



# Human athletic paleobiology; using sport as a model to investigate human evolutionary adaptation

Daniel P. Longman<sup>1</sup> | Jonathan C. K. Wells<sup>2</sup> | Jay T. Stock<sup>3,4,5</sup>

<sup>1</sup>School of Sport, Exercise and Health Sciences, Loughborough University, Loughborough, UK

<sup>2</sup>Childhood Nutrition Research Centre, UCL Institute of Child Health, London, UK

<sup>3</sup>Department of Anthropology, University of Western Ontario, London, Ontario, Canada

<sup>4</sup>Department of Archaeology, Max Planck Institute for the Science of Human History, Jena, Germany

<sup>5</sup>Department of Archaeology, University of Cambridge, Cambridge, UK

## Correspondence

Daniel P. Longman, School of Sport, Exercise and Health Sciences, Loughborough University, Clyde Williams Building, Epinal Way, Loughborough LE11 3TU, UK.  
Email: d.longman@lboro.ac.uk

## Abstract

The use of sport as a conceptual framework offers unprecedented opportunities to improve our understanding of what the body does, shedding new light on our evolutionary trajectory, our capacity for adaptation, and the underlying biological mechanisms. This approach has gained traction over recent years. To date, sport has facilitated exploration not only of the evolutionary history of our species as a whole, but also of human variation and adaptation at the interindividual and intraindividual levels. At the species level, analysis of lower and upper limb biomechanics and energetics with respect to walking, running and throwing have led to significant advances in the understanding of human adaptations relative to other hominins. From an interindividual perspective, investigation of physical activity patterns and endurance running performance is affording greater understanding of evolved constraints of energy expenditure, thermoregulatory energetics, signaling theory, and morphological variation. Furthermore, ultra-endurance challenges provoke functional trade-offs, allowing new ground to be broken in the study of life history trade-offs and human adaptability. Human athletic paleobiology—the recruitment of athletes as study participants and the use of contemporary sports as a model for studying evolutionary theory—has great potential. Here, we draw from examples in the literature to provide a review of how the use of athletes as a model system is enhancing understanding of human evolutionary adaptation.

## KEYWORDS

adaptation, human athletic paleobiology, human evolution, plasticity, sport

## 1 | INTRODUCTION

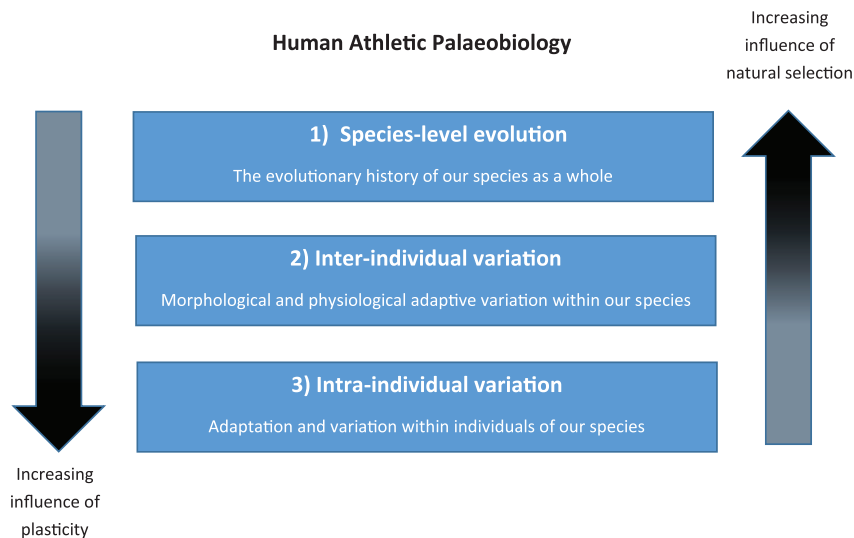
The fossil record provides evidence about the form and physical characteristics of the human or hominin body, and their changes over time. However, a central challenge of hominin paleobiology is the interpretation of the body's function from its form; how do we walk, run, use tools, and move within the landscape, and how did these functions themselves evolve? Stemming from this, what is the nature of the physiological mechanisms that underpin observed variation in form and function?

The use of sport as a conceptual framework offers unprecedented opportunities to improve our understanding of what the body does, shedding new light on our evolutionary trajectory, our capacity for adaptation, and the underlying biological mechanisms.

There has been increasing interest in the model system provided by athletes to enhance our understanding of human evolutionary theory. To date, studies of athletes have facilitated exploration of three key levels of variation and adaptation within the field of human evolution (Figure 1).

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2020 The Authors. *American Journal of Physical Anthropology* published by Wiley Periodicals, Inc.



**FIGURE 1** Conceptual diagram highlighting the levels of adaptation studied using sport

**TABLE 1** How sports and athletes have been used to study different levels of adaptation

Level of adaptation	How are using sports and athletes being used?	Which component of adaptation is being addressed?	Examples highlighted from the literature
Species-level evolution	Sportspeople as being representative of past populations	Natural selection acting on lower and upper limbs	Runners and javelin throwers
Interindividual variation	Physical activity as a proxy for subsistence activity in the past	Natural selection, population history, developmental plasticity leading to: <ul style="list-style-type: none"> <li>• Constrained energy expenditure</li> <li>• Ecogeographical patterning</li> <li>• Intersexual selection</li> </ul>	Various endurance competitions
Intraindividual variation	Skeletal analysis of sportspeople to infer adaptations to particular loading patterns, informing interpretation of fossil record	Details how the body adapts through plasticity to demands of subsistence tasks	Cross-country runners, swimmers, rowers
	Sport as a tool to reveal morphological traits and behaviors that are under selection and the dynamic response to competition	Intrasexual selection	Football, skiing, rowing
	To impose an energetic load and provoke functional trade-offs	Plasticity	Ultra-endurance sport, rowing

In parallel, different types of adaptation can be investigated through the lens of sports studies. Table 1 highlights this and provides an overview of this article. At the level of species-level evolution, sports can provide an inferential model for the study of natural selection. At the other end of the spectrum, sports can be used to examine short-term intraindividual plasticity. It is important to note, however, that the capacity for plastic adaptation also has a heritable component (Wells & Stock, 2011).

Firstly, studies utilizing athletic protocols and/or analyzing athletes have elucidated the evolutionary history of our species. This approach has facilitated significant advances in understanding human form and function relative to other hominins in both the upper and lower limbs. Observational and experimental investigations integrating laboratory and field studies with the fossil record have furthered understanding of evolved athletic activities such as bipedal endurance running (Bramble & Lieberman, 2004; Lieberman, 2010, 2012a, 2012b, 2015), the use of projectile technology and spear thrusting

(Milks, Parker, & Pope, 2019; Rhodes & Churchill, 2009; Shaw, Hofmann, Petraglia, Stock, & Gottschall, 2012). This methodology has provided new perspectives toward a range of human morphological traits.

Secondly, this approach is shedding new light on human inter-individual variation. Variation within the human species may reflect the response to selection acting on different groups in the past (e.g., environmental conditions and sex-specific energetic pressures). Alternatively, it could also arise through early developmental exposures with effects that may be irreversible later in life (e.g., low birth weight and later-life constraints in lean body mass), or due to the effects of population history. Investigators in this area have highlighted the influence of physical activity as a selective pressure driving variability in metabolic efficiency (Pontzer, 2015a; Pontzer et al., 2016; Pontzer et al., 2012) and body proportions (Longman et al., 2019).

Thirdly, sport is providing valuable insights into intraindividual variation. Adaptation and variability at the intraindividual level may be more rapid in nature. Much intraindividual variation is achieved via

the process of phenotypic plasticity (Hill & Hurtado, 1996). One key adaptive response is the dynamic nature of internal energy distribution in response to environmental energy availability. Life history theory, a branch of evolutionary theory, seeks to characterize the competitive allocation of limited resources between physiological functions throughout the lifespan (Leonard, 2012; Stearns, 1989, 1992; Zera & Harshman, 2001). The study of contemporary sports and athletes in an evolutionary context has the potential to significantly enhance knowledge of our adaptive capabilities as a phenotypically plastic species. This is because athletic events themselves can be used to provoke functional trade-offs, allowing new ground to be broken in the study of life history trade-offs and human adaptability.

This article will review the areas of human evolutionary theory already benefitting from the application of this novel approach, considering human variation at the species, interindividual and intra-individual levels in turn. It is hoped that this review will highlight the potential of athletic models not only to complement existing methodologies in human paleobiology, but also to provide unique advances beyond the scope of traditional approaches.

## 1.1 | Species-level evolution

Athletic disciplines, particularly those associated with locomotion and throwing, are providing insights toward the evolutionary history of our species as a whole. This section will review the contributions to current understanding of aspects of the form and function of the human lower and upper limb. In an increasingly sedentary contemporary Western society (Owen, Sparling, Healy, Dunstan, & Matthews, 2010) athletes are often the study participants most aligned with the ancestral populations of interest. The importance of studying athletes with specific training in the activities of interest will be highlighted.

## 2 | LOWER LIMB VARIATION

The use of experimental sporting protocols and the analysis of athletes is shedding new light on hominin lower limb morphological variation. Alongside the development of an enlarged and elaborated brain, the adoption of bipedalism is considered a defining characteristic of human evolution (Dart, 1925; Napier, 1967; Rodman & McHenry, 1980a). In his comprehensive review, Niemitz (2010) describes the range of theories that have been suggested to explain this phenomenon. While theories developed before the early 1990s described a savannah environment as the environment of origin of hominin bipedalism (Rose, 1976), it is now generally accepted that a fragmented and variable environment, including woodland, was more likely (Cerling et al., 2010). An explanation which has gained significant traction suggests that hominin bipedalism was instead driven by gains in locomotor efficiency, reducing the cost of foraging (Haile-Selassie, 2001; Pontzer, Raichlen, & Sockol, 2009; Senut & Pickford, 2004; Sockol, Raichlen, & Pontzer, 2007). Toward the end of the Miocene, when the cooler and drier climate may have made food patches more sparse

(Cerling et al., 1997), energetic savings in locomotion would have been increasingly beneficial. This allowed early hominins to travel further distances to find food sources (Rodman & McHenry, 1980b).

This section will draw examples from the literature to highlight how both the deployment of sporting protocols and the analysis of athletes is driving understanding of the development of this key feature of our evolutionary history.

Firstly, anthropological investigations employing techniques typically found in kinesiology and sports science laboratories have shone new light on lower limb evolution. Studies using treadmills and respiratory gas analysis have compiled evidence supporting the theory that lower limb mechanical efficiency may have been driven by selective pressures enhancing locomotion economy when both walking and running (Bramble & Lieberman, 2004; Pontzer, 2007; Steudel-Numbers & Tilkins, 2004; Steudel-Numbers, Weaver, & Wall-Scheffler, 2007; Will, Pablos, & Stock, 2017; Wright & Weyand, 2001). Although it is possible that the shorter lower limbs of *Australopithecus afarensis* conferred an economical advantage when walking (albeit with the disadvantage of a slower walk-run transition speed; Jungers, 1982; Kramer & Eck, 2000; Kramer, 1999; Ward, 2002), there have been several reports that the longer legs which emerged later in the *Homo* lineage brought demonstrable benefits at a variety of walking speeds (Steudel-Numbers & Tilkins, 2004). Elongated lower limbs confer an increased optimal walking pace (Bramble & Lieberman, 2004) and enhanced running efficiency across a range of species (Pontzer, 2007; Steudel-Numbers et al., 2007). While the rationale behind this is complex (Pontzer, 2005), an intuitive explanation is that an individual with longer legs has to take fewer strides to cover a given distance, and would match the speed of a smaller individual while maintaining a lower cadence (see Bramble & Lieberman, 2004; Heglund & Taylor, 1988; Higgins & Ruff, 2011; Jungers, 1982). This results in increased locomotor efficiency as the energetic requirement of a single step is a function of leg length and is largely invariant (Weyand, Smith, Puyau, & Butte, 2010).

Selective pressures acting to improve walking efficiency (Schmitt, 2003; Susman, Stern, & Jungers, 1984), and those favoring the development of endurance running ability (Bramble & Lieberman, 2004), may explain the transition to modern locomotor anatomy from *Australopithecus* to *Homo* (Lieberman, 2015). Consequently, contemporary human habitual bipedalism is distinctive and efficient among extant mammals. Our optimal walking speed is approximately 20% faster and four times more efficient than our closest living relatives, the chimpanzee (Pontzer, Raichlen, & Rodman, 2014; Rubenson et al., 2007; Taylor, Heglund, & Maloiy, 1982). It is noted, however, that Halsey and White (2012) have suggested that the hominin locomotion does not differ in its locomotion costs in comparison with other mammals.

The value of studying athletes has been demonstrated in the barefoot running literature. Humans have been performing endurance running for more than two million years, either barefoot or with minimal footwear over the last 50,000 years (Bramble & Lieberman, 2004; Pinhasi et al., 2010; Trinkaus, 2005). However, the last 50 years has seen the running market flooded with specialist running shoes exhibiting thick cushioned soles and heels (Shawcross, 2014). Dan

Lieberman's group has been at the forefront of research investigating the biomechanical consequences of this technological innovation, making significant advances through investigation of trained runners.

Considering first the biomechanical effect of wearing running shoes, Lieberman argues that the cushioning and support creates an environment to which the human foot is not evolved (Lieberman, 2014). Comparative analyses of the biomechanics of running with no or minimal footwear with running shoes have revealed key differences in running techniques. Patterns of barefoot running are typically characterized by a forefoot or mid-foot strike before the heel contacts the ground. Rearfoot striking, in which the heel contacts the ground first, is rare. In contrast, running in cushioned trainers is associated with an increased tendency to land on the heel. Rearfoot striking generates a rapid and high-impact ground reaction force that must be absorbed by the skeleton. In contrast, forefoot striking, in which the ball of the foot contacts the ground before the heel, avoids the generation of impact peaks as the foot is in a more plantarflexed position upon landing and ankle compliance is increased (see Perl, Daoud, & Lieberman, 2012). Even on hard surfaces, shod rearfoot striking generates larger collision forces than barefoot forefoot striking, potentially increasing the risk of injury (Aibast et al., 2017; Lieberman et al., 2010; Lieberman, 2012b; Perl et al., 2012).

While analyzing running foot strike biomechanics, Lieberman and colleagues found that different foot strike angles were observed depending on whether or not the participant was an athlete. Study participants with higher levels of previous running experience, and with faster mile times, were more likely to forefoot or mid-foot strike than those who were less athletic (Lieberman et al., 2015).

This illustrates an important point—sportsmen and sportswomen are invaluable to anthropologists because they are more representative of past populations than the average person. Numerous metrics indicate that contemporary Western society is growing more sedentary. Jobs are becoming less physically demanding, screen time is increasing (time spent using a computer or phone, watching a television or playing video games), as is time spent sitting (see Owen et al., 2010). As a result, the average member of sedentary Western society may not be a representative model for investigations of biomechanical and energetic aspects of evolved habitual activities such as running, or even walking. The fundamental differences in the running gait between those who do and do not regularly run highlights the value of examining athletes when attempting to model behavior from our past. To gain more accurate insight into the evolved characteristics of locomotion, it is necessary to recruit study participants with repetitive habitual activity profiles more aligned with our active ancestors.

### 3 | UPPER LIMB VARIATION

Investigations employing sporting protocols and analyzing athletes trained in the relevant discipline have also provided insights into hominin morphological variation in the upper limb. This new approach is challenging pre-existing behavioral interpretations of physical traits found in the fossil record. Two examples from the literature will be

reviewed to illustrate the value of the model system provided by athletes.

Relative to Holocene *Homo sapiens*, *Homo neanderthalensis* exhibits significant asymmetry in the strength of the humeral diaphysis, as well as asymmetry in anteroposterior strengthening as observed in humeral diaphyseal shape (Churchill & Rhodes, 2009; Churchill, 2002; Churchill, Weaver, & Niewoehner, 1996; Rhodes & Churchill, 2009; Trinkaus, Churchill, & Ruff, 1994). This degree of asymmetry is so pronounced that it is only mirrored in contemporary tennis players and cricketers; groups who regularly load their upper limbs in an asymmetrical manner (Shaw & Stock, 2009a; Trinkaus, 1984).

A proposed explanation for this asymmetry is the use of projectile technology. The use of hand-thrown spears during the Pleistocene is considered an important event in human evolution (Milks et al., 2019), and could provide an explanation for this observed asymmetry. Prior to the relatively recent invention of the atlatl and bow (Shea, 2006), spears facilitated activities such as hunting (Bunn & Gurtov, 2014; Gamble, 1987; Iovita & Sano, 2016; Thieme, 1999), defense against predators (Serangeli, Van Kolschoten, Starkovich, & Verheijen, 2015), and interpersonal violence (Churchill, Franciscus, McKean-Peraza, Daniel, & Warren, 2009). However, initial investigations of the effective range of thrown spears, observing that reasonable accuracy was only possible over 5–10 m, discounted throwing as an explanation for observed Neanderthal upper limb asymmetry and provided evidence that spear thrusting could engender similar patterns of asymmetry in mechanical loading (Churchill, 1993).

Recognizing the important role played by skill and training, Milks and colleagues challenged this perception by studying trained male javelin throwers to attempt to hit a hay bale from a series of distances with replicas of the Schöningen Spear II (Schoch, Bigga, Böhner, Richter, & Terberger, 2015; Thieme, 1997). The results revealed that trained throwers were able to throw spears as least twice the distance previously reported and suggest that further improvements would be possible with target-specific training. As with the analysis of runners to examine evolved barefoot running biomechanics (Lieberman et al., 2015), examination of activity-specific athletes, more aligned with the activities of our ancestors, provides greater value and insight. It is worth noting, however, that fewer than 25% of attempts from 20 m hit the target, and as Churchill notes, it is unclear how many of these successful hits would have been sufficiently powerful to penetrate an animal's hide (Yong, 2019).

The debate surrounding humeral torsion and retroversion provides a second example from the upper limb literature illustrating the value of studying athletes. Humeral torsion reflects the angular difference between the orientation of the proximal humeral head and the axis of the elbow at the distal humerus (Roach, Lieberman, Gill, Palmer, & Gill, 2012). The degree of humeral torsion has changed during evolution of the *Homo* lineage, with modern humans displaying greater torsion than early *Homo* (Larson, 2007, 2009).

Within *Homo sapiens*, humeral torsion shows great variation, and increases with age between birth and adulthood. Activity patterns

throughout life also influence the degree of torsion, likely as a result of a functional imbalance between muscles involved in medial and lateral rotation (Birch, 1997; Cowgill, 2007; L'Episcopo, 1934). For example, tool use such as knapping generates strong internal rotational forces acting to modify the humerus, and increase humeral torsion (discussed in Roach & Richmond, 2015). In contrast, overhand throwing leads to a posterior orientation of the humeral head, generating external rotational forces and decreasing the humeral torsion of the dominant arm by 10°–20°. As a result, individuals regularly performing overhand throwing during adolescence and young adulthood acquire decreased humeral torsion in the throwing arm, leading to high levels of bilateral torsional asymmetry (Bigliani et al., 1997; Borsa, Dover, Wilk, & Reinold, 2006; Borsa et al., 2005; Brown, Niehues, Harrah, Yavorsky, & Hirshman, 1988; Chant, Litchfield, Griffin, & Thain, 2007; Crockett et al., 2002; King, Brelsford, & Tullos, 1969; Magnusson, Gleim, & Nicholas, 1994; Osbahr, Cannon, & Speer, 2002; Pieper, 1998; Reagan et al., 2002). Studies analyzing trained baseball players determined that low humeral torsion enhances elastic energy storage in the shoulder's soft tissues, enabling faster throwing (Roach & Lieberman, 2014; Roach, Venkadesan, Rainbow, & Lieberman, 2013).

Collation of evidence from developmental studies and throwing performance allowed the synthesis of a new argument to counter previous interpretations of the fossil record. Instead of torsional asymmetry being interpreted as a skeletal hallmark of throwing (Rhodes & Churchill, 2009), torsional asymmetry may reflect the opposing effects of

1. The internal rotational forces arising from recent tool use which lead to higher torsion in the nondominant arm, and
2. The external rotational forces stemming from throwing serving to maintain lower torsion in the dominant arm (Roach & Richmond, 2015).

In this way, the model system provided by athletes has provided unique insight and interpretation of function from form in the fossil record, contributing to our understanding of human evolution. The extinction of our *Homo* relatives brings variation within our species into sharper focus, and variation at the interindividual level will be considered in the next section.

#### 4 | HUMAN INTERINDIVIDUAL VARIATION

Significant morphological and physiological variation exists within the human species (Eveleth & Tanner, 1990; Katzmarzyk & Leonard, 1998; Ruff, 2002; Wells, 2012), and this applies equally to the fossil record of ancestral hominins, even though the evidence is more sparse. Such interindividual variation may arise following past selection or following exposure to environmental stresses early in life that irreversibly influence later-life phenotype. Studies employing sports and physical activities to answer questions related to each of these will now be considered.

#### 5 | EVOLVED CONSTRAINTS OF ENERGY EXPENDITURE

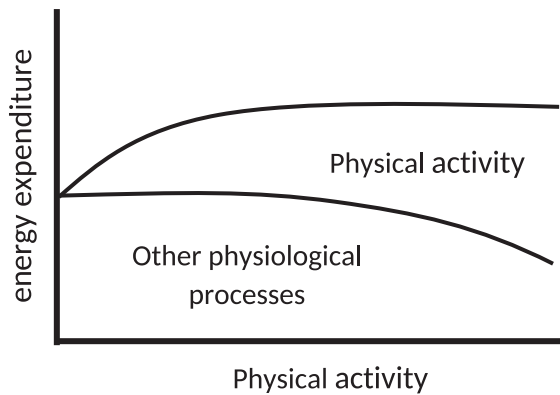
Hominin evolutionary history is characterized by repeated cycles of dispersal and colonization of new environments (Wells & Stock, 2007). This evolutionary strategy leads to exposure to energetic stress, which may push physiological functions to the limits of adaptive plasticity. Examples of such stressors include unreliable food availability or increased energy demands, and climactic stressors such as extremes of temperature. The significant role played by energy homeostasis in the process of evolution has long been recognized. Building upon the work of early proponents of the idea that energy is critical to the development of species (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).

Strong selective pressures encourage the effective capture and appropriate distribution of energy and resources between competing physiological processes, relating to reproduction, maintenance, growth and defense, though these "allocation decisions" may include the storage of reserves for use at a later date (Leonard, 2012; Leonard & Ulijaszek, 2002; Stearns, 1989; Ulijaszek, 1995; Wells, Nesse, Sear, Johnstone, & Stearns, 2017; Zera & Harshman, 2001). The individual is challenged to develop efficient and effective strategies to acquire and distribute energy and resources toward these key life processes; those that have developed effective systems for both energy acquisition and optimal allocation are thereby advantaged in their particular ecological niche (Angilletta, Wilson, Navas, & James, 2003; Kaplan & Gangestad, 2005; Lotka, 1922).

Traditional models of energy expenditure are additive in nature, considering total energy expenditure as the sum of the energetic demands of an individual's basal metabolism and daily activities (FAO/WHO/UNU, 2001). It would follow that highly active populations expend more energy than groups with comparatively sedentary lifestyles. It was quite striking, therefore, when Pontzer and colleagues found the standardized total daily energy expenditure of Hadza hunter gatherers to be similar to that of Western populations, despite significantly higher estimated physical activity levels (Pontzer et al., 2012).

Further investigation, considering the energetics of populations with differing levels of habitual physical activity, identified an apparent limit to daily energy expenditure (Pontzer, 2015a, 2015b; Pontzer et al., 2016). The resultant constrained total energy expenditure model proposes that daily energy expenditure is homeostatically maintained within a narrow evolved physiological range. In this model, daily energy expenditure is maintained when levels of physical activity increase, bringing the benefits of reducing energy requirements and pursuant reduced mortality risk (Figure 2).

Consistent with these reports, recent analysis of energy expenditure during pregnancy (Dunsworth, Warrener, Deacon, Ellison, & Pontzer, 2012) and by athletes participating in contests ranging from half-day triathlons to multimonth ultra-endurance runs revealed an ultimate limit of sustainable energy expenditure (Thurber et al., 2019).



**FIGURE 2** The constrained total energy model, adapted from Pontzer et al. (2016)

Thurber and colleagues found that over time the maximal daily energy output decreases curvilinearly to a value below three times basal metabolic rate. This level of energy expenditure persists despite ongoing physical activity.

When coupled with high levels of physical activity, this apparent restriction of daily total energy expenditure requires dynamic redistribution of limited available energy within the body. Not all biological functions can continue to receive “normal” levels of energetic funding. Priority is given to biological functions offering the greatest immediate survival value. The constrained total energy expenditure model does not explain this process, and this insight underpins the work of Longman, Stock, and Wells, whose research seeks to determine the hierarchy of functional preservation under conditions of energetic stress (Longman, Prall, et al. 2017), as discussed in more detail later in this review.

## 6 | THERMOREGULATORY ENERGETICS, PHYSICAL ACTIVITY, AND SELECTIVE PRESSURES FOR MORPHOLOGICAL THERMAL ADAPTATION

The ability to achieve effective thermoregulation is a key challenge facing individuals in different environments. The physiological processes associated with the maintenance of core body temperature impose a significant energetic burden (Hill, Muhich, & Humphries, 2013). Here, we review studies of physical activity and exercise as proxies for subsistence tasks. As physical activity, influences heat generation and hence the degree of thermoregulatory activation, there is a dynamic relationship between physical activity, thermoregulation and energy expenditure (McArdle, Magel, Gergley, Spina, & Toner, 2017; McArdle, Magel, Spina, Gergley, & Toner, 1984). Depending on ambient conditions and activity levels, thermoregulation has the potential to form a considerable component of human daily energy expenditure, while also constraining the amount of energy that can be directed to other functions.

In cold climates, the heat produced by physical activity contributes significantly to the maintenance of core body temperature, reducing the thermoregulatory energetic load (Tikuisis, Jacobs, Moroz, Vallerand, & Martineau, 2000; Toner, Sawka, Foley, & Pandolf, 1986). In contrast, in warm climates exercise-induced heat production increases the thermoregulatory burden, and hyperthermia may ensue if the rate of heat production exceeds the rate of heat loss (Montain, Sawka, Cadarette, Quigley, & McKay, 1994).

Ocobock has made important contributions to the field of evolutionary energetics through analysis of the interactions between physical activity, thermoregulatory energy costs, and total daily energy expenditure. Using medical technology designed to monitor patterns of physical activity (namely ActiTrainer devices), Ocobock studied total energy expenditure and its components in highly active people living and working in cold, temperate, and hot environments. The heat produced during exercise was found to be sufficient to differentially influence thermoregulatory costs in hot and cold environments (Ocobock, 2016).

The high energetic costs of active thermoregulation reduce the energy available for other physiological processes. We propose that the selective pressures this generated led to the adoption of temperature-adapted morphologies in a range of species, acting to reduce thermal stress. Recent investigations of ultra-endurance running performance in hot and cold environments have provided a unique perspective on the selective forces driving the emergence of these temperature-adapted morphologies (Longman et al., 2019).

Both extinct and extant hominin species demonstrate morphological traits consistent with Bergmann's (Bergmann, 1847) and Allen's (Allen, 1887) rules (Foster & Collard, 2013; Holliday, 1997a, 1997b; Holliday & Trinkaus, 1991; Tilkins, Wall-Scheffler, Weaver, & Steudel-Numbers, 2007). These ecogeographical rules describe patterns of morphological variation with respect to environmental temperature and are based on the principle that heat production is proportional to body mass (heat is produced through cellular activity) and is lost in proportion to body surface area. Consequently, endotherms in warmer climates are proposed to be smaller (Bergmann, 1847) and have longer limbs (Allen, 1887) than those living in colder climates. Early work in humans has demonstrated that annual temperature correlates negatively with body mass (Roberts, 1953) and positively with leg length (Roberts, 1973, 1978). Subsequent research has broadly supported the applicability of Bergmann's and Allen's rules to humans (Crognier, 1981; Foster & Collard, 2013; Hiernaux, 1968; Hiernaux & Fromont, 1976; Katzmarzyk & Leonard, 1998; Ruff, 1994; Stinson, 1990; Trinkaus, 1981).

The mechanisms underpinning morphological adaptation to environmental temperature are unclear and have tended to be relatively adaptationist in nature. For a time, the majority of studies considered natural selection to be the driving force behind ecogeographical patterning (Ashton, Tracy, & Queiroz, 2000), however it is likely that developmental plasticity also plays an important role (Paterson, 1996). Vasomotor changes, functioning to vary the supply of growth factors and blood nutrients, were considered to mediate temperature-growth effects (Trinkaus, 1981; Weaver & Ingram, 1969). However, more



recent experimental work performed by Serrat et al. (2008) suggests that vasoconstriction and vasodilation effect temperature-mediated changes in growth, not because of variation in the delivery of essential growth-related blood constituents, but instead by inducing variation in the temperature within developing cartilage (Serrat, King & Lovejoy, 2008).

The majority of studies analyzing the influence of environment on natural selection have to some degree assumed that all groups are consistent in their genetic relatedness and have evolved by natural selection. In reality, population history and structure leads to genetic dependencies between the mean phenotypic values of human groups, which in turn influences patterns of morphological variation (Betti, von Cramon-Taubadel, & Lycett, 2012; Betti, von Cramon-Taubadel, Manica, & Lycett, 2013). Through the application of computer simulations and generalized linear mixed models, Roseman and Auerbach (2015) found that population structure explains a significant proportion of among-group morphological variation. As a result, human ecogeographic patterning cannot be entirely explained by clinally distributed natural selection, but rather is multifactorial and population-history contingent (Roseman & Auerbach, 2015).

By analyzing the performance of runners competing in multiday ultra-foot races in hot and cold environments, Longman et al. (2019) recently demonstrated the functional benefits of ecogeographical patterning in thermally challenging environments for the first time. Consistent with the hypothesis that climate-appropriate body types would reduce thermoregulatory load, morphologies consistent with Bergmann's and Allen's Rules were associated with enhanced performance in hot and cold environments in both sexes (Longman et al., 2020, under review).

The physiological demand for heat conservation and dissipation is intensified during prolonged physical activity, generating powerful selective forces that could have driven the emergence of temperature-adapted morphologies. It may therefore be the interaction between environment and prolonged physical activity that led to the development of environmentally appropriate morphologies (rather than adaptation to an environment allowing for resultant activity). This hypothesis is described in Figure 3.

In addition to providing unique insight regarding morphological adaptation, this study of ultra-endurance performance also underlined the unique reproductive energetic context of human female adaptation. While both male and female athletes exhibited ecogeographical patterning as predicted by Bergmann's and Allen's rules, the relationship was more pronounced in female athletes; climate-appropriate morphologies appear to enhance ultra-running performance to a greater degree in female athletes (Longman et al., 2020, under review). Despite the smaller sample size, the female subgroup displayed a greater number of statistically significant relationships relating to both Bergmann's (weight, BMI, hip circumference, waist circumference, and ponderal index) and Allen's rules (relative leg length). Conversely, the trends in the male data relating to Bergmann's rule did not achieve statistical significance (Longman et al., 2019).

These data suggest that human women have greater sensitivity to thermal stress than men. An explanation for this stems from an



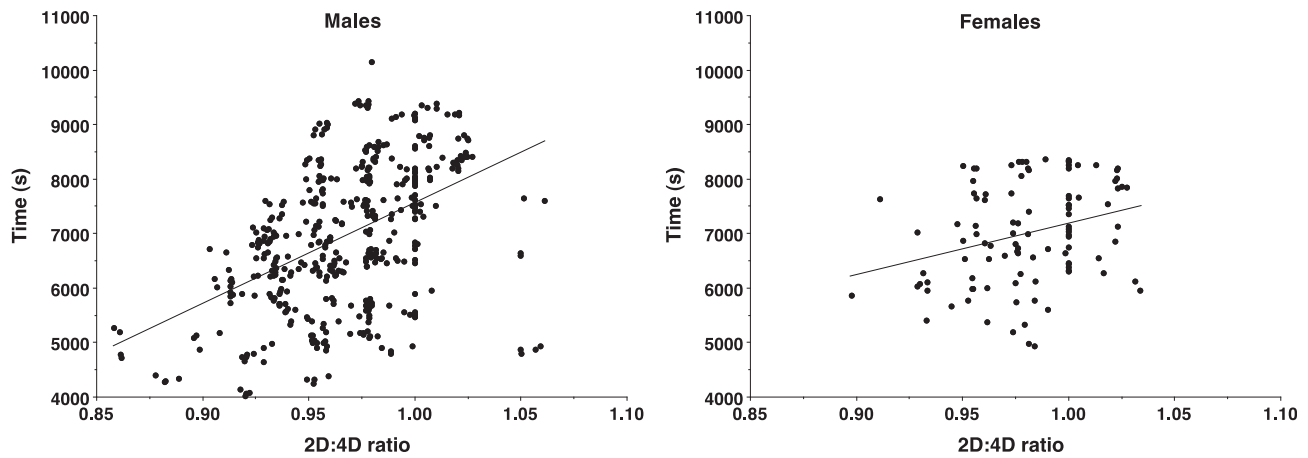
**FIGURE 3** Prolonged physical activity in thermally challenging environments provides the selective pressure for the generation of morphologies through natural selection or developmental plasticity. Taken from Longman et al. (2019)

adaptive perspective, considering dimorphism in sex-specific evolutionary trajectories relating to energetic biology. Humans exhibit significant sexual dimorphism in relation to body composition. On average, men have a lower fat mass and a greater lean mass relative to body weight than women, as well as being taller and having increased bone mineral content (Gustafsson & Lindenfors, 2004; Maynard et al., 1998; Rico, Revilla, Hernandez, Villa, & Del Buergo, 1992; Stini, 1972; Wells, 2007). These differences have implications for thermoregulation during physical activity in thermally challenging environments. Sexual dimorphism in body composition and sensitivity to thermal stress may have stemmed from differential selective forces in our evolutionary past, arising from the need for female fat accumulation to buffer infant energy supply from ecological fluctuations (Wells, 2010).

## 7 | INTERSEXUAL SELECTION— SIGNALING GENETIC QUALITY

Status within a social hierarchy has important implications for male reproductive success in a range of animal populations (Ellis, 1995; Strier, 2003). The enhanced reproductive success enjoyed by those with high status stem from factors such as increased access to resources, reduced harassment from other group members, and reduced risk of predation. The consequent health benefits lead to an enhanced probability of copulation, conception, and birth of healthy progeny (Ellis, 1995). Similarly, male social status in human groups such as the !Kung of the Kalahari and the Aché of Paraguay is positively associated with the number of surviving offspring, and in contemporary Western societies increasing male income promotes proxies of reproductive success and desirability as a marriage partner (Buss, 1989; Buunk, Dijkstra, Fetchenhauer, & Kenrick, 2002; Hopcroft, 2006; Kaplan & Hill, 1985a; Nettle & Pollet, 2008; R. Pennington & Harpending, 1993; Pollet & Nettle, 2008; Vining, 1986).

Prior to agriculture, hunting may have been a key mechanism for the display of male resourcefulness and the acquisition of social status. Although successful hunters have been shown to enjoy heightened reproductive success (Hill & Kaplan, 1993; Kaplan & Hill, 1985b; Smith, 2004), the mechanism linking the two traits was unknown. On the one hand, the “direct provisioning hypothesis” asserted that successful hunters are more able to share food with their mate and offspring, enhancing reproductive success through physiological means (Hawkes, 1993). Conversely, as successful hunters benefit the community through the sharing of meat in many forager societies (Kaplan & Hill,



**FIGURE 4** Scatter plot of male and female right hand 2D:4D ratio versus half-marathon performance (s). The steeper male gradient is visible. Taken from Longman et al. (2015)

1984), hunting success may act as a reliable signal of underlying desirable traits such as athleticism (endurance running may be an important contributor to hunting success [Lieberman & Bramble, 2007]), intelligence or altruism. Based on Zahavi's "handicap principle" (Zahavi, 1975), the elevated social status attained may attract potential mates because of the benefits of association (e.g., protection; Blurton Jones, Marlowe, Hawkes, & O'Connell, 2000).

A research design studying athletes provided a valuable contribution toward the clarification of this question. Runners competing at a large-scale half-marathon were recruited to elucidate the nature of the link between hunting success and elevated reproductive fitness. The large sample size made accessible through this methodology ( $n = 542$ ;  $m = 439$ ,  $f = 103$ ) allowed for a meaningful sex comparison to be made (Longman, Wells, & Stock, 2015; Figure 4).

This study found that a marker of prenatal testosterone exposure (2D:4D ratio) is associated with endurance running ability; an attribute that has been ethnographically shown to be an important component of hunting ability (Liebenberg, 2006). As testosterone has repeatedly been linked with reproductive success (see Manning & Fink, 2008), this investigation provides mechanistic evidence in support of the theory that running capability may serve as a reliable signal of male reproductive quality and potential (Longman, Wells & Stock, 2015). Due to the egalitarian nature of many forager societies, in which meat is widely distributed throughout the group (Kaplan & Hill, 1984), this work suggests that women may be attracted to men with the capacity to acquire resources, rather than those who have resources. It is worth noting that recent work, assessing the link between Hadza hunting reputation, bow pull strength and bow and arrow aiming skill found no association with digit ratio in a relatively small sample (Stibbard-hawkes, n.d.). A study with a larger sample size is needed to clarify this.

## 8 | INTRAINDIVIDUAL VARIATION

The model system provided by athletes and contemporary sporting events is proving increasingly valuable in studying variation at the

intraindividual level. Adaptation within an individual's lifetime may be mediated by the process of phenotypic plasticity, whereby an individual's genome produces different phenotypes in response to exposure to varying environmental cues (Pigliucci, Murren, & Schlichting, 2006). Plasticity can be mediated at the behavioral, biochemical, physiological, or developmental levels, each differing in the degree of reversibility (Pigliucci, Murren & Schlichting, 2006). Commonplace human examples of phenotypic plasticity include immune system adaptation to pathogen exposure, as well as mechanisms of learning (Fusco & Minelli, 2010). Although not all plasticity is beneficial (Sultan, 1995), the ability of an individual to modify its phenotypic status in response to changes in the environment affords great adaptive potential and responsiveness to nonstatic conditions (Garland & Kelly, 2006). In this section we discuss recent advances provided by athlete-based models of investigation concerning the plasticity of long bone structure, intrasexual selection and life history theory. It is important to note that plasticity influences variation at both the interindividual and intra-individual levels, and that there is no intention to imply a hard-dividing line between these two sections.

## 9 | SPORT AS A TOOL TO INFER BEHAVIORAL PATTERNS FROM THE FOSSIL RECORD

Biomechanical movement creates strain in bones, both through muscle contraction and ground reaction forces, and these have been measured in vivo using implanted strain gauges (Burr et al., 1996; Lanyon, Hampson, Goodship, & Shah, 1975; Rubin & Lanyon, 1984). Mechanical loading is consistently linked with cross-sectional limb bone size, rigidity, and shape (Hseih, Robling, Abmbrosius, Burr, & Turner, 2001; Jones, Priest, Hayes, Tichenor, & Nagel, 1977; Judex, Gross, & Zernicke, 1997; Nikander, Sievänen, Uusi-Rasi, Heinonen, & Kannus, 2006; Shaw & Stock, 2009a, 2009b; Woo et al., 1981). Considerable experimental evidence demonstrates that long bone diaphyses display plasticity within a lifetime and adaptively respond to increased loading



by structurally augmenting their mass in the direction of the deformation (Lanyon, 1992; Rubin, McLeod, & Basin, 1990). The organization of bone tissue may be driven by, and be reflective of, the range of daily strains imposed by a wide range of activities imposing different strain intensities (McLeod, Rubin, Otter, & Qin, 1998).

Studies seeking to infer patterns of activity in prehistoric hominin groups depend upon comparative analysis of skeletal morphology (Churchill et al., 1996; Holt, 2003; Holt & Formicola, 2008; Marchi, 2008; Ruff, 2008, 2009; Trinkaus, Churchill & Ruff, 1994). The interpretive power of such studies has been enhanced by comparison of the morphology evolutionary and archaeological hominin record to that of living groups (see Ruff, 2000; Ruff, Trinkaus, & Holliday, 1998; Trinkaus et al., 1994), whose activity patterns and skeletal morphology are well documented (Shaw, 2010, 2011; Shaw & Stock, 2009a, 2009b).

The study of athletes, whose discipline-specific training has subjected their long bones to a particular set of forces, is providing valuable comparative data from which to infer prehistoric activity patterns. This approach is exemplified by work performing a comparative analysis of interlimb patterns of robusticity (tibial J/humeral J) in living athletes (cross-country runners and swimmers), living controls, Pleistocene fossil hominins (Neanderthals and anatomically modern and Upper Paleolithic *H. sapiens*), and Holocene foragers (terrestrial LSA southern Africans and marine Andaman islanders; Shaw & Stock, 2013). As expected, among the living cohort, runners had higher levels of tibial rigidity relative to humeral rigidity than the swimmers. Similarly, the relative tibial rigidity of terrestrial and marine Holocene foragers resembled the athlete groups with comparable patterns of habitual activity (runners and swimmers, respectively). The Pleistocene fossil hominins resembled terrestrial Holocene foragers and runner subsamples. Furthermore, almost half of the Pleistocene individuals sampled displayed tibial rigidities suggestive of volumes of walking/running exceeding that of contemporary runners (80–100 miles per week).

The value of studying analyzing athletes to enhance the interpretation of prehistoric skeletal robusticity has been further demonstrated in work investigating sexual dimorphism and labor across the transition to agriculture (Macintosh, Pinhasi, & Stock, 2017). Comparative analyses with contemporary athletes demonstrated that for over 5,000 years of prehistory in central Europe, women had stronger humeral cross-sectional properties than contemporary female rowers. The results highlight sex differences in the norms of reaction of bone to patterns of mechanical loading, emphasizing the need for sex-specific analyses to infer past female behavior from the mechanobiology of skeletal tissue.

Present interpretations of behavioral patterns from fossils often lack consistency (Shaw & Stock, 2009b). In order to further understanding of prehistoric activity patterns, further clarification of the complex relationship between habitual loading patterns and diaphyseal adaptation is required. Competitive athletes repeatedly perform the same activities in training and in competition, often from a young age. As a result, investigations of living athletes can provide detailed information linking habitual activities to diaphyseal morphology. The use of athletes in this way, across a range of disciplines encompassing varying

intensities, repetitiveness, and planes of movement, are adding to previous understanding of the influence of habitual activity on diaphyseal rigidity and shape patterns (Shaw & Stock, 2009a). Research in this area has demonstrated that differences in the manner of loading, as well as frequency, are linked to variation in long bone shape (Richmond & Jungers, 2008; Ruff, 1995; Ruff et al., 2006; Trinkaus, 1997). A recent study of trabecular bone microarchitecture in living human distance runners has demonstrated that runners with a forefoot strike, interpreted to have greatest summative loading stimulus due to training, have greater trabecular thickness (Best, Holt, Troy, & Hamill, 2017). Ultimately, this line of research will contribute to a unifying theory explaining the influence of different activities on the skeleton and allow the inference of mobility patterns from hominin skeletal remains.

## 10 | SPORT AS A MODEL OF INTRASEXUAL SELECTION

Manning and colleagues have drawn parallels between athletic competition and intrasexual selection, highlighting the similarities between the traits required for success in each. Taking football (soccer) or rugby as examples, to be successful a player must have spatial judgment to pass to and receive the ball from team-mates, and cardiovascular development and efficiency to play competitively for 90 or 80 min, respectively. Speed to reach the ball first and use it effectively, and strength to shield it from opponents, are also required (Manning & Taylor, 2001). Sport further mirrors abilities in male–male competition through the prominence of actions such as throwing, punching, kicking, and running (Hönekopp, Manning, & Müller, 2006). As all these attributes are beneficial in male–male combat, performance in sport may reflect potential ability in this domain.

Furthermore, intense rivalry often exists between sporting opponents. An official with total control is almost always required to police contests, as competitors constantly test the behavioral limits as dictated by the rules of the contest (Hönekopp, Bartholdt, Beier & Liebert, 2006; Manning & Taylor, 2001). Perhaps unsurprisingly then, athletic ability across a range of sports has been linked to 2D:4D digit ratio (Longman, Stock & Wells, 2011; Manning 2002; Manning, Morris & Caswell, 2007; Manning & Taylor, 2001; Paul, Kato, Hunkin, Vivekanandan & Spector, 2006; Pokrywka, Rachon, Suchecka-Rachon & Bitel, 2005)—an early life indicator of subsequent reproductive fitness (Berenbaum et al., 2009; Hönekopp et al., 2007; Manning, Scutt, Wilson & Lewis-Jones, 1998; Manning, Barley, Walton, Lewis-Jones & Trivers, 2000; Manning & Fink, 2008). Sport also mirrors intrasexual selection insofar as the status-enhancing and monetary rewards facilitate resource acquisition, promoting access to mating opportunities (Buss, 1989; Edwards, 2006; Manning & Taylor, 2001).

Androgenization, positively linked with reproductive success in many animal populations, is also positively related to status within a social hierarchy (Ellis, 1995; Strier, 2003). Status is often determined by male–male competition (Altmann, Sapolski, & Licht, 1995), and testosterone levels have been shown to closely track the results of such

dominance interactions across a range of mammalian species (Zilioli & Watson, 2012).

The validity of sport as a proxy for male–male competition in a selective context is supported by reports of testosterone tracking the outcomes of both athletic and nonathletic contests in contemporary Western societies, as well as in the vicarious experience of winning among sports fans (Apicella et al., 2008; Archer, 2006; Bernhardt & Dabbs, 1997; Bernhardt, Dabbs, Fielden, & Lutter, 1998; Booth, Shelley, Mazur, Tharp, & Kittik, 1989; Elias, 1981; Gladue, Boechler, & McCaul, 1989; Longman, Surbey, Stock, & Wells, 2018; Mazur, Booth, & Dabbs, 1992; Mazur & Lamb, 1980; McCaul, Gladue, & Joppa, 1992). This mirrors the increases in testosterone that have been observed in primates following a dominance interaction (Muller & Wrangham, 2001), and in pre-industrialized communities following hunting success (Trumble, Smith, Connor, Kaplan, & Gurven, 2013). It is worth noting, however, that nonsignificant differences in testosterone levels between winners and losers have been reported in sporting and video gaming contests (Gonzalez-Bono, Salvador, Ricarte, Serrano, & Arnedo, 2000; Mazur, Susman, & Edelbrock, 1997; Salvador, Simón, Suay, & Llorens, 1987; Salvador, Suay, & Cantón, 1990; Suay et al., 1999).

Recent work employing a rowing contest as a model of intrasexual selection has enhanced understanding of the dynamic relationship between testosterone, status and a key trade-off relating to reproductive strategy (the allocation of energetic resources toward either mating or parenting [McGlothlin, Jawor, & Ketterson, 2007]). Perceived victory in an experimentally manipulated head-to-head rowing machine competition between young adult male trained rowers led to both a surge in androgenization, as well as psychological changes pertaining to reproductive strategy. Self-perceived mate value, self-esteem, inclination toward engaging in casual sexual relationships and increased intention to instigate such relationships all increased in winners, while the propensity toward caring for or mentoring children decreased (Longman, Surbey, Stock & Wells, 2018). The tandem hormonal and psychological shifts in male reproductive effort following victory represent a significant shift to the mating end of the mating-parenting trade-off. The use of sport as a model of intrasexual competition not only allowed for analysis of the trade-off between mating and parenting effort, but also facilitated an experimental design in which the physical effort of winning was uncoupled from the social perception of winning. The utilization of a manipulated competition result highlights that the social experience of winning causes the testosterone surge of a “victory,” and strongly influences reproductive investment and strategy.

## 11 | ULTRA-ENDURANCE SPORT AS A MODEL TO STUDY HUMAN LIFE HISTORY THEORY

### 11.1 | Trade-offs in energy allocation

Life history theory describes the competitive allocation of limited resources between physiological functions (Leonard, 2012; Stearns,

1989, 1992; Zera & Harshman, 2001). During periods of energetic stress, life history theory hypothesizes that trade-offs between competing processes arise (Bronson, 1991; Stearns, 1992); a life history strategy involving a greater allocation of resources toward a given function necessitates a reduction in the resources available for other functions. Hence, there is a strong selective pressure for energetic efficiency. Limited resources are predicted to be preferentially allocated to biological functions offering the greatest immediate survival value. However, the hierarchy of functional preservation, and how this varies with population, age, sex, and body composition, is unknown.

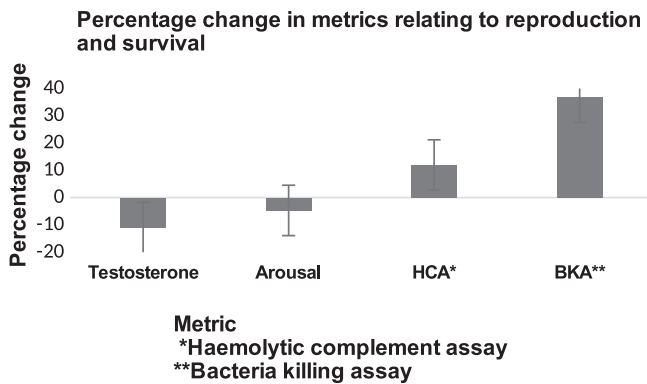
The energetic cost of reproduction is central to many life history trade-offs (Stearns, 1989). Although reproduction is only one of the key functions described by life history theory, the other processes are only of value from a fitness perspective in that combined, these processes increase the opportunities for reproduction in the future. Evolutionary theory argues that individuals should, at every reproductive opportunity, exhibit behavior intended to enhance genetic contributions to subsequent generations. However, a life history strategy involving a greater allocation of energetic resources toward reproduction imposes reduced allocation to other functions, such as survival.

While the concept of a life history trade-offs is appealing, negative correlations between investment in two competing physiological functions are frequently absent when phenotypic comparisons are made between individuals within a population (Cody, 1966; Glazier, 1999). This may be due, at least in part, to the finding that inter-individual variation in resource acquisition often exceeds variation in resource allocation (van Noordwijk & de Jong, 1986).

Recently published research (Longman et al., 2017) identified ultramarathon competitions as a valuable experimental model enabling observation of negative covariations between investment in competing physiological functions in the field. Although it is not possible to control individual energy intake without compromising ecological validity (or, perhaps, reasonable research ethics), it is possible to experimentally control energy balance. This innovative model utilizes the pre-existing energy deficit inherent in ultramarathons (Knechtle & Bircher, 2005; Knechtle, Enggist, & Jehle, 2005) to nullify the effect of variation in resource acquisition. This negative energy balance pushes physiological and cognitive systems to the limits of adaptive plasticity, provoking detectable functional trade-offs. This allows us, for the first time, to directly test physiological trade-offs and observe how the body prioritizes different tissues or functions.

We used ultra-endurance events to study human life history trade-offs during a 100-mile foot race. This study revealed an acute-level trade-off between reproduction and survivorship in male athletes during which athletes lost body weight. The data highlighted a shift in energetic priorities away from reproduction (as measured by levels of testosterone and libido), and toward short-term survival (as measured by innate immune function, a marker of defense; Longman et al., 2017). The changes in each of the four metrics achieved statistical significance (Figure 5).

The sample populations tested in ultramarathons are, by their very nature, highly trained and physically fit individuals. The precise



**FIGURE 5** Changes in investment in measures of reproduction (testosterone and arousal) and survival (hemolytic complement assay and bacteria killing assay) following participation in a 100-mile footrace. Taken from Longman et al. (2017)

results may not therefore be generalizable to the wider population. For example, the high levels of physical conditioning may buffer the study cohort from detrimental health consequences of malnutrition during prolonged and strenuous physical exercise. However, given the universality of general life history theory predictions, one can argue that results in different populations should be broadly comparable due to the evolutionary (Carrier, 1984; Lieberman, Bramble, Rachlen & Shea, 2006; Longman et al., 2015) and cross-cultural ecological relevance of endurance running (Liebenberg, 2006; Pennington, 1963).

We have since developed this model through the incorporation of more detailed measures of immune function, which promises to shed further light on the survival versus reproductive trade-off. This work spans a range of environmental conditions, incorporating both multiday ultramarathons and ocean rows spanning more than 4 weeks in duration. In addition, we have actively addressed the need to increase the number of female study participants. Female participation in ultramarathons is often significantly lower than males (Knechtle, Knechtle, & Lepers, 2011). It is worth noting that the model of using ultra-endurance events to study life history trade-offs and human adaptability offers a smooth route to navigate the ethical concerns inherent in studying participants under physical stress. This is because the sporting events under investigation are often taking place independently of the study protocol.

As previously described, Pontzer's constrained total energy expenditure model (Pontzer et al., 2016) suggests that daily energy expenditure is maintained within a narrow evolved physiological range. Pontzer suggests that the additional energy demand of increased levels of physical activity is absorbed through metabolic adaptations to save energy in other physiological systems, which are yet to be described (Pontzer et al., 2015). The novel approach to studying life history trade-offs using ultramarathons is beginning to answer questions concerning this metabolic adaptation. Over the next few years we hope to be able to characterize the hierarchy of functional preservation under conditions of energetic stress. In doing so, this will shed new light on our adaptive capabilities as a phenotypically plastic species.

Ultra-endurance events have demonstrated that the energy load generated by sporting activities can be used to reveal coherent energetic allocations across *functions*. In parallel, recent experimental work has highlighted that this energy load can also be used to reveal moment-by-moment differences in fuel allocation between *tissues*.

The development of an enlarged and elaborated brain is a defining characteristic of human evolution (Foley & Lee, 1991; Hawks, Hunley, Lee, & Wolpoff, 2000; Lee & Wolpoff, 2003; Ruff, Trinkaus, & Holliday, 1997). This has brought a plethora of benefits to the *Homo* clade (Barrickman, Bastian, Isler, & van Schaik, 2008; Byrne & Corp, 2004; Gibson, 1986; Parker & McKinney, 1999; Reader & Laland, 2002), but at the cost of the brain having the highest metabolic requirements relative to size of all organs (Attwell & Laughlin, 2001; Bullmore & Sporns, 2012; Isler & van Schaik, 2006; Mink, Blumenshine, & Adams, 1981). As a result, the issue of how an enlarged and elaborated brain can be metabolically afforded is a prominent and persistent question within human evolution (Aiello & Dunbar, 1993; Aiello & Wheeler, 1995; Byrne, 1997; Isler & van Schaik, 2006, 2011; McNab & Eisenberg, 1989; Navarrete, van Schaik, & Isler, 2011). Skeletal muscle mass is also an expensive tissue to maintain (Elias, 1992; Snodgrass, Leonard, & Robertson, 1999), and, like the brain, its glucose demands increase with activation (Bélanger, Allaman, & Magistretti, 2011; Brooks & Mercier, 1994; McArdle, Katch, & Katch, 2001; Romijn, Gastaldelli, Horowitz, Endert, & Wolfe, 1993; Wahren, Felig, Ahlborg, & Jorfeldt, 1971). During such circumstances, muscle tissue may compete with the brain for glucose and oxygen.

An experimental design applied to a sporting contest was employed to investigate the hypothesis of a trade-off involving the brain at the acute, rather than the evolutionary or developmental, level. Simultaneous challenge of both cognitive and physical functions resulted in relative preservation of cognitive function over physical power output (Longman, Stock, & Wells, 2017), lending support to the selfish brain hypothesis (Peters et al., 2004) and highlighting the metabolically privileged niche occupied by the human brain. This metabolic hierarchy may be an evolved trait, as the chances of survival may be boosted more by a well-fuelled brain than well-fuelled muscles when facing an environmental challenge (Beedie & Lane, 2012).

Research seeking to understand the competitive allocation of resources between key functions is central to life history theory, and cuts to the heart of our nature as a phenotypically plastic, colonizing species (Wells & Stock, 2007). The study of modern sports in this context has the promise to enhance understanding of this process, and consequently knowledge of our plasticity and adaptive capabilities.

## 12 | SUMMARY AND FUTURE PERSPECTIVES

A plethora of scientific disciplines have contributed to the study of human evolution, ranging from primatology and bioarchaeology to paleontology and genetics. Each approach has added a unique perspective, building knowledge of the origins and development of our

species. Here, we have reviewed a new methodology. Human athletic paleobiology—the analysis of athletes as study participants and the use of contemporary sports as a model for studying evolutionary theory—has great potential.

The appeal of utilizing athletes and sport to study human variation is multifactorial. The varying characteristics of the wide range of existing sporting contests offer diverse and unique opportunities as a methodological tool. From a research design perspective, this model facilitates a variety of data collection protocols. These range from field-based observational studies to laboratory-based rigorous randomized controlled trials with experimental designs. The opportunity to design and perform controlled experimental investigations is particularly valuable to anthropology. Furthermore, interdisciplinary collaborations are possible through collaborations between researchers in anthropology and sport science, kinesiology, physiology and psychology. This allows for the application of specialized equipment and complementary expertise with the potential to provide alternative, valuable perspectives to our discipline.

From a biological perspective, the range of contemporary athletic events allows for the functional assessment of a variety of different biological systems. For example, it has been proposed that the contrasting morphologies of humans and Neanderthals may reflect the selective pressures imposed by endurance versus sprinting or other power-related hunting styles (Bramble & Lieberman, 2004; Liebenberg, 2006; Stewart et al., 2018). Insights toward the selective pressures imposed by these opposing hunting styles are made possible by studying athletic physiologies associated with enhanced performance in endurance events (e.g., marathon running) in comparison to power-based disciplines (e.g., weightlifting, sprinting or rugby). This would allow analysis of the cardiovascular and aerobic system, and of muscular and anaerobic energy systems. In tandem with the large sample sizes available across a range of athletic disciplines, the increased depth and breadth of viable metrics arising from the use of living subjects often allows for the derivation of clearer insights.

To date, this model has been shown capable of enhancing understanding of variation at the species, inter-individual and intra-individual levels. The potential to develop this avenue of research is vast. One approach to realize this potential is to establish collaborations with specialized sports science or kinesiology departments. This will allow laboratory-based investigations to be performed, with the aim of standardizing field measurements and analyzing interesting field observations in greater depth.

Aspects of the literature cited in this article have been selected to illustrate not only how this approach can enhance understanding of our evolutionary past, but also how this knowledge can be forward-facing in its application. Energetic stress presents as a prominent problem in contemporary society. Situations such as famine, war and migration bring inherent food insecurity, and the potential for energy deficit (Abubakar et al., 2018; The World Bank, 2018). The recent UCL–Lancet Commission on Migration and Health stressed that migration and health are inextricably linked, and are key to sustainable development (Abubakar et al., 2018). A comprehensive understanding of biological adaptation to energetic stress, as described at the level

of intraindividual variation here, is therefore critical to health and medical outcomes. Evolutionary scientists understand that energy allocation underpins multiple functional relationships, but this perspective has yet to emerge in biomedical science. Increased knowledge of the scope of human plasticity and the adaptive stress response outside the context of overt disease can be applied to numerous areas of public health, enhancing understanding of the interrelationship between body weight regulation, physical activity, dietary intake, and health. This understanding will contribute to the emerging field of evolutionary public health, which is using knowledge derived from life history theory trade-offs to improve the efficacy of public health interventions (Wells, Nesse, Sear, Johnstone & Stearns, 2017).

## DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data was created or analyzed in this study.

## ORCID

Daniel P. Longman  <https://orcid.org/0000-0003-3025-7053>

## REFERENCES

- Abubakar, I., Aldridge, R., Devakumar, D., Orcutt, M., Burns, R., Barreto, M., ... Zimmerman, D. (2018). The UCL–lancet commission on migration and health: The health of a world on the move. *The Lancet*, 6736(18), 2606–2654.
- Aibast, H., Okutoyi, P., Sigei, T., Adero, W., Chemjor, D., Ongaro, N., ... Pitsiladis, Y. (2017). Foot structure and function in habitually barefoot and shod adolescents in Kenya. *Current Sports Medicine Reports*, 16(6), 448–458.
- Aiello, L., & Dunbar, R. (1993). Neocortex size, group size, and the evolution of language. *Current Anthropology*, 34(2), 183–193.
- Aiello, L., & Wheeler, P. (1995). The expensive-tissue hypothesis the brain and the digestive evolution. *Current Anthropology*, 36(2), 199–221.
- Allen, J. (1887). The influence of physical conditions in the genesis of species. *Radical Review*, 1, 108.
- Altmann, J., Sapolski, R., & Licht, P. (1995). Baboon fertility and social status. *Nature*, 377, 668–669.
- Angilletta, M., Wilson, R., Navas, C., & James, R. (2003). Tradeoffs and the evolution of thermal reaction norms. *Trends in Ecology and Evolution*, 18(5), 234–240.
- Apicella, C., Dreber, A., Campbell, B., Gray, P., Hoffman, M., & Little, A. (2008). Testosterone and financial risk preferences. *Evolution and Human Behavior*, 29(6), 384–390.
- Archer, J. (2006). Testosterone and human aggression: An evaluation of the challenge hypothesis. *Neuroscience and Biobehavioral Reviews*, 30(3), 319–345.
- Ashton, K., Tracy, M., & Queiroz, A. (2000). Is Bergmann's rule valid for mammals? *The American Naturalist*, 156(4), 390–415.
- Attwell, D., & Laughlin, S. (2001). An energy budget for signaling in the grey matter of the brain. *Journal of Cerebral Blood Flow and Metabolism*, 21(10), 1133–1145.
- Barrickman, N., Bastian, M., Isler, K., & van Schaik, C. (2008). Life history costs and benefits of encephalization: A comparative test using data from long-term studies of primates in the wild. *Journal of Human Evolution*, 54(5), 568–590.
- Beedie, C., & Lane, A. (2012). The role of glucose in self-control: Another look at the evidence and an alternative conceptualization. *Personality and Social Psychology Review*, 16(2), 143–153.



- Bélanger, M., Allaman, I., & Magistretti, P. (2011). Brain energy metabolism: Focus on astrocyte-neuron metabolic cooperation. *Cell Metabolism*, 14(6), 724–738.
- Berenbaum, S. A., Bryk, K. K., Nowak, N., Quigley, C. A., & Moffat, S. (2009). Fingers as a marker of prenatal androgen exposure. *Endocrinology*, 150(11), 5119–5124.
- Bergmann, C. (1847). Increase in the effectiveness of heat conservation in large subjects. *Göttinger Studien*, 3, 595–708.
- Bernhardt, P., & Dabbs, J. (1997). Testosterone increases in basketball fans. In Meeting of American Psychological Society. Washington, DC.
- Bernhardt, P., Dabbs, J., Fielden, J., & Lutter, C. (1998). Testosterone changes during vicarious experiences of winning and losing among fans at sporting events. *Physiology & Behavior*, 65(1), 59–62.
- Best, A., Holt, B., Troy, K., & Hamill, J. (2017). Trabecular bone in the calcaneus of runners. *PLoS ONE*, 12(11), 1–14.
- Betti, L., von Cramon-Taubadel, N., & Lycett, S. (2012). Human pelvis and long bones reveal differential preservation of ancient population history and migration out of Africa. *Human Biology*, 84(2), 139–152.
- Betti, L., von Cramon-Taubadel, N., Manica, A., & Lycett, S. (2013). Global geometric morphometric analyses of the human pelvis reveal substantial neutral population history effects, even across sexes. *PLoS ONE*, 8(2), e55909.
- Bigliani, L., Codd, T., Connor, P., Levine, W., Littlefield, M., & Hershon, S. (1997). Shoulder motion and laxity in the professional baseball player. *The American Journal of Sports Medicine*, 25, 609–613.
- Birch, R. (1997). Birth lesions of the brachial plexus. In R. Birch, G. Bonney, & C. Wyn Parry (Eds.), *Surgical disorders of the peripheral nerves* (pp. 209–234). London: Churchill Livingstone.
- Blurton Jones, N., Marlowe, F., Hawkes, K., & O'Connell, J. F. (2000). Hunter-gatherer divorce rates and the paternal provisioning theory of human monogamy. In L. Cronk, N. Chagnon, & W. Irons (Eds.), *Adaptation and human behaviour: An anthropological perspective* (pp. 65–84). New York, NY: Aldine de Gruyter.
- Boltzmann, L. (1886). Der zweite Hauptsatz der mechanischen Wärmetheorie. *Almanach Der Kaiserlichen Akademie Der Wissenschaften*, 36, 225–259.
- Booth, A., Shelley, G., Mazur, A., Tharp, G., & Kittik, R. (1989). Testosterone, and winning and losing in human competition. *Hormones and Behavior*, 55, 556–571.
- Borsa, P., Dover, G., Wilk, K., & Reinold, M. (2006). Glenohumeral range of motion and stiffness in professional baseball pitchers. *Medicine and Science in Sports and Exercise*, 38(1), 21–26.
- Borsa, P., Wilk, K., Jacobson, J., Cibek, J., Dover, G., Reinold, M., & Andrews, J. (2005). Correlation of range of motion and glenohumeral translation in professional baseball pitchers. *The American Journal of Sports Medicine*, 33(9), 1392–1399.
- Bramble, D., & Lieberman, D. (2004). Endurance running and the evolution of *Homo*. *Nature*, 432(7015), 345–352.
- Bronson, F. (1991). *Mammalian reproductive biology*. Chicago, US: University of Chicago Press.
- Brooks, G., & Mercier, J. (1994). Balance of carbohydrate and lipid utilization during exercise: The “crossover” concept. *Journal of Applied Physiology*, 76(6), 2253–2261.
- Brown, L., Niehues, S., Harrah, A., Yavorsky, P., & Hirshman, H. (1988). Upper extremity range of motion and isokinetic strength of the internal and external shoulder rotators in major league baseball players. *The American Journal of Sports Medicine*, 16(6), 577–585.
- Bullmore, E., & Sporns, O. (2012). The economy of brain network organization. *Nature Reviews. Neuroscience*, 13(5), 336–349.
- Bunn, H., & Gurtov, A. (2014). Prey mortality profiles indicate that Early Pleistocene *Homo* at Olduvai was an ambush predator. *Quaternary International*, 322–323, 44–53.
- Burr, B., Milgrom, C., Fyhrie, D., Forwood, M., Nyska, M., Finestone, A., ... Simkin, A. (1996). In vivo measurement of human tibial strains during vigorous activity. *Bone*, 18, 405–410.
- Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioural and Brain Sciences*, 12(1), 1–49.
- Buunk, B. P., Dijkstra, P., Fetchenhauer, D., & Kenrick, D. T. (2002). Age and gender differences in mate selection criteria for various involvement levels. *Personal Relationships*, 9(3), 271–278.
- Byrne, R. (1997). The technical intelligence hypothesis: An additional evolutionary stimulus to intelligence? In A. Whiten & R. Byrne (Eds.), *Machiavellian intelligence II: Extension and evaluations* (pp. 289–311). Cambridge, UK: Cambridge University Press.
- Byrne, R., & Corp, N. (2004). Neocortex size predicts deception rate in primates. *Proceedings. Biological Sciences/The Royal Society*, 271(1549), 1693–1699.
- Carrier, D. R. (1984). The energetic paradox of human running and hominid evolution. *Current Anthropology*, 25(4), 483–495.
- Cerling, T., Harris, J., MacFadden, B., Leakey, M., Quade, J., Eisenmann, V., & Ehleringer, J. (1997). Global vegetation change through the Miocene/Pliocene boundary. *Nature*, 389(6647), 153–158.
- Cerling, T., Levin, N., Quade, J., Wynn, J., Fox, D., Kingston, J., ... Brown, F. (2010). Comment on the paleoenvironment of *ardipithecus ramidus*. *Science*, 328(5982), 1105.
- Chant, C., Litchfield, R., Griffin, S., & Thain, L. (2007). Humeral head retroversion in competitive baseball players and its relationship to glenohumeral rotation range of motion. *Journal of Orthopaedic & Sports Physical Therapy*, 37(9), 514–520.
- Churchill, S., & Rhodes, J. (2009). The evolution of the human capacity of “killing at a distance”: The human fossil evidence for the evolution of projectile weaponry. In J. Hublin & M. Richards (Eds.), *The evolution of hominin diets: Integrating approaches to the study of Palaeolithic Subsistence*. Dordrecht: Springer.
- Churchill, S., Weaver, A., & Niewoehner, W. (1996). Late Pleistocene human technological and subsistence behavior: Functional interpretations of upper limb morphology. *Quaternaria Nova*, 6, 413–447.
- Churchill, S. E. (1993). Weapon technology, prey size selection, and hunting methods in modern hunter-gatherers: Implications for hunting in the Palaeolithic and Mesolithic. *AP3A. Archeological Papers of the American Anthropological Association*, 4, 11–24.
- Churchill, S. E. (2002). Of assegais and bayonets: Reconstructing prehistoric spear use. *Evolutionary Anthropology*, 11, 185–186.
- Churchill, S. E., Franciscus, R., McKean-Peraza, H., Daniel, J., & Warren, B. (2009). Shanidar 3 Neandertal rib puncture wound and paleolithic weaponry. *Journal of Human Evolution*, 57, 163–178.
- Cody, M. (1966). A general theory of clutch size. *Evolution*, 20(2), 174–184.
- Cowgill, L. (2007). Humeral torsion revisited: A functional and ontogenetic model for population variation. *American Journal of Physical Anthropology*, 134(472–480), 2–48.
- Crockett, H., Gross, L., Wilk, K., Schwartz, M., Reed, J., OMara, J., & Reilly, M. (2002). Osseous adaptation and range of motion at the glenohumeral joint in professional baseball pitchers. *The American Journal of Sports Medicine*, 30(1), 20–26.
- Crognier, E. (1981). Climate and anthropometric variations in Europe and the Mediterranean area. *Annals of Human Biology*, 8(2), 99–107.
- Dart, R. (1925). The man-ape of South Africa. *Nature*, 115, 195–199.
- Dunsworth, H., Warren, A., Deacon, T., Ellison, P., & Pontzer, H. (2012). Metabolic hypothesis for human altriciality. *Proceedings of the National Academy of Sciences of the United States of America*, 109(38), 15212–15216.
- Edwards, D. (2006). Competition and testosterone. *Hormones and Behavior*, 50(5), 681–683.
- Elias, M. (1981). Serum cortisol, testosterone, and testosterone-binding globulin responses to competitive fighting in human males. *Aggressive Behaviour*, 7.3, 215–224.

- Elias, M. (1992). Organ and tissue contribution to metabolic rate. In J. McKinney & H. Tucker (Eds.), *Energy metabolism: Tissue determinants and cellular corollaries* (pp. 51–79). New York, NY: Raven Press.
- Ellis, L. (1995). Dominance and reproductive success among nonhuman animals: A cross-species comparison. *Ethology and Sociobiology*, 16, 257–333.
- Eveleth, P., & Tanner, J. (1990). *Worldwide variation in human growth* (2nd ed.). Cambridge, UK: Cambridge University Press.
- FAO/WHO/UNU. (2001). Human energy requirements. FAO Food and Nutrition Technical Report Series, 1.
- Foley, R., & Lee, P. (1991). Ecology and energetics of encephalization in hominid evolution. *Philosophical Transactions—Royal Society of London, B*, 334(1270), 223–232.
- Foster, F., & Collard, M. (2013). A reassessment of Bergmann's rule in modern humans. *PLoS ONE*, 8(8), e72269.
- Fusco, G., & Minelli, A. (2010). Phenotypic plasticity in development and evolution: Facts and concepts. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1540), 547–556.
- Gamble, C. (1987). Man the shoveler: Alternative models for middle Pleistocene colonization and occupation in northern latitudes. In O. Soffer (Ed.), *The Pleistocene Old World: Regional perspectives* (pp. 81–98). New York, NY: Plenum.
- Garland, T., & Kelly, S. (2006). Phenotypic plasticity and experimental evolution. *Journal of Experimental Biology*, 209(12), 2344–2361.
- Gibson, K. (1986). Cognition, brain size and the extraction of embedded food resources. *Primate Ontogeny, Cognition and Social Behaviour*, 3, 92–10.
- Gladue, B., Boechler, M., & McCaul, K. (1989). Hormonal response to competition in human males. *Aggressive Behaviour*, 15(6), 409–422.
- Glazier, D. S. (1999). Trade-offs between reproductive and somatic (storage) investments in animals: A comparative test of the Van Noordwijk and De Jong model. *Evolutionary Ecology*, 13, 539–555.
- Gonzalez-Bono, E., Salvador, A., Ricarte, J., Serrano, M. A., & Arnedo, M. (2000). Testosterone and attribution of successful competition. *Aggressive Behaviour*, 26(July 1999), 235–240.
- Gustafsson, A., & Lindfors, P. (2004). Human size evolution: No evolutionary allometric relationship between male and female stature. *Journal of Human Evolution*, 47(4), 253–266.
- Haile-Selassie, Y. (2001). Late Miocene hominids from the middle Awash, Ethiopia. *Nature*, 412(6843), 178–181.
- Halsey, L. G., & White, C. R. (2012). Comparative energetics of mammalian locomotion: Humans are not different. *Journal of Human Evolution*, 63(5), 718–722.
- Hawkes, K. (1993). On why male foragers hunt and share food: Reply to Hill and Kaplan. *Current Anthropology*, 34(5), 706–710.
- Hawks, J., Hunley, K., Lee, S. H., & Wolpoff, M. (2000). Population bottlenecks and Pleistocene human evolution. *Molecular Biology and Evolution*, 17(1), 2–22.
- Heglund, N., & Taylor, C. (1988). Speed, stride frequency and energy cost per stride: How do they change with body size and gait? *Journal of Experimental Biology*, 138, 301–318.
- Hiernaux, J. (1968). *La diversité humaine en Afrique subsaharienne*. Bruxelles: Editions de l'Institut de Sociologie de l'Université Libre de Bruxelles.
- Hiernaux, J., & Fromont, A. (1976). The correlations between anthropobiological and climatic variables in sub-Saharan Africa: Revised estimates. *Human Biology*, 1, 757–767.
- Higgins, R. W., & Ruff, C. B. (2011). The effects of distal limb segment shortening on locomotor efficiency in sloped terrain: Implications for Neandertal locomotor behavior. *American Journal of Physical Anthropology*, 146(3), 336–345.
- Hill, K., & Hurtado, A. M. (1996). *Ache life history*. New York, NY: Aldine de Gruyter.
- Hill, K., & Kaplan, H. (1993). On why male foragers hunt and share food. *Current Anthropology*, 34(5), 701–710.
- Hill, R., Muhich, T., & Humphries, M. (2013). City-scale expansion of human thermoregulatory costs. *PLoS ONE*, 8(10), 1–8.
- Holliday, T. (1997a). Body proportions in late Pleistocene Europe and modern human origins. *Journal of Human Evolution*, 32, 423–447.
- Holliday, T. (1997b). Postcranial evidence of cold adaptations in European Neanderthals. *American Journal of Physical Anthropology*, 104(May 1996), 245–258.
- Holliday, T., & Trinkaus, E. (1991). Limb/trunk proportions in Neandertals and early anatomically modern humans. *American Journal of Physical Anthropology*, 12, 93–94.
- Holt, B. (2003). Mobility in Upper Paleolithic and Mesolithic Europe: Evidence from the lower limb. *American Journal of Physical Anthropology*, 122, 200e215.
- Holt, B., & Formicola, V. (2008). Hunters of the ice age: The biology of Upper Paleolithic people. *Yearbook of Physical Anthropology*, 137, 70e99.
- Hönekopp, J., Manning, J., & Müller, C. (2006). Digit ratio (2D:4D) and physical fitness in males and females: Evidence for effects of prenatal androgens on sexually selected traits. *Hormones and Behavior*, 49(4), 545–549.
- Hönekopp, J., Bartholdt, L., Beier, L., & Liebert, A. (2007). Second to fourth digit length ratio (2D:4D) and adult sex hormone levels: New data and a meta-analytic review. *Psychoneuroendocrinology*, 32(4), 313–321.
- Hopcroft, R. L. (2006). Sex, status, and reproductive success in the contemporary United States. *Evolution and Human Behavior*, 27(2), 104–120.
- Hsieh, Y., Robling, A., Ambrosius, W., Burr, B., & Turner, C. (2001). Mechanical loading of diaphyseal bone in vivo: The strain threshold for an osteogenic response varies with location. *Journal of Bone and Mineral Research*, 16, 2291–2297.
- Iovita, R., & Sano, K. (2016). Summary and conclusions. In R. Iovita & K. Sano (Eds.), *Multidisciplinary Approaches to the Study of Stone Age Weaponry* (pp. 289–297). Dordrecht: Springer.
- Isler, K., & van Schaik, C. (2011). Costs of encephalization: The energy trade-off hypothesis tested on birds. *Journal of Human Evolution*, 51(3), 228–243.
- Isler, K., & van Schaik, C. P. (2006). Metabolic costs of brain size evolution. *Biology Letters*, 2(4), 557–560.
- Jones, H., Priest, J., Hayes, W., Tichenor, C., & Nagel, D. (1977). Humeral hypertrophy in response to exercise. *The Journal of Bone and Joint Surgery. American Volume*, 59(2), 204–208.
- Judex, S., Gross, T., & Zernicke, R. (1997). Strain gradients correlate with sites of exercise-induced bone-forming surfaces in the adult skeleton. *Journal of Bone and Mineral Research*, 12, 1737–1745.
- Jungers, W. (1982). Lucy's limbs: Skeletal allometry and locomotion in *Australopithecus afarensis*. *Nature*, 297, 676–678.
- Kaplan, H., & Hill, K. (1984). Food sharing among ache foragers: Tests of exploratory hypotheses. *Current Anthropology*, 26(2), 223–246.
- Kaplan, H., & Hill, K. (1985a). Food sharing among ache foragers: Tests of explanatory hypotheses. *Current Anthropology*, 26(2), 223–246.
- Kaplan, H., & Hill, K. (1985b). Hunting ability success among male ache foragers: Preliminary research conclusions. *Current Anthropology*, 26(1), 131–133.
- Kaplan, H. S., & Gangestad, S. (2005). Life history theory and evolutionary psychology. In D. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 68–95). New York, NY: John Wiley.
- Katzmarzyk, P., & Leonard, W. (1998). Climatic influences on human body size and proportions: Ecological adaptations and secular trends. *American Journal of Physical Anthropology*, 50(3), 483–503.
- King, J., Brelsford, H., & Tullos, H. (1969). Analysis of the pitching arm of the professional baseball pitcher. *Clinical Orthopaedics and Related Research*, 67, 116–123.
- Knechtel, B., & Bircher, S. (2005). Changes in body composition during an extreme endurance run. *Praxis*, 94, 371–377.



- Knechtle, B., Enggist, A., & Jehle, T. (2005). Energy turnover at the Race Across America (RAAM)—A case report. *International Journal of Sports Medicine*, 26(6), 499–503.
- Knechtle, B., Knechtle, P., & Lepers, R. (2011). Participation and performance trends in ultra-triathlons from 1985 to 2009. *Scandinavian Journal of Medicine and Science in Sports*, 21(6), e82–e90.
- Kramer, P. A., & Eck, G. G. (2000). Locomotor energetics and leg length in hominid bipedality. *Journal of Human Evolution*, 38(5), 651–666.
- Kramer, P. A. (1999). Modelling the locomotor energetics of extinct hominids. *The Journal of Experimental Biology*, 202(Pt 20), 2807–2818.
- L'Episcopo, J. (1934). Tendon transplantation in obstetrical paralysis. *American Journal of Surgery*, 25, 122–125.
- Lanyon, L., Hampson, W., Goodship, A., & Shah, J. (1975). Bone deformation recorded in vivo from strain gauges attached to the human tibial shaft. *Acta Orthopaedica Scandinavica*, 46, 256–268.
- Lanyon, L. E. (1992). Control of bone architecture by functional load bearing. *Journal of Bone and Mineral Research*, 7, S369–S375.
- Larson, S. (2007). Evolutionary transformation of the hominin shoulder. *Evolutionary Anthropology*, 16, 172–187.
- Larson, S. (2009). Evolution of the hominin shoulder: Early Homo. In *The first humans—Origin and early evolution of the genus Homo* (pp. 65–75). Dordrecht: Springer.
- Lee, S., & Wolpoff, M. (2003). The pattern of evolution in Pleistocene human brain size. *Paleobiology*, 29(2), 186–196.
- Leonard, W. R. (2012). Laboratory and field methods for measuring human energy expenditure. *American Journal of Human Biology*, 24(3), 372–384. doi:10.1002/ajhb.20000
- Leonard, W. R., & Ulijaszek, S. J. (2002). Energetics and evolution: An emerging research domain. *American Journal of Human Biology*, 550, 547–550.
- Liebenberg, L. (2006). Persistence hunting by modern hunter gatherers. *Current Anthropology*, 47(6), 1017–1026.
- Lieberman, D. (2014). The story of the human body: Evolution, health, and disease. *Vintage*.
- Lieberman, D. E., & Bramble, D. M. (2007). The evolution of Marathon running. *Sports Medicine*, 37, 288–290.
- Lieberman, D. E. (2010). Four legs good, two legs fortuitous: Brains, brawn, and the evolution of human bipedalism. In J. LOSOS (Ed.), *The light of evolution* (2nd ed., pp. 55–71). Greenwood Village, CO: Roberts and Company.
- Lieberman, D. E. (2012a). Those feet in ancient times. *Nature*, 483, 550–551.
- Lieberman, D. E. (2012b). What can we learn about running from barefoot running: An evolutionary medical perspective. *Exercise and Sport Sciences Reviews*, 40(2), 63–72.
- Lieberman, D. E. (2015). Human locomotion and heat loss: An evolutionary perspective. *Comprehensive Physiology*, 5(1), 99–117.
- Lieberman, D. E., Bramble, D., Raichlen, D., & Shea, J. (2006). Brains, brawn, and the evolution of human endurance running capabilities. In F. E. Grine, J. G. Fleagle, & R. E. Leakey (Eds.), *The first humans—Origin and early evolution of the genus Homo*. Springer.
- Lieberman, D. E., Castillo, E., Otarola-Castillo, E., Sang, M., Sigei, T., Ojiambo, R., ... Pitsiladis, Y. (2015). Variation in foot strike patterns among habitually barefoot and shod runners in Kenya. *PLoS ONE*, 10(7), e0131354. doi:10.1371/journal.pone.0131354
- Lieberman, D. E., Venkadesan, M., Werbel, W., Daoud, A., Dandrea, S., Davis, I., ... Pitsiladis, Y. (2010). Foot strike patterns and collision forces in habitually barefoot versus shod runners. *Nature*, 463(7280), 531–535.
- Lodge, O. (1906). *Life and matter*. London: Williams & Norgate.
- Longman, D., Stock, J. T., & Wells, J. C. K. (2011). Digit ratio (2D:4D) and rowing ergometer performance in males and females. *American Journal of Physical Anthropology*, 144(3), 337–341.
- Longman, D., Wells, J., & Stock, J. (2015). Can persistence hunting signal male quality? A test considering digit ratio in endurance athletes. *PLoS One*, 10(4), e0121560. doi:10.1371/journal.pone.0121560
- Longman, D. P., Macintosh, A., Roberts, R., Oakley, S., Wells, J., & Stock, J. (2019). Ultra-endurance athletic performance suggests energetics drive human morphological thermal adaptation. *Evolutionary Human Sciences*, 1, e16. doi:10.1017/ehs.2019.1
- Longman, D. P., Macintosh, A., Roberts, R., Oakley, S., Wells, J., & Stock, J. (2020). Female ultra-endurance athletic performance reflects sex-specific evolutionary energetics. *Evolutionary Human Sciences*, 2, e16. doi:10.1017/ehs.2020.1
- Longman, D. P., Prall, S., Shattuck, E., Stephen, I., Stock, J., Wells, J., & Muehlenbein, M. (2017). Short-term resource allocation during extensive athletic competition. *American Journal of Human Biology*, 30(1), e23052. doi:10.1002/ajhb.20000
- Longman, D. P., Stock, J., & Wells, J. (2017). A trade-off between cognitive and physical performance, with relative preservation of brain function. *Scientific Reports*, 7(1), 13709. doi:10.1038/s41598-017-01370-9
- Longman, D. P., Surbey, M., Stock, J., & Wells, J. (2018). Tandem androgenic and psychological shifts in male reproductive effort following a manipulated “win” or “loss” in a sporting competition. *Human Nature*, 29(3), 283–310. doi:10.1007/s12110-018-9310-1
- Lotka, J. (1922). Contribution to the energetics of evolution. *Proceedings of the National Academy of Sciences of the United States of America*, 8, 147–151.
- Macintosh, A., Pinhasi, R., & Stock, J. (2017). Prehistoric women's manual labor exceeded that of athletes through the first 5500 years of farming in Central Europe. *Science Advances*, 3(November), ea03893. doi:10.1126/sciadv.a03893
- Magnusson, S., Gleim, G., & Nicholas, J. (1994). Shoulder weakness in professional baseball pitchers. *Medicine and Science in Sports and Exercise*, 26, 5–9.
- Manning, J. (2002). The ratio of the 2nd to 4th digit length and performance in skiing. *The Journal of Sports Medicine and Physical Fitness*, 42(4), 446–450.
- Manning, J., Morris, L., & Caswell, N. (2007). Endurance running and digit ratio (2D:4D): implications for fetal testosterone effects on running speed and vascular health. *American Journal of Human Biology*, 421, 416–421.
- Manning, J., Scutt, D., Wilson, J., & Lewis-Jones, D. (1998). The ratio of 2nd to 4th digit length: A predictor of sperm numbers and concentrations of testosterone, luteinizing hormone and oestrogen. *Human Reproduction (Oxford, England)*, 13(11), 3000–3004.
- Manning, J., & Taylor, R. (2001). Second to fourth digit ratio and male ability in sport: Implications for sexual selection in humans. *Evolution and Human Behavior*, 22(1), 61–69.
- Manning, J. T., Barley, L., Walton, J., Lewis-jones, D. I., & Trivers, R. L. (2000). The 2nd:4th digit ratio, sexual dimorphism, population differences, and reproductive success: Evidence for sexually antagonistic genes? *Evolution and Human Behavior*, 21, 163–183.
- Manning, J. T., & Fink, B. (2008). Digit ratio (2D:4D), dominance, reproductive success, asymmetry, and sociosexuality in the BBC Internet Study. *American Journal of Human Biology*, 20(4), 451–461.
- Marchi, D. (2008). Relationships between lower limb cross-sectional geometry and mobility: The case of a Neolithic sample from Italy. *American Journal of Physical Anthropology*, 137, 188e200. doi:10.1002/ajpa.20000
- Maynard, L., Guo, S., Chumlea, W., Roche, A., Wisemandle, W., Zeller, C., ... Siervogel, R. (1998). Total-body and regional bone mineral content and areal bone mineral density in children aged 8–18 y: The Fels Longitudinal Study. *The American Journal of Clinical Nutrition*, 68(5), 1111–1117.
- Mazur, A., Booth, A., & Dabbs, J. (1992). Testosterone and chess competition. *Social Psychology Quarterly*, 55(1), 70–77.
- Mazur, A., & Lamb, T. (1980). Testosterone, status, and Mood in Human Males. *Hormones and Behavior*, 14(3), 236–246.
- Mazur, A., Susman, E., & Edelbrock, S. (1997). Sex difference in testosterone response to a video game contest. *Evolution and Human Behavior*, 18(5), 317–326.

- McArdle, W., Katch, F., & Katch, V. (2001). *Exercise physiology: Energy, nutrition and human performance*. Philadelphia, PA: Lippincott, Williams & Wilkins.
- McArdle, W., Magel, J., Gergley, T., Spina, R., & Toner, M. (2017). Thermal adjustment to cold-water exposure in resting men and women. *Journal of Applied Physiology*, 56(6), 1565–1571.
- McArdle, W., Magel, J., Spina, R., Gergley, T., & Toner, M. (1984). Thermal adjustment to cold-water exposure in exercising men and women. *Journal of Applied Physiology*, 56(6), 1572–1577.
- McCaul, K. D., Gladue, B. A., & Joppa, M. (1992). Winning, losing, mood, and testosterone. *Hormones and Behavior*, 26(4), 486–504.
- McGlothlin, J. W., Jawor, J. M., & Ketterson, E. D. (2007). Natural variation in a testosterone-mediated trade-off between mating effort and parental effort. *The American Naturalist*, 170(6), 864–875.
- McLeod, K., Rubin, C., Otter, M., & Qin, Y. (1998). Skeletal cell stresses and bone adaptation. *The American Journal of the Medical Sciences*, 316, 176–183.
- McNab, B., & Eisenberg, J. F. (1989). Brain size and its relation to the rate of metabolism in mammals. *The American Naturalist*, 133(2), 157–167.
- Milks, A., Parker, D., & Pope, M. (2019). External ballistics of Pleistocene hand-thrown spears: Experimental performance data and implications for human evolution. *Scientific Reports*, 9(1), 31–34.
- Mink, J., Blumenshine, R., & Adams, D. (1981). Ratio of central nervous system to body metabolism in vertebrates: Its constancy and functional basis. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 241(3), R203–R212.
- Montain, S., Sawka, M., Cadarette, B., Quigley, M., & McKay, J. (1994). Physiological tolerance to uncompensable heat stress: Effects of exercise intensity, protective clothing, and climate. *Journal of Applied Physiology*, 77(1), 216–222.
- Muller, M., & Wrangham, R. (2001). The reproductive ecology of male hominoids. In *Reproductive ecology and human evolution* (pp. 397–427). New York: Aldine.
- Napier, J. (1967). The antiquity of human walking. *Scientific American*, 216(4), 56–67.
- Navarrete, A., van Schaik, C. P., & Isler, K. (2011). Energetics and the evolution of human brain size. *Nature*, 480(7375), 91–93.
- Nettle, D., & Pollet, T. V. (2008). Natural selection on male wealth in humans. *The American Naturalist*, 172(5), 658–666.
- Niemitz, C. (2010). The evolution of the upright posture and gait—A review and a new synthesis. *Die Naturwissenschaften*, 97(3), 241–263.
- Nikander, R., Sievänen, H., Uusi-Rasi, R., Heinonen, A., & Kannus, P. (2006). Loading modalities and bone structures at nonweight-bearing upper extremity and weight-bearing lower extremity: A pQCT study of adult female athletes. *Bone*, 39, 886–894.
- Ocobock, C. (2016). Human energy expenditure, allocation, and interactions in natural temperate, hot, and cold environments. *American Journal of Physical Anthropology*, 161(4), 667–675.
- Osbahr, D., Cannon, D., & Speer, K. (2002). Retroversion of the humerus in the throwing shoulder of college baseball pitchers. *The American Journal of Sports Medicine*, 30, 347–353.
- Owen, N., Sparling, P., Healy, G., Dunstan, D., & Matthews, C. (2010). Sedentary behavior: Emerging evidence for a new health risk. *Mayo Clinic Proceedings*, 85(12), 1138–1141.
- Parker, S., & McKinney, M. (1999). *Origins of intelligence: The evolution of cognitive development in monkeys, apes, and humans*. Baltimore: Johns Hopkins University Press.
- Paterson, J. (1996). Coming to America: Acclimation in macaque body structures and Bergmann's rule. *International Journal of Primatology*, 17(4), 585–611.
- Paul, S., Kato, B., Hunkin, J., Vivekanandan, S., & Spector, T. (2006). The Big Finger: The second to fourth digit ratio is a predictor of sporting ability in women. *British Journal of Sports Medicine*, 40(12), 981–983.
- Pennington, C. (1963). *The Tarahumara of Mexico*. Salt Lake City, UT: University of Utah Press.
- Pennington, R., & Harpending, H. (1993). *The structure of an African pastoralist community: Demography, history, and ecology of the Ngamiland Herero*. New York, NY: Oxford University Press.
- Perl, D., Daoud, A., & Lieberman, D. (2012). Effects of footwear and strike type on running economy. *Medicine and Science in Sports and Exercise*, 44(7), 1335–1343.
- Peters, A., Schweiger, U., Pellerin, L., Hubold, C., Oltmanns, K., Conrad, M., ... Fehm, H. (2004). The selfish brain: Competition for energy resources. *Neuroscience and Biobehavioral Reviews*, 28, 143–180.
- Pieper, H. (1998). Humeral torsion in the throwing arm of handball players. *The American Journal of Sports Medicine*, 26, 247–253.
- Pigliucci, M., Murren, C., & Schlichting, C. (2006). Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology*, 209(12), 2362–2367.
- Pinhasi, R., Gasparian, B., Areshian, G., Zardaryan, D., Smith, A., Bar-Oz, G., & Higham, T. (2010). First direct evidence of chalcolithic footwear from the near eastern highlands. *PLoS ONE*, 5(6), 3–7.
- Pokrywka, L., Rachoń, D., Suchecka-Rachoń, K., & Bitel, L. (2005). The second to fourth digit ratio in elite and non-elite female athletes. *American Journal of Human Biology: The Official Journal of the Human Biology Council*, 17(6), 796–800.
- Pollet, T., & Nettle, D. (2008). Driving a hard bargain: Sex ratio and male marriage success in a historical US population. *Biology Letters*, 4(1), 31–33.
- Pontzer, H. (2005). A new model predicting locomotor cost from limb length via force production. *The Journal of Experimental Biology*, 208(Pt 8), 1513–1524.
- Pontzer, H. (2007). Effective limb length and the scaling of locomotor cost in terrestrial animals. *The Journal of Experimental Biology*, 210(Pt 10), 1752–1761.
- Pontzer, H. (2015a). Constrained total energy expenditure and the evolutionary biology of energy balance. *Exercise and Sport Sciences Reviews*, 43(3), 110–116.
- Pontzer, H. (2015b). Energy expenditure in humans and other Primates: A new synthesis. *Annual Review of Anthropology*, 44, 169–187.
- Pontzer, H., Durazo-Arvizu, R., Dugas, L., Plange-Rhule, J., Bovet, P., Forrester, T., ... Luke, A. (2016). Constrained total energy expenditure and metabolic adaptation to physical activity in adult humans. *Current Biology*, 26(3), 410–417.
- Pontzer, H., Raichlen, D., & Rodman, P. (2014). Bipedal and quadrupedal locomotion in chimpanzees. *Journal of Human Evolution*, 66(1), 64–82.
- Pontzer, H., Raichlen, D., & Sockol, M. (2009). The metabolic cost of walking in humans, chimpanzees, and early hominins. *Journal of Human Evolution*, 56(1), 43–54.
- Pontzer, H., Raichlen, D., Wood, B., Emery Thompson, M., Racette, S., Mabulla, A., & Marlowe, F. (2015). Energy expenditure and activity among Hadza hunter-gatherers. *American Journal of Human Biology*, 27(5), 628–637.
- Pontzer, H., Raichlen, D., Wood, B., Mabulla, A., Racette, S., & Marlowe, F. (2012). Hunter-gatherer energetics and human obesity. *PLoS ONE*, 7(7), 1–8.
- Reader, S., & Laland, K. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America*, 99(7), 4436–4441.
- Reagan, K., Meister, K., Horodyski, M., Werner, D., Carruthers, C., & Wilk, K. (2002). Humeral retroversion and its relationship to glenohumeral rotation in the shoulder of college baseball players. *The American Journal of Sports Medicine*, 30(3), 354–360.
- Rhodes, J., & Churchill, S. (2009). Throwing in the Middle and Upper Paleolithic: Inferences from an analysis of humeral retroversion. *Journal of Human Evolution*, 56(1), 1–10.
- Richmond, B., & Jungers, W. (2008). Orrorin tugenensis femoral morphology and the evolution of hominin bipedalism. *Science*, 319, 1662–1665.

- Rico, H., Revilla, M., Hernandez, E., Villa, L., & Del Buergo, M. (1992). Sex differences in the acquisition of total bone mineral mass peak assessed through dual-energy X-ray absorptiometry. *Calcified Tissue International*, 51(4), 251–254.
- Roach, N., & Lieberman, D. (2014). Upper body contributions to power generation during rapid, overhand throwing in humans. *Journal of Experimental Biology*, 217(12), 2139–2149.
- Roach, N., Lieberman, D., Gill, T., Palmer, W., & Gill, T. (2012). The effect of humeral torsion on rotational range of motion in the shoulder and throwing performance. *Journal of Anatomy*, 220(3), 293–301.
- Roach, N., & Richmond, B. (2015). Humeral torsion does not dictate shoulder position, but does influence throwing speed. *Journal of Human Evolution*, 85, 206–211.
- Roach, N., Venkadesan, M., Rainbow, M., & Lieberman, D. (2013). Elastic energy storage in the shoulder and the evolution of high-speed throwing in Homo. *Nature*, 498(7455), 483–486.
- Roberts, D. (1953). Body weight, race and climate. *American Journal of Physical Anthropology*, 11(4), 533–558.
- Roberts, D. (1973). *Climate and human variability. An Addison-Wesley module in anthropology* (Vol. 34). Reading, MA: Addison-Wesley.
- Roberts, D. (1978). *Climate and human variability*. Menlo Park, CA: Cummings.
- Rodman, P., & McHenry, H. (1980a). Bioenergetics and the origin of hominid bipedalism. *American Journal of Physical Anthropology*, 52, 103–106.
- Rodman, P., & McHenry, H. (1980b). Bioenergetics and the origin of human bipedalism. *American Journal of Physical Anthropology*, 52, 103–106.
- Romijn, J. A., Gastaldelli, A., Horowitz, J. F., Endert, E., & Wolfe, R. R. (1993). Regulation in relation of endogenous fat and carbohydrate to exercise intensity and duration metabolism. *American Journal of Physiology*, 265, 380–391.
- Rose, M. (1976). Bipedal behavior of olive baboons (*Papio anubis*) and its relevance to an understanding of the evolution of human bipedalism. *American Journal of Physical Anthropology*, 44(2), 247–261.
- Roseman, C., & Auerbach, B. (2015). Ecogeography, genetics, and the evolution of human body form. *Journal of Human Evolution*, 78, 80–90.
- Rubenson, J., Heliam, D., Maloney, S., Withers, P., Lloyd, D., & Fournier, P. (2007). Reappraisal of the comparative cost of human locomotion using gait-specific allometric analyses. *Journal of Experimental Biology*, 210(20), 3513–3524.
- Rubin, C., & Lanyon, L. (1984). Regulation of bone formation by applied dynamic loads. *The Journal of Bone and Joint Surgery. American Volume*, 66-A, 397–402.
- Rubin, C., McLeod, K., & Basin, S. (1990). Functional strains and cortical bone adaptation: Epigenetic assurance of skeletal integrity. *Journal of Biomechanics*, 23, 43–54.
- Ruff, C. (2002). Variation in human body size and shape. *Annual Review of Anthropology*, 31(1), 211–232.
- Ruff, C., Trinkaus, E., & Holliday, T. (1997). Body mass and encephalization in Pleistocene Homo. *Nature*, 387(6629), 173–176.
- Ruff, C. B. (1994). Morphological adaptation to climate in modern and fossil hominoids. *Yearbook of Physical Anthropology*, 37, 65–107.
- Ruff, C. B. (1995). Biomechanics of the hip and birth in early Homo. *American Journal of Physical Anthropology*, 98, 527–574.
- Ruff, C. B. (2000). Body mass prediction from skeletal frame size in elite athletes. *American Journal of Physical Anthropology*, 112(112), 507e517.
- Ruff, C. B. (2008). Femoral/humeral strength in early African Homo erectus. *Journal of Human Evolution*, 54, 383e390.
- Ruff, C. B. (2009). Relative limb strength and locomotion in Homo habilis. *American Journal of Physical Anthropology*, 138, 90e100.
- Ruff, C. B., Holt, B., Sladek, V., Berner, M., Murphy, W., Jr., Nedden, D., ... Recheis, W. (2006). Body size, body proportions, and mobility in the Tyrolean "Iceman". *Journal of Human Evolution*, 51, 91–101.
- Ruff, C. B., Trinkaus, E., & Holliday, T. (1998). Body mass estimation in Olympic athletes and Pleistocene Homo. *American Journal of Physical Anthropology*, 26, 192e193.
- Salvador, A., Simón, V., Suay, F., & Llorens, L. (1987). Testosterone and cortisol responses to competitive fighting in human males: A pilot study. *Aggressive Behaviour*, 13(1), 9–13.
- Salvador, A., Suay, F., & Cantón, E. (1990). Efectos del resultado de una competición y de la categoría deportiva sobre los cambios en la testosterona y el cortisol séricos. *Actas Del II Congreso Nacional Del Colegio Oficial de Psicólogos*.
- Schmitt, D. (2003). Insights into the evolution of human bipedalism from experimental studies of humans and other primates. *Journal of Experimental Biology*, 206, 1437–1448.
- Schoch, W., Bigga, G., Böhner, U., Richter, P., & Terberger, T. (2015). New insights on the wooden weapons from the Paleolithic site of Schöningen. *Journal of Human Evolution*, 89, 214–225.
- Senut, B., & Pickford, M. (2004). La dichotomie grands singes-homme revisitée. *Comptes Rendus Palevol*, 3(4), 265–276.
- Serangeli, J., Van Kolfschoten, T., Starkovich, B., & Verheijen, I. (2015). The European saber-toothed cat (*Homotherium latidens*) found in the 'Spear Horizon' at Schöningen (Germany). *Journal of Human Evolution*, 89, 172–180.
- Serrat, M., King, D., & Lovejoy, C. (2008). Temperature regulates limb length in homeotherms by directly modulating cartilage growth. *Proceedings of the National Academy of Sciences of the United States of America*, 105(49), 19348–19353.
- Shaw, C. (2010). 'Putting flesh back onto the bones?' Can we predict soft tissue properties from skeletal and fossil remains? *Journal of Human Evolution*, 59, 484e492.
- Shaw, C. (2011). Is 'hand preference' coded in the hominin skeleton? An in-vivo study of bilateral morphological variation. *Journal of Human Evolution*, 61, 480e487.
- Shaw, C., Hofmann, C., Petraglia, M., Stock, J., & Gottschall, J. (2012). Neandertal humeri may reflect adaptation to scraping tasks, but not spear thrusting. *PLoS ONE*, 7(7), 1–8.
- Shaw, C., & Stock, J. (2009a). Habitual throwing and swimming correspond with upper limb diaphyseal strength and shape in modern human athletes. *American Journal of Physical Anthropology*, 140(1), 160–172.
- Shaw, C., & Stock, J. (2009b). Intensity, repetitiveness, and directionality of habitual adolescent mobility patterns influence the tibial diaphysis morphology of athletes. *American Journal of Physical Anthropology*, 140(1), 149–159.
- Shaw, C., & Stock, J. (2013). Extreme mobility in the Late Pleistocene? Comparing limb biomechanics among fossil Homo, varsity athletes and Holocene foragers. *Journal of Human Evolution*, 64(4), 242–249.
- Shawcross, R. (2014). *Shoes: An illustrated history*. London, UK: Bloomsbury.
- Shea, J. (2006). The origins of lithic projectile point technology: Evidence from Africa, the Levant, and Europe. *Journal of Archaeological Science*, 33, 823–846.
- Smith, E. A. (2004). Why do good hunters have higher reproductive success? *Human Nature*, 15(4), 343–364.
- Snodgrass, J. J., Leonard, W. R., & Robertson, M. L. (1999). Interspecific variation in body composition and its influence on metabolic variation in primates and other mammals. *American Journal of Physical Anthropology*, 28, 255.
- Sockol, M., Raichlen, D., & Pontzer, H. (2007). Chimpanzee locomotor energetics and the origin of human bipedalism. *Proceedings of the National Academy of Sciences of the United States of America*, 104(30), 12265–12269.
- Stearns, S. C. (1989). Trade-offs in life-history evolution. *British Ecological Society*, 3, 259–268.
- Stearns, S. C. (1992). *The evolution of life histories*. Oxford: Oxford University Press.



- Studel-Numbers, K. L., Weaver, T. D., & Wall-Scheffler, C. M. (2007). The evolution of human running: Effects of changes in lower-limb length on locomotor economy. *Journal of Human Evolution*, 53(2), 191–196.
- Studel-Numbers, K., & Tilkens, M. (2004). The effect of lower limb length on the energetic cost of locomotion: Implications for fossil hominins. *Journal of Human Evolution*, 47(1–2), 95–109.
- Stewart, J., García-rodríguez, O., Knul, M., Sewell, L., Montgomery, H., Thomas, M., & Diekmann, Y. (2018). Palaeoecological and genetic evidence for Neanderthal power locomotion as an adaptation to a woodland environment. *Quaternary Science Reviews*.
- Stibbard-hawkes, D. (n.d.). No association between 2D:4D ratio and hunting success among Hadza hunters. *Human Nature*. (in press).
- Stini, W. (1972). Malnutrition, body size and proportion. *Ecology of Food and Nutrition*, 1(2), 1210126.
- Stinson, S. (1990). South American Indians. *American Journal of Human Biology*, 2, 37–51.
- Strier, K. (2003). Primate behavioral ecology: From ethnography to ethology and back. *American Anthropologist*, 105(1), 16–27.
- Suay, F., Salvador, A., González-Bono, E., Sanchis, C., Martínez, M., Martínez-Sanchis, S., ... Montoro, J. B. (1999). Effects of competition and its outcome on serum testosterone, cortisol and prolactin. *Psychoneuroendocrinology*, 24(5), 551–566.
- Sultan, S. (1995). Phenotypic plasticity and plant adaptation. *Acta Botanica Neerlandica*, 44(4), 363–383.
- Susman, R., Stern, J. J., & Jungers, W. (1984). Arboreality and bipedality in the Hadar hominids. *Folia Primatologica*, 43, 113–156.
- Taylor, C., Heglund, N., & Maloij, G. M. O. (1982). Energetics and mechanics of terrestrial locomotion. *Journal of Experimental Biology*, 97, 1–21.
- The World Bank. (2018). *Fragility, Conflict and Violence*. The World Bank. <https://www.worldbank.org/en/topic/fragilityconflictviolence>.
- Thieme, H. (1997). Lower Palaeolithic hunting spears from Germany. *Nature*, 385, 807–810.
- Thieme, H. (1999). Lower Palaeolithic throwing spears and other wooden implements from Schöningen, Germany. In H. Ullrich (Ed.), *Hominid evolution: lifestyles and survival strategies* (pp. 383–395). Gelsenkirchen, Germany: Edition Archaea.
- Thurber, C., Dugas, L., Ocobock, C., Carlson, B., Speakman, J., & Pontzer, H. (2019). Extreme events reveal an alimentary limit on sustained maximal human energy expenditure. *Science Advances*, 5(6), 1–9.
- Tikuisis, P., Jacobs, I., Moroz, D., Vallerand, A., & Martineau, L. (2000). Comparison of thermoregulatory responses between men and women immersed in cold water. *Journal of Applied Physiology*, 89(4), 1403–1411.
- Tilkens, M., Wall-Scheffler, C., Weaver, T., & Studel-Numbers, K. (2007). The effects of body proportions on thermoregulation: An experimental assessment of Allen's rule. *Journal of Human Evolution*, 53(3), 286–291.
- Toner, M., Sawka, M., Foley, M., & Pandolf, K. (1986). Effects of body mass and morphology on thermal responses in water. *Journal of Applied Physiology (Bethesda, MD)*, 60(2), 521–525.
- Trinkaus, E. (1981). Neanderthal limb proportions and cold adaptation. In C. Stringer (Ed.), *Aspects of human evolution* (pp. 187–224). London: Taylor & Francis.
- Trinkaus, E. (1997). Appendicular robusticity and the paleobiology of modern human emergence. *Proceedings of the National Academy of Sciences of the United States of America*, 94, 13367–13373.
- Trinkaus, E. (2005). Anatomical evidence for the antiquity of human footwear use. *Journal of Archaeological Science*, 32(10), 1515–1526.
- Trinkaus, E., Churchill, S., & Ruff, C. (1994). Postcranial robusticity in Homo. II: Humeral bilateral asymmetry and bone plasticity. *American Journal of Physical Anthropology*, 93, 1e34.
- Trinkaus, E. (1984). Comment on: Human running and hominid evolution, by DR Carrier. *Current Anthropology*, 25, 491.
- Trumble, B. C., Smith, E. A., Connor, K. A. O., Kaplan, H. S., & Gurven, M. D. (2013). Successful hunting increases testosterone and cortisol in a subsistence population. *Proceedings of the Royal Society B: Biological Sciences*, 281(1776), 20132876.
- Ulijaszek, S. J. (1995). *Human energetics in biological anthropology*. Cambridge, UK: Cambridge University Press.
- van Noordwijk, A., & de Jong, G. (1986). Acquisition and allocation of resources: Their influence on variation in life history tactics. *The American Naturalist*, 128(1), 137–142.
- Vining, D. (1986). Social versus reproductive success: The central theoretical problem of human sociobiology. *Behavioral and Brain Sciences*, 9(1), 167–187.
- Wahren, J., Felig, P., Ahlborg, G., & Jorfeldt, L. (1971). Glucose metabolism during leg exercise in man. *The Journal of Clinical Investigation*, 50(12), 2715–2725.
- Ward, C. (2002). Interpreting the posture and locomotion of *Australopithecus afarensis*: Where do we stand? *American Journal of Physical Anthropology*, 119(S35), 185–215.
- Weaver, M., & Ingram, D. (1969). Morphological changes in swine associated with environmental temperature. *Ecological Society of America*, 50(4), 710–713.
- Wells, J. (2007). Sexual dimorphism of body composition. *Best Practice and Research: Clinical Endocrinology and Metabolism*, 21(3), 415–430.
- Wells, J. (2010). *The evolutionary biology of human body fatness: Thrift and control*. Cambridge, UK: Cambridge University Press.
- Wells, J. (2012). Ecogeographical associations between climate and human body composition: Analyses based on anthropometry and skinfolds. *American Journal of Physical Anthropology*, 147(2), 169–186.
- Wells, J., Nesse, R., Sear, R., Johnstone, R., & Stearns, S. (2017). Evolutionary public health: Introducing the concept. *The Lancet*, 390(10093), 500–509.
- Wells, J., & Stock, J. (2007). The biology of the colonizing ape. *Yearbook of Physical Anthropology*, 222, 191–222.
- Wells, J., & Stock, J. (2011). Re-examining heritability: Genetics, life history and plasticity. *Trends in Endocrinology and Metabolism*, 22(10), 421–428.
- Weyand, P. G., Smith, B. R., Puyau, M. R., & Butte, N. F. (2010). The mass-specific energy cost of human walking is set by stature. *The Journal of Experimental Biology*, 213(Pt 23), 3972–3979.
- Will, M., Pablos, A., & Stock, J. (2017). Long-term patterns of body mass and stature evolution within the hominin lineage. *Subject Category: Subject Areas: Royal Society Open Science*, 4, 171339.
- Woo, S., Kuei, S., Amiel, D., Gomez, M., Hayes, W., White, F., & W, A. (1981). The effect of prolonged physical training on the properties of long bone. A Study of Wolff's Law. *Journal of Bone and Joint Surgery*, 63, 780–787.
- Wright, S., & Weyand, P. G. (2001). The application of ground force explains the energetic cost of running backward and forward. *The Journal of Experimental Biology*, 204(1), 1805–1815.
- Yong, E. (2019). When modern men throw ancient weapons. Retrieved July 30, 2019, from The Atlantic website: <https://www.theatlantic.com/science/archive/2019/01/neanderthal-spears-threw-pretty-well/581218/>
- Zahavi, A. (1975). Mate selection—A selection for a handicap. *Journal of Theoretical Biology*, 53, 205–214.
- Zera, A. J., & Harshman, L. G. (2001). The physiology of life history trade-offs in animals. *Ecology*, 32, 95–126.
- Zilioli, S., & Watson, N. V. (2012). The hidden dimensions of the competition effect: Basal cortisol and basal testosterone jointly predict changes in salivary testosterone after social victory in men. *Psychoneuroendocrinology*, 37(11), 1855–1865.

**How to cite this article:** Longman DP, Wells JCK, Stock JT. Human athletic paleobiology; using sport as a model to investigate human evolutionary adaptation. *Am J Phys Anthropol*. 2020;1–18. <https://doi.org/10.1002/ajpa.23992>