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Thermoregulation and endurance running in extinct hominins: Wheeler's models revisited

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ABSTRACT

Thermoregulation is often cited as a potentially important influence on the evolution of hominins, thanks to a highly influential series of papers in the Journal of Human Evolution in the 1980s and 1990s by Peter Wheeler. These papers developed quantitative modeling of heat balance between different potential hominins and their environment. Here, we return to these models, update them in line with new developments and measurements in animal thermal biology, and modify them to represent a running hominin rather than the stationary form considered previously. In particular, we use our modified Wheeler model to investigate thermoregulatory aspects of the evolution of endurance running ability. Our model suggests that for endurance running to be possible, a hominin would need locomotive efficiency, sweating rates, and areas of hairless skin similar to modern humans. We argue that these restrictions suggest that endurance running may have been possible (from a thermoregulatory viewpoint) for *Homo erectus*, but is unlikely for any earlier hominins.

Introduction

In an influential paper, Bramble and Lieberman (2004) argued that modern humans are conspicuously unusual in comparison to other mammals in their ability to run continuously for long periods of time. They further argued that the evolution of this unusual ability requires explanation, because it seems unlikely to be a byproduct of selection for walking long distances. It has been suggested that such endurance running may have played an important role in hominin evolution (Carrier, 1984; Bramble and Lieberman, 2004; Lieberman et al., 2009). Specifically, if the ancestors of humans had similar abilities, then these could have been used for hunting, giving them access to otherwise difficult-to-catch but highly-rewarding large mammalian prey. Such persistence hunting would have involved chasing prey continually, and not allowing it time to rest until the prey was overcome by hyperthermia (Lieberman et al., 2009).

The viewpoint that endurance hunting was important in hominin evolution remains contentious (see Pickering and Bunn, 2007; Lieberman et al., 2007; Liebenberg, 2008). Previous works (e.g., Bramble and Lieberman, 2004) considered the structural basis and fossil evidence for endurance running in extinct hominins. However, one of the keys to endurance running in modern humans is our ability to shed heat. Specifically, humans are considerably derived in terms of our number and function of eccrine sweat glands and near-bare skin, and these adaptations play a vital role in heat dissipation. Since running is a highly energy-expensive activity and persistence hunting is likely to be most effective in hot conditions and in open habitats with little available shade (Liebenberg, 2006; Lieberman et al., 2009), heat balance is a central aspect of the evolutionary importance of endurance running in hominins. Further, persistence hunting is predicted only to be effective against otherwise healthy prey if the prey is driven to move at high speeds. At moderate speeds, many mammalian quadrupeds (e.g., dogs, horses, and deer) can trot for long distances at speeds that exceed human walking. Only if the human pursuers run such that the prey must often break into a gallop, will the chase ultimately be successful. This occurs because of both the high rate of heat generated during galloping and the inability to lose heat by panting whilst galloping (Lieberman et al., 2009). Thus, the key to success in persistence hunting is to achieve hyperthermia in the prey (rather than simple physical exhaustion) by chasing sufficiently quickly enough that the prey must regularly move faster than a trot. This will often require sustained running from the hominin pursuers (but see Pickering and Bunn [2007] for an alternative viewpoint), and thus very effective dissipation of the considerable heat produced.

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Here, we use a mathematical modeling approach to explore heat balance in putative persistence hunting hominins. Specifically, we modify the most widely-cited model of thermoregulation in hominins (Wheeler, 1984, 1985, 1991a,b, 1992a,b, 1993, 1996). Wheeler's model dealt with a hominin standing still, so we have developed a model to allow for both the heat generated by a running individual and the increase in convective heat loss due to an individual moving quickly through the surrounding air. We also modify the model in a number of small ways to take into account improved estimates of some parameter values as a result of research done since the original models were published. Our aim is to explore whether or not endurance running would have been thermally possible for extinct hominins: that is whether or not extinct hominins could have run in the heat of the day for sustained periods of time without overheating. We also seek to identify what thermal adaptations would have been required to make such activity possible. We stress that such a modeling approach *cannot* demonstrate that persistence hunting actually happened at any point during human evolution *but could potentially rule it out as a possibility on thermoregulatory grounds.*

A revised Wheeler model of hominin thermoregulation

In order to facilitate comparison with Wheeler's works and other papers that refer to his ideas, we have endeavored to retain as much of the structure of his model as we can. We have also kept as much of the same nomenclature and use of symbols as possible. Where we deviate from his model, we make the difference clear and we explain our motivation for the change.

The thermal environment

We define the thermal environment exactly as Wheeler did (see Wheeler, 1991b). He was interested in the period from dawn at 06:00 to dusk at 18:00 on a cloudless day in an environment without cover. Let t be the time in hours, $t = 0$ being midnight. He assumed that the air temperature at a height of 200 cm (T_{200}) varied sinusoidally with a minimum at $t = 5$ and a maximum at $t = 14$. Wheeler considered various values for the maximum value (τ_{200}): 35°C, 40°C, or 50°C. For comparison, in modern African savannas the *mean* maximum temperature ranges from 18°C to 36°C, depending on location. For example, in southern Africa there is more seasonal variation in temperature, and so lower annual means (Shorrocks, 2007). Here, we assume a maximum value of 40°C throughout. As in Wheeler's model, the minimum value was set at 25 degrees less than τ_{200}. Thus, at any given time t, the air temperature 200 cm above the ground was given by:

$$T_{200}(t) = \tau_{200} - 25 + 25Sin\left(\frac{\pi(t-5)}{18}\right). \quad (1)$$

The ground temperature (T_g) is assumed to reach a maximum that was 5°C higher than the maximum air temperature, and to have a daily range of 35°C. The minimum temperature occurs at $t = 5$ and the maximum at $t = 13$. Thus, the ground temperature at any time (t) is given by:

$$T_g(t) = \tau_{200} + 5 - 35 + 35Sin\left(\frac{\pi(t-5)}{16}\right). \quad (2)$$

The air temperature (T_a) actually experienced by a hominin would depend on its characteristic height. Specifically, Wheeler used a parameter (α) to specify this characteristic height, such that:

$$T_a = T_{200} + \alpha(T_g - T_{200}). \quad (3)$$

A larger value of α suggests a lower characteristic height. We adopt the same value as Wheeler used for a bipedal posture: α is 0.41. This value was calculated from scale models (details provided in Wheeler, 1991a). The value of α will be affected by hominin height as well as posture. However, the change in air temperature with height off the ground is highly non-linear, with most change occurring in the first few tens of centimeters (e.g., Oke, 1978); thus, variation in hominin height (ranging between 1 m and 2 m) would have such a sufficiently small effect on the value of α that we can safely ignore it.

Windspeed

An assumption in Wheeler's original modeling was that windspeed was very low, with the value at 200 cm above the ground being 1 ms^{-1}. However, Wheeler (1991a) suggested that (because of the exponential decrease in airspeed with reducing height above the ground) this would decline to an average characteristic windspeed of 0.67 ms^{-1} for a biped (estimated from Wheeler, 1991a: Fig. 3a).

Here, we will assume that the air movement past the body is produced by the travel of the individual rather than by wind. For simplicity, we will ignore the acceleration and deceleration of different body parts, and simply characterize movement by a constant velocity. This assumption is supported by the recent modeling study of Cross et al. (2008). They compared a rigid-structure model like ours with a more complex model of a running human that captured the complex range of body part movement. While the two models produced very different predictions for heat exchange between the human and the environment at low air temperatures, at high air temperatures like those considered here, the two models agreed to within 1%.

Many walkers seem to adopt an energetically efficient walking speed such that their Froude number is approximately 0.3 (Alexander, 2006). If we assume that our organism has a leg length L (in m), then (since Froude number is velocity squared divided by the product of leg length and acceleration due to gravity) this suggests an energetically efficient walking speed of $1.7L^{0.5}$ ms^{-1}. However, for endurance running, we are interested in the running speed that minimizes the energetic cost of traveling unit distance, which in humans occurs at a Froude number of around 1.5 (Alexander, 2006; and calculations from data in Steudel-Numbers and Wall-Scheffler [2009]). For an individual of leg length L, this translates into a speed of $3.5L^{0.5}$ ms^{-1}. We are not seeking to model the maximum aerobic running speed, but rather the running speed that minimizes energy expenditure per unit distance. Marathon runners are trying to run as quickly as possible, not as energetically efficiently as possible. In contrast, when modern humans are jogging for recreational purposes without concern for maximizing speed, they generally select running speeds of between 3.5 ms^{-1} and 4 ms^{-1}, which corresponds to Froude numbers of 1.3–1.6 (Delattre et al., 2009, and references therein). These running speeds also correspond to those that Steudel-Numbers and Wall-Scheffler (2009) suggested minimize the cost of traveling unit distance. Although we use Froude number because of its success in describing variation in speed between taxa, we note that concerns have been raised about its use in anthropological studies (e.g., Steudel-Numbers and Weaver, 2006; but see Weyand et al., 2010).

The radiation environment

In none of his papers did Wheeler provide the exact functional form he used to describe daily variation in the intensity of direct solar irradiance incident on a surface at right angles to the ray path (S); however, it is illustrated in Wheeler (1991b: Fig. 1). He stated that the maximum is 865 Wm^{-2} when the sun is directly overhead at noon. Oke (1978) suggested that daily variation in the strength of