

# Are humans evolved specialists for running in the heat? Man vs. horse races provide empirical insights

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## Abstract

Many mammals run faster and for longer than humans and have superior cardiovascular physiologies. Yet humans are considered by some scholars to be excellent endurance runners at high ambient temperatures, and in our past to have been persistence hunters capable of running down fleeter quarry over extended periods during the heat of the day. This suggests that human endurance running is less affected by high ambient temperatures than is that of other cursorial ungulates. However, there are no investigations of this hypothesis. We took advantage of longitudinal race results available for three annual events that pit human athletes directly against a hyper-adapted ungulate racer, the thoroughbred horse. Regressing running speed against ambient temperature shows race speed deteriorating with hotter temperatures more slowly in humans than in horses. This is the first direct evidence that human running is less inhibited by high ambient temperatures than that of another endurance species, supporting the argument that we are indeed adapted for high temperature endurance running. Nonetheless, it is far from clear that this capacity is explained by an endurance hunting past because in absolute terms humans are slower than horses and indeed many other ungulate species. While some human populations have persistence hunted (and on occasion still do), the success of this unlikely foraging strategy may be best explained by the application of another adaptation – high cognitive capacity. With dedication, experience and discipline, capitalising on their small endurance advantage in high temperatures, humans have a chance of running a more athletic prey to exhaustion.

## KEYWORDS

evolution, persistence hunting, temperature

## 1 | INTRODUCTION

'Humans are the sole species of mammal that excels at long distance trekking and running in extremely hot conditions' (Lieberman, 2015). This claim is the culmination of arguments put forward by a number of authors including Bramble and Lieberman (2004), Carrier (1984) and

Liebenberg (2013) purporting that humans are excellent endurance runners at high ambient temperatures. Often the explanation given for this claimed capacity is that it was an adaptation in our ancestors for foraging – the chasing down of prey over many hours during the heat of the day, known as persistence hunting. Yet humans do not possess exceptional cardiovascularities in contrast to, for example,

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dogs (*Canis lupus familiaris*) and horses (*Equus caballus*; see Williams, Bengtson, Steller, Croll, & Davis, 2015, Figure 1). Even non-elite dogs and horses have far superior oxygen delivery systems including hearts that are proportionally much larger, elevated haematocrit levels and greater muscle mass. Compared with humans, these equine and canine adaptations facilitate considerably higher maximum rates of oxygen delivery to the body ( $\dot{V}_{O_2\max}$ ; summarized in Figure 3 of Poole & Erickson, 2011).

If not cardiovascular, what attributes, might humans possess to make them elite endurance runners, and indeed capable of wearing down quarry on the move at high temperatures? Liebenberg (2013) argues that for hominins to have evolved a fitness-enhancing capacity for endurance running, they would have become adapted for speed, distance, heat loss and energy economy, among other things. We briefly consider these arguments and the available data that humans are adapted for each of these traits.

### 1.1 | Running speed and distance

Humans are markedly slow runners compared to many similarly sized non-primate animals (Garland, 1983; Hirt, Jetz, Rall, & Brose, 2017). This is demonstrably true over short distances, but also over long distances including, pertinently, when compared to obligate persistence-hunters and their ungulate prey. African wild dogs have a mean preferred travelling speed while ranging and hunting of  $8.3 \text{ km h}^{-1}$  (Hubel et al., 2016), which is similar to grey wolves ( $8.6\text{--}10.1 \text{ km h}^{-1}$ ; Mech, 1994), and hound dogs pursuing pumas ( $9.7 \text{ km h}^{-1}$ ; Bryce, Wilmers, & Williams, 2017), while humans that were observed over eight persistence hunts averaged  $6.1 \text{ km h}^{-1}$  (Table 1 in Liebenberg, 2013). Pronghorn antelope can apparently maintain  $65 \text{ km h}^{-1}$  for over 10 min (covering some 11 km; Costello, 1969). Race horses ridden in a 161 km race (e.g. the Vermont 100 Endurance Ride) typically average speeds in excess of  $11 \text{ km h}^{-1}$  while bearing a rider, the event therefore lasting around 15 h.

### 1.2 | Heat loss and tolerance

Due to the heat generated by active muscles, thermoregulation is a key challenge during endurance running (Longman et al., 2019). Evaporative water loss as a means of heat dissipation is by far the predominant method of temperature reduction in mammals, usually through perspiring and/or panting (Belval & Armstrong, 2018). Humans, the only 'hairless' animals to possess eccrine sweat glands (Marino, 2008; McGowan, 1979), are probably the most perspirative of all species, and thus able to lose heat more rapidly than do other animals. This difference is even more pronounced in environments so hot that the body gains heat convectively (Lieberman, 2015; Lindinger, 1999; Schmidt-Nielsen, 1964). Moreover, reduced body hair promotes convective heat loss while the upright gait limits radiative heat stress (Lieberman & Bramble, 2007; Wheeler, 1992). However, certain cursorial species appear adapted to the heat by facultative hyperthermia (i.e. adaptive heterothermy) – they tolerate a high heat

### New Findings

- **What is the central question of this study?**

Do available comparative data provide empirical evidence that humans are adapted to endurance running at high ambient temperatures?

- **What is the main finding and its importance?**

Comparing the results of races that pit man against horse, we find that ambient temperature on race day has less deleterious effects on running speed in humans than it does on their quadrupedal adversary. This is evidence that humans are adapted for endurance running at high ambient temperatures. We debate whether this supports the hypothesis that early man was evolutionarily adapted for persistence hunting.

load. English pointer dogs show no obvious loss in hunting performance during days that are particularly hot and humid (Davenport, Kelley, Altom, & Lepine, 2001). Horses, swine, goats and sled dogs can tolerate their core body temperatures reaching  $42^\circ\text{C}$  (Armstrong, Delp, Goljan, & Laughlin, 1987; Caputa, Feistkorn, & Jessen, 1986; Hodgson et al., 1993; Marlin et al., 1996; McConaghy, Hales, Rose, & Hodgson, 1995; Phillips, Coppinger, & Schimel, 1981; Poole & Erickson 2011), and both cheetah (Hetem et al., 2013, 2019) and African wild dogs (Taylor, Schmidt-Nielsen, Dmi'el, & Fedak, 1971) have been recorded in the wild with core temperatures over  $41^\circ\text{C}$ , although this is uncommon. In comparison, human distance runners and cyclists rarely attain core temperatures above  $40^\circ\text{C}$  (hyperpyrexia) even in high ambient temperatures (Laursen et al., 2006; Figures 3 and 4 of Nybo & González-Alonso 2015; Williams, Wickes, Gilmour, Barker, & Scott, 2014; Valentino, Stuempfle, Kern, & Hoffman, 2016), and heat stress resulting in failure to complete races (i.e. voluntary fatigue) typically occurs at around  $40^\circ\text{C}$  (see references in Brück & Olschewski, 1987; Lindinger, 1999; Nielsen et al., 1993; Nielsen, Strange, Christensen, Warberg, & Saltin, 1997), although core temperatures above  $40^\circ\text{C}$  have been observed on occasion in field studies and without necessarily a deterioration in performance (Byrne, Lee, Chew, Lim, & Tan, 2006; Ely et al., 2009; Racinais, Périard, Karlsen, & Nybo, 2015). Compared with sweating, facultative hyperthermia provides the advantage of retained body fluids and salts (reviewed in Mitchell et al., 2002). Furthermore, while heightened temperatures in the brain are associated with the cessation of activity in animals (e.g. goats, Caputa et al., 1986; guinea pigs, Caputa, Kądziela, & Narębski, 1983; hamsters, Gordon & Heath, 1980), and selective cooling mechanisms in the brain have been found in some ungulates including horses (Baptiste, 1998; McConaghy et al., 1995; Strauss et al., 2017), there is no evidence that they are present in humans or other primates (Bregelmann, 1993; Nelson & Nunneley, 1998; Nybo, 2012). Potentially, increases in brain temperature limit the

motor performance of active humans (Nybo, 2012) and yet they have no apparent adaptations to defend against this (Nelson & Nunneley, 1998; Strauss et al., 2017).

Consequently, it is not surprising that, contrary to documented claims, humans are not the only species that can withstand protracted locomotion in high-temperature environments. The assertion that 'no horse or dog could possibly run a marathon in 30 degree heat' (Lieberman, 2015) is demonstrably untrue. In the annual Tevis Cup race held in California (USA), where horses are ridden over the Sierra Nevada mountain range for 161 km at an average pace that can exceed 10 km h<sup>-1</sup>, mean ambient temperature is often above 28°C, even 30°C. In the 2019 Marathon des Sables in the deserts of Morocco, a now-celebrity pet dog named Cactus, which lived locally to the race, voluntarily completed several stages including the 'double marathon' stage 4 (76.3 km, video). Its speed averaged around 9 km h<sup>-1</sup> on stage 3 (37.1 km), at high daytime temperatures probably exceeding 30°C (<https://www.marathondessables.com/en/news/all-runners-are-grey-night-186>). Similarly, a small stray dog, later named Gobi, followed the heels of ultrarunner Dion Leonard at an average speed of 8.5 km h<sup>-1</sup> across the rugged Tian Shan Mountains of northwest China. The pair even averaged a speed of 12.3 km h<sup>-1</sup> on Day 3's 42 km stage in heat exceeding 49°C (Leonard, 2017). Thus, while cultural interventions (e.g. water carriage and scheduling work for cooler parts of the day; Lupo, 2019) are applied to working dogs in hot environments to limit the chances of heat stress, dogs are nonetheless typically able to exert moderate endurance activity such as trotting for extended periods.

### 1.3 | Energy economy of locomotion

Humans are believed to have a number of anatomical traits that enhance their locomotion efficiency, including relatively long legs and Achilles tendons, large gluteus muscles and arched feet with short toes (Bramble & Lieberman, 2004; Lieberman, 2015; Lieberman, Bramble, Raichlen, & Shea, 2009). However, there is no evidence that humans or other hominins are energetically economical movers compared to other primates (Studel-Numbers, 2003) or other mammals in general, either when walking or when running. Rather, for a mammal of their size they have a fairly typical energy expenditure per unit distance (Halsey & White, 2012). If anything, they are relatively inefficient runners but efficient walkers. Humans have a net cost of transport (NCOT; the whole-animal energy cost to move a unit distance) while walking that is 25% lower than predicted based on the best fit NCOT-mass relationship across mammalian species, but an NCOT while running that is 27% higher (Halsey & White 2012). Horses have an NCOT about 20% above predicted (Wickler, Hoyt, Cogger, & Myers, 2003). All measured canids – the African wild dog and the grey wolf (both persistence hunters) and mongrel dogs and Walker foxhounds – have NCOTs close to that predicted for their size (Bryce & Williams, 2017; Halsey & White 2012; Seeherman, Taylor, Maloiy, & Armstrong, 1981; Taylor, Heglund, & Maloiy, 1982; Taylor, Schmidt-Nielsen, & Raab, 1970).

In summary of the above, humans may well be more adapted for running, coping with activity in the heat, and locomotion economy than are other extant primates (Bramble & Lieberman, 2004). However, given that many of these human adaptations are substantially inferior to the equivalents of other mammalian species clearly designed for endurance running, again the evidence does not strongly support the concept that humans are a species truly evolved for endurance running, or indeed persistence hunting. An alternate possibility is that our enhanced endurance capacity compared to our primate cousins instead evolved as an adaptation to decrease the time taken to descend on carcasses that had been spotted from distance, thus increasing the calories available to scavenge upon arrival (Bramble & Lieberman, 2004; Lieberman & Bramble, 2007; but see Pickering & Bunn, 2007).

Nonetheless, today a handful of disparately located tribes (thus probably culturally independent of each other) at least occasionally procure meat through the persistence hunting of large ungulates (see Glaub & Hall, 2017 and references therein). Field documentation of persistence hunting indicates that the factor enabling human hunters to catch up with their fleeter quarry appears to be the latter's hyperthermia resulting in heat exhaustion (the proximal factor probably being dehydration of the intracellular fluids; Lindinger, 1999). Indeed, triggering hyperthermia in their prey seems to be the aim of the hunters, who undertake pursuit running at the hottest time of the day, when ambient temperatures can exceed 40°C (Lieberman, 2013). Perhaps, then, despite the heat tolerance adaptations that are present in many, perhaps all, ungulate species (McConaghy et al., 1995; Strauss et al., 2017; Yousef, 1976), the human ability to sweat profusely proves to be a superior heat adaptation under certain circumstances, in turn making us veritable endurance athletes and persistence hunters in that moment.

We investigated this proposition by analysing the effects of ambient temperature on the running speeds of humans and an ungulate model, the horse, in directly comparable races – events in which the two species compete against each other, commonly called 'Man vs. Horse' (MvH) races. Humans have long debated and tested their ability to outrun horses on foot, in race distances ranging from 100 m sprints to 160 km ultramarathons and beyond (Crockett, 2018). In recent decades, MvH events have been held annually, typically at marathon (42 km) or ultramarathon (160 km) distances. We took advantage of yearly variations in weather on race day to describe the relationships between mean running speed and mean ambient temperature for each species. We hypothesized that mean running speed would decrease with increasing ambient temperature in both horses and humans, but more so in horses, represented by a greater negative slope for the relationship in this species.

## 2 | METHODS

### 2.1 | Data collection

Historical records from MvH races in excess of 30 km were identified and compiled from eight international competitions, but the data

available for most of them were sparse. Ultimately, sufficient results for analysis (>30 years) were obtained from three races (Table 1).

From each race, we collated the annual race distance and finishing times of the top three horses and top three (non-relay) human competitors. For most races and years, results were available online, but in some cases (especially finish times >15 years old), we obtained historical results from race organizers directly. In addition to finish times, we compiled ambient race-day temperature (°C) from archival weather records at the nearest weather station of similar elevation. Historical race day temperature and precipitation were extracted from the National Oceanic and Atmospheric Administration's (NOAA) National Centers for Environmental Information (NCEI) online data repository and NOAA's Global Surface Summary of the Day (GSOD) records using the R package GSODR (R Core Team, 2019). In some cases, we used weather data from multiple stations for a given race to provide full temporal coverage across all race years (Table 1).

## 2.2 | Analysis

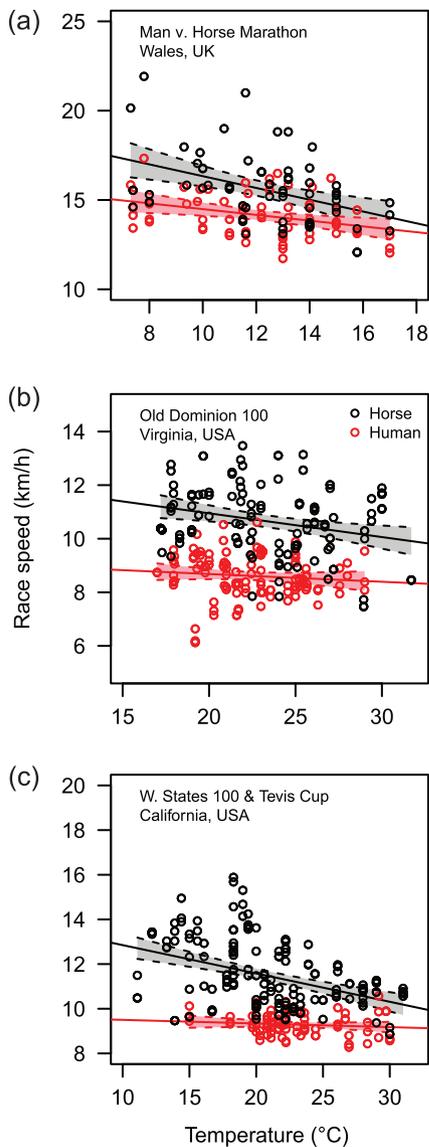
We calculated running speed ( $\text{km h}^{-1}$ ) in both species based on race length and finishing time. To investigate the effect of ambient temperature on running speed for both horse and human competitors, we fitted two generalized linear mixed models (GLMMs) using the R packages 'lmer', and used 'lmerTest' to assign estimated *P*-values for interaction terms. Year and race were input as random factors (with year nested within race), and species as a fixed factor. Our full model included the interaction of temperature and species, while our reduced model did not. We report marginal  $R^2$  to quantify the variance explained by the fixed factors in the models (thus excluding the variance explained that is simply due to differences between the three races) (*R*<sup>2</sup><sub>m</sub>; Nakagawa & Schielzeth, 2013). We compared the two models using Akaike's information criterion (AIC; Akaike, 1973). We checked the assumptions of linearity, normality and homoscedasticity by visual inspection of plotted residuals and utilized a combined dataset of results from all three races.

## 3 | RESULTS

Data from a total of 260 humans and 358 horses racing in three independent annual MvH events were analysed. As predicted, hotter temperatures resulted in slower race speeds for both species (Figure 1). The slope of the relationship between race speed and ambient temperature was statistically significantly steeper for horses than it was for humans (horses:  $-0.11$ ; humans:  $-0.07$ ,  $t = 3.17$ ,  $P = 0.002$ ; model  $R^2_m = 0.21$ ). Thus, per  $1^\circ\text{C}$  increase in ambient temperature, the race pace of horses decreased by on average  $0.11 \text{ km h}^{-1}$  and that of humans by  $0.07 \text{ km h}^{-1}$  – a 36% smaller decrease for humans. The AICs for the full model and reduced model were 1740 and 1741, respectively.

**TABLE 1** Summary of the MvH races retained in our analyses

Race	Location (approx. finish line coordinates)	Years of collated data ( <i>n</i> )	Distance (km)	Temperature, mean $\pm$ SD (range) (°C)	Weather stations used ( <i>n</i> )	Station distance from finish line, mean $\pm$ SD (km)
Man vs. Horse Marathon	Llanwrtyd Wells, Wales, UK (52.107, $-3.637$ )	1980–2019 (38)	33–38	$12.3 \pm 2.5$ (7.3–17.0)	2	$6.1 \pm 3.8$
Tervis Cup 100 (TC, horses) and Western States 100 (WS, humans)	Auburn, CA, USA (38.897, 121.072)	TC: 1962–2018 (57) WS: 1974–2019 (45)	160	TC: $21.2 \pm 5.0$ (11.1–31.0) WS: $23.7 \pm 3.7$ (15.0–30.8)	2	$2.1 \pm 0.6$
Old Dominion 100	Woodstock, VA, USA (38.874, $-78.523$ )	Horses: 1975–2019 (44) Humans: 1979–2019 (40)	160	Horses: $23.6 \pm 3.9$ (17.2–31.7) Humans: $22.3 \pm 3.0$ (17.0–29.0)	4	$31.0 \pm 15.8$



**FIGURE 1** Running speed ( $\text{km h}^{-1}$ ) against mean ambient temperature ( $^{\circ}\text{C}$ ) in three Man vs. Horse races for the first three horses (black data points) and first three humans (red data points) of each year. The two continuous lines are the least squares best fit regressions, and the associated dashed lines and shaded areas are 95% confidence intervals of those fits. (a) Man vs. Horse Marathon, Wales, UK; (b) Old Dominion 100, Virginia, USA; (c) Tevis Cup 100 (horses) and Western States 100 (humans), California, USA. The y-axis is truncated to start at  $4 \text{ km h}^{-1}$  in all three panels

## 4 | DISCUSSION

Although horses are substantially larger animals than humans (approx. 500 vs. 70 kg, respectively), they have comparable stride lengths at endurance running speeds (Figure 4 of Bramble & Lieberman, 2004; Heglund & Taylor, 1988). However, because they have superior cardiovascular systems (Williams et al., 2015), it is not surprising that horses typically traverse MvH courses more quickly than do human competitors (Figure 1). Yet the time gap between the two species closes on hotter days; in the heat, the degree of deterioration in race

performance of horses is greater than that of humans. This finding was sometimes subtle but always apparent in each of the three race events we analysed (Figure 1). Being larger, horses have a lower surface area-to-volume ratio and greater thermal inertia meaning that all else being equal, they lose heat to a cooler ambient environment more slowly. But even accounting for size, data provided in Lindinger (1999) on human and horse sweat rates (the percentage of sweat used for cooling, and the percentage of heat loss from various routes) indicates that the rate of evaporative heat loss of horses is about half that of humans. Consequently core temperature rises much more slowly in humans than horses, and this probably explains why humans experience a relatively slow loss of physical capability compared to horses when running in the heat. Clearly, humans have an exceptional capacity to dump excess heat through sweating (Lindinger, 1999; Schmidt-Nielsen, 1964).

Can this subtle advantage be enough to proclaim that humans have a heat adaptation enabling them to out-run prey in hot environments? The very high sweat rates of humans, the fact that human persistence hunters tend to select the hottest time of day to hunt, the heat exhaustion exhibited by their prey, and the reduced detriment of high ambient temperatures to running speed (Figure 1) together suggest that heat tolerance during running is key to the success of human persistence hunters. Yet horses in MvH races are still running more quickly than humans, even on hotter days, all, of course, while carrying a human rider and without it being imperative to survival. And data for wild endurance species such as African wild dogs and grey wolves indicate that they too travel faster while hunting than do humans (Hubel et al., 2016; Mech, 1994), although ambient temperature was not reported. Thus in answer to the question as to whether humans are comparatively well adapted to endurance running at high temperatures, the evidence suggests no – in absolute terms, even in the heat humans are not fast runners.

While horses are not a prey species of human persistence hunters, the MvH comparison highlights that humans will be off the pace in trying to chase down ungulate prey even at high ambient temperatures. During persistence hunts, what are the choices that humans can make that can bridge this performance gap? Human persistence hunting involves a group of communicating individuals, with only the very best completing the final stages (Liebenberg, 2013). After spending time carefully observing a herd, they predominantly target an animal weakened from age, injury or emaciation, or otherwise an individual with large, heavy horns (e.g. Liebenberg, 2013). They know that as they get close to their quarry, it will flee at pace. Although hunter and hunted cover approximately the same distance, the latter is doing so through stop-start bursts of intermittent locomotion, which could be energetically less economic (Kramer & McLaughlin, 2001; Seethapathi & Srinivasan 2015), thus generating more heat. Furthermore, if pauses are too short, intermittent locomotion can result in detrimental high-energy phosphate depletion and lactate accumulation from anaerobic metabolism (Edwards & Gleeson, 2001; Kramer & McLaughlin, 2001; Weinstein & Full, 2000). Persistence hunters assess information on their own physical state and their perceptions of the physical state of their quarry, then attempt to optimise the pace at which they track

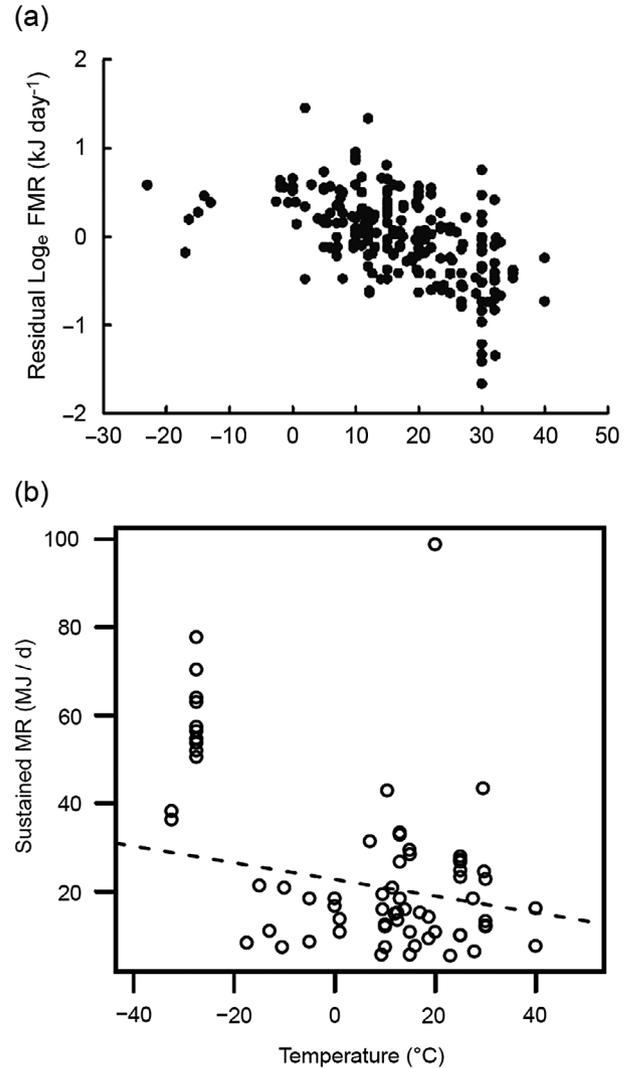
their prey so that the prey overheats, and they do not. Finally, humans persistence hunters have the advantage of hands – some stave off dehydration-induced fatigue by carrying water on hunts, for example in ostrich shells (Liebenberg, 2013).

Our synthesis of the current literature, coupled with our analysis of MvH race times, leads us to the following interpretation, which we put forward for debate and critique. We humans clearly have a superior capacity for endurance than do other primates (Pontzer, 2017), allowing us to expend more energy on foraging – an investment humans pay back with a greater calorie intake (Leonard & Robertson 1997; Pontzer et al., 2016). Nonetheless, compared to a broader range of species, human endurance is not exceptional. Carnivores in general travel further than herbivores in search of food (Carbone, Cowlshaw, Isaac, & Rowcliffe, 2005; Joly et al., 2019) requiring a capacity to locomote for extended periods, and humans appear to fit this mould with anatomical adaptations such as a significant bias toward slow-twitch skeletal muscle fibres (O'Neill, Umberger, Holowka, Larson, & Reiser, 2017). Yet our general running endurance is not as impressive as that of many other mammals. Rather than being the elite heat-endurance athletes of the animal kingdom, humans are instead using their elite *intellect* to leverage everything they can from their moderate endurance capabilities, optimising their behaviours during a hunt to bridge the gap between their limited athleticism and that of their more physically capable prey. Our capacity for profuse sweating provides a subtle but essential boost to our endurance capabilities in hot environments. This is a slight but critical advantage that our ingenuity magnifies to achieve the seemingly impossible: the running down of a fleeter-footed quarry.

#### 4.1 | Future research

Of course, further data on the endurance capabilities and adaptations of prey and predatory animals in the heat would advance our understanding of man's place in the pantheon of persistence hunters. Of particular intrigue is whether human endurance activity can be limited because of increases in brain temperature, as is the case for a diversity of other species. Data on goats and rodents are widely cited (Caputa et al., 1986; Caputa, Wasilewska, & Swiecka, 1985; Gordon & Heath, 1980), while data on humans are widely desired (Nybo, 2012).

Physical endurance is not necessarily confined to the context of running and may be a factor in other intensive activities. Across mammalian species, there is a clear reduction in daily metabolic rate in those species that inhabit higher mean ambient temperatures (Figure 2a; Speakman & Król, 2010), suggesting that ambient temperature limits activity intensity. Is this also the case for humans? This question is yet unanswered. As a first and tentative approximation, we collated data from the literature on daily energy expenditure during high intensity activities, from running and cycling races to military training and polar expeditions, along with mean ambient temperatures where available (which otherwise were estimated based on latitude and time of year). In contrast to the data for other mammals, our analyses show no relationship between sustainable daily energy



**FIGURE 2** Relationships between long-term metabolic rate (MR) and mean ambient temperature (°C). (a) Mass-independent field metabolic rate (kJ day<sup>-1</sup>) measured in mammals against ambient temperature of their habitat. Reproduced from Speakman and Król (2010) with permission. (b) Sustained metabolic rate (MJ day<sup>-1</sup>) of people undertaking arduous tasks and events for at least 1 day against (estimated) mean ambient temperature. The metabolic rate data are adjusted for body mass, proportion of participants who are male, and event duration. The black trend line is the best linear fit accounting for multiple measures within studies; it is dashed to indicate non-significance ( $P = 0.15$ ). References to these data are: (Ainslie et al., 2002; Beals et al., 2019; Bircher et al., 2006; Bourrilhon et al., 2009; Castellani et al., 2006; Clemente-Suárez, 2015; Coker et al., 2018; Costa et al., 2014; Diaz et al., 1991; Ebine et al., 2002; Edwards et al., 1993; Forbes-Ewen et al., 1989; Frykman et al., 2003; Fudge et al., 2006; Geismann et al., 2014; Glace et al., 2002; Hill and Davies, 2001; Hoyt et al., 1991; Hoyt et al., 1994; Hulton et al., 2010; Johnson et al., 2017; Jones et al., 1993; Knechtle et al., 2010; Knechtle et al., 2011; Koehler et al., 2011; Margolis et al., 2013; Margolis et al., 2016; Mudambo et al., 1997; Mullie et al., 2018; Plasqui et al., 2019; Pulfrey and Jones, 1996; Rehner et al., 2010; Reynolds et al., 1999; Ryder et al., 2004; Schulz et al., 1992; Sjodin et al., 1994; Stroud, 1998; Stroud et al., 1993; Stroud et al., 1997; Verma et al., 2018; Westerterp et al., 1986; Westerterp et al., 1992; Westerterp et al., 1994)

expenditure and mean ambient temperature (Figure 2b). Together, these analyses might very cautiously be interpreted as suggesting that profuse sweating, which only humans do (perhaps supported by their unique ability to guarantee the availability of water), is the adaptation most capable of nullifying the effects of heat during chronic extreme activity. However, there is very considerable noise inherent in this dataset on human activities since few of the included studies were designed to directly address our question of interest, and ambient temperatures were often not stated and, in many cases, would have varied considerably over the duration of the activity. Moreover, other environmental factors can be as important as temperature in influencing heat load, such as radiant heat, humidity and wind speed. There is currently a gap in the empirical literature on how the maximum daily energy expenditure of humans relates to ambient conditions.

While investigations into human persistence hunting have been conducted through research in the fields of social and biological anthropology, and both comparative and macrophysiology, there have been few attempts to gain insight from a psychological perspective. Animals are believed to enjoy the behaviours that they are adapted for (Markowitz, 1982; Markowitz & LaForse, 1987). What proportion of people enjoy running? The percentages appear very low. For example, New York City has the highest reported number of runners per capita of any city in the USA, with some 410,000 people reported going for a run at least once in the previous 12 months (Seligman & Nolan, 2017). The population of New York is about 8.6 million, and thus less than 5% of New Yorkers do even a modicum of running. While the nature of Western societies typically eschews the need to run, and it cannot be assumed that everyone who would enjoy running partakes in this activity, we might anticipate that if our species was 'born to run' we would find excuses to do so despite the constraints of modern society and the environment (cf. Speakman, 2020). On the other hand, some runners report experiencing a 'natural high' from high endorphin or cannabinoid levels (Dietrich & McDaniel, 2004; Schulkin, 2016). These heightened neurotransmitter levels presumably increase real-time enjoyment of the endurance activity and promote habitual aerobic exercise (Raichlen, Foster, Gerdeman, Seillier, & Giuffrida, 2012). But is this common in voluntary runners, or an experience of the few, and do persistence hunters also experience this natural high?

While the sport of endurance running is participated in worldwide, persistence hunting is a dying art. Hunter-gatherers in the Kalahari Desert of Botswana, for example, have shifted away from a significant dependence on hunting in all forms (Marshall Thomas, 2006). Those that continue to hunt often utilize dogs and horses to improve efficiency (Liebenberg, 2006) – bow-and-arrow and pure persistence hunting have become increasingly obsolete there and elsewhere (Liebenberg, 2013). There is now very limited scope for direct investigations into the physiology, ecology and psychology of persistence hunting. Nonetheless, we can at least further progress our understanding of the human experience of running *per se*; better comprehension about feats of human endurance in the present can help us better comprehend the realities of human endurance in the past.

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## COMPETING INTERESTS

The authors declare no competing or financial interests.

## AUTHOR CONTRIBUTIONS

Both authors contributed to conceptualization, methodology, validation, formal analysis, investigation, resources, data curation, writing, review and editing, and visualization. Both authors have read and approved the final version of this manuscript and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. All persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

## DATA AVAILABILITY STATEMENT

Man vs. Horse race data utilized in analyses.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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