



ELSEVIER

Contents lists available at ScienceDirect

## Journal of Human Evolution

journal homepage: [www.elsevier.com/locate/jhevol](http://www.elsevier.com/locate/jhevol)

## Comparing walking and running in persistence hunting

Martin Hora<sup>a, b, \*</sup>, Herman Pontzer<sup>b, c</sup>, Michal Struška<sup>a</sup>, Pauline Entin<sup>d</sup>, Vladimír Sládek<sup>a</sup><sup>a</sup> Department of Anthropology and Human Genetics, Charles University, Viničná 7, Prague, 12800, Czech Republic<sup>b</sup> Department of Evolutionary Anthropology, Duke University, 130 Science Drive, Durham, NC, 27708, USA<sup>c</sup> Global Health Institute, Duke University, 310 Trent Drive, Durham, NC, 27710, USA<sup>d</sup> College of Arts & Sciences, University of Massachusetts Dartmouth, 285 Old Westport Road, Dartmouth, MA, 02747, USA

## ARTICLE INFO

## Article history:

Received 28 January 2022

Accepted 28 July 2022

Available online xxx

## Keywords:

Endurance

Human evolution

Locomotion

Thermoregulation

## ABSTRACT

It has been proposed that humans' exceptional locomotor endurance evolved partly with foraging in hot open habitats and subsequently about 2 million years ago with persistence hunting, for which endurance running was instrumental. However, persistence hunting by walking, if successful, could select for locomotor endurance even before the emergence of any running-related traits in human evolution. Using a heat exchange model validated here in 73 humans and 55 ungulates, we simulated persistence hunts for prey of three sizes (100, 250, and 400 kg) and three sweating capacities (nonsweating, low, high) at 6237 combinations of hunter's velocity (1–5 m s<sup>-1</sup>, intermittent), air temperature (25–45 °C), relative humidity (30–90%), and start time (8:00–16:00). Our simulations predicted that walking would be successful in persistence hunting of low- and nonsweating prey, especially under hot and humid conditions. However, simulated persistence hunts by walking yielded a 30–74% lower success rate than hunts by running or intermittent running. In addition, despite requiring 10–30% less energy, successful simulated persistence hunts by walking were twice as long and resulted in greater exhaustion of the hunter than hunts by running and intermittent running. These shortcomings of pursuit by walking compared to running identified in our simulations could explain why there is only a single direct description of persistence hunting by walking among modern hunter-gatherers. Nevertheless, walking down prey could be a viable option for hominins who did not possess the endurance-running phenotype of the proposed first persistence hunter, *Homo erectus*. Our simulation results suggest that persistence hunting could select for both long-distance walking and endurance running and contribute to the evolution of locomotor endurance seen in modern humans.

© 2022 Elsevier Ltd. All rights reserved.

## 1. Introduction

Humans have exceptional locomotor endurance among mammals (Carrier, 1984; Bramble and Lieberman, 2004; Pontzer, 2017; Raichlen et al., 2019). Our body seems to be tuned to perform prolonged moderate to vigorous physical activity, such as walking and running, to the extent that the absence of physical activity increases vulnerability to poor physical and mental health and contributes to diseases such as heart disease, osteoporosis, obesity, and Alzheimer's disease (Morris et al., 1953; Paffenbarger et al., 1986; Donnelly et al., 2009; Guadalupe-Grau et al., 2009; Mattson, 2012; Lieberman, 2020). Human locomotor endurance has been explained as resulting from selection for long-distance

walking and running (Bramble and Lieberman, 2004). Initially, foraging by walking in hot open habitats with sparsely distributed resources might have selected for locomotor endurance (e.g., Brace and Montagu, 1965; Lieberman, 2015; Pontzer, 2017). Further increase in locomotor endurance may have stemmed from selection for endurance running used in scavenging and persistence hunting (Carrier, 1984; Bramble and Lieberman, 2004; Pontzer, 2017). The importance of endurance running in these evolutionary scenarios was based largely on observations of modern hunter-gatherer populations, some of which use running or intermittent running (alternation of running and walking) to drive their prey to exhaustion, heatstroke, or otherwise into traps or other means by which they can be killed by hunters (Liebenberg, 2006; Lieberman et al., 2020). However, other research has suggested that walking without running could also result in successful persistence hunting (Pickering and Bunn, 2007). If so, persistence hunting would not have required endurance running as a prerequisite (Nickels, 1984;

\* Corresponding author.

E-mail address: [mrtnh@seznam.cz](mailto:mrtnh@seznam.cz) (M. Hora).

Pickering and Bunn, 2007), and could have been used by hominins before the emergence of the running-related traits in *Homo erectus* (Nickels, 1984). Nevertheless, the records of persistence hunting by walking in modern hunter-gatherers are limited to the report of Pickering and Bunn (2007; and perhaps Bartram et al., 1991 see Discussion section), which may suggest a lower success rate compared to running. However, the relative success rates of walking and running in persistence hunting remain unclear.

Owing to differences in mechanics and energetical and thermoregulatory demands between walking and running, different aspects of locomotor endurance might be favored by selection for each gait. Locomotor endurance, defined as the maximum duration of locomotion sustainable at a given velocity (Pontzer, 2017), is determined by several factors including aerobic capacity, volume of mitochondria in muscles, locomotor economy, and heat loss capacity (for a more complex discussion of endurance see, e.g., Bassett and Howley, 2000; Hutchinson, 2018). Aerobic capacity ( $VO_{2max}$ ) determines how much oxygen can be delivered to and used by muscles active during locomotion and since one cannot operate above  $VO_{2max}$  for extended periods, it sets the upper limit for endurance performance (Bassett and Howley, 2000). Aerobic capacity is affected by, among other factors, cardiorespiratory capacity and volume of mitochondria in active muscles, which itself is primarily a function of muscle volume, muscle fiber type (Weibel et al., 2004), and mitochondrial volume density (Hoppeler et al., 1973). Volume of mitochondria in muscles also positively affects endurance at submaximal aerobic velocities by allowing to perform at higher percentage of aerobic capacity because of slower accumulation of metabolites, lower rates of glycogen depletion, and increase of fat oxidation (Holloszy and Coyle, 1984). The need for higher aerobic capacity and mitochondrial volume would rise with intensity of the locomotion, e.g., due to challenging terrain, carried loads, and velocity. As modern hunter-gatherers usually walk relatively slowly (e.g., about  $1.1 \text{ m s}^{-1}$  in Hadza; Pontzer et al., 2015), foraging might not require high aerobic capacity. Similarly, persistence hunting by walking would not be expected to select for higher aerobic capacity unless it benefited from faster velocities which require higher oxygen uptake (e.g., Ralston, 1958). More intensive running-based scavenging or persistence hunting would put stronger selection pressure for increased aerobic capacity in hominins compared to walking (Bramble and Lieberman, 2004; Pontzer, 2017).

The locomotor economy is defined as the mass-specific distance traveled per unit of energy (and thus oxygen) expended (Pontzer, 2017). Keeping aerobic capacity constant, individuals with better locomotor economy would travel at lower percentage of their aerobic capacity and hence have greater endurance (Conley and Krahenbuhl, 1980; Daniels and Daniels, 1992). Although some morphological characteristics improve the economy of both walking and running (e.g., long lower limbs; Steudel-Numbers and Tilkens, 2004; Pontzer, 2005; Steudel-Numbers et al., 2007), others are relevant for only a single gait (e.g., energy storage in a long Achilles tendon and a plantar arch during running; Bramble and Lieberman, 2004). Thus, we suggest that selection for walking economy, whether due to persistence hunting or other long-distance walking foraging behaviors, could act on some of the same traits (e.g., long lower limbs) as those selected for running economy.

In hot, open environments, hyperthermia and dehydration become the key limits of locomotor endurance (Adolph, 1947; Carrier, 1984; Steudel-Numbers et al., 2007; Ruxton and Wilkinson, 2011a, b; Lieberman, 2015; Rathkey and Wall-Scheffler, 2017; Longman et al., 2019, 2021; Hora et al., 2020). Modern humans are characterized by several traits that facilitate heat loss such as high sweating capacity and loss of functional hair cover (Lieberman,

2015). It has been argued that heat loss capacity might have been under selection in hominins foraging in open habitats (Wheeler, 1992; Ruxton and Wilkinson, 2011a), especially in the middle of the day to avoid predators (Brace and Montagu, 1965; Lieberman, 2015). Persistence hunting by walking was reported in a hot open environment (Pickering and Bunn, 2007) so it would also benefit from the derived heat loss capacity. As high-intensity locomotion is more thermogenic, heat loss capacity would be more important for persistence hunting if performed at faster walking velocities and would be essential with the adoption of persistence hunting by running (Montagu, 1964; Carrier, 1984; Bramble and Lieberman, 2004; Lieberman, 2015).

There are several factors that could contribute to the optimal gait and velocity for a successful persistence hunt, including the prey sweating capacity, body size of the prey, and preferred velocity of the prey, as well as environmental factors such as air temperature and relative humidity. Although terrestrial ungulates (the typical prey in persistence hunting; Liebenberg, 2006; Lieberman et al., 2020) dissipate heat primarily by panting and many rely on panting exclusively (e.g., wildebeest, wild boar, mule deer; Taylor et al., 1969a; Ingram, 1965; Parker and Robbins, 1984), some wild ungulate species also have heat-induced sweating capacity (Robertshaw and Taylor, 1969a; Bullard et al., 1970; Robertshaw and Dmi'el, 1983; Parker and Robbins, 1984), which would provide them with an additional route to lose heat while fleeing from the hunter. In contrast to human eccrine glands which produce sweat through exocytosis of secretory granules of specific content, in ungulates, sweat is produced by apocrine glands through discharging a portion of the cell, including cell membrane, cell cytoplasm, and intracellular fragments (Farkaš, 2015). The resulting sweat ranges from highly concentrated to watery (Weiner and Hellmann, 1960). As such, the evaporative capacity of the apocrine sweat might be lower than that of the eccrine sweat. However, experiments show that cutaneous evaporation can surpass the evaporation from respiratory tract in some sweating ungulate species (Knapp and Robinson, 1954; McLean, 1963; Taylor, 1969; Taylor et al., 1969b; Finch, 1972; Robertshaw and Dmi'el, 1983) and other animals (Dawson et al., 1974) and account for up to 95% of overall evaporation (McLean, 1963), although most data come from resting animals. More data are needed from animals during physical activity when ventilation is increased and so would be the evaporation from the respiratory tract. On the other hand, cutaneous evaporation would also be enhanced during locomotion due to airflow over the body surface. Nonequid ungulates seem to lack the direct humoral control of sweating through circulating catecholamines (studied in cattle and black bedouin goat; Robertshaw and Whittow, 1966; Dmi'el et al., 1979) that can contribute to sweating during physical activity (in addition to neural control) in equids (Evans et al., 1956; Robertshaw and Taylor, 1969b) and primates (Wada, 1950; Robertshaw et al., 1973). Nevertheless, because of increased metabolic heat production, sweating should be induced by heat during physical activity also in nonequid ungulates, which is illustrated, e.g., in eland whose cutaneous evaporation "increased by 4- to 10-fold during a run and the sweat literally dripped off them after they stopped" as reported by Taylor and Lyman (1972: 116). The observed increase of body core temperature in eland during running was below  $1 \text{ }^\circ\text{C}$  compared to the up to  $4.5 \text{ }^\circ\text{C}$  increase in gazelle, who increased cutaneous evaporation by only 40%, which suggests that sweating is an effective route for heat dissipation in eland (Taylor and Lyman, 1972). As such, the sweating capacity of the prey could have a negative effect on the success of the persistence hunt.

Larger animals have lower body surface area to body mass ratios that limit their relative heat dissipation capacity (Bergmann, 1848; Ruff, 1994). This characteristic should make larger animals prone to

overheating at lower levels of physical activity (i.e., at lower velocities). Thus, walking might be better suited for the persistence hunting of large prey. On the other hand, larger animals might have adaptations to moderate the size-induced limits of thermoregulation. Among African ungulates, larger species have been reported to have greater sweating capacity (Robertshaw and Taylor, 1969a), lower pelage depth, and lower thermal conductance of the pelage (Hofmeyr, 1985). All these characteristics would enhance heat dissipation in larger animals. Although larger-bodied animals have relatively more muscle mass compared with smaller-bodied animals (Alexander et al., 1981), their mass-specific cost of locomotion is lower (Taylor et al., 1970, 1982) and thus they should generate relatively less heat when moving.

Quadrupeds use narrow ranges of energetically optimal velocities within each gait (Hoyt and Taylor, 1981). The hunter might thus benefit from selecting velocities just above those preferred ranges to force prey to switch to a faster gait and hasten the rate of heat accumulation (Carrier, 1984). As hunting by walking would elicit lower heat production in the prey compared to running (Hoyt and Taylor, 1981), it might require a higher air temperature (which increases heat gain from the environment and limits heat loss) or higher relative humidity (which limits evaporative heat loss) to push the game to overheat. Owing to the circadian oscillation of air temperature and humidity, the success of walking in persistence hunting could also be affected by the time of day.

In this study, we simulated the success of walking and running in persistence hunting using a heat exchange model. We adjusted and validated (in humans, horses, sheep, cattle, and elands) a previously published heat exchange model (Hora et al., 2020) to simulate persistence hunts for prey of three sizes and three levels of sweating capacity by a modern human hunter at combinations of the hunter's aerobic velocity, air temperature, relative humidity, and start time. The heat exchange model was used to estimate body core temperature and water loss of the hunter and prey. The prey was modeled as fleeing from the hunter at its preferred velocity (equal or faster than the actual velocity of the hunter), stopping after reaching a certain distance from the hunter and resting in the shade until the hunter gets closer again. We identified successful simulated hunts as those in which the hunter had greater locomotor endurance (limited by hyperthermia, dehydration, and sunset) than the prey. We calculated the success rate of simulated persistence hunts by dividing the number of successful simulated hunts under given conditions by the number of simulated hunts under the given conditions, thus assuming that the hunter can track the prey at a given velocity and never loses the trail. We tested two hypotheses: 1) walking is as successful as running in persistence hunting of medium to very large prey and 2) the success of walking is greater in larger prey, in animals with low sweating capacity, at velocities that force the prey to trot, and under hot and humid ambient conditions.

## 2. Methods

### 2.1. Heat exchange model

We used a previously published heat exchange model (Hora et al., 2020), described in detail in Supplementary Online Material (SOM S1), to estimate the body core temperature and water loss as the primary factors that delineate the endurance capacity of the hunter and prey moving within their aerobic velocities in a hot, open environment. The heat exchange model is a set of equations that model the metabolic heat production, heat flow between the body core and skin and between the skin and hair, and convective, radiative, and evaporative routes of heat exchange between the body surface and ambient environment (Fig. 1). The input variables

of the model included body mass, stature, gait, velocity, air temperature, relative humidity, and sun elevation, and the output variables estimated at each second of simulation were the body core temperature and water loss due to respiratory and cutaneous evaporation (Fig. 1).

The heat exchange model was adjusted (SOM S1) and validated (SOM S2) using newly collected data (three experiments on outdoor running and walking humans:  $n = 12$ , air temperature = 22–35 °C, relative humidity = 31–61%; SOM Table S1) and previously published data in humans (SOM Table S1; 18 experiments:  $n = 61$ , air temperature = 30–45 °C, relative humidity = 23–85%; Mitchell et al., 1976; Shvartz, 1976; Marino et al., 2004; Jack, 2010; Maughan et al., 2012; Moyen et al., 2014; Che Muhamed et al., 2016), horses (SOM Table S2; 17 experiments:  $n = 38$ , air temperature = 19–35 °C, relative humidity = 40–85%; Hodgson et al., 1993; Geor et al., 1995, 2000; Marlin et al., 1996, 1999; McCutcheon and Geor, 1996; Kingston et al., 1997), sheep (SOM Table S2; 10 experiments:  $n = 12$ , air temperature = 18–33 °C, relative humidity = 22–50%; Bell et al., 1983; Ueno et al., 1989; Entin et al., 1998, 1999), cattle (SOM Table S2; six experiments:  $n = 3$ , air temperature = 18–40 °C, relative humidity = 48–88%; Hales and Findlay, 1968; Ueno et al., 2001), and eland (SOM Table S2; four experiments:  $n = 2$ , air temperature = 27.5 °C, relative humidity = 23.5%; Taylor and Lyman, 1972). Each human participant provided written informed consent before participation in our validation study, and the protocol was approved by the Institutional Review Board of Charles University, Faculty of Science (approval number 2019/21).

Simulated and reported body core temperatures were compared using the mean error and root mean square error (RMSE) following previous validation studies for human heat exchange models (Haslam and Parsons, 1994; Fiala et al., 2001; Martínez et al., 2016) as:

$$\text{Mean core temperature error} = \frac{\sum_1^q (T_{c\text{Simulated}} - T_{c\text{Observed}})}{q} \quad [1]$$

$$\text{Core temperature RMSE} = \frac{\sqrt{\sum_1^q (T_{c\text{Simulated}} - T_{c\text{Observed}})^2}}{q} \quad [2]$$

where  $q$  is the number of reported body core temperatures for a given experiment excluding the temperature at the beginning of the experiment,  $T_{c\text{Simulated}}$  is the simulated body core temperature (°C), and  $T_{c\text{Observed}}$  is the observed body core temperature (°C). Water loss difference was calculated as:

$$\text{Water loss difference} = WL_{\text{Simulated}} - WL_{\text{Observed}} \quad [3]$$

where  $WL_{\text{Simulated}}$  is the simulated water loss at the end of the experiment (kg), and  $WL_{\text{Observed}}$  is the observed water loss at the end of the experiment (kg). In addition, water loss difference was also adjusted to the initial body mass at the beginning of the experiment.

Comparisons of observed and estimated body core temperatures and human water loss are provided in SOM Tables S1 and S2 and Figure 2. Body core temperature was estimated with a mean error (positive values represent overestimation) of –0.25 °C in humans, 0.26 °C in horses, and –0.06 °C in low-sweating species (i.e., –0.14 °C in sheep, –0.05 °C in cows, and 0.12 °C in elands), and with an RMSE of 0.41 °C in humans, 0.75 °C in horses, and 0.30 °C in low-sweating species (i.e., 0.29 °C in sheep, 0.34 °C in cows, and 0.26 °C in elands). In heat exchange modeling studies, models are usually considered acceptable when the RMSE is within the

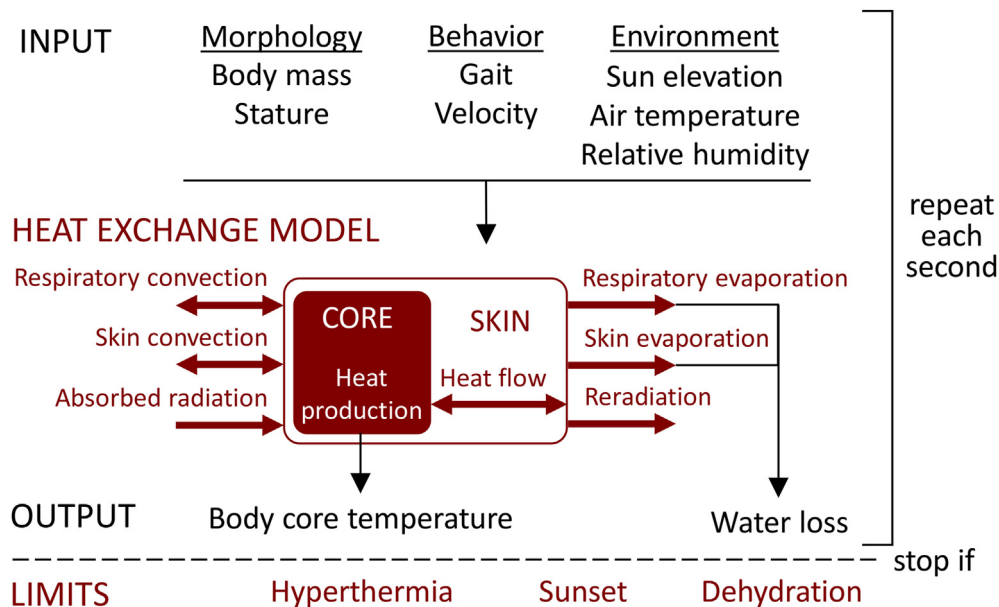


Figure 1. Heat exchange model and simulation.

standard deviation of the experimental data (Haslam and Parsons, 1994; Fiala et al., 2001; Psikuta et al., 2012; Martínez et al., 2016). Both the mean error and RMSE were lower than the average standard deviation of the body core temperatures measured at the end of the experiments in humans (0.46 °C) and low-sweating species (0.44 °C; data available only for sheep), but not in horses (0.46 °C) where only the mean error was lower. The high RMSE in horses was particularly driven by four experiments in hot ( $\geq 30$  °C) and humid ( $\geq 80\%$ ) conditions with body core temperature RMSE  $\geq 1.0$  °C (Fig. 2A, B). Water loss was estimated with the mean error at the end of the experiment to be  $-0.54\%$  of the body mass in humans (SOM Tables S1). Estimation of water loss was not validated in prey because of lack of appropriate data, but the prey's endurance was not limited by dehydration in any of the hunts simulated in the present study.

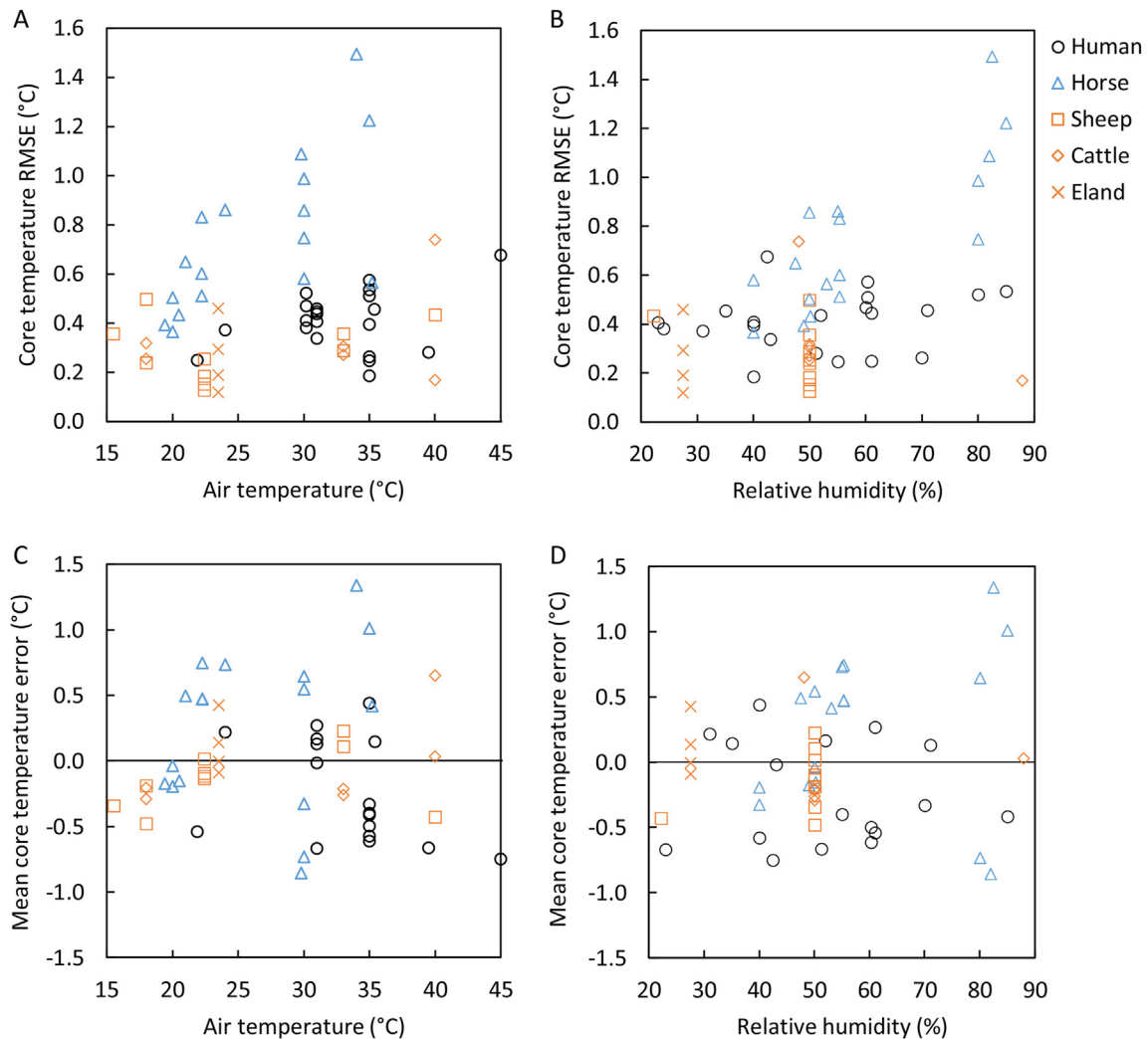
To evaluate the effect of ambient conditions on estimates of body core temperature and water loss, we analyzed relationships of mean error and RMSE with air temperature and relative humidity using product–moment correlation (four tests in which data conformed to a bivariate normal distribution) and Spearman rank order correlation (remaining 12 tests) with Holm-Bonferroni correction for multiple comparisons. We identified two significant relationships. In horses, body core temperature RMSE was significantly correlated with air temperature ( $r_s = 0.697$ ;  $p = 0.002$ ;  $n = 17$ ; Fig. 2A) and relative humidity ( $r_s = 0.737$ ;  $p = 0.001$ ;  $n = 17$ ; Fig. 2B), which suggests that our model estimated body core temperature in horses with greater error in hot and humid conditions. However, this error was nondirectional (i.e., not biased to more positive or negative values in hot humid compared to cold dry conditions) as evidenced by the absence of significant relationship of mean error with either air temperature ( $r_s = 0.323$ ;  $p = 0.206$ ;  $n = 17$ ; Fig. 2C) or relative humidity ( $r_s = 0.390$ ;  $p = 0.122$ ;  $n = 17$ ; Fig. 2D) in horses. Our model estimates of body core temperature in humans and low-sweating species and of water loss in humans were not affected by either air temperature or relative humidity.

## 2.2. Simulated hunts

We simulated a total of 56,133 persistence hunts which were all possible combinations of 11 velocities of the hunter, three prey sizes,

three prey sweating capacities, nine air temperatures, seven relative humidities, and nine starting times (Table 1). The hunter was modeled as a modern human with the body size and shape of *H. erectus* (adult projection of KNM-WT 15000: body mass = 76.7 kg, stature = 178 cm, relative body surface area = 254 kg cm<sup>-2</sup>; Ruff and Burgess, 2015; Ruff et al., 2018). To determine the sensitivity of our results to the body size and shape of the hunter, we also modeled the hunter as having a body mass of 50 kg, stature of 160 cm, and relative body surface area of 300 kg cm<sup>-2</sup>, which corresponds to an average male in modern hunter-gatherers such as !Kung San (Kirchengast, 2000) or Hadza (Hiernaux and Hartono, 1980).

We simulated that the hunter followed the prey at three variants of constant walking velocities, six variants of constant running velocities, and two variants of intermittent running/walking velocities. Walking hunts were simulated at 1.0, 1.5, and 2.0 m s<sup>-1</sup>. All these walking velocities were below the reported walk-to-run transition (Hreljac, 1993) and metabolic heat production estimated by our model at all these walking velocities was lower than at any running velocity. Running hunts were simulated as slow at 2.5 and 3.0 m s<sup>-1</sup>, medium at 3.5 and 4.0 m s<sup>-1</sup>, and fast at 4.5 and 5.0 m s<sup>-1</sup>. Slow intermittent running was simulated as alternating running at 3 m s<sup>-1</sup> and walking at 1 m s<sup>-1</sup>, which corresponds to running speeds in ethnographic records (Liebenberg, 2006; Lieberman et al., 2020). Fast intermittent running was simulated as alternating running at 4.5 m s<sup>-1</sup> and walking at 1.5 m s<sup>-1</sup>, which corresponds to the theoretical model of Carrier (1984) that the hunter should force the prey to gallop. Alternations of running and walking were determined according to the activity of the prey: the hunter ran when the prey was moving (we assumed that the prey is in sight or that its trail can be predicted so that the hunter can move quickly), whereas the hunter walked when the prey was resting (we assumed the hunter had to slow down to track the prey; see below how we modeled when the prey was moving and resting). For intermittent running, duration of the running period was determined by preferred velocity of the prey, which varies with prey size in our model (see below). As a result, duration of the running period varied with prey size. During slow intermittent running, the hunter ran for 282 min after a 100 kg prey (fleeing at 3.06 m s<sup>-1</sup>), for 95 min after a 250 kg prey (fleeing at 3.18 m s<sup>-1</sup>), and for 61 min after a 400 kg prey (fleeing at 3.28 m s<sup>-1</sup>), before



**Figure 2.** Core temperature root mean square error (RMSE) (A, B) and mean core temperature error (C, D) estimated by our model in relation to air temperature (A, C) and relative humidity (B, D) for human (black circle), horse (blue triangle), sheep (orange square), cattle (orange diamond), and eland (orange cross). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

**Table 1**  
Variables characterizing the simulated hunts.

Variable	Number of variants	Variants
Hunter		
Velocity ( $m s^{-1}$ )	11	Constant: 1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5; Intermittent: 3/1, 4.5/1.5
Prey		
Body mass (kg)	3	100, 250, 400
Sweating capacity	3	High, low, nonsweating
Ambient conditions		
Air temperature (°C)	9	25, 27.5, 30, 32.5, 35, 37.5, 40, 42.5, 45
Relative humidity (%)	7	30, 40, 50, 60, 70, 80, 90
Starting time	9	8:00, 9:00, 10:00, 11:00, 12:00, 13:00, 14:00, 15:00, 16:00

switching to walking which took 17 min (regardless of the prey size) and was followed by another running period. During fast intermittent running, hunter ran for 51 min after a 100 kg prey (fleeting at  $4.83 m s^{-1}$ ), for 14 min after a 250 kg prey (fleeting at  $5.72 m s^{-1}$ ), and for 11 min after a 400 kg prey (fleeting at  $5.99 m s^{-1}$ ) before switching to walking which took 11 min for prey of all sizes. Our intermittent running simulations might over-emphasize time spent running versus walking since real hunters might walk more because of tracking difficulties (Liebenberg, 2006; Lieberman et al., 2020).

We modeled prey of three sizes: 100, 250, and 400 kg, which represent respectively size classes 2 (medium), 3 (large), and 4 (very large; Bunn and Kroll, 1986). For each prey size, we modeled three variants of prey sweating capacity: high-sweating model based on a horse to represent prey such as zebra (maximum wettedness i.e., maximum proportion of body surface area that can be covered by sweat = 1.0), low-sweating model based on African bovids with heat-induced sweating capacity to represent sweating antelopes (maximum wettedness varied with body size: 0.06 for a 100-kg prey, 0.2 for a 250-kg prey, and 0.3 for a 400-kg prey), and

nonsweating model to represent nonsweating prey like a wildebeest or mule deer (maximum wettedness = 0.02 to allow for diffusion). All variants could increase ventilation >7-fold over the normothermic resting value due to the thermal drive alone to account for panting. The high-, low-, and nonsweating prey models lost on average ( $\pm$ SD)  $90 \pm 5.0\%$ ,  $69 \pm 18.1\%$ , and  $30.3 \pm 18.8\%$ , of evaporated heat, respectively, by cutaneous evaporation during the hunts simulated here, which corresponds well to the reported 71–94% for cattle (McLean, 1963), 81% for goat (Robertshaw and Dmi'el, 1983), 80% for eland (Finch, 1972), 61–77% for sheep (Knapp and Robinson, 1954), 75% for oryx (Taylor, 1969), 63% for waterbuck (Taylor et al., 1969b), and 35% for hartebeest (Finch, 1972). The average sweat rate of the high-sweating prey during our simulations ( $640 \text{ g h}^{-1} \text{ m}^{-2}$ ) was lower than the reported  $2000 \text{ g h}^{-1} \text{ m}^{-2}$  in a running horse (Hodgson et al., 1993). Our simulations yielded similar sweating rates in our low-sweating prey as reported in the literature:  $94 \text{ g h}^{-1} \text{ m}^{-2}$  for a 100-kg prey compared to the reported  $100 \text{ g h}^{-1} \text{ m}^{-2}$  in the 100-kg waterbuck and 110-kg oryx during resting (Robertshaw and Taylor, 1969a),  $254 \text{ g h}^{-1} \text{ m}^{-2}$  for a 250-kg prey compared to the reported  $266 \text{ g h}^{-1} \text{ m}^{-2}$  in the 200-kg running eland (Taylor and Lyman, 1972), and  $344 \text{ g h}^{-1} \text{ m}^{-2}$  for a 400-kg prey compared to the reported  $500 \text{ g h}^{-1} \text{ m}^{-2}$  in the 400-kg resting eland (Finch, 1972). The simulated rate of cutaneous water loss in our nonsweating prey was on average lower ( $34 \text{ g h}^{-1} \text{ m}^{-2}$ ) but had a maximum rate ( $72 \text{ g h}^{-1} \text{ m}^{-2}$ ) comparable to values reported for a 150-kg resting wildebeest ( $60 \text{ g h}^{-1} \text{ m}^{-2}$ ; Robertshaw and Taylor, 1969a) or a 15-kg resting ( $56 \text{ g h}^{-1} \text{ m}^{-2}$ ) and running ( $78 \text{ g h}^{-1} \text{ m}^{-2}$ ) Thompson's gazelle (Taylor and Lyman, 1972). In addition, to test if our model can predict the outcome of the reported successful persistence hunt by walking (Pickering and Bunn, 2007), we simulated the prey as a 20-kg duiker with maximum wettedness of 0.02, body surface area of  $0.74 \text{ m}^2$  (Schmidt-Nielsen, 1984), hair conductance of  $4.5 \text{ W m}^{-2} \text{ }^\circ\text{C}^{-1}$  (estimated for ungulate of such body mass from data of Hofmeyr, 1985), metabolic heat production estimated as  $\text{Body mass} \times [3.36543 \times \text{Velocity} + 3.20885]$  (based on data for 23-kg gazelle; Taylor et al., 1974), and relative minute volume estimated as  $1.0513 \times \text{Core temperature} - 40$  (based on data for 52-kg sheep; Entin, 1997). Owing to the duiker's reported "nervous disposition" (Keymer and Garnham, 1969:52), we simulated that it would never walk from the hunter but instead use trot or gallop. All other parameters and equations were same as in the low-sweating and nonsweating model. As Pickering and Bunn (2007) have not reported any details about velocity of the hunter or ambient conditions, we simulated the hunt of the duiker across all the above-listed velocities and below-listed ambient conditions. The average cutaneous water loss in our simulations ( $32 \text{ g h}^{-1} \text{ m}^{-2}$ ) was similar as reported for a resting duiker exposed to  $40 \text{ }^\circ\text{C}$  (Robertshaw and Taylor, 1969a).

Simulations were performed for nine daily maximum air temperatures (25.0, 27.5, 30.0, 32.5, 35.0, 37.5, 40.0, 42.5, and  $45.0 \text{ }^\circ\text{C}$ ; Fig. 3A) and seven daily average relative humidities (30%, 40%, 50%, 60%, 70%, 80%, and 90%; Fig. 3B). Both the air temperature and relative humidity varied with time of the day as a sine wave (Fig. 3A, B) determined by our Ambient model (SOM S3). Hunts were simulated as starting at each hour from 8:00 to 16:00. Sun elevation profile reflected a representative day (August 15) in the Turkana Basin (4.13 N, 35.9 E; Fig. 3C; SOM S3). We simulated that both the hunter and prey were exposed to direct solar radiation at all times except for the prey during resting.

### 2.3. Endurance limits

Each simulations provided estimates of endurance of the hunter and prey which were compared to determine if the hunt could be

successful at the given conditions. A successful simulated persistence hunt was defined here as a hunt in which the prey had a lower endurance than the hunter. Endurance was delimited by reaching hyperthermia, dehydration, or sunset.

The hyperthermia threshold was defined here as the body core temperature of  $41 \text{ }^\circ\text{C}$  for the hunter (Ely et al., 2009) and  $42 \text{ }^\circ\text{C}$  for the prey (Lindinger, 1999). Body core temperatures up to  $40.9 \text{ }^\circ\text{C}$  were reported in humans during running races (Lee et al., 2010) and experiments (Ely et al., 2009), and  $40.5 \text{ }^\circ\text{C}$  was reached by one of the participants of our validation study which makes our hyperthermia threshold of  $41 \text{ }^\circ\text{C}$  a reasonable choice. Nevertheless, to determine the sensitivity of our results to setting the hyperthermia threshold of the hunter, we also modeled the hunter's hyperthermia threshold at  $40 \text{ }^\circ\text{C}$ .

The dehydration threshold was defined here as water loss equivalent to 10% body mass for the hunter (Hora et al., 2020) and 30% body mass for the prey (Schmidt-Nielsen, 1964). Water loss equivalent to 10% of body mass was reported for marathon winners (Beis et al., 2012) and even 25% of body mass loss was anecdotally reported in the literature (Noakes, 2012). Nevertheless, to determine the sensitivity of our results to setting of the dehydration threshold, we modeled the dehydration threshold of the hunter also as water loss equivalent to 7.5% and 5.0% of body mass.

Sunset at the given date and location was at 18:45. Although there are reports that hunters sometimes resume the hunt the next morning (Liebenberg, 2006; Levi, 2020; Lieberman et al., 2020), we have chosen not to simulate any hunts that span over more than one day. Sunset was thus an end of the hunt in our simulations.

### 2.4. Prey behavior

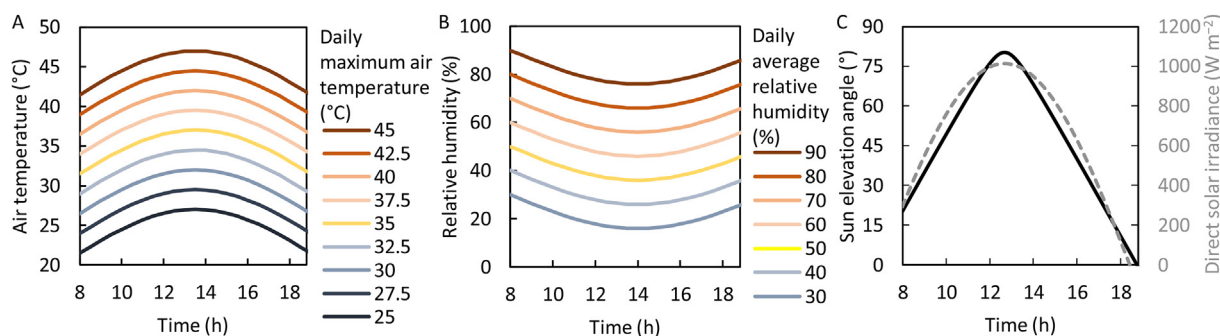
The actual velocity and gait of the prey were determined by three factors: the velocity of the hunter (see above), preferred velocities of the prey, and distance between the hunter and prey.

We defined the preferred velocities of the prey as those at which the mass-specific cost of transport (COT) was within 3% from the minimum cost of transport for a given gait (walk, trot, and gallop). We derived size- and gait-specific quadratic function equations for estimation of mass-specific COT from prey velocity (SOM S1 Eq. 6) based on published equations for ponies (Hoyt and Taylor, 1981) and horses (Minetti et al., 1999). We then calculated the energetically optimal velocity ( $v_{opt}$ ,  $\text{m s}^{-1}$ ) for each gait as:

$$v_{opt} = \frac{-b}{2a} \quad [4]$$

where  $a$  and  $b$  are the coefficients of the quadratic equation for mass-specific COT estimation (SOM S1 Eq. 6). Minimum mass-specific COT was then determined by solving the SOM S1 Eq. 6 for  $v_{opt}$ .

We assumed that the prey aims to keep within a range of safe distances from the hunter, delimited by a minimum and maximum safe distance. Distances shorter than the minimum safe distance would be avoided by the prey due to immediate danger from the hunter, whereas distances longer than the maximum safe distance would be avoided due to unnecessary heat production. We assumed that the prey would stop when reaching the maximum safe distance from the hunter and would rest in shade until the hunter reached the minimum safe distance. The difference between the maximum and minimum safe distance along with the velocity of the hunter determined the duration of the resting periods of the prey. Note that the absolute value for the minimum safe distance, i.e., flight initiation distance (Wolf and Croft, 2010), was irrelevant to our modeling approach. The difference between maximum and minimum safe distance could be about 73 m for greater kudu



**Figure 3.** Modeled air temperatures (A), relative humidity (B), sun elevation angle (black solid), and direct solar irradiance (grey dashed; C). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(based on reported flight length of 73 m and an unmoving human, [Muposhi et al., 2016](#), estimated as flight length  $\times [1 - \text{hunter's velocity/prey velocity}]$ , where flight length is a distance moved by the prey) and about 1310 m for red deer (based on reported flight length of 3500 m, [Jeppesen, 1987](#), and assuming human velocity of  $1.5 \text{ m s}^{-1}$  and prey velocity of  $2.4 \text{ m s}^{-1}$ ). However, low values estimated for kudu are likely a consequence of the experimental design in which the approaching human stopped moving when flight was initiated by the animal. Data on red deer should be more relevant for our simulations as they were collected during actual hunts. We chose the value of 1000 m as the difference between the maximum and minimum safe distance for our simulations. Nevertheless, to determine the effect of the setting of the difference between the maximum and minimum safe distance on our results, we ran the simulations also with a 100 m value.

To maintain the distance from the hunter within the safe range, the prey needs to move at a velocity equal to or higher than the velocity of the hunter. We assumed that if the velocity of the hunter was within the range of the preferred velocities of the prey, the prey would match the velocity of the hunter (and keep constant distance from the hunter). If the velocity of the hunter fell outside the range of preferred velocities of the prey, the prey used the slowest preferred velocity from the range of the next faster gait (and increased the distance from the hunter). Following these assumptions, the prey was simulated as walking from the hunter when the hunter approached at  $1 \text{ m s}^{-1}$  (prey of all sizes) and  $1.5 \text{ m s}^{-1}$  (400 kg prey only). Such behavior can be elicited by following the animal at the edge of its flight zone (i.e., close to the flight initiation distance) as is used by animal handlers to move cattle and sheep forward at walking pace ([Grandin, 2019](#)) and was proposed to be used by Neandertals for hunting of aurochs ([White et al., 2016](#)). When we exploratively forbid the prey to walk, the simulated walking hunting success rate increased by 6% for low-sweating prey.

## 2.5. Analyses

We calculated the success rate of simulated persistence hunting at the given conditions (defined by velocity, gait, prey size, prey evaporation mode, and start time) by dividing the number of successful simulated hunts at the given conditions by the number of simulated hunts under the given conditions. The success rate here is thus derived exclusively from the difference between the endurance of the hunter and prey, and assumes that the hunter can track the prey at a given velocity without losing the trail.

To account for the error of our heat exchange model in the estimation of body core temperature and water loss, we performed two more sets of persistence hunting simulations with altered thresholds for hyperthermia and dehydration in the hunter and

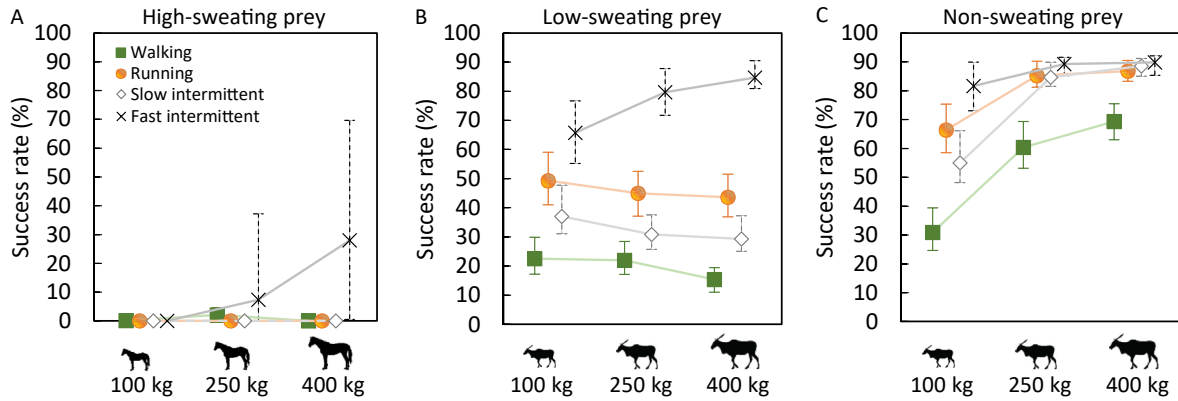
prey models. The thresholds were altered by addition or subtraction of the body core RMSE ( $0.41 \text{ }^\circ\text{C}$  for hunter,  $0.75 \text{ }^\circ\text{C}$  for high-sweating prey, and  $0.30 \text{ }^\circ\text{C}$  for low- and nonsweating prey) and water loss difference (only in hunter: 0.54%) revealed in our validation analysis. Results of these additional simulations were used to construct confidence intervals (CIs) for our success rate estimates. For the upper confidence limit, the success rate was calculated from a set of simulations with increased thresholds in the hunter's model and decreased thresholds in the preys' model. In other words, the hunter had greater endurance due to higher hyperthermia and dehydration thresholds, whereas the prey had lower endurance due to lower hyperthermia threshold in this set of simulations which led to higher success rates. For the lower confidence limit, the success rate was calculated from simulations at which thresholds were decreased for the hunter and increased for the prey. Consequently, the hunter's endurance was lowered and the prey's endurance improved in this set of simulations which led to lower success rates.

Hunt duration (h) of successful simulated hunts was determined as equal to the endurance of the prey. Energy expenditure of the hunter (kcal) was calculated as metabolic rate summed over the duration of the successful hunt. Relative exhaustion of the hunter (percentage of hunter's endurance) was calculated as duration of the successful hunt divided by hunter's endurance under given conditions and multiplied by 100. Relative exhaustion was determined only for simulations in which hunter's endurance would be limited by hyperthermia or dehydration threshold, i.e., simulations in which hunter's endurance was limited by sunset were excluded.

We compared the differences in simulated hunt duration, energy expenditure of the hunter, and relative exhaustion of the hunter between walking and running using the nonparametric Mann–Whitney U test, and between walking, slow running, medium running, fast running, and slow and fast intermittent running using the nonparametric Kruskal–Wallis analysis of variance by ranks and post-hoc multiple comparisons of mean ranks for all groups (two-tailed) with Statistica v. 8.0 (StatSoft, Tulsa). All simulations were performed using Visual Basic in Excel, Microsoft Office 365 ProPlus v. 2205 (Microsoft, Redmond). The simulation code is provided in a separate SOM file. The results of the individual simulations are provided in [SOM Table S4](#).

## 3. Results

Simulated persistence hunts of prey with high sweating capacity were not successful regardless of the hunter's gait, except for the 250-kg prey hunted by walking (success rate: 2.1%, CI: 0.2–4.5%) and 400 kg-prey hunted by fast intermittent running (success rate: 28% but wide CI: 0.5–70%; [Fig. 4A](#)). In contrast, hunts of low-sweating prey and nonsweating prey were successful at all



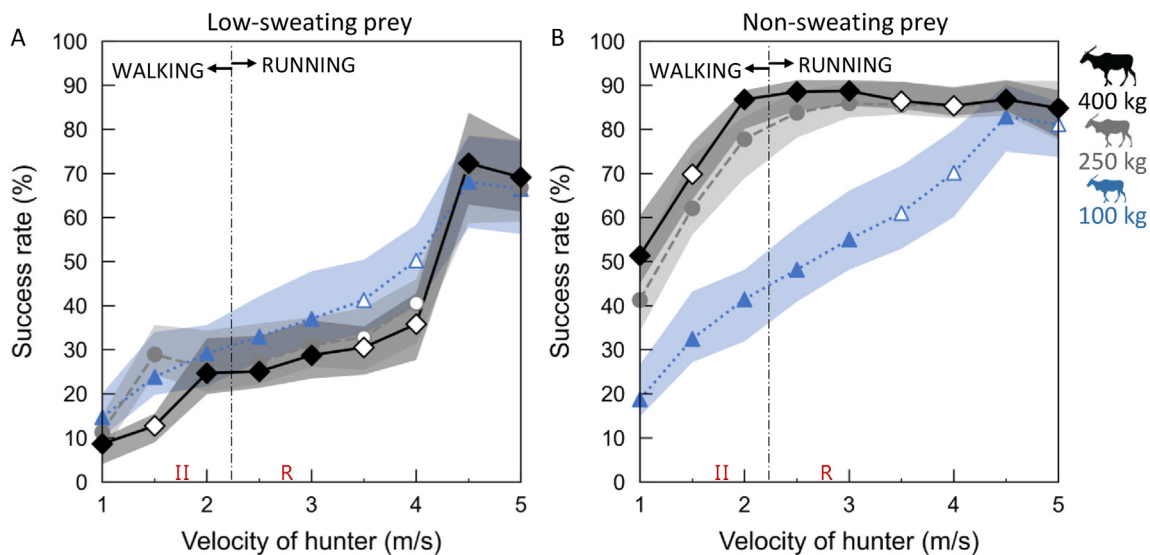
**Figure 4.** Effect of prey size and hunter's gait on the success rate of simulated persistence hunts of high-sweating (A), low-sweating (B), and nonsweating (C) prey by walking ( $n = 5103$ , green square), running ( $n = 10,206$ , orange circle), slow intermittent running ( $n = 1701$ , grey diamond), and fast intermittent running ( $n = 1701$ , black cross). Whiskers indicate confidence intervals based on the estimation error of our heat exchange model (see Methods section 2.5). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

simulated gaits (Fig. 4B, C). Therefore, we only present the results for hunts of low-sweating and nonsweating prey. Walking was the least successful gait for the simulated persistence hunting of low-sweating and nonsweating prey followed by slow intermittent running, running, and fast intermittent running. Prey size had little effect on the success rate of the simulated persistence hunts of low-sweating prey (42% for a 100-kg prey, 41% for a 250-kg prey, and 38% for a 400-kg prey). In nonsweating prey, the success rate was lower in the 100-kg prey (57%) compared to the remaining 250-kg and 400-kg prey (79% and 82%, respectively).

The velocity of the hunter affected the success rate of simulated persistence hunts (Fig. 5). The success rate of simulated hunting low-sweating prey increased nonlinearly with velocity (Fig. 5A) from 9–15% (depending on prey size) at the hunter's velocity of  $1 \text{ m s}^{-1}$  up to 68–72% at the hunter's velocity of  $4.5 \text{ m s}^{-1}$ . The greatest increase in success rate (compared to success rate at the previous simulated velocity) was observed just above the prey's preferred walking (9–18% increase) and trotting (18–37% increase) speed. Persistence

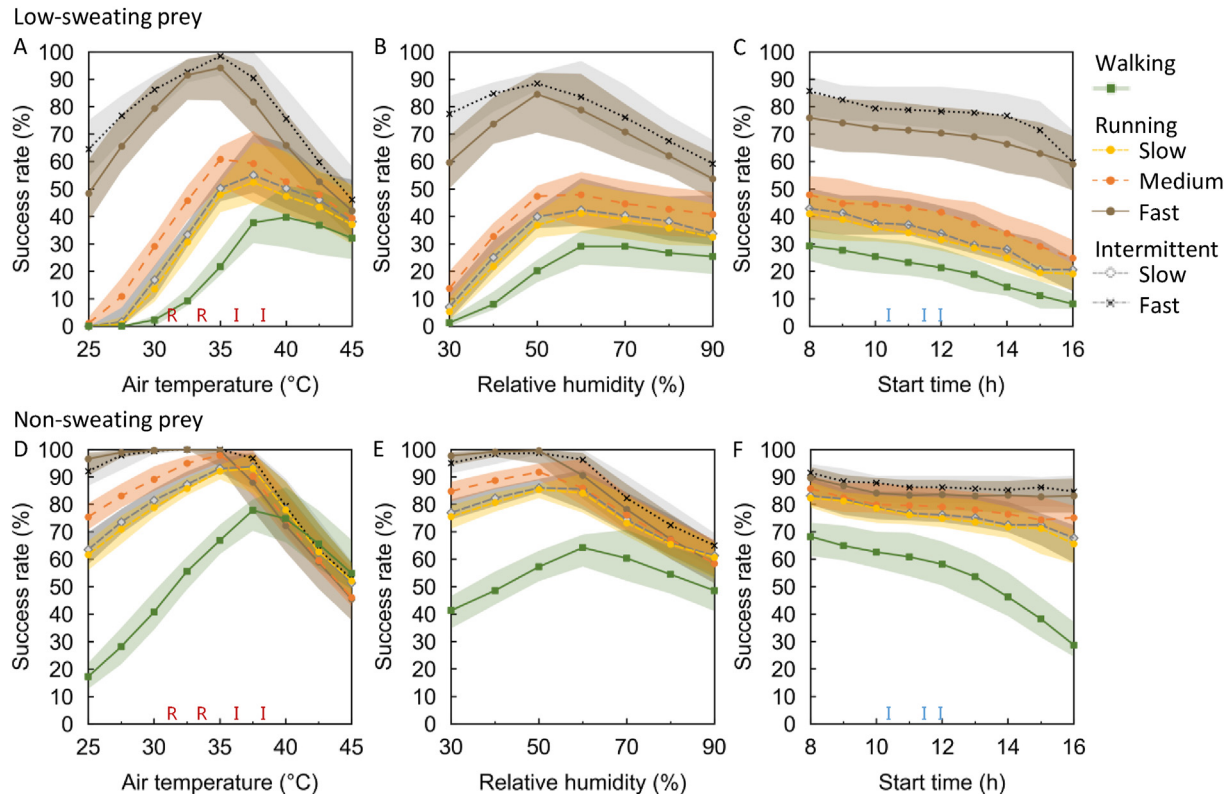
hunting of all sizes of the low-sweating prey was most successful at a velocity just above the prey's range of preferred trotting speed (success rate: 68–72%), which corresponded to the hunter's fast running ( $4.5 \text{ m s}^{-1}$ ). Nevertheless, medium to very large low-sweating prey could be hunted across all simulated velocities including the preferred velocities of the prey. The success rate of simulated hunting a 100-kg nonsweating prey increased almost linearly with velocity (Fig. 5B) from 19% to 83% between the hunter's velocity of  $1 \text{ m s}^{-1}$  and  $4.5 \text{ m s}^{-1}$ . For 250-kg and 400-kg nonsweating prey, the success rate increased with velocity only within the walking gait and remained relatively constant throughout the running velocities (Fig. 5B).

Environmental factors and the start time of the hunt affected the success of simulated persistence hunts for low-sweating and nonsweating prey (Fig. 6). Walking was most successful at high air temperature ( $37.5\text{--}40 \text{ }^\circ\text{C}$ ; Fig. 6A, D) and high relative humidity (60–70%; Fig. 6B, E). Running and intermittent running were generally most successful at lower temperature ( $32.5\text{--}37.5 \text{ }^\circ\text{C}$ ) and



**Figure 5.** Effect of velocity on the success rate of simulated persistence hunts for medium (blue triangles, dotted line), large (grey circles, dashed line), and very large (black diamonds, solid line) low-sweating (A) and non-sweating (B) prey. Open symbols indicate velocities that fall into the range of the preferred velocities of the prey. Shaded areas indicate confidence intervals based on the estimation error of our heat exchange model (see Methods). For each combination of prey size and velocity:  $n = 567$ . The average velocities of three successful hunts of kudu ( $\sim 230 \text{ kg}$ ) in the Kalahari (red letters: R, running, I, intermittent running; Liebenberg, 2006) are shown for comparison. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)





**Figure 6.** Effect of daily maximum air temperature (A, D), daily average relative humidity (B, E), and start time (C, F) on the success of simulated persistence hunts by walking ( $n = 5103$ ; green square), slow running ( $n = 3402$ ; yellow circle), medium running ( $n = 3402$ ; orange circle), fast running ( $n = 3402$ ; brown circle), and slow ( $n = 1701$ ; grey diamond) and fast ( $n = 1701$ ; black cross) intermittent running. Shaded areas indicate confidence intervals based on the estimation error of our heat exchange model (see Methods). The daily maximum air temperature for four successful (red letters: R, running, I, intermittent running) and start time for five failed (blue letters) hunts of kudu in Kalahari (Liebenberg, 2006; Hora et al., 2020) is shown for comparison (start times for successful hunts were not published). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

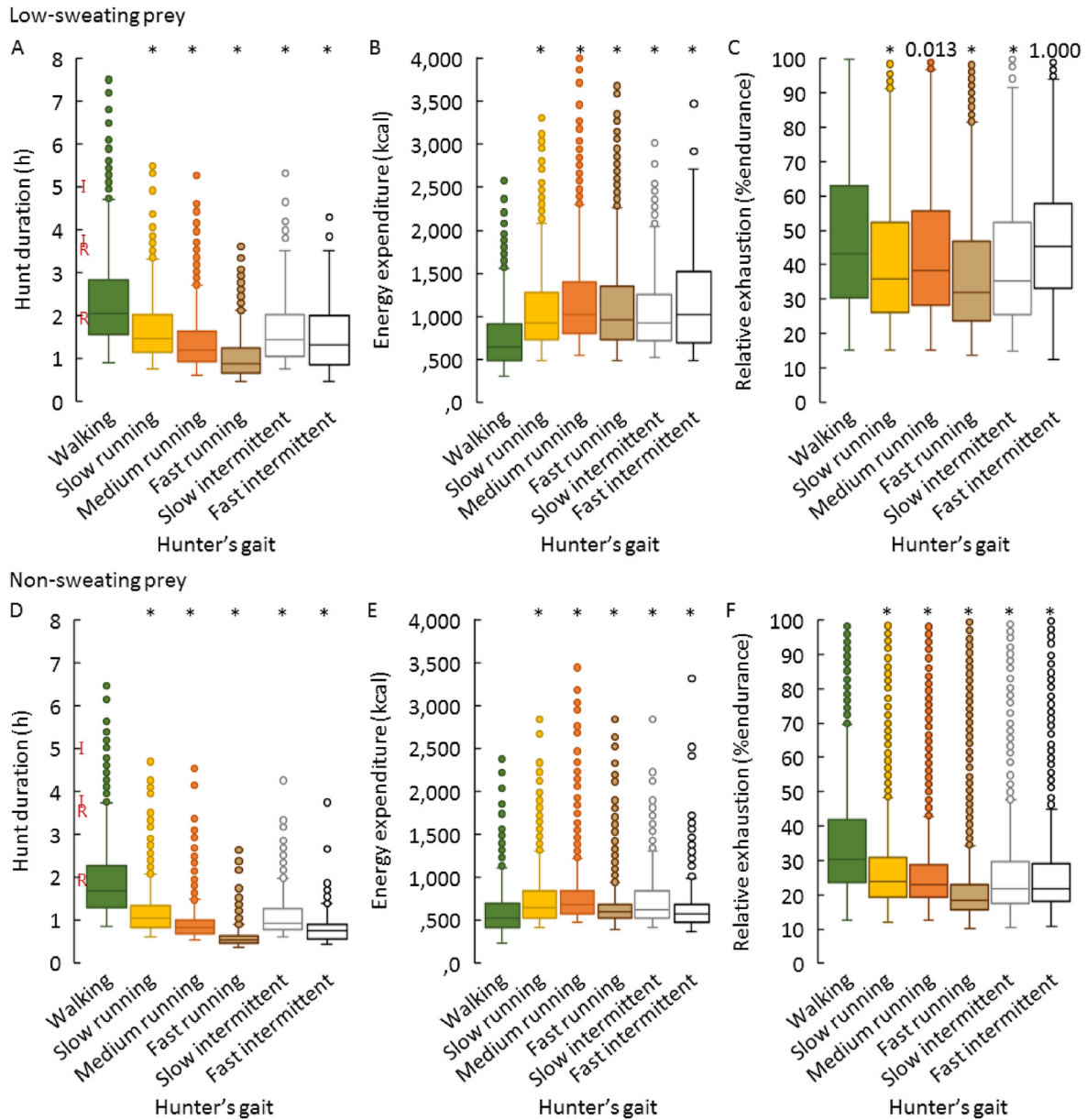
lower humidity (50–60%) than walking and the optimal temperature and humidity were inversely related to running velocity (Fig. 6A, B, D, E). At high air temperatures ( $>37.5$  °C), the success rate of the simulated walking hunts approached (low-sweating prey) and even overlapped with (nonsweating prey) running hunts. Similarly, at high humidity ( $>50\%$ ), the success rate of the simulated walking hunts was closest to running hunts. Walking was the only successful gait in hot humid conditions (SOM Figs. S1 and S2). By contrast, running and intermittent running were the only successful gaits in cold dry conditions (SOM Figs. S1 and S2). The success rate of simulated persistence hunts decreased with starting time regardless of the hunter's gait (Fig. 6C, F).

Differences in hunt duration, energy expenditure of the hunter, and relative exhaustion of the hunter in successful simulated hunts for low- and nonsweating prey by walking, running, and intermittent running are shown in Figure 7. The hunt duration was greater for walking than running (low sweating prey median: 2.1 h vs. 1.1 h,  $U = 769,875$ ,  $p < 0.001$ ; nonsweating prey: 1.7 vs. 0.8 h,  $U = 1,838,484$ ,  $p < 0.001$ ), and it decreased with velocity (Fig. 7A, D). Walking hunt duration was also greater compared to intermittent running. Successful simulated hunts by walking resulted in lower energy expenditure than by running (low sweating prey: 644 kcal vs. 973 kcal,  $U = 1,176,070$ ,  $p < 0.001$ ; nonsweating prey: 523 vs. 638 kcal,  $U = 6,965,636$ ,  $p < 0.001$ ), especially due to the high costs of hunts by medium running (Fig. 4B, E). Energy expenditure of walking hunts was also lower in comparison to hunts by slow and fast intermittent running. Relative exhaustion of the hunter at the end of the hunt was higher for walking than for running (low sweating prey: 43% vs. 35%,  $U = 867,718$ ,  $p < 0.001$ ;

nonsweating prey: 30% vs. 21%,  $U = 2,456,204$ ,  $p < 0.001$ ). Relative exhaustion of the hunter for walking was also higher than for intermittent running except for the fast intermittent running in low-sweating prey (Fig. 7C, F).

The results of our sensitivity analyses are shown in Table 2. The body size and shape of the hunter had relatively low effect on our results. A hunter of 50 kg body mass, 160 cm stature, and 300 kg  $\text{cm}^{-2}$  relative body surface area hunting for a low-sweating prey had simulated hunting success rate 1% higher for walking and 2% higher for running compared to the KNM-WT 15000-sized model (76.7 kg, 178 cm, 254 kg  $\text{cm}^{-2}$ ). Setting of the hyperthermia threshold of the hunter to 40 °C (compared to the original 41 °C) decreased the overall hunting success rate for low sweating prey by 4% for walking and by 7% for running, i.e., the hunts at higher velocities would be more affected by the threshold change. Our simulations were relatively robust to setting of the dehydration threshold. Lowering the dehydration threshold from 10% to 7.5% of body mass decreased the simulated hunting success rate for low-sweating prey by 1% for walking and by 2% for running; further lowering of the threshold to 5% of body mass decreased the success rate by 3% for walking and by 7% for running. Our results changed little when 100 m (instead of 1000 m) was used as the difference between the maximum and minimum safe distance: the overall hunting success rate for low-sweating prey decreased by 2% for walking and did not change for running.

Our simulations of the persistence hunting of a 20-kg duiker had 50% success rate for walking and 90% success rate for running (Table 2). The simulated success rate increased with velocity across both gaits (SOM Figs. S3). Success rate was also strongly positively



**Figure 7.** Hunt duration (A, D), energy expenditure of the hunter (B, E), and relative exhaustion of the hunter (C, F) for successful simulated persistence hunts of low-sweating (A–C) and non-sweating (D–F) prey (walking:  $n_{(A),(B)} = 1018$ ,  $n_{(C)} = 558$ ,  $n_{(D),(E)} = 2731$ ,  $n_{(F)} = 1346$ , slow running:  $n_{(A),(B)} = 1032$ ,  $n_{(C)} = 809$ ,  $n_{(D),(E)} = 2552$ ,  $n_{(F)} = 1823$ , medium running:  $n_{(A),(B)} = 1311$ ,  $n_{(C)} = 1115$ ,  $n_{(D),(E)} = 2687$ ,  $n_{(F)} = 2149$ , fast running:  $n_{(A),(B)} = 2349$ ,  $n_{(C)} = 2063$ ,  $n_{(D),(E)} = 2872$ ,  $n_{(F)} = 2485$ , slow intermittent running:  $n_{(A),(B)} = 551$ ,  $n_{(C)} = 431$ ,  $n_{(D),(E)} = 1294$ ,  $n_{(F)} = 913$ , fast intermittent running:  $n_{(A),(B)} = 1305$ ,  $n_{(C)} = 1039$ ,  $n_{(D),(E)} = 1478$ ,  $n_{(F)} = 1149$ ). Multiple comparisons of mean ranks *p*-values (two-tailed) for difference from walking are presented above each plot (\*,  $p < 0.001$ ). Horizontal line: median; boxes: interquartile range; whiskers: minimum–maximum excluding outliers; circles: outliers  $> 1.5$  times the interquartile range beyond the box. The hunt duration of four successful hunts of kudu in the Kalahari (red letters: R, running, I, intermittent running; Liebenberg, 2006) is shown for comparison. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

**Table 2**  
Success rate (%) for simulated persistence hunts.

Prey model	Walking	Running	Slow intermittent	Fast intermittent
Model alteration				
High sweating	0.8	0.0	0.0	11.8
Low sweating	19.9	46.0	32.4	76.7
Small hunter	20.6	48.3	34.6	78.6
40 °C threshold	15.6	38.9	26.9	40.4
7.5 %BM threshold	19.3	44.4	31.2	74.1
5 %BM threshold	16.7	39.2	26.9	61.1
100 m	18.0	46.2	28.6	58.1
Nonsweating	53.5	79.5	76.1	86.9
Duiker	50.2	90.4	81.7	98.8

BM, body mass.

related to air temperature and relative humidity (SOM Figs. S4). For example, the success rate of simulated walking hunts increased linearly from 2% at 25 °C to 94% at 45 °C. The median duration of the simulated hunts for the duiker by walking was 0.65 h (minimum: 0.2 h, maximum: 5.2 h).

#### 4. Discussion and conclusions

Walking was simulated here as a successful gait for persistence hunting, especially in hot and humid conditions, although it was generally less successful than running. Both walking and running were successful in the simulated persistence hunting of medium to very large low-sweating and nonsweating prey across a wide range of ambient conditions. Compared to running and intermittent

running, walking yielded a 30–74% lower success rates, simulated successful hunts by walking were twice as long, and resulted in greater relative exhaustion of the hunter, but had 10–30% lower energy expenditure.

Results from our hunting simulations were consistent with the ethnographic observation of persistence hunting by running. The hunt durations estimated by our model matched well the reported hunts performed using running (one hunt reported by Liebenberg, 2006, took less than 2 h which corresponds to our median hunt duration for low-sweating prey using slow running: 1.5 h; the other hunt took 3.5 h which is within our range for slow running; Fig. 7A) but were lower than two reported hunts performed by slow intermittent running (although both were within the range of our simulations of low-sweating prey and one within the range estimated for the nonsweating prey; Fig. 7A, D). This could be due to a large proportion of running in our intermittent running simulations compared to real hunts in which the hunter is often forced to walk due to tracking difficulties (Liebenberg, 2006; Lieberman et al., 2020). Our simulations were compatible with the single persistence hunt by walking reported in detail for a 20-kg duiker (Pickering and Bunn, 2007). Our model predicted a 50% success rate for persistence hunting for duiker by walking with a higher success rate at air temperatures above 35 °C. The 3-h duration of the hunt reported by Pickering and Bunn (2007) was greater than the median duration (0.65 h, but well below the maximum duration of 5.2 h) of the successful hunts simulated here which was to be expected. In our simulations, the hunter walked at a constant pace, never losing the trail, whereas Pickering and Bunn (2007) reported that the real hunter was often slowed down by tracks of other animals. Although our simulation supported the applicability of the persistence hunting by walking for small prey such as a duiker, it also indicated that the success rate would be almost twice as high if the hunter used running.

The lack of successful hunts for high-sweating prey in our simulations is inconsistent with the records of few persistence hunts of zebra (Schapera, 1934) and horse (Lieberman et al., 2020) and of human runners who often beat some horses in races (Lieberman, 2020). However, in contrast to our simulations, modern hunters rehydrate during the persistence hunt (Liebenberg, 2006; Lieberman et al., 2020), and might improve their chances by working in groups and focusing on disadvantaged (e.g., injured, pregnant) animals as suggested for other persistence hunted prey species (Liebenberg, 2006; Lieberman et al., 2020). Similarly, human racers also rehydrate during the race and compete against horses whose metabolic heat production is increased by the weight of the carried rider.

Simulated persistence hunts were most successful in hot conditions, which fits well with ethnographic reports (Bartram et al., 1991; Liebenberg, 2006). Yet, our simulations resulted in successful hunts at all simulated temperatures (25–45 °C) which agrees with ethnographic sources indicating that persistence hunting has been performed throughout the year in both winter and summer and in both dry and wet seasons (Liebenberg, 2006; Lieberman et al., 2020). The facilitative effect of high air temperature for hunting at slower velocities has indirect support in ethnography. The two reported successful hunts in the Kalahari (Liebenberg, 2006), which were accomplished by slow intermittent running (average velocity  $<2 \text{ m s}^{-1}$ ), were performed on hotter days (by about 5 °C) compared to the hunts performed entirely at a slow running velocity ( $>2.5 \text{ m s}^{-1}$ ; Fig. 6A, D; Hora et al., 2020).

The success rate of simulated persistence hunting was highest in the morning and decreased throughout the day, which may be due to the increasing proportion of hunts terminated by sunset. Sunset terminated 4% of the simulated hunts that started at 8 AM compared to 64% of hunts that started at 4 PM. In agreement with

our results, Tarahumara hunters were reported to start the persistence hunts early in the morning (Levi, 2020; Lieberman et al., 2020). Although the timing of the actual pursuit might be later in the day (e.g., Liebenberg, 2006 reported start times of three failed pursuits between 10:30 AM and noon), the delay could be explained by the fact that some time needs to be allocated to finding a promising track before one can start the pursuit. The success of the morning persistence hunts could be further enhanced due to better visibility of the tracks under the morning sun, which casts longer shadows (Liebenberg, 1990), but this aspect was not considered in our simulations.

Future studies should validate our simulation results with ethnographic and experimental data. The implication of our simulations that persistence hunting by walking should be successful across wide ranges of ambient conditions and prey currently contrasts with the ethnographic literature that, to our knowledge, describes persistence hunting by walking only in Kua San in Kalahari (Pickering and Bunn, 2007). Pickering and Bunn (2007) reported that persistence hunting by walking was used by Kua San primarily for small prey represented most often by duiker and steenbok but also for large prey such as greater kudu. Nevertheless, the only witnessed hunt by walking described in detail is successful pursuit of a duiker (Pickering and Bunn, 2007). Bartram and colleagues reported that one of the three hunting techniques used by Kua San in the hot dry season is “walking animals to death, with or without dogs” (Bartram et al., 1991: 99). They specified that in this season, hunters obtained generally small animals (principally duiker, steenbok, and springhare) partly due to absence of several large migratory species and lower availability of arrow poison (Bartram et al., 1991). Further detailed description of the pursuit hunting without dogs in Bartram et al. (1991) is however not specific about gait used during pursuits, so it is not clear if hunts were performed entirely by walking or included some running. In contrast, other ethnographic reports of persistence hunting in Kalahari and elsewhere include running (Sollas, 1911; Lowie, 1924; Schapera, 1930; Steyn 1984; Liebenberg, 1990, 2006; Lieberman et al., 2020).

The shortcomings of pursuit by walking identified in our simulations (i.e., lower success rate, greater duration of the hunt, and greater relative exhaustion of the hunter) could explain why there is not a single direct description of persistence hunting for large prey exclusively by walking in modern hunter ethnographies. Modern humans adapted to long-distance running in hot environments (Bramble and Lieberman, 2004; Hora et al., 2020) might prefer running, or a mixture of running and walking, over exclusive walking in persistence hunting to maximize chances and save time at the cost of higher energy expenditure which would be repaid many times if the hunt was successful (Lieberman et al., 2007; Glaub and Hall, 2017). Moreover, in some environments such as in Kalahari, the success of persistence hunting by walking could be lowered due to sandy substrate. It has been shown that sandy substrate increases the cost of transport more for walking compared to running (Lejeune et al., 1998). As a result, the walk-to-run transition on sand would be shifted to lower velocities and consequently the hunter might use walking only at slow velocities that were shown in our simulations to yield the lowest success rates. Nevertheless, our simulations suggest that running may not be a persistence hunting prerequisite, and that persistence hunting could also be viable for hominins who did not possess the endurance-running phenotype of the proposed first persistence hunter, *H. erectus* (Lieberman et al., 2009). Our estimates of the relative exhaustion of the hunter at the end of the hunt (Fig. 7C, F) suggest that the derived thermoregulatory capacity of modern humans would not have been necessary at the origin of persistence hunting. Even hominins with 50% of the modern human endurance

would accomplish over half of the successful hunts by walking simulated here for the modern hunter. Yet, we expect strong selection pressure for the endurance running phenotype, as the ability to run for at least part of the hunt would allow for making up delays due to tracking difficulties. Running would thus make persistence hunting a more reliable strategy with a higher success rate.

Our simulation results provide a plausible scenario for the evolution of persistence hunting behaviors. The hot (Passey et al., 2010) and generally more humid climate with periodic phases of extreme wetness (Levin et al., 2004; Wynn, 2004; Deino et al., 2006; Trauth et al., 2007) of the Pliocene and Early Pleistocene East Africa might have provided opportunities for early *Homo* or late australopithecines (already accustomed to scavenging; Thompson et al., 2019; Pobiner, 2020) to walk down prey. Successful persistence hunting by walking requires prolonged locomotion (0.8–7.5 h as simulated here, 3 h recorded for small prey by modern Kalahari hunters; Pickering and Bunn, 2007) and would thus select for locomotor endurance, perhaps along with foraging in habitats with sparsely distributed resources (Isbell et al., 1998; Lieberman, 2015) or with the adoption of a central place provisioning strategy in which food is taken back to a central place (Marlowe, 2010). Besides selection for covering long distances, persistence hunting by walking would select for higher walking velocity that, as we simulated here, should increase the success rate of pushing the prey to exhaustion. Faster walking speeds would also allow hunters to recover from delays due to tracking difficulties. Persistence hunting by walking could thus partially pre-adapt hominins for slow endurance running through selection for greater aerobic capacity, volume of muscle mitochondria, and non-gait-specific locomotor economy (e.g., longer limbs), which would allow for higher walking velocities, and for greater heat loss capacity that would be particularly needed in hot habitats in which walking yielded the highest success rates in our simulations.

Persistence hunting by walking provides a plausible alternative to scenarios suggested by Carrier (1984) and Bramble and Lieberman (2004) for the evolution of endurance running. Carrier (1984) argued that hominins first used running to pursue less cursorial prey like hares and small artiodactyls and gradually built running endurance by targeting more athletic species. According to Bramble and Lieberman (2004) and Lieberman (2015), endurance running might have initially evolved with scavenging as an advantage in competition with other scavengers. Instead, the results of our simulations offer up an alternative possible scenario that hominins started pursuing animals using walking—a familiar gait already used for prolonged locomotion, to which they would be already well adapted—and gradually incorporated longer and more frequent periods of running. Incorporation of running would result in selection for further increase in aerobic capacity and, as summarized by Bramble and Lieberman (2004), in heat dissipation capacity and new selection pressures for running economy. Adoption of endurance running might then increase the success of persistence hunts, especially under more demanding tracking conditions and in colder environments. Thus, persistence hunting could select for both long-distance walking and endurance running and could have contributed to the evolution of locomotor endurance seen in modern humans.

### Conflict of interest

There is no conflict of interest.

### Acknowledgments

This work was supported by the Czech Science Foundation, grant number 18-16287S. M.H. has been supported by Czech

Fulbright Commission and Charles University Research Centre program No. 204069. We thank attendees of the Annual Meeting of the American Association of Physical Anthropologists 2019 in Cleveland for their feedback and our participants and members of the Bone Tissue Anthropology Lab at Charles University for their help with the validation study.

### Supplementary Online Material

Supplementary online material related to this article can be found at <https://doi.org/10.1016/j.jhevol.2022.103247>.

### References

- Adolph, E.F. (Ed.), 1947. *Physiology of Man in the Desert*. Interscience Publishers, New York.
- Alexander, R.M.N., Jayes, A.S., Maloij, G.M.O., Wathuta, E.M., 1981. Allometry of the leg muscles of mammals. *J. Zool.* 194, 539–552.
- Bartram, L.E., Kroll, E.M., Bunn, H.T., 1991. Variability in camp structure and bone food refuse patterning at Kua San Hunter-Gatherer camps. In: Kroll, E.M., Price, T.D. (Eds.), *The Interpretation of Archaeological Spatial Patterning*. Springer US, Boston, pp. 77–148.
- Bassett, D.R., Howley, E.T., 2000. Limiting factors for maximum oxygen uptake and determinants of endurance performance. *Med. Sci. Sports Exerc.* 32, 70–84.
- Beis, L.Y., Wright-Whyte, M., Fudge, B., Noakes, T., Pitsiladis, Y.P., 2012. Drinking behaviors of elite male runners during marathon competition. *Clin. J. Sport Med.* 22, 254–261.
- Bell, A.W., Hales, J.R., King, R.B., Fawcett, A.A., 1983. Influence of heat stress on exercise-induced changes in regional blood flow in sheep. *J. Appl. Physiol.* 55, 1916–1923.
- Bergmann, C., 1848. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Größe. Vandenhoeck and Ruprecht, Göttingen.
- Brace, C.L., Montagu, M.A., 1965. *Man's Evolution: An Introduction to Physical Anthropology*. The Macmillan Company, New York.
- Bramble, D.M., Lieberman, D.E., 2004. Endurance running and the evolution of *Homo*. *Nature* 432, 345–352.
- Bullard, R.W., Dill, D.B., Yousef, M.K., 1970. Responses of the burro to desert heat stress. *J. Appl. Physiol.* 29, 159–167.
- Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania [and comments and reply]. *Curr. Anthropol.* 27, 431–452.
- Carrier, D.R., 1984. The energetic paradox of human running and hominid evolution. *Curr. Anthropol.* 25, 483–495.
- Che Muhamed, A.M., Atkins, K., Stannard, S.R., Mündel, T., Thompson, M.W., 2016. The effects of a systematic increase in relative humidity on thermoregulatory and circulatory responses during prolonged running exercise in the heat. *Temperature* 3, 455–464.
- Conley, D.L., Krahenbuhl, G.S., 1980. Running economy and distance running performance of highly trained athletes. *Med. Sci. Sports Exerc.* 12, 357–360.
- Daniels, J., Daniels, N., 1992. Running economy of elite male and elite female runners. *Med. Sci. Sports Exerc.* 24, 483–489.
- Dawson, T., Robertshaw, D., Taylor, C., 1974. Sweating in the kangaroo: A cooling mechanism during exercise, but not in the heat. *Am. J. Physiol.* 227, 494–498.
- Deino, A.L., Kingston, J.D., Glen, J.M., Edgar, R.K., Hill, A., 2006. Precessional forcing of lacustrine sedimentation in the late Cenozoic Chemon Basin, Central Kenya Rift, and calibration of the Gauss/Matuyama boundary. *Earth Planet Sci. Lett.* 247, 41–60.
- Dmi'el, R., Robertshaw, D., Choshniak, I., 1979. Sweat gland secretion in the black bedouin goat. *Physiol. Zool.* 52, 558–564.
- Donnelly, J.E., Blair, S.N., Jakicic, J.M., Manore, M.M., Rankin, J.W., Smith, B.K., 2009. Appropriate physical activity intervention strategies for weight loss and prevention of weight regain for adults. *Med. Sci. Sports Exerc.* 41, 459–471.
- Ely, B.R., Ely, M.R., Cheuvront, S.N., Kenefick, R.W., DeGroot, D.W., Montain, S.J., 2009. Evidence against a 40°C core temperature threshold for fatigue in humans. *J. Appl. Physiol.* 107, 1519–1525.
- Entin, P.L., Robertshaw, D., Rawson, R.E., 1998. Thermal drive contributes to hyperventilation during exercise in sheep. *J. Appl. Physiol.* 85, 318–325.
- Entin, P.L., Robertshaw, D., Rawson, R.E., 1999. Effect of locomotor respiratory coupling on respiratory evaporative heat loss in the sheep. *J. Appl. Physiol.* 87, 1887–1893.
- Evans, C.L., Smith, D.F.G., Weil-Malherbe, H., 1956. The relation between sweating and the catechol content of the blood in the horse. *J. Physiol.* 132, 542–552.
- Farkaš, R., 2015. Apocrine secretion: New insights into an old phenomenon. *Biochim. Biophys. Acta* 1850, 1740–1750.
- Fiala, D., Lomas, K.J., Stohrer, M., 2001. Computer prediction of human thermoregulatory and temperature responses to a wide range of environmental conditions. *Int. J. Biometeorol.* 45, 143–159.
- Finch, V., 1972. Thermoregulation and heat balance of the East African eland and hartebeest. *Am. J. Physiol.* 222, 1374–1379.

- Geor, R.J., McCutcheon, L.J., Ecker, G.L., Lindinger, M.I., 1995. Thermal and cardio-respiratory responses of horses to submaximal exercise under hot and humid conditions. *Equine Vet. J.* 27, 125–132.
- Geor, R.J., McCutcheon, L.J., Ecker, G.L., Lindinger, M.I., 2000. Heat storage in horses during submaximal exercise before and after humid heat acclimation. *J. Appl. Physiol.* 89, 2283–2293.
- Glaub, M., Hall, C.A., 2017. Evolutionary implications of persistence hunting: An examination of energy return on investment for !Kung hunting. *Hum. Ecol.* 45, 393–401.
- Grandin, T., 2019. Behavioural principles of handling beef cattle and the design of corrals, lairages, races and loading ramps. In: Grandin, T. (Ed.), *Livestock Handling and Transport*. CABI, Wallingford, pp. 80–109.
- Guadalupe-Grau, A., Fuentes, T., Guerra, B., Calbet, J.A.L., 2009. Exercise and bone mass in adults. *Sports Med.* 39, 439–468.
- Hales, J.R.S., Findlay, J.D., 1968. Respiration of the ox: Normal values and the effects of exposure to hot environments. *Respir. Physiol.* 4, 333–352.
- Haslam, R.A., Parsons, K.C., 1994. Using computer-based models for predicting human thermal responses to hot and cold environments. *Ergonomics* 37, 399–416.
- Hiernaux, J., Hartono, D.B., 1980. Physical measurements of the adult Hadza of Tanzania. *Ann. Hum. Biol.* 7, 339–346.
- Hodgson, D.R., McCutcheon, L.J., Byrd, S.K., Brown, W.S., Bayly, W.M., Brengelmann, G.L., Gollnick, P.D., 1993. Dissipation of metabolic heat in the horse during exercise. *J. Appl. Physiol.* 74, 1161–1170.
- Hofmeyr, M.D., 1985. Thermal properties of the pelages of selected African ungulates. *Afr. Zool.* 20, 179–189.
- Holloszy, J.O., Coyle, E.F., 1984. Adaptations of skeletal muscle to endurance exercise and their metabolic consequences. *J. Appl. Physiol.* 56, 831–838.
- Hoppeler, H., Lüthi, P., Claassen, H., Weibel, E.R., Howald, H., 1973. The ultrastructure of the normal human skeletal muscle. *Pflügers Arch.* 344, 217–232.
- Hora, M., Pontzer, H., Wall-Scheffler, C.M., Sládek, V., 2020. Dehydration and persistence hunting in *Homo erectus*. *J. Hum. Evol.* 138, 102682.
- Hoyt, D.F., Taylor, C.R., 1981. Gait and the energetics of locomotion in horses. *Nature* 292, 239–240.
- Hreljac, A., 1993. Preferred and energetically optimal gait transition speeds in human locomotion. *Med. Sci. Sports Exerc.* 25, 1158–1162.
- Hutchinson, A., 2018. *Endure: Mind, Body, and the Curiously Elastic Limits of Human Performance*, 1st ed. Harper Collins, New York.
- Ingram, D.L., 1965. Evaporative cooling in the pig. *Nature* 207, 415–416.
- Isbell, L.A., Pruett, J.D., Lewis, M., Young, T.P., 1998. Locomotor activity differences between sympatric patas monkeys (*Erythrocebus patas*) and vervet monkeys (*Cercopithecus aethiops*): Implications for the evolution of long hindlimb length in *Homo*. *Am. J. Phys. Anthropol.* 105, 199–207.
- Jack, A., 2010. Einfluss hoch funktioneller sporttextilien auf die thermoregulation von ausdauerathleten bei unterschiedlichen umgebungstemperaturen. Ph.D. dissertation, University of Bayreuth.
- Jeppesen, J.L., 1987. Impact of human disturbance on home range, movements and activity of red deer (*Cervus elaphus*) in a Danish environment. *Dan. Rev. Game Biol.* 13, 1–38.
- Keymer, I.F., Garnham, P.C.C., 1969. Investigations on the Duiker (*Sylvicapra grimmia*) and its blood protozoa in Central Africa. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 255, 33–108.
- Kingston, J.K., Geor, R.J., McCutcheon, L.J., 1997. Rate and composition of sweat fluid losses are unaltered by hypohydration during prolonged exercise in horses. *J. Appl. Physiol.* 83, 1133–1143.
- Kirchengast, S., 2000. Differential reproductive success and body size in !Kung San people from northern Namibia. *Coll. Anthropol.* 24, 121–132.
- Knapp, B.J., Robinson, K.W., 1954. The role of water for heat dissipation by a Jersey cow and a Corriedale ewe. *Aust. J. Agric. Res.* 5, 568–577.
- Lee, J.K.W., Nio, A.Q.X., Lim, C.L., Teo, E.Y.N., Byrne, C., 2010. Thermoregulation, pacing and fluid balance during mass participation distance running in a warm and humid environment. *Eur. J. Appl. Physiol.* 109, 887–898.
- Lejeune, T.M., Willems, P.A., Heglund, N.C., 1998. Mechanics and energetics of human locomotion on sand. *J. Exp. Biol.* 201, 2071–2080.
- Levi, J.M., 2020. Comment on: Running in Tarahumara (Rarámuri) culture: Persistence hunting, footracing, dancing, work, and the fallacy of the athletic savage. *Curr. Anthropol.* 61, 369–370.
- Levin, N.E., Quade, J., Simpson, S.W., Semaw, S., Rogers, M., 2004. Isotopic evidence for Plio–Pleistocene environmental change at Gona, Ethiopia. *Earth Planet Sci. Lett.* 219, 93–110.
- Liebenberg, L., 1990. *The Art of Tracking: The Origin of Science*. David Philip Publishers, Claremont.
- Liebenberg, L., 2006. Persistence hunting by modern hunter-gatherers. *Curr. Anthropol.* 47, 1017–1026.
- Lieberman, D., 2020. *Exercised: Why Something We Never Evolved to Do Is Healthy and Rewarding*. Pantheon Books, New York.
- Lieberman, D.E., 2015. Human locomotion and heat loss: An evolutionary perspective. *Compr. Physiol.* 5, 99–117.
- Lieberman, D.E., Bramble, D.M., Raichlen, D.A., Shea, J.J., 2007. The evolution of endurance running and the tyranny of ethnography: A reply to Pickering and Bunn (2007). *J. Hum. Evol.* 53, 439–442.
- Lieberman, D.E., Bramble, D.M., Raichlen, D.A., Shea, J.J., 2009. Brains, brawn, and the evolution of human endurance running capabilities. In: Grine, F.E., Fleagle, J.G., Leakey, R.E. (Eds.), *The First Humans: Origin and Early Evolution of the Genus Homo*. Springer, Dordrecht, pp. 77–92.
- Lieberman, D.E., Mahaffey, M., Cubesare Quimare, S., Holowka, N.B., Wallace, I.J., Baggish, A.L., 2020. Running in Tarahumara (Rarámuri) culture: Persistence hunting, footracing, dancing, work, and the fallacy of the athletic savage. *Curr. Anthropol.* 61, 356–379.
- Lindinger, M.I., 1999. Exercise in the heat: Thermoregulatory limitations to performance in humans and horses. *Can. J. Appl. Physiol.* 24, 152–163.
- Longman, D.P., Murray, A., Roberts, R., Oakley, S., Wells, J.C.K., Stock, J.T., 2021. Energetics as a driver of human morphological thermal adaptation; evidence from female ultra-endurance athletes. *Evol. Hum. Sci.* 3, e22.
- Longman, D.P., Murray, A.M., Roberts, R., Oakley, S., Wells, J.C.K., Stock, J.T., 2019. Ultra-endurance athletic performance suggests that energetics drive human morphological thermal adaptation. *Evol. Hum. Sci.* 1, e16.
- Lowie, R.H., 1924. *Notes on Shoshonean Ethnography*. American Museum Press, New York.
- Marino, F.E., Lambert, M.I., Noakes, T.D., 2004. Superior performance of African runners in warm humid but not in cool environmental conditions. *J. Appl. Physiol.* 96, 124–130.
- Marlin, D.J., Scott, C.M., Schroter, R.C., Mills, P.C., Harris, R.C., Harris, P.A., Orme, C.E., Roberts, C.A., Marr, C.M., Dyson, S.J., Barrelet, F., 1996. Physiological responses in nonheat acclimated horses performing treadmill exercise in cool (20°C/40%RH), hot dry (30°C/40%RH) and hot humid (30°C/80%RH) conditions. *Equine Vet. J.* 28, 70–84.
- Marlin, D.J., Scott, C.M., Schroter, R.C., Harris, R.C., Harris, P.A., Roberts, C.A., Mills, P.C., 1999. Physiological responses of horses to a treadmill simulated speed and endurance test in high heat and humidity before and after humid heat acclimation. *Equine Vet. J.* 31, 31–42.
- Marlowe, F., 2010. *The Hadza: Hunter-gatherers of Tanzania*. University of California Press, Berkeley.
- Martinez, N., Psikuta, A., Kuklane, K., Priego Quesada, J.I., Cibrián Ortiz de Anda, R.M., Soriano, P.P., Palmer, R.S., Corberán, J.M., Rossi, R.M., Anaheim, S., 2016. Validation of the thermophysiological model by Fiala for prediction of local skin temperatures. *Int. J. Biometeorol.* 60, 1969–1982.
- Mattson, M.P., 2012. Energy intake and exercise as determinants of brain health and vulnerability to injury and disease. *Cell Metabol.* 16, 706–722.
- Maughan, R.J., Otani, H., Watson, P., 2012. Influence of relative humidity on prolonged exercise capacity in a warm environment. *Eur. J. Appl. Physiol.* 112, 2313–2321.
- McCutcheon, L.J., Geor, R.J., 1996. Sweat fluid and ion losses in horses during training and competition in cool vs. hot ambient conditions: Implications for ion supplementation. *Equine Vet. J. Suppl.* 54–62.
- McLean, J.A., 1963. Measurement of cutaneous moisture vaporization from cattle by ventilated capsules. *J. Physiol.* 167, 417–426.
- Minetti, A.E., Ardigo, L.P., Reinach, E., Saibene, F., 1999. The relationship between mechanical work and energy expenditure of locomotion in horses. *J. Exp. Biol.* 202, 2329–2338.
- Mitchell, D., Senay, L.C., Wyndham, C.H., van Rensburg, A.J., Rogers, G.G., Strýdom, N.B., 1976. Acclimatization in a hot, humid environment: Energy exchange, body temperature, and sweating. *J. Appl. Physiol.* 40, 768–778.
- Montagu, A., 1964. Natural selection and man's relative hairlessness. *JAMA* 187, 356–357.
- Morris, J.N., Heady, J.A., Raffle, P.A.B., Roberts, C.G., Parks, J.W., 1953. Coronary heart-disease and physical activity of work. *Lancet* 6796, 1111–1120.
- Moyen, N.E., Ellis, C.L.V., Ciccone, A.B., Thurston, T.S., Cochrane, K.C., Brown, L.E., Coburn, J.W., Judelson, D.A., 2014. Increasing relative humidity impacts low-intensity exercise in the heat. *Aviat Space Environ. Med.* 85, 112–119.
- Muposhi, V.K., Gandiwa, E., Makuza, S.M., Bartels, P., 2016. Trophy hunting and perceived risk in closed ecosystems: Flight behaviour of three gregarious African ungulates in a semi-arid tropical savanna. *Austral Ecol.* 41, 809–818.
- Nickels, M.K., 1984. Comment on: The energetic paradox of human running and hominid evolution. *Curr. Anthropol.* 25, 490, 490.
- Noakes, T., 2012. *Waterlogged: The Serious Problem of Overhydration in Endurance Sports*. Human Kinetics Publishers, Champaign.
- Paffenbarger, R.S., Hyde, R., Wing, A.L., Hsieh, C., 1986. Physical activity, all-cause mortality, and longevity of college alumni. *N. Engl. J. Med.* 314, 605–613.
- Parker, K.L., Robbins, C.T., 1984. Thermoregulation in mule deer and elk. *Can. J. Zool.* 62, 1409–1422.
- Passy, B.H., Levin, N.E., Cerling, T.E., Brown, F.H., Eiler, J.M., 2010. High-temperature environments of human evolution in East Africa based on bond ordering in paleosol carbonates. *Proc. Natl. Acad. Sci. USA* 107, 11245–11249.
- Pickering, T.R., Bunn, H.T., 2007. The endurance running hypothesis and hunting and scavenging in savanna-woodlands. *J. Hum. Evol.* 53, 434–438.
- Pobiner, B.L., 2020. The zooarchaeology and paleoecology of early hominin scavenging. *Evol. Anthropol.* 29, 68–82.
- Pontzer, H., 2005. A new model predicting locomotor cost from limb length via force production. *J. Exp. Biol.* 208, 1513–1524.
- Pontzer, H., 2017. Economy and endurance in human evolution. *Curr. Biol.* 27, R613–R621.
- Pontzer, H., Raichlen, D.A., Wood, B.M., Emery Thompson, M., Racette, S.B., Mabulla, A.Z.P., Marlowe, F.W., 2015. Energy expenditure and activity among Hadza hunter-gatherers. *Am. J. Hum. Biol.* 27, 628–637.
- Psikuta, A., Fiala, D., Laschewski, G., Jendritzky, G., Richards, M., Błażejczyk, K., Mekjavic, I., Rintamäki, H., Dear, R. de Havenith, G., 2012. Validation of the Fiala multi-node thermophysiological model for UTCI application. *Int. J. Biometeorol.* 56, 443–460.
- Raichlen, D.A., Webber, J.T., Pontzer, H., 2019. The evolution of the human endurance phenotype. In: Lightfoot, J.T., Hubal, M.J., Roth, S.M. (Eds.), *Routledge*

- Handbook of Sport and Exercise Systems Genetics. Routledge, New York, pp. 135–147.
- Ralston, H.J., 1958. Energy-speed relation and optimal speed during level walking. *Int. Z. für Angew. Physiol. Einschl. Arbeitsphysiol.* 17, 277–283.
- Rathkey, J.K., Wall-Scheffler, C.M., 2017. People choose to run at their optimal speed. *Am. J. Phys. Anthropol.* 163, 85–93.
- Robertshaw, D., Whittow, G.C., 1966. The effect of hyperthermia and localized heating of the anterior hypothalamus on the sympatho-adrenal system of the ox (*Bos taurus*). *J. Physiol.* 187, 351–360.
- Robertshaw, D., Taylor, C.R., 1969a. A comparison of sweat gland activity in eight species of East African bovines. *J. Physiol.* 203, 135–143.
- Robertshaw, D., Taylor, C.R., 1969b. Sweat gland function of the donkey (*Equus asinus*). *J. Physiol.* 205, 79–89.
- Robertshaw, D., Taylor, C., Mazzia, L., 1973. Sweating in primates: Secretion by adrenal medulla during exercise. *Am. J. Physiol.* 224, 678–681.
- Robertshaw, D., Dmi'el, R., 1983. The effect of dehydration on the control of panting and sweating in the black bedouin goat. *Physiol. Zool.* 56, 412–418.
- Ruff, C.B., 1994. Morphological adaptation to climate in modern and fossil hominids. *Yearbk. Phys. Anthropol.* 37, 65–107.
- Ruff, C.B., Burgess, M.L., 2015. How much more would KNM-WT 15000 have grown? *J. Hum. Evol.* 80, 74–82.
- Ruff, C.B., Burgess, M.L., Squyres, N., Junno, J.-A., Trinkaus, E., 2018. Lower limb articular scaling and body mass estimation in Pliocene and Pleistocene hominins. *J. Hum. Evol.* 115, 85–111.
- Ruxton, G.D., Wilkinson, D.M., 2011a. Avoidance of overheating and selection for both hair loss and bipedality in hominins. *Proc. Natl. Acad. Sci. USA* 108, 20965–20969.
- Ruxton, G.D., Wilkinson, D.M., 2011b. Thermoregulation and endurance running in extinct hominins: Wheeler's models revisited. *J. Hum. Evol.* 61, 169–175.
- Schaper, L., 1934. *The Khoisan Peoples of South Africa*. Routledge & Kegan Paul, London.
- Schmidt-Nielsen, K., 1964. *Desert Animals: Physiological Problems of Heat and Water*. Clarendon Press, Oxford.
- Schmidt-Nielsen, K., 1984. *Scaling, Why Is Animal Size So Important?* Cambridge University Press, Cambridge.
- Shvartz, E., 1976. Effect of neck versus chest cooling on responses to work in heat. *J. Appl. Physiol.* 40, 668–672.
- Sollas, W.J., 1911. *Ancient Hunters and Their Modern Representatives*. Macmillan and Company, London.
- Stuedel-Numbers, K.L., Tilkens, M.J., 2004. The effect of lower limb length on the energetic cost of locomotion: Implications for fossil hominins. *J. Hum. Evol.* 47, 95–109.
- Stuedel-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. *J. Hum. Evol.* 53, 191–196.
- Steyn, H.P., 1984. Southern Kalahari San subsistence ecology: A reconstruction. *S. Afr. Archaeol. Bull.* 39, 117–124.
- Taylor, C.R., 1969. The eland and the oryx. *Sci. Am.* 220, 88–97.
- Taylor, C.R., Lyman, C., 1972. Heat storage in running antelopes: Independence of brain and body temperatures. *Am. J. Physiol.* 222, 114–117.
- Taylor, C.R., Robertshaw, D., Hofmann, R., 1969a. Thermal panting: A comparison of wildebeest and zebu cattle. *Am. J. Physiol.* 217, 907–910.
- Taylor, C.R., Spina, C., Lyman, C., 1969b. Water relations of the waterbuck, an East African antelope. *Am. J. Physiol.* 217, 630–634.
- Taylor, C.R., Schmidt-Nielsen, K., Raab, J.L., 1970. Scaling of energetic cost of running to body size in mammals. *Am. J. Physiol.* 219, 1104–1107.
- Taylor, C.R., Dmi'el, R., Shkolnik, A., Bahar, D., Borut, A., 1974. Heat balance of running gazelles: Strategies for conserving water in the desert. *Am. J. Physiol.* 226, 439–442.
- Taylor, C.R., Heglund, N.C., Maloiy, G.M., 1982. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. Exp. Biol.* 97, 1–21.
- Thompson, J.C., Carvalho, S., Marean, C.W., Alemseged, Z., 2019. Origins of the human predatory pattern: The transition to large-animal exploitation by early hominins. *Curr. Anthropol.* 60, 1–23.
- Trauth, M.H., Maslin, M.A., Deino, A.L., Strecker, M.R., Bergner, A.G.N., Dühnforth, M., 2007. High- and low-latitude forcing of Plio-Pleistocene East African climate and human evolution. *J. Hum. Evol.* 53, 475–486.
- Ueno, T., Takemura, Y., Shijimaya, K., Ohtani, F., Furukawa, R., 2001. Effects of high environmental temperature and exercise on cardiorespiratory function and metabolic responses in steers. *Jpn. Agric. Res. Q.* 35, 137–144.
- Ueno, T., Yamagishi, N., Otani, F., Shijimaya, K., Furukawa, R., 1989. Effects of high environmental temperature and exercise on cardiorespiratory functions in ewe. *Jpn. J. Biometeorol.* 26, 71–77.
- Wada, M., 1950. Sudorific action of adrenalin on the human sweat glands and determination of their excitability. *Science* 111, 376–377.
- Weibel, E.R., Bacigalupe, L.D., Schmitt, B., Hoppeler, H., 2004. Allometric scaling of maximal metabolic rate in mammals: Muscle aerobic capacity as determinant factor. *Respir. Physiol. Neurobiol.* 140, 115–132.
- Weiner, J.S., Hellmann, K., 1960. The sweat glands. *Biol. Rev.* 35, 141–186.
- Wheeler, P.E., 1992. The influence of the loss of functional body hair on the water budgets of early hominids. *J. Hum. Evol.* 23, 379–388.
- White, M., Pettitt, P., Schreve, D., 2016. Shoot first, ask questions later: Interpretative narratives of Neanderthal hunting. *Quat. Sci. Rev.* 140, 1–20.
- Wolf, I.D., Croft, D.B., 2010. Minimizing disturbance to wildlife by tourists approaching on foot or in a car: A study of kangaroos in the Australian rangelands. *Appl. Anim. Behav. Sci.* 126, 75–84.
- Wynn, J.G., 2004. Influence of Plio-Pleistocene aridification on human evolution: Evidence from paleosols of the Turkana Basin, Kenya. *Am. J. Phys. Anthropol.* 123, 106–118.