Dehydration and persistence hunting in *Homo erectus*

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A B S T R A C T

Persistence hunting has been suggested to be a key strategy for meat acquisition in *Homo erectus*. However, prolonged locomotion in hot conditions is associated with considerable water losses due to sweating. Consequently, dehydration has been proposed to be a critical limiting factor, effectively curtailing the usefulness of persistence hunting prior to the invention of water containers. In this study, we aimed to determine the extent to which dehydration limited persistence hunting in *H. erectus*.

We simulated ambient conditions and spatiotemporal characteristics of nine previously reported persistence hunts in the Kalahari. We used a newly developed and validated heat exchange model to estimate the water loss in *H. erectus* and a recent Kalahari hunter. Water loss equivalent to 10% of the hunter's body mass was considered the physiological limit of a hunt with no drinking. Our criterion for ruling dehydration out of being a limit for persistence hunting was the ability to hunt without drinking for at least 5 h, as this was the longest duration reported for a successful persistence hunt of large prey.

Our results showed that *H. erectus* would reach the dehydration limit in 5.5−5.7 h of persistence hunting at the reported Kalahari conditions, which we argue represent a conservative model also for Early Pleistocene East Africa. Maximum hunt duration without drinking was negatively related to the relative body surface area of the hunter. Moreover, *H. erectus* would be able to persistence hunt over 5 h without drinking despite possible deviations from modern-like heat dissipation capacity, aerobic capacity, and locomotor economy. We conclude that *H. erectus* could persistence hunt large prey without the need to carry water.

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1. Introduction

Persistence hunting is a form of pursuit hunting in hot environments in which the hunter runs or uses a mixture of running and walking to drive prey into exhaustion (Liebenberg, 2006). Persistence hunting has been suggested to be a key strategy for meat acquisition in human evolution (Carrier, 1984; Bramble and Lieberman, 2004; though see; Pickering and Bunn, 2007). There is a vast body of ethnographic evidence from hot open environments around the world that persistence hunting not only works (Sollas, 1911; Lowie, 1924; Bennett and Zingg, 1935; McCarthy, 1957; Pennington, 1963; Liebenberg, 1990; Heinrich, 2002) but under certain conditions can be more effective than other hunting approaches (Liebenberg, 2006). The fact that persistence hunting does

not require any sophisticated weapons like spears with lithic points, atlatl, or bow-and-arrow, which all appear in the fossil record relatively recently (Shea, 2006), has lent support for ascribing persistence hunting to the subsistence repertoire of the Early Pleistocene *Homo* (Carrier, 1984). As such persistence hunting could initiate or promote the development of several characteristics which are often used to define the genus *Homo* such as tool production and usage (butchering), encephalization (tracking), high sweating capacity and loss of hair coat (heat dissipation), plantar arch and long Achilles tendon (locomotor economy), speech (precise communication between hunters), or social cooperation (tracking in group, meat sharing) (Liebenberg, 1990; Bramble and Lieberman, 2004; Lieberman et al., 2009; Ruxton and Wilkinson, 2011a; Raichlen and Polk, 2013; Zink and Lieberman, 2016).

It has been argued that *Homo erectus*, which appeared in Africa about 1.8 Ma (Antón, 2003) and is characterized by modern human-like body size and body proportions (Ruff and Walker, 1993), was the first effective persistence hunter (Lieberman et al., 2009). A key

prerequisite of persistence hunting is locomotor endurance. Several morphological traits which either promote endurance (e.g., long Achilles tendon, foot arch, long lower limb) or reflect prolonged locomotion (e.g., robust joints of lower limb) first emerged or were already present in *H. erectus* (Bramble and Lieberman, 2004; Lieberman et al., 2009). Physiology and soft-tissue morphology, which do not fossilize, would also need to adapt to allow *H. erectus* to use persistence hunting, or any long-distance transport in hot open environments (Aiello and Wells, 2002; Pontzer, 2017). Traits which increase heat dissipation to prevent hyperthermia are of special importance for endurance in hot environments (Carrier, 1984; Porter, 1993) as suggested also by mathematical simulations (Ruxton and Wilkinson, 2011a) and data (Wall-Scheffler, 2014, 2015). Thus, it is expected that *H. erectus* possessed effective heat dissipation mechanisms, likely including the loss of hair cover and high sweating capacity, to persistence hunt effectively (Jablonski and Chaplin, 2000; Rogers et al., 2004; Jablonski, 2012; Lieberman, 2015).

The very same mechanisms which effectively dissipate heat under the equatorial midday sun have made our taxon prone to dehydration. In hot environments, humans sweat at rates between 1.0 and 1.7 kg h^{-1} during walking (Adolph and Dill, 1938) and up to 3.2 kg h^{-1} during running (Beis et al., 2012) which is exceptionally high in comparison to our poor ability to preload with water and our low dehydration tolerance. Humans can ingest about one liter of water before reaching the limits of stomach capacity. Of that liter, about 0.85 L of the ingested water is available for sweat production, the rest appears as increase of urine volume (Brown, 1947). Preloading with water by drinking one liter prior hunting would delay dehydration in hot conditions by only 15−50 min, depending on gait and velocity. Consequently, humans in deserts regularly lose water equivalent to 3−5% of body mass between meals (Schmidt-Nielsen, 1964). Water losses of up to 10% body mass were reported for 2-h runs at aerobic velocities even under moderate climate in marathon winners (Beis et al., 2012). The 10% body mass loss seems to be at the upper limit of dehydration a highly motivated hunter would willingly undergo, since at only 12% body mass loss humans lose the ability to swallow and rehydration is then possible only with assistance (Schmidt-Nielsen, 1964). In comparison, heat adapted ungulates like camels and donkeys can tolerate dehydration up to 30% of their body mass and can fully restore their body fluids by drinking water in just few minutes (Schmidt-Nielsen, 1964).

Dehydration was identified by Scott (1984) as a likely limit of persistence hunting in response to Carrier's (1984) initial proposal of the persistence hunting hypothesis. In his reply to Scott's comments, Carrier (1984) noted that before the invention of water containers, the hominin proneness to dehydration could limit the coverable distances of the hunter. He continued that susceptibility to dehydration might have constrained which prey could be acquired through persistence hunting without water containers to smaller species with lower endurance, such as hare (Carrier, 1984). Twenty years later, the resurrected persistence hunting hypothesis (Bramble and Lieberman, 2004; Liebenberg, 2006) was first criticized from points other than dehydration (Pickering and Bunn, 2007). But Steudel-Numbers and Wall-Scheffler (2009) and more recently Ruxton and Wilkinson (2011a) and Rathkey and Wall-Scheffler (2017) have noted the potential dehydration limits of persistence hunting, and proposed that dehydration may have inhibited the importance of persistence hunting in human evolution until the invention of water containers. Yet despite the likely importance of dehydration, the limits of persistence hunting without water carriers have not been quantified.

The first water containers were likely made of perishable materials like skin, gourd, eggshell or animal intestine (Sollas, 1911;

Rathkey and Wall-Scheffler, 2017), thus the timing of their emergence will be difficult to pinpoint. Yet, the determination of whether persistence hunting could be applied to large prey in the Early Pleistocene has critical relevance for studies of human evolution. Persistence hunting has been proposed to be a key way of meat acquisition in the Early Pleistocene and also explain the evolution of several locomotor and thermoregulatory adaptations (Carrier, 1984; Bramble and Lieberman, 2004; Lieberman et al., 2009; Lieberman, 2015). If water containers were an unavailable prerequisite for persistence hunting of large prey in Early Pleistocene, then the archeological evidence of human early access to meat of large animals (e.g., Bunn, 1981, 2001; Bunn and Kroll, 1986) would need to be explained by other means of meat acquisition such as active searching for unexploited carcasses (Bramble and Lieberman, 2004; Pickering and Bunn, 2007), power scavenging (Bunn, 2001; Domínguez-Rodrigo and Pickering, 2003), or ambush hunting (Bunn and Pickering, 2010). In addition, the evolution of heat dissipation capacity and locomotor adaptations in the human lineage would require alternative models of selection such as long-distance walking and running-based scavenging (Lieberman, 2015).

Direct observations of Kalahari hunters have shown that it takes between about two and 5 h to catch a large prey like kudu using persistence hunting (Liebenberg, 2006). However, hunters were provided with water from an accompanying vehicle during most of these observed hunts (Liebenberg, 2006), so it is questionable whether these hunts could be undertaken for the same duration without water provisioning (Steudel-Numbers and Wall-Scheffler, 2009; Ruxton and Wilkinson, 2011a; Rathkey and Wall-Scheffler, 2017). It is, thus, to be determined how long a human hunter can perform persistence hunt before reaching the dehydration limit.

Direct measurement of the dehydration status during persistence hunting is difficult due to unavailability of the hunters who still practice persistence hunting. The last reported successful hunt was performed 17 years ago by a Kalahari hunter, Karoha (Liebenberg, 2006), who if still living is now 55 years old. An alternative way to assess the water loss during persistence hunting is available: mathematical modeling and simulation.

The advantage of the modeling approach is the ability to explore wide ranges of variation in morphology, physiology, ambient conditions, and duration of the hunt by reparametrizing the model. Modeling is especially convenient for application to studies of past species for which values of many of the physiologic and soft-tissue-related morphologic variables are not known. In these cases, the modeling approach allows us to iterate the values of the variables in question (e.g., proportion of skin covered by dense hair) within the realistic boundaries and to evaluate the relative impact of the different variables on the model outputs. For persistence hunting, the iterative power of the modelling approach allows also to overcome the lack of detailed information about changes of velocity and gait during the hunt.

Several previous studies employed mathematical modeling and simulation to assess the water loss due to evaporation in past hominins including early hominins (Wheeler, 1991a, 1992a) and *H. erectus* (Wheeler, 1993). However, only overall daytime water loss was provided in these studies with no specific consideration of persistence hunting. These studies took advantage of the tight link between water loss and heat loss and estimated water loss by modeling evaporation from the respiratory tract and skin using a heat exchange model. Heat exchange modeling is a well-established approach in a wide spectrum of research areas including physiology, ecology, thermal comfort, aerospace, textile engineering, meteorology, medicine, and military (Porter and Gates, 1969; Stolwijk, 1971; Kerslake, 1972; Haslam and Parsons, 1988; Malchaire et al., 2001; Fiala et al., 2012; Parsons, 2014), and also human evolution (Austin and Lansing, 1986; Wheeler, 1991a,

1992a, 1992b, 1993; Chaplin et al., 1994; Queiroz do Amaral, 1996; Cross et al., 2008; Ruxton and Wilkinson, 2011a, 2011b; Dávid-Barrett and Dunbar, 2016; Collard and Cross, 2017). We built on this vast body of research and use heat exchange modeling and simulation to estimate water loss during persistence hunting in *H. erectus* who is considered to have already possessed most traits related to endurance locomotion in the heat (Bramble and Lieberman, 2004; Lieberman et al., 2009; Jablonski, 2012). In addition, we will estimate water loss in a recent Kalahari hunter.

In this study, we aimed to determine whether dehydration was a limit for persistence hunting in *H. erectus*. Our criterion for ruling dehydration out of being a limit for persistence hunting was the ability to hunt for at least 5 h without drinking. The 5-h time limit was derived from the ethnographic reports as the longest successful persistence hunt observed (Liebenberg, 2006). To assess how long *H. erectus* could hunt without drinking in realistic settings, we simulated ambient conditions and spatiotemporal characteristics of nine persistence kudu hunts in Kalahari reported by Liebenberg (2006). The semi-arid Kalahari is a useful model also for habitats assessible to *H. erectus* e.g., in the Turkana Basin which by Early Pleistocene already comprised seasonally arid savanna (Cerling, 1992; Wynn, 2004; Bobe and Leakey, 2009) characterized by high solar radiation and high air temperatures (Passey et al., 2010). We used a newly developed and validated heat exchange model to estimate water loss in *H. erectus* and for comparison also in recent Kalahari hunter during these hunting simulations. A water loss equivalent to 10% of the hunter's body mass was taken as the physiological limit determining the maximal duration of hunt without drinking.

2. Materials and methods

2.1. Materials

Published body mass and stature of two contrasting adult extrapolations of KNM-WT 15000 (Ruff and Burgess, 2015; Cunningham et al., 2018; Ruff et al., 2018), and OH 28 (Stringer et al., 1998; Ruff et al., 2018) fossils were used to model *H. erectus*. Published data on an average !Kung San male (Kirchengast, 2000) were used to model the recent Kalahari hunter. The characteristics of the hunter models are presented in Table 1.

2.2. Layout

The layout of our modeling and simulation approach is presented in Figure 1. Data on four hunters and nine persistence hunts were used to estimate water loss. The hunt data were first inputted

Table 1
Characteristics of the hunter models.

Model	Body mass (kg)	Stature (cm)	Body surface area[a] (m²)	Body surface area/body mass (cm² kg⁻¹)	Sources[b]
Homo erectus					
KNM-WT 15000 Large	76.7	178.0	1.95	254	1,2
KNM-WT 15000 Small	65.9	163.3	1.71	260	3
OH 28	69.4	164.8	1.76	254	2,4
Recent Kalahari hunter	49.4	160.4	1.50	303	5

[a] Estimated from body mass and stature using equation of DuBois and DuBois (1916).
[b] Sources: 1, Ruff and Burgess (2015); 2, Ruff et al. (2018); 3, Cunningham et al. (2018); 4, Stringer et al. (1998); 5, Kirchengast (2000).

to the Ambient model and Gait generator, which estimated five ambient variables (sun elevation, three air temperatures, and relative humidity) and two gait variables (gait and velocity), respectively, at each second of the hunt. These ambient and gait variables together with hunter data (body mass and stature) were then inputted to the heat exchange model, which estimated water loss.

2.3. Heat exchange model

Water loss is estimated here as a sum of respiratory water loss and sweat loss. This summation corresponds to water loss assessed empirically as a change in body mass corrected for fluid intake and excreted urine. Respiratory water loss and sweat loss were estimated for each second of the hunt using the heat exchange model (Fig. 2) and summed to provide a total water loss over the hunt.

Respiratory water loss Respiratory water loss (RWL, kg s⁻¹) was estimated for each second of the hunt as:

$$RWL = \frac{E_{resp}}{h_{vap}}, \tag{1}$$

where E_{resp} is the respiratory evaporation (W) and h_{vap} is the heat of vaporization of the water ($h_{vap} = 2426000$ J kg⁻¹; Wenger, 1972).

The respiratory evaporation (E_{resp}; W) was estimated following Fanger (1970):

$$E_{resp} = 0.0173 \times M_i \times (5.87 - P_{air}). \tag{2}$$

where M_i is the metabolic heat production during walking or running (W), and P_{air} is the water vapor pressure of the ambient air (kPa).

Metabolic heat production (M; W) was estimated using gait-specific equations for walking and running. For walking, the metabolic heat production (M_{walk}; W) was estimated using the equation of Weyand et al. (2013) based on a heterogeneous sample of 45 males and 33 females (age: 5–48 years; body mass: 15.9–112.8 kg; stature: 107–211 cm) walking at 0.4–1.9 m s⁻¹:

$$M_{walk} = \left(2 \times RMR + 5.6 \times v^2 \times st\right) \times m_{act}, \tag{3}$$

where RMR is the resting metabolic rate (ml O₂ kg⁻¹ min⁻¹), v is the velocity (m s⁻¹), st is the stature (m), and m_{act} is the actual body mass (kg) continuously, i.e., at each second of simulation, corrected for body mass decrease due to evaporation of water from the respiratory tract and skin. The resting metabolic rate was estimated using the equation of Schofield et al. (1985) for males 18–30 years of age (Weyand et al., 2013; their Table 4):

$$RMR = 2.177 + \frac{100.055}{m_{init}}, \tag{4}$$

where m_{init} is the initial body mass of the subject, i.e., uncorrected for water losses. For running, several published equations allow the estimation of the metabolic heat production. However, the relationship between velocity and energetic cost is modeled linearly in most of these equations which does not correspond with the recently described polynomial relationship, i.e., the existence of an energetically optimal running speed (Steudel-Numbers and Wall-Scheffler, 2009; Willcockson and Wall-Scheffler, 2012; Cher et al., 2015; Rathkey and Wall-Scheffler, 2017). Only one published equation modeled the effect of the velocity on the energetic rate polynomially (Walt and Wyndham, 1973). Nevertheless, the equation of Walt and Wyndham (1973) was based on a small sample of non-athletes running at slow speeds (below 3.6 m s⁻¹) and may not
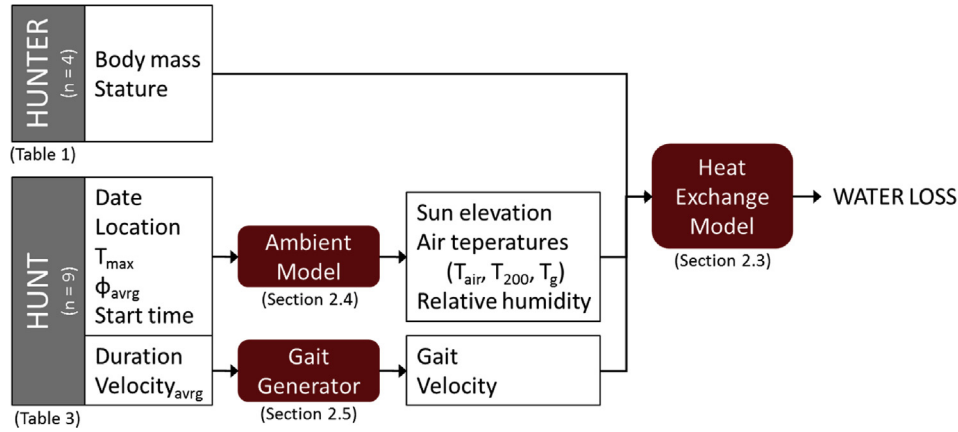
Figure 1. Layout of the modeling and simulation approach for water loss estimation (T_{max}, the daily maximum air temperature; ϕ_{avrg}, daily average relative humidity; velocity$_{avrg}$, average velocity; T_{air}, air temperature experienced by hunter; T_{200}, air temperature at 200 cm above the ground; T_g, air temperature at ground).
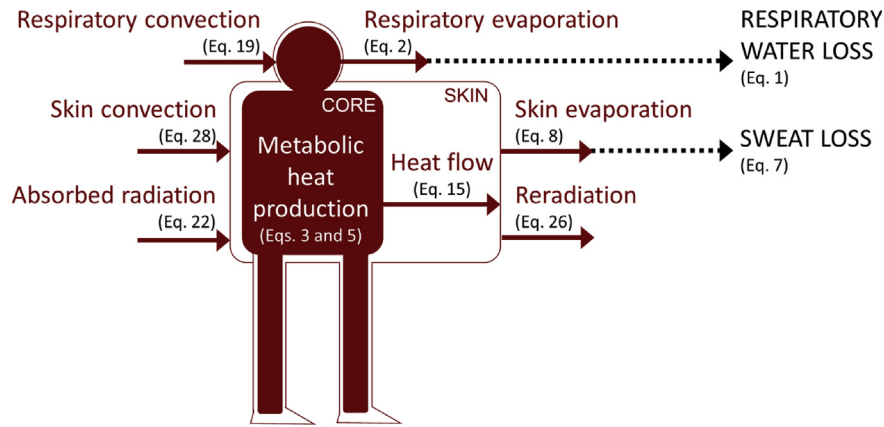

Figure 2. Heat exchange model for estimation of water loss.

provide accurate estimates of the energetic cost of running in the physically active population. Thus, we use here a newly derived equation to predict the cost of locomotion and hence the metabolic heat production during running (M_{run}; W) based on previously published data on 16 experienced male runners (body mass: 57.7–81.3 kg; stature: 170–192 cm) running at 2.0–4.9 m s^{-1} (Steudel-Numbers and Wall-Scheffler, 2009; Willcockson and Wall-Scheffler, 2012; Rathkey and Wall-Scheffler, 2017):

$$M_{run} = \left(0.41 \times v^2 + 1.357 \times v + 5.331\right) \times m_{act}. \tag{5}$$

We tested the accuracy of this equation on newly collected data on seven males and three females running at 2.0–3.5 m s^{-1}, individual data from Rathkey and Wall-Scheffler (2017) (nine males running at 2.0–4.4 m s^{-1}) and Steudel-Numbers et al. (2007) (11 males and seven females running at 2.68 m s^{-1}), and mean data on Baka Pygmies (Minetti et al., 1994) (13 males running at 1.9–3.2 m s^{-1}) with mean percentage error of the estimate 2.0%, 0.4%, 2.7%, and 0.4%, and mean absolute percentage error of estimate 5.9%, 4.0%, 7.2%, and 3.5% for the four samples, respectively. The limits of agreement, and the effect of body mass and velocity on the percentage difference between the estimated and measured metabolic heat production are presented in Figure 3. Each participant of our new testing sample provided written informed consent prior to participation, and the protocol was approved by the University Integrated

Institutional Review Board, Hunter College, City University of New York. The participants ran on a treadmill for 6–8 min at each of the four velocities (2.0, 2.5, 3.0, and 3.5 m s^{-1}) while their cost of locomotion was measured using a portable respiratory system (Cosmed K4b2). Only trials with respiratory quotient ≤1.0 were included in the analysis.

Water vapor pressure of the air (P_{air}; kPa) was calculated using the Arden Buck equation and corrected for relative humidity as follows:

$$P_{air} = 0.61121 \times \exp\left(\left(18.678 - \frac{T_{air}}{234.5}\right) \times \frac{T_{air}}{257.14 + T_{air}}\right)$$
$$\times \frac{\phi}{100}, \tag{6}$$

where T_{air} is the air temperature experienced by the subject (°C) and ϕ is the relative humidity of the air (%).

Sweat loss The sweat loss in our model comprises only the evaporated sweat. We did not attempt to account for the sweat dripping down from the body. Previous studies (Kuno, 1956; Shvartz et al., 1973; Hori et al., 1976; Lee et al., 2004) showed that acclimatization, and especially long-term acclimatization, to dry hot conditions results in greater efficiency of sweating which means that the sweating rate is better tuned to actual evaporation and less sweat is dripped. Since we expected that
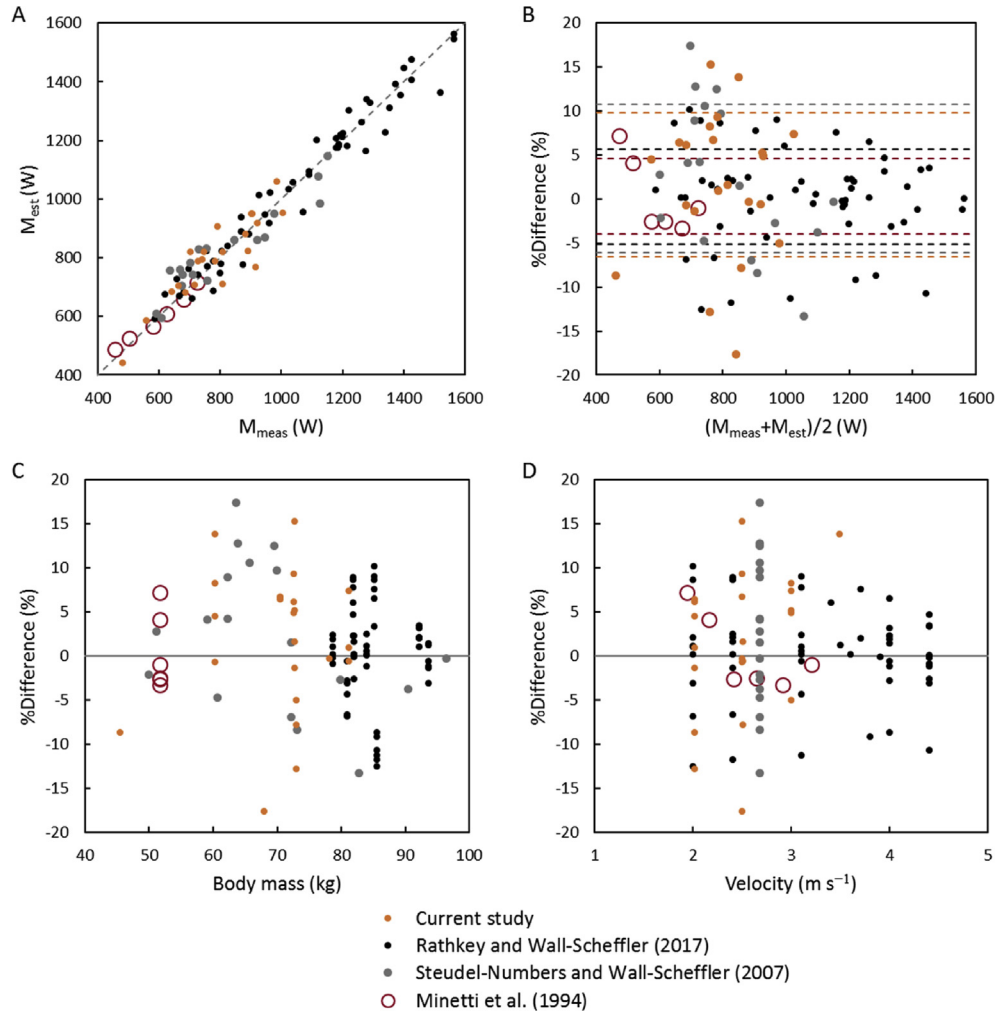
Figure 3. (A) Estimated metabolic heat production (M_{est}) during running against measured metabolic heat production (M_{meas}) (orange, current study; black, data from Rathkey and Wall-Scheffler, 2017; grey, data from Steudel Numbers and Wall-Scheffler, 2007; red, data from Minetti et al., 1994; grey dashed line represents isometry). (B) Evaluation of agreement between measured and estimated metabolic heat production using the approach of Bland and Altman (1986): percentage difference between the estimated and measured heat production, ($M_{est} - M_{meas}$)/[($M_{meas} + M_{est}$)/2] × 100, against the mean of the two metabolic heat productions, ($M_{meas} + M_{est}$)/2, with limits of agreement (dashed lines). (C and D) Percentage difference between estimated and measured metabolic heat production against body mass and velocity. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

both the *H. erectus* and Kalahari hunters would be acclimatized to dry hot conditions it seemed justified to estimate only the evaporated sweat loss acknowledging that this parameter undervalues to some degree the overall sweat loss.

Sweat loss (SL; kg s^{-1}) was estimated at each second of the hunt as:

$$SL = \frac{E_{skin}}{\frac{f_{hair} \times (e_{hair}-1)+1}{h_{vap}}}, \quad (7)$$

where E_{skin} is the skin evaporation (W), f_{hair} is the fraction of body surface covered by dense hair (i.e., containing large pigmented terminal hairs), and e_{hair} is the hair evaporation efficiency, i.e., the constant relating heat loss by evaporation from hair-covered skin to heat loss by evaporation from "hairless" skin. The f_{hair} was assumed to be 0.15 which corresponds to hair covering the head and shoulders (Wheeler, 1992a) but no assumptions about the location of hair on the body have been used in our model. Since the presence of hair moves the location of some portion of evaporation away from the skin (heat of vaporization is then taken from surrounding air rather than the body) and reduces air

convection at the skin surface (humid air trapped in the hair then restricts further evaporation), the heat lost by evaporation from the hair-covered skin is reduced (Wheeler, 1991a; Lieberman, 2015). The degree of the reduction is difficult to quantify but some researchers assumed that e_{hair} in fossil hominins was about 0.8 (Wheeler, 1991a, 1992a). Such relatively high e_{hair} is supported by the notion of others that the helical hair which is often seen in equatorial and south African recent human populations may keep the rate of skin evaporation relatively little affected (Porter, 1993). Since we simulate heat exchange in southern Africans and fossil hominins here, we followed these assumptions and used e_{hair} = 0.8 throughout this study.

The skin evaporation (E_{skin}; W) is estimated as:

$$E_{skin} = E_{max} \times w, \quad (8)$$

where E_{max} is the maximum skin evaporation at given conditions and w is the wettedness.

The maximum skin evaporation (E_{max}; W) is estimated as follows:

$$E_{max} = (P_{skin} - P_{air}) \times \sqrt{v} \times A \times 124 \times (f_{hair}[e_{hair} - 1] + 1), \tag{9}$$

where P_{skin} is the saturated water pressure (kPa) at skin temperature, v is the velocity of locomotion which represents the mean velocity of air movement across the body (Parsons, 2014), and A is the body surface area (m^2). The P_{skin} (kPa) was estimated using the Arden Buck equation as:

$$P_{skin} = 0.61121 \times \exp\left(\left(18.678 - \frac{T_{skin}}{234.5}\right) \times \frac{T_{skin}}{257.14 + T_{skin}}\right), \tag{10}$$

where T_{skin} is the temperature of the skin (°C). The body surface area was estimated from stature and initial body mass using the formula of DuBois and DuBois (1916) which has been shown to be accurate in individuals varying widely in body size and shape including neonates and pregnant women (Wang et al., 1992). The initial skin temperature was estimated from T_{air}, ϕ, velocity, metabolic heat production, and T_{core} following Mairiaux et al. (1987: their Eq. (7)). The subsequent changes in skin temperature (ΔT_{skin}; °C) were estimated as:

$$\Delta T_{skin} = \frac{H_{dry} - E_{skin} + H_{flow}}{c_{body} \times m_{skin}}, \tag{11}$$

where H_{dry} is the dry heat gain from the environment to the skin due to radiation and convection (W), H_{flow} is the heat flow from the body core to the skin (W); c_{body} is the specific heat capacity of the body (3500 J °C^{-1} kg^{-1}), and m_{skin} is the mass of the skin (kg). The m_{skin} (kg) was estimated as:

$$m_{skin} = A \times d_{skin} \times \rho_{skin}, \tag{12}$$

where d_{skin} is the skin thickness (m) and ρ_{skin} is the skin density (kg m^{-3}). We assumed that skin thickness is 0.002 m (Roddie, 2011) and skin density is 1060 kg m^{-3} (Morales et al., 1945).

The wettedness is a proportion of body surface area covered by sweat (Gagge, 1937). The maximum attainable wettedness (w_{max}) is dependent on the acclimatization and training (Ravanelli et al., 2018). Fully acclimatized subjects are believed to be able to fully wet their skin and thus reach the maximum wettedness of 1 (International Organization for Standardization, 1989). We assumed that both the H. erectus and Kalahari hunters were fully acclimatized to a hot environment and in consequence their $w_{max} = 1$. Within the appropriate w_{max}, the wettedness was estimated as:

$$w = 0.94 \times w_{req} + w_{min}, \tag{13}$$

where w_{req} is the wettedness required to maintain the heat balance in the skin and w_{min} is the minimum wettedness due to insensible perspiration ($w_{min} = 0.06$; Kenny and Jay, 2013). The wettedness required to maintain the heat balance in the skin (w_{req}) was estimated as:

$$w_{req} = \frac{H_{flow} + H_{dry}}{E_{max}}. \tag{14}$$

Heat flow from core to skin (H_{flow};W) was estimated as:

$$H_{flow} = K_{skin} \times A \times (T_{core} - T_{skin}), \tag{15}$$

where K_{skin} is the skin conductance (W m^{-2} °C^{-1}) and T_{core} is the temperature of the body core (°C).

Here, the skin conductance is a sum of two components: the tissue conductance which is derived at maximum peripheral vasoconstriction and dependent largely on thickness of the subcutaneous fat, and the blood conductance. We assume that during the maximum peripheral vasoconstriction, the K_{skin} is 9 W m^{-2} °C^{-1} which is a value typical for lean individual (Witzmann, 2013). The blood conductance (K_{blood}; W m^{-2} °C^{-1}) is estimated as:

$$K_{blood} = \frac{SkBF * c_{blood}}{A}, \tag{16}$$

where SkBF is the skin blood flow (L s^{-1}) and c_{blood} is the volume-specific heat capacity of blood (3850 J L^{-1} °C^{-1}). We assume that the skin blood flow is zero at maximum vasoconstriction but can reach up to 0.133 L s^{-1} at maximum vasodilation and maximum cardiac output (Witzmann, 2013). We assume that within the above defined limits, the K_{skin} is adjusted to the conductance required to maintain the heat balance in the body core. Based on the previous empirical findings (reviewed in Kenny and Jay, 2013; Kenny and McGinn, 2017), it is further assumed that during major changes in the activity level, particularly after the initiation of locomotion, cease of locomotion, and switch between gaits, the K_{skin} is fully adjusted to the new rate of metabolic heat production with a time delay (t_{delay}; s). We used 435 s as the time delay here, which reflects closely the mean thermal inertia reported by Kenny et al. (2009). The actual value of K_{skin} during the adjustment period is modeled non-linearly as a circular arc:

$$K_{skin} = K_{skin0} + (K'_{skin} - K_{skin0}) * \sin\left(\arccos\left(1 - \frac{t_{lag}}{t_{delay}}\right)\right), \tag{17}$$

where K_{skin0} (W m^{-2} °C^{-1}) is the value of K_{skin} at the time of the change in metabolic heat production rate, K'_{skin} (W m^{-2} °C^{-1}) is the estimated value of K_{skin} if there was no delay, and t_{lag} is the time (s) elapsed since the change in metabolic heat production rate.

The initial body core temperature was assumed to be 37 °C. The subsequent changes in body core temperature (ΔT_{core}; °C) were estimated as:

$$\Delta T_{core} = \frac{M + C_{resp} - E_{resp} - H_{flow}}{c_{body} \times m_{core}}, \tag{18}$$

where C_{resp} is the heat gain due to respiratory convection (W) and m_{core} is the mass of the body core (kg). The C_{resp} (W) was estimated following Fanger (1970):

$$C_{resp} = 0.0014 \times M \times (T_{air} - 34), \tag{19}$$

The mass of the body core (kg) was estimated as:

$$m_{core} = m_{act} - m_{skin}. \tag{20}$$

Dry heat gain (H_{dry}; W) is a result of heat transfer between the skin and the environment through radiation and convection. The dry heat gain of the whole body is a summation of dry heat gains of four body surface sections which differ in dense hair cover (present/absent) and exposure to direct solar radiation (exposed/non-exposed). For each body surface section (j), the dry heat gain (H_{dryj}; W) was calculated as:

$$H_{dryj} = \left(Q_{absj} - Q_{rj} + C_{skinj}\right) \times A_j \tag{21}$$

Table 2
Description of experiments and results of heat exchange model validation.

Exp. No	Body mass (kg)	Stature (cm)	Sample size	Activity[a]	Duration (h)	Air temperature (°C)	Relative humidity (%)	Water loss					Source[e]
								Observed (kg)	Estimated (kg)	Difference[b] (kg)	%Error[c] (%)	Difference[d] (%BM)	
1	59.3	167.4	6	Run	1	35.0	60.3	1.43	1.37	−0.06	−4	−0.10	1
2	76.6	183.4	6	Run	1	35.0	60.3	1.97	1.73	−0.24	−12	−0.31	1
3	63.3	166.0	4	Cycle	4	45.0	42.4	3.19	2.51	−0.68	−23	−1.08	2
4	68.0	175.0	6	Bench	2	39.5	51.2	1.43	0.73	−0.69	−49	−1.02	3
5	72.0	180.0	11	Run	1	31.0	23.0	1.47	1.49	0.01	1	0.02	4
6	72.0	180.0	11	Run	1	31.0	43.0	1.44	1.38	−0.06	−4	−0.09	4
7	72.0	180.0	11	Run	1	31.0	52.0	1.44	1.33	−0.11	−8	−0.16	4
8	72.0	180.0	11	Run	1	31.0	61.0	1.40	1.28	−0.13	−9	−0.17	4
9	72.0	180.0	11	Run	1	31.0	71.0	1.41	1.22	−0.19	−13	−0.26	4
10	73.5	181.9	7	Run	0.7	35.0	40.0	0.95	0.91	−0.04	−4	−0.05	5

[a] Run, running on treadmill; Cycle, cycling on ergometer; Bench, bench stepping.
[b] Difference [kg] = (estimated [kg] − observed [kg]).
[c] %Error [%] = difference [kg]/observed [kg] × 100.
[d] Difference [%body mass] = difference [kg]/body mass [kg] × 100.
[e] Sources: 1, Marino et al. (2004); 2, Mitchell et al. (1976); 3, Shvartz (1976); 4, Che Muhamed et al. (2016); 5, Jack (2010).

where Q_{abs} is the absorbed radiation (W m^{-2}), Q_r is the heat loss from re-radiation (W m^{-2}), and C_{skin} is the heat gain through convection (W m^{-2}).

The absorbed radiation (Q_{abs}; W m^{-2}) was estimated following Porter and Gates (1969) as:

$$Q_{abs} = a \times S + 0.5 \times \left(a \times s + a \times r \times [S+s] + R_{sky} + R_g \right), \quad (22)$$

where a is the absorptivity of the hominin surface exposed to radiation (skin or hair), S is the direct solar irradiance (W m^{-2}), s is the diffuse irradiance (W m^{-2}), r is the surface reflectivity of the environment, R_{sky} is the thermal radiation emitted from the atmosphere (W m^{-2}), and R_g is the thermal radiation emitted from the surfaces of the environment (W m^{-2}). For the part of the body surface which is not exposed to direct sunlight, the term $a \times S$ is omitted from the equation. For absorptivity of the skin and hair, we adopted a value of 0.8 which has been used previously in hominin models and reflects dark blackish color (Wheeler, 1991a; Ruxton and Wilkinson, 2011a). The direct solar irradiance (S; W m^{-2}) was estimated following Farber and Morrison (1977) as:

$$S = 1121 \times (\cos(\beta + 90°) - 0.08251), \quad (23)$$

where β is the elevation of the sun (°). We assumed zero solar irradiance between sunset and sunrise. For surface reflectivity, the value of 0.15 was adopted from Wheeler (1991a). Following Wheeler (1991a), we assumed that the diffuse irradiance comprises 10% of the total non-reflected shortwave radiation (S + s). Longwave radiation R_{sky} (W m^{-2}) and R_g (W m^{-2}) was estimated following Monteith and Unsworth (2013) and Wheeler (1991a), respectively:

$$R_{sky} = 213 + 5.5 \times T_{200}, \quad (24)$$

$$R_g = \sigma \times (T_g + 273)^4, \quad (25)$$

where T_{200} is the air temperature at 200 cm above the ground (°C), σ is the Stefan−Boltzmann constant (5.67×10^{-8} W m^{-2} K^{-4}), and T_g is the air temperature at the ground (°C).

Heat loss from re-radiation (Q_r; W m^{-2}) was calculated as:

$$Q_r = \sigma \times T_k^4, \quad (26)$$

where T_k is the temperature at the skin or hair surface (°C). The temperature at the outer surface of the hair (T_{hair}; °C) was estimated by solving the following equation (Porter and Gates, 1969):

$$K_{hair} \times (T_{hair} - T_{skin}) - C_{skin} + Q_r - Q_{abs} = 0, \quad (27)$$

where K_{hair} is the hair conductance (W m^{-2} °C^{-1}). Eq. (27) is based on assumption that heat is not stored in the hair. In previous models of hominin thermoregulation, various values have been used for K_{hair} ranging from 1 W m^{-2} °C^{-1} (Ruxton and Wilkinson, 2011a) to 10 W m^{-2} °C^{-1} (Wheeler, 1991a; Chaplin et al., 1994; Queiroz do Amaral, 1996). Since we simulate running which is a highly physically demanding activity associated with high rates of sweating, it can be expected that the hair will be wet during running. Water has a high conductivity and, thus, its presence in hair should increase the overall conductivity of the hair. For this reason, we use the highest from the previously considered values for K_{hair} in our simulations (i.e., 10 W m^{-2} °C^{-1}). Nevertheless, due to the low proportion of hair cover in our human models, the actual value of the K_{hair} parameter has little effect on the results of our simulations.
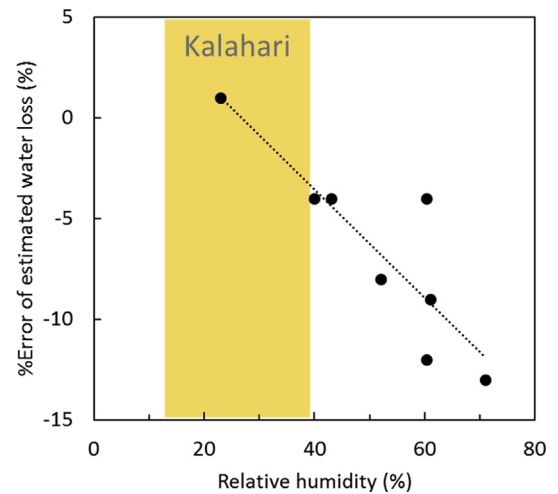

Figure 4. Percentage error of estimated water loss against relative humidity for experiments in which air flow matched running velocity. The line is an ordinary least squares regression. Yellow area represents relative humidity used in our simulations of persistence hunting in Kalahari. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)
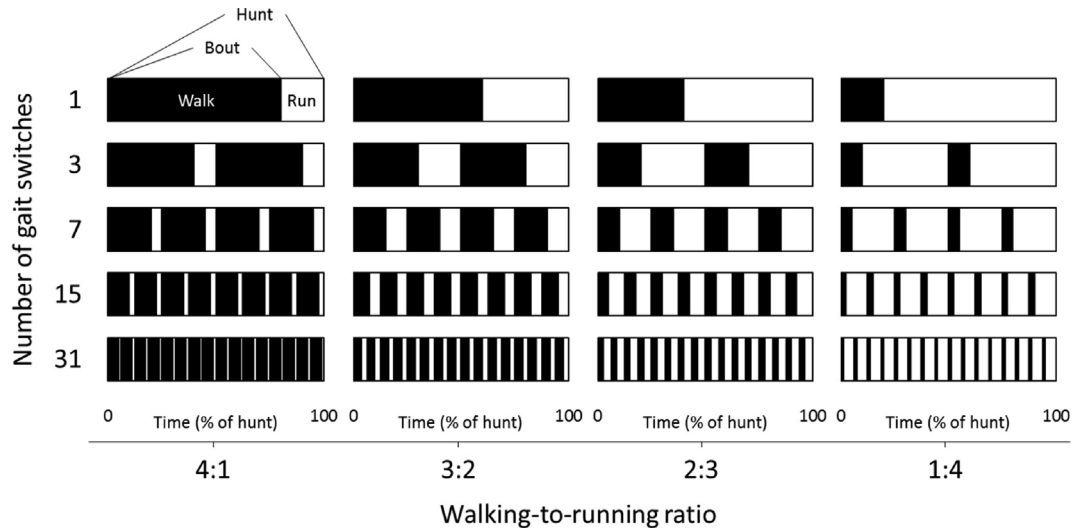
Figure 5. Diagram of explored combinations of walking ratios and numbers of switches between gaits. Walking bouts are in black, running bouts are in white. Seven walking velocities were explored at each of these 20 combinations which resulted in total of 140 combinations generated by the gait generator + one at a single gait and velocity.

Table 3
Description of simulated persistence hunts.

Hunt date	Hunt result	T_{max} (°C)	ϕ_{avrg} (%)	Hunt duration (h)	Average velocity (m s^{-1})	Start time
August 29, 1990	Successful	32.9	**27.0**	**1.9**	**3.00**	**13:00**
November 12, 1998	Failed	**35.7**	**31.9**	5.1	1.67	**11:30**
November 18, 1998	Successful	31.0	**31.9**	3.6	2.78	**12:30**
October 5, 2001	Failed	36.1	**23.1**	4.1	1.72	**11:30**
October 6, 2001	Successful	36.1	**23.1**	5.0	1.83	**11:00**
October 9, 2001	Failed	36.8	**23.1**	3.7	1.33	12:00
October 10, 2001	Failed	34.6	**23.1**	4.9	1.17	10:30
October 12, 2001	Failed	36.5	**23.1**	6.6	1.47	11:30
October 13, 2001	Successful	37.8	**23.1**	3.8	1.75	**12:00**

T_{max}, daily maximum air temperature; ϕ_{avrg}, daily average relative humidity; data on T_{max} from Ghanzi meteorological station, other data from Liebenberg (2006), values in bold are estimated (see text about details).
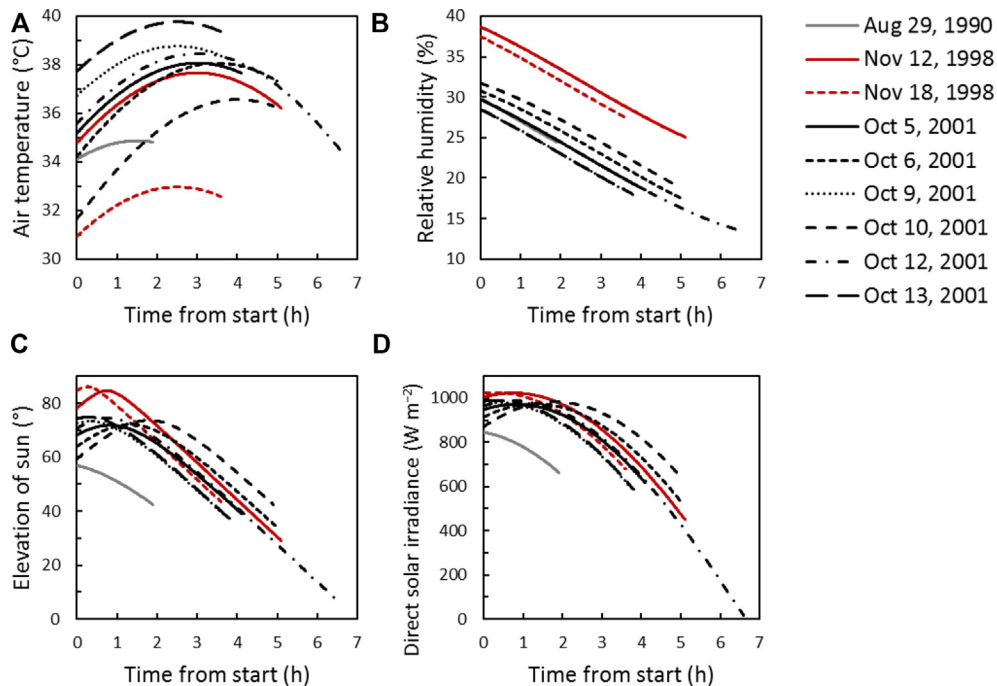

Figure 6. Ambient conditions during the simulated hunts: (A) air temperature experienced by hunter; (B) relative humidity; (C) sun elevation; and (D) direct solar irradiance.

Table 4
Estimated water loss (kg).

Hunt date	KNM-WT 15000 Large		KNM-WT 15000 Small		OH 28		Recent Kalahari hunter	
	Mean (SD)	Min−max	Mean (SD)	Min−max	Mean (SD)	Min−max	Mean (SD)	Min−max
Aug 29, 1990	3.7 (−)	−	3.4 (−)	−	3.5 (−)	−	2.6 (−)	−
Nov 12, 1998	6.8 (0.3)	6.3−7.2	6.0 (0.2)	5.5−6.3	6.2 (0.2)	5.7−6.6	5.0 (0.1)	4.6−5.2
Nov 18, 1998	6.3 (0.2)	5.9−6.6	5.5 (0.1)	5.2−5.8	5.7 (0.1)	5.4−6.0	4.5 (0.1)	4.2−4.6
Oct 5, 2001	6.0 (0.2)	5.5−6.5	5.3 (0.2)	4.8−5.7	5.5 (0.2)	5.0−5.9	4.4 (0.1)	4.0−4.6
Oct 6, 2001	7.5 (0.3)	6.8−8.0	6.6 (0.2)	6.0−7.0	6.8 (0.2)	6.2−7.2	5.4 (0.2)	5.1−5.7
Oct 9, 2001	4.7 (0.2)	4.3−4.9	4.1 (0.1)	3.8−4.3	4.3 (0.1)	3.9−4.5	3.5 (0.1)	3.2−3.6
Oct 10, 2001	5.5 (0.2)	5.2−5.9	4.9 (0.2)	4.6−5.2	5.1 (0.2)	4.7−5.4	4.1 (0.1)	3.8−4.3
Oct 12, 2001	8.5 (0.3)	7.9−9.2	7.5 (0.2)	7.0−8.0	7.8 (0.3)	7.3−8.4	6.3 (0.1)	5.9−6.6
Oct 13, 2001	5.8 (0.2)	5.3−6.3	5.1 (0.2)	4.7−5.5	5.3 (0.2)	4.8−5.7	4.3 (0.1)	3.9−4.5

Table 5
Estimated sweat rate (kg h^{-1}).

Hunt date	KNM-WT 15000 Large		KNM-WT 15000 Small		OH 28		Recent Kalahari hunter	
	Mean (SD)	Min−max	Mean (SD)	Min−max	Mean (SD)	Min−max	Mean (SD)	Min−max
Aug 29, 1990	1.94 (−)	−	1.69 (−)	−	1.76 (−)	−	1.36 (−)	−
Nov 12, 1998	1.28 (0.05)	1.18−1.36	1.13 (0.04)	1.04−1.19	1.17 (0.04)	1.08−1.24	0.94 (0.02)	0.88−0.98
Nov 18, 1998	1.66 (0.04)	1.55−1.75	1.45 (0.03)	1.35−1.52	1.51 (0.04)	1.41−1.58	1.17 (0.02)	1.09−1.22
Oct 5, 2001	1.40 (0.05)	1.27−1.51	1.23 (0.04)	1.12−1.32	1.27 (0.05)	1.16−1.37	1.02 (0.03)	0.95−1.09
Oct 6, 2001	1.43 (0.06)	1.31−1.53	1.26 (0.04)	1.16−1.33	1.30 (0.05)	1.20−1.38	1.04 (0.03)	0.97−1.09
Oct 9, 2001	1.22 (0.04)	1.11−1.28	1.07 (0.04)	0.98−1.13	1.11 (0.04)	1.01−1.17	0.90 (0.03)	0.83−0.94
Oct 10, 2001	1.09 (0.04)	1.01−1.16	0.96 (0.37)	0.89−2.15	0.99 (0.04)	0.92−1.05	0.81 (0.02)	0.75−0.85
Oct 12, 2001	1.24 (0.04)	1.15−1.34	1.10 (0.03)	1.02−1.17	1.13 (0.04)	1.05−1.21	0.92 (0.02)	0.86−0.97
Oct 13, 2001	1.47 (0.06)	1.34−1.59	1.30 (0.05)	1.18−1.39	1.34 (0.05)	1.22−1.44	1.08 (0.03)	1.00−1.14

Heat gain through skin convection (C_{skin}; W m^{-2}) was estimated as follows:

$$C_{skin} = k \times \sqrt{v} \times (T_{air} - T_k), \tag{28}$$

where k is the convection coefficient (8.3 W m^{-2} °C^{-1}; Kerslake, 1972) and T_k is the temperature at the skin or hair surface (°C).
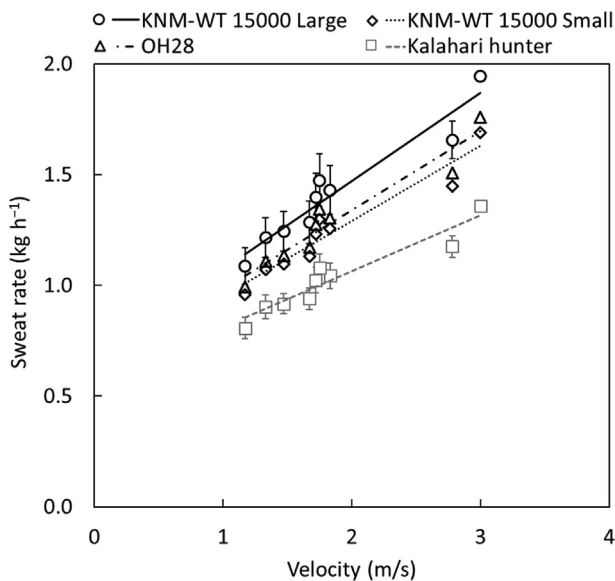

Figure 7. Estimated sweat rate against average velocity for KNM-WT 15000 Large (black circles; black solid line), KNM-WT 15000 Small (black diamonds, black dotted line), OH 28 (black triangles; black dot dashed line), and recent Kalahari hunter (grey squares; grey dashed line). Error bars are ±2 standard deviations (note that error bars are presented only for KNM-WT 15000 Large and recent Kalahari hunter to enhance clarity of figure). Lines are ordinary least square regressions.

Fraction of the body surface area exposed to the direct solar radiation (f_r) was estimated using the following equation derived from the data of Fanger (1970) graphed in Kubaha et al. (2004: their Fig. 13b):

$$f_r = 4.8276 \times 10^{-7} \times \beta^3 - 8.1371 \times 10^{-5} \times \beta^2 + 9.6369 \times 10^{-4} \times \beta + 0.3036. \tag{29}$$

The negative effect of body water loss on skin blood flow, sweat rate and other components of human thermoregulation associated with hypovolemia and hyperosmolality (Sawka et al., 1985, 1992; Armstrong et al., 1997) was not reflected in the present model. We acknowledge that such simplification may overestimate the evaporative heat loss from the skin, and hence the sweat loss, at least in simulations in which a higher degree of hypohydration is achieved.

H. erectus was modeled here using the same values for variables describing heat dissipation capacity as in recent Kalahari hunters. We had initially built three models which differed in heat dissipation capacity: a poor model ($f_{hair} = 0.9$; $w_{max} = 0.5$), intermediate model ($f_{hair} = 0.9$; $w_{max} = 0.8$), and modern-like model ($f_{hair} = 0.15$; $w_{max} = 1$). However, the modern-like model consistently resulted in the highest estimated water loss. Thus, we report here only the results for the modern-like heat dissipation model of *H. erectus* which is the one most prone to dehydration limits.

<u>Validation</u> We searched the published literature for experimental studies of exercise in hot conditions which used minimally clothed subjects. We identified five studies which met these conditions (Table 2). We reproduced eight experiments (some studies reported more than one experiment using different samples for different ambient conditions) by using the reported mean body mass (59.3−76.6 kg) and stature (167.4−183.4 cm) of the sample, air temperature (31−45 °C), relative humidity (23−71%), air flow (0.2−4.2 m s^{-1}), duration (0.7−4 h), either running velocity (2.9−4.6 m s^{-1}; experiments 1, 2 and 10) or metabolic heat

Table 6
Estimated relative water loss (%body mass).

Hunt date	KNM-WT 15000 Large		KNM-WT 15000 Small		OH 28		Recent Kalahari hunter	
	Mean (SD)	Min−max	Mean (SD)	Min−max	Mean (SD)	Min−max	Mean (SD)	Min−max
Aug 29, 1990	5.1 (−)	−	5.1 (−)	−	5.1 (−)	−	5.5 (−)	−
Nov 12, 1998	8.9 (0.3)	8.2−9.4	9.1 (0.3)	8.4−9.6	9.0 (0.3)	8.3−9.5	10.1 (0.3)	9.4−10.5
Nov 18, 1998	8.2 (0.2)	7.7−8.7	8.4 (0.2)	7.9−8.8	8.3 (0.2)	7.8−8.7	9.0 (0.2)	8.4−9.4
Oct 5, 2001	7.8 (0.3)	7.1−8.5	8.0 (0.3)	7.3−8.6	7.9 (0.3)	7.2−8.5	8.8 (0.3)	8.2−9.4
Oct 6, 2001	9.7 (0.4)	8.9−10.4	10.0 (0.3)	9.2−10.6	9.8 (0.4)	9.0−10.4	11.0 (0.3)	10.2−11.5
Oct 9, 2001	6.1 (0.2)	5.6−6.4	6.3 (0.2)	5.8−6.6	6.1 (0.2)	5.6−6.5	7.0 (0.2)	6.5−7.3
Oct 10, 2001	7.2 (0.3)	6.7−7.7	7.4 (0.3)	6.9−7.9	7.3 (0.3)	6.8−7.7	8.3 (0.2)	7.8−8.7
Oct 12, 2001	11.1 (0.4)	10.4−12.0	11.4 (0.4)	10.6−12.2	11.2 (0.4)	10.5−12.0	12.7 (0.3)	11.9−13.4
Oct 13, 2001	7.6 (0.3)	6.9−8.2	7.8 (0.3)	7.1−8.3	7.7 (0.3)	7.0−8.2	8.6 (0.3)	8.0−9.1

production (325−1083 W; experiments 3−9), and initial body core temperature and skin temperature. In cases when the input and output data were available only in figures, we digitized the figures using Gimp 2.8.14 and Microsoft Office Excel 365. All subjects in running experiments were well-trained runners (Marino et al., 2004; Jack, 2010; Che Muhamed et al., 2016). Subjects in the bicycle ergometer experiment underwent intensive physical training prior to the experiment (Mitchell et al., 1976). Subjects in the bench stepping experiment engaged regularly in physical activities but were not specifically trained in any discipline (Shvartz, 1976). Since none of the studies reported maximum wettedness of the subjects, we used the following values derived from the literature (Ravanelli et al., 2018): $w_{max} = 0.72$ for untrained heat-unacclimatised subjects in experiment 4, $w_{max} = 0.85$ for trained heat-unacclimatised subjects in experiments 1−3 and 5−7, and $w_{max} = 1$ for heat-acclimatized subjects in experiment 10. For each experiment, we
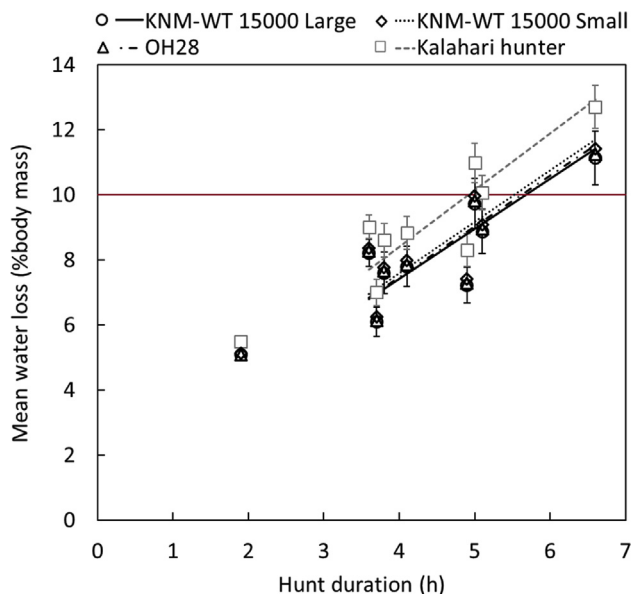

Figure 8. Estimated water loss against hunt duration in KNM-WT 15000 Large (black circles; black solid line), KNM-WT 15000 Small (black diamonds, black dotted line), OH 28 (black triangles; black dotdashed line), and recent Kalahari hunter (grey squares; grey dashed line). Error bars are ±2 standard deviations (note that error bars are presented only for KNM-WT 15000 Large and recent Kalahari hunter to enhance clarity of figure). Lines are reduced major axis regressions through the hunts which lasted over 3 h. The 10% body mass threshold is highlighted by red solid horizontal. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
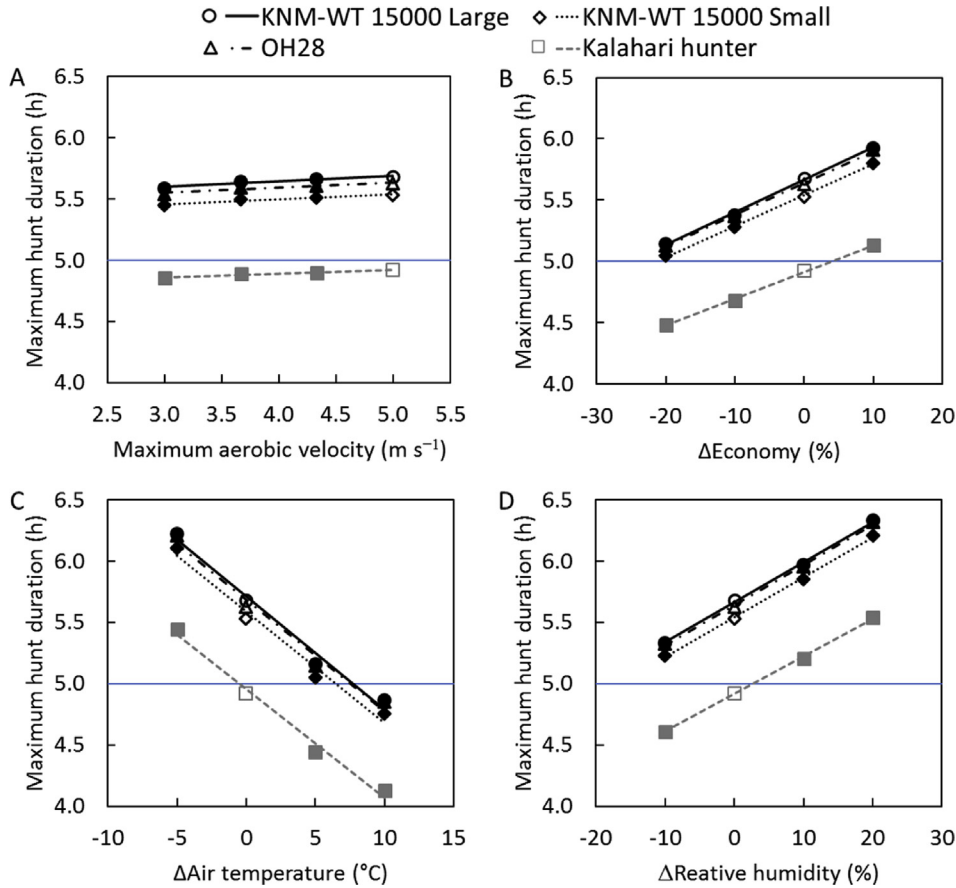
calculated the difference between the estimated and observed water loss. In experiments 5−9, we subtracted respiratory water loss from the estimated water loss prior to comparison with the observed value to reflect the reported data.

The differences between reported and estimated water loss and percentage errors of the estimates are provided in Table 2. The mean difference in water loss was −0.22 kg. The mean difference in relative water loss was −0.32% of body mass. Mean percentage error of estimated water loss was −12.4%. For each experiment except one, the estimated water loss was lower than the observed loss which was to be expected because our model estimates only the evaporated water and does not account for water which drips off of the body. It has been shown (Shapiro et al., 1982) that dripping sweat is a consequence of overshoot in sweating when the rate of required evaporation is close to or higher than the rate of maximum evaporation such as in hot humid conditions and/or low air flow conditions. Our validation results correspond well to these previous observations. The highest percentage errors of estimated water loss were found in indoor experiments 3 and 4 which were characterized by low (1 m s^{-1}) and absent artificial air flow, respectively. In the remaining experiments (1, 2, and 5−10) in which the artificial air flow was high (2.9−4.2 m s^{-1}) and matched the running velocity, the percentage error of estimated water loss was low and negatively related to relative humidity ($b = -0.27$; $r^2 = 0.76$; $p = 0.005$; Fig. 4). Since air flow matched the velocity of locomotion in our simulations of persistence hunting, it may be more relevant for the aims of this study to consider only experiments 1, 2, and 5−10 which yield a mean percentage error of estimated water loss of −6.6%. Accounting for the effect of relative humidity presented in Figure 4 and considering only the Kalahari conditions simulated here (relative humidity: 13%−39%), it can be anticipated that the percentage error of estimated water loss in our persistence hunting simulations would be within ±5%.

2.4. Ambient model

Sun elevation, air temperature, and relative humidity change throughout the day as a function of time. To account for these changes, we used the ambient model to estimate the time specific sun elevation, air temperature, and relative humidity experienced by the hunter.

The elevation of the sun (β) was modeled using equations provided by the National Oceanic and Atmospheric Administration (accessed at https://www.esrl.noaa.gov/gmd/grad/solcalc/NOAA_-Solar_Calculations_day.xls; 11/30/2018) based on Meeus (1991) with a date of the hunt and geographic coordinates as the input data.

The temperature of the air (T_{air};°C) experienced by the subject is estimated following Wheeler (1991a):

Figure 9. Maximum hunt duration against (A) maximum aerobic velocity, (B) locomotor economy, (C) air temperature, and (D) relative humidity in KNM-WT 15000 Large (black circles, black solid line), KNM-WT 15000 Small (black diamonds, black dotted line), OH 28 (black triangles, black dotdashed line), and recent Kalahari hunter (grey squares, grey dashed line). Open symbol is the original model/simulation, filled symbols are adjusted models and simulations. Black and grey lines are ordinary least square regressions, blue solid horizontal line highlights the 5-h maximum successful hunt duration observed in the Kalahari hunting sample (Liebenberg, 2006). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)
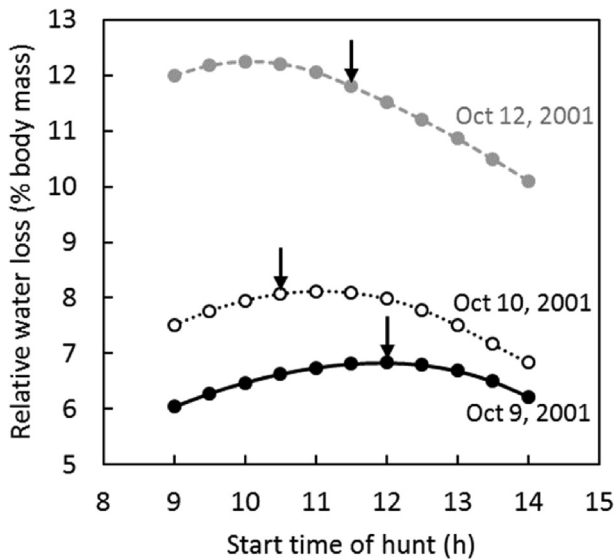

Figure 10. Relative water loss against start time of the hunt for recent Kalahari hunter. Arrows show the observed start time of the hunt (Liebenberg, 2006). Simulations are for walking at the reported average velocity for the whole hunt.

$$T_{air} = T_{200} + \alpha \times (T_g - T_{200}), \tag{30}$$

where T_{200} is the air temperature at 200 cm above the ground (°C), T_g is the air temperature at the ground (°C), and α is the proportion of the gradient between T_g and T_{200} experienced by the subject. An α value of 0.41 introduced for a biped by Wheeler (1991b) was used here. The T_{200} (°C) and T_g (°C) are modeled here as sine waves:

$$T_{200} = \frac{T_{range}}{2} \times sin\left(\frac{2\pi \times (t + t_{Tmax})}{24}\right) + T_{max} - \frac{T_{range}}{2}, \tag{31}$$

$$T_g = \frac{1.4 \times T_{range}}{2} \times sin\left(\frac{2\pi \times (t + t_{Tmax} + 1)}{24}\right) + T_{max} + T_{diff}$$
$$- \frac{1.4 \times T_{range}}{2}, \tag{32}$$

where T_{range} is the daily range of air temperature (°C), t is the time (h), T_{max} is the daily maximum air temperature at 200 cm above the ground (°C), t_{Tmax} is the time (h) of T_{max}, and T_{diff} is the difference between T_{max} and daily maximum T_g (°C). The T_{range}, t_{Tmax}, and T_{diff} were assumed to be characteristic for the central Kalahari whereas T_{max} was specific for each day of the hunt. The daily range of air temperature and time of the T_{max} were estimated from Ghanzi meteorological data (https://www.worldweatheronline.com/
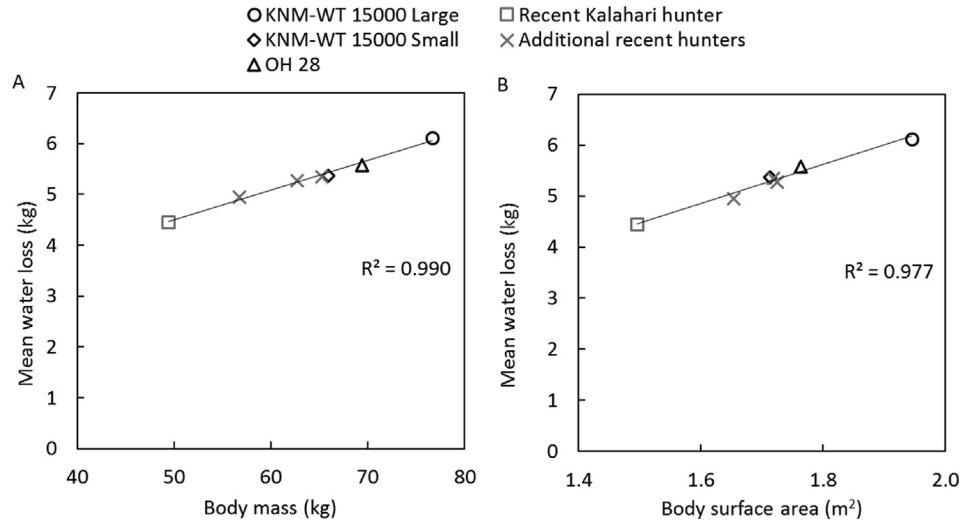
Figure 11. Mean water loss against (A) body mass, and (B) body surface area in KNM-WT 15000 Large (black circle), KNM-WT 15000 Small (black diamond), OH 28 (black triangle), recent Kalahari hunter (grey square), and three additional recent hunters (Aboriginal Australian, Navajo, and Tarahumara; grey crosses). Lines are ordinary least square regressions.

Table 7
Characteristics of models of additional recent hunters.

Model	Body mass (kg)	Stature (cm)	Body surface area[a] (m²)	Body surface area/body mass (cm² kg⁻¹)	Sources[b]
Aboriginal Australian	56.7	169.8	1.65	291.6	1
Navajo	62.7	169.6	1.72	275.0	2
Tarahumara	65.2	165.0	1.72	263.5	3

[a] Estimated from body mass and stature using equation of DuBois and DuBois (1916).
[b] Sources: 1, Abbie (1957); 2, Gabel (1949); 3, Lieberman (2014).

ghanzi-weather-history/ghanzi/bw.aspx; 11/30/2018) as 17 °C and 15:00, respectively. The T_{diff} was assumed to be 5 °C (Wheeler, 1991a).

The relative humidity (ϕ; %) was modeled here as sine wave:

$$\phi = \frac{\phi_{range}}{2} \times sin\left(\frac{2\pi \times (t-2)}{24}\right) + \phi_{avrg}. \tag{33}$$

where ϕ_{range} is the daily range of relative humidity (%) and ϕ_{avrg} is the daily average relative humidity (%). The daily range of relative humidity was estimated from the Ghanzi meteorological data (https://www.worldweatheronline.com/ghanzi-weather-history/ghanzi/bw.aspx; 11/30/2018) as 22%.

2.5. Gait generator

The gait and velocity used by a hunter at each second of the hunt were modeled using the gait generator. We assumed that each hunt comprised of either a single bout of gait at the reported average velocity or of a mixture of walking and running bouts. Since the timing of switches between gaits and the velocity of each gait bout was not reported for the simulated hunts by Liebenberg (2006), we systematically explored 141 combinations of gait switches, bout durations, and bout velocities for each hunt using the gait generator. At first, each hunt was modeled at a single gait and reported average velocity (v_{avrg}) as a walk for hunts at $v_{avrg} < 2$ m s⁻¹ or run for hunts at $v_{avrg} \geq 2$ m s⁻¹. To explore the 140 mixtures of walking and running, the gait generator iterated through four walking-to-running ratios, i.e., ratios of walking to running duration (4:1, 3:2, 2:3, 1:4), five numbers of switches between gaits (1, 3, 7, 15, and 31 switches), and seven walking

velocities (0.5, 0.75, 1.0, 1.25, 1.5, 1.75, and 2.0 m s⁻¹). The combinations of walking-to-running ratios and number of gait switches are shown in Figure 5. At each iteration, running velocity (v_{run}; m s⁻¹) was calculated as:

$$v_{run} = \frac{distance - v_{walk} \times t_{walk}}{t_{run}}, \tag{34}$$

where t_{walk} is duration of walking (h), and t_{run} is the duration of running (h). The t_{walk} (h) and t_{run} (h) were calculated as:

$$t_{walk} = walking\ ratio \times t_{hunt}, \tag{35}$$

$$t_{run} = t_{hunt} - t_{walk}, \tag{36}$$

where t_{hunt} is the duration of the hunt (h). Only iterations which produced running velocity between the assumed walk-to-run transition velocity and maximum aerobic velocity, i.e., between 2 m s⁻¹ and 5 m s⁻¹, were used in further simulations; all the other iterations were discarded.

2.6. Simulations

We simulated nine persistence kudu hunts of recent Kalahari hunters (Table 3) documented by Liebenberg (2006). Although hunters carried water during these hunts and in all but one hunt (August 29, 1990) they were also able to refill their water containers from the accompanying vehicle (Liebenberg, 2006), we simulated the hunts without any water carrying or ingestion. The maximum air temperature and mean relative humidity were taken from the Ghanzi (Botswana) meteorological reports either as day-specific or long-term average value. Ghanzi is located in Central Kalahari about 170 km north-west from the Lone Tree area where the
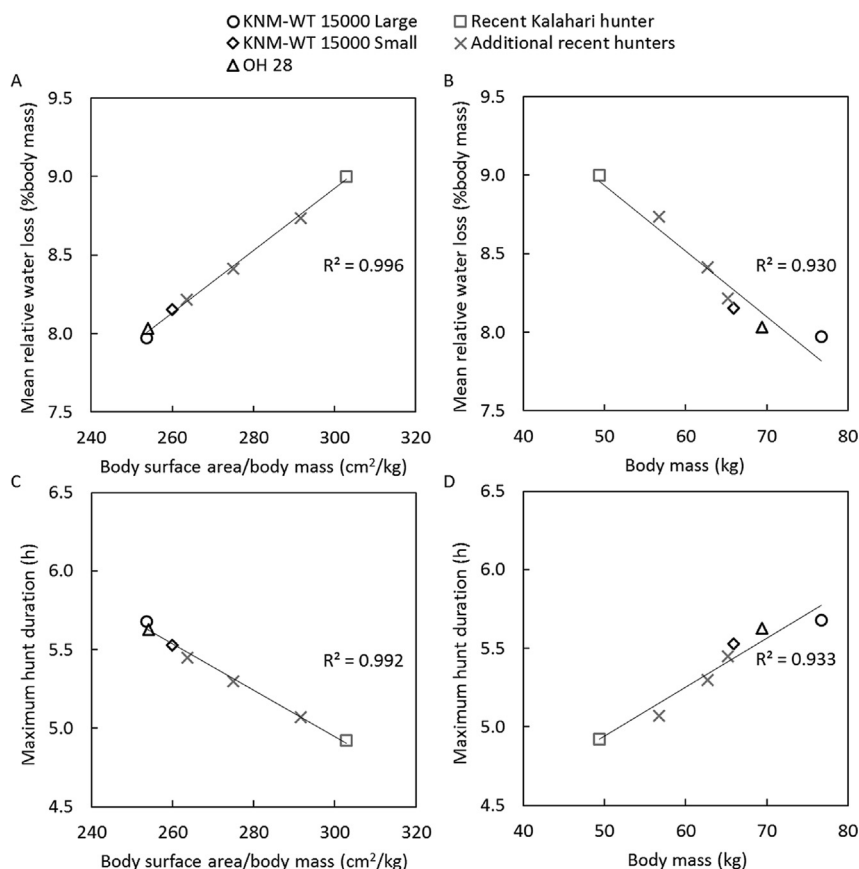
Figure 12. Mean relative water loss (A, B) and maximum hunt duration (C, D) against relative body surface are (A, C) and body mass (B, D) in KNM-WT 15000 Large (black circle), KNM-WT 15000 Small (black diamond), OH 28 (black triangle), recent Kalahari hunter (grey square), and three additional recent hunters (Aboriginal Australian, Navajo, and Tarahumara; grey crosses). Lines are ordinary least square regressions.

hunters observed by Liebenberg (2006) lived. The time of the start of the hunt, duration of the hunt, and average velocity were taken from Liebenberg (2006) and missing values were estimated.

The maximum air temperature for the given day was taken from the Ghanzi meteorological reports (https://geographic.org/global_weather) rather than from Liebenberg (2006). There are no details about measurements of the highest temperature provided by Liebenberg (2006). In the field conditions, the highest temperature reported by Liebenberg was hardly taken at the standardized conditions 200 cm above ground. More likely, the temperature was measured by a car thermometer which is usually located in the front bumper about 0.5–1 m above the ground where the temperature is higher than the T_{200} (Mildrexler et al., 2011). Indeed, the maximum temperature reported by Liebenberg (2006) was on average 6.3 °C higher than the maximum temperature reported for the same dates by the meteorological station in Ghanzi. For one day (November 12, 1998), the Ghanzi temperature data were not available and the T_{max} was estimated by subtracting the average difference between the Ghanzi and Liebenberg reports (i.e., 6.3 °C) from the value reported by Liebenberg (2006). The daily average relative humidity was approximated as the reported mean relative humidity for the given month during 2009–2017 at Ghanzi (https://www.worldweatheronline.com/ghanzi-weather-averages/ghanzi/bw.aspx; 11/30/2018). The actual time-specific elevation of the sun (β) was estimated for the geographic location (latitude = −23.097, longitude = 22.269) of the Lone Tree. The time-specific values (at each second) of the air temperature experienced by the hunter, relative humidity of the air, sun elevation, and direct solar irradiance for each hunt are shown in Figure 6.

The start time was not provided for six hunts. We simulated these six hunts as starting at each half an hour between 9:00 and 14:00 and then selected the start time at which the hunt resulted in the greatest body mass loss. The duration of one hunt (August 29, 1990) was provided only approximately as "less than 2 h" (Liebenberg, 2006: 1018) which we approximate here as 1.9 h. Using the average velocity and duration of each hunt, the gait generator produced between 16 and 86 meaningful simulations per hunt, i.e., simulations in which the running velocity was within the desired range of 2–5 m s^{-1}. The average velocity was missing for one hunt (August 29, 1990) but it was specified that the hunter "ran the entire way" (Liebenberg, 2006: 1018). We assumed, that the running velocity would be close to that reported for the fastest of the other hunts (November 18, 1998) and simulated this hunt as a single running bout at 3 m s^{-1} velocity.

To account for unknown aerobic capacity and locomotor economy of *H. erectus*, we built six additional models of each hunter which differed in maximum aerobic velocity and metabolic heat production, respectively. To simulate lower aerobic capacity, we additionally reduced the maximal aerobic running velocity from 5 m s^{-1} to 4.33, 3.67, and 3 m s^{-1}. To simulate different locomotor economy, we additionally increased the estimated metabolic heat production by 10% and 20%, and also decreased it by 10%.

To assess how sensitive our water loss estimations are to air temperature and relative humidity, we simulated the hunts also at maximum daily temperature changed by −5 °C, +5 °C, and +10 °C, and at mean daily relative humidity changed by −10%, +10%, and +20%. All these changes are related to values provided in Table 3.
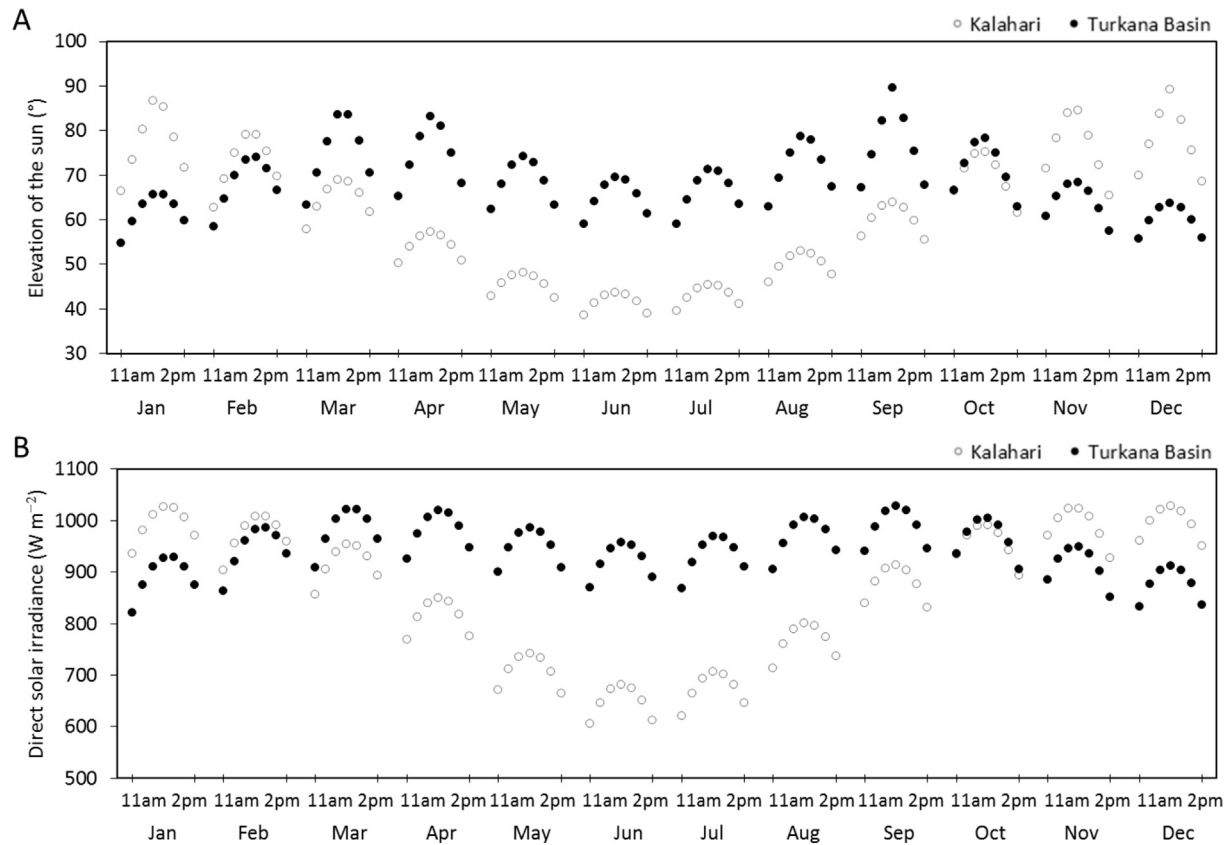
Figure 13. Comparison of elevation of the sun and direct solar irradiance between Kalahari and Turkana Basin (Lodwar, Kenya) around midday (11:00−14:00) on the 15th day of each month of the year. Elevation of the sun was modeled using equations provided by National Oceanic and Atmospheric Administration based on Meeus (1991), direct solar irradiance was estimated using Eq. (23).

2.7. Evaluation of water loss

We provided absolute volume of total water loss in kilograms per hunt. For comparison with previously reported sweat rates, we also provided the average sweat rate (kg h^{-1}) per hunt. Finally, we evaluated the relative water loss as a percentage body mass loss, which is widely used in sport research and medicine as an easily obtainable proxy for dehydration (Sawka et al., 2007). For each hunter, we performed a reduced major axis regression of estimated percentage body mass loss on hunt duration. The hunt performed on August 29, 1990 was excluded from the regression due to lower confidence in the estimate related to unreported average velocity. A maximum hunt duration at which the hunter loses 10% of body mass was then determined using the regression equation. We evaluated the dehydration as being a limit for persistence hunting if the maximum hunt duration was less than 5 h.

3. Results

The absolute values of estimated water loss and sweat rate are presented in Tables 4 and 5, respectively. *H. erectus* lost on average 5.7 kg of water per hunt (min−max: 3.4−8.5 kg) which was 1.2 kg more than the recent Kalahari hunter. Sweat rate was between 1.0 and 1.9 kg h^{-1} in *H. erectus* and between 0.8 and 1.4 kg h^{-1} in the recent Kalahari hunter. A plot of sweat rate against average velocity in *H. erectus* and the recent Kalahari hunter is shown in Figure 7. Sweat loss accounted on average for 96% of total water loss (KNM-WT 15000 Large mean ± SD: 95.7 ± 0.65%; KNM-WT 15000 Small:

95.7 ± 0.63%; OH 28: 95.7 ± 0.64%; Kalahari hunter: 96.0 ± 0.60%), the remaining 4% being the respiratory water loss.

The relative water loss as percentage of body mass is presented in Table 6. *H. erectus* lost on average 8.1% of body mass per hunt (min−max: 5.1% and 11.1%) which was 0.9% of body mass less than the recent Kalahari hunter. A plot of relative water loss against hunt duration in recent Kalahari hunters and *H. erectus* is shown in Figure 8. The relative water loss is significantly positively related to hunt duration in both *H. erectus* (KNM-WT 15000 Large: b = 1.544, r = 0.817, p = 0.013; KNM-WT 15000 Small: b = 1.581, r = 0.824, p = 0.012; OH 28: b = 1.557, r = 0.820, p = 0.013) and the Kalahari hunter (b = 1.745, r = 0.853, p = 0.007). KNM-WT 15000 Large lost 10% of body mass in 5.68 h of persistence hunting, KNM-WT 15000 Small in 5.53 h, OH 28 in 5.63 h, and the recent Kalahari hunter in 4.92 h.

The sensitivity of the maximum hunt duration to maximum aerobic velocity, locomotor economy, air temperature, and relative humidity is shown in Figure 9. The maximum hunt duration was positively related to maximum aerobic velocity (b = 0.040−0.044 and 0.033 h s m^{-1} for *H. erectus* and the recent Kalahari hunter, respectively), locomotor economy (b = 0.025−0.027 and 0.022 h %$^{-1}$), and relative humidity (b = 0.033 and 0.031 h %$^{-1}$), whereas it was negatively related to air temperature (b = −0.092−(−0.091) and −0.089 h °C^{-1}).

4. Discussion

Our results suggest that dehydration would not limit persistence hunting in *H. erectus*. In our simulations, *H. erectus* could hunt for

between 5 h and 32 min and 5 h and 40 min with no drinking before reaching the dehydration limit. The longest reported successful persistence kudu hunt by modern hunters took 5 h (Liebenberg, 2006) at which time *H. erectus* would lose about 9.0% of body mass. Such a degree of dehydration is not life-threatening for humans and other primates (Adolph, 1947; Schmidt-Nielsen, 1964; Zurovsky et al., 1984; Beis et al., 2012). Thus, the persistence hunting of prey of similar or lower endurance to modern-day kudu by *H. erectus* in Kalahari-like savanna conditions would not be limited by a lack of water containers.

4.1. Effect of physiology and soft-tissue morphology

The maximum hunt duration with no water would be affected by deviations from the assumed physiology and soft-tissue morphology of *H. erectus* related to heat dissipation capacity, locomotor economy, and aerobic capacity. Previous studies linked the evolution of heat dissipation capacity in hominins to evolution of bipedal walking in open habitats in early hominins (Wheeler, 1984, 1985; Zihlman and Cohn, 1988) and alternatively to evolution of the hunting and gathering in the genus *Homo* (Jablonski, 2012; Lieberman, 2015). Although both of these hypotheses assume that *H. erectus* already had derived eccrine sweating system and lacked a hair coat, the exact state of the heat dissipation capacity of *H. erectus* is not known. Our model predicted that if the heat dissipation capacity of *H. erectus* was lower than in modern humans, *H. erectus* would reach the 10% dehydration threshold later. The poor model and intermediate model of heat dissipation capacity in KNM-WT 15000 Large resulted in reduced relative water loss, by 1.66% and 0.93% body mass, respectively, in comparison to the modern-like model. Consequently, the maximum hunt duration of the poor model and intermediate model would be 64 and 36 min longer, respectively. The lower water loss in the poor model and intermediate model is primarily a consequence of lower maximum wettedness. These models were able to cover lower proportion of their skin with sweat, which resulted in lower skin evaporation and sweat rate. Dehydration would thus be even less a limit for a hominin with lower heat dissipation capacity which makes our conclusions based on modern-like model of *H. erectus* conservative. On the other hand, although more resistant to dehydration, the poor model and intermediate model would be more prone to hyperthermia which may affect the ability to complete the hunts. Our results suggest that it was not dehydration or the absence of water containers what limited the use of persistence hunting in human evolution, but another important limiting factor of persistence hunting − hyperthermia, has not been evaluated here. Future studies need to model both water loss and changes in body temperatures to evaluate the limits of persistence hunting in *H. erectus* and earlier hominins.

Our model predicted that a decrease in locomotor economy by as much as 20% would still allow *H. erectus* to hunt with no drinking for more than 5 h. Since previous studies ascribed to *H. erectus* an economy of locomotion similar to modern humans (Wang et al., 2004; Steudel-Numbers, 2006; Pontzer, 2017) the actual deviation of *H. erectus* from the modern human economy was likely within the 20% modeled here.

A decrease of the maximum aerobic velocity from 5 to 3 m s^{-1} shortened the maximum hunt duration of *H. erectus* by only 5 min. If *H. erectus* had the same walk-to-run transition velocity as modern humans at about 2 m s^{-1} (Thorstensson and Roberthson, 1987; Hreljac, 1993), a further reduction of maximum aerobic velocity (below 3 m s^{-1}) would be unjustified because it would preclude *H. erectus* from using endurance running or at least from using it economically (Steudel-Numbers and Wall-Scheffler, 2009). Previous interpretations of the lower limb morphology of *H. erectus*

(Bramble and Lieberman, 2004) suggest that it was capable of endurance running. Our estimates of the maximum hunt duration without drinking in *H. erectus* are thus conservative in relation to possible deviations from the heat dissipation capacity, locomotor economy, and aerobic capacity of modern humans.

4.2. Effect of ambient conditions

Key variables in our model – air temperature and relative humidity – which characterized the ambient conditions were not measured (at standardized conditions) at the place of the hunts but were taken from a nearby meteorological station. Thus, the simulated conditions could deviate to some degree from the actual conditions at the hunt. Our sensitivity analysis (Fig. 9C) showed that undervaluation of the daily maximum air temperature by up to 5 °C would not change the conclusion of our study. A 5 °C increase of the daily maximum temperature would result in a maximum hunt duration of 3−10 min above our 5-h threshold. A decrease of the maximum daily temperature would, on the other hand, lead to a greater maximum hunt duration. A decrease of relative humidity by 10% (i.e., to values of relative humidity during the hunts between 3% and 30%) shortened the maximum hunt duration by 18−21 min to the resulting 5.23−5.33 h. A further decrease of relative humidity would result in values reaching zero for some hunts and thus was not modeled here.

Since ambient conditions vary with the time of day in our model and the start time of the hunt was not reported by Liebenberg (2006) for the six hunts, we first simulated these six hunts as starting at each half an hour between 9:00 and 14:00. In further analyses, we used the start time which produced the greatest water loss. This approach might overestimate water loss in at least some of these six hunts because the actual start time does not always coincide with the most-water-demanding time as can be seen in the three remaining hunts (Fig. 10) for which the start time was reported by Liebenberg (2006). In one of the three remaining hunts (October 9), the reported start time coincided with the simulated most-water-demanding time. In two other hunts (October 10 and 12), the reported start time differed by 0.5 and 1.5 h from the simulated most-water-demanding time, respectively. Our approach, which uses the most-water-demanding time, would overestimate the relative water loss in these two hunts in recent Kalahari hunter by 0.1−0.4% of body mass.

The maximum hunt duration with no water could be underestimated here due to modeling the hunter as being exposed to direct solar radiation throughout the whole hunt. In real world conditions, solar radiation may occasionally be blocked by clouds or trees. Using the reported average number of sunshine hours per year in the Kalahari (Andringa, 1986), it can be deduced that cloudy hours comprise about 21−23% of daytime per year. It had been partially cloudy in at least one of the successful modern human hunts simulated here (November 18, 1998) as is illustrated in the documentary film The Great Dance by Craig and Damon Foster about this hunt. In addition, the prey would likely be attracted to tree shade and the hunter would subsequently spend part of the hunt in the shade while following the prey. To illustrate the magnitude of the effect of direct solar exposure on relative water loss and maximum hunt duration with no drinking, we performed additional simulations of the hunts with no exposure to direct solar radiation in KNM-WT 150000 Large. No exposure to direct solar radiation resulted in reduction of sweat rate by 0.32 ± 0.03 kg h^{-1} (mean ± SD) and a decrease in relative water loss of 1.8 ± 0.41% body mass in comparison to simulations with permanent direct solar exposure. Such decrease of relative water loss would prolong the maximum duration of hunt in *H. erectus* by 68−70 min.

4.3. Effect of body size and shape

Since the ambient conditions and hunt characteristics were the same for all hunters, the differences in water loss and maximum hunt duration should be attributable to differences in body size and/or body shape of the hunters. At heat balance, i.e., assuming no change in core temperature and skin temperature, a combined evaporation from skin and respiratory tract which determines the water loss can be expressed by combining Eq. (11) and Eq. (18) as follows:

$$E_{skin} + E_{resp} = M + C_{resp} + H_{dry}. \qquad (37)$$

Since M and C_{resp} are proportional to body mass (Eqs. (3), (5) and (19)) and H_{dry} is proportional to body surface area (Eq. (21)), it follows that water loss should be positively related to both body mass and body surface area:

$$\text{Water Loss} \sim m + A, \qquad (38)$$

which is what we see in our extended sample of past and recent hunters in Figure 11 (for details about three additional models of recent persistence hunters see Table 7; Gabel, 1949; Abbie, 1957; Lieberman, 2014). Division of both sides of Eq. (38) by body mass results in relative water loss being proportional to relative body surface area:

$$\text{Relative Water Loss} \sim 1 + \frac{A}{m}, \qquad (39)$$

which reflects well our data presented in Figure 12A. The low variation in relative water loss (range: 0.18% body mass) and maximum hunt duration (range: 9 min) estimated here for *H. erectus* is thus a consequence of low variation in relative body surface area (254−260 cm^2 kg^{-1}; Fig. 12A and C).

The negative relationship between maximum hunt duration and relative body surface area presented in Figure 12C also could be used to assess dehydration limits in other human species or populations. Small-bodied early *Homo* taxa would have greater relative body surface area (due to the scaling of area to volume; e.g., Ruff, 1994) and hence shorter maximum hunt duration than a larger-bodied *H. erectus* (relationship illustrated in Fig. 12B and D). This relationship also has been pointed out theoretically by Wheeler (1992b) and experimentally by Brown (1947) who has reported that soldiers of greater body mass endure marching through the desert without water longer than individuals of lower body mass. Persistence hunting in small-bodied early *Homo* would thus be more limited by dehydration than in large-bodied *H. erectus*. An increase of body mass in African *H. erectus* (Ruff et al., 2018) may then reflect selection for increased resistance to dehydration induced by persistence hunting. In this scenario, the increase of body mass in African *H. erectus* in comparison to early *Homo* may reflect either initiation or intensification of persistence hunting. Nevertheless, even if early *Homo* had a relative body surface area similar to that of the recent Kalahari hunter, early *Homo* would still be able to hunt for almost 5 h without water (Fig. 12C). If dehydration was the most limiting factor of endurance in small-bodied *Homo*, it would probably not preclude them from persistence hunting entirely, but rather may lower their success rate or modulate focus on specific optimal conditions (Liebenberg, 2006). Increased maximum hunt duration due to greater resistance to dehydration would improve fitness of *H. erectus* thanks to increased reliability of food (due to higher success rate) and a greater amount of food (due to focusing on more persistent and likely larger prey).

Our Dehydration Resistance Model is in opposition to Bergman's rule. According to Bergman's rule, hot environments should be inhabited by smaller individuals with high relative body surface area which would allow them to lose more heat through the skin relatively to their metabolic heat production (Bergmann, 1848; Ruff, 1994). From this view, large relative body surface area would be beneficial during activities associated with high metabolic heat production in hot environments, such as during persistence hunting. Although variation in body mass and relative body surface area in recent human populations reflects the Bergman's rule (Roberts, 1953; Ruff, 1994; Katzmarzyk and Leonard, 1998), recent humans possess water containers which make them less limited by dehydration in comparison to past human taxa. It has been pointed out by Pontzer (2012) that elite endurance runners also fit the underlying principles of Bergman's rule by having low body mass and high relative body surface area, which is in contrast to the body size increase seen in the proposed first endurance runners − *H. erectus*. However, recent athletes are not limited by dehydration because water is provided during races. On the other hand, relative body surface area in ancient persistence hunters with no water containers might reflect a compromise between selection for resistance to dehydration and selection for the ability to lose enough heat to avoid hyperthermia (but note that body size and consequently relative body surface area are also under selection for reasons not related to thermoregulation, see e.g., Walker et al., 2006; Pontzer, 2012). Future studies of the evolution of body size and body shape in hominins in a thermoregulatory context would thus benefit from modeling together both limiting factors – dehydration and hyperthermia. The present heat exchange model may be expedient for such applications after its validation for estimation of body temperatures. Simulations of other subsistence activities relevant for Early Pleistocene *Homo* such as gathering or scavenging in addition to persistence hunting would enrich the discussion about evolution of human body size and body shape.

4.4. Persistence hunting in East Africa

In this study, we have simulated persistence hunting in semi-arid conditions of Southern African Kalahari, for which ethnographic records are available. However, the KNM-WT 15000, OH 28 and many other fossils of *H. erectus* come from the equatorial East Africa, where water loss during persistence hunting might be different due to differences in climate. Although elevation of the sun around midday is on average higher at the Equator than in Kalahari, the nine hunts simulated in this study happen most often in October (n = 6) and November (n = 2), when the elevation of the sun in Kalahari is close to the average and even close to the highest observed elevation at the Equator (Lodwar, Turkana Basin, Kenya), respectively (Fig. 13A). The heat loads due to direct solar radiation simulated in this study for Kalahari thus represent well the radiation loads at the equatorial East Africa (Fig. 13B). Daily maximum air temperatures in equatorial East Africa vary little throughout the year and are similar to those simulated here for Kalahari conditions (annual average maximum temperature in Lodwar, Turkana Basin, Kenya: 34 °C, min−max monthly average maximum temperature: 33−36 °C; https://weather-and-climate.com/average-monthly-min-max-Temperature,Lodwar,Kenya; 05/31/2019). The Kalahari would thus be a useful model also for East African air temperatures. Relative humidity in equatorial East Africa is also relatively stable throughout the year, but on average 22% higher than relative humidity simulated here for Kalahari (annual average relative humidity in Lodwar, Turkana Basin, Kenya: 47%, min−max monthly averages: 42−52%; https://weather-and-climate.com/average-monthly-Humidity-perc,Lodwar,Kenya; 05/31/2019). As discussed above, our model predicts lower water loss and thus greater endurance in more humid conditions. In consequence, dehydration should be even less limiting factor for persistence hunting in

today's East Africa than in Kalahari. On the other hand, greater relative humidity would limit heat dissipation capacity of both the hunter and prey which would likely result in shorter duration of the hunt due to hyperthermia of the prey or in failure of the hunt due to hyperthermia of the hunter.

Paleoenvironmental studies suggest oscillation of drier and wetter periods in equatorial East Africa during Pleistocene (deMenocal, 2004; Trauth et al., 2007). Yet, at least the Turkana Basin, which revealed many key H. erectus fossils including the KNM-WT 15000, has been continually hot during the past 4 million years with air temperatures and solar radiation similar to today's levels (Passey et al., 2010). Faunal (Bobe and Leakey, 2009) and carbon isotope (Cerling, 1992; Wynn, 2004) studies show a shift to more open seasonally arid savanna in the Turkana Basin prior the emergence of H. erectus in the area. The current Kalahari ambient conditions simulated here thus seem to be a conservative model for persistence hunting in H. erectus in East Africa since they are characterized by similar elevations of the sun and air temperatures and reflect the drier climatic periods during which persistence hunting is most limited by dehydration.

Although it is tempting to manipulate the ambient conditions in our simulations to explore maximum hunt duration of H. erectus in more diverse environments, such results would have little ecological meaning without also modeling the endurance of the prey. It is only the difference between the endurance of the hunter and its prey in favor of the hunter which makes persistence hunting a feasible strategy (Carrier, 1984). Future studies should model the dehydration and hyperthermia of the prey to explore the range of possible prey species and sizes as different prey may be tackled by human hunters at different environments, ambient conditions (i.e., parts of the year), and even by different Homo taxa.

4.5. Water containers

Although our study shows that African H. erectus would not need to carry water to persistence hunt, the present model can be used to explore the possible benefits of water containers to increasing the duration of a hunt. At mean estimated sweat rate of 1.315 kg h^{-1}, a liter of carried water would allow H. erectus to hunt for about 46 min longer before reaching the dehydration limit. A hunter of the size and relative body surface area of our recent Kalahari hunter with mean sweat rate of 1.027 kg h^{-1} could hunt for 58 min longer with one liter of water. The actual benefit of the carried water would be somewhat lower as the carried load would increase metabolic heat production (Watson et al., 2008) which would subsequently increase evaporation.

4.6. Prey

A prerequisite of a successful persistence hunt is that the hunter has greater endurance in the given ambient conditions than the prey. Midday hot ambient conditions seem best for persistence hunting since these make the prey more prone to hyperthermia (Carrier, 1984) and lower the competitivity from other predators who are generally more active around dusk and dawn (Schaller, 1976; Kimura, 1984). Generally, the easiest prey to acquire would be large (thus having low relative surface area) heterothermic (thus allowing its body core temperature to rise closer to the life-threatening level during the day) and relying primarily on panting to dissipate heat (thus having difficulties dissipating heat during locomotion) (Carrier, 1984). Nevertheless, a wide variety of species have been reported to be prey in persistence hunting including gemsbok, wildebeest (Schapera, 1934), deer (Bennett and Zingg, 1935; Pennington, 1963), pronghorn antelope (Lowie, 1924), but also small animals like hare (Schmidt-Nielsen, 1964), duicker and

steenbok (Schapera, 1934), and even sweating animals like kangaroo (Sollas, 1911; McCarthy, 1957) and zebra (Schapera, 1934). Prey with greater endurance than kudu could likely also be hunted without the need to carry water, however it may require more favorable conditions that would decrease the endurance of the prey. Liebenberg (2006) reported that some species are hunted in rainy season because wet sand forces open their hoofs and stiffens the joints, other species are known to tire more easily in loose sand during the dry season. Heavy horns, pregnancy, injury, illness or poor nourishment at the end of dry season were also reported to decrease the endurance of the prey and so was a full moon (animals are more active during night and hence more tired during day) (Liebenberg, 2006). Alternatively, persistence hunting prey with greater endurance in similar ambient conditions to those modelled here would yield lower a success rate. However, even such lower success rate of persistence hunting may still be comparable or higher than the success rates of other hunting approaches (Liebenberg, 2006).

4.7. Rehydration at the end of hunt

Our model predicted only the water lost during the persistence hunt itself, but additional water loss would be associated with after−hunt activities like defending the prey against other predators, butchering, carrying the prey back to camp, or even just waiting for other members of the hunting group. In many instances the prey would be driven into exhaustion well before the water loss threshold of the hunter is reached and thus the hunter would have a reserve to perform the activities needed to secure, process, and transport the prey. In cases when the hunter would be at the edge of his or her dehydration threshold, the hunter could utilize body liquids of the prey, water sources around the killing site, or assistance from other members of the hunting group. Rumen fluid would likely be the first choice of the thirsty hunter as it is basically pure water with some electrolytes − an additional benefit for a hunter who lost much salt in his sweat (Schmidt-Nielsen, 1964). Moreover, usage of rumen fluid as a drinking water has been observed at several places in Africa (Schmidt-Nielsen, 1964; Liebenberg, 2013) including Kalahari at the end of persistence hunt as shown in David Attenborough's documentary film Life of Mammals. Nevertheless, rumen fluid may not be drinkable in occasions when the prey had eaten plants poisonous to humans (Liebenberg, 2013). Blood is generally not a good source of water because processing its protein requires more water than the blood contains (Moran, 2008). The suitability of blood as a water source at the end of persistence hunting might be further lowered due to presence of endotoxins like lipopolysaccharides (Slawinska et al., 2016; Vargas and Marino, 2016), although the effects of drinking such blood are unexplored. Surface water sources are possible but not likely to be used in generally hot dry environments, but water-rich tubers and melons could be available around the kill site at least during some parts of the year. In addition, other members of the hunting group might bring water e.g., in form of tuber or vegetables for the lead hunter. It seems reasonable to assume that persistence hunting was a collaborative group activity in past hominins since it is so in modern human hunters (Liebenberg, 2006) and also other primates pursuit prey in groups (e.g., baboons and chimpanzees; Harding and Strum, 1976; Boesch, 1994). It is, however, less clear when in human evolution the collaboration could reach the complexity of providing water to a group member in need. It should also be noted that the killing site might not be far from the other hunters or even from the home base. Liebenberg (2006) observed that prey often crosses its own path during the hunt and as a result the hunt might end close to where it started. It is thus likely that known water sources and/or help with

rehydration, processing, securing, and transporting the prey would be close to the killing site.

4.8. Limitations of the heat exchange model

Our heat exchange model does not account for sweat lost from dripping, mass loss due to substrate oxidation, and dehydration-related reduction in heat dissipation. Our model estimates only sweat evaporated from the skin that has a thermoregulatory function. Because sweat lost from dripping is wasted, omission of dripping sweat in our model resulted in systematic underestimation of water loss in our validation study (Table 2). Previous studies have shown that overproduction of sweat is associated with conditions in which heat balance is not achieved due to required evaporation being close to or greater than the maximum evaporation (Shapiro et al., 1982). Heat balance was achieved in all our simulations suggesting that there should be little overproduction of sweat. If we use the mean percentage error of estimated water loss (-6.6%.) from the relevant validation experiments (1, 2 and 5–10; Table 2) as an approximation of the error in our simulations of hunts by *H. erectus*, we will get an underestimation of water loss of about 0.5% body mass which would result in overestimation of the maximum hunt duration by 19 min. The resulting maximum hunt duration of *H. erectus* would still be well above our 5-h threshold. If we account also for the effect of relative humidity on percentage error of estimated water loss (Fig. 4), the error of estimated water loss in the Kalahari would be within 5%. The higher relative humidity in the Turkana Basin (47%) would then correspond to percentage error of estimated water loss of about 6.5%.

Our model underestimates body mass loss due to omission of the mass loss due to substrate oxidation. The mass loss due to substrate oxidation however is low because a large amount of water is produced during the oxidation process which remains within the body (Maughan et al., 2007). Oxidation of one gram of carbohydrate results in a 0.4 g loss of body mass, whereas oxidation of one gram of fat actually results in a 0.13 g gain of body mass (Maughan et al., 2007). Using the metabolic heat production estimated here and the data of Maughan et al. (2007: their Table 2) which link the contribution of carbohydrate and fat to the relative intensity of exercise (% VO_{2max}), we can estimate the mass loss due to substrate oxidation (Table 8). In two hunts (August 29, 1990 and November 18, 1998) performed at average running velocities (intensity of about 60% VO_{2max}), the contribution of carbohydrates to fats would be about 3:1, which would result in 0.13–0.22% body mass loss per hunt. During the remaining seven slower hunts (intensity of about 25% VO_{2max}), the energy would be derived mainly

from fats (carbohydrates to fats proportion: 2:3) and the resulting loss would be only 0.04–0.09% of body mass per hunt. The mean underestimation of relative water loss in all the nine simulated hunts would be 0.09% of body mass which would shorten the maximum hunt duration by 3.5 min. The omission of substrate oxidation in our model therefore had no significant impact on the conclusions of this study.

The deterioration effect of dehydration above 3–5% of body mass loss on skin blood flow, sweat rate and other components of human thermoregulation (Sawka et al., 1985, 1992; Armstrong et al., 1997) is not accounted for in the present model. Consequently, our model somewhat overestimates the sweat loss at higher degrees of hypohydration. This simplification is conservative because incorporation of the dehydration effect on sweat loss would result in lower estimates of water loss and hence longer duration of the hunt without reaching the dehydration threshold.

4.9. Long-term effect of persistence hunting and dehydration

Whereas recurring dehydration has historically been viewed as having reversible effects on organs of the body, particularly on the kidneys, more recent research has clearly identified recurring dehydration as a risk factor for chronic kidney disease in modern humans (Johnson et al., 2014; Robey, 2014; Roncal Jimenez et al., 2014; García-Trabanino et al., 2015; Roncal-Jimenez et al., 2015; Wegman et al., 2018). Chronic kidney disease creates a host of physiological problems, and leads to damage in virtually every other system – it leads to bone loss and its associated anemia, as well as nerve damage and whole-system cardiovascular disease (Webster et al., 2017). While it might seem most likely that chronic kidney disease only influences the post-reproductive life span and thus may not influence fitness, in actuality, recurring dehydration leads to the onset of chronic kidney disease (and subsequent death) in reproductive-aged people (O'Donnell et al., 2011; Correa-Rotter et al., 2014; Crowe, 2014). Up to this point, recurring dehydration has meant consistent dehydration over a shorter-term period – like daily throughout a dry season – which may not be how regularly humans practiced endurance hunting (Liebenberg, 2006). Nonetheless, the strong relationship between regularly occurring dehydration and the deterioration of kidney health could reasonably trigger selection for improved kidney function. Such selection would most likely be on a regulatory rather than morphological level (Skov et al., 1999; MacManes, 2017), but currently, we are not aware of any data that would support derived kidney function in humans in comparison to other apes.

Table 8
Estimated body mass loss due to substrate oxidation in KNM-WT 15000 Large during persistence hunts reported by Liebenberg (2006) and simulated as a single gait bout at reported average velocity.

Hunt date	M (W)	%VO_{2max} (%)	Carb:Fat contribution (%)	Energetic expenditure (kcal)	Substrate oxidation (g)		Body mass loss (g)			Relative body mass loss (%body mass)
					Carb	Fat	Carb	Fat	Total	
Aug 29, 1990	1004	60	67:33	1642	269	58	−108	8	−100	−0.131
Nov 12, 1998	425	25	42:58	1865	191	116	−76	15	−61	−0.080
Nov 18, 1998	941	56	65:35	2916	459	111	−184	14	−169	−0.221
Oct 5, 2001	439	26	43:57	1550	161	96	−64	12	−52	−0.068
Oct 6, 2001	473	28	44:56	2033	218	122	−87	16	−71	−0.093
Oct 9, 2001	338	20	38:62	1077	100	72	−40	9	−31	−0.040
Oct 10, 2001	304	18	37:63	1283	115	87	−46	11	−34	−0.045
Oct 12, 2001	372	22	40:60	2111	204	137	−82	18	−64	−0.083
Oct 13, 2001	448	27	43:57	1466	153	90	−61	12	−50	−0.065

M [W], metabolic heat production estimated using Eqs. (3) and (5); %VO_{2max} [%] = M [W]/VO_{2max} [W] × 100, assuming VO_{2max} = 1688 W (Maughan et al., 2007); Carb contribution [%] = %VO_{2max} [%] × 0.738 + 23.29 (equation derived from data of Maughan et al., 2007, their Table 2); Energetic expenditure [kcal] = M [W] × t_{hunt} [s]/4184 [J kcal^{-1}]; Substrate oxidation [g] = energetic expenditure [kcal] × contribution of substrate [%]/100/energy in substrate (carbohydrate: 4.1 kcal g^{-1}; fat: 9.3 kcal g^{-1}); Body mass loss [g] = substrate oxidation [g] × mass change due to substrate oxidation (carbohydrate: 0.6 g g^{-1}; fat: 1.13 g g^{-1}).

5. Conclusions

In ambient conditions characteristic of persistence hunting in the modern Kalahari, which we argue is a conservative model for Early Pleistocene East Africa, African *H. erectus* would reach a dehydration limit of 10% body mass loss in 5.5–5.7 h. As such, *H. erectus* would be able to accomplish all reported successful persistence hunts of large prey (kudu) by modern humans, as the longest of these hunts took 5 h. Moreover, our model shows that *H. erectus* would be able to persistence hunt over 5 h with no drinking despite possible deviations from modern-like heat dissipation capacity, aerobic capacity, and locomotor economy. Maximum hunt duration without drinking was negatively related to relative body surface area of the hunter which may have implications for the evolution of human body size and body shape prior to the invention of water containers. We conclude that *H. erectus* could persistence hunt large prey without the need to carry water. Since water loss would be even lower in hominins with lower heat dissipation capacity, we conclude that neither dehydration nor absence of water containers, but rather hyperthermia was the likely limit for inclusion of persistence hunting into hominin subsistence strategy. Future studies need to model both water loss and changes in body temperatures to evaluate the limits of persistence hunting in *H. erectus* and other hominins.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jhevol.2019.102682.

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