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Walking separately, together, or in mixed groups: Energetic modeling of hominin group locomotion using the Engare Sero archaeological footprint assemblage

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ABSTRACT

Locomotor coordination is a fundamental pillar of human sociality, yet reconstructing group dynamics in deep time remains a significant challenge. The Late Pleistocene footprint site of Engare Sero (Tanzania) provides a unique record of anatomically modern humans moving collectively across a volcanic landscape. While previous studies have inferred group composition and speed from footprint morphology, the energetic implications of these movement patterns have remained unexplored. This study models the Cost of Transport (*CoT*) and energetic penalties for three representative profiles: adult male, adult female, and non-adult, using experimentally validated quadratic equations. Multiple walking scenarios derived from the Engare Sero assemblage were evaluated, including age-sex-specific means, directional mean speeds (northeast [NE] and southwest [SW]), and the total group average, which were compared with the calculated Optimal Locomotion Speed (*OLS*) for each profile. The results identify an energetically efficient range between 1.35 and 1.41 $m \cdot s^{-1}$ (4.86–5.08 $km \cdot h^{-1}$), where individual optima overlap. The reconstructed group mean speed (1.41 $m \cdot s^{-1}$) yielded the mathematically lowest overall penalty (0.26%). However, given the female-biased demography of the site (77% adult females), the SW scenario (1.35 $m \cdot s^{-1}$) appears demographically favorable, reducing the energetic penalty for the majority group to 0.09%. These findings support the interpretation of cooperative mobility in the Late Pleistocene and suggest that prehistoric human locomotion balanced metabolic efficiency with group cohesion.

KEYWORDS: Hominin footprints; human behavioral ecology; energy expenditure; hunter-gatherers; Engare Sero; group locomotion.

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TEXT PAGE

1. INTRODUCTION

Locomotor behavior in humans is not merely a biomechanical activity; it is fundamentally shaped by social, ecological, and evolutionary pressures (Hamilton et al. 2016; Venkataraman et al. 2017; Wagnild & Wall-Scheffler, 2013; Wall-Scheffler, 2012a). In mobile foraging societies, movement typically occurs in groups composed of individuals with varying morphologies, life stages, and physiological needs, in both past and present contexts (Binford, 2001; Duveau et al. 2019; Venkataraman et al. 2017). Coordinating locomotion across such heterogeneous profiles likely required behavioral strategies that balanced energetic efficiency with social cohesion. While experimental biomechanics, bioenergetics, and ethnographic studies have provided insight into inter-individual variation in walking performance (Bouterse & Wall-Scheffler, 2018; Mateos et al. 2022; Wall-Scheffler, 2012a, 2012b), understanding how prehistoric humans moved collectively remains a central challenge in paleoanthropology and studies of the human past.

Fossil footprint sites may offer a unique window into this issue. Unlike skeletal assemblages, which reflect static morphology, ichnological records preserve direct evidence of locomotor dynamics, spatial interaction, and contemporaneous group movement (Bennett et al. 2013; Hatala et al. 2020). While several significant sites exist worldwide (Ashton et al. 2014; Bennett et al. 2020; Cherin et al. 2019; Clarke, 1979; Dingwall et al. 2013; Duveau, 2021; Masao et al. 2016; Mayoral et al. 2022; McNutt et al. 2021; Sellers et al. 2005), one of the most remarkable is Engare Sero, a Late Pleistocene site in northern Tanzania that preserves over 400 hominin footprints on a lakeshore surface (Balashova et al. 2016; Hatala et al. 2020; Liutkus-Pierce et al. 2016). The trackways, attributed to anatomically modern humans, include traces from multiple adults and non-adults moving in the same direction and timeframe, strongly suggesting coordinated group travel (Hatala et al. 2020).

Previous analyses of Engare Sero have inferred walking speeds and group composition based on footprint morphology and spacing. However, the energetic implications of such movement remain largely unexplored. Since walking speed is a primary determinant of energy cost per distance (Bastien et al. 2005; Ralston, 1958), quantifying the extent to which individuals walked near or far from their Optimal Locomotion Speed (*OLS*) can offer key insights into group decision-making and reinterpret or confirm previous results reported by Hatala et al. (2020). Walking at non-optimal speeds imposes additional energetic costs, which may disproportionately affect individuals based on age and sex, as reported by previous studies on human walking energetics and locomotor behavior (Wagnild & Wall-Scheffler, 2013; Wall-Scheffler, 2012a, 2012b; Zorrilla-Revilla et al. 2024; Zorrilla-Revilla et al. 2025).

This study addresses these questions by modeling the Cost of Transport (*CoT*, expressed in energy expenditure per distance walked, e.g., $J \cdot m^{-1}$ or $kcal \cdot km^{-1}$) across multiple walking scenarios for three hypothetical Engare Sero individuals (an adult male, an adult female, and a non-adult), using experimentally validated *CoT*-speed equations. Energetic penalties are quantified across the range of walking speeds observed in the footprint assemblage, including speeds specific to adult males, adult females, and non-adults; the mean speed derived from the entire footprint sample; the maximum and minimum recorded speeds; and the speeds inferred for the two groups moving in opposite directions (northeast and southwest). All these conditions are compared with the *OLS* (and its associated *CoT*) calculated for an average adult male, adult female, and non-adult modern human.

This approach builds on established work showing that non-adults and adult females often exhibit greater tolerance for suboptimal pacing than adult males, whose higher body mass and stride mechanics make them energetically less flexible (Mateos et al. 2022; Wall-Scheffler & Myers, 2013; Zorrilla-Revilla et al. 2024; Zorrilla-Revilla, 2022; Zorrilla-Revilla et al. 2025). Studies

have shown that women's wider pelvis may allow them to maintain walking efficiency across a broader range of speeds, even while carrying frontal loads such as infants (Wall-Scheffler, 2012a, 2012b; Wall-Scheffler & Myers, 2013). Experimental research further demonstrates that children and adolescents can often match adult speeds without incurring significant energetic penalties due to their higher walking flexibility (Zorrilla-Revilla et al. 2024) and that deviations from *OLS* may lead to steeper energy costs, particularly for adult males.

These findings provide new evidence that Late Pleistocene *Homo sapiens* groups could have minimized collective energy expenditure by adjusting pace according to the most constrained individuals, while taking advantage of the adaptive flexibility of the rest. By quantifying these energetic compromises, this study offers a new framework for interpreting cooperation, group integration, and locomotor decision-making in deep human history.

2. MATERIALS AND METHODS

2.1. Study site and individuals

This study focuses exclusively on fossil human footprints from the archaeological site of Engare Sero, located near Lake Natron in northern Tanzania. The site preserves more than 400 human footprints interpreted as the traces of a group of anatomically modern humans traversing a lacustrine substrate, representing one of the largest assemblages of footprints currently known from the human fossil record in Africa (Balashova et al. 2016).

For the present analyses, the subset of trackways described by Hatala et al. (2020), for which walking speeds were estimated from stride length, was used. Excluding the single running trackway (trackway B), the assemblage contains 22 walking trackways with predicted velocities and age-sex attributions. Of these, 5 trackways are oriented toward the northeast (NE group) and 17 toward the southwest (SW group). Across the full walking sample, adult females dominate the assemblage (17/22 trackways), adult males are less frequent (4/22), and one juvenile individual (represented by 1/22 trackway) is identified. The NE group (n = 5, all walking) includes 3 adult female and 2 adult male trackways, with relatively fast estimated walking speeds. In contrast, the SW group (n = 17) is strongly female-biased, with 14 adult females, 2 adult males, and 1 juvenile trackway, clustering around a slightly slower mean walking speed. This single juvenile trackway is hereafter modeled as the non-adult profile in the energetic analyses. Following Hatala et al. (2020), the SW group has been interpreted as a relatively large, predominantly female set of individuals moving in the same general direction and time frame, whereas the smaller NE group may reflect separate or partially overlapping locomotor episodes.

2.2. Estimating optimal locomotion speed and minimum cost of transport

Following prior morphometric analyses of the Engare Sero individuals (Hatala et al. 2020), the *OLS* and the corresponding minimum cost of transport (*minCoT*) were estimated for three representative modern human models: an adult male, an adult female, and a sex-averaged non-adult.

To evaluate walking energetics, CoT ($J{\cdot}m^{-1}$) was modeled as a function of walking speed (v) for each individual. For adult males and females, the *CoT*-speed equations published by Wall-Scheffler (2012b) were used. Although the single Engare Sero juvenile was originally described as male (Hatala et al. 2020), a more conservative approach was adopted due to the limited sexual dimorphism at this developmental stage. Consequently, a sex-averaged non-adult model was constructed by calculating the mean of the sex-specific equations (boys and girls) provided by Mateos et al. (2022).

The *CoT*-speed equations for adults (expressed in $J{\cdot}m^{-1}$):

$$CoT_{\text{male}} = 178.7v^2 - 517.8v + 649.8$$

$$CoT_{\text{female}} = 132.9v^2 - 348.6v + 453.8$$

The equations describing non-adult walking energetics ($J \cdot m^{-1}$) are:

$$CoT_{\text{boy}} = 130.2v^2 - 379.1v + 445.7$$

$$CoT_{\text{girl}} = 123.0v^2 - 355.2v + 442.2$$

A sex-averaged non-adult energetic model was calculated as:

$$CoT_{\text{non-adult}} = \frac{CoT_{\text{boy}} + CoT_{\text{girl}}}{2}$$

All *CoT* values were converted from $J \cdot m^{-1}$ to $kcal \cdot km^{-1}$ using the thermochemical conversion factor 0.239006 (1 kJ = 0.239006 *kcal*) and adjusting for distance (1,000 *m* = 1 *km*). Thus, *CoT* ($kcal \cdot km^{-1}$) = *CoT* ($J \cdot m^{-1}$) × 0.239006

For each quadratic function of the form: $CoT = av^2 + bv + c$, the *OLS* was obtained by calculating the vertex of the parabola:

$$OLS = -\frac{b}{2a}$$

The *minCoT* was then computed by evaluating the equation at that speed.

2.3. Walking-speed energetic scenarios

For each of the three modeled profiles (adult male, adult female, non-adult), energetic costs were evaluated across a range of potential walking-speed scenarios derived from the footprint assemblage (Hatala et al. 2020):

a) *Individual optimal speeds:*

First, each individual's own *OLS* was considered, as calculated in Section 2.2:

- Adult male *OLS*
- Adult female *OLS*
- Non-adult *OLS*

These values represent the speed that minimizes *CoT* (*minCoT*) for each profile.

b) *Age-sex category mean speeds derived from all Engare Sero footprints:*

Next, the category-specific average walking speeds estimated from the full Engare Sero trackway dataset were used (Hatala et al. 2020):

- *MaleAver*: adult male mean speed (n = 4 trackways)
- *FemaleAver*: adult female mean speed (n = 17 trackways)
- *Non-adultAver*: non-adult mean speed (n = 1 juvenile trackway)

These footprint-derived means were treated as representative observed speeds for each age-sex class.

c) Mixed group-relevant speeds derived from Hatala et al. (2020):

In addition to individual-based speeds, three assemblage-level velocities were examined:

- Fast walking speed (Fast): the fastest sustained walking speed in the assemblage (Trackway F; as shown in Table 1 of Hatala et al. 2020), excluding the single running trackway.
- Slow walking speed (Slow): the slowest sustained walking speed among the Engare Sero walking trackways (Trackway X; as shown in Table 1 of Hatala et al. 2020).

- Group mean speed: the average walking speed calculated from all Engare Sero trackways (n = 22 trackways), used as a representative collective pace under the assumption of a cohesive group movement.

i. Additionally, the mean walking speeds of the NE and SW groups are also reported:

- SW mean speed (n = 17 trackways)
- NE mean speed (n = 5 trackways),

representing directional subsets used to contextualize differences between the two putative movement episodes.

For each scenario and each individual, the imposed speed v was substituted into the corresponding *CoT* equation (adult male, adult female, or non-adult averaged model) and converted to *kcal·km⁻¹* as described above. This procedure produced a matrix of scenario-specific energetic costs, $CoT_{(i,s)}$, for each individual *i* across all walking-speed scenarios *s*. For readability, some speeds are also reported in *km·h⁻¹*, but all calculations use *m·s⁻¹*; 1 *m·s⁻¹* = 3.6 *km·h⁻¹*.

Graphical plots illustrating the *CoT*-speed relationships and locomotor scenarios were generated from the modeled data using Python (Python Software Foundation) and subsequently edited for clarity and layout using Adobe Photoshop CS6 (Adobe Systems Inc., San Jose, CA, USA).

2.4. Energetic cost and individual penalties

Energetic penalties quantify the additional energy an individual expends when walking at a given scenario speed relative to their own *OLS*. For each individual profile *i* and scenario *s*, the scenario-specific *CoT* in *kcal·km⁻¹* was first calculated as:

$$CoT_{(i,s)} = CoT_i(v_s) \times 0.239006$$

where $CoT_i(v_s)$ is the value of the individual's *CoT*-speed quadratic function (expressed in *J·m⁻¹*) evaluated at the imposed speed v_s, and 0.239006 is the conversion factor from *J·m⁻¹* to *kcal·km⁻¹*.

Each individual's minimum cost of transport was then defined as:

$$minCoT_i = \mathrm{CoT_i}(v_{OLS,i}) \times 0.239006$$

where $v_{OLS,i}$ corresponds to the optimal locomotion speed for individual i.

For each walking-speed scenario, energetic penalties were quantified in two complementary forms:

- Absolute energetic penalty (*kcal·km⁻¹*):

$$\Delta CoT_{i,s} = CoT_{i,s} - minCoT_i$$

- Relative energetic penalty (%):

$$\mathrm{Penalty_{i,s}}(\%) = 100 \times \left(\frac{CoT_{i,s} - minCoT_i}{minCoT_i}\right)$$

Positive values indicate an increased energetic cost relative to the individual's optimal walking speed, whereas values approaching zero indicate locomotion close to the individual's energetic optimum. These penalties are expressed both in *kcal·km⁻¹* and %.

For each locomotor scenario, a mean group energetic penalty was calculated as the average relative energetic penalty (%) across the adult male, adult female, and non-adult models for each locomotor scenario, providing an integrated estimate of the group-level energetic burden imposed by each walking speed.

3. RESULTS

3.1. Optimal locomotion speeds and minimum energetic costs

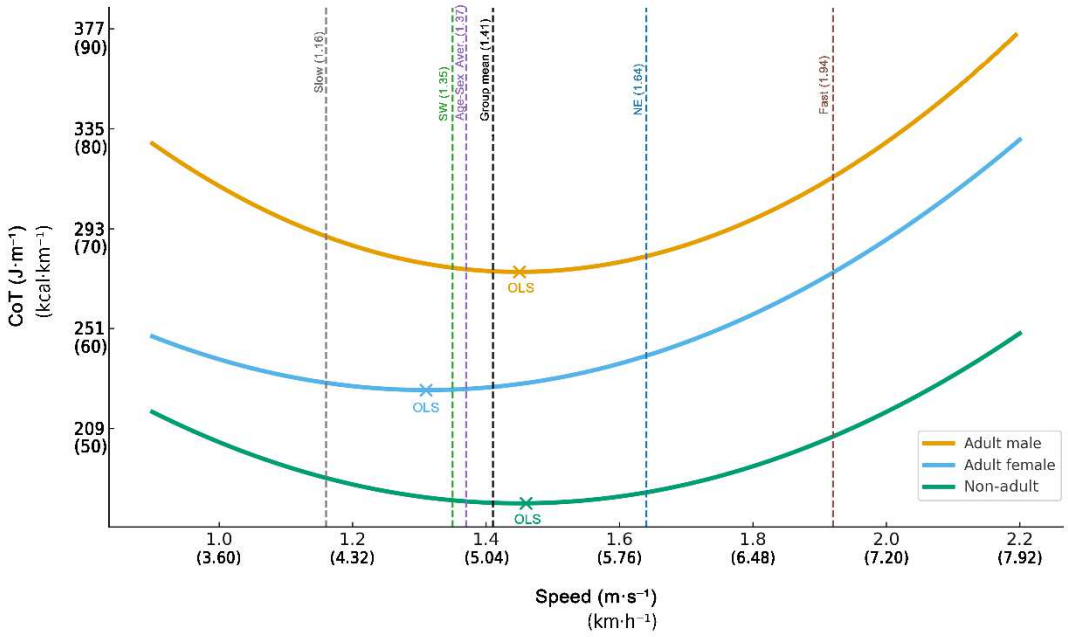
The three modeled individuals showed *OLS* tightly clustered between 1.31 and 1.46 $m \cdot s^{-1}$ (Table 1). An adult male reached his *OLS* at 1.45 $m \cdot s^{-1}$ ($minCoT = 65.66\ kcal \cdot km^{-1}$), an adult female at 1.31 $m \cdot s^{-1}$ ($minCoT = 53.83\ kcal \cdot km^{-1}$), and a non-adult at 1.46 $m \cdot s^{-1}$ ($minCoT = 42.49\ kcal \cdot km^{-1}$) (Fig. 1).

Table 1. Optimal locomotion speed (*OLS*) and minimum energetic cost (*minCoT*) for the three modeled profiles.

Individual	*OLS* ($m \cdot s^{-1}$)	*minCoT* ($kcal \cdot km^{-1}$)
Adult male	1.45	65.66
Adult female	1.31	53.83
Non-adult	1.46	42.49

Note. OLS corresponds to the speed minimizing each individual's CoT-speed function; minCoT values are derived from the quadratic equations described in the methods and expressed in $kcal \cdot km^{-1}$.

Fig. 1 *OLS*, min*CoT*, and several potential scenarios.



Note: The graph displays OLS in $m \cdot s^{-1}$ ($km \cdot h^{-1}$ *in parentheses), CoT in* $J \cdot m^{-1}$ ($kcal \cdot km^{-1}$ *in parentheses), and the different modeled walking scenarios (Slow, SW, Age-sex Aver., Group mean, NE, and Fast). Each scenario illustrates the deviation from each individual's OLS. OLS and CoT refer to optimal locomotion speed and cost of transport, respectively.*

3.2. Modeled energetic cost at footprint-derived age-sex mean walking speeds (MaleAver, FemaleAver, Non-adultAver)

Footprint-derived mean walking speeds differed among age-sex categories in the Engare Sero assemblage. Based on stride-length estimates reported by Hatala et al. (2020, Table 1 data), the

category-specific average speeds were 1.44 $m \cdot s^{-1}$ (5.18 $km \cdot h^{-1}$) for adult males (MaleAver; n = 4 trackways), 1.37 $m \cdot s^{-1}$ (4.93 $km \cdot h^{-1}$) for adult females (FemaleAver; n = 17), and 1.30 $m \cdot s^{-1}$ (4.68 $km \cdot h^{-1}$) for non-adults (Non-adultAver; n = 1 juvenile trackway) (Table 2).

When these velocities were substituted into the corresponding *CoT*-speed equations, the adult-male model walking at the MaleAver was predicted to expend 65.66 $kcal \cdot km^{-1}$, exactly matching its *minCoT* and therefore incurring no energetic penalty. The adult female model walking at the FemaleAver speed expended 53.93 $kcal \cdot km^{-1}$, corresponding to a small increase of 0.11 $kcal \cdot km^{-1}$ relative to her minimum (0.20% energetic penalty). The non-adult model walking at the Non-adultAver speed showed a *CoT* of 43.17 $kcal \cdot km^{-1}$, representing an increase of 0.68 $kcal \cdot km^{-1}$ above its minimum and resulting in the highest relative energetic penalty under this scenario (1.60%). Thus, when each age-sex category is assumed to walk at its own footprint-derived mean speed, non-adults experience the largest relative deviation from their *OLS*, although energetic penalties remain extremely small across all three profiles.

Table 2. Energetic Penalties Relative to Each Individual's *OLS*

Individual	*Scenario (speed = $m \cdot s^{-1}$; $km \cdot h^{-1}$) and CoT ($kcal \cdot km^{-1}$)*	*Absolute Penalty ($kcal \cdot km^{-1}$)*	*Relative Penalty (%)*	*Mean relative energetic penalty across all scenarios (%)*
Adult male *(OLS = 1.45 $m \cdot s^{-1}$; 5.22 $km \cdot h^{-1}$; minCoT = 65.66 $kcal \cdot km^{-1}$)*	MaleAver (1.44; 5.18) → 65.66	0.00	0.00	4.03
	Fast (1.94; 6.98) → 75.95	10.29	15.67	
	Slow (1.16; 4.18) → 69.22	3.56	5.43	
	SW mean (1.35; 4.86) → 66.07	0.41	0.63	
	NE mean (1.64; 5.90) → 67.22	1.56	2.38	
	Group mean speed (1.41; 5.08) → 65.72	0.06	0.09	
Adult female *(OLS = 1.31 $m \cdot s^{-1}$; 4.72 $km \cdot h^{-1}$; minCoT = 53.83 $kcal \cdot km^{-1}$)*	FemaleAver (1.37; 4.93) → 53.93	0.11	0.20	6.05
	Fast (1.94; 6.98) → 66.39	12.56	23.33	
	Slow (1.16; 4.18) → 54.55	0.73	1.35	
	SW mean (1.35; 4.86) → 53.87	0.05	0.09	
	NE mean (1.64; 5.90) → 57.25	3.42	6.37	
	Group mean speed (1.41; 5.08) → 54.13	0.31	0.57	
Non-adult *(OLS = 1.46 $m \cdot s^{-1}$; 5.26 $km \cdot h^{-1}$; minCoT = 42.49 $kcal \cdot km^{-1}$)*	Non-adultAver (1.30; 4.68) → 43.17	0.68	1.60	5.03
	Fast (1.94; 6.98) → 49.70	7.21	16.97	
	Slow (1.16; 4.18) → 45.03	2.54	5.98	
	SW mean (1.35; 4.86) → 42.79	0.30	0.71	
	NE mean (1.64; 5.90) → 43.58	1.09	2.57	
	Group mean speed (1.41; 5.08) → 42.53	0.05	0.11	

Note. Energetic penalties represent the difference between the scenario-specific cost of transport (CoT expressed as $kcal \cdot km^{-1}$) and each individual's minimum CoT at their optimal locomotion speed (OLS), calculated as: Penalty = $CoT_{scenario}$ - CoT_{OLS}. Penalties are also expressed as a percentage of CoT_{OLS}. NE and SW scenario values correspond to the mean walking velocities reconstructed for the NE and SW groups reported by Hatala et al. (2020), reflecting distinct directional locomotor episodes within the Engare Sero assemblage. Group mean speed represents the average walking speed calculated from all Engare Sero trackways and is interpreted as a cohesive group pace. Fast and slow speeds correspond to the maximum and minimum walking speeds estimated from individual trackways reported by Hatala et al. (2020). MaleAver, FemaleAver, and Non-adultAver represent the mean walking speeds calculated for each age-sex category across the entire footprint assemblage. Mean relative energetic penalty across all scenarios (%) corresponds to the average relative energetic penalty calculated for each individual profile across the full set of modeled walking scenarios.

3.3. Energetic cost at fast walking speed (1.94 $m \cdot s^{-1}$)

A high-velocity walking scenario corresponding to the highest sustained speeds inferred from the Engare Sero assemblage (1.94 $m \cdot s^{-1}$; 6.98 $km \cdot h^{-1}$) was also examined. At this speed, all three individuals incur substantial energetic penalties relative to their respective optima.

The adult male's *CoT* rose to 75.95 $kcal \cdot km^{-1}$, representing an energetic penalty of 10.29 $kcal \cdot km^{-1}$ (15.67%). The adult female expended 66.39 $kcal \cdot km^{-1}$, which is 12.56 $kcal \cdot km^{-1}$ (23.33%) above her minimum. The non-adult showed a similarly strong response, with a *CoT* of 49.70 $kcal \cdot km^{-1}$, corresponding to 7.21 $kcal \cdot km^{-1}$ (16.97%).

3.4. Energetic effects of slow walking (1.16 $m \cdot s^{-1}$)

To explore the effects of a potentially suboptimal slow group movement, the slowest sustained walking speed inferred from the Engare Sero assemblage was examined, 1.16 $m \cdot s^{-1}$ (4.18 $km \cdot h^{-1}$). At this speed, all three individuals experienced increased energetic costs relative to their *OLS*. The adult male's *CoT* rose to 69.22 $kcal \cdot km^{-1}$, representing an additional 3.56 $kcal \cdot km^{-1}$ and a 5.43% relative penalty. The adult female's cost increased to 54.55 $kcal \cdot km^{-1}$, corresponding to 0.73 $kcal \cdot km^{-1}$ (1.35%) above her minimum. Notably, the non-adult showed the strongest response to this slow pace, with a *CoT* of 45.03 $kcal \cdot km^{-1}$, a penalty of 2.54 $kcal \cdot km^{-1}$ (5.98%).

3.5. Energetic costs at the NE and the SW mean walking speeds

The energetic implications of the average walking speeds reconstructed for the NE and SW groups were evaluated. The NE group shows a higher mean walking speed (1.64 $m \cdot s^{-1}$; 5.90 $km \cdot h^{-1}$), whereas the SW group walks more slowly (1.35 $m \cdot s^{-1}$; 4.86 $km \cdot h^{-1}$). The analysis of directional movement revealed distinct energetic profiles for the two putative travel episodes:

At the NE mean speed, all individuals incurred moderate energetic penalties, but the costs were especially pronounced for the adult female. The adult male expended 67.22 $kcal \cdot km^{-1}$, a modest 2.38% increase relative to his minimum, remaining within the low-cost portion of his *CoT* curve. In contrast, the adult female's expenditure rose to 57.25 $kcal \cdot km^{-1}$, representing a 6.37% penalty, the highest among the three profiles, indicating a higher energetic cost for adult females. The non-adult's cost of 43.58 $kcal \cdot km^{-1}$ corresponded to a 2.57% penalty, suggesting a manageable but suboptimal deviation from its *OLS*.

By contrast, walking at the SW mean speed of 1.35 $m \cdot s^{-1}$ produced very low energetic costs across all profiles. The adult male's *CoT* rose only slightly above his minimum (66.07 $kcal \cdot km^{-1}$; 0.63%), while the adult female's expenditure remained essentially unchanged relative to her *OLS* (53.87 $kcal \cdot km^{-1}$; 0.09%). The non-adult likewise showed a minimal penalty (42.79 $kcal \cdot km^{-1}$; 0.71%).

Overall, the SW scenario appears energetically highly favorable for individuals of all age-sex categories, in contrast with the more demanding NE scenario. This comparison suggests that the SW scenario represents a metabolically efficient, coordinated group travel phase, whereas the faster NE scenario may reflect a distinct, more energetically costly locomotor episode.

3.6. Energetic cost at the reconstructed Group mean speed (total Engare Sero footprints)

The calculated average speed for the entire walking assemblage (Group mean speed) was 1.41 $m \cdot s^{-1}$ (5.08 $km \cdot h^{-1}$) and was evaluated as a representative collective pace. At this speed, the adult male expended 65.72 $kcal \cdot km^{-1}$, effectively identical to his *minCoT* (penalty 0.06 $kcal \cdot km^{-1}$; 0.09%). The non-adult's cost was 42.53 $kcal \cdot km^{-1}$, again essentially equal to his minimum (penalty 0.05 $kcal \cdot km^{-1}$; 0.11%). The adult female expended 54.13 $kcal \cdot km^{-1}$, incurring a modest penalty of 0.31 $kcal \cdot km^{-1}$ (0.57%) relative to her minimum (Table 2).

3.7. Group-level energetic penalties across locomotor scenarios

Across all scenario comparisons, a clear pattern emerges. The group mean speed (1.41 $m \cdot s^{-1}$; 5.08 $km \cdot h^{-1}$) produced the lowest theoretical energetic burden, with an average penalty of 0.26% (Table 3). Next, the SW mean speed (1.35 $m \cdot s^{-1}$) and the age-sex footprint averages likewise yielded very

low penalties (0.48 and 0.60%, respectively). Under this criterion, the NE mean speed (1.64 $m \cdot s^{-1}$) produced a moderate group penalty of 3.77%. By contrast, scenarios of unusually slow (1.16 $m \cdot s^{-1}$) or fast walking (1.94 $m \cdot s^{-1}$) imposed substantially higher group costs, resulting in collective penalties of 4.25% and 18.70%, respectively.

Table 3. Mean group energetic penalties across modeled locomotor scenarios.

Scenario (speed = m·s⁻¹; km·h⁻¹)	*Mean group energetic penalty (%)*
Group mean speed (1.41; 5.08)	0.26%
SW mean (1.35; 4.86)	0.48%
MaleAver / FemaleAver / Non-adultAver (1.37; 4.93)	0.60%
NE mean (1.64; 5.90)	3.77%
Slow (1.16; 4.18)	4.25%
Fast (1.94; 6.98)	18.70%

Note. Mean group energetic penalty (%) represents the average relative cost across the adult male, adult female, and non-adult models for each locomotor scenario. Walking speeds are expressed in meters per second ($m \cdot s^{-1}$) with kilometer-per-hour equivalents ($km \cdot h^{-1}$) provided for readability. Scenarios are ordered from lowest to highest energetic penalty. Blue colors (represented here as gradient cues) correspond to penalty magnitude, with darker blue indicating higher energetic penalties.

4. DISCUSSION

Fossil footprints provide exceptional insights into the groups that produced them, including estimates of locomotor speed, demographic composition, sexual dimorphism, and, in some cases, more complex behavioral patterns (Altamura et al. 2018; Alvarado et al. 2022; Ashton et al. 2014; Avanzini et al. 2008; Bennett et al. 2020; Dingwall et al. 2013; Duveau, 2021; Duveau et al. 2019; Hatala et al. 2016; Helm et al. 2022; Mayoral et al. 2021). The present study demonstrates that energetic modeling represents a necessary complement to these traditional ichnological approaches because energy minimization represents a widespread principle influencing movement strategies across organisms (Alexander, 1996; Ralston, 1958; Sirotkin, 2025; Zarrugh et al. 1974). By quantifying the energetic consequences of walking at the speeds represented in the Engare Sero footprint assemblage, the interpretations offered by Hatala et al. (2020) are extended, and the likelihood of different locomotor scenarios in terms of energetic suitability is evaluated.

Below, the implications of these results are discussed for several categories of locomotor scenarios, including movement at age-sex-specific mean speeds, extreme walking speeds (slow and fast), SW and NE subsets, the overall group mean pace, and a broader group-level synthesis.

4.1. Modeled energetic implications of footprint-derived age-sex mean walking speeds (MaleAver, FemaleAver, Non-adultAver)

A possible scenario can be inferred in which each age-sex group walked at its own mean speed, estimated from the full set of footprints found in the archaeological context. Adult males, adult females, and non-adults may have moved in partially distinct clusters, although all of them followed a common path. Under this scenario, non-adults would move more slowly than their energetic optima, adult females would walk faster than theirs, whereas adult males would tend to walk essentially at their OLS and therefore without incurring markedly higher costs per distance. This scenario is particularly favorable for adult males and remains relatively efficient for adult females and non-adults; at the group level, it also ranks among the most efficient modeled alternatives when mean energetic penalties across the three categories are considered (Table 3). This pattern likely reflects the fact that the mean speeds calculated for each age-sex group based on the footprints approximate the adults' estimated *OLS*.

It is also noteworthy that the Non-adultAver and FemaleAver speeds are the most similar, with values around 1.3 $m{\cdot}s^{-1}$. This similarity may have favoured adult females and non-adults moving nearly side by side, with adult females remaining closer to their estimated *OLS* and non-adults somewhat farther from theirs. However, since non-adults have been shown to exhibit the greatest energetic flexibility (Zorrilla-Revilla et al. 2024), they may tolerate non-optimal speeds with minimal penalty (Zorrilla-Revilla et al. 2025). Adult males, by contrast, may have tended to walk closer to their estimated OLS, which is higher than that of adult females, when moving in same-sex groups, because they consistently show a sharper *CoT*-speed parabola, implying reduced flexibility in walking performance (Fig. 1). Some ethnographic and biomechanical research suggests that foraging mobility is often structured by sex and age, with females and children typically moving together, while adult men preferentially engage in solitary or male-group travel associated with hunting activities (Binford, 2001; Blurton Jones et al. 1989; Hill & Hurtado, 2017; Jang et al. 2022; Marlowe, 2010; Wall-Scheffler, 2012a).

However, two considerations are worth noting. Firstly, the non-adult category is represented by a single trackway, limiting its statistical representativeness. Secondly, although this scenario is energetically attractive at the individual level, it may be behaviorally risky. Group travel in prehistoric contexts likely required maintaining visual contact and ensuring protection of non-adults; therefore, allowing each subgroup to walk at different paces may not have been behaviorally feasible.

4.2. Fast walking and slow walking speed scenarios

Walking as fast as 1.94 $m{\cdot}s^{-1}$ is energetically costly for all individuals, and is particularly demanding for adult females and non-adults. As shown in the Results, this scenario represents the most energetically taxing condition for each profile and for the group as a whole (18.70%; Table 3).

Importantly, the footprint corresponding to this high velocity was attributed to an adult female (trackway F), yet the energetic models indicate that adult females are the individuals most strongly penalized when walking far above their *OLS* (23.33%). This elevated cost reflects the position of this speed at the upper extreme of the walking cost-speed curve relative to the female *OLS*, a pattern consistent with the results presented here showing sharply increasing energetic demands at high walking speeds (Fig. 1) and, moreover, such speeds may approach the walk-run transition zone, where running can become energetically more efficient than fast walking (Rotstein et al. 2005), a transition that has been shown to occur at lower absolute speeds in females than in males (Gill et al. 2022).

These findings suggest that this speed is unlikely to represent a sustained long-distance travel pace for a mixed-age, mixed-sex group. Instead, it more plausibly reflects a brief, isolated locomotor episode driven by short-term behavioral or environmental circumstances. Although a similar walking speed (1.81 $m{\cdot}s^{-1}$) was reported by Hatala et al. (2024), it is important to note that this trackway was interpreted as the solitary movement of a single individual belonging to a different hominin species.

At the opposite extreme, walking at 1.16 $m{\cdot}s^{-1}$ is also energetically suboptimal for all three individuals, although the degree of penalty varies. The non-adult and adult male incur penalties above 5%, consistent with their higher *OLS* values. In contrast, the adult female experiences only a modest penalty. As noted in Wall-Scheffler (2012b), adult females tend to have greater energetic flexibility across speeds, likely due to pelvic morphology and gait mechanics.

Despite this relative flexibility, the slow walking scenario remains one of the least efficient scenarios for group movement, indicating that this pace would still have been suboptimal at the collective level, as revealed in Table 3. Although this speed corresponds to a footprint attributed

to an adult female (as well as another at 1.19 $m \cdot s^{-1}$ reported by Hatala et al. 2020), it still lies outside the most energetically favorable range for the group as a whole. It is noteworthy that, although this represents the lowest walking speed potentially associated with the Engare Sero group, it remains considerably higher than speeds estimated for other fossil trackways interpreted as group movement. For example, Dingwall et al. (2013) reported walking speeds ranging between 0.45 and 1.0 $m \cdot s^{-1}$. The reasons for such slow locomotion remain unclear, particularly because these speeds lie far from the predicted energetic optima regardless of whether the individuals were adult males, adult females, or non-adults. However, these trackways have been attributed to Early Pleistocene hominins, which may reflect different locomotor or ecological contexts.

4.3. Two directional groups with distinct locomotor patterns (NE and SW).

Hatala and colleagues (2020) proposed that the Engare Sero trackways might represent at least two distinct locomotor episodes. The SW group likely represents a mixed age-sex group moving together at speeds between 1.2 – 1.5 $m \cdot s^{-1}$. Fourteen of those trackways were most likely produced by adult females, with two adult males and one juvenile male, leading to the hypothesis that males may have reduced their pace to accommodate the females' velocity.

This hypothesis proposed by Hatala and colleagues (2020) is supported by the energetic patterns identified here, as the SW mean speed lies closest to the *OLS* estimated for adult females. Consequently, this scenario appears especially favorable for adult females, while requiring only slight adjustments by adult males and non-adults, both of whom would remain close to their estimated optima. Under this possible scenario, adult males and non-adults would be required to walk at speeds about 0.1 $m \cdot s^{-1}$ below their estimated *OLS*, with the latter incurring a very small energetic penalty (0.70%). Although adult males and non-adults would not be walking under their individually most favorable conditions, the SW mean speed still ranks among the most efficient modeled alternatives at the group level (Table 3). In this sense, it seems to represent a plausible compromise pace, combining low individual penalties with a low collective energetic burden across the three modeled profiles. Moreover, this mixed composition movement would have reduced potential risks associated with group fragmentation, as ethnographic and socioecological research on hunter-gatherers empirically shows (Lew-Levy et al. 2022; Marlowe, 2010). In contrast, the NE scenario presents a different energetic signature. At this speed, the collective penalty increases, with a disproportionate impact on adult females, for whom this represents the second-highest energetic cost. These presented results suggest that the NE scenario may reflect urgency or a different social context in which energy minimization was temporarily deprioritized.

4.4. Group mean speed

Assuming that this plausible scenario reflects a cohesive group moving together rather than independent individuals walking at random paces, the reconstructed group mean speed emerges as the mathematically most plausible locomotor strategy identified in the Engare Sero assemblage. The results indicate that this pace represents an excellent compromise, balancing individual physiological limits with the collective need for social cohesion. At this speed, the collective energetic penalty is the lowest of all modeled scenarios, suggesting a highly optimized movement pattern. Such mixed-age group dynamics align with other Late Pleistocene records, including *Homo sapiens* sites such as Pech-Merle cave (France) (Pastoors et al. 2017) and Larache in Morocco (Sedrati et al. 2024), the latter being strongly dominated by non-adults, as well as Neanderthal sites such as Le Rozel (France) and Monte Clérigo (Portugal) (de Carvalho et al. 2025; Duveau et al. 2019).

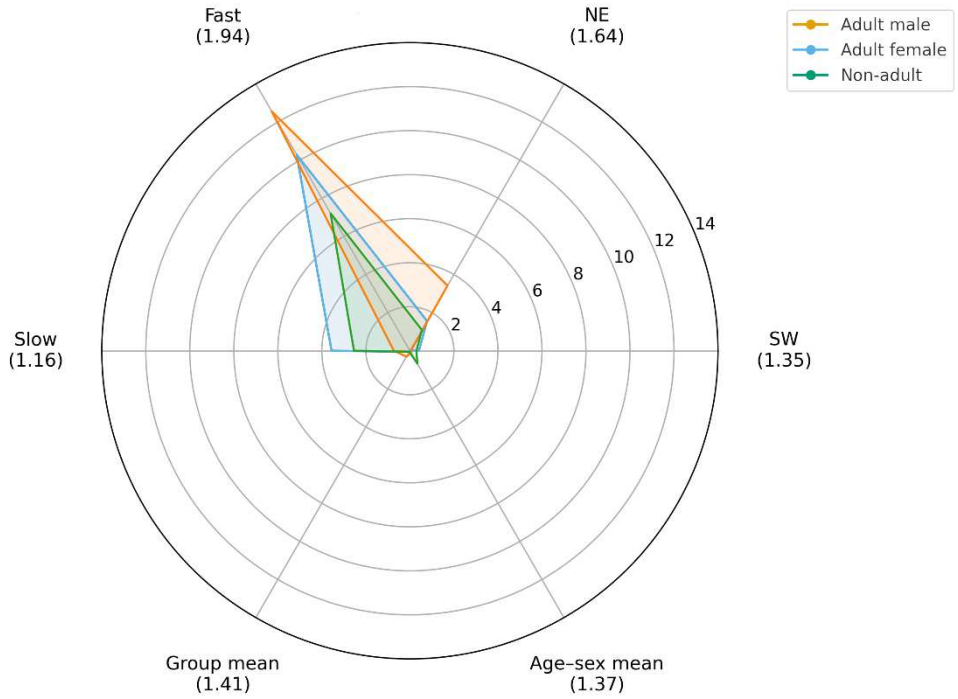
From a behavioral perspective, this pace is virtually optimal for adult males and non-adults, who incur negligible penalties (see Table 2). While it lies slightly above the adult female's *OLS*, the resulting penalty cost (0.57%) remains well within a tolerable range. This finding suggests that collective movement was not the result of a "forced" pace, but rather a mutually compatible

strategy. By operating within this energetically efficient range, the group could have remained synchronized without imposing excessive energetic demands on adult males, who show a more sharply curved *CoT*-speed relationship around their *OLS*, or on adult females, the most numerous group in the assemblage. Ultimately, this evidence supports the hypothesis that Late Pleistocene groups may have favored social stability and collective economy over individual performance, reflecting a coordinated social unit where locomotor decision-making was intrinsically tied to the needs of the entire community. While this pace represents a mathematical ideal for the collective sample, a deeper look at the site's specific demography suggests further nuances (see Section 4.5).

4.5. Group-level energetic penalties and the female-biased group pace

The distribution of energetic penalties across scenarios highlights a consistent pattern in the collective energetic burden (Fig. 2). The group mean speed yields the lowest overall penalty, followed closely by the SW scenario and the age-sex footprint averages, whereas the NE scenario and, especially, the extreme slow and fast conditions impose substantially higher costs. This gradient reinforces the existence of a narrow range of energetically efficient walking speeds for the group as a whole.

Fig. 2 Absolute energetic penalties (*kcal·km⁻¹*) for adult male, adult female, and non-adult profiles across walking-speed scenarios in the Engare Sero footprint assemblage.



Note. Values represent absolute energetic penalties (kcal·km⁻¹) calculated for adult male, adult female, and non-adult profiles under each walking-speed scenario. Concentric rings indicate increasing energetic costs as walking speeds diverge from each individual's optimal locomotion speed (OLS), at which cost of transport (CoT) is minimized (minCoT). Values closer to the center represent speeds near the energetic optimum, whereas values toward the outer rings indicate progressively higher energetic costs. The radar plot shows that the Group mean and SW scenarios impose minimal energetic costs, whereas the NE scenario and, especially, the extreme slow and fast scenarios result in progressively higher energetic penalties. Numbers in parentheses indicate walking speeds in m·s⁻¹.

Overall, these findings show that the most plausible collective movement speeds, particularly the group mean and SW scenarios, fall very close to the energetic optima of all modeled individuals.

However, a purely statistical approach may overlook the social reality of the Engare Sero group. It is essential to highlight that adult females represent 77% of the identified trackmakers (17 out of 22). Consequently, even a minor individual penalty for females has a significant impact on the cumulative energetic cost of the community.

From this demographic perspective, the SW scenario emerges not just as an energetically efficient alternative, but also as a potentially socially advantageous walking pace. By shifting from the group mean speed (1.41 $m{\cdot}s^{-1}$) to the SW mean speed (1.35 $m{\cdot}s^{-1}$), the energetic burden on the female majority is virtually eradicated, dropping from 0.57% to a negligible 0.09%.

This suggests that the group mean speed may represent a statistical optimum, whereas the SW mean speed could better reflect a socially optimized reality. If the community's energetic success depends on the efficiency of its most numerous members, often the primary caregivers or gatherers, then the group's pace may have been strongly influenced by the energetic landscape of adult females. In this light, the few males in the SW group were not just "walking"; they may have actively accommodated their pace to the female-juvenile core of the traveling group. This evidence reinforces the interpretation of Late Pleistocene groups as highly integrated units where locomotor decisions favored the energetic efficiency of the demographic majority.

4.6. Study Limitations

Despite the robustness of the observed patterns, it is necessary to consider certain limitations inherent to bioenergetic modeling in archaeological contexts. First, these estimations are based on physiological profiles of experimentally studied modern human populations acting as proxies. While these models are well-established, they may not fully capture the exact individual variability, the specific body proportions of African Pleistocene hunter-gatherers, or the potential metabolic adaptations of the Late Pleistocene inhabitants of Engare Sero.

Second, this study's *CoT* calculations assume movement over flat or unobstructed terrain (see Murray, 2022, for a discussion of this debate), as assumed by the equations used here (Mateos et al. 2022; Wall-Scheffler, 2012b). However, the reality of the archaeological environment suggests that factors such as substrate consistency, specifically wet volcanic ash, and the presence of environmental obstacles would have increased total metabolic expenditure, potentially shifting individual optima (*OLS*) slightly. Additionally, walking speeds inferred from stride length involve uncertainty related to substrate properties and footprint preservation. Consequently, the energetic penalties reported here should be interpreted as approximate estimates rather than precise physiological values. Moreover, the present analysis does not account for the transport of loads, such as tools, food, or infants, which likely represented an important component of daily mobility in Late Pleistocene populations. The inclusion of these variables would not only increase the absolute cost but would likely narrow the identified energetically efficient range, making group coordination even more critical.

Third, the energetic differences identified between locomotor scenarios are relatively small in absolute terms. However, the aim of the model is not to demonstrate large energetic disparities but to evaluate whether the reconstructed walking speeds fall within or outside the energetically efficient range for different demographic profiles. Even small energetic differences may become relevant when accumulated over longer travel distances or when considered at the scale of group movement.

Finally, the non-adult profile is derived from a single juvenile trackway, which limits the statistical representativeness of this demographic group.

5. CONCLUSIONS

The Engare Sero trackways suggest that Late Pleistocene humans coordinated their movement through a balance between physiological efficiency and social cohesion. The present analysis identifies an energetically efficient range (between 1.35 and 1.41 $m \cdot s^{-1}$) where the overlap of individual optima allowed for group travel with minimal metabolic compromise. While the group mean speed minimizes the collective burden to a negligible 0.26%, the demographic importance of females within the assemblage suggests that the SW scenario may also have represented a similarly strategic locomotor pace. By favoring the energy savings of the group's majority, this pace reduces the female penalty to a minimal 0.09%, thereby reducing the cumulative metabolic burden of the group.

This dynamic suggests an adaptive asymmetry: the heightened sensitivity of adult males to speed deviations may have been offset by the energetic flexibility of females and non-adults, who may have acted as stabilizing elements for the group. Ultimately, mobility at Engare Sero was not a matter of unilateral adjustment, but rather a cooperative strategy based on shared energetic landscapes. These results suggest that prehistoric human locomotion was a fundamentally social act, where metabolic efficiency and group stability were inseparable objectives.

6. REFERENCES

Alexander RM (1996) Optima for animals. Princeton University Press, Princeton

Altamura F, Bennett MR, D'Août K, Gaudzinski-Windheuser S, Melis RT, Reynolds SC, Mussi M (2018) Archaeology and ichnology at Gombore II-2, Melka Kunture, Ethiopia: everyday life of a mixed-age hominin group 700,000 years ago. Sci Rep 8(1):2815. https://doi.org/10.1038/s41598-018-21158-7

Alvarado E, Paliard C, Rohmer D, Cani MP (2022) Real-time locomotion on soft grounds with dynamic footprints. Front Virtual Real 3:801856. https://doi.org/10.3389/frvir.2022.801856

Ashton N, Lewis SG, De Groote I, Duffy SM, Bates M, Bates R, Hoare P, Lewis M, Parfitt SA, Peglar S, Williams C, Stringer C (2014) Hominin footprints from early Pleistocene deposits at Happisburgh, UK. PLoS ONE 9(2):e88329. https://doi.org/10.1371/journal.pone.0088329

Avanzini M, Mietto P, Panarello A, De Angelis M, Rolandi G (2008) The devil's trails: middle Pleistocene human footprints preserved in a volcanoclastic deposit of southern Italy. Ichnos 15(3–4):179–189. https://doi.org/10.1080/10420940802470458

Balashova A, Mattsson HB, Hirt AM, Almqvist BSG (2016) The Lake Natron Footprint Tuff (northern Tanzania): volcanic source, depositional processes and age constraints from field relations. J Quat Sci 31(5):526–537. https://doi.org/10.1002/jqs.2876

Bastien GJ, Willems PA, Schepens B, Heglund NC (2005) Effect of load and speed on the energetic cost of human walking. Eur J Appl Physiol 94(1–2):76–83. https://doi.org/10.1007/s00421-004-1286-z

Bennett MR, Bustos D, Odess D, Urban TM, Lallensack JN, Budka M, Santucci VL, Martinez P, Wiseman ALA, Reynolds SC (2020) Walking in mud: remarkable Pleistocene human trackways from White Sands National Park (New Mexico). Quat Sci Rev 249, 106610. https://doi.org/10.1016/j.quascirev.2020.106610

Bennett MR, Falkingham P, Morse SA, Bates K, Crompton RH (2013) Preserving the impossible: conservation of soft-sediment hominin footprint sites and strategies for three-dimensional digital data capture. PLoS ONE 8(4): e60755. https://doi.org/10.1371/journal.pone.0060755

615 Binford LR (2001) Constructing frames of reference: an analytical method for archaeological
616 theory building using ethnographic and environmental data sets. University of California
617 Press, Berkeley

618 Blurton Jones NG, Hawkes K, O'Connell JF (1989) Modelling and measuring costs of children
619 in two foraging societies. In: Standen V, Foley RA (eds) Comparative socioecology: the
620 behavioural ecology of humans and other mammals. Blackwell Scientific, Oxford, pp
621 367–390

622 Bouterse LM, Wall-Scheffler C (2018) Children are not like other loads: a cross-cultural
623 perspective on the influence of burdens and companionship on human walking. PeerJ
624 6:e5547. https://doi.org/10.7717/peerj.5547

625 Cherin M, Barili A, Boschian G, Ichumbaki EB, Iurino DA, Masao FT, Menconero S, Moggi-
626 Cecchi J, Sarmati S, Santopuoli N, Manzi G (2019) New footprints from Laetoli
627 (Tanzania, 3.66 Ma): discovery, analysis, inferences, research project and conservation
628 plans. In: di Lernia S, Gallinaro M (eds) Archaeology in Africa: potentials and
629 perspectives on laboratory & fieldwork research. Arid Zone Archaeology Monographs 8,
630 Sapienza Università di Roma, pp 141–148

631 Clarke RJ (1979) Early hominid footprints from Tanzania. S Afr J Sci 75(4):148–149.

632 de Carvalho C, Cunha PP, Belo J, Muñiz F, Baucon A, Cachão M, Figueiredo S, Buylaert J-P,
633 Galán JM, Belaústegui Z, Cáceres LM, Zhang Y, Ferreira C, Rodríguez-Vidal J, Finlayson
634 S, Finlayson G, Finlayson C (2025) Neanderthal coasteering and the first Portuguese
635 hominin tracksites. Sci Rep 15(1): 23785. https://doi.org/10.1038/s41598-025-06089-4

636 Dingwall HL, Hatala KG, Wunderlich RE, Richmond BG (2013) Hominin stature, body mass,
637 and walking speed estimates based on 1.5 million-year-old fossil footprints at Ileret,
638 Kenya. J Hum Evol 64(6): 556–568. https://doi.org/10.1016/j.jhevol.2013.02.004

639 Duveau J (2021) The Le Rozel footprints: snapshots of Neandertal groups in the Late
640 Pleistocene. A combined morphometric and experimental approach. Bull Mem Soc
641 Anthropol Paris 33(2). https://doi.org/10.4000/bmsap.7900

642 Duveau J, Berillon G, Verna C, Laisné G, Cliquet D (2019) The composition of a Neandertal
643 social group revealed by the hominin footprints at Le Rozel (Normandy, France). Proc
644 Natl Acad Sci USA 116(39): 19409 – 19414. https://doi.org/10.1073/pnas.1901789116

645 Gill N, Hollands K, O'Leary TJ, Roberts AJ, Greeves JP, Jones RK (2022) The effect of sex,
646 stature, and limb length on the preferred walk-to-run transition speed. Gait Posture 98:1–5.
647 https://doi.org/10.1016/j.gaitpost.2022.08.006

648 Hamilton MJ, Lobo J, Rupley E, Youn H, West GB (2016) The ecological and evolutionary
649 energetics of hunter-gatherer residential mobility. Evol Anthropol 25(3):124–132.
650 https://doi.org/10.1002/evan.21485

651 Hatala KG, Harcourt-Smith WEH, Gordon AD, Zimmer BW, Richmond BG, Pobiner BL,
652 Green DJ, Metallo A, Rossi V, Liutkus-Pierce CM (2020) Snapshots of human anatomy,
653 locomotion, and behavior from Late Pleistocene footprints at Engare Sero, Tanzania. Sci
654 Rep 10(1):7740. https://doi.org/10.1038/s41598-020-64095-0

655 Hatala KG, Roach NT, Ostrofsky KR, Wunderlich RE, Dingwall HL, Villmoare BA, Green DJ,
656 Harris JWK, Braun DR, Richmond BG (2016) Footprints reveal direct evidence of group
657 behavior and locomotion in Homo erectus. Sci Rep 6(1): 1–9.
658 https://doi.org/10.1038/srep28766

659 Hatala KG, Roach NT, Behrensmeyer AK, Falkingham PL, Gatesy SM, Williams-Hatala EM,
660 Feibel CS, Dalacha I, Kirinya M, Linga E, Loki R, Longaye AA, Longaye M, Lonyericho
661 E, Loyapan I, Nakudo N, Nyete C, Leakey LN (2024) Footprint evidence for locomotor

diversity and shared habitats among early Pleistocene hominins. Science 386(6725):1004–1010. https://doi.org/10.1126/science.ado5275

Helm CW, Cawthra HC, De Vynck JC, Hattingh R, Lockley MG (2022) Possible Pleistocene hominin tracks from South Africa's west coast. S Afr J Sci 118(1–2): 1–3. https://doi.org/10.17159/sajs.2022/11842

Hill K, Hurtado AM (2017) Ache life history: the ecology and demography of a foraging people. Routledge, New York

Jang H, Janmaat KRL, Kandza V, Boyette AH (2022) Girls in early childhood increase food returns of nursing women during subsistence activities of the BaYaka in the Republic of Congo. Proc R Soc B 289(1987):20221407. https://doi.org/10.1098/rspb.2022.1407

Lew-Levy S, Reckin R, Kissler SM, Pretelli I, Boyette AH, Crittenden AN, Hagen RV, Haas R, Kramer KL, Koster J, O'Brien MJ, Sonoda K, Surovell TA, Stieglitz J, Tucker B, Lavi N, Ellis-Davies K, Davis HE (2022) Socioecology shapes child and adolescent time allocation in twelve hunter-gatherer and mixed-subsistence forager societies. Sci Rep 12(1): 8054. https://doi.org/10.1038/s41598-022-12217-1

Liutkus-Pierce CM, Zimmer BW, Carmichael SK, McIntosh W, Deino A, Hewitt SM, McGinnis KJ, Hartney T, Brett J, Mana S (2016) Radioisotopic age, formation, and preservation of Late Pleistocene human footprints at Engare Sero, Tanzania. Palaeogeogr Palaeoclimatol Palaeoecol 463:68–82. https://doi.org/10.1016/j.palaeo.2016.09.019

Marlowe FW (2010) The Hadza: hunter-gatherers of Tanzania. University of California Press, Berkeley

Masao FT, Ichumbaki EB, Cherin M, Barili A, Boschian G, Iurino DA, Menconero S, Moggi-Cecchi J, Manzi G (2016) New footprints from Laetoli (Tanzania) provide evidence for marked body size variation in early hominins. ELife 5, e19568. https://doi.org/10.7554/eLife.19568

Mateos A, Zorrilla-Revilla G, Rodríguez J (2022) At their own pace: optimal walking speed in children and adolescents. Am J Biol Anthropol 178(4):593–604. https://doi.org/10.1002/ajpa.24562

Mayoral E, Díaz-Martínez I, Duveau J, Santos A, Rodríguez Ramírez A, Morales JA, Morales LA, Díaz-Delgado R (2021) Tracking late Pleistocene Neandertals on the Iberian coast. Sci Rep 11(1): 4103. https://doi.org/10.1038/s41598-021-83413-8

Mayoral E, Duveau J, Santos A, Rodríguez Ramírez A, Morales JA, Díaz-Delgado R, Rivera-Silva J, Gómez-Olivencia A, Díaz-Martínez I (2022) New dating of the Matalascañas footprints provides new evidence of the Middle Pleistocene (MIS 9-8) hominin paleoecology in southern Europe. Sci Rep 12(1): 17505. https://doi.org/10.1038/s41598-022-22524-2

McNutt EJ, Hatala KG, Miller C, Adams J, Casana J, Deane AS, Dominy NJ, Fabian K, Fannin LD, Gaughan S, Gill SV, Gurtu J, Gustafson E, Hill AC, Johnson C, Kallindo S, Kilham B, Kilham P, Kim E, Liutkus-Pierce CM, Maley B, Prabhat A, Reader J, Rubin S, Thompson NE, Thornburg R, Williams-Hatala EM, Zimmer B, Musiba CM, DeSilva JM (2021) Footprint evidence of early hominin locomotor diversity at Laetoli, Tanzania. Nature 600(7889): 468–471. https://doi.org/10.1038/s41586-021-04187-7

Murray AA (2022) Variability and the form–function framework in evolutionary biomechanics and human locomotion. Evol Hum Sci 4, e29. https://doi.org/10.1017/ehs.2022.28

Pastoors A, Lenssen-Erz T, Breuckmann B, Ciqae T, Kxunta U, Rieke-Zapp D, Thao T (2017) Experience based reading of Pleistocene human footprints in Pech-Merle. Quat Int 430, 155–162. https://doi.org/10.1016/j.quaint.2016.02.056

Ralston HJ (1958) Energy-speed relation and optimal speed during level walking. Int Z Angew Physiol Einschliessl Arbeitsphysiol 17(4): 277–283. https://doi.org/10.1007/BF00698754

Rotstein A, Inbar O, Berginsky T, Meckel Y (2005) Preferred transition speed between walking and running: effects of training status. Med Sci Sports Exerc 37(11):1864–1870. https://doi.org/10.1249/01.mss.0000177217.12977.2f

Sedrati M, Morales JA, Duveau J, El M'rini A, Mayoral E, Díaz-Martínez I, Anthony EJ, Bulot G, Sedrati A, Le Gall R, Santos A, Rivera-Silva J (2024) A Late Pleistocene hominin footprint site on the North African coast of Morocco. Sci Rep 14(1): 1962. https://doi.org/10.1038/s41598-024-52344-5

Sellers WI, Cain GM, Wang W, Crompton RH (2005) Stride lengths, speed and energy costs in walking of Australopithecus afarensis: Using evolutionary robotics to predict locomotion of early human ancestors. J R Soc Interface 2(5):431–441. https://doi.org/10.1098/rsif.2005.0060

Sirotkin AV (2025) Animal and human behavior to maximize energy income and to minimize its expenditure. Biosystems, 254, 105523. https://doi.org/10.1016/j.biosystems.2025.105523

Venkataraman VV, Kraft TS, Dominy NJ, Endicott KM (2017) Hunter-gatherer residential mobility and the marginal value of rainforest patches. Proc Natl Acad Sci USA 114(12): 3097–3102. https://doi.org/10.1073/pnas.1617542114

Wagnild J, Wall-Scheffler C (2013) Energetic consequences of human sociality: walking speed choices among friendly dyads. PLoS ONE, 8(10): e76576. https://doi.org/10.1371/journal.pone.0076576

Wall-Scheffler C (2012a) Energetics, locomotion, and female reproduction: implications for human evolution. Annu Rev Anthropol 41(1): 71–85. https://doi.org/10.1146/annurev-anthro-092611-145739

Wall-Scheffler C (2012b) Size and shape: morphology's impact on human speed and mobility. J Anthropol 2012, 1–9. https://doi.org/10.1155/2012/340493

Wall-Scheffler C, Myers MJ (2013) Reproductive costs for everyone: how female loads impact human mobility strategies. J Hum Evol 64(5):448–456. https://doi.org/10.1016/j.jhevol.2013.01.014

Zarrugh MY, Todd FN, Ralston HJ (1974) Optimization of energy expenditure during level walking. Eur J Appl Physiol Occup Physiol 33(4):293–306. https://doi.org/10.1007/BF00430237

Zorrilla-Revilla G, Volpe SL, Prado-Nóvoa O, Howard KR, Laskaridou E, Marinik EL, Ramadoss R, Davy KP, García-González R (2024) Far from the walking pace: ecological and evolutionary consequences of the suboptimal locomotion speeds in non-adult humans. Am J Hum Biol:e24138. https://doi.org/10.1002/ajhb.24138

Zorrilla-Revilla G (2022) Demandas energéticas de actividades de subsistencia en individuos subadultos. Contribuciones a la Ecología del Comportamiento Humano. Universidad de Burgos

Zorrilla-Revilla G, Prado-Nóvoa O, Davy KP, García-González R, Laskaridou E, Howard KR, Marinik EL, Carretero J-M, Volpe SL (2025) Morphological influences and energetic walking flexibility in determining preferred vs. optimal speeds: an evolutionary human ecology perspective on children and adolescents. Am J Biol Anthropol 188(3):e70152. https://doi.org/10.1002/ajpa.70152