



Alternative Metabolic Strategies are Employed by Endurance Runners of Different Body Sizes; Implications for Human Evolution

Adaptive Human Behaviour and Physiology Special Issue

Daniel P. Longman¹ · Viviane Merzbach² · Jorge Marques Pinto² ·
Laura Hope Atkinson³ · Jonathan C. K. Wells⁴ · Dan Gordon² ·
Jay T. Stock^{3,5}

Received: 17 September 2021 / Revised: 16 December 2021 / Accepted: 17 December 2021
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Abstract

Objective A suite of adaptations facilitating endurance running (ER) evolved within the hominin lineage. This may have improved our ability to reach scavenging sites before competitors, or to hunt prey over long distances. Running economy (RE) is a key determinant of endurance running performance, and depends largely on the magnitude of force required to support body mass. However, numerous environmental factors influence body mass, thereby significantly affecting RE. This study tested the hypothesis that alternative metabolic strategies may have emerged to enable ER in individuals with larger body mass and poor RE.

Methods A cohort of male ($n = 25$) and female ($n = 19$) ultra-endurance runners completed submaximal and exhaustive treadmill protocols to determine RE, and $\text{VO}_{2\text{Max}}$.

Results Body mass was positively associated with sub-maximal oxygen consumption at both LT1 (male $r=0.66$, $p<0.001$; female LT1 $r=0.23$, $p=0.177$) and LT2 (male $r=0.59$, $p=0.001$; female $r=0.23$, $p=0.183$) and also with $\text{VO}_{2\text{Max}}$ (male $r=0.60$, $p=0.001$; female $r=0.41$, $p=0.046$). Additionally, sub-maximal oxygen consumption varied positively with $\text{VO}_{2\text{Max}}$ in both male (LT1 $r=0.54$, $p=0.003$; LT2 $r=0.77$, $p<0.001$) and female athletes (LT1 $r=0.88$, $p<0.001$; LT2 $r=0.92$, $p<0.001$).

Conclusions The results suggest that, while individuals with low mass and good RE can glide economically as they run, larger individuals can compensate for the negative effects their mass has on RE by increasing their capacity to consume oxygen. The elevated energy expenditure of this low-economy high-energy turnover

Dan Gordon and Jay T. Stock are joint senior authors.

Extended author information available on the last page of the article

approach to ER may bring costs associated with energy diversion away from other physiological processes, however.

Keywords Evolution · Endurance running · Running economy · Energetics

Introduction

Humans as Endurance Runners

Humans are unique amongst primates in being able to run distances of multiple kilometres using aerobic metabolism (Carrier, 1984). This ability emerged during evolution of the hominin lineage. Although anatomically modern humans are poor sprinters compared to most quadrupeds, amateur human runners are typically able to sustain speeds of 5 m/s, which compares favourably with specialised quadrupedal cursors. For example, a 65 kg dog would be expected to have a trot-gallop transition speed of 3.8 m/s, and could then only gallop at around 7.8 m/s for up to 15-minutes under ideal conditions (Heglund & Taylor, 1988; Lieberman et al., 2006). A similar comparison can be made with horses, despite their selective breeding for running ability. Horses can maintain a gallop speed of 8.9 m/s for 10 km (much faster than humans), but are limited to a canter at around 5.8 m/s for distances around 20 km/day (beatable by well-trained humans) (Lieberman & Bramble, 2007; Minetti, 2003). This capability allows human runners to comfortably cover daily distances in excess of 10 km, which is comparable with the scavenging and hunting of hunting dogs and hyenas (Lieberman et al., 2006).

Scavenging and hunting may have provided the primary selective pressure leading to the evolution of endurance running, which likely emerged in the hominin lineage after our divergence from our last common ancestor with the chimpanzee (Lieberman et al., 2006). The ability to run long distances to hunt prey over long distances using methods such as persistence hunting (the pursuit of prey to the point of prey exhaustion / hyperthermia), may have improved the chances of acquiring meat (Bunn, 2001; Lieberman et al., 2006; Longman et al., 2015).

A suite of evolved features facilitate endurance running (Bramble & Lieberman, 2004; Lieberman, 2010, 2012a, b, 2015). These adaptations may be considered relative to four main demands posed by endurance running; energetics, strength, stabilisation and thermoregulation (Bramble & Lieberman, 2004). Considering energetics, humans exhibit a range of anatomical traits enhancing running economy (RE).

First, we are unique amongst primates due to the large number of long spring-like tendons allowing the energetically economic generation of force. Running employs a mass-spring mechanism, which handles the exchange between gravitational potential energy and kinetic energy differently to the walking gait. Energy is stored during the initial breaking when the foot lands, and released during the subsequent propulsive phase. The multitude of spring-like tendons (for example the Achilles tendon) that developed during the hominin lineage allows for the efficient storage and release of energy during running. While these tendons have little effect during walking, they

may reduce the energetic cost of running by around 50%. Tendons found in the longitudinal arch of the foot confer further energetic gains, returning almost a fifth of the energy generated during each stride (Ker, 1987).

Second, humans may gain further energetic efficiency whilst running by varying stride length. In contrast to quadrupeds, humans tend to increase running speed by increasing stride length, rather than by increasing stride rate [discussed in (Bramble & Lieberman, 2004)]. Thirdly, the lower limb elongation characterising the hominin lineage allows for not only a longer stride length, but also increased ground contact time, which reduces the metabolic cost of running (Roberts et al., 1998). Increasing ground contact time decreases the required rate of ground force application, reducing the energetic cost. As a result, the energy expenditure of running animals is an inverse function of ground contact time [discussed in (Wright & Weyand, 2001)]. The low resultant stride frequency of humans may also offset the drawback of long legs – an increased limb mass moment of inertia. This cost is also reduced by the compact feet of humans, which are smaller than those of Chimpanzees relative to body mass (Zihlman & Bruner, 1979).

The importance of energy in the process of evolution has long been recognised. Building upon the work of early proponents of the central role played by energy homeostasis (Boltzmann, 1886; Lodge, 1906), Lotka wrote that “...the fundamental object of contention in the life-struggle, in the evolution of the organic world, is available energy” (Lotka, 1922). The effects of the powerful influence of energy on our evolutionary journey are visible throughout our biology and function. For example, the adoption and persistence of bipedalism – considered a defining characteristic of human evolution (Dart, 1925; Napier, 1967; Rodman & McHenry, 1980) and instrumental in the development of endurance running ability – is understood to be driven by gains in locomotor efficiency serving to reduce the energetic cost of calorie acquisition (Cerling et al., 2010; Haile-Selassie, 2001; Pontzer et al., 2009; Senut & Pickford, 2004; Sockol et al., 2007). As the cooler and drier climate of the late Miocene is thought to have made food patches more sparse (Cerling et al., 1997), more economical locomotion allowed early hominins to travel greater distances in search of food (Rodman & McHenry, 1980).

Influence of Environmental Factors on Running Economy

RE is a key determinant of endurance running performance (di Prampero, 2003; Ingham et al., 2008; Joyner, 1991; Lucia et al., 2002; McLaughlin et al., 2010). While a range of physiological factors influence running economy [including mechanical efficiency (Cavanagh et al., 1977; Williams & Cavanagh, 1985), muscles' ability to store and release elastic energy by increasing lower-body stiffness (Dalleau et al., 1998) and intramuscular metabolic adaptations including increased mitochondria and oxidative enzymes (Holloszy et al., 1977)], RE depends largely on the magnitude of force generation required to support body mass. This force generation accounts for up to 74% of the total energetic cost of running (Ackerman & Seipel, 2016; Epstein et al., 1987; Farley & McMahon, 1992; Kram & Taylor, 1990;

Maldonado-Martin & Padilla, 2002; Taylor et al., 1980; Teunissen et al., 2007). Body mass is therefore an important driver of RE (Anderson, 1996; Pate et al., 1992).

Body mass is affected by a range of environmental factors. Considering climate, Bergmann's rule describes patterns of variation both within and across species relative to the temperature of their environment, with endotherms expected to be larger in colder environments (Bergmann, 1847). Recent research combining comprehensive palaeontological data with climate models demonstrates that temperature is the only environmental variable to correspond with variation in body size across the last one million years of hominin evolution (Will et al., 2021). While earlier Plio-Pleistocene increases in body size may have been driven by early hominin migrations into more variable environments and through changes in the hominin dietary niche (Will et al., 2017; Will & Stock, 2015), the recent analyses suggest that that thermal stress was the primary driver of variation in hominin body size within the genus *Homo* (Will et al., 2021). Modern humans also show patterns of phenotypic variation consistent with Bergmann's rule Crognier 1981; Foster & Collard, 2013; Hiernaux, 1968; Hiernaux & Fromont, 1976; Holliday, 1997a, b; Holliday & Trinkaus, 1991; Ruff, 1994; Stinson, 1990; Tilkens et al., 2007; Trinkaus, 1981). Early work by Roberts identified a negative relationship between mean annual temperature and body mass in humans (Roberts, 1953). The trends at higher latitudes have been reported to be diminishing in strength (Katzmarzyk & Leonard, 1998), and the pattern is only observable with a sufficiently large temperature (or latitude) range (Foster & Collard, 2013). Recent analyses of the relationship between body composition and environment found that lean mass, a metabolically expensive tissue, increases with food supply and decreases with a marker of food insecurity and infectious disease. In contrast, adiposity increases with temperature volatility, an indicator of the risk of infectious disease (Wells et al., 2019). These findings suggest that the relationship between climate and morphology extend beyond body mass, as predicted by Bergmann's Rule. The extent to which ecogeographic variation in human body-size is driven by natural selection or plasticity remains unknown, but it is likely that developmental plasticity is a key component of phenotypic variation in body size and proportions among homeotherms (Rogers, 2003; Serrat et al., 2008; Te Velde et al., 2003).

Body Mass and Metabolic Approaches to Endurance Running

It is clear from the sports science literature that excellent RE is necessary for success as an elite endurance runner (di Prampero, 2003; Ingham et al., 2008; Joyner, 1991; Lucia et al., 2002; McLaughlin et al., 2010; Shaw et al., 2015). However, the aim of ancestral endurance running was not to be the *fastest*, but rather, to be able to run *well enough* to hunt or scavenge successfully in order to survive. As previously discussed, numerous environmental factors influence adult body mass, potentially through both selection and plastic responses during development, which in turn significantly affects RE. As the ability to run long

distances would have been advantageous irrespective of body mass, it is possible that alternative metabolic strategies emerged, facilitating endurance running in individuals with larger body masses.

Here, we seek to test the hypothesis that, while individuals with low mass can perform endurance running economically, heavier runners may be able to compensate for their low economy by increasing their maximal capacity to consume oxygen ($\text{VO}_{2\text{Max}}$) and meet their elevated energetic costs of running. More specifically, in a cohort of successful ultra-endurance runners, we predict an inverse correlation between RE and $\text{VO}_{2\text{Max}}$.

Previous work has considered the relationship of RE and $\text{VO}_{2\text{Max}}$. Positive relationships have been reported from several studies with relatively small (Fletcher et al., 2009; Morgan & Daniels, 1994; Pate et al., 1992), and more recently in a larger cohort of 168 trained distance runners (males $r = 0.26$, female $r = 0.25$) (Shaw et al., 2015).

Methods

Study Design

Following local institutional ethical approval (Faculty Research and Ethics Panel, Anglia Ruskin University), $n = 46$ ultra-endurance runners (27 males, 19 females) agreed to participate and gave their written informed consent. All runners had previously competed in one of four multi-stage ultra-marathon events in 2016/17 (Rovaniemi150 (Finland), Jungle Ultra (Peru), Al Andalus Ultimate Trail (Spain) and Everest Trail Race (Nepal)) to be eligible for this study. This investigation stems from a wider research theme using contemporary sports as a tool to examine evolutionary theory Longman et al., 2015, 2018, 2019, 2020, 2021; Longman et al., 2017a, b). More specifically, the current study is part of the ADaPt Project, which is developing the use of ultra-endurance challenges as experimental scenarios to study trade-offs relating to life history theory (Longman et al., 2017a, b).

All participants attended the Cambridge Centre for Sport and Exercise Sciences on one occasion for the assessment of isokinetic knee extensors and flexors peak torques across a range of angular speeds during concentric and eccentric loading for both legs. Furthermore, all participants ($n = 44$, 2 male participants had to be excluded: 1 due to medical reasons, 1 due to equipment failure) performed an incremental treadmill test for the evaluation of running economy, sub-maximal blood lactate responses and the assessment of maximal oxygen uptake ($\dot{\text{V}}\text{O}_{2\text{max}}$). Body mass (kg) was measured using electronic scales (Seca, Hamburg, Germany) and body height (cm) was determined using a stadiometer (Seca, Hamburg, Germany) prior to all testing.

Submaximal Treadmill Protocol

Each participant completed a submaximal incremental speed-based protocol for the determination of lactate threshold 1 (LT1), lactate turn-point 2 (LT2), and running economy (RE) (Gordon et al., 2017). The starting speed was selected on an individual basis to coincide with a speed that the participant would normally warm-up at, and thereafter was increased by $1 \text{ km}\cdot\text{h}^{-1}$ every 3 min. Throughout the test, the gradient was kept constant at 1%. After each 3-minute increment, there was a 1-minute break where upon the participant was asked to stand astride of the treadmill to facilitate the collection of a capillary fingertip blood sample ($20 \mu\text{L}$) for the immediate determination of blood lactate concentrations. Once the sample was collected, the participants were asked to ease themselves back onto the treadmill and complete the remaining time of the 1-minute recovery at walking pace ($4 \text{ km}\cdot\text{h}^{-1}$). Throughout the test, individual blood lactate responses ($\text{mmol}\cdot\text{L}^{-1}$) were plotted against exercise intensity ($\text{km}\cdot\text{h}^{-1}$) for the determination of lactate LT1 and LT2. Identification of LT1 was based on the first initial rise above baseline, whilst LT2 was the sudden and sustained increase in blood lactate, determined through visual inspection of the blood lactate curve (Bourdon, 2000; Gordon et al., 2017). Two physiologists present in the laboratory independently validated both LT1 and LT2. The test was terminated once the participant had reached LT2. Gas exchange responses were recorded throughout all trials on a breath-by-breath basis with a pre-calibrated metabolic cart (MetaLyzer 3B-R2, Cortex Ltd, Germany) and HR responses were tracked using a telemetric system (T31 heart rate strap, Polar, Kempele, Finland). Oxygen consumption at LT1 and LT2 was used to provide the measure of RE used in subsequent analyses.

$\text{VO}_{2\text{max}}$ Protocol

Upon completion of the submaximal treadmill protocol and following a 7-minute recovery, each participant was asked to complete an incremental gradient-based treadmill test to volitional exhaustion. The running speed was based on the speed at which LT2 occurred in the previous protocol and kept constant throughout. Every minute, the gradient was increased by 1% (starting at 1%) until volitional exhaustion was reached, or when the participant was unable to maintain a predetermined position at the front of the treadmill. Verbal encouragement was provided towards the end of the test to facilitate a maximal effort of the participant. Immediately after completion of the $\dot{\text{V}}\text{O}_{2\text{max}}$ test, a capillary blood sample ($20 \mu\text{L}$) was collected for the determination of post-exercise blood lactate and glucose concentrations. Throughout the trial, expired air was recorded on a breath-by-breath basis and HR responses were documented using a telemetric system.

For both treadmill protocols, participants wore a harness connected to an emergency stop system of the treadmill for safety purposes.

Blood Lactate and Glucose Analysis

Capillary blood samples (20 μL) for the determination of blood lactate and glucose were collected from the fingertip. For each blood sample, the fingertip was pierced with a single-use lancet device system (ACCU-CHEK Safe-T-Pro Plus). The blood was drawn into an end-to-end haemolysed micro-capillary and placed into a pre-filled (with haemolysing solution) sample test tube (2 mL). To prepare the sample for immediate measurement with a lactate and glucose analyser (Bio-sen C-Line, EKF-diagnostic, Germany), the test tube was gently agitated until a uniform solution was produced. The analyser was set to self-calibrate every 60 min according to the manufacturer's instructions.

Pulmonary Gas Exchange Responses

Expired air was recorded for the assessment of pulmonary gas exchange responses. Participants wore a facemask secured with headgear (7600 Face Mask with Headgear, Hans Rudolph, USA) where the size of the mask was selected so that a seal could be achieved. A low-resistance volume transducer and capillary sample line for gases were secured to the facemask with both connected to an online metabolic cart (MetaLyzer 3B-R2, Cortex Ltd, Germany) which allowed for breath-by-breath analysis. Through the sample line, O_2 and CO_2 were drawn off at a rate of $60 \text{ mL}\cdot\text{min}^{-1}$ to determine expired gas concentrations. To align gas concentrations and respiratory responses, custom metabolic cart software (MetaSoft Studio V4.60, Cortex Ltd, Germany) was used to display breath-by-breath gas exchange variables (volume of oxygen ($\dot{V}\text{O}_2$), volume of carbon dioxide ($\dot{V}\text{CO}_2$), minute ventilation ($\dot{V}\text{E}$), respiratory exchange ratio (RER)). According to the manufacturer's specifications, the metabolic cart was calibrated for volume, flow, and gas concentrations prior to each trial. Anglia Ruskin University have previously achieved a 3.7% internal coefficient of variation for this technique.

Statistics

SPSS v27 was used for all analyses, with a significance benchmark of 0.05. Independent samples t-tests were used to compare male and female descriptive statistics. Correlations between body mass, RE and $\text{VO}_{2\text{Max}}$ were evaluated using Pearson's Product Moment Correlations. Scatter plots were made to visualize the relationship between variables. Finally, a multiple linear regression model was used.

Results

Descriptive Statistics

As expected, the cohort exhibited sexual dimorphism. Males were 17.7 (95% CI 12.0, 22.5)kg heavier, 14.6 (95% CI 11.2, 19.0)cm taller, 1.0 (95% CI 0.3, 1.7) km/h faster at LT1, 1.2 (95% CI 0.3, 2.2) km/h faster at LT2 and had a $\text{VO}_{2\text{Max}}$ 4.4 (95% CI 0.8, 8.0)ml/kg/min larger. Males were also 5.4 (95% CI 0.4, 10.4) years older. There were no significant sex differences in oxygen consumption at either LT1, LT2, or between oxygen consumption at LT1 or LT2 as a percentage of $\text{VO}_{2\text{Max}}$. A description of the male and female cohorts is given in Table 1.

Body Mass, RE and $\text{VO}_{2\text{Max}}$

Regression analysis was performed to analyse the relationship between body mass and oxygen consumption at LT1 and LT2.

At LT1, a significant positive correlation was observed in male ($n = 25$, $r = 0.66$, $p < 0.001$, 1-tailed; standardized 95% CI, 0.012 to 0.034) and a positive trend was seen in female athletes ($n = 18$, $r = 0.23$, $p = 0.177$, 1-tailed; standardized 95% CI, -0.013 to 0.034). At LT2, a positive correlation was observed in male ($n = 25$, $r = 0.59$, $p = 0.001$, 1-tailed; standardized 95% CI, 0.012 to 0.047) and female athletes ($n = 18$, $r = 0.23$, $p = 0.183$, 1-tailed; standardized 95% CI, -0.015 to 0.039). See Fig. 1.

Regression analysis revealed a significant positive correlation between body mass and $\text{VO}_{2\text{Max}}$ in both male athletes ($n = 25$, $r = 0.60$, $p = 0.001$, 1-tailed; standardized 95% CI, 0.016 to 0.062) and female athletes ($n = 18$, $r = 0.41$, $p = 0.046$, 1-tailed; standardized 95% CI, -0.004 to 0.047). See Fig. 2.

$\text{VO}_{2\text{Max}}$ and RE

Regression analysis revealed significant positive correlations between $\text{VO}_{2\text{Max}}$ and RE in both male and female athletes. At LT1 there was a significant positive correlation with both male ($n = 25$, $r = 0.54$, $p = 0.003$, 95% CI 0.332 to 1.722) and female athletes ($n = 18$, $r = 0.88$, $p < 0.001$, 95% CI 0.681 to 1.230). Similarly, at LT2 there was a significant positive correlation with both male ($n = 25$, $r = 0.77$, $p < 0.001$, 95% CI 0.635 to 1.342) and female athletes ($n = 18$, $r = 0.92$, $p < 0.001$, 95% CI 0.677 to 1.067). See Fig. 3.

A partial correlation was run to determine the relationship between $\text{VO}_{2\text{Max}}$ and running economy whilst controlling for body mass. This is necessary as both variables are expressed relative to body mass, creating a common denominator which can lead to spurious correlations (Atkinson et al., 2003). Both sexes displayed a significant positive correlation between $\text{VO}_{2\text{Max}}$ (ml/kg/min) and RE (ml/kg/min). At LT1 the correlation was significant in males ($r(22) = 0.420$, $p = 0.041$) but not females ($r(15) = 0.138$, $p = 0.598$) while at LT2 the correlation was significant in both males ($r(22) = 0.765$, p

Table 1 Sample descriptive statistics

	Males (n = 25)			Females (n = 18)			Delta	95% CI	p
	Mean	SD	Range	Mean	SD	Min, Max			
	Age (years)	46.0	8.2	24, 65	40.9	8.10			
Body mass (kg)	81.3	9.9	64.5, 98.7	63.5	5.9	53.0, 73.2	17.8	2.4, 12.9	<0.001
Height (cm)	180.3	5.7	169.1, 190.8	165.6	5.5	154.0, 172.4	14.7	11.2, 18.3	<0.001
Speed at LT1 (km/h)	10.0	1.2	8.0, 12.0	9.1	1.2	7.0, 11.0	1.0	0.3, 1.7	0.009
Oxygen cost at LT1 (ml/kg/km)	199.2	16.7	173.5, 230.2	201.8	13.9	181.1, 234.1	-2.6	-12.4, 7.1	0.591
Oxygen cost at LT1 as % of VO _{2max} (%)	67.9	7.4	48.5, 83.4	68.1	4.8	56.5, 75.9	-0.3	-4.3, 3.7	0.887
Speed at LT2 (km/h)	12.5	1.6	10.0, 16.0	11.2	1.5	9.0, 14.0	1.3	0.3, 2.3	0.009
Oxygen cost at LT2 (ml/kg/km)	193.0	19.0	162.5, 238.3	196.0	15.6	178.3, 230.8	-3.0	-14.1, 8.0,	0.580
Oxygen cost at LT2 as % of VO _{2max} (%)	81.6	6.4	63.4, 93.1	81.9	4.9	73.6, 89.7	-0.3	-3.9, 3.4	0.876
VO _{2max} (ml/kg/min)	49.3	6.3	39.4, 62.7	44.6	5.0	38.9, 56.6	4.7	1.0, 8.3	0.013

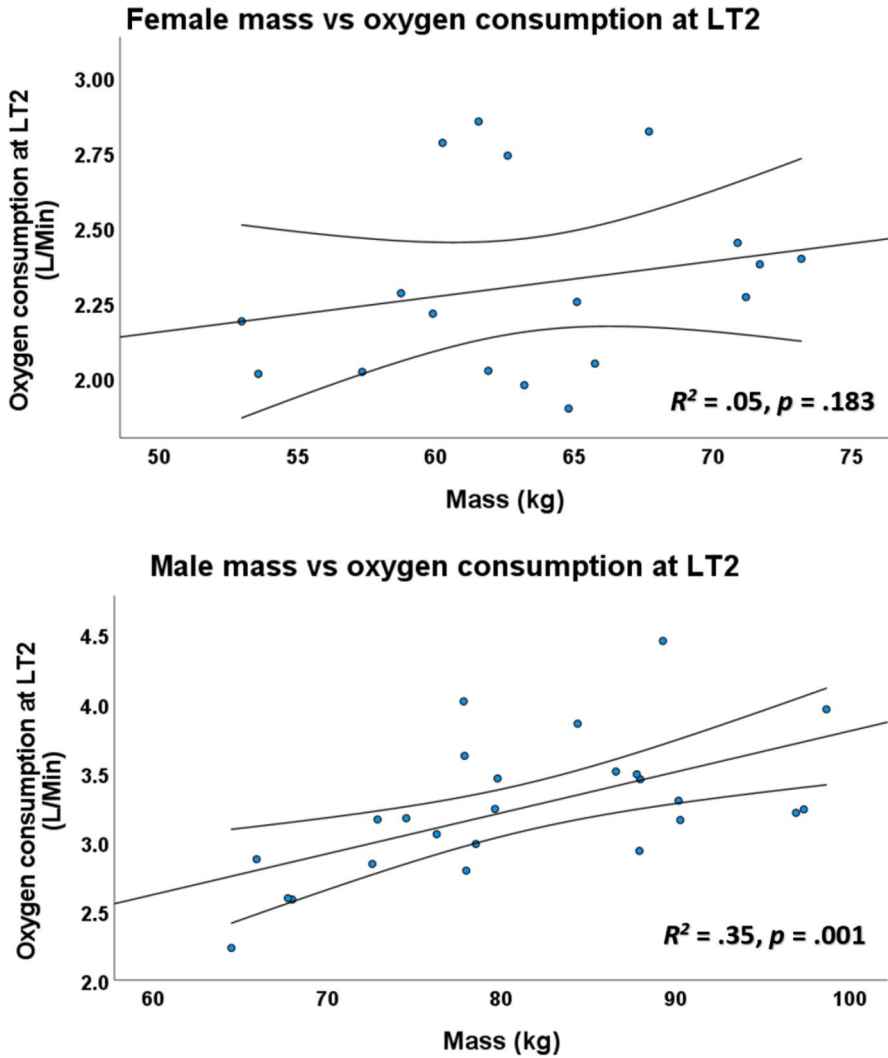


Fig. 1 Scatter plot of body mass and oxygen consumption at LT2 for male and female participants (95% confidence interval)

< 0.001) and females ($r(15) = 0.904, p < 0.001$). Zero-order correlations showed that these correlations persisted, indicating that body mass had little influence in controlling for the relationship between VO_{2Max} and RE.

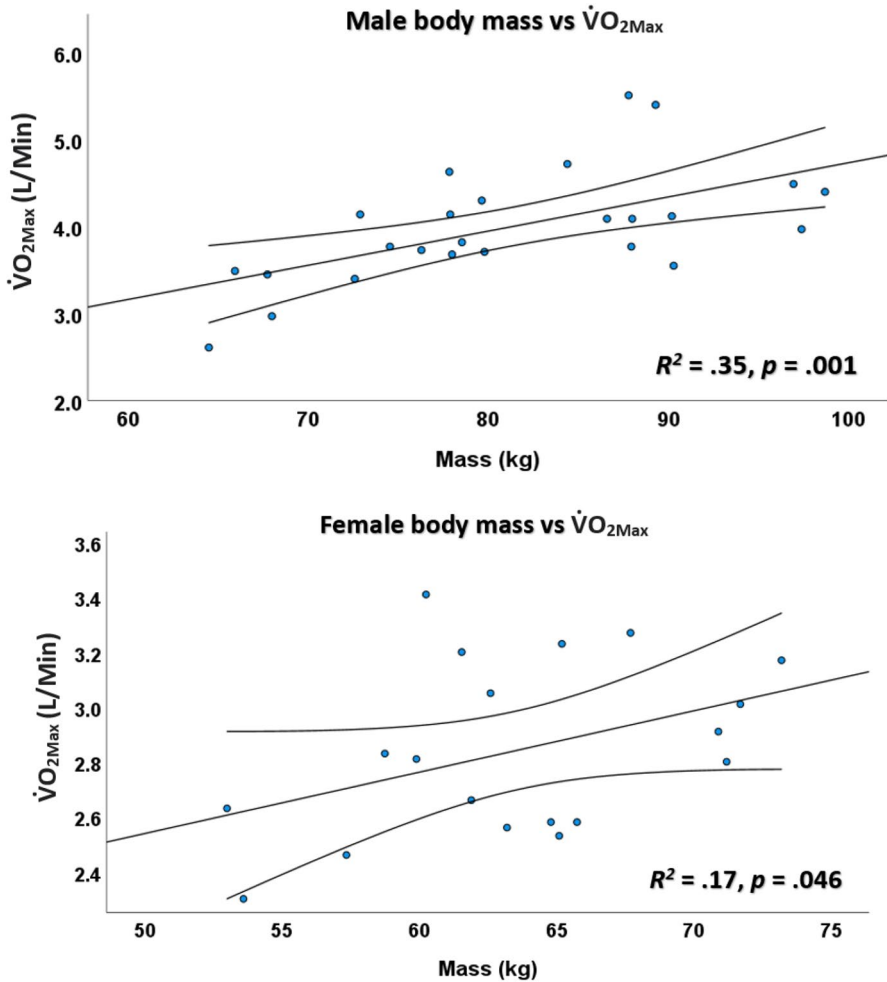


Fig. 2 Scatter plot of body mass and $\dot{V}O_{2Max}$ for female and male participants (95% confidence intervals)

Discussion

Body mass was found to vary negatively with RE in both male and female athletes (as observed by positive correlations between mass and oxygen consumption at both LT1 and LT2 in male and female athletes). This was consistent with the existing literature (Anderson, 1996; Pate et al., 1992). Other variables that might be expected to contribute to variation in RE include mechanical efficiency (Cavanagh et al., 1977; Williams & Cavanagh, 1985), the muscles' ability to store and release elastic energy by increasing lower-body stiffness (Dalleau et al., 1998) as well as intramuscular metabolic adaptations, which include increased mitochondria and oxidative enzymes (Holloszy et al., 1977). Further, this study

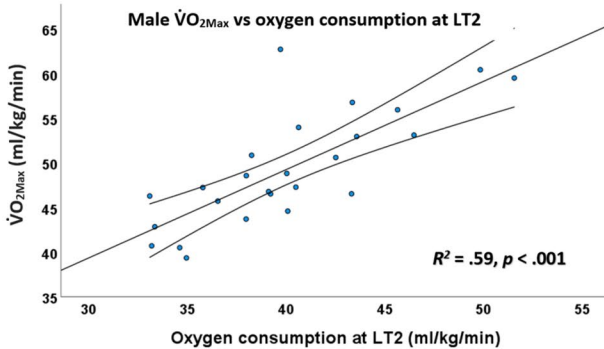
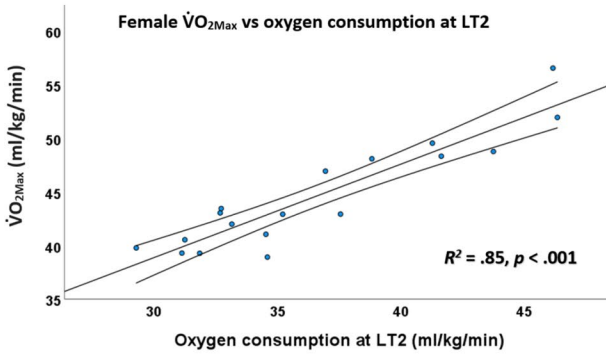
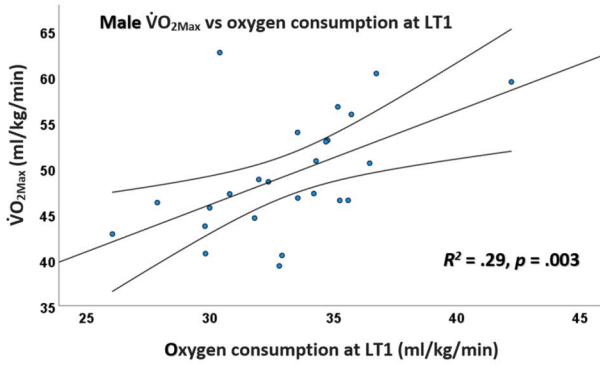
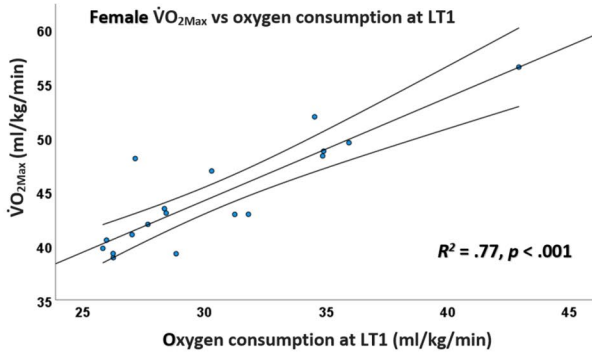
Fig. 3 Scatter plot of RE at LT1 & LT2 and VO_{2Max} for female and male participants (95% confidence intervals) ▶

identified an inverse relationship between VO_{2Max} and RE. This was observed as a positive correlation between VO_{2Max} and oxygen consumption at both LT1 and LT2 in male and female athletes. This inverse relationship has previously been reported in elite cyclists (Lucia et al., 2002; Santalla et al., 2009) as well as trained endurance runners (Fletcher et al., 2009; Morgan & Daniels, 1994; Pate et al., 1992; Shaw et al., 2015), leading to the suggestion that competitive runners may compensate for a lower VO_{2Max} with superior RE. To our knowledge, this is the first study demonstrating a negative association between VO_{2Max} and RE in ultra-endurance athletes.

Prehistoric hominin foragers engaged in persistence hunting differ from modern-day endurance athletes in that they did not strive to be the *fastest*. Instead, the challenge was to be able to run *well enough* to enhance survival by scavenging and/or hunting to access nutrition. They did so using bodies of variable mass and proportions, shaped by environmental stress such as temperature, with larger body sizes typically found in colder, more open environments with greater frequencies of large game (Will et al., 2021). Individuals with good RE and lower body mass, common in warmer environments, could likely *glide* economically as they ran. In contrast, our results suggest that larger individuals typical of hominins living in colder environments may be able to compensate for the negative effects that their mass has on RE by increasing their capacity to consume oxygen. This may allow them to *power* their way to calories. The findings reported in this study, which recruited a cohort of athletes who have successfully completed an ultramarathon (150–300 km in distance), are thereby suggestive of the existence of alternative metabolic approaches to performing endurance running. These different strategies allow humans, irrespective of their adult body size, to occupy the same behavioural niche of endurance running as a means of acquiring calories.

The elevated energy expenditure associated with the low-economy high-energy turnover approach may bring costs, however. Recent work has identified preliminary evidence suggestive of an apparent limit to daily energy expenditure, with daily energy expenditure being homeostatically maintained within a narrow evolved physiological range (Pontzer, 2015a, b; Pontzer et al., 2016). The constrained total energy expenditure model contends that the addition of further physical activity, with associated additional energy costs, to individuals who are already moderately active does not result in increased total energy expenditure. This is achieved through a redistribution of energy away from other biological functions.

The allocation of limited energy and resources between physiological functions is described by life history theory (Leonard, 2012; Leonard & Ulijaszek, 2002; Stearns, 1989; Ulijaszek, 1995; Wells et al., 2017; Zera & Harshman, 2001). When an individual encounters an energetic deficit, such as during periods of limited food availability or when energy demands unexpectedly increase, life history theory contends that trade-offs arise in the energetic allocation between



competing processes (Bronson, 1991; Stearns, 1992). In such conditions, energy is expected to be allocated towards processes offering the greatest immediate survival value. For example, the prioritisation of immune function over reproduction (Longman, Prall, et al., 2017) and growth (Urlacher et al., 2018) has been reported. A large runner adopting the low-economy high-energy turnover approach to endurance running experiences a greater metabolic burden, which may in turn push physiological functions to the limits of adaptive plasticity (Longman et al., 2020).

This increased metabolic turnover may also be detrimental in the long term. Reactive oxygen species (ROS) are by-products of aerobic metabolism, and induce pathology via oxidative stress by damaging proteins, lipids and DNA (Cross et al., 1987; Schieber & Chandel, 2014). The generation of harmful ROS, and the associated physiological response to protect against oxidative stress, is a key determinant of longevity (Finkel & Holbrook, 2000). A recent analysis of the life expectancy of elite athletes found that, independent of weight, high jumpers and marathon runners outlived sprinters and discus throwers (Lee-Heidenreich et al., 2017). Although further work is clearly needed, our results suggest that the higher rates of oxygen turnover associated with a larger lean body mass may partially explain the observed decreased longevity.

It is appreciated that numerous factors affecting both RE and $\text{VO}_{2\text{Max}}$, including training status, body composition and morphology, age and running technique (see (Morgan et al., 1989; Saunders et al., 2004) for a detailed discussion) were not controlled for in this study. Finally, we acknowledge that the sample size of this study was small, and the findings will require confirmation with a larger sample.

To conclude, we observed a strong negative relationship between $\text{VO}_{2\text{Max}}$ and RE in a cohort of ultra-endurance athletes. This relationship suggests that our hominin ancestors may have been able to occupy the behavioural niche of endurance running irrespective of their body mass by adopting different metabolic approaches. Specifically, larger individuals may have been able to compensate for low running economy by burning more energy. However, this approach may incur costs as energy may be drawn away from other biological functions, potentially including homeostatic maintenance.

Funding European Research Council under the European Union's Seventh Framework Programme, Grant/Award Number: (FP/ 2007-2013)/ERC Grant Agreement n.617627 to JTS.

Data Availability The datasets generated and analysed during the current study are available from the corresponding author upon reasonable request.

Declarations

Conflict of Interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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Authors and Affiliations

Daniel P. Longman¹  · **Viviane Merzbach**²  · **Jorge Marques Pinto**²  ·
Laura Hope Atkinson³  · **Jonathan C. K. Wells**⁴  · **Dan Gordon**²  ·
Jay T. Stock^{3,5} 

✉ Daniel P. Longman
D.Longman@lboro.ac.uk

✉ Dan Gordon

✉ Jay T. Stock

¹ School of Sport, Exercise and Health Sciences, Loughborough University,
LE11 3TU Loughborough, UK

² Cambridge Centre for Sport & Exercise Sciences, Anglia Ruskin University,
Cambridge CB1 1PT, UK

³ Department of Anthropology, University of Western Ontario, London, Ontario, Canada

⁴ Childhood Nutrition Research Centre, UCL Institute of Child Health, WC1N 1EH London, UK

⁵ Department of Archaeology, Max Planck Institute for the Science of Human History, Kahlaische
Strasse 10, D-07745 Jena, Germany