic mean of individual  $r_h$  values based on body mass ( $r_h = 1.31 \times \text{body mass}^{0.33}$ ; [Pontzer et al., 2009](#)) and hip height ( $r_h = 0.062 \times \text{hip height}$ ; [Griffin et al., 2003](#));  $r_k$  was approximated by tibial condylar displacement ([Trinkaus, 1983](#)); and  $r_a$  was approximated by the posterior pedal moment arm ([Trinkaus, 1975](#)). We are aware that using a point-estimate for  $r$  is a simplification since  $r$  changes with joint angle (e.g., [Kellis and Baltzopoulos, 1999](#)). However, point estimates for  $r$  greatly simplify the calculation of  $V_{\text{muscle}}$ . Although tibial condylar displacement and the posterior pedal moment arm have not yet been validated as reliable proxies for the active muscle–tendon unit moment arms in recent humans, their usage is inevitable and justified in fossil specimens ([Trinkaus, 1975, 1983; Trinkaus and Rhoads, 1999](#)). Values of  $r_i$  are given in [Table 3](#). Neandertal  $r_k$  is in

particular longer than that of EUP (males) and the Holocene mean (both sexes) and, similarly,  $r_a$  is longer than that of EUP in males.

Step length ( $L_{\text{step}}$ ) was also estimated using the model of locomotor posture ([Fig. 4](#)). The  $L_{\text{step}}$ , defined as horizontal distance covered by  $\text{COM}_{\text{trunk}}$  during the stance phase ([Pontzer et al., 2009](#)), was determined as:

$$L_{\text{step}} = d_{\text{hs}} + d_{\text{to}} + d_{\text{cop}}, \quad (3)$$

where  $d_{\text{hs}}$  is the horizontal distance between  $\text{COM}_{\text{trunk}}$  and COP at heel strike,  $d_{\text{to}}$  is the horizontal distance between  $\text{COM}_{\text{trunk}}$  and COP at toe off, and  $d_{\text{cop}}$  is the distance covered by COP during the stance phase. We assumed the angle between the sole of the foot and the ground to be 14.9° at heel strike and 66.1° at toe off ([Perry and Burnfield, 2010](#)). The  $L_{\text{step}}$  values are given in [Table 3](#). The mean estimated  $L_{\text{step}}$  of Holocene males and females accord well with those values reported previously for recent males and females of similar stature by [Crosbie et al. \(1997\)](#). The average Neandertal has a shorter  $L_{\text{step}}$  than does the AMH of the same sex.

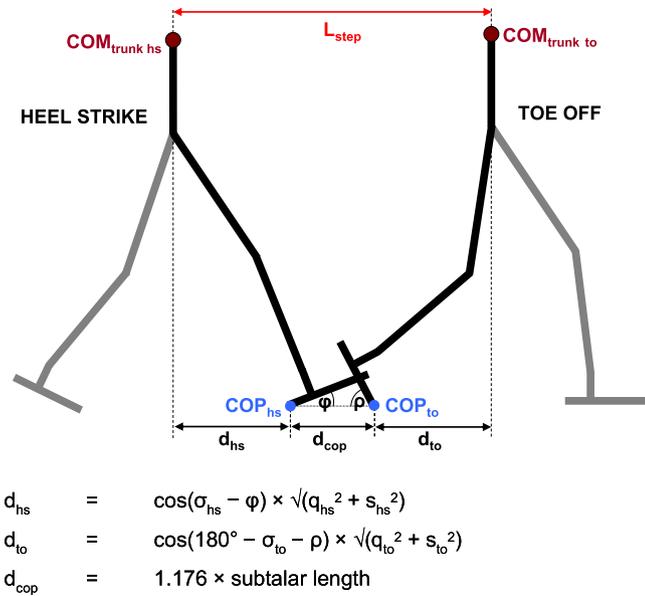
#### *Influence of particular features of lower limb configuration on walking cost*

Aiming to understand the basis for the expected walking cost differences between Neandertals and AMH, we independently manipulated the  $r_i$ ,  $R_i$  and lower limb length from AMH values to Neandertal values and analyzed their effects on mass-specific netCOT. We obtained estimates of mass-specific netCOT for each average AMH representative while one parameter at a time had its AMH value substituted by the Neandertal value. We evaluated the change from originally estimated mass-specific netCOT as a percentage of the original mass-specific netCOT of the particular AMH representative. Since  $R_i$  is a product of lower limb segment lengths and their proportions, we also manipulated the proposed

**Table 3**

Predicted dimensions and locomotor parameters of average sex-specific representatives of Neandertal (Nea), Middle Paleolithic modern humans (MPMH), and early Upper Paleolithic Europeans (EUP). The comparative Holocene sample is characterized by sex-specific sample size, mean, and standard deviation (in parentheses).

	Sex	Muscle fascicle length (l)			Muscle moment arm (r)			Moment arm of the GRF (R)			$L_{\text{step}}$ (m)
		Hip (cm)	Knee (cm)	Ankle (cm)	Hip (cm)	Knee (cm)	Ankle (cm)	Hip (cm)	Knee (cm)	Ankle (cm)	
Nea	M	11.15	7.26	3.68	5.47	4.73	5.72	2.82	1.98	10.24	0.739
	F	9.98	6.49	3.22	4.93	3.60	4.60	2.66	1.59	8.89	0.646
MPMH	M	12.35	8.04	4.39	5.72	4.85	5.90	2.89	2.67	9.99	0.831
	F	11.34	7.38	3.81	5.27	4.20	4.50	2.76	1.87	9.85	0.744
EUP	M	12.05	7.84	4.21	5.61	4.12	5.17	3.02	2.17	10.36	0.806
	F	10.73	6.98	3.78	5.20	3.60	4.90	2.76	1.91	9.55	0.723
Holocene	M (n = 15)	11.65 (0.39)	7.58 (0.25)	3.91 (0.16)	5.45 (0.16)	3.78 (0.39)	5.80 (0.30)	2.91 (0.11)	2.05 (0.13)	10.66 (0.38)	0.769 (0.028)
	F (n = 6)	10.70 (0.35)	6.96 (0.22)	3.60 (0.07)	5.10 (0.13)	3.02 (0.30)	5.13 (0.20)	2.79 (0.12)	1.78 (0.06)	9.75 (0.47)	0.704 (0.019)



**Figure 4.** Diagram of step length ( $L_{step}$ ) computation as sum of distance between trunk's center of mass ( $COM_{trunk}$ ) and center of pressure (COP) at heel strike ( $d_{hs}$ ), distance between center of mass and center of pressure at toe off ( $d_{to}$ ), and distance between center of pressure at heel strike and center of pressure at toe off ( $d_{cop}$ ). For calculation of parameters  $\sigma$ ,  $\varphi$  and  $s$  at heel strike (hs) and toe off (to), see Fig 2.

determinants of  $R_k$  (lower limb length and relative tibial length), and the determinant of  $R_a$  (anterior pedal moment arm = subtalar length minus posterior pedal moment arm; Trinkaus, 1975), then analyzed their effects on  $R_i$ ,  $L_{step}$  and walking cost.

## Results

### GrossCOT

The total energy used by an individual to cover a given distance, the grossCOT, is presented in Table 4 and Fig. 5. GrossCOT of the average Neandertal male ( $11.50 \text{ ml O}_2 \text{ m}^{-1}$ ) is 9–14% higher than the grossCOT for an AMH male, indicating that Neandertal males used more energy to walk a given distance. However, the 9–14% difference between Neandertal and AMH grossCOT is substantially less than the previously reported 30% (which was based on a pooled-sex sample, albeit with a majority of males; Steudel-Numbers and Tilkens, 2004). The average Neandertal female grossCOT ( $9.53 \text{ ml O}_2 \text{ m}^{-1}$ ) is far closer to the values for AMH females than was that in the case of the average Neandertal male: being 1–6% higher than the grossCOT of the AMH females and thereby falling just above the upper margin of the comparative Holocene female range of  $\pm 1$  standard error of the mean.

**Table 4**  
Predicted walking costs of average sex-specific representatives of Neandertal (Nea), Middle Paleolithic modern humans (MPMH), and early Upper Paleolithic Europeans (EUP). The comparative Holocene sample is characterized by sex-specific sample size, mean, and standard deviation (in parentheses). Walking cost is expressed as gross cost of transport (grossCOT), net cost of transport (netCOT), and mass-specific netCOT.

	Sex	GrossCOT ( $\text{ml O}_2 \text{ m}^{-1}$ )	NetCOT ( $\text{ml O}_2 \text{ m}^{-1}$ )	Mass-specific netCOT ( $\text{ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ )	Daily energy expenditure for walking per se ( $\text{kcal day}^{-1}$ )
Nea	M	11.50	6.78	0.0853	479
	F	9.53	5.47	0.0877	402
MPMH	M	10.06	6.07	0.0868	425
	F	9.03	5.39	0.0894	389
EUP	M	10.51	6.25	0.0895	440
	F	9.42	5.50	0.0888	401
Holocene	M ( $n = 15$ )	10.36 (0.69)	6.07 (0.52)	0.0884 (0.0010)	430 (9)
	F ( $n = 6$ )	9.20 (0.52)	5.37 (0.45)	0.0900 (0.0012)	390 (12)

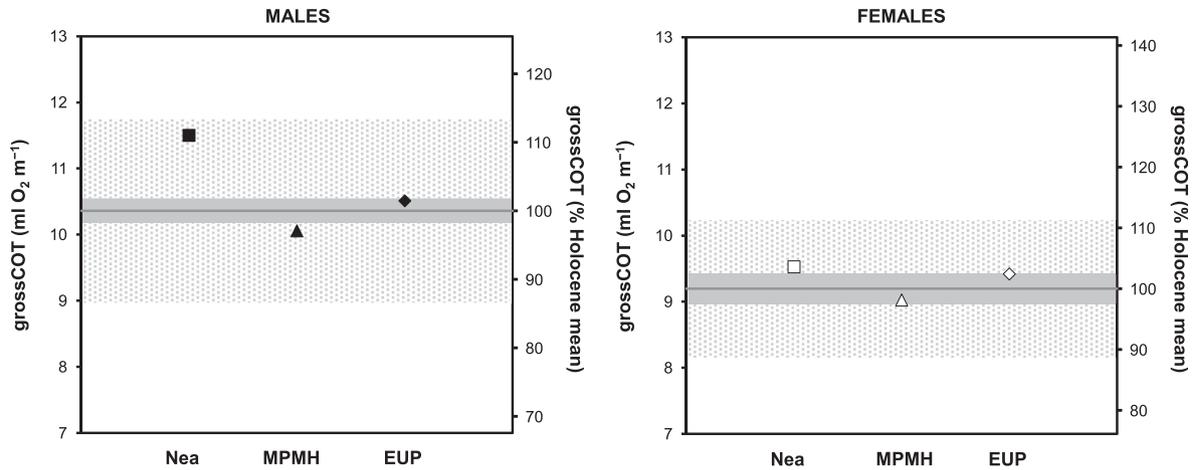
### NetCOT

To better understand the basis for the differences in grossCOT between Neandertals and AMH, we compare their netCOT (i.e., cost of transport excluding cost of maintaining an upright body position and of general metabolism) in which the non-locomotor cost inherently included into grossCOT is subtracted (Table 4 and Fig. 6). The netCOT of the average Neandertal male ( $6.78 \text{ ml O}_2 \text{ m}^{-1}$ ) is 8–12% higher than is the netCOT of AMH males. The netCOT of the average Neandertal female ( $5.47 \text{ ml O}_2 \text{ m}^{-1}$ ) differs less than 2% from that for AMH females and it is actually 1% lower than the netCOT of the average EUP female, thereby falling within the comparative Holocene female range of  $\pm 1$  standard error of the mean.

Thus after subtracting non-locomotor cost, the walking cost difference between Neandertals and AMH decreased slightly in males but virtually vanished in females. Since the excluded non-locomotor cost is a quotient of BMR and walking speed, it follows that BMR and walking speed have only minor influence on walking cost differences between Neandertal and AMH males but constitute the basic causes of walking cost differences in females. In males, parameters other than BMR and walking speed (presumably body mass and/or lower limb configuration) are thus responsible for the substantial size of the walking cost differences between Neandertals and AMH. In females, it is primarily the assumed lower walking speed of Neandertals (4–7% slower than AMH), which in the present model is dependent on lower limb length, that is responsible for increased grossCOT in Neandertals in comparison with AMH. Thus, a Neandertal female would have expended about the same amount of energy to move her body through space (netCOT) as would an AMH female, but it would have taken her more time to cover a given distance (if walking at the same Froude number) and thus she would have spent more energy for keeping her body in an upright position and for BMR during that locomotion than would an AMH female.

### Mass-specific netCOT

To evaluate the individual effect of lower limb configuration and of body mass on walking cost, we compare the Neandertal and AMH values for mass-specific netCOT, i.e., the netCOT divided by body mass (Table 4 and Fig. 7). The mass-specific netCOT of the average Neandertal male ( $0.0853 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ ) is 2–5% lower than the mass-specific netCOT of the AMH males, falling outside of the comparative Holocene male range of  $\pm 2$  standard deviations. The mass-specific netCOT of the average Neandertal female ( $0.0877 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ ) is 1–3% lower than the mass-specific netCOT of the AMH females, falling at the margin of the comparative Holocene female range of  $\pm 2$  standard deviations. Neandertals thus had a more cost-saving lower limb configuration for walking than did AMH, that trend being more pronounced in males. The 9–



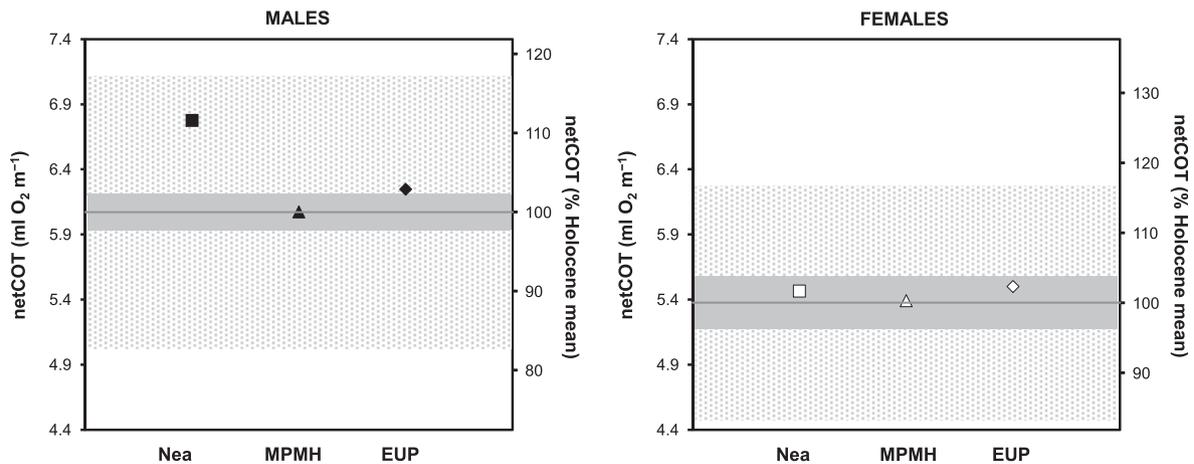
**Figure 5.** Estimated gross cost of transport (grossCOT) of average representatives of Neandertal (Nea), Middle Paleolithic modern humans (MPMH), and early Upper Paleolithic Europeans (EUP) in relation to variation of the Holocene human sample (black line, mean; dark gray area,  $\pm 1$  standard error of the mean; light gray area  $\pm 2$  standard deviation), divided by sex.

14% difference in grossCOT between Neandertal and AMH males was thus primarily a consequence of large body mass in Neandertals (13–16% greater than in AMH males), which was not offset by their cost-moderating lower limb configuration.

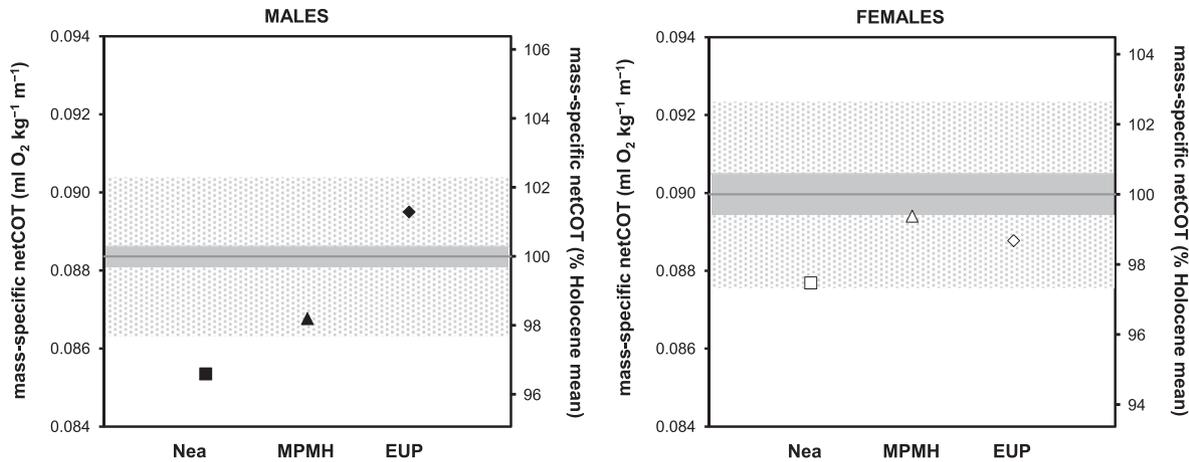
*Influence of particular features of lower limb configuration on walking cost*

Generally, the sum of  $(R_i \times l_i)/r_i$  is so low in Neandertals that it overcomes their short  $L_{step}$  and leads to a prediction of lower mass-specific netCOT. The question remains as to which parameters in particular are responsible for low mass-specific netCOT in Neandertals. Since both muscle fascicle length ( $l$ ) and step length ( $L_{step}$ ) are proportional to lower limb length, we investigate their effect on mass-specific netCOT together. The effects of muscle moment arm ( $r_i$ ), moment arm of the GRF ( $R_i$ ) and lower limb length on mass-specific netCOT are given in Table 5. We estimated mass-specific netCOT of the sex-specific AMH representatives (MPMH, EUP, Holocene) while varying  $r_i$ ,  $R_i$  and lower limb length independently between the AMH and Neandertal values. In MPMH males, most of the parameters had little effect on mass-specific netCOT, although a

change of  $R_k$  alone to the Neandertal value decreased the mass-specific netCOT of the average MPMH male over that of the average Neandertal male. In the EUP male, no change of any single parameter decreased the mass-specific netCOT to anywhere near that of the average Neandertal male, although a change of  $r_a$  resulted in the greatest decrease of mass-specific netCOT for the average EUP male. In the Holocene male, a change of  $r_k$  to the Neandertal value resulted in the greatest decrease of mass-specific netCOT of the mean Holocene male, although it did not reach the level of the average Neandertal male. In the MPMH female, a change of  $R_a$  alone to the Neandertal value decreased the mass-specific netCOT of the average MPMH female just to that of the average Neandertal female. In the EUP female, a change of either  $R_k$  or  $R_a$  alone to the Neandertal value decreased the mass-specific netCOT of the average MPMH female to that of the average Neandertal female. In the Holocene female, a change of any single parameter to its Neandertal value did not decrease the mass-specific netCOT to that of the average Neandertal female. A change of  $r_k$  followed by  $R_a$  to the Neandertal value did, however, result in the greatest decreases of mass-specific netCOT for the mean Holocene female.



**Figure 6.** Estimated net cost of transport (netCOT) of average representatives of Neandertal (Nea), Middle Paleolithic modern humans (MPMH), and early Upper Paleolithic Europeans (EUP) in relation to variation of the Holocene human sample (black line, mean; dark gray area,  $\pm 1$  standard error of the mean; light gray area  $\pm 2$  standard deviation), divided by sex.



**Figure 7.** Estimated mass-specific net cost of transport (mass-specific netCOT) of average representatives of Neandertal (Nea), Middle Paleolithic modern humans (MPMH), and early Upper Paleolithic Europeans (EUP) in relation to variation of the Holocene human sample (black line, mean; dark gray area,  $\pm 1$  standard error of the mean; light gray area  $\pm 2$  standard deviation), divided by sex.

Given our results, Neandertals' low mass-specific netCOT is a consequence of their increased  $r$  and/or decreased  $R$  at the knee and ankle in comparison with AMH. While  $r_i$  can be approximated by a single osteological measurement,  $R_i$  is a product of lengths of lower limb segments and their proportions (the effect of posture is not considered since it is the same for each representative/individual in the present study). However, several parameters have been proposed as having the greatest impact on  $R_k$  (lower limb length and relative tibial length) and on  $R_a$  (subtalar length and particularly the anterior pedal moment arm). We indirectly analyzed the influence of these parameters on  $R_i$ , along with their influence on walking cost, by independent manipulation of lower limb length, relative tibial length and anterior pedal moment arm. Boundary average Neandertal and EUP male values were chosen for lower limb length and relative tibial length manipulation, because these differ substantially and yet are well within the range of human variation. Similarly, boundary average Neandertal and MPMH female values were chosen for anterior pedal moment arm manipulation because they differ substantially.

The influence of lower limb length and relative tibial length on walking cost,  $R_i$  and  $L_{\text{step}}$  is presented in Fig. 8. The 10.3% increase in lower limb length (i.e., the difference between the lengths of the average Neandertal and EUP male) generated a 2.3% increase of mass-specific netCOT and of netCOT and 0.6% decrease of grossCOT. The increase in mass-specific netCOT and of netCOT was caused

**Table 5**

Percentage changes in mass-specific net cost of transport (mass-specific netCOT) for average sex-specific representative of Middle Paleolithic modern humans (MPMH), early Upper Paleolithic Europeans (EUP) and Holocene sample with changes in lower limb length, muscle moment arms ( $r_i$ ) and moment arms of the ground reaction force ( $R_i$ ) at particular joints ( $h$ , hip;  $k$ , knee;  $a$ , ankle) from value of particular anatomical modern human representative to value of Neandertal representative of the same sex.

Parameter	% Change in mass-specific netCOT					
	Males			Females		
	MPMH	EUP	Holocene	MPMH	EUP	Holocene
$r_h$	0.6	0.4	0.0	0.9	0.7	0.5
$r_k$	0.2	-1.1	-1.8	1.2	0.0	-1.5
$r_a$	0.5	-1.6	0.2	-0.4	1.1	1.8
$R_h$	-0.3	-0.9	-0.4	-0.4	-0.4	-0.6
$R_k$	-2.3	-0.7	-0.3	-1.1	-1.4	-1.0
$R_a$	0.4	-0.2	-0.6	-1.8	-1.2	-1.4
Lower limb length <sup>a</sup>	-0.5	-0.6	-0.4	-0.2	0.1	0.0

<sup>a</sup> Proportional change of femoral and tibial length, its effect being restricted to  $l_i$  and  $L_{\text{step}}$ .

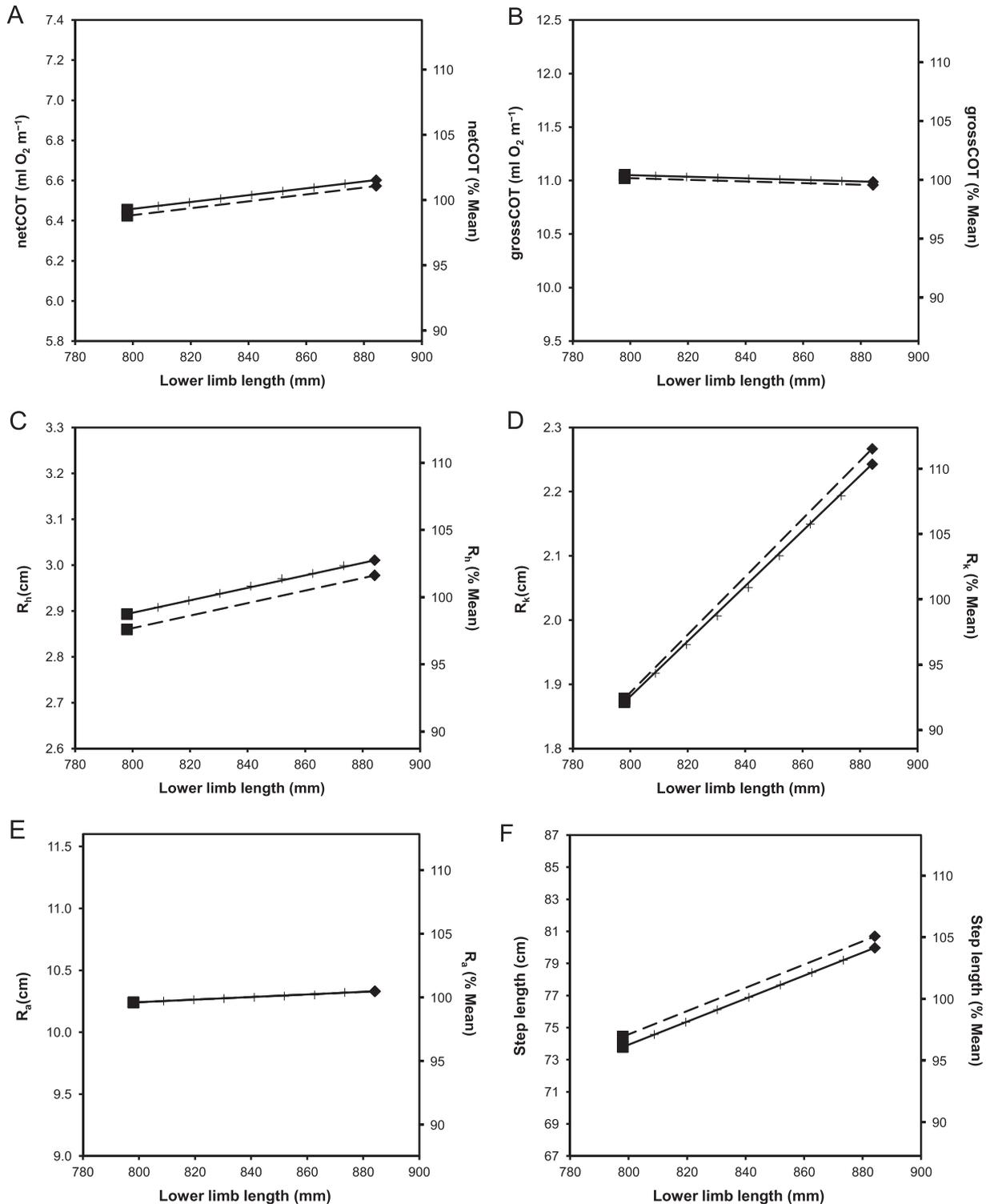
mainly by an 18.7% increase in  $R_k$ , (for comparison,  $R_h$  increased by 4.0%,  $R_a$  increased by 0.9%) and by a 10.3% increase of muscle fascicle length at each of the three joints. The increment of these cost-increasing parameters could not be wholly offset by the 8.1% increase in step length. The 0.6% decrease of grossCOT was caused by a 4.7% increase of walking speed, which in our model is dependent on lower limb length. Longer lower limbs thus lead to higher walking cost primarily through elongation of  $R_k$ , but if walking speed is related to lower limb length (as in our model) then the elongation of  $R_k$  can be offset by the walking speed increment and walking cost remains almost the same as in a short-limbed, slower-walking individual.

The increase of relative tibial length from 79.3 of the average Neandertal male to 83.9 of the average EUP male while holding lower limb length constant generated 0.5% of the decrease in mass-specific netCOT and of netCOT and 0.3% of the decrease in grossCOT. The decrease in mass-specific netCOT and netCOT was caused mainly by a 2.6% decrease of  $l_h$  and  $l_k$  and by a 1.1% decrease of  $R_h$  (for comparison,  $R_k$  increased by 0.7%,  $R_a$  decreased by 0.01%). The decrease in these cost-increasing parameters was, however, almost offset by a 3.1% increase of  $l_a$  and a 0.9% increase in step length. The relative tibial length has negligible effect on walking cost and on  $R_k$ . Short  $R_k$  in Neandertals is thus a consequence of their short lower limbs and not of their relatively short tibia.

The influence of anterior pedal moment arm on walking cost,  $R_i$  and  $L_{\text{step}}$  is as follows. The 6.6% increase in anterior pedal moment arm (i.e., the difference between the moment arms of the average Neandertal and of the MPMH female) generated a 0.2% increase of mass-specific netCOT and netCOT and a 0.1% increase of grossCOT. The increases in mass-specific netCOT, netCOT and grossCOT were caused by an 8.5% increase in  $R_a$ , (for comparison,  $R_h$  increased by 0.4%, step length increased by 1.1%). The increment of these cost-increasing parameters was, however, almost offset by a 12.7% decrease in  $R_k$ . Prolongation of the anterior pedal moment arm thus increases  $R_a$  but at the same time decreases  $R_k$ , and thus its overall effect on walking cost per se is minimal.

## Discussion

Our results suggest that Neandertal walking cost was not so different from that of AMH as previously estimated. Not only did Neandertals have at maximum only a 14% higher estimated grossCOT than did AMH (which is much lower than the previously



**Figure 8.** Influence of relative tibial length (ratio of tibial length to femoral length) and lower limb length (sum of tibial length and femoral length) on net cost of transport (A), gross cost of transport (B), moment arms of the ground reaction force at the hip (C), knee (D) and ankle (E) and step length (F). Relative tibial length of the average Neandertal male (0.793) is represented by the solid line, that of the average EUP male (0.839) by the dashed line. Lower limb length of the average Neandertal male (798.0 mm) is represented by the square, that of the average EUP male (884.2 mm) by the diamond.

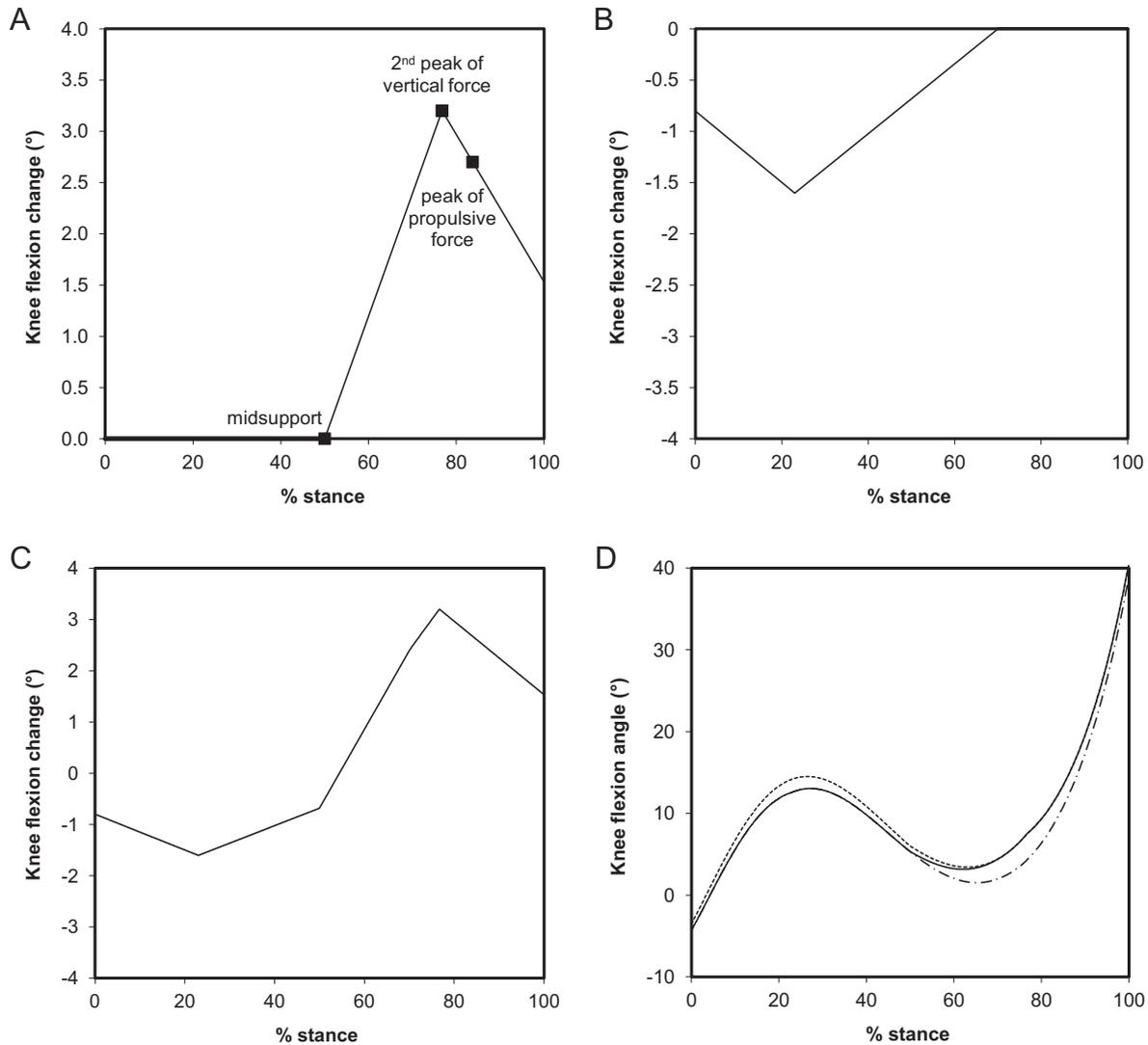
estimated 30% difference), but in estimated mass-specific netCOT Neandertals even outperformed AMH. We also detected that the estimated differences between Neandertal and AMH walking cost were far more pronounced in males than in females (e.g., netCOT was almost the same in Neandertal and AMH females), which is attributable to sex-specific differences in body mass between

Neandertal and AMH (or from another viewpoint, to greater sexual dimorphism in body mass of Neandertals versus AMH). The estimated low mass-specific netCOT of Neandertals is generally a consequence of their increased muscle moment arm ( $r_i$ ) and decreased moment arm of the ground reaction force ( $R_i$ ) at the knee and ankle in comparison with AMH.

### Limitations of the model and sensitivity analyses

The results presented here are based on assumptions that Neandertals and AMH had the same locomotor posture and the same  $COM_{trunk}$  position (as a percentage skeletal trunk height distance from hip) and that muscle fascicle lengths correlate with the length of the given limb segment. In addition, our grossCOT estimate is affected also by BMR, a parameter considerably variable on both the intra- and inter-population level in recent humans. Locomotor posture substantially affects the walking cost through its effect on  $R_i$  (Pontzer et al., 2009), but, unfortunately, it is not recordable in nonliving specimens. We argue, however, that it is reasonable to assume the same locomotor posture in Neandertals and AMH. Although the crural index was reported to influence posture in six closely related cercopithecine monkeys (Polk, 2002) and subsequently Neandertals were proposed to use a more flexed posture due to their lower crural index (Polk, 2004), such effect was not detected empirically in recent humans (Gruss, 2005, 2007). Even

such differences in body size and proportions as between recent males and females do not imply differences in locomotor postures (Kerrigan et al., 1998; Cho et al., 2004; Hurd et al., 2004). However, there is some evidence that body mass and lower limb length might influence locomotor posture, and particularly the degree of knee flexion during specific parts of the stance phase of walking (DeVita and Hortobágyi, 2003; Gruss, 2007). To investigate the sensitivity of our analysis to this potential change in posture, we manipulated the posture of Neandertal males to reflect the Neandertal–MPMH differences in lower limb length and/or body mass as expected by DeVita and Hortobágyi (2003) and Gruss (2007) (see Fig. 9 for procedure details) and we report the resulting walking cost,  $R_i$  and  $L_{step}$  estimations in Table 6. As expected, increased knee flexion leads to higher walking cost while decreased knee flexion leads to lower walking cost. The simulated postural changes result in less than a 1% change of grossCOT, netCOT and mass-specific netCOT. We thus consider the assumption of the same locomotor posture among the fossil representatives satisfactory for our purposes.



**Figure 9.** Knee flexion change of three different locomotor posture simulations during stance (A–C) evaluated as deviations from originally assumed posture of the average Neandertal male: (A) increased knee flexion at late stance due to 115.5 mm shorter lower limbs of Neandertal in comparison with MPMH male based on results of Gruss (2007), (B) decreased knee flexion at early stance due to 9.6 kg greater body mass of Neandertal in comparison to MPMH male based on results of DeVita and Hortobágyi (2003), (C) presumed combined effect of shorter lower limb and greater body mass of Neandertal. (D) Knee flexion angle of the three posture simulations during stance phase of walking (dotted line, increased knee flexion at late stance following Gruss (2007); dot-and-dashed line, decreased knee flexion at early stance following DeVita and Hortobágyi (2003); solid line, combination of increased knee flexion at late stance and decreased knee flexion at early stance).

**Table 6**

Estimations of moment arms of ground reaction force ( $R_i$ ) at the hip ( $h$ ), knee ( $k$ ) and ankle ( $a$ ); step length ( $L_{\text{step}}$ ); gross cost of transport (grossCOT); net cost of transport (netCOT); and mass-specific netCOT of the average Neandertal male using four different locomotor posture simulations.

Posture simulation	$R_h$ (cm)	$R_k$ (cm)	$R_a$ (cm)	$L_{\text{step}}$ (m)	GrossCOT (ml O <sub>2</sub> m <sup>-1</sup> )	NetCOT (ml O <sub>2</sub> m <sup>-1</sup> )	Mass-specific netCOT (ml O <sub>2</sub> kg <sup>-1</sup> m <sup>-1</sup> )
Original posture	2.82	1.98	10.24	0.74	11.50	6.78	0.0853
Increased knee flexion at late stance	2.82	2.06	10.11	0.72	11.57	6.84	0.0862
Decreased knee flexion at early stance	2.98	1.47	10.24	0.73	11.46	6.73	0.0848
Combination of increased knee flexion at late stance and decreased knee flexion at early stance	2.98	1.63	10.12	0.71	11.54	6.82	0.0859

Further, we manipulated the COM<sub>trunk</sub> position of the average Neandertal male and we report the resulting walking cost and  $R_i$  in Table 7. Positioning COM<sub>trunk</sub> further from the hip increases walking cost linearly by 0.4% (grossCOT) and 0.7% (netCOT and mass-specific netCOT) per 5% of trunk length.

The muscle fascicle lengths ( $l_i$ ) are unfortunately also impossible to reconstruct from fossil or skeletal evidence where muscle tissue is not available. Muscle fascicle lengths were nevertheless previously approximated by particular limb segment lengths (Pontzer et al., 2009), and this approach is well founded on human cadaver studies (Griffin et al., 2003; Biewener et al., 2004). Nevertheless, we additionally modified  $l_i$  of the average Neandertal male and we report the resulting walking cost estimations in Table 8. When all other parameters are held constant, walking cost is directly proportional to  $l_i$ . In the average Neandertal male, simultaneous 10% change of  $l_h$ ,  $l_k$  and  $l_a$  results in a 2.1% change in grossCOT and a 3.6% change in netCOT and mass-specific netCOT.

In our model, grossCOT is affected by BMR, which is estimated from body mass and annual temperature (Froehle, 2008; Froehle and Churchill, 2009). Use of this method to estimate BMR in fossil humans brings possible sources of error such as from estimates of body mass, geological age and mean annual temperature, which cannot be fully evaluated. To evaluate at least the sensitivity of our grossCOT estimate to BMR, we manipulated the BMR of the average Neandertal male and we report the resulting grossCOT in Fig. 10. The GrossCOT is directly proportional to BMR. In the average Neandertal male, a 10% change of BMR results in a 4.1% change in grossCOT.

The sagittal plane force–cost approach used in the present study to estimate walking cost of Neandertals and AMH omits those costs related to swinging the limb and the costs related to controlling the hip frontal movement and stability during walking. The cost to swing the limb was estimated to comprise ca. 10–30% of the total cost of walking (Doke et al., 2005; Gottschall and Kram, 2005; Pontzer, 2007a), the cost to produce force in hip abductors is ca. 8% of the total cost of walking (Warrener, 2011), and both of these contributions to total cost were successfully disregarded in previous estimations (Sockol et al., 2007; Pontzer et al., 2009). Nevertheless, since the cost to swing the limb is proportional to limb moment of inertia, which is itself strongly affected by lower limb length (Witte et al., 1991), Neandertals, with their shorter lower limb, would presumably have lower cost to swing the limb than

would AMH and that may further diminish the Neandertal–AMH walking cost differences.

#### Lower limb length and walking cost

Our estimated difference between Neandertal and AMH grossCOT is less than half of that estimated by Steudel-Numbers and Tilkens (2004). The discrepancy between the estimated differences is mainly due to using a different approach (mechanical versus inductive). Half of the Neandertal–AMH difference estimated in the previous study was ascribed to the difference in lower limb length, since a longer lower limb has been determined empirically to be energetically advantageous for human walking (Steudel-Numbers and Tilkens, 2004). Although long lower limbs can be energetically advantageous in a homogenous human sample (as detected by Steudel-Numbers and Tilkens, 2004), this relationship may not be extendable to hominins differing widely in their lower limb configurations (as suggested also by Crompton et al., 1998; Kramer and Eck, 2000). The present model shows that a long lower limb is not energetically advantageous per se unless it is accompanied by an increase of  $r_k$  (which is expectable in homogenous samples; Fig. 11) and/or it is accompanied by a decrease of  $R_k$  (through shift to more erect locomotor postures of the knee). Longer limbs will tend to increase step length (decreasing cost) but will also be associated with greater  $R$  and fascicle length ( $l$ ), which will increase cost. In particular, the relationship between lower limb length and  $r_k$  is shifted in Neandertals as compared with AMH (Neandertals had greater  $r_k$  for their lower limb length than did AMH; Fig. 11). As a consequence, the relationship between lower limb length and walking cost, too, must be modified, and that makes the predictive equation of Steudel-Numbers and Tilkens (2004) inappropriate for Neandertal walking cost estimation.

We emphasize that our results are not necessarily in contradiction with inter-specific studies across mammals and intra-specific studies of recent humans, which have reported that longer limbs are associated with lower locomotor cost (Steudel-Numbers and Tilkens, 2004; Pontzer, 2007b). Although our simulation suggests that longer lower limbs induce cost-increasing prolongation of  $R$  (in humans especially at the knee as also detected empirically by Gruss (2007)), such  $R$  prolongation can be counteracted by proportional increase of  $r$  or even avoided by a

**Table 7**

Estimations of moment arms of ground reaction force ( $R_i$ ) at the hip ( $h$ ), knee ( $k$ ) and ankle ( $a$ ); step length ( $L_{\text{step}}$ ); gross cost of transport (grossCOT); net cost of transport (netCOT); and mass-specific netCOT of the average Neandertal male using five different COM<sub>trunk</sub> vertical distances from hip joint center, expressed in percentages of skeletal trunk height (STH).

Hip–COM <sub>trunk</sub> distance	$R_h$ (cm)	$R_k$ (cm)	$R_a$ (cm)	$L_{\text{step}}$ (m)	GrossCOT (ml O <sub>2</sub> m <sup>-1</sup> )	NetCOT (ml O <sub>2</sub> m <sup>-1</sup> )	Mass-specific netCOT (ml O <sub>2</sub> kg <sup>-1</sup> m <sup>-1</sup> )
40% STH	2.36	2.21	10.26	0.74	11.40	6.68	0.0841
45% STH	2.60	2.09	10.26	0.74	11.45	6.73	0.0847
50% STH (original)	2.82	1.98	10.24	0.74	11.50	6.78	0.0853
55% STH	3.04	1.88	10.22	0.74	11.55	6.82	0.0859
60% STH	3.25	1.79	10.21	0.74	11.60	6.87	0.0866

**Table 8**  
Estimations of the gross cost of transport (grossCOT), net cost of transport (netCOT) and mass-specific netCOT of the average Neandertal male after increasing its muscle fascicle length ( $l_i$ ) at the hip ( $h$ ), knee ( $k$ ) and ankle ( $a$ ) by 5%, 10%, 15% and 20%.

Muscle fascicle length increase	$l_h$ (cm)	$l_k$ (cm)	$l_a$ (cm)	GrossCOT (ml O <sub>2</sub> m <sup>-1</sup> )	NetCOT (ml O <sub>2</sub> m <sup>-1</sup> )	Mass-specific netCOT (ml O <sub>2</sub> kg <sup>-1</sup> m <sup>-1</sup> )
0%	11.15	7.26	3.68	11.50	6.78	0.0853
5%	11.71	7.62	3.86	11.62	6.90	0.0869
10%	12.27	7.99	4.05	11.74	7.02	0.0884
15%	12.83	8.35	4.23	11.87	7.14	0.0899
20%	13.39	8.71	4.42	11.99	7.26	0.0915

shift to more erect postures. Since the  $r$  is positively correlated with lower limb length (Fig. 11) and longer limbed animals (or individuals of the same species) use more erect postures (Biewener, 1989, 2005; Polk, 2002; Gruss, 2007), longer limbed animals or individuals are generally expected to have lower walking cost and this expectation is consistent with findings of Steudel-Numbers and Tilkens (2004) and Pontzer (2007b).

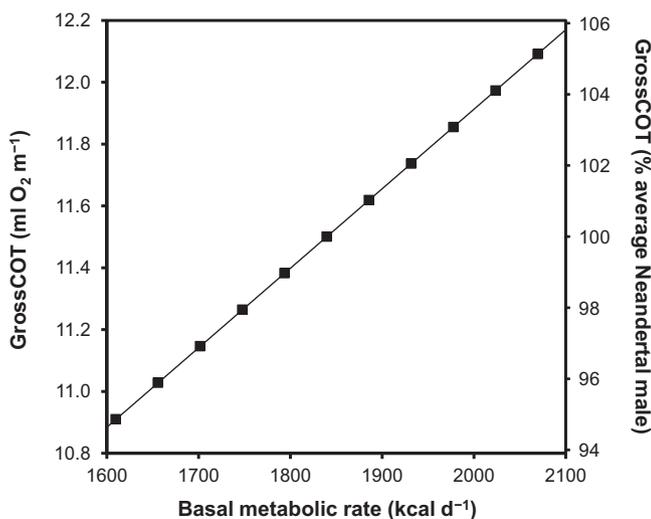
#### Lower limb configuration and walking cost

Our results suggest that Neandertals had lower mass-specific netCOT compared with AMH, and this is generally a result of their increased  $r_i$  and/or decreased  $R_i$  at the knee and/or ankle. The increased  $r_i$  at the knee and ankle of Neandertals had been reported previously, and energy benefits for walking also were proposed (e.g., Trinkaus, 1975, 1983, 1986). The approach of the present study allowed us to estimate how the increased  $r_k$  and  $r_a$  affect mass-specific netCOT. The Neandertals had increased  $r_k$  especially when compared with the Holocene sample means (both sexes) and increased  $r_a$  when compared with the EUP male. Change of the  $r_k$  in Holocene samples and  $r_a$  in EUP males from the particular AMH value to Neandertal value decreased the mass-specific netCOT by 2% in either AMH group. The demonstrated energetic advantage in walking of Neandertal's increased  $r_a$  could compensate for a previously proposed Neandertal energetic disadvantage in running due to the very same  $r_a$  increase (Raichlen et al., 2011). This might lend further support to the notion that Neandertal morphology was better suited for walking than for running, as suggested by Spoor et al. (2003). The lower  $R_i$  at the knee and ankle of Neandertals compared with AMH predicted in the present study is in accordance with previous estimations (Trinkaus, 1975, 1983; Trinkaus and Rhoads, 1999). In agreement with results from Gruss (2007),

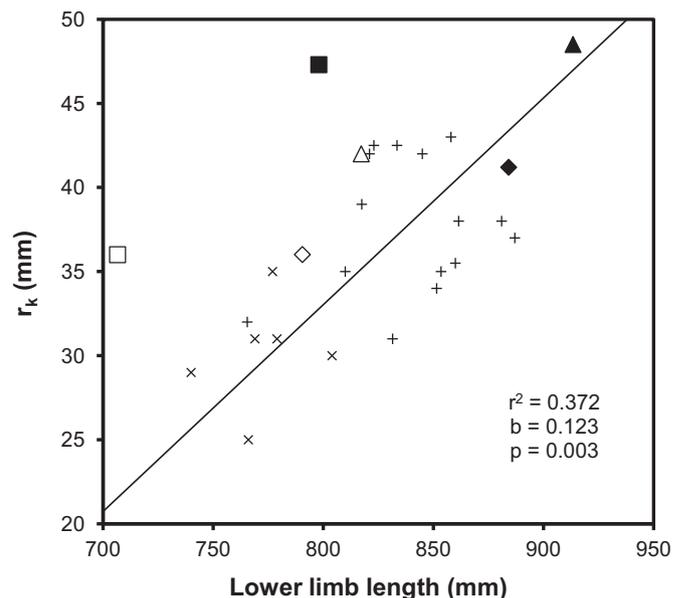
who empirically detected that  $R_k$  is positively correlated with lower limb length in recent humans when posture is constant, the low  $R_k$  of Neandertals is not a consequence of their relatively short tibia but rather of their absolutely short lower limbs. The difference in  $R_k$  accounts for most of the difference in mass-specific netCOT between Neandertal and MPMH males and between Neandertal and EUP females. Our simulation also indicates that  $R_a$  is greatly affected by the anterior pedal moment arm, as proposed by Trinkaus (1975), and, as such, it is responsible for a great part of the difference in mass-specific netCOT between AMH and Neandertal females, who differed in the length of the anterior pedal moment arm (Neandertal females had shorter anterior pedal moment arms than did AMH females). The overall lower mass-specific netCOT of Neandertals, and particularly of Neandertal males, accords well with the general interspecies tendency toward a decrease of mass-specific netCOT with body mass (Schmidt-Nielsen, 1972; Taylor et al., 1982; Rubenson et al., 2007).

#### Body mass estimation and walking cost

Although our results indicate that the Neandertals spent less energy for walking per kilogram of body mass, males were still less economical (i.e., Neandertals spent more energy to cover a given distance) than AMH due to their higher body mass. The striking sexual dimorphism in estimated grossCOT and netCOT of



**Figure 10.** Effect of change in basal metabolic rate on gross cost of transport (grossCOT) in the average Neandertal male.



**Figure 11.** Reduced major axis regression of the muscle moment arm at the knee ( $r_k$ ) on lower limb length (i.e., sum of femoral length and tibial length) in Holocene human sample (males, plus signs; females crosses). The average Neandertal male (filled square) and female (open square), Middle Paleolithic modern human male (filled triangle) and female (open triangle) and early Upper Paleolithic European male (filled diamond) and female (open diamond) graphed for comparison.

Neandertals does not correspond well with other evidence, which suggests that Neandertals had sexual dimorphism similar to that of AMH (Trinkaus, 1980; Ruff, 2002). Since both netCOT and grossCOT are strongly affected by body mass (most of the locomotor energy is spent to resist gravity, i.e., body weight), the increased Neandertal sexual dimorphism might be a reflection of body mass estimation or of sample composition in Neandertals. Generally, body mass is a delicate parameter to estimate. Even well-established equations for body mass estimations give different results. Furthermore, in Neandertals (and in fossils generally) the measurements used for body mass estimation are often not available directly and are themselves estimated from other dimensions. With such a series of multiple estimations, the differences between body mass estimations using different approaches are not surprising (e.g., compare Ruff et al., 1997 and Trinkaus and Rhoads, 1999). In the present study, we used body mass estimation of ten Neandertal specimens from Trinkaus and Rhoads (1999) and five additional specimens from Ruff et al. (1997). In addition, we included into our sample the recently published Neandertal female Palomas 96 (Walker et al., 2011). Although, Ruff et al. (1997) estimated body mass for more sexually identifiable specimens than are used here, we did not use those because they did not offer additional measurements other than body mass usable for walking cost estimation. The mean sex-specific body mass of Neandertals in this study differs by less than 0.6 kg from that of Trinkaus and Rhoads (1999), and also the sexual dimorphism in body mass is similar (27.4% versus 27.8%). Greater difference is found, however, when the present mean sex-specific body mass is compared with that of Ruff et al. (1997). Mean Neandertal male body mass in the present study is 2.8 kg greater than that in Ruff et al. (1997), whereas the present mean Neandertal female body mass is 3.5 kg lower than that in Ruff et al. (1997). The 27.4% sexual dimorphism in Neandertal body mass in the present study is thus considerably greater than the 16.5% in Ruff et al. (1997). Using the sex-specific mean body masses from Ruff et al. (1997) for Neandertal walking cost estimation would have decreased the grossCOT and netCOT of males to 11.23 ml O<sub>2</sub> m<sup>-1</sup> and 6.54 ml O<sub>2</sub> m<sup>-1</sup>, respectively, and increased the grossCOT and netCOT of females to 9.90 ml O<sub>2</sub> m<sup>-1</sup> and 5.76 ml O<sub>2</sub> m<sup>-1</sup>. In comparison with AMH, Neandertal males would have a 7–12% higher grossCOT and 5–8% higher netCOT while Neandertal females would have a 5–10% higher grossCOT and 5–7% higher netCOT. Thus the percentage difference between Neandertal and AMH males would be almost equal to that between Neandertal and AMH females. Since we have no information about lower limb configuration of the additional specimens, however, it is not possible to estimate how it would have affected their walking cost. We cannot rule out the possibility that lower limb configuration of the additional specimens would reflect their body mass and regulate the impact of their body mass on walking cost.

#### *Neandertal–AMH walking cost difference and daily energy intake*

To explore the biological importance of the estimated walking cost difference between Neandertal and AMH males, we need to know how it would have been manifested in their daily energy intake. Using an earlier assumption (Weaver and Steudel-Numbers, 2005) that a Pleistocene human walked 12.2 km per day based on recent hunter-gatherer data of Binford (2001), we calculated the energy spent on walking per day by the average Neandertal and AMH male (Table 4). If we compare only the energy spent on walking per se (netCOT) plus energy to maintain upright posture (thus excluding only the cost of general metabolism, which would be spent in any case whether walking, lying or otherwise) the Neandertal male would have needed 39–54 kcal more energy to walk the assumed 12.2 km daily distance than would have an AMH

male. To acquire the calories in such an amount, one would only have needed to eat one pheasant egg or about 30 g of cooked venison or bison meat (or, to use a modern-day comparison, to drink 100 ml of Coca-Cola). The 39–54 kcal would account for only 0.8–1.7% of the daily energy expenditure of the Neandertal (3339–4701 kcal) or AMH (3131–4414 kcal) male recently estimated by Froehle and Churchill (2009).

## Conclusions

Our results suggest that Neandertal males had 9–14% higher grossCOT and 8–12% higher netCOT than did AMH, which is less than would be expected considering the difference in body mass. The estimated walking cost difference between Neandertal and anatomically modern females was far less pronounced than in males, being 1–6% when comparing grossCOT. The difference in females vanishes entirely when netCOT is compared. Posteriorly displaced tibial condyles, a long posterior pedal moment arm, and short moment arms of the GRF at the knee and ankle (due to a short lower limb and short anterior pedal moment arm, respectively) decrease the Neandertal mass-specific netCOT by 2–5% (males) and 1–3% (females) below the AMH level for the same sex. The estimated walking cost difference between Neandertal and AMH males would account for about 1% of the estimated daily energy expenditure in either a Neandertal or AMH male.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2013.09.011>.

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