EMBO reports

The evolution of human endurance

Research on the biology of extreme endurance gives insights into its evolution in humans and animals

Philip Hunter

The popularity of extreme sports—in running, cycling, rowing and swimming—provides an interesting laboratory for studying the underlying metabolic and other factors, as well as the evolution of the stamina required to achieve these impressive feats of human endurance. Although our ancestors did not row across the Atlantic in the Talisker Whisky Race, or swim four times across the English channel as Sarah Thomas did this September, they did undergo selection for endurance. Studying these extreme athletes has helped to identify some of these adaptations and the ultimate limits on performance they impose.

Some of these insights have proved helpful to endurance athletes themselves, but they have also underlined again the enormous health benefits of exercise for most humans. They have further helped to either confirm or refute theories on the selective pressures early humans were subject to, particularly concerning long-distance running.

The key systems of stamina

Recent studies have the key systems or mechanisms involved in endurance, which include the heart, liver, alimentary canal, nervous system, temperature regulations and psychological factors, such as pain tolerance. In addition, the body is able to deploy its total energy expenditure (TEE), a measure of calories burned, as efficiently as possible within its limits by diverting resources from some processes such as digestion towards muscle activity.

Many of these insights are qualitative rather than quantitative, but one that has attracted considerable interest appears to define a fairly precise limit not so much on the duration of human endurance, but the maximum energy that can be generated at a sustained rate over long periods. A recent study provides evidence that the digestive system restricts the maximum metabolic rate for sustained activities to about two and a half times an individual's resting energy use, with only slight individual variations [1].

> *“Although our ancestors did not row across the Atlantic [. . .], or swim four times across the English channel as Sarah Thomas did this September, they did undergo selection for endurance.”*

The authors followed runners completing the equivalent of a marathon distance of around 42 km 6 days a week for nearly 5 months, comparing their metabolic rate and other markers of high-energy activities. They found that, initially, runners were able to sustain metabolic rates considerably greater than 2.5 times the base rate, but only for a time. As the event went on, their metabolic rate would decline towards that 2.5 times the base rate, which determines the body's TEE. The researchers concluded that this limit was imposed by the rate at which the human alimentary canal is able to absorb calories.

However, this limit is not an absolute constraint on human performance, but more draws a line on how much energy can be converted through consumption of food during an endurance event, according to John Speakman, head of the Energetics Research Group at the University of Aberdeen in the UK and corresponding author on that study. “Humans can sustain performance above 2.5 but only by drawing on your stored reserves”, he said. “People on the Tour de France (cycling) or Race Across America (running) can sustain levels of expenditure greater than 2.5, initially up to four times basal, then it declines to around 3, but only by continually losing weight”.

In other words, these athletes consume their own fat or structural protein to sustain a level above 2.5. “Total Energy Expenditure is quite interesting because it requires burning of fat or muscle for you to exceed it. But if you burn tissue, that tissue is no longer using energy as well. If you use up part of your muscle that reduces your BMR [Basal Metabolic Rate], so that gives a bit more scope for endurance”, Speakman added.

Yet, the type of extreme endurance events some humans indulge in were not performed by our ancestors—in fact not until the last few decades in most cases—and so humans have not evolved the ability to reduce BMR excessively to boost endurance. The same applies even more to most mammals: selective pressures have tended to favour short-term speed bursts either to evade predators or to catch prey, rather than endurance. There is just one notable exception in the animal kingdom, migratory birds, where selection operated on the necessity of crossing increasingly large stretches of water without landing for food or rest in order to reach favourable sites for nesting and rearing young.

Masters of endurance

Some of these migratory birds are able to achieve extremes of endurance far beyond

Freelance journalist in London, UK. E-mail: ph@philiphunter.com

DOI 10.15252/embr.201949396 | EMBO Reports (2019) 20: e49396 | Published online 21 October 2019

other animals, as well as humans, by consumption of significant BMR during the flight. Indeed, the record for non-stop distance flights now stands at 11,000 km, by the Alaskan bar-tailed godwit (*Limosa lapponica baueri*) during its 8-day autumn migration from Alaska to New Zealand with no stopovers to rest or refuel at an average speed of almost 60 km/h [2].

> *“. . . selective pressures have tended to favour short-term speed bursts either to evade predators or catch prey, rather than endurance.”*

Such feats have prompted revisions over the degree of extreme endurance animals are capable of evolving when under selective pressure. The first point is the average speed, which seems surprisingly high. After all, air resistance is proportional to the square of the velocity so that energy consumed per km increases with air speed for any flying object, including birds or planes.

But there are two other factors, the first being that a bird loses water during flight and has to be constantly awake, which together impose strong selective pressure to keep the total journey time down. Secondly, and equally crucially, flying at slower speeds would increase the relative impact of cross-winds and particularly head winds, so that in practice more energy might be needed. A bird flying at just 20 km/h into a headwind of the same speed would make no progress at all, while at 60 km/h, it would progress at 40 km/h, which would still be acceptable.

Nonetheless, in order to sustain flight at 60 km/h requires a phenomenal amount of energy. “Flying birds expenditure energy is 15× BMR, sustained for 3–4 days”, Speakman said. “Humans can’t do that for more than 1/10th of a day”. This sustained elevation of energy expenditure is achieved through systematic consumption of bodily tissue that begins even before the migration in order to eliminate all tissues that do not contribute to the flight. The birds reduce their gut size, for example, because they will not be needing to digest any food during the journey. That brings weight down and in turn energy required to stay airborne. It may also cut air resistance slightly. But, as Speakman noted, the birds then have to regain their gut very rapidly after landing to start feeding and the lost tissues. Later in the migratory journey, the birds even consume their own flight muscle on the basis that, as their mass comes down, the power needed to maintain the average speed is reduced. They can therefore manage with reduced lean muscle in the wings; regaining that upon landing is less urgent than the gut.

Evolved to run

While this insight is not helpful for increasing human endurance, there is interest comparing humans with other mammals to ascertain both the origins of endurance and other constraints apart from maximum rate of calorie intake. Humans differ from many other mammals in their early selection for persistence hunting where they would rely on endurance to catch animals such as deer that can easily outrun them over short or middle distances. This was partly a result of becoming bipedal, which made outsprinting four-legged animals impossible, coupled with the fact that, unlike most primates, humans became genuinely omnivorous and therefore dependent on hunting. Even today, some human groups, such as the Tarahumara Indians in Mexico, pursue deer over periods of up to 2 days to exhaust them. Perhaps at least some early humans were subject to more extreme selection for endurance than is sometimes supposed [3].

Apart from humans, wolves and wild dogs also pursue persistence hunting, which enables comparisons over overall energy costs with cheetahs—that have gone for the opposite strategy of achieving a high kill rate through short bursts at very high speed. One study of six wild dogs in northern Botswana has found that their strategy of opportunistic persistence hunting in small packs is slightly more efficient energetically than that of the cheetah engaging in highly athletic chases at high speed and acceleration [4].

Such adaptations involve differing distributions of fast and slow muscle fibres in response to opposing selective pressures. High-speed predators such as cheetahs undergo selection for fast-twitch muscles, as do some of their prey, while persistent hunters have higher proportions of slow-twitch muscles. Slow-twitch or type 1 muscle is optimized for endurance with lower contraction rates and deriving energy primarily from mitochondria that convert triglycerides into ATP. Fast-twitch muscles come in two types, IIa and IIb. Type IIa shares some characteristics of slow-twitch, while type IIb is even more optimized for short bursts of rapid contraction for acceleration, speed and power. These fibres produce energy in the absence of oxygen through glycolytic oxidation of phosphocreatine to drive explosive movements such as jumping and sprinting, but this temporary nutrient source is quickly exhausted. While little evidence has been found that exercise can transform type I into type II fibres or the other way round, it is clear that conversions between IIa and IIb do occur. Endurance training therefore tends to elevate levels of type IIa, while power training does the same for IIb.

> *“Some of these migratory birds are able to achieve extremes of endurance far beyond other animals, as well as humans, by consumption of significant BMR during the flight.”*

Beyond biomechanics, endurance athletes tend to have higher aerobic capacities measured by their VO^2 max, the maximum millilitres of oxygen they can consume per kilogram of body weight. Endurance training increases VO^2 max considerably, although there are individual variations. One point to note is the distinction between absolute VO^2 max for an individual and relative VO^2 max per unit weight. Athletes such as rowers who require both power and stamina have the highest absolute values reflecting their greater body weight, while ultra-long-distance runners have high relative VO^2 max scores per unit weight.

For humans, there is also the psychological dimension of high pain thresholds which also appears to vary greatly between individuals and clearly plays an important role for elite athletes. The key finding from most research is that psychological “fitness” for endurance may be partly inherited, but is mostly acquired through hard training that replicates as closely as possible the fatigue generated by the actual events themselves.

Temperature control

Another very important aspect of human endurance is body temperature control which is regulated by the autonomic nervous system. When exercising, the heat created from muscle work is transported via the blood to the skin where it is dissipated through radiation and sweating. The main cardiovascular challenge during sustained endurance is therefore to maintain sufficient blood flow to the exercising skeletal muscle to support metabolism while simultaneously delivering blood quickly enough to the skin to dissipate heat. Especially in hot weather, skin blood flow must be great enough to transfer heat quickly enough to prevent a rise in core temperature.

> *“For humans, there is also the psychological dimension of high pain thresholds which [. . .] clearly plays an important role for elite athletes.”*

One of the earliest findings in the field of exercise came in 1936 with the observation that humans tend to maintain a constant core temperature irrespective of the external environment, providing they are neither dehydrated nor suffering from hyperthermia. That, after all, is the objective of being warm-blooded. It also gives clues to early selective forces for human endurance, which are believed to have occurred in warm climates before migrations to higher latitudes. The selection for endurance may have come with loss of hair for better cooling and that in turn required mechanisms for coping with dehydration and exposure to the sun. Recent research has started to unpick the molecular factors behind the distribution of hair follicles in mammals and how these may have evolved [5] and it seems likely a number of selective factors may have contributed. These may include greater resistance to lice infection through being largely hairless and superior non-verbal communication at the emotional level. But whatever the factors, becoming hairless was clearly associated with adaptation for more efficient cooling via sweating and therefore higher endurance.

However, heat loss is much less of a problem for smaller mammals such as mice, because they have a much higher surface-area-to-volume ratio. As Speakman noted, most studies in mammals have therefore focused on lactation rather than exercise because that is the one activity that calls for sustained high levels of energy conversion in most cases. “We’ve done a lot of work on lactation in mice”, Speakman commented. “They can expend and consume energy at a much higher rate, taking in energy at about 7× basal rate”. That is partly a function of size, but Speakman pointed out that dairy cows can also reach incredible rates of energy turnover, with heat loss being a constraint. “Cattle are limited by heat”, he explained. “If you look at mortality in heatwaves, lactating cattle are one of the first that go to the wall”.

An adaptable heart

Given that both heat dissipation and nutrient distribution require efficient blood circulation, it is not surprising that the cardiovascular systems, and especially the heart as the pump, have been implicated in selection for endurance. A recent study indicates that the human heart has evolved to respond to training, being initially adapted at the same time for short bursts of intense activity or sustained endurance at lower rates of energy conversion [6]. “We’re actually saying that there is a specific cardiac adaptation to the type of training performed”, commented Rob Shave, Director of the School of Health and Exercise Sciences at University of British Columbia in Canada and a co-author on the study. “Those who do endurance have a heart that responds well to a volume stimulus, while those who do resistance become better able to deal with a pressure challenge”, he added.

> *“. . . becoming hairless was clearly associated with adaptation for more efficient cooling via sweating and therefore higher endurance.”*

The study also examined inactive individuals who took little exercise and found that their hearts responded better to increases in pressure associated with short bursts of activity, which suggests that this is a default state. Such individuals are more likely to engage in occasional short bursts of activity out of necessity, while unlikely to find themselves having to exert themselves for long periods. “This adaptation or response is likely related to their inactivity, they are not stimulating their cardiovascular system as required, and as was likely experienced by early hunter gatherers and subsistence farmers, so the heart starts to remodel towards a more pressure adapted heart”, Shave explained.

The study tested the hypothesis that preindustrial humans were adapted for endurance not just through the musculoskeletal and thermoregulatory adaptations but through their hearts’ capability of adapting to increased demand for sustained pumping at higher volume. The authors compared left ventricular (LV) structure and function across semi-wild sanctuary chimpanzees, gorillas and a sample of humans exposed to markedly different physical activity patterns. Perhaps a slight surprise was that, while the results did confirm that the human LV evolved to help augment cardiac output and thereby enable endurance activities, there was also a high degree of phenotypic plasticity. The human LV can remodel differentially in response to chronic pressure associated with intense activity, as well as to endurance and inactivity. This indicates that early humans were under selective pressure for both distance running and occasional intense activity.

According to Daniel Liebermann, the lead author and Professor of Biology at the Department of Human Evolutionary Biology at Harvard University, Cambridge, USA, there is evidence this cardiac adaptation for endurance running occurred early during the history of humans, rather than during later hunter gathering or with the demands of subsistence farming after the dawn of agriculture. “We suspect, but cannot prove, that selection for more endurance adapted hearts had occurred by 2 million years ago when we have other skeletal evidence for long distance running in the genus *Homo*”, he said. “In terms of future studies we need to understand the physiology that underpins the interaction between regular physical activity and the maintenance of stable blood pressures in the subsistence farmers”, Shave added.

There are also unanswered questions over the psychological dimension and the greater variations between individual performance in humans compared with most other mammals. “There are some situations some individuals are performing “away from the line” with high levels of expenditure, without appearing to draw too much on the body weight, as with Tour de France cyclists", Speakman commented. "Understanding these specialist groups is an interesting way forward. It may be that some groups have cracked it and can sustain metabolic scopes of 3.5 or 4.5 much longer and don't have to draw down all their fat reserves and proteins to do that". Insights such as this, along with research on the evolution of and the biological factors influencing endurance, can help to tailor training programmes for athletes and provide lifestyle guidance to everybody else.

References

1. Thurber C, Dugas LR, Carlson B, Speakman JR, Pontzer H (2019) Extreme events reveal an alimentary limit on sustained maximal human energy expenditure. *Sci Adv* 5: eaaw0341
2. Hedenström A (2010) Extreme endurance migration: what is the limit to non-stop flight? *PLoS Biol* 8: e1000362
3. Liebenberg L (2008) The relevance of persistence hunting to human evolution. *J Hum Evol* 55: 1156 – 1159
4. Hubel TZ, Myatt JP, Jordan NR, Dewhirst OP, McNutt JW, Wilson AM (2016) Energy cost and return for hunting in African wild dogs and cheetahs. *Nat Commun* 29: 11034
5. Song Y, Boncompagni AC, Kim SS, Gochnauer HR, Zhang Y, Loots GG, Wu D, Li Y, Xu M, Millar SE (2018) Regional control of hairless versus hair-bearing skin by *Dkk2*. *Cell Rep* 25: 2981 – 2991.e3
6. Shave RE, Lieberman DE, Drane AL, Brown MG, Batterham AM, Worthington S, Atencia R, Feltrer Y, Neary J, Weiner RB *et al* (2019) Selection of endurance capabilities and the trade-off between pressure and volume in the evolution of the human heart. *Proc Natl Acad Sci USA* 116: 19905 – 19910