



Patterns of energy allocation during energetic scarcity; evolutionary insights from ultra-endurance events

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ABSTRACT

Exercise physiologists and evolutionary biologists share a research interest in determining patterns of energy allocation during times of acute or chronic energetic scarcity. Within sport and exercise science, this information has important implications for athlete health and performance. For evolutionary biologists, this would shed new light on our adaptive capabilities as a phenotypically plastic species.

In recent years, evolutionary biologists have begun recruiting athletes as study participants and using contemporary sports as a model for studying evolution. This approach, known as human athletic palaeobiology, has identified ultra-endurance events as a valuable experimental model to investigate patterns of energy allocation during conditions of elevated energy demand, which are generally accompanied by an energy deficit. This energetic stress provokes detectable functional trade-offs in energy allocation between physiological processes. Early results from this model suggest that limited resources are preferentially allocated to processes which could be considered to confer the greatest immediate survival advantage (including immune and cognitive function). This aligns with evolutionary perspectives regarding energetic trade-offs during periods of acute and chronic energetic scarcity.

Here, we discuss energy allocation patterns during periods of energetic stress as an area of shared interest between exercise physiology and evolutionary biology. We propose that, by addressing the ultimate “why” questions, namely why certain traits were selected for during the human evolutionary journey, an evolutionary perspective can complement the exercise physiology literature and provide a deeper insight of the reasons underpinning the body’s physiological response to conditions of energetic stress.

1. Energy allocation is a key driver of both evolution and athletic performance

Energy is the fundamental currency of life. All biological function depends on an individual’s ability to acquire and appropriately distribute this key and often limited resource between competing life processes. Indeed, as the prominent and influential biologist Norman Cheetham writes, “*Nothing in biology (or in any other science for that matter) makes sense except in the context of energy and its transformations*” (Sharpe, 2011). As energy is required for all biological processes, it can be viewed as a fundamental driver of both evolutionary adaptation and athletic performance. Each will now be considered.

The significant role played by energy 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; Darwin, 1859; Lodge, 1906), Alfred Lotka wrote that “...*the fundamental object of contention in the life-struggle, in the evolution of the organic world, is available energy*” (Lotka, 1922). Due to the significant challenges associated with acquiring sufficient energy to sustain life and function, powerful selective pressures for energetic efficiency have shaped the evolution of our species. Selection for metabolic frugality is evident in contemporary human physiology, which enhance our ability to cope with periods of both chronic and acute energetic stress (as described in the next subsection).

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The investigation of energy allocation is also of fundamental importance within the field of sport and exercise science. At an acute level, success in many sporting events involves “*solving the fuel crisis*” (Burke and Hawley, 2018). This requires that the rate of ATP regeneration is commensurate to the demands of the sport, which can range from all-out efforts lasting seconds or minutes, to prolonged, sub-maximal efforts lasting hours or even days (Hargreaves and Spriet, 2020). Acute exercise can require a 50–100-fold increase in ATP requirements over baseline, yet intramuscular ATP rarely declines during exercise. This is achieved by the remarkable responsiveness of the body’s energy transfer systems, and their capacity to ensure that cellular energy provision corresponds to demand during various exercise intensities and durations, ensuring a constant energy charge (Neufer, 2018).

Improved understanding of patterns of energy allocation during longer periods of energetic scarcity (lasting, for example, days, weeks, months and even years) is also of paramount importance to athlete health and performance. Energy availability is defined as the amount of energy that is accessible to fuel bodily processes after the demands of exercise training have been met (Loucks et al., 2011). Brief exposure to planned low energy availability within a periodized training program may bring about beneficial outcomes, such as reducing unnecessary body fat or increasing metabolic efficiency, which in turn may support attainment of performance goals (Shirley et al., 2022; Stellingwerff et al., 2019), however more severe and prolonged low energy availability can lead to negative health consequences (Areta et al., 2021), including disrupted reproductive function, compromised bone health and increased injury risk (Mountjoy et al., 2018; Nattiv et al., 2007). Recently our group discussed the concept of LEA from a life history perspective and in light of the trade-offs that may occur when energy availability is low (Oliveira-Junior et al., 2022; Shirley et al., 2022). Yet much remains unknown about the nature of these trade-offs, and how different factors such as the extent and duration of deficit, or characteristics such as age, sex, body composition, health, or training status, may affect them. This renders development of targeted risk identification and management strategies difficult. A better understanding of energy allocation patterns during periods of energetic stress (whether driven by high training energy expenditures, dietary restriction, or a combination of the two), has substantial potential to inform such strategies.

Fields such as molecular biology and exercise physiology allow us to answer the “*how*” and the “*what*” questions. That is, what are the biochemical mechanisms responsible for biological phenomena, and how do they work? For example, the potentially negative consequences of prolonged low energy availability have been conceptualised with models including the male and female athlete triad (Nattiv et al., 1994, 2007, 2021; Yeager et al., 1993) and RED-S (Mountjoy et al., 2014). Although these models do an excellent job of describing *what* happens within the body during periods of low energy availability and *how* it happens, gaps persist in the understanding of *why* the human body responds as it does to stressors such as energy scarcity. In other words, what were the ancestral conditions driving selection for observed contemporary human biology? Specifically, why is energy preferentially allocated to certain processes during periods of scarcity, and not others? This evolutionary perspective complements the existing exercise physiology regarding energy allocation on a conceptual level by acknowledging that the physiological response to low energy availability is an evolved trait, and is influenced by a variety of interindividual and environmental factors (Lieberman, 2015b).

Appropriate and effective allocation of energy can therefore be considered key to success in both the evolutionary and athletic arena. Recognising this common area of interest, this paper draws on data provided from a unique model of energetic stress, namely ultra-endurance athletic events, to demonstrate how an evolutionary perspective can complement the exercise physiology literature to provide insight into energy allocation strategies at the limits of human

adaptive plasticity.

2. The human evolutionary journey has conferred adaptations allowing us to cope with energetic stress

The influence of ancestral selective pressures for energetic efficiency is apparent in the physiology of modern *Homo sapiens*. This can be seen in both the long-term adaptive solutions that developed throughout the hominin lineage, as well as in the fast acting and reversible adaptive mechanisms that allow us to cope with transient bouts of energetic stress within a lifetime. The former can be illustrated by considering two defining features of human evolution; the adoption of upright bipedal locomotion (Dart, 1925; Napier, 1967; Rodman and McHenry, 1980), and the development of an enlarged and elaborated brain (Foley and Lee, 1991; Lee and Wolpoff, 2003; Ruff et al., 1997; Will et al., 2021).

A range of theories have been posed to explain why our hominin ancestors began walking on two, rather than four, limbs (Niemitz, 2010). One potential explanation that has gained significant traction argues that the emergence of bipedalism was driven by gains in locomotor efficiency at a time characterised by a diversification and fragmentation of terrestrial environments (Haile-Selassie, 2001; Pontzer et al., 2009; Senut et al., 2018; Senut and Pickford, 2004; Sockol et al., 2007). During the late Miocene (around 5 million years ago), our ancestral African climate grew cooler and drier. This led to a fragmentation of the dominant rainforests and increased environmental diversification (Cazenave and Kivell, 2023; Cerling et al., 2011; Davies et al., 2020; Drummond-Clarke et al., 2022; Levin, 2015; Magill et al., 2013; Potts, 2013). The transition to an upright gait, as evidenced in the earliest hominins (Zollikofer et al., 2005), conferred metabolic savings while walking (Jungers, 1982; Kramer, 1999; Kramer and Eck, 2000; Ward, 2002). This was succeeded by further improvements in the energetic efficiency of both walking and running throughout the genus *Homo* due to significant lower limb elongation (Bramble and Lieberman, 2004; Pontzer, 2007; Steudel-Numbers et al., 2007; Steudel-Numbers and Tilkins, 2004). Today, human walking is approximately 75% less energetically costly than the quadrupedal knuckle walking of our nearest living relative, the chimpanzee (Pontzer et al., 2014; Sockol et al., 2007).

In parallel with the emergence of bipedalism and subsequent lower limb elongation, the influence of energy on human evolution can be seen in the development of the human brain. While this unique feature has conferred a plethora of benefits to our species such as an improved ability to acquire food, to solve ecological problems and to develop more complex social strategies (Barrickman et al., 2008; Gibson, 1986; Parker and McKinney, 1999; Reader and Laland, 2002), it imposes a significant energetic burden. The brain confers the highest absolute metabolic demand of any human organ (Elia, 1991; Isler and van Schaik, 2006; Shirley et al., 2019), accounting for 20–25% of adult resting metabolic rate – a fig. 2–3 times higher than for chimpanzees (Judaš et al., 2013; Peters et al., 2004). This high cost, coupled with the brain’s continuous consumption of energy, represents a pressure which is likely to generate physiological trade-offs in other systems. Candidate tissues or organs that may display energy savings allowing energetic diversion to the brain (without the need to increase overall metabolic expenditure (Isler and van Schaik, 2011, Isler and van Schaik, 2006) include a reduced digestive tract development (Aiello and Wheeler, 1995) and reduced adiposity (Navarrete et al., 2011).

In addition to bipedalism and encephalisation, *Homo sapiens* have also developed fast acting and reversible mechanisms of adaptation allowing us to cope with bouts of energetic stress within a lifetime. The human evolutionary journey is characterised by repeated cycles of dispersal and colonisation of new environments (Flatt and Heyland, 2011; Wells and Stock, 2007). The food insecurity and increased energy demands associated with this evolutionary strategy brought regular exposure to energetic stress. Similarly, the hunter-gatherer lifestyle adopted by all human groups for around 95% of the evolutionary history

of our species (Hamilton and Walker, 2018) required high levels of physical activity and resulted in lean body types (Pontzer et al., 2012). Consequently, strong selective pressures have encouraged the development of adaptive responses to allow us to survive transient conditions of low environmental energy availability. One such adaptation is our evolved ability to dynamically reallocate energy between different physiological processes during times of scarcity. This is achieved through the process of phenotypic plasticity, whereby morphological, physiological, and behavioural traits vary in response to changing environmental conditions without the need for genetic change (Flatt and Heyland, 2011; Pigliucci et al., 2006; West-Eberhard, 1989).

Life history theory, a branch of evolutionary theory, describes the competitive allocation of finite energy between physiological processes (Leonard, 2012; Stearns, 1989, 1992; Zera and Harshman, 2001). As energy used for one function cannot be used for another, life history theory predicts that during conditions of energetic scarcity, competition between functions becomes heightened and trade-offs arise (Bronson, 1991; Stearns, 1992). Under such conditions, limited resources are predicted to be allocated to processes conferring the greatest immediate survival advantage, although what these processes may be is likely to vary widely between individuals (is likely to vary significantly between individuals (e.g., by population, age, sex, body composition, nutrition, and patterns of physical activity) and by environment (e.g., temperature and altitude)). As such, further investigation of the specific.

The specific hierarchy of functional preservation – the pattern by which certain processes are prioritised or sacrificed (Wells, 2013), along with how this pattern may be influenced by individual and environmental factors – represents an essential and exciting avenue for ongoing investigation. Enhanced knowledge of the hierarchy of functional preservation would not only shed new light on our adaptive capabilities as a phenotypically plastic species but would also allow sports science practitioners to anticipate physiological changes that occur during periods of acute or chronic energetic scarcity (which may be driven by high energy expenditure, low energy intake, or a combination of the two).

3. Ultra-endurance events as a model to investigate energy allocation during conditions of energetic scarcity

In recent years, the concept of recruiting athletes as study participants and using contemporary sports as a model for studying evolution has attracted increasing attention. This approach, known as human athletic palaeobiology, offers unique and valuable opportunities to improve our understanding of how the body responds to periods of energetic scarcity, shedding new light on our evolutionary trajectory, our capacity for adaptation, and the underlying biological mechanisms (Longman et al., 2020). To date, sport has facilitated exploration not only of the evolutionary history of our species (e.g., Bramble and Lieberman, 2004; Lieberman, 2010, 2012b; Lieberman, 2012a; Lieberman, 2015a; Milks et al., 2019; Rhodes and Churchill, 2009; Shaw et al., 2012), but also of human variation and adaptation at the interindividual (i.e., between individuals) (Longman et al., 2019, 2021; Ocobock, 2016; Pontzer, 2015a; Pontzer et al., 2012, 2016; Thurber et al., 2019) and intraindividual levels (i.e. within the individual) (e.g., Longman et al., 2018; Macintosh et al., 2017; Manning et al., 2007; Manning and Taylor, 2001; Shaw, 2010, 2011; Shaw and Stock, 2009a, 2009b).

At the intraindividual level, ultra-endurance events represent a valuable experimental model to investigate acute patterns of energy allocation between physiological processes during conditions of energetic scarcity (Longman et al., 2017a). Ultra-endurance events are typically defined as those exceeding 6 h (Zaryski and Smith, 2005). However, they can often last for days (e.g., the 220 km 5-day Ultra-X ultramarathon series) or weeks (e.g., the Talisker Whisky Atlantic Challenge – a 3000 nautical mile trans-Atlantic rowing race from the Canary Islands to Antigua) on end. Training for, and participation in these events has a very high energetic cost. Further, energy intake is often limited during the events themselves, due to practical or

gastrointestinal difficulties in consuming sufficient food to fuel the event. As such, ultra-endurance events challenge both sides of the energy balance equation (intake and expenditure, and the energy stress inherent within these events (Knechtle et al., 2005; Knechtle and Bircher, 2005) pushes both physiological and cognitive systems to the limits of adaptive plasticity, provoking detectable functional trade-offs in energy allocation between different physiological processes.

This novel approach addresses a significant methodological constraint that had previously limited investigators' ability to observe negative covariation in energetic allocation between two physiological processes. Negative correlations in energetic allocation to different processes can be difficult to detect because inter-individual variation in the ability to acquire resources is often greater than variation in the allocation of these resources (van Noordwijk and de Jong, 1986). That is to say, the ability to acquire calories is likely to differ substantially between individuals, and this can mask individual-level trade-offs in resource allocation. This concept can be illustrated by considering the analogy of the cost of a hypothetical person's rent, and the cost of their car repayments. At the individual level, we would expect there to be a trade-off between the two, as money spent on a house is no longer available to be spent on a car (and vice versa). However, high levels of income variation at the population level masks this negative covariation; people with expensive houses tend also to have expensive cars. Negative correlations and trade-offs at the individual level may well exist, but large population-level variation in resource acquisition masks this. Within the context of energy allocation, high population-level inter-individual variation can obscure intra-individual biological trade-offs that may occur during periods of energetic scarcity. Ultramarathons circumvent this issue by inducing a high metabolic demand, which in turn imposes a negative energy balance on (almost) all participants. By negating the effect of inter-individual variation in resource acquisition and provoking detectable life history trade-offs, this model allows for the observation of perturbations of function and of potential physiological trade-offs in internal resource allocation.

4. Emerging insights towards functional preservation during ultra-endurance events

We first trialled the use of ultra-endurance events to observe functional trade-offs at the North Downs Way 100-mile foot race (UK). To investigate the hypothesised trade-off between energy allocation towards reproduction and survivorship, we measured biomarkers representing both functions in male athletes before and after the race (testosterone and libido for reproduction, and the bacteria killing assay and haemolytic complement assay to consider the innate immune system, which served as a marker of survival ability). Comparison of pre-race and post-race levels revealed a shift of energy flow away from reproduction and towards short-term survival. Following the race, levels of both markers of reproductive function decreased significantly, while both markers of short-term survival significantly increased (Longman et al., 2017a). See Fig. 1 below. These findings add to pre-existing and varied observations of the effect of ultramarathon participation on immune function (Gill et al., 2014; Knez et al., 2007; McKune et al., 2005; Neubauer et al., 2008; Nieman, 2009; Pacque et al., 2007; Turner et al., 2011).

While the biomarkers of reproduction and survival used in this study were not comprehensive, this work served as a proof of concept of the use of ultra-endurance events to investigate patterns of energy allocation during conditions of LEA. This model has since been developed to gain a more nuanced insight towards patterns of energy allocation and the hierarchy of functional preservation by incorporating more detailed measures of physiological function in our analyses. In addition, the physiological response of athletes competing in events varying by both environment (including hot-dry, hot-humid, cold, and high-altitude) and duration (ultramarathons lasting 3–5 days and ocean rows lasting >4 weeks) have been studied. Importantly, we have also specifically

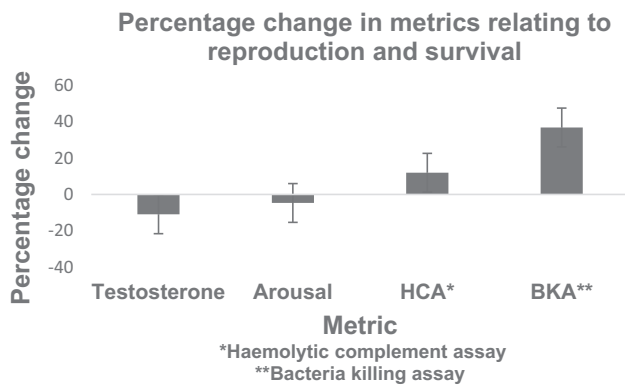


Fig. 1. Changes in investment in measures of reproduction (testosterone and arousal) and survival (haemolytic complement assay and bacteria killing assay) following participation in a 100-mile footrace. Taken from Longman et al., 2017.

selected ultramarathons which attract a greater number of female athletes to address the participatory sex imbalance currently evident in ultra-endurance events (Knechtle et al., 2011; Scheer, 2019).

This approach is providing unique insight towards the rapid and reversible adaptive changes to energy allocation during a situation of extreme energetic stress, and has been used to explore both cognitive as well as physiological domains. We recently measured performance in key cognitive domains in athletes before and after 250 km multiday ultramarathons in Jordan and Sri Lanka (www.ultra-x.co/). Upon completion of the races, the spatial working memory of athletes who's body mass reduced (indicating a negative energy balance) improved, while psychomotor speed remained unchanged, and episodic memory declined (Longman et al., 2023). Spatial working memory temporarily stores location information, enhancing ability to navigate a landscape. This is beneficial during energetic deficit because it may improve one's ability to acquire food by facilitating recollection of the location and quality of previously visited feeding sites, and also the ability to find the way home following a foraging or long-distance hunting trip. It is therefore likely that the prioritisation of spatial working memory function, at the expense of episodic memory, confers a survival advantage during conditions of energetic deficit. This work builds on recent advances considering neuroplasticity in response to bioenergetic challenges (Raefsky and Mattson, 2017), and on lines of enquiry considering the role played by ecological variation in shaping cognitive abilities (Rosati, 2017).

In addition to providing a model to explore potential trade-offs between physiological and cognitive traits, ultra-endurance events have also been used to provide insight to how adaptive responses to energetically challenging environments may differ by sex. Our preliminary findings indicate potential sex differences in the relationship between temperature-adapted body morphological features and performance in multiday ultramarathons in hot and cold climates. While longer legs (associated with increased heat dissipation) and lower body mass (associated with reduced heat generation) were associated with better performance in hot-condition events than cold-condition events for both male and female runners, the relationship between morphology and performance appeared to be stronger in female athletes (Longman et al., 2019, 2021). This may be due to female athletes' increased adiposity (Wells, 2006), reduced muscle mass (Welle et al., 2008), reduced thermosensitivity in the whole-body sudomotor response when hot (Gagnon and Kenny, 2011) and reduced sweat gland output at high exercise intensity (Gagnon and Kenny, 2012) relative to male athletes. Similarly, the aforementioned changes to spatial working memory and episodic memory were also more pronounced amongst female athletes. Meta-analytic data indicate a female advantage in a subdivision of tasks relating to spatial working memory in a non-athletic context (Voyer et al., 2017), which may have arisen

from the unique energetic context of human female reproduction. Both pregnancy and lactation require the mother to provide a steady source of nutrition for her offspring (Butte and King, 2005; Ecuyer-Dab and Robert, 2007; Holliday, 1971). As males lack these direct metabolic reproductive demands, females potentially face a larger penalty if they are unable to successfully navigate their environment and acquire calories when experiencing LEA. While a continuum of responses exists between the sexes, the adaptive response to enhance spatial working memory during conditions of energetic deficit appears to be stronger in females.

In parallel to our studies recruiting ultra-endurance athletes, acute exercise-induced energetic stress can also be used to reveal moment-by-moment prioritisation of fuel allocation between functions. An experimental protocol simultaneously challenging both cognitive (a free recall task) and physical (a maximum effort row) functions over a short timescale (3-min) resulted in relative preservation of cognitive function at the expense of physical power output (Longman et al., 2017b). This pattern of functional preservation may also be an evolved trait. Within the cognitive niche that we have created (Whiten and Erdal, 2012), our survival chances when confronted with an environmental challenge may be greater with a well-fuelled brain than with well-fuelled muscles (Beedie and Lane, 2012). This is consistent with the results of our previous work in that, during conditions of energetic stress, energy is internally reallocated towards physiological processes providing the greatest immediate survival value.

The patterns emerging from our work suggest that, under conditions of energetic stress, limited resources are preferentially allocated to processes conferring the greatest immediate survival advantage. This was seen when innate immune function was prioritised over reproductive function (Longman et al., 2017a), when cognitive function was prioritised over the ability to generate power (Longman et al., 2017b), and when spatial working memory was prioritised over episodic memory (Longman et al., 2023). It is important to highlight that to date we have primarily focused on acute or shorter-term stressors, as occur in events or interventions lasting minutes, hours, and days. Energy allocation patterns during periods of deficit are likely to vary depending on the extent and duration of the deficit (Shirley et al., 2022). Ultra-endurance events can vary from hours to weeks, however, and thus represent the opportunity to investigate energy allocation strategies during a range of timescales. Importantly, ultra-endurance athletes habitually live highly active lives, and their arduous training schedules also offer an opportunity to investigate these concepts across longer time periods (months to years). It is also important to highlight that the ultra-endurance events described herein are likely to induce an energetic stress due to a combination of their very high energetic demand, in combination with limited opportunity to eat, thus creating a large deficit based on both the energy intake and expenditure sides of the equation. It is likely that equivalent deficits, induced by either increased expenditure, or reduced intake alone, may induce differential biological responses, which is another important avenue for ongoing research within this topic area.

5. Summary and future perspectives

The fields of evolutionary energetics and exercise physiology are highly complementary due to their shared interest in patterns of energy allocation during conditions of energetic stress. In this article we suggest that collaboration between researchers in these fields can lead to an enhanced understanding of the physiological response to energetic stress. Specifically, current evidence suggests that energy is internally reallocated towards physiological processes providing the greatest immediate survival value (Longman et al., 2023; Longman et al., 2017a; Longman et al., 2017b; Pontzer, 2015a; Urlacher et al., 2018). In the coming months and years, it is anticipated that the field of human athletic palaeobiology will improve current understanding of the hierarchy of functional preservation, and how this varies inter-individually

(Longman et al., 2020). This has clear relevance for athletes, many of whom may struggle to avoid energetic deficit due to high training volume and/or inadequate energy intake at both acute and chronic timescales.

Future work with larger athlete sample sizes and employing a richer suite of markers of physiological function will facilitate a greater understanding of evolved patterns of energy allocation under conditions of energetic stress. In addition to shedding further light on the hierarchy of functional preservation, we will examine how this varies inter-individually by population, age, sex, body composition, nutrition, and patterns of physical activity. From an evolutionary perspective, this will provide a step-change in the understanding of human energetic trade-offs, contribute to knowledge underpinning recent advances in human energetics (Pontzer, 2015b; Pontzer, 2015a) and shed new light on our adaptive capabilities as a phenotypically plastic species (Longman et al., 2020).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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