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INVITED REVIEW

A century of exercise physiology: concepts that ignited the study of human thermoregulation. Part 4: evolution, thermal adaptation and unsupported theories of thermoregulation

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Abstract

This review is the final contribution to a four-part, historical series on human exercise physiology in thermally stressful conditions. The series opened with reminders of the principles governing heat exchange and an overview of our contemporary understanding of thermoregulation (Part 1). We then reviewed the development of physiological measurements (Part 2) used to reveal the autonomic processes at work during heat and cold stresses. Next, we re-examined thermal-stress tolerance and intolerance, and critiqued the indices of thermal stress and strain (Part 3). Herein, we describe the evolutionary steps that endowed humans with a unique potential to tolerate endurance activity in the heat, and we examine how those attributes can be enhanced during thermal adaptation. The first of our ancestors to qualify as an athlete was *Homo erectus*, who were hairless, sweating specialists with eccrine sweat glands covering almost their entire body surface. *Homo sapiens* were skilful behavioural thermoregulators, which preserved their resource-wasteful, autonomic thermoeffectors (shivering and sweating) for more stressful encounters. Following emigration, they regularly experienced heat and cold stress, to which they acclimatised and developed less powerful (habituated) effector responses when those stresses were re-encountered. We critique hypotheses that linked thermoregulatory differences to ancestry. By exploring short-term heat and cold acclimation, we reveal sweat hypersecretion and powerful shivering to be protective, transitional stages *en route* to more complete thermal adaptation (habituation). To conclude this historical series, we examine some of the concepts and hypotheses of thermoregulation during exercise that did not withstand the tests of time.

Keywords Adaptation · Acclimation · Acclimatisation · Body temperature · Exercise · Evolution · Genetic · Homeostasis · Thermoeffector · Thermoregulation

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Abbreviations

$T_{b\text{-}i}$	Body temperature at time *i*
$T_{b\text{-}0}$	Basal body temperature
d*t*	The duration of the thermal stimulus

Introduction

Many small mammals, both wild-caught and captive-bred, engage in voluntary endurance activity when in captivity (*e.g.*, wheel running), but why they do so is unknown (Sherwin 1998; Halsey 2016); "*wheel running has no directly analogous naturally occurring behaviour*" (Sherwin 1998 [P. 11]). Of course, many animal species play, but *Homo sapiens* is the only species that engages voluntarily in arduous endurance exercise for recreational or occupational purposes (Fig. 1), which draws the question. Why is it that humans of widely varying abilities run marathons, often

in the heat, and swim across the English channel, which is rarely anything other than cold? Why do highly trained military personnel and emergency workers (occupational athletes) frequently push themselves very hard, and sometimes into oblivion?

No other extant primate species is capable of such endurance exercise (Bramble and Lieberman 2004). Nevertheless, humans do not routinely walk the thousands of kilometres each year that reindeer, Asian asses and wolves do (Teitelbaum et al. 2015; Joly et al. 2019). Those species are obliged to move for nutritional reasons, and they walk slowly and in cool weather. Humans are fast endurance mammals and have evolved to be so. During the evolution of all species, successful individuals, through natural variations or mutations, acquired attributes that enabled them to survive. Humans did not evolve with the traits of competitive sprinters. The fastest sprinters are quadrupeds: a cheetah can run 200 m in less time than it takes the fastest human sprinter to run 100 m (Hetem et al. 2013). Humans are not even the fastest bipedal sprinters; ostriches are (Alexander et al. 1979). The Australian emu (Patak and Baldwin 1998) and South American rhea (Roberts et al. 1998) are also faster than humans.



Fig. 1 **A** Participants in the Comrades Marathon, held annually in South Africa, and regarded as the world's most-famous ultramarathon (Burfoot 2007). The course is 90 km long with a climb of 870 m on the uphill run. The field is capped at 25,000 participants, and winners run at an average speed of 16.5 km h^{-1} for over five hours. Over that distance humans are as fast as horses; over longer distances humans are faster (Minetti 2003). Source: Used with permission of The Comrades Marathon Association, which retains copyright. **B** Zasson (Jason) Zirganos (Greece) at the completion if his English Channel swim from Dungeness Point (France) to Folkestone (England; 1951 [14 h 10 min]). Source: https://www.channelswimmingdover.org.uk/content/photo/major-jason-zirganos-of-greece-with-sam-rockett Accessed: July 11th, 2022. This photograph is in the Public Domain

In this, the final part our series of historical reviews on thermoregulation during exercise (Notley et al. 2023a, 2023b, 2023c), we explore the evolutionary steps that endowed each of us with the potential to be fast endurance mammals and sweating specialists. We have not included recent developments in the fields of epigenetics, gene mapping or heat-shock proteins. Against that genotypic background, we will examine how we are able to enhance those attributes by acquiring, either naturally or artificially, the physiological (phenotypic) adaptations necessary for us to tolerate endurance running in the heat and endurance swimming in cold water. Those attributes, if developed, allow us to play and compete for pleasure in today's world. Over the centuries, those characteristics allowed our ancestors to be selected ahead of other hominids, but our largely sedentary contemporary lifestyles within a warming climate will mean that natural selection will again test human survival.

How thermoregulation enabled fast endurance exercise in *Homo sapiens*

Before our ancestors could evolve the traits for fast endurance exercise, they needed to acquire thermoeffectors to dissipate metabolic heat, a regulatory system to control heat dissipation and bipedal locomotion. Bipedality enabled those hominins to carry water, which supported thermoregulation. Indeed, we possess a curious collection of attributes and regulatory systems selected by nature through the random application of environmental and competitive stresses that could be tolerated only by a unique species (Balter 2002; Grigg et al. 2004), or members of species. In achieving those capabilities, non-thermoregulatory mechanisms were co-opted to serve thermoregulation (Euler and Söderberg 1958; Simon et al. 1986). Indeed, "*it would be unnecessarily burdensome to require the evolutionary process to create a new system to solve a problem already solved by an existing system*" (Satinoff 1978 [P. 21]). Since our thermoeffectors operate from soft tissues, they left no evidence within the fossil record. Fortunately, archeological and genetic clues enabled anthropologists and physiologists

to divine evidence-based interpretations of how our ancestors evolved into the bipedal, less-hairy sweating specialists that we are today.

Thermoeffector evolution: vascular networks, homeothermy, sweating and hairlessness

For our hominid ancestors and ourselves, there were crucial steps in acquiring the traits necessary for fast endurance exercise: the emergence of bipedality occurred perhaps 6 million years ago, the drying and opening up of parts of the African continent happened about 2 million years ago and its conversion from a cold to a tropical climate occurred ~ 250,000 years ago (Gowlett 2001). Owen-Smith suggested that the evolution of the genus *Homo* could have occurred nowhere else other than in Africa, because that process required warm savanna grasslands and plentiful large-animal protein (Owen-Smith 2021). Those events gave rise to the *Anthropocene* epoch, the era dominated by humans, our activities and our often adverse influences on our shared home. Our evolving traits were superimposed on structures and functions with a much longer evolutionary history.

We have discovered, from observations on primitive organisms, that learned behaviours are the most-ancient mechanism that animals use to manipulate their body temperatures (Malvin and Wood 1992; Nelson et al. 1984). Indeed, behavioural thermoregulation (*e.g.*, clothing, buildings, air conditioning) is our most effective method for manipulating and defending our body temperatures. For more precise regulation, those behaviours were supplemented by autonomic mechanisms (Cabanac 1972; Nelson et al. 1984), and inter-species comparisons have revealed that progression has occurred across animal phyla, and may have been driven by selective pressures that favoured animals with a preference for thermal stability, rather than heterothermy (Bligh 1998).

The first autonomic thermoeffectors to evolve were likely to have been those that depended upon vascular networks. Those networks appeared > 600 million years ago (Fig. 2), predicated by increases in body size, which necessitated transportation networks to supply the metabolic requirements for, and the removal of wastes from, all cells, which are diffusion dependent when organisms are very small (Monahan-Earley et al. 2013). Jump forwards some 300 million years to the appearance of reptiles (Carroll 1970; Simões et al. 2020), and we find animals that exploited their cutaneous vasculature, in combination with behavioural strategies, to use external heat to warm their deeper tissues (Templeton 1970), and to reduce heat loss in the absence of an ambient heat source. That transportation is bi-directional and gradient dependent, with all heat exchanges obeying the *Laws of Thermodynamics* (Notley et al. 2023a). It is not only the reptiles that possess such a capability, but all

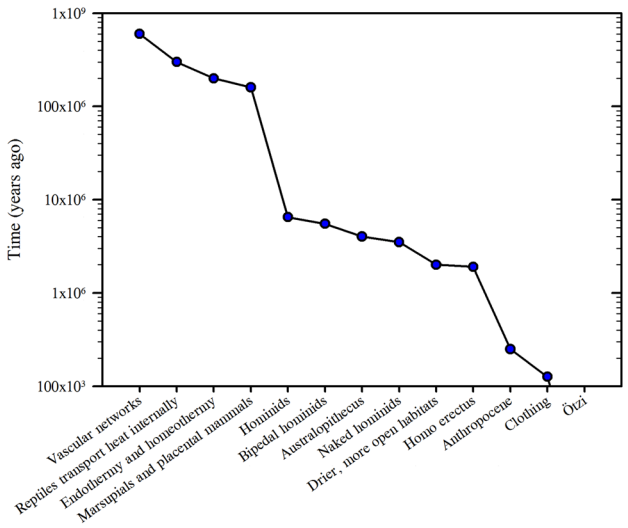


Fig. 2 A probable timeline for the development of autonomic and behavioural thermoregulatory phenomena that contributed to the evolution and survival of the endurance capabilities of the first *Homo sapiens*, as they progressed from *Homo sudomotor* to become *Homo cursor* (Sands 2010). In the lower right, we find the oldest mummified athlete of his time (>3000 years old), Ötzi, a Neolithic hunter and farmer, who was found with his personal protective clothing and equipment, trapped within the Niederjoch Glacier in the Ötztal Alps (Italy)

ectotherms that rely on their environments as a heat source and a heat sink use their cutaneous vasculature in this way (Smith 1979; Dzialowski and O'Connor 1999).

Jump another 80–140 million years forwards, and we find evidence for the existence of endothermy and homeothermy (Fig. 2), especially amongst mammals and birds (Ruben 1995; Hillenius and Ruben 2004). Endotherms can produce enough metabolic heat (tachymetabolism) to regulate their body temperature using both shivering and non-shivering mechanisms. That capability became a feature of mammals and birds ~ 200 million years ago (Phillips et al. 2009; Benton 2021), possibly as a consequence of different selective pressures (Legendre and Davesne 2020).

Homeothermic mammals, with their stable body temperatures, appeared around 160–220 million years ago (Phillips et al. 2009; Benton 2021), when egg-laying mammals (*monotremata*) diverged from amphibious reptiles (Phillips et al. 2009). Neither the addition of endothermy to ectothermy, nor the emergence of homeothermy, occurred instantaneously. Those transitions probably related to a decline in body size (Lovegrove 2017; Rezende et al. 2020). By virtue of their high thermal inertia, large dinosaurs may well have had stable enough body temperatures to qualify as homeotherms (McNab 1978), or at least as mesotherms (Grady et al. 2014), and the energy requirements of running for large, bipedal dinosaurs may have required them to be

tachymetabolic, so they too were endothermic (Pontzer et al. 2009).

The biochemical mechanism selected for elevating metabolic heat production across mammals and birds was mitochondrial oxidative phosphorylation. That highly inefficient process liberates significant amounts of thermal energy (thermogenesis), which becomes problematic for occupational athletes working hard in protective clothing. That oxidation is not unique to animals. It occurs in higher plants and in organisms that have cell nuclei (eukaryotes; Müller et al. 2012; Poole and Gribaldo 2014). What had been selected in mammals and birds was the ability to use that metabolic engine to continually produce heat. For example, the metabolic rates of mammals, measured in the field (doubly-labelled water), are about 12 times higher than those of similarly sized reptiles (Nagy 2005).

Let us now consider the evolution of tachymetabolism from an exercise perspective, and how our oxidative capability may have provided a selective advantage. Of course, it was a double-edged sword, because it not only kept the engine running, but the conversion of chemical potential energy into kinetic energy, which was used to exercise and perform external (mechanical) work, incurs a significant heat load (Helmholtz 1848; Hill and Hartree 1920; Christensen 1931; Nielsen 1938). In the Part 3 of this review series, we examined the physiological and health implications of excessive heat storage and the corresponding increases in tissue temperatures (Notley et al. 2023c).

The resting heat production of humans is dominated by the metabolic activities of our brain and intra-thoracic organs (Müller et al. 2011). When we commence exercising, there is an intensity-dependent elevation in heat produced by the skeletal muscles, which, on its own, can approach 90% of the overall heat production during maximal exercise (Mitchell and Blomqvist 1971; Hochachka 1994). That energy conversion is irreversible (Wilkie 1954, 1960), so the heat generated must either be stored or dissipated, and that is the other edge of this sword, since excessive heat storage can be life threatening.

The egg-laying monotremes of Australia and New Guinea (Holz 2015; Wagstaff et al. 2020; Flannery et al. 2022) thermoregulate with less precision, and at lower temperatures than do other mammals (Miklouho-Maclay 1884a, 1884b; Martin 1903). Since they were the next mammalian order that diverged from reptiles, it is not unreasonable to assume that they possessed some control over their cutaneous vasculature, although those mechanisms probably differed widely across species (Morgareidge and White 1969). The next mammals to evolve seem to have been the marsupials (*metatheria* or *marsupalia*; Fig. 2), the neonates of which complete their development within a pouch, attached to a mammary gland. They inhabit Asia, Australia, North and South America (Vogelnest 2015; Taylor et al. 2022) and appeared 140–180 million years ago (Phillips et al. 2009; Luo et al. 2011). Our forebears also appeared at about that time (placental [eutherian] mammals; Phillips et al. 2009; Luo et al. 2011), and were likely to have been proficient thermoregulators.

After nearly 200 million years of evolution within the endotherms and homeotherms, the hominid lineage emerged. They would become the most-proficient of the thermoregulators (Fig. 2). The phylogenetic tree of primates provides compelling evidence that *Hominidae* (humans, their predecessors and the other great apes) shared a common ancestor with the other catarrhine primates: the *Cercopithecidae* (Old World monkeys) and *Hylobatidae* (gibbons and siamangs; Mittermeier et al. 2013). The human clade (hominids) split from the chimpanzees and bonobos ~ 6 to 7 million years ago, and the oldest known hominid fossils are those of *Sahelanthropus tchadensis* (Pontzer 2012a), which then lived in the tropical and sub-tropical habitats of Africa. Those habitats were characterised by abundant water, maximum dry-bulb temperatures of 30–32 °C, low wind speeds, little or no penetrating solar radiation due to the dense vegetation, and almost fully saturated air (close to 100% relative humidity; Newman 1970; WoldeGabriel et al. 2001). Although the African Equatorial Belt contracted progressively, the hominids and other great apes did not have to leave those habitats until ~ 2 million years ago, though they may well have explored the forest edges and the nearby woodlands (Kingston et al. 1994). Indeed, it was unlikely that they had any reason to travel far on any one day (Pontzer 2017a).

We know nothing of the skin of *Sahelanthropus tchadensis*, but the ancestors of chimpanzees, bonobos and gorillas shared the same habitat as *Sahelanthropus*, and they have dense body hair. We therefore assume that *Sahelanthropus* also had dense body hair. All three primate families possess a unique, whole-body distribution of apocrine and eccrine sweat glands (Gelineo 1964; Szabo 1967; Newman 1970; Jenkinson 1973; Taylor and Machado-Moreira 2013; Best and Kamilar 2018). The eccrine glands secrete a serous fluid (Folk and Semken 1991), and its evaporation fulfilled a significant thermoregulatory role (Johnson and Elizondo 1979; Mahoney 1980). In the catarrhine primates, those sweat glands are distributed over the entire body surface (Montagna and Yun 1963; Folk and Semken 1991; Best and Kamilar 2018). That enabled evaporative cooling without inhibiting locomotion. Animals that pant tend to remain stationary while panting. Unless those primate families evolved sweating independently after their divergence, their last common ancestor was likely to have been an eccrine sweater.

The last common ancestor of *Hominidae* lived ~ 20 million years ago (Pontzer 2012a) and would have inherited that trait. The oldest date proposed for the loss of body hair

in that lineage was 4 million years ago. So for at least 16 million years, to the extent that they relied on evaporative cooling to dissipate metabolic heat, ancestors of the great apes had a sweating system that operated through their body hair. The fastest of the extant primates (easily outstripping humans) is the patas monkey (*Erythrocebus patas*), which inhabits the savannas of tropical Africa. It has a dense hair coat, but thermoregulates effectively using eccrine sweating (Mahoney 1980; Kolka and Elizondo 1983), challenging the contention that "*that the benefits of sweating only accrue to hairless animals*" (Dávid-Barrett and Dunbar 2016 [P. 75]). It is not even necessary to have an eccrine sweating system to achieve potent cutaneous evaporative cooling. Elephants, which lack eccrine sweat glands, achieve controlled evaporative cooling of up to 360 W m^{-2} (>500 g m^{-2} h^{-1}), which is greater than that of any extant non-human primate (Dunkin et al. 2013).

Only two thirds of the fluid-producing cutaneous glands of our closest phylogenetic relatives (chimpanzees) are eccrine glands (Lieberman 2015), and their glandular density is about a tenth that of humans (Kamberov et al. 2018). The maximum sweat rate of chimpanzees is ~ 80 g m^{-2} h^{-1} (Hiley 1976), which can achieve ~ 53 W m^{-2} of cooling if it all evaporates on the skin. That is just enough to dissipate its resting metabolic heat, and is rather modest compared to human endurance athletes (Hora et al. 2020). For example, the sweat rate of Alberto Salazar, an elite marathon runner, was 3.7 L h^{-1} (~2 kg $m^{-2}h^{-1}$, achieving ~ 1.3 kW m^{-2}) during an Olympic marathon (1984; Armstrong et al. 1986a). He lost 8.1% of his body mass durings the race, despite drinking just before (1 L) and during the race. It is presumed the evaporative cooling achieved by our ancestral great apes was adequate for their lifestyle, but would have been inadequate for hominids engaged in endurance exercise.

Humans have hair-follicle densities similar to those of chimpanzees, but a density much lower than is found in other primates (Kamberov et al. 2018). Moreover, the majority of human body hairs are microscopic (vellus hair; Szabo 1967). It appears that the *in-utero* determination of human hair-follicle and eccrine-gland densities, which arise from the same epithelial appendages, results from the competing influences of two genes: sonic hedgehog proteins (hair-follicle formation) and bone morphogenetic proteins (eccrine-gland formation; Lu et al. 2016). Aldea et al. (2021) have now shown that an ectodermal enhancer gene (hECE18) determines the number of sweat glands. Compared to other great apes, and presumably our hominid ancestors, humans are unequivocally naked (though not hairless). When our ancestors lost their body hair, they lost most of their apocrine sweat glands, which secrete into hair follicles (Folk and Semken 1991); eccrine glands secrete onto the skin surface. Humans retained apocrine glands only where we have dense body hair on our torsos. So it was nakedness that enabled our ancestors to become almost completely eccrine sweaters, with human sweat-gland densities being ~ 10 times those of the chimpanzee (Kamberov et al. 2018). Nakedness became particularly important for humans (Kuno 1934; List 1948; Weiner and Hellmann 1960; Sato 1977) as it optimised evaporative cooling, although that optimisation was not the evolutionary force behind nakedness.

Nakedness does not fossilise, so the question of when our lineage became naked has to be approached indirectly, and it has provided an arena for entertaining and ongoing disputes (Rantala 2007; Allen et al. 2013). According to Ebling (1985 [P. 33]), "*the evolution of near nakedness in the human species has been accounted for by a series of myths which owe more to the predilections of their creators than to the available evidence*". One indirect way of estimating when hominids became naked is to track the genetic clock of a gene locus associated with skin darkening by the sun (MC1R), which establishes that hominids were naked and regularly sun exposed 1.2 million years ago (Rogers et al. 2004). But whatever the evolutionary forces were that drove nakedness, it was unlikely to be those that enhanced thermoregulation when exercising in the sun (Newman 1970; do Amaral 1996). Mutations selected for that outcome would have carried more hair not less, in a hair coat that allowed the free transport of water vapour, but which intercepted solar radiation before it reached the skin, as seen in the patas monkey (do Amaral 1996). Indeed, we would have retained more than just scalp hair to act as a sunshield (Lasisi et al. 2023). Consequently, behavioural practices were needed, such as the loose-fitting Bedouin robe (Shkolnik et al. 1980; Horowitz 2022), which supports evaporation while intercepting solar radiation.

Though it is a topic unlikely to grace the dinner tables of the *International Olympic Committee*, the most-compelling evidence for when and how hominid nakedness occurred, we believe, relates to ectoparasites. The only human hairs to which the louse (*Pthirus pubis*) could attach were the pubic hairs, which co-evolved with nakedness; hairy great apes have no pubic hairs. The louse's molecular clock tells us that they first attached to the pubic hair of hominids ~ 3–4 million years ago, probably host-switching from the coarse hair of gorillas (Reed et al. 2007). Our ancestors were not yet exploiting the savannas, so nakedness emerged within enclosed forest habitats. Global temperatures in the Pliocene (1.6–5 million years ago) were higher than they would be again until the current *Anthropocene*, so nakedness imposed little risk of cold stress for forest dwellers, and would have facilitated evaporation, which is helpful in an environment with low water vapour-pressure gradients. The louse may tell us when nakedness occurred, but not why.

Hairy primates were vulnerable to another class of ectoparasite, blood-sucking ticks, which are powerful vectors of disease. Evolution would have favoured the less hairy

members of a species, which were less vulnerable to ticks (Pagel and Bodmer 2003; Allen et al. 2013) because they would have been more visible and easily removed during grooming (Brown 2021). That parasite hypothesis was put forward by Belt (1874), and rejected by Charles Darwin (1809–1882, England; Darwin 1888) because he could not envisage why it applied to hominids, and not to other great apes (Rantala 2007). So why did hominids become naked, and not other great apes? At that time, hominids started functioning in groups, sharing activities and food, and living in communal lairs and dens (Rantala 2007). Those social circumstances can lead to lethal tick infestations in extant primates (Brain 1992; Brain and Bohrman 1992), and could well have done so for our hominid ancestors. So it would appear that our naked ancestors may have been selected by ticks, and our hairy ancestors (with notable contemporary exceptions) died out. Any benefits for evaporative cooling were secondary. The cost of that was lice, but human life was not meant to be easy!

Which hominids first became naked? Gilligan (2010) says it was early *Homo* that became naked, but there are no *Homo* fossils from 3–4 million years ago (Pontzer 2012a). That was the age of *Australopithecus*, but Dávid-Barrett and Dunbar (2016) argue that nakedness did not emerge in *Australopithecus*, because they lived at high altitude, and had an over-riding need to stay warm, rather than to lose heat. They assert that nakedness appeared within the genus *Homo* ~ 2.5 million years ago. Macdonald (2018) has suggested several ways in which a hominin could cope with low temperatures without either hair or fire.

Whichever hominin species entered the Pleistocene epoch naked (12,000–2.6 million years ago), it needed thermoregulatory competence in both hot and cold environments. During the Pleistocene, the earth experienced successive periods of falling and rising air temperatures, resulting in continental ice sheets and glaciers forming (the ice age; Pisias and Moore 1981). The advantage that mammals and birds possessed, in addition to their tachymetabolism, was their ability to modify their thermal insulation, through anatomical, autonomic and behavioural changes (Irving 1966). For our now-naked ancestors, the critical behavioural change was adopting clothing, and it is another louse species that allows us to estimate when that happened.

Pediculus humanus lives exclusively in clothing, and its molecular clock indicates that *Homo sapiens* first used clothing to between 83,000 and 170,000 years ago (Fig. 2; Allen et al. 2013; Gilligan 2018; Hallett et al. 2021). So when the most recent wave of *Homo sapiens* left Africa, *en route* to Australia and tropical Asia, they were clothed, which was necessary in the colder winters of Europe and Asia (Toups et al. 2011). Any reversion to near-nakedness by subsequent indigenes was a matter of choice. Those who travelled north and into the colder European climates certainly needed clothing, and Notley et al. (2023c) introduced Ötzi, an occupational athlete of his time (>3000 years B.C.E.), as the person who provided the earliest example of thermally protective clothing during exercise in the cold. Our objective for this section has been to highlight phenomena and developmental stages that accompanied the evolution of both human thermoregulation (Fig. 2), but why did humans adopt bipedal exercise and eventually become endurance specialists?

Why we needed bipedality for endurance exercise: not what you might think

When the hominid lineage split from chimpanzees and bonobos, our ancestors were quadrupedal and arboreal, though they were likely to have made excursions to the ground. But within 1–2 million years, the hominids changed their mode of locomotion, with successive hominid genera developing progressively better capacities for bipedal movement, presumably due to random genetic changes and mutations that served their arboreal activity (Drummond-Clarke et al. 2022). Those changes gave them a selective advantage by allowing them to venture into more open habitats, with bipedal locomotion eventually becoming their usual, and ultimately their only, mode of locomotion.

Paleoanthropologists adduce evidence for proficiency in bipedal locomotion primarily from the orientation between the skull and spinal column, the size and shape of the forelimb and hindlimb bones, and their alignment, and the shape and alignment of the foot bones. Bipedality was claimed for *Sahelanthropus tchadensis* (Zollikofer et al. 2005), but recent analysis does not support habitual bipedal locomotion (Macchiarelli et al. 2020). There seems to be agreement that the fossils of *Orrorin tugenensis* (~6 million years old) were from an habitually bipedal hominid (Senut et al. 2001; Pickford et al. 2002), although it would not have been naked, nor was it a prolific eccrine sweater.

Which evolutionary forces led to habitual bipedal locomotion in our ancestors? We know it was not selection for speed, because not just patas monkeys, but baboons and quadrupedal primates are faster than modern humans. The effortless grace of the Kenyan athlete, Eliud Kipchoge, might beguile us into thinking that it was locomotor efficiency, but we would be wrong. When our hominid ancestors first walked bipedally, it was with bodies better suited to arboreal movement. Think not of Kipchoge, but of the inelegant crouching walks of modern chimpanzees that are reluctantly bipedal over short distances. It would take 2 million years after *Orrirn* walked bipedally before *Australopithecus* walked comfortably (Fig. 2), and another 2 million years of bipedalism before *Homo erectus* walked and ran competitively with other mammalian species (Pontzer 2017b).

We believe that the evolutionary forces behind bipedal locomotion had more to do with forelimbs than with hindlimbs. That was also Charles Darwin's explanation, and he proposed that bipedality freed the hands and arms for defence and food acquisition (Darwin 1888; Pontzer 2012b). Whilst that is true, we do not believe those were the most important benefits, since freeing the forelimbs enabled carrying to become a normal behaviour of our bipedal ancestors (Berecz et al. 2020), with no more precious load to be carried than one's offspring (Fig. 3). Hominid primates carry their offspring for at least the first few weeks of its life, and sometimes much longer, with the offspring of haired hominids clinging to the mother (Berecz et al. 2020). That form of offspring carriage fell away when our ancestors became naked. Chimpanzees and gorillas use one arm to assist the attachment of infants, but locomotion is difficult, although it would have been much easier once genetic changes allowed hominids to become bipedal. Parents could then use both arms, with an upright posture resulting in a better load distribution (do Amaral 2008; Berecz et al. 2020; Brown 2021). Although the asymmetry of such load carriage is energetically costly (Watson et al. 2008), that posture freed the arms for other functions, and possibly improved reproductive success. Collectively, those changes would have withstood selective pressures, so it is believed that bipedality and nakedness were co-selected.

Our bipedal ancestors could now also carry water. That would not have been required in the forested habitats, but would have been a substantial advantage when our ancestors began to encounter more open and drier habitats (deMenocal 2011), where they would have to range much further for food. They would also have been exposed to more solar radiation, because they were forced into diurnal activity by nocturnal predators, such as leopards (Brain 1983). Reed (1997) insists that ancestor was *Paranthropus* (Constantino 2013), which survived another 600,000 years. In some ways, various hominins were pre-adapted for life under greater heat stress, with eccrine sweat glands secreting directly onto to their near-naked skin. In one important respect, though, they were not prepared.

They were about to embark on an evolutionary journey that would lead to them having a lower daily water turnover than other primates (Pontzer et al. 2021), but there had been no evolutionary pressure to prepare them for habitats in



Fig. 3 Offspring carriage by hairy and naked primates. **A** Baboon offspring cling to the hair of their mothers. Source: Royalty-free image from Pixabay. **B** Chimpanzee offspring also cling, but mothers assist very young offspring with an arm; locomotion is then more difficult. Source: Royalty-free image from Pixabay. **C**: Human infants cannot cling, but our upright posture, which freed the arms, made offspring carriage possible. Source: Netpix.com (https://www.needpix.com/photo/1345586/), used under Creative Commons Zero License for Public Domain

which drinking water was not readily available. Their ability to range widely would have been constrained by access to water to replace that lost as sweat. If their ability to withstand hypohydration was similar to that of modern humans (Beis et al. 2012), they were unlikely to encounter lethal hypohydration (Hora et al. 2020), even from the sweating required to range at pace. But if their thermoregulatory characteristics resembled those of modern humans, hypohydration would have made them progressively hyperthermic during exercise in the heat, and perhaps dangerously so. When body-fluid homeostasis and homeothermy come into regulatory conflict, the regulation of blood volume and pressure might be given a higher priority than the regulation of body temperature (Notley et al. 2023a [Table 1]). Thus, hypohydration may suppress sweating (Greenleaf and Castle 1971; Fortney et al. 1984; Sawka et al. 1985), although sudomotor suppression is not always seen (Ladell 1955; Strydom et al. 1966; van den Heuvel et al. 2020b), particularly if the resulting increase in body temperature leads to extra sweating (Notley et al. 2023c). Whether they became hyperthermic or not, they may have carried water or water-rich food (Hewes 1961) to counteract hypohydration. Since our hominin ancestors had ample access to water in their earlier forest-dwelling forms, there was no selection pressure for them, or other primates, to evolve a physiological mechanism, such as selective brain cooling, that would help them to conserve water when they moved into arid regions (Maloney et al. 2007; Strauss et al. 2017).

Some dismiss the idea that hominins carried water, because it would have required carrying several kilograms (Hanna and Brown 1983), for which they did not have the means (Ruxton and Wilkinson 2011a). However, the provision of just a little water to hyperthermic (non-human) mammals following the suppression of evaporative cooling, can restore cooling and reverse hyperthermia within minutes (*e.g.*, McKinley et al. 2009). The sensory cues for that seem to be related to the act of drinking (Takamata et al. 1995), but it can even be sufficient just to show water to an hypohydrated animal (Claus Jessen, personal communication), so the response seems to resemble a Pavlovian (classical conditioning) mechanism. That phenomenon occurs in baboons (Fig. 4; Brain and Mitchell 1999; Mitchell et al. 2009), modern humans (Lee and Mulder 1935; Senay and Christensen, 1965; Takamata et al. 1995; Nose and Takamata 1997) and presumably within our ancestors. Remarkably little water is required, so carrying small volumes, or water-rich plants, could have allowed our ancestors to roam widely, for some time after drinking, in dry and open habitats without incurring lethal hyperthermia. Whilst hyperthermia was temporarily averted, neither the blood volume nor its osmolality would be modified, although the suppression of hyperthermia reduces water loss via evaporative cooling, and in

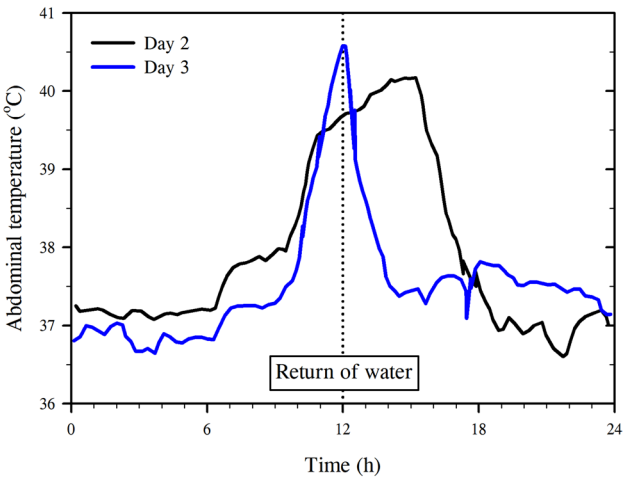


Fig. 4 Baboons exposed to a simulated desert environment, including solar radiation, showed progressive hyperthermia when deprived of water, and fed only dry food for three days. Providing water at 38 ℃ at peak hyperthermia on Day 3 resulted in complete resolution of the hyperthermia, with abdominal (implanted retroperitoneal loggers) temperatures falling very rapidly to <38 ℃. Redrawn from Mitchell et al. (2009)

Namib Desert baboons (Brain and Mitchell 1999) that effect can last from noon into the night, when body heat could be lost non-evaporatively.

Wheeler (1991a, 1991b) provided an alternative explanation for the avoidance of hyperthermia in those dry and open habitats. That is, a bipedal posture reduced the skin surface area exposed to direct solar radiation and enhanced both convective and evaporative cooling. Wheeler's modelling was confined to a standing hominin, but his hypothesis was endorsed for a walking hominin by Ruxton and Wilkinson (2011a, 2011b). When running, evaporation is further elevated by the relative air movements that accompany locomotion, but that does not imply that a thermoregulatory disadvantage existed for quadrupedal primates in those environments. For example, quadrupedal baboons, which exploited those habitats at the same time as hominins, do not show any disadvantage, providing they have access to water (Mitchell et al. 2009). It is hard to conceive of any thermoregulatory pressures being an evolutionary driving force for bipedality, if being quadrupedal confers no thermoregulatory disadvantage. Of course, that does not deny the possibility that bipedality might confer secondary thermoregulatory benefits.

Thermoregulation in our ancestral *Homo cursor*

By the time that our hominin ancestors began exploiting open and dry habitats, they had acquired the thermoregulatory capacity to dissipate the heat they generated when roaming, as well as the radiant heat gained during diurnal

activity. The key to that thermoregulatory capacity was their prolific, whole-body sweating from naked skin. Resource density would have been reduced in those habitats, so one can envisage more expansive roaming, presumably achieved by walking. But unless running emerged only with *Homo sapiens*, then our hominin ancestors also ran. Why did they incur the energy costs, thermoregulatory demands and the water requirements of running? How did running humans evolve? Sands (2010), who coined the pseudonym *Homo cursor*, believes that it had nothing to do with exercise performance.

For our body mass, compared to other endotherms and particularly to other primates, running is energetically costly, except for highly trained athletes, whilst walking is energetically less costly and more economical (Steudel-Numbers 2003). Those differences are of thermoregulatory importance. During horizontal locomotion, if heat storage is to be avoided, every Joule of metabolically released thermal energy has to be dissipated (Notley et al. 2023a). In hot environments, heat dissipation is reliant upon evaporative cooling.

The metabolic heat production of humans during horizontal (unloaded), steady-state walking and running is a non-linear (allometric) function of body mass (Bowes et al 2021b; steady-state oxygen consumption = $0.023 \times \text{mass}^{0.865}$). We assume that was similar for our hominin ancestors. Thus, a 60-kg hominin, moving at 4.8 km h^{-1} would consume oxygen at a rate of 9.9 L km^{-1}. That equates with a heat production of 217 kJ km^{-1}, and dissipating that heat would require a sweat secretion of 89 g km^{-1}, if all of that sweat evaporated on the skin, which does not happen (Candas et al. 1979a, 1980). If walking constantly for 20 km, that hominin would need to evaporate 1.9 kg of sweat if sweating was 100% efficient. Consequently, in the absence of fluid replacement, our hominin would end up hypohydrated by > 3%, and by analogy with modern humans (Wyndham and Strydom 1969a, b; Notley et al. 2023c; Fig. 11]), its deep-body temperature might exceed 39.0 °C, even in temperate conditions.

Whilst the energetic cost of locomotion is both speed- and efficiency-dependent, the overall cost of locomotion is determined principally by exercise duration. Let us return to Alberto Salazar, whose metabolic power generation during a marathon would not have exceeded 1.5 kW (Costill et al. 1971). To dissipate the resulting metabolic heat, he would have to evaporate sweat at 2.2 L h^{-1}. In hot-humid environments, only ~ 60% of discharged sweat can evaporate (Stewart 1981). Greater evaporation can be expected during marathons, which are rarely run in unfavourable thermal environments, although a 60% evaporation rate of Salazar's peak sweat rate (3.7 L h^{-1}) matches the 2.2 L h^{-1} required to dissipate the metabolic heat. Solar heat might add 100–150 W to the metabolic load (Nielsen 1990). That can be offset by his running speed (5.8 m s^{-1}), because it would require the dry-bulb temperature to be only 4 °C below his skin temperature to dissipate all of that solar heat via convective cooling (Mitchell et al. 1969). His performance would not have been limited by his capacity to dissipate metabolic heat through evaporation. Our hominin ancestors were unlikely to have run for hours at such a high metabolic power generation (Halsey 2016), nor would they have the fatigue resistance of contemporary athletes (Marino et al. 2022). Whilst we do not know when their sweating capacity evolved to match that of modern humans, their running speed may have been limited by their sweating capacity.

Which of our ancestors could have been the first *Homo cursor*? Experts in hominin energetics believe that the first to have the posture, limb length and hind-limb extension necessary for endurance running was *Homo erectus* (*e.g.*, Steudel-Numbers and Wall-Scheffler 2009; Pontzer 2012b, 2017b; Raichlen and Pontzer 2021), which emerged ~ 1.9 million years ago (Pontzer 2012a). Initially, it may only have been the male *Homo erectus* that was capable of endurance running, because the pelvis of his average female counterpart seems less suited to running (Simpson et al. 2008). The australopithecine precursors of early *Homo* were prey, not predators (Brain 1983), who ate predominantly underground tubers (Dávid-Barrett and Dunbar 2016), and their skeletal morphology indicates they would not have been proficient runners (Carrier et al. 1984; Pontzer 2012b). Early *Homo* was omnivorous, not carnivorous. They had the capacity to be hunters, and not the hunted.

Homo erectus, the hunter, has been the source of enthusiastic conjecture about the origin of running. We have restricted our enthusiasm to the thermoregulatory aspects and to the hypotheses advanced about why *Homo erectus* needed to run. The first theory was that it enabled them to get to carcasses faster than other scavengers, while the second hypothesis was based on persistence hunting (Lieberman 2015). Scavenging could have occurred at any time, but persistence hunting, which entailed running prey, usually the ungulates (hooved animals), to exhaustive hyperthermia, would have been most effective in the hottest part of the day. That would require resistance to fatigue (Marino et al. 2022), and would impose a combined metabolic and environmental heat load on the hunter, with the inevitable hypohydration. The question of whether *Homo erectus* could tolerate hypohydration has been asked more often than the question of whether he could tolerate hyperthermia better than his prey. Like Ruxton and Wilkinson (2011a), we suspect that hyperthermia imposed the greater risk, and we have elaborated on that within Part 3 of this historical series (Notley et al. 2023c).

Scavenging is unlikely to have challenged thermoregulation. On the other hand, persistence hunting would have

relied on the thermoregulatory competence of *Homo erectus* outperforming that of its prey. Much of the conjecture about persistence hunting by our ancestral hominins is based on observations of how persistence hunting has been carried out by modern hunter-gatherers in arid and semi-arid, sub-Saharan Africa (Liebenberg 2006; Glaub and Hall 2017), although they are not the only indigenous persistence hunters (Liebenberg 2006). Persuasive in conjectures about hominin persistence hunting has been the view of Liebenberg (2006) that "*data from observations of !Xo and /Gwi hunters of the central Kalahari in Botswana … suggest that persistence hunting was a very efficient method under certain conditions. Compared with other forms of hunting, it may have been one of the most efficient*" (P. 1017). Those Kalahari hunters pursued their prey relentlessly, often tracking its footprints without stopping their running. One successful hunt covered 33 km in 4 h 57 min, at an average speed of 6.6 km h^{-1}. If that was typical of the speed of persistence hunting for our hominin ancestors, it is slow by modern standards, since winning the Comrades Marathon (Fig. 1) requires running at 16.5 km h^{-1} for five hours. Nevertheless, persistence hunting by running was likely to have been more successful than persistence walking (Hora et al. 2022).

It was that Kalahari persistent hunt that was modelled by Hora and colleagues (2020) when evaluating whether the thermoregulatory capacity of *Homo erectus* was compatible with persistence hunting. They set as a criterion that hypohydration from sweating should not exceed 10% of the body mass, and, according to their model, it would not have done so. They considered, but did not analyse, the likely concomitant hyperthermia. Though it requires extrapolation of the predictive equation of Wyndham and Strydom (1969a, b) well beyond the original data (a potentially dangerous practice), a predicted deep-body temperature of 43.4 °C at 10% hypohydration would result. Our *Homo erectus* persistence hunter would have increased his risk of developing heat stroke, even if he survived dehydration, although marathon runners often experience similarly high deep-body temperatures without sequelae (Pugh et al. 1967; Maron et al. 1977; Maughan et al. 1985).

Not everyone shares the enthusiasm for the idea that either scavenging or persistence hunting contributed to the evolution of fast endurance running in modern humans. The sceptics, Pickering and Bunn (2007), pointed out that high carcase densities would not have required running to scavenge, and the habitat encountered by *Homo erectus* was not open, but savanna-woodland, with reduced visibility. They suggested that tracking prey in those habitats was very difficult and that persistence hunting is extraordinarily rare in modern hunter-gatherers. Indeed, they believe that main motivation for the Kalahari hunt described by Liebenberg (2006) was that the hunters were being filmed for a television documentary. Sands (2010) was also sceptical about the role of subsistence hunting in the evolution of *Homo cursor*, instead supporting the possibility that the runner's high might have driven the desire to engage in fast endurance running. Whatever the reason, endurance running (and swimming) will disturb one or more of our regulated variables (Notley et al. 2023a [Table 1]), and when those practices become habitual, they will induce a suite of physiological adaptations that are overlayed onto the genotypic attributes acquired during the ascent of *Homo sapiens*, and the progression of our ancestral sweating specialists (*Homo sudomotor*; Notley et al. 2023c) through to *Homo cursor* (running man; Sands 2010).

Physiological adaptations to changes in body temperature

We embark on the last topic from this review series recognising that it could form two independent reviews, one on the adaptations to heat (*e.g.*, Sundstroem 1927; Kuno 1934, 1956; Yoshimura 1964; Wenger 1988; Taylor 2006a, 2014; Horowitz 2014) and another on cold adaptation (*e.g.*, Hammel 1964; Hicks 1964; LeBlanc 1992; Himms-Hagen 1996; Young 1988, 1996; Launay and Savourey 2009; Mäkinen 2010; Daanen and Van Marken Lichtenbelt 2016; Yurkevicius et al. 2021). Nevertheless, in the footsteps of Wyndham (1969), Bligh (1973), Zeisberger and Roth (1996) and Tipton et al. (2008), we proceed with the enthusiasm of the brave, a desire for thoroughness, but with a wish to avoid reader exhaustion, as we discuss the critical historical steps that led to our contemporary understanding of human adaptations to hot and cold conditions. As with Parts 1–3 of this series, our work has been divided into three epochs: the period before 1900, the Krogh-Hill epoch (1900–1930), named after August Krogh (1874–1949, Denmark) and Archibald V. Hill (1886–1977, England), and the modern epoch. Our primary emphasis is upon the potential benefits that thermal adaptation has for those who engage in endurance-dependent athletic and occupational pursuits for which *Homo sapiens* have a genetic capability. Our focus is upon the thermoeffectors that defend the thermal integrity of the deep-body tissues, but in the cold, there is the hazard of peripheral soft-tissue injuries, so it is of interest to know whether local adaptation of those peripheral tissues can be protective.

At the end of the nineteenth Century, some were anxious about living and working in unfamiliar tropical climates (Sambon 1898a). Some believed Europeans could neither tolerate nor adapt to those climates. Therefore, we open this section by showing how opinions on that theme changed from 1771 to 1923. The last statement, which reveals the

cardinal sins of bias and unfamiliarity with the literature, appeared within one of Britain's most prestigious medical journals and was made by the Director-in-Chief of a prestigious scientific trust.

> "*... some employments, which are of such a nature, as cannot well be performed in hot and unhealthy countries, by such as are lately arrived, without imminent danger of their health and lives ...*" (Lind 1771: P. 104).
> "*So late as 1850 Dr Knox of London declared that Englishmen transplanted to America and Australia must inevitably deteriorate and would die out in a few generations. The absurdity of such a statement does not need to be pointed out ...*" (Cutler 1902 [P. 421]).
> "*THE title of this lecture is intended to indicate that the white race, under existing circumstances, cannot be looked upon as more than wayfarers in the tropics, as people who have there no continuing city in the sense that they can settle and rear a progeny blessed with the energy and virility ...*" (Balfour 1923a [P. 1329]).

On the nature of adaptation

Notley et al. (2023c) reviewed the acute thermoeffector responses of humans that defend body temperatures when confronted with diverse thermal stresses, and thereby reduce physiological strain. Those processes are forms of physiological accommodation, since they allow us to remain within, and to tolerate, thermally stressful conditions. Our individual capacities for accommodation are a function of our genetically determined anatomical and physiological characteristics (our genotype), but we can modify our phenotype through physiological adaptation.

Over millennia, the genotypic characteristics of some individuals provided them with survival advantages, so nature gave them the opportunity to transmit their genes (Darwin 1859). Through natural selection, humans acquired, and then inherited, the genetic attributes of sweaty, endurance specialists ("Thermoeffector evolution: vascular networks, homeothermy, sweating and hairlessness"). Given the wide, inter-individual variations that exist within our genetically determined characteristics, our attention now turns towards the degree to which we can modify those anatomical and physiological attributes during adaptation. Phenotypic adaptations can enhance stress tolerance during athletic and occupational pursuits, and they are revealed through modifications in thermoeffector control and the stability of our regulated variables (Notley et al. 2023a [Table 1]). Such changes can occur when living, working or exercising in one's natural environment (acclimatisation), or through artificially imposed environmental conditions (acclimation), both of which repeatedly disturb thermal homeostasis. Whilst acclimatisation is a long-term process that takes years to be fully expressed, acclimation effects occur within a few days (short-term process), with ergogenic advantages occurring within a few weeks.

In this section, we consider thermal adaptation as it pertains to physiologists with interests in athletic performance, physiologists who focus upon occupational pursuits and thermal physiologists with interests in both resting and exercising states. Since increased thermal tolerance can be induced either passively or actively (exercise), one might wonder whether sitting in a hot bath or a sauna with a good book is advantageous for marathon runners preparing to race in the heat. Will sitting in an ice bath be beneficial for swimmers of the English Channel? Will the regular exposure of hands and feet to ice-cold water help to protect them from cold injuries? Which athletes and workers would benefit more from thermal adaptation; those who are about to experience the heat or those embarking on stressful cold exposures? How important are the physiological changes relative to the benefits gained from experiencing and discovering how stressful heat and cold conditions can dramatically affect athletic and work performance?

Well-trained endurance athletes may already be so well adapted to the applicable climatic conditions, that additional physiological improvements may be quite small, and perhaps not even quantifiable. However, the experience and psychological benefit obtained from trying to race at personal-best pace in oppressive conditions may well lead to the development of a strategic approach that makes the difference between successful racing and failing to complete the race (Taylor and Cotter 2006), or worse still, succumbing to heat illness (Notley et al. 2023c). Such exposures afford opportunities to prepare and rehearse behavioural strategies, including race pacing and rehydration strategies. The significance of those benefits depends upon factors that are beyond the expertise of most physiologists.

We may describe adaptations according to their impact upon our regulated or controlled variables, with thermal adaptation truly being an integrated physiological process; "*every adaptation is an integration*" (Barcroft 1934 [P. 187]). Thus, our observations will always be constrained by our methodological limitations (Notley et al. 2023b) or the scope of our research questions, since they are just pieces of the overall puzzle. No single measurement or mechanism will enable us to explain the entire process of thermal adaptation. Moreover, whilst our emphasis is not behavioural thermoregulation, behaviours are among our first, as well as our most powerful responses (Cabanac 1972; Nelson et al. 1984; Malvin and Wood 1992). They can ensure that modern humans seldom encounter stress, with such stress

avoidance possibly being disadvantageous to the survival of individuals and our species (Selye 1973). Furthermore, we advise caution concerning the application of observations from the general population to athletes, who have unique and more homogeneous genotypes and phenotypes. The reverse application is also cautioned.

One reason for caution lies in the different capacities of those sub-populations for adaptation. The general population contains stress-intolerant, sedentary individuals who respond vigorously to acutely applied homeostatic disturbances. Following repeated disturbances, they will undergo pronounced physiological adaptations that increase their stress tolerance. Those individuals are high responders. At the other end of that spectrum are the adventurers, and the occupational and recreational athletes. Through those activities, they will already be physiologically adapted, although perhaps not completely. They are low responders. It is a mistake to assume that large physiological adaptations changes observed in high responders will also occur in low responders exposed to the same stresses. A classical example of that truism is seen with increases in the maximal ability to extract and consume oxygen during exercise (peak aerobic power; Hill and Lupton 1923) that occur in response to endurance training. Whilst substantial changes to those attributes may occur in the general population (Saltin et al. 1968b; Ekblom 1969), well-trained individuals exhibit little or no change. Indeed, our adaptation responses even seem to be genetically linked (Prud'homme et al. 1984; Vollaard et al. 2009), with most elite athletes attaining their genetic potential for training induced adaptations. Thus, the measurement of peak aerobic power is of limited value with regard to predicting athletic performance in elite athletes, and that myth has been domesticated elsewhere (Noakes and Ekblom 2008).

At the close of the Krogh-Hill epoch, two scientists from the Southern Hemisphere highlighted the implications of inter-individual variability, as it related to thermal adaptation. Edward S.J. Sundstroem ([Sundström] 1880–1970, Finland and Australia; Sundstroem 1927) wrote that most populations include individuals lacking any thermal adaptation, those who are in the process of adapting and those who are well adapted. Moreover, he recognised "*that individuals may not be all alike in their choice of the acclimatization mechanisms which nature has placed at their disposal. Some may succeed in striking the medium road preferring to divide up the burden imposed by a trying environment on several functions without unduly overtaxing any of them*" (Sundstroem 1927 [P. 352]). Secondly, Aldo O. Dreosti (1902–1971, South Africa; Dreosti 1935, 1950), when evaluating the heat tolerance of recruits from different African communities prior to their employment within hot-humid mines, found that, from more than 42,000 miners tested, 15% were intolerant, while 25% had acquired heat tolerance naturally. Almost a century earlier, Johnson and Martin (1841), wrote that "*the Constitution of Man is better adapted to bear those changes of temperatures and other circumstances, experienced in migrating from the northern to a tropical region, and vice versâ, than that of any other animal … this … is a distinctive characteristic of the human species …*" (Johnson and Martin 1841 [P. 1]).

Modern occupational athletes are required to wear protective clothing, but recreational athletes may choose clothing best suited to the thermal stress imposed by the expected ambient conditions. What can those athletes learn from the physiological responses of different populations that lived and worked their entire lives in hot climates? What can they learn from clothed workers in hot industries? Clothing compromises heat loss, with physiological strain being dramatically elevated when metabolic heat production approaches its maximal rate. For those wearing protective clothing, the advantage of increasing sweat rate, a common feature of short-term heat adaptation, is negligible, with heavy sweating significantly degrading thermal protection and elevating discomfort (McLellan et al. 2013; Taylor 2015). Whilst elevating sweat rate may be advantageous when competing in the heat, high sweat rates can be problematic during ultra-distance events, even when drinking is possible, because water absorption rates do not match sweat rates (Gisolfi et al. 2001; Notley et al. 2023c).

In the cold, clothing choices are generally aimed at reducing heat loss, but the swimmers of *Ice Miles*, as well as those in events controlled by the *International Winter Swimming Association*, compete without thermal protective or buoyancy clothing. Those are worst-case scenarios that are normally associated with unintentional cold exposures. Not surprisingly, the wearing of wetsuits when racing in water temperatures <18 °C has been mandated for many events (*Fédération Internationale de Natation*). However, insulated clothing often results in individuals who live in very cold conditions, only briefly experiencing the cold, with those exposures rarely being of the entire body (Rodahl 1958). There are some occupations in which the hands (*e.g.*, fish filleters) or entire bodies (*e.g.*, military personnel) are regularly cold exposed. Much has been learned about the physiology of human cold adaptation from sub-populations that live and work in cold climates. But before we examine different forms of thermal adaptation, it is useful to consider the first principles of physiological adaptation.

To which thermal stimuli do humans adapt?

We open this sub-section with a strength-training analogy, during which repeated loading of the skeletal muscles with an external resistance (stress) will induce

neuromuscular adaptations that result in subsequent exercise with the same external resistance imposing less physiological strain (Edgerton et al. 1996). That is an habituated response. As adaptation progresses, the strain experienced when that same external stress is re-applied diminishes. However, for the strength athlete to continue to adapt and improve, that external stress (forcing function) must be progressively increased (load, repetitions, volume [cumulative mass]) and that is the cornerstone of the overload principle (DeLorme and Watkins 1951). Indeed, regardless of which physiological function one examines, adaptation will not occur unless sufficiently large disturbances are repeatedly applied (Adolph 1956, 1964, 1972). As time progresses, our responses to the application of those same external stimuli will become progressively less pronounced.

Let us weave that general principle into that which is known about regulated and controlled physiological variables (Notley et al. 2023a [Table 1]). Repeated disturbances to one or more of our regulated, but not our controlled, variables will induce physiological adaptation. Thermal adaptations occur when one (or more) of our regulated variables is sufficiently and frequently disturbed from its normothermic state. Consider our body temperatures, with the temperatures of our deep-body, skin and other thermosensitive tissues combining to form the regulated variable. Repeatedly changing any of those temperatures may lead to local or whole-body thermal adaptations. During heat adaptation, thermal stress can be imposed externally (exogenous heat stress), which elevates both deep-body and skin temperatures, or metabolically (endogenous stress), which elevates deep-body temperature, but not necessarily skin temperatures, depending on the environment. For cold adaptation, heat passes through the skin to the environment, so there is no natural equivalent whereby the deep tissues can be cooled independently of the skin, although internal cooling could be achieved using extracorporeal cooling of the blood. Thus, cooling of the deep-body tissues is invariably accompanied by cooling of the superficial tissues.

The stimuli for thermal adaptation are those body temperature disturbances (physiological strain), which can be induced passively and actively. One might quantify the physiological overloads that induce adaptation, just as coaches might quantify their training programmes using indices that reflect the size (intensity) of each stimulus, the duration and frequency of their application and the volume of each overload. They might even seek to evaluate the cumulative physiological burden of each training session. We are not seeking to quantify the stimulus per se (*e.g.*, ambient temperature or metabolic heat production), but its impact on physiological strain, as reflected within changes in a regulated variable. For endurance training, Banister and Calvert (1980, Canada) developed the concept of the endurance-training impulse, within which strain was quantified using heart-rate data. However, to apply that concept to physiological adaptations, we must replace heart rate, which is a controlled variable, with one of our regulated variables (*e.g.*, body temperature), since they are the variables to which our regulatory centres respond. Therefore, Taylor and Cotter (2006) modified the training-impulse concept for use during thermal adaptation, resulting in a thermal impulse (Eq. 1), which enabled the quantification of either heat- or cold-adaptation stimuli.

$$\text{Thermal impulse} = \int \left(T_{b-i} - T_{b-0}\right) \mathrm{d}t \ [^{\circ}\mathrm{C\,min}] \quad (1)$$

where: $T_{\text{b-i}}$ is body temperature at time i, $T_{\text{b-0}}$ is the basal body temperature, dt is duration of the thermal stimulus

Unbeknown to those authors, a similar concept (thermal response or fever index) had been used for investigating the pathophysiology of fever (*e.g.*, Kenedi et al. 1982). Since we do not know the integrated body temperature to which our regulatory centres respond, we use a surrogate of one of its components (deep-body temperature), but that surrogate must faithfully track changes in the temperature of the blood perfusing those centres (Notley et al. 2023b). The impact of successive thermal loads can be estimated by adding individual impulses, which then becomes the cumulative adaptation impulse. Details of these concepts and adaptation theory are available elsewhere (Taylor 2014). During natural forms of thermal adaptation, our regulatory centres are responding to those same stimuli.

Natural adaptation: acclimatisation within hot and cold climates

Interests in thermal adaptation were initially driven by pragmatic issues (*e.g.*, colonisation, the industrial revolution, international conflicts), and preceded athletic pursuits. An outcome of colonisation that ignited the interests of scientists was the apparent inability of Europeans to tolerate tropical climates (Lind 1771; Balfour 1923a), relative to tropical indigenes. Did they possess anatomical or physiological attributes that were not present in Europeans? If they did, then how did they acquire that advantage? Our summary timeline (Fig. 5) highlights critical historical steps in the development of our understanding of human heat adaptation.

Perhaps the person of greatest current relevance in the nineteenth Century was James Johnson (1777–1845, England), who, with James R. Martin (1796–1874, England), had just published the sixth edition of *The Influence of Tropical Climates on European Constitutions* (Johnson and Martin 1841 [colonial India]). That text preceded the birth of Patrick Manson (1844–1922, England), the first Director of the London School of Hygiene and Tropical Medicine (To and Yuen 2012), which was established in 1899, following its counterpart in Liverpool (1898). Both were part of the *constructive imperialism* (an oxymoron) policy of the British

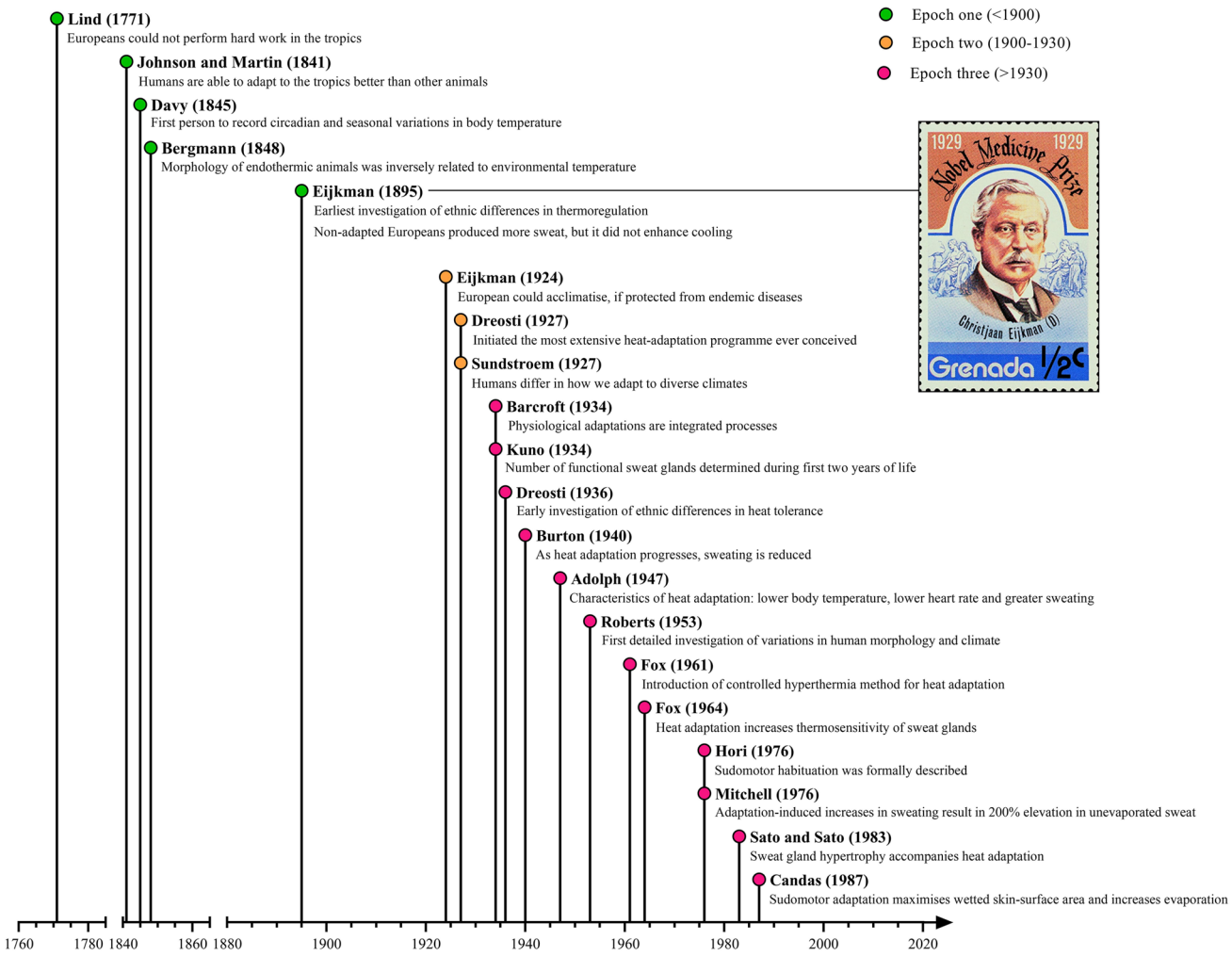


Fig. 5 Human heat adaptation: mileposts in the progression of our understanding over the past two centuries. The image is a stamp issued in Grenada to commemorate the Nobel laureate Christiaan Eijkman. Source: Singapore Medical Journal (Merritt and Tan 2011). Accessed: March 17th, 2022

Colonial Secretary of the time (Harrison 1992). Johnson and Martin (1841) knew that we could elevate heat production in the cold, and dissipate excess thermal energy in the heat. Whilst they did not understand either mechanism, Johnson did not accept prevailing teachings without question (Harrison 1992), and he believed the view that humans could not adapt to the heat to be a misconception; he was not alone.

> "*... the almost universal opinion that the European cannot colonize the tropics, but must inevitably fall, sooner or later, a victim to the influence of their deadly climate. I will endeavour to prove that this statement is wrong ... there is no reason why the European should not conquer the tropical world.*" (Sambon 1898a [P. 589]).

We introduced John Davy (1790–1868, England) in Parts 1 and 2 of this series (Notley et al. 2023a, 2023b), and noted that he was possibly the first person to record deep-body temperatures during exercise, as well as circadian and seasonal variations (Davy 1845). We now accompany him on a cruise to Barbados (West Indies), during which he replicated those measurements within a tropical climate (Davy 1850 [tabulated data: Pp. 449–466]). Those data provided some of the earliest records for the acute impact of the tropics on body temperatures, and soon became the accepted dogma. Davy noted deep-body (sublingual) temperatures were almost 1 °C higher in the tropics than within temperate regions, and its circadian variation covered almost 2 °C, but with the nadir in the morning, rather than the evening (as recorded in England).

To those data, we add the observations of Richard Neuhauss (1855–1915, Germany) on deep-body temperature (rectum and axilla), heart rate and urine production, recorded four times daily (0600, 1200, 1800 and 2200 h)

on his trip around the world in 1884 (March-November; Neuhauss 1893 [Pp. 373–379]). That trip included northern and southern temperate zones, as well as tropical regions. Like Wunderlich (1871) and Richet (1889), he found rectal temperature to be ~ 0.6 °C warmer than the axilla, and observed slightly higher body temperatures when in the tropics (also see: Pembrey 1898; Castellani and Chalmers 1913). However, the data of Davy (1850) and Neuhauss (1893) involved tropical sojourners, so they offer little to our understand of thermal adaptation.

To address that limitation, we return to William J. Young (1878–1942, England and Australia), whom we introduced in Notley et al. (2023b). He studied the rectal, sublingual and urine temperatures of tropical residents of European ancestry (Young 1915a [tabulated data: Pp. 225 and 227–229]). Under basal conditions, he found no significant variation between the rectal temperatures of Europeans acclimatised to the tropics, and those of their counterparts living in Europe. From that apparently unremarkable, yet important observation, we turn our attention to studies in which the possibility that differences in thermal tolerance (cold and hot) might exist between indigenes and transplanted Europeans, for it was within the former that physiologists first observed thermal adaptation. They completed physically demanding work in their local climates without undue strain, while their recently arrived, European counterparts could not (Lind 1771). Over 150 years later, Eijkman (1924) described tropical indigenes as "*permanent summermen*", and their relevance to our interests is that they were the occupational athletes of their time, so it is from those athletes that we gain our first insights into human heat adaptation.

Heat-induced acclimatisation in indigenous populations

Another colonial power was The Netherlands, and working almost right through the Krogh-Hill epoch was the Dutch physician Christiaan Eijkman (1858–1930, Fig. 5; Nobel Prize in Medicine in 1929; Nobelstiftelsen 1965). He led the Medical Laboratory at the Military Hospital in Indonesia (1888–1896; Pietrzak 2019), and discovered that *polyneuritis endemica perniciosa* (beriberi), which was common in soldiers of the Dutch East Indies, was nutritionally related (Jansen 1950; Merritt and Tan 2011; Pietrzak 2019). Whilst unknown at the time, it was the result of a thiamine deficiency, but our interest in him stems from his thermal investigations.

Unlike Woodruff (1900, U.S.A.) and Balfour (1923a, England), Eijkman believed that people of European ancestry could indeed attain a state of acclimatisation similar to the indigenes, if they were protected from endemic diseases (Eijkman 1924). Nevertheless, there existed a belief that tropical climates were associated with, and perhaps causally linked to, the origin of many diseases (Sargent 1960). Two so-called neurological disorders highlight that school of thought: tropical neurasthenia (Woodruff 1900; Taylor 1916; Huntington 1924) and Arctic hysteria (Aberle 1952). The former was a type of climatic determinism (Taylor et al. 2022), in which the climate was believed to predetermine both the choice of where to live and one's health following the making of that choice. Tropical climates were thought to result in a "*… lack of industry, an irascible temper, drunkenness, and sexual indulgence …*" (Huntington 1924 [P. 68]). That state is colloquially known as "*going troppo*", but tropical neurasthenia was domesticated by Cilento (1925), Sundstroem (1926) and Ladell (1958/59). With regard to Arctic hysteria, Sargent (1960 [P. 243]) said that it "*is not only not an Arctic disease but it is not even a climatic disease*". Scientific advancement required people to step away from a "*prefabricated set of interpretations*" (Kennedy 1962), and Johnson and Martin (1841) stepped away in the first half of the nineteenth Century, with Eijkman (1895, 1924) following that lead.

Christiaan Eijkman also investigated the affects of tropical climates on indigenes and recent European arrivals. He challenged the conclusions of Woodruff (1900) that Europeans could withstand cold stress better than could people of African ancestry, but they were less able to lose heat via radiation. Whilst the first statement has been supported within the modern epoch (Burgess and Macfarlane 2009; Maley et al. 2015), Eijkman knew that radiative heat loss was a function of temperature (first principle), and unrelated to skin colour. Woodruff's interpretation was "*physical heresy*" (Eijkman 1924 [P. 890]). Although he could not measure radiant heat loss, he used skin dissected from European and Malaysian cadavers (Malaysia was then a Dutch colony), wrapped the skin around a cylinder of heated water and observed equivalent heat loss from both skin types (Eijkman 1895). Indeed, as demonstrated when radiant heat loss could be measured accurately, skin colour differences have no affect on the emissivity of human skin in the heat-loss waveband (Mitchell et al. 1967), although darker objects absorb radiation better across a wider range of the electromagnetic spectrum, as Eijkman (1895) observed. In recognition of his wide-ranging contributions to topical medicine and health, the Royal Tropical Institute (previously the Colonial Institute, Amsterdam; Notley et al. 2023b [Table 2]) initiated The Christiaan Eijkman Medal in 1927.

Further evidence that people of European ancestry were not precluded from successfully adapting to work in the heat, came from the research of Joseph S. Weiner (1915–1982, South Africa and England), whom we have met throughout this series. Weiner had observed that, after six months of hard physical work in hot-humid mines, miners of African ancestry appeared not to be as well adapted (acclimatised) to work in the heat as artificially adapted (acclimated) Europeans (Weiner 1950). Those physiological differences

disappeared if both groups went through the same heat-acclimation programme (Wyndham et al. 1964b). From a collaboration among South African, French and Australian scientists, Nick Strydom and Cyril H. Wyndham (1916–1987, South Africa; Anonymous 1987; Wolstenholme 1987; Mitchell and Laburn 2022) compared the acclimatisation state of various indigenous groups with Europeans who lived with them (Strydom and Wyndham 1963). They found that different indigenous groups had the same deep-body (rectal) temperature response to exercise in the heat, but desert-dwelling Bushmen and Arabs had higher sweat rates. Most remarkable was how similar the responses were for both the tropical indigenous men and the European men with whom they lived. They all revealed similar adaptations to exercising in the heat.

Sudomotor responses The colonial powers sent both administrative and military personnel to their colonies. Whilst the administrators were just uncomfortably hot, the soldiers suffered heat-related problems, including many deaths from exertional heat stroke (Notley et al. 2023c). Christiaan Eijkman decided to investigate the causes, and whether or not they could be managed. He compared people of European and Malaysian ancestry, in possibly the earliest investigation of ethnic differences in thermoregulation (Eijkman 1895, 1924), and observed equivalent deep-body (axilla) temperatures in the morning (37.0 and 36.9 ℃, respectively).

Of greater interest, however, are his observations concerning sweating, and the experimental design he developed for that study. Eijkman (1895) studied pairs of Europeans and Malaysians, matched for body mass, averaging 57.4 and 55.6 kg (respectively). From 27 parallel experiments (75 min) in humid air (32 ℃ dry bulb), presumably at rest, he found their average deep-body temperatures to be equivalent (37.1 and 37.0 ℃, respectively), whilst the Europeans lost sweat 30.4 g h^{-1} more rapidly. He also recognised that sudorific response to be superfluous and wasteful (Eijkman 1895), since not all of that sweat evaporated on the skin. Superfluous sweating was rare in the Malaysians, but common in the Europeans, especially in new arrivals (Eijkman 1924). Those observations provided perhaps the first illustration of what would become known as the acute (physiological accommodation) and short-term adaptation responses of the Europeans, and the longer-term habituated responses of the Malaysians.

To explore those ethnic differences, Eijkman examined sweat-glands densities across ten skin regions, observing "*no perceptible difference between the two races*" (Eijkman 1924 [P. 891]). The average glandular density of the Malaysians was 160 glands cm^{-2}, that of the Europeans was 162 glands cm^{-2}. Next, he studied both groups resting in air at 30 ℃ (360 min; 200 mL water provided), with urine volumes and body masses determined before and after exposure. Both sweat secretion and urine production were higher in the Europeans (Eijkman 1924). When those trials were repeated (120 min, 32 ℃ dry bulb, artificially humidified air), but with the Europeans water deprived, their sweat and urine flows were still higher than those of the Malaysians. In another first, he observed that "*unevaporated sweat, the quantity of which, weighed together with the clothing, amounted to more than three times as much in the thirsting white as in the water-drinking Malayan*" (Eijkman 1924 [P. 891]). Since those Europeans had lived and worked in Malaysia for some time, they were partially heat acclimatised. We now know that only ~ 10% of the increase in sweating, following short-term adaptation to exercise in a hot-humid environment, actually contributes to evaporative cooling, with the rest being superfluous (Mitchell et al. 1976).

Eijkman (1895, 1924) was also well aware of the morphological differences between Europeans and Malaysians, and the impact those differences might have on heat exchange and storage. Indeed, he designed his experiments to negate those effects (P. 138), with his matching of participants marking possibly the earliest attempt to control for differences in the surface area to body-mass ratio (mass-specific surface area), although few followed his lead (Havenith and van Middendorp 1990; Havenith et al. 1995; Taylor 2006a; Notley et al. 2016, 2017). Since dry-heat exchanges are energy-efficient avenues for heat dissipation, then larger mass-specific surface areas tend to support heat tolerance during rest and exercise, although other factors are sometimes equally important (Wyndham 1965). Because humans have the same general (allometric) shape, then larger mass-specific surface areas are found in smaller individuals, such as children, many women and all slender individuals. As a consequence, such people are less dependent on activating their autonomically driven avenues for heat loss (Notley et al. 2016, 2017).

During our first epoch, Carl Bergmann (1847, Germany) described broad differences in the morphology of endothermic, non-human animals living in different climates, and suggested that body mass appeared to be inversely related to environmental temperature, and was possibly a climatic adaptation. Joel Allen (1877, 1907; U.S.A.) described differences in limb shape which varied with climate, with animals in colder climates tending to have shorter and thicker limbs. In possibly the first detailed investigation of variations in human morphology, Derek Roberts (1953, England; Crawford 2017) reported evidence across 116 indigenous groups (also see: Suominen 1929; Roberts 1978), finding that body mass was inversely related to the average annual temperature of their country of origin.

That outcome for humans was consistent with the ecological generalisation of Bergmann (1847), in that sphericity favours heat conservation (Sundstroem 1927). Whilst the

physical principle remains valid, whether Bergmann's Rule indeed was a biological rule was challenged by Per F. Scholander (1905–1980, Norway; Scholander, 1959, 1955; Blix et al. 2022) and Ernst Mayr (Mayr 1956), with challenges of its applicability to humans continuing (*e.g.*, Foster and Collard 2013). Whether any rule relating human body size to climate is currently relevant is doubtful, given the extensive immigration and world-wide improvements in dietary resources and health services that occurred during the second half of the twentieth Century. Nevertheless, when we examine research from the Krogh-Hill epoch, during which adequate diets and immigration were much less common, we should be sceptical about comparisons of climate-related raw data from different ethnic groups, unless those data are have been corrected for variations in body size, either by the authors or the readers. Eijkman (1895) recognised that requirement.

Similar caution is required when comparing the microanatomy of eccrine sweat glands, their regional distribution and their functional characteristics across people of varying ancestry. That material is covered in detail by Smith and Havenith (2011, England) and Taylor and Machado-Moreira (2013, Australia and Brazil), and summarised by Notley et al. (2023b, 2023c). With that precaution, we now turn to emphasise possible ethnic differences in sudomotor activity, and commence with contributions from Yas Kuno (1882–1977, Japan; Morimoto 2015; Nagasaka 2022; Notley et al. 2023b [Table 1]). In his seminal monograph (Kuno 1934, 1956), he hypothesised that the number of functional sweat glands was determined within the first two years of life. Whilst there is a well-established postnatal conversion of the sudomotor neurons from an adrenergic to a cholinergic phenotype (Schotzinger and Landis 1988; Landis 1990; Guidry et al. 2005), it may be impossible ever to test Kuno's hypothesis.

However, that hypothesis may imply an ancestral attribute, if being born and raised within warmer climates resulted in higher sweat-gland densities. Whilst there are historical and contemporary data consistent with that possibility (Schiefferdecker 1922; Homma 1926; Kawahata and Sakamoto 1951; Kuno 1956; Toda 1967; Hwang and Baik 1997), others have either challenged those observations (Woollard 1930; Weiner and Hellmann 1960) or provided contradictory evidence (Eijkman 1924; Thompson 1954; Collins and Weiner 1965; Roberts et al. 1970; Green 1971; Knip 1972; Garcia et al. 1977; Samueloff 1987; Inoue et al. 2009). We are amongst the sceptics, as ancestry-related differences in glandular densities seem to be more artefactual than real (Taylor 2014). Instead, we suggest that the whole-body density of eccrine sweat glands for adults of all ancestries will be about 112 glands cm^{-2}, with extensive inter-segmental variation (Taylor and Machado-Moreira 2013). If glandular densities are similar, then the observation of greater sweat rates for Europeans than Malaysians (Eijkman 1895, 1924) must be attributable to differences in glandular function.

How glandular function can differ across individuals was established within the modern epoch, and there are several functional and morphological characteristics of sudomotor activity that are amenable to modification during the course of both passive (resting) and active heat adaptation. Those changes might also explain differences in sweating across short- and long-term residents of tropical and equatorial climates, when compared with residents of temperate climates. Those adaptations relate to three primary changes: an alteration in the initiation of sweating (sudomotor threshold), an increased capacity of the glands to secrete sweat (glandular hypertrophy) and a change in the reactivity of the sweat glands to a given change in body temperature (sudomotor sensitivity). Such changes can reflect adaptations within the regulatory centre itself (threshold) or process adaptations that can occur at the sweat glands. Modifications in sudomotor sensitivity can occur both centrally, via altered thermoefferent drive, and peripherally, through changes in cholinergic sensitivity of the glands themselves (Folk 1974; Brück 1986; Werner et al. 2008).

With regard to adaptations to the regulatory centre, we will examine four studies that are relevant to thermoregulation within indigenous populations. The first two were led by Cyril Wyndham, who introduced the most extensive programme of supervised heat adaptation (acclimation) within climatic chambers, sometimes holding 1000 miners and operating over four shifts a day. Miners worked in simulated underground conditions for four hours a day for ten days (Mitchell and Laburn 2022), with hundreds of thousands of miners being heat acclimated (Wyndham and Strydom 1969b; Wyndham et al. 1973). From trials conducted in research-specific climate chambers, Wyndham and his colleagues found lower sudomotor thresholds in miners of African ancestry and in *Bushmen* (the *MaSarwa*, the original modern inhabitants of southern Africa; Wyndham et al. 1966, 1967b). Unfortunately, in neither study was there a control group, so those observations could simply reflect a controller adaptation that might occur within any group of people.

The next two studies included experimental controls. The first was led by Ronald H. Fox (1923–2009, England), and it was he who developed the controlled-hyperthermia technique for artificially inducing thermal adaptation (Fox et al. 1963a). Some contemporary thermal physiologists seem unfamiliar with both the method and its true origin. Those studies were indirectly linked to South Africa, since Wyndham had studied in Oxford (England; Wolstenholme 1987), following in the footsteps of another expatriate, Joseph Weiner (Milton 2022). Weiner had a strong interest in ethnic differences in thermoregulation, which he pursued with vigour in the 1970s (Collins and Weiner 1977a, b), and

Fox was part of that team. Fox and his colleagues compared indigenes from a tropical region of New Guinea with two control groups: indigenes of similar ancestry, but who lived in a cool-dry climate, and people of European ancestry (Fox et al. 1974). In another of the twists that we have sought to illuminate, our fourth investigation came from a combined Malaysian and Japanese team who also compared indigenes from those countries (Wijayanto et al. 2011). Neither of those research groups found evidence for differences in sudomotor thresholds that might be attributable to ethnicity. Thus, the central control of sudomotor function seemed not to differ systematically with ancestry, at least among those experimental groups.

If we accept that conclusion, and the interpretation that eccrine-gland densities do not differ with ancestry and that heat adaptation, at least in the short term, does not change the number of active sweat glands (Sargent et al. 1965 [U.S.A.]; Peter and Wyndham 1966; Inoue et al. 1999a [Japan]), then we must entertain the possibility that differences might exist in the secretion capacity or cholinergic sensitivity of those glands. Indeed, heat adaptation was classically defined on the basis of greater sweat rates (hypersecretion) during subsequent heat exposures (Adolph 1947d), and it was once the consensus that adaptation was incomplete unless sweating was more prolific (Wyndham et al. 1964a; Duncan and Horvath 1988). That is the second of our three possible adaptation responses.

That interpretation is still held by many modern thermal and applied physiologists, although it has long been contested (Burton et al. 1940; Yoshimura 1964; Candas 1987; Hori et al. 1976; Taylor 2006a). Since both genotypic and phenotypic adaptations tend to move physiological mechanisms towards more efficient states, then an increase in the sudomotor capacity of indigenes from hot, and particularly from tropical climates, might seem counter-intuitive, because evaporative cooling depletes body water. Therefore, minimising excessive (superfluous) sweating would improve physiological efficiency, and that is precisely what Eijkman (1895, 1924) had observed in his Malaysian volunteers, whilst his Europeans produced much wasteful sweat. Similarly, Sundstroem (1927) reported that well-adapted individuals, regardless of their ancestral origin, lost less heat through evaporation, and more through the less wasteful dry-heat exchanges. An elevated sudomotor efficiency, with reduced sweat dripping, has also been described (Eijkman 1924; Hori et al. 1976). Such responses are ideally suited to life in humid climates (Garden et al. 1966) and the wearing of protective clothing (Taylor et al. 2021), whilst short-term, adaptation-induced increases in sweating during exercise in humid heat can result in as much as a 200% elevation in unevaporated, wasteful or superfluous sweat production (Mitchell et al. 1976).

Perhaps unsurprising is the observation that long-term heat adaptation does not necessarily result in hypersecretion, particularly for those living and working in the tropics for many years (Eijkman 1895; Burton et al. 1940; Ladell 1958/59 Yoshimura 1964; Candas 1987; Hori et al. 1976; Taylor 2006a). Instead, a more resource-conservative sudorific response is typically observed, with lower sweat rates during exposures to hot-humid conditions. Ladell wrote that "*we were never able to get an African to sweat more than a "fully acclimatized" European under the same temperature conditions and working at the same rate*" (Ladell 1958/59 [P. 4]). Such responses reflect less pronounced effector activity and reduced physiological strain. That outcome reflects an attenuation of our thermoeffector responses, which we now call an habituation process (Henane 1980).

The phenomenon of sudomotor habituation was described by Seiki Hori and colleagues (Japan; Hori et al. 1976; Nagasaka 2022): "*… people born and raised in Okinawa have been exposed to heat constantly for years, it is presumed that the sweating center may have been habituated to the stimulation of heat*" (Hori et al. 1976 [P. 243]). They attributed the descriptor "habituation" to Glaser and Whittow (1953, England), and it was then adopted by the IUPS Thermal Commission (2001). Victor Candas (France) hypothesised the existence of a long-term (third) phase of heat adaptation, during which evaporation was optimal and sweat dripping minimal (Candas 1987). As Sundstroem (1927) had suggested, there are three stages of heat adaptation, with the last (habituated) stage perhaps being most easily seen in long-term residents and individuals with a morphological configuration suited to resource-conservative, dry-heat exchanges (*e.g.*, those of Asian ancestry). Such an outcome is entirely consistent with adaptations increasing physiological efficiency and enhancing survival, so it perhaps should have been anticipated.

It follows from this domestication of a very persistent hypothesis, that lower sweat rates during heat exposure might reflect more complete heat adaptation, a phenomenon hypothesised by others (*e.g.*, Dreosti 1935; Burton et al. 1940; Thompson 1954; Yoshimura 1964; Fox et al. 1974; Senay et al. 1976). Indeed, if one examines the literature with that possibility also in mind, there is ample evidence of lower sweat rates in indigenes from the tropics, relative to similarly heated individuals from cooler climates (Eijkman 1924; Thompson 1954; Edholm et al. 1964; McCance and Purohit 1969; Fox et al. 1974; Samueloff 1987; Duncan and Horvath 1988; Kosaka et al. 1994; Saat et al. 2005; Bae et al. 2006; Inoue et al. 2009; Wijayanto et al. 2011). Thorough and careful consideration of the literature can lead to reduced adherence to a "*prefabricated set of interpretations*" (Kennedy 1962).

The third form of sudomotor adaptation is an elevated effector (cholinergic) sensitivity, wherein, for a given

amount of acetylcholine released from the axonal terminals, more precursor sweat is produced. That process is analogous to the sweat-gland training described by Ken J. Collins (1929–2017, England; Collins et al. 1965) and Kenzo Sato (1939–2010, U.S.A.; Sato et al. 1990; Anonymous 2010), yet, until relatively recently, it had not been investigated across different ethnic groups. Using acetylcholine iontophoresis, Inoue et al. (2009, Japan) found that the eccrine glands of Thai nationals from a hot-humid climate were less responsive to acetylcholine. It appeared that a sudorific habituation in those individuals was associated with a reduced cholinergic sensitivity. Was that a genotypic or a phenotypic adaptation?

Thoicharoen and Taylor studied Thai women who had lived in a cooler Australian climate for > 1 year (Taylor 2014). Each woman was matched with an anthropometrically similar woman of European ancestry, and with equivalent physical activity behaviours, and then studied during light-intensity, steady-state cycling (90 min; 35.0 ℃ dry bulb). Sudomotor thresholds (37.1 [Thai] versus 37.0 ℃), sensitivities (4.07 [Thai] versus 3.06 mg cm^{-2} min^{-1} $^{o}C^{-1}$) and steady-state sweat rates did not differ significantly. Since a genotypic difference would be retained when moving to, and living in, a cooler climate, those data were consistent with the absence of a genotypic difference related to sweating between those ethnic groups. More recently, Muia et al. (2020) used direct calorimetry to quantify whole-body heat storage, dry and evaporative heat exchange and total heat loss in second-generation males of African and European ancestry living in a temperate, continental climate (Canada). When cycling (light, moderate and vigorous; 30 min each) in conditions that resulted in matched heat-loss requirements (40 ℃ dry bulb), heat storage, when averaged across exercise bouts, did not differ significantly between those groups (568 kJ [African] and 623 kJ [European]). Similarly, total heat losses were not significantly different (177, 217 and 244 W m^{-2} [African]; and 172, 212 and 244 W m^{-2} [European]). Those observations were interpreted to show that ancestral differences did not appreciably influence either whole-body heat exchange or heat storage when exercising in the heat.

Vasomotor responses In the heat, cutaneous heterothermy is replaced by more uniform skin temperatures (Werner and Reents 1980; Notley et al. 2023c [Fig. 7]), driven by increased convective heat delivery to the skin. That delivery reduces the core-skin thermal gradient and, if the air temperature is above that of the skin, the skin-air thermal gradient and the associated dry-heat exchanges (Sundstroem 1927; Eichna et al. 1950). There is also a simultaneous increase in the cutaneous water-vapour pressure, which increases evaporative cooling, even when the ambient vapour pressure and sweating remain stable. Those vascular effects were first described by Alan C. Burton (1904–1979, Canada and U.S.A.; Tikuisis 2022) and colleagues as part of the heat-adaptation process (Burton et al. 1940). However, few have examined the cutaneous vascular responses of people from different ancestral backgrounds during heat adaptation.

Two exceptions are highlighted. Firstly, Fox et al. (1974) measured hand blood flows in indigenes from both the hot-humid and cool-dry regions of New Guinea, during deep-body temperature thermal clamping (38 °C for 30 min; controlled hyperthermia). They also studied two groups of European ancestry. One group lived in the same conditions and was assumed to be acclimatised, while the second (control) group was unacclimatised. In comparison with the European controls, the blood flows of indigenes were ~ 50% lower during controlled hyperthermia. When the two European groups were examined, the acclimatised group revealed blood flows that were ~ 30% lower. The indigenous subjects showed an habituation of both their sudorific and cutaneous vascular responses.

The second experiment involved comparisons of Japanese-born, long-term residents of tropical Brazil with Japanese participants who lived in Japan. Katsuura et al. (1993, Japan) observed significantly lower forearm blood flows and higher skin temperatures in the former group, when they were heat exposed. Higher skin temperatures during heat exposure have also been reported for people of African ancestry relative to Europeans (Thompson 1954), as well as for Malaysians relative to Japanese residents (Saat et al. 2005). Finally, Thoicharoen and Taylor measured cutaneous vascular-conductance during elevated, but equivalent mean body temperatures in exercising Thai and European women (Taylor 2014), and found their vasomotor sensitivities to be almost identical, as were their vasomotor threshold temperatures (36.2° versus 36.3 °C [Thai]).

Postscript These observations of adaptation in residents of thermally stressful climates ignited interests in examining their underlying mechanisms, from which arose the possible ergogenic advantages that might be obtained by heat-adapted athletes and workers. Collectively, the studies from different ancestral groups did not support the existence of genotypic differences in thermoregulation among people of varying ancestry. Instead, it is the view of the current authors that many of the apparent differences in heat tolerance and physiological accommodation, sometimes attributed to ancestry, can adequately be explained on the basis of phenotypic variations associated with differences in lifestyles and the opportunity to experience one's natural environment, and thereby to acquire the appropriate physiological adaptations. Does that interpretation also apply to cold adaptation?

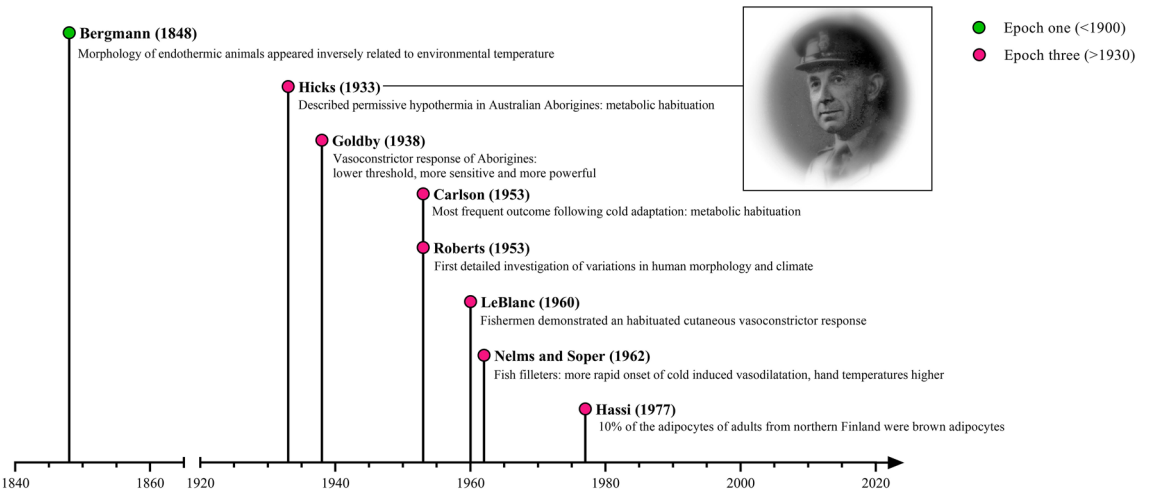


Fig. 6 Historical timeline for critical steps in the development of our physiological knowledge of human cold adaptation. The photograph of Stanton Hicks was obtained from the Virtual War Memorial Australia (https://vwma.org.au/explore/people/534729). Accessed: March 17th, 2022 and used with permission

Cold-induced acclimatisation within indigenous and occupational groups

Significant historical steps in the development of critical concepts concerning cold adaptation are revealed in our second timeline (Fig. 6). Morphological configurations that provide smaller mass-specific surface areas will be advantageous in the cold, since spherical objects tend to conserve heat better, particularly if they also have a larger mass. That physical argument is consistent with Bergmann's Rule (1847), but the universal validity of that principle has been contested, and there are many examples that conform to, but also diverge away from, that principle (*e.g.*, Scholander et al. 1950a, b; Roberts 1953; Wyndham 1965; Feist and White 1989; Ruff 1994; Foster and Collard 2013). In Fig. 7, people with the typical morphological characteristics of tribesmen from the hot climate of Kilimanjaro (the *Wadshagga* people, Tanzania) and the cold Alaskan climate (the *Inuit*, U.S.A.) are shown. Both examples, at least when photographed during the Krogh-Hill epoch, conformed to Bergmann's generalisation.

According to data compiled by Derek Roberts (1953), the average African *Bushmen* at that time had a mass-specific surface area ~ 25% larger (0.033 m^2 kg^{-1}) than that of a typical *Inuit* from the same epoch (0.026 m^2 kg^{-1}). Both were morphologically suited to their climates (hot-dry versus very cold, respectively), and those with such characteristics will have a slight advantage during low-level thermal stress. In Fig. 7C are data extracted from the more extensive work of Foster and Collard (2013). When mass-specific surface areas for people from the ten coldest climates (0.026 m^2 kg^{-1}) were compared with those data for people from the ten hottest climates (0.029 m^2 kg^{-1}), the latter was only 10% higher. Across 108 data sets, only about 23% of the variance in that morphological characteristic could be explained on the basis of differences in local climates. A low mass-specific surface area bestows an advantage when resting in the cold, where heat needs to be retained, but it becomes disadvantageous during exercise, and particularly during ambulatory activities when heat production is mass-dependent (Notley et al. 2023a, 2023b). On the other hand, heat loss is elevated when mass-specific surface areas are high.

Physiological (phenotypic) adaptations to the cold must be interpreted within the context of genetically acquired anatomical and morphological attributes. During the Krogh-Hill epoch, adaptations to cold weather were explored, again within first-nations people, with authors from the modern epoch classifying those sometimes dissimilar observations as if they were different and possibly independent forms, or stages, of cold adaptation, such as hypothermic or insulative forms of adaptation (Hammel 1964; Webster 1974; LeBlanc 1978; Tipton et al. 2008; Mäkinen 2010). Whilst such classifications can be useful, though perhaps more for authors than readers, they can restrict how other eyes might interpret experimental data, and they might be misleading. Indeed, such classifications of responses may imply that apparently different responses (adaptation strategies) are either predetermined, due to inherent characteristics of physiological regulation, or exclusive, such that other adaptations are precluded. Accordingly, whilst we have similarly sub-divided the literature, we acknowledge the possibly artificial nature of those divisions, which will become apparent as we proceed, particularly when considering adaptation specificity. Practitioners may wonder what they can learn for English Channel swimmers from those early studies. Does it matter whether those adaptations are investigated in resting or

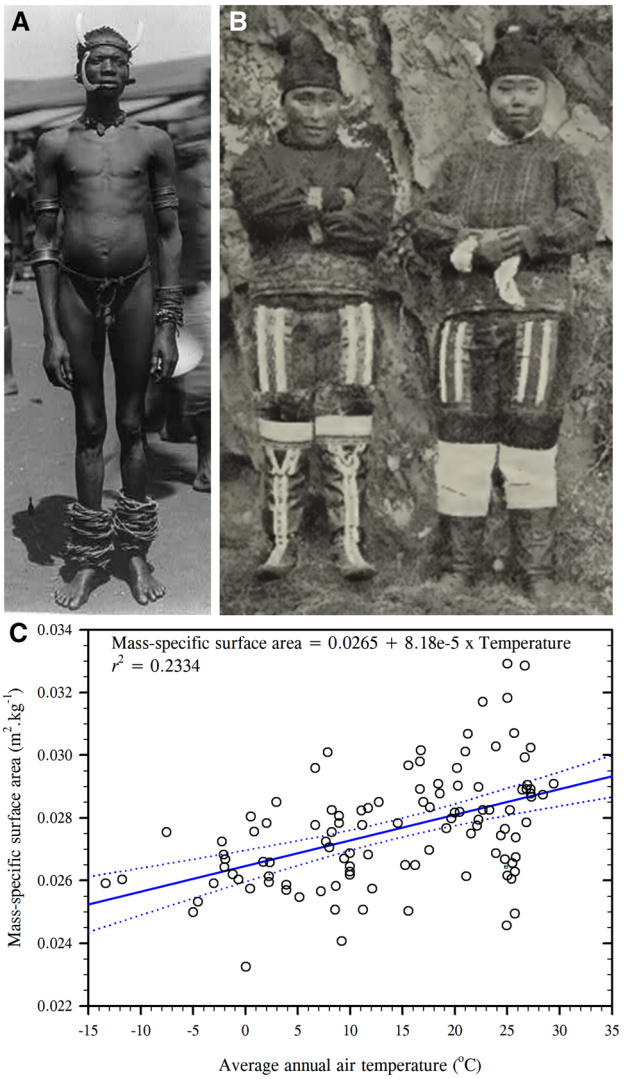


Fig. 7 Typical morphological characteristics observed during the Krogh-Hill epoch for indigenous people from hot and cold climates. **A** A member of Wadshagga tribe of Kilimanjaro (Tanzania). Photograph taken between 1890 and 1923, and retrieved from the Library of Congress (U.S.A.). Source: https://www.loc.gov/item/2001705606/ Accessed: March 17th, 2022. **B** Two Inuit women from Greenland, after spending four days in a portable, open-circuit respirometer. Photograph taken in 1908 during the Danish expedition to the northeast coast, and extracted from the report of Krogh and Krogh (1913). Source: https://archive.org/details/studyofdietmetab51krog/page/n9/mode/2up?ref=ol&view=theater&pg=PA18 Accessed: March 17th, 2022. **C** Variations in ethnic differences in mass-specific surface area associated with climatic differences. Data were extracted from Forster and Collard (2013), redrawn and re-analysed to show a linear function with 95% confidence intervals

exercising individuals? If the stimulus to adapt is simply the repeated reduction in body temperatures, then we suspect that it may not.

Hypothermic-insulative adaptation To the best of our knowledge, the first person to undertake detailed investigations of naturally induced cold tolerance (acclimatisation) in first-nations people, who still lived in their traditional lifestyle, was C. Stanton Hicks (1892–1976; Hicks 1974; Nash 1996; University of Adelaide 2013; Taylor et al. 2022). He is claimed as an Australian, as he completed his entire academic career in Australia, but he was born in New Zealand and he was educated there and in England. Some readers may wonder why Hicks was interested in cold adaptation for people who lived on the driest inhabited continent on earth, with ~ 40% of its land mass above the Tropic of Capricorn. It was all about deserts, with their clear skies and cold nights! But let us rewind the clock.

We introduced Francis G. Benedict (1870–1957, U.S.A.) within Parts 1–3 of this historical series (Notley et al. 2023a, 2023b), and we return now to his research on metabolic heat production (Atwater and Benedict 1905). Throughout the Krogh-Hill epoch, Benedict and his colleagues investigated the relationships between metabolism and body size, gender (sex) and age (Benedict and Cady 1912; Harris and Benedict 1918, 1919; Benedict and Talbot 1921). Following the possibly serendipitous observation that some Asian students had a lower basal metabolic rate than did their American counterparts (MacLeod et al. 1925), Benedict became interested in the possibility that differences in metabolic rate may be related to ancestral differences. He developed a portable system for field-based data collection (Benedict 1927) and recruited scientists to collect data from different ethnic groups: the *Maya* (Yucatan, Mexico; Steggerda, Shattuck and Williams), *Tamil Indians* (Madras, India; Mason), the *Kokatha Mula* aboriginal people (Eyre Peninsula, Australia; Hicks) and Chinese Americans (U.S.A.; Henderson and Benedict). That respirometric system was cumbersome (Fig. 8A), but could be used for measuring metabolic rate during rest or stationary exercise, while the system developed by Zuntz and Schumburg (1901, Germany; Notley et al. 2023b) was designed for exercising soldiers. It would have been beyond their comprehension that, within a century, it would be possible to measure the metabolic rates of competitors during *le Tour de France* without any equipment being attached to the cyclists (Westerterp 2018).

The studies that Benedict oversaw revealed lower basal metabolic rates for the Indian (17.4%; Mason and Benedict 1931), Australian (14% [men] and 16% [women]) and the Chinese (9%) participants, relative to those of European ancestry and of the same sex (Benedict 1932). The exception was with the *Mayan* people, who had a metabolic rate 6.5% higher than their European counterparts (Williams and Benedict 1928; Shattuck and Benedict 1931; Steggerda and Benedict 1932). Hicks et al. (1931) independently reported the Australian data, although he felt that little was gained from those first trials (Hicks 1974), other than learning how to perform a better experiment. Scientists frequently

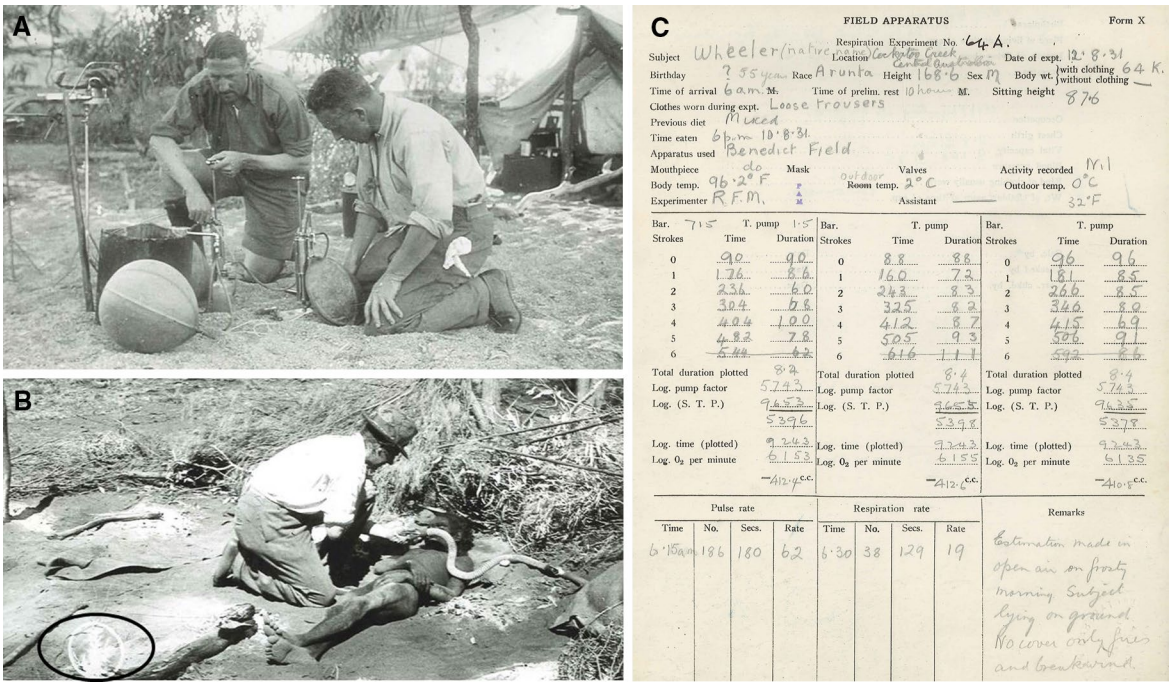


Fig. 8 Photographs and raw data from the field trials of Stanton Hicks (1929–1931), conducted in Cockatoo Creek (Central Australia), where he collected data from the *Walpiri* people (the *Anmatjera* and *Ilpira*). **A** Francis Matters and Stanton Hicks calibrating the portable apparatus, developed by Benedict (1927), for measuring respiratory gas exchange. **B** Ernest Eldridge collecting exhaled air, from a resting Aboriginal man, and into a Douglas bag. Note the wind break near the head of the participant and the remnants of a fire near his feet, with our black (oval) annotation highlighting Hicks' marker for the fire. **C** experimental records for one individual (64A; Hicks and Matters 1933). See Table 1 of that manuscript for the metabolic data of all participants, and Tables 3 and 4 for their anthropometric and physiological data (including body temperatures). Note the description on the lower right (fire and windbreak). Source: University of Adelaide (2013: http://www.adelaide.edu.au/library/special/mss/hicks/). Both photographs are in the Public Domain

relearn that lesson. Those were resting studies, and have often been forgotten or ignored. However, without a sound understanding of basal metabolism, exercise and applied physiologists have critical gaps in their knowledge. Moreover, those experiences led Hicks to his classical observations of an habituated metabolic response when traditional-living, desert Aborigines of Australia were studied in the field during cold desert mornings (Hicks and Matters 1933; Hicks et al. 1934).

In another curious coincidence, a physiologist from over 1,350 km to the east of Adelaide (University of Sydney) was also collaborating with Benedict. His name is Halcro Wardlaw, whom we introduced with regard to measuring insensible water losses (Benedict and Wardlaw 1932; Notley et al. 2023b). He was independently using a gravimetric method to determine carbon dioxide production (soda-lime absorption), from which he estimated the basal metabolic rate of the Aboriginal people from Central and Northern Australia (*Loritja* and *Aranda*; Wardlaw and Horsley 1928; Wardlaw and Lawrence 1932; Wardlaw et al. 1934). Hicks and Wardlaw were aware of, and cited each other's work. However, it seemed that neither Benedict nor his collaborators were aware of a publication on the basal metabolism of the *Inuit* people (Krogh and Krogh 1913). So we must return to Denmark, where August and Marie Krogh (1874–1943) were participating in an expedition to Greenland. The Kroghs were studying diets and metabolic rates (Fig. 7B), although they did not provide comparative data, and we identify this work primarily for those wishing to compare field-based experimental methods from that epoch.

Back to Hicks. For his second study, Hicks went to Central Australia (1929–1931; Hicks 1974), where he recruited participants from the *Walpiri* people (the *Anmatjera* and *Ilpira*). Australian first-nations people are from the longest continuous culture beyond Africa (Cane 2013; Clarkson et al. 2017; Rasmussen et al. 2011), and during the Krogh-Hill epoch, they were the closest approximation to the genotype of their ancestors, and many had retained their traditional lifestyle and thermal behavioural strategies. Many slept semi-naked on the ground (Fig. 8B; Spencer and Gillen 1899), protected by bush windbreaks and camp fires (Hicks et al. 1934). Those circumstances represented a unique opportunity, as he reflected in the title of his accounts of that research: *Just in Time* (Hicks 1974).

The Aborigines "*did not shiver or show signs of discomfort*" although "*their body temperatures (mouth and skin)*

were low" (Hicks and Matters 1933 [P. 178]). Was that a permissive or regulated form of mild hypothermia? What implications does that have for temperature regulation during exercise? If that was a genetically determined attribute, as some would later suggest (Hammel 1964), does it mean that they would be less likely to maintain homeothermy during exercise? The European scientists also slept outside on the ground, and were uncomfortably cold, even with their clothing and blankets. Metabolic measurements were performed early in the morning, at which time air temperatures ranged from − 2° to 10 °C (dry-bulb), as they do with the clear night skies of the desert spring. During the day, air temperatures were > 30 °C, with a strong solar load. Hicks and Matters (1933) reported very low deep-body (sublingual; rectal measurements were culturally offensive) temperatures in most Aborigines: 22 of 33 observations were < 36 °C, with eight < 35 °C. Nonetheless, their behaviours were more consistent with thermally comfortable Europeans. No effort was made to examine inter-individual differences.

In subsequent manuscripts, Hicks and O'Connor (1938b) described the skin temperatures of sleeping Aborigines to be 5 ℃ cooler than those their European counterparts, who slept in beds. Those cooler temperatures were dictated by the ambient conditions. Indeed, Jules Lefèvre (1863–1944, France) described the peripheral tissues as if they were poikilothermic (Lefèvre, 1911). As relatively hairless mammals, our ability to modify physiological insulation through piloerection and seasonal changes in hair coverage is ineffectual. Nevertheless, from estimations of cutaneous blood flow, as determined from the radial artery, Goldby et al. (1938) found the vasoconstrictor response of the Aborigines to be initiated at a lower threshold, and it was also more sensitive and more powerful.

Such adaptation-induced increases in physiological insulation would be protective for cold-water marathon swimmers, as would the morphology of the *Inuit* (Figs. 1B and 7B) and the accumulation of a thicker anatomical insulation. Both would reduce the convective transport of heat to the skin and the skin-environment thermal gradient in the cold, thereby reducing, but not eliminating, heat loss (Johnson and Kellogg 2018). For stationary soldiers it would be disadvantageous, since it elevates the risk of cold injuries to the hands and feet (Notley et al. 2023c).

Consequently, the Aborigines studied by Goldby et al. (1938) were cooler despite exhibiting greater vasoconstrictor tone, yet their metabolic heat production was much lower than similarly cooled Europeans. They showed no evidence of a metabolic compensation for the heat they lost, with their resting metabolic rates remaining stable throughout the night and morning (Hicks et al. 1934). They did not shiver. Since shivering is energetically wasteful and accelerates convective heat loss, it is tempting to suggest those observations might reflect a long-term form of thermal adaptation, wherein physiological adaptations, in combination with behavioural practices, moved towards a state that is more efficient and conducive to survival (Selye 1973).

Such repetitive deep-body and superficial cooling provided powerful stimuli for thermal adaptation, which Hicks summarised in the *Handbook of Physiology* (Hicks 1964). Those contributions led others to the concept of a metabolic habituation (Glaser and Whittow 1953); reduced heat production. That is, the Aboriginal participants provided a classical illustration of a blunted, or desensitised, metabolic response to cold stress, relative to non-adapted Europeans. They displayed the combination of a strong cutaneous vasoconstrictor (insulative) response with a permissive, mild-moderate hypothermia (Hicks and Matters 1933; Hicks et al. 1934; Goldby et al. 1938). Hicks and his colleagues had provided the first human description of this form of cold adaptation. Others subsequently described that as an hypothermic-insulative adaptation (Hammel 1964; Webster 1974; LeBlanc 1978).

The limitation of that classification comes from the experiments themselves. That is, the researchers were examining thermal exposures that might normally be experienced during daily life, and without limiting behavioural practices, so we have no information concerning how those participants might have responded when faced with a more challenging cold stress. Whilst permissive hypothermia is now widely reported for resting subjects (LeBlanc, 1956b; Keatinge 1961; Golden and Tipton 1988; Janský et al. 1996; Mäkinen 2010; Yurkevicius et al. 2021), it is not observed when cold-adapted individuals exercise in cold water (Golden and Tipton 1988). In the workplace, however, a reduced shivering response would certainly be beneficial to the performance of fine-motor tasks during cold exposures.

There is little doubt that pioneering research ignited the interests of other thermal physiologists, due to the possibility that other ethnic groups might also reveal unique thermal adaptations, and time was short, as European lifestyles were becoming ubiquitous. The first to follow that trail were Per Scholander and H.T. "Ted" Hammel (1921–2005, U.S.A.; Blatteis and Schneider 2022). Scholander recruited a team from America (Ted Hammel), Australia (Hugh Le Messurier), Canada (Sandy Hart) and Norway (Johan Steen), they were assisted by Hicks, and they also travelled to Central Australia in Spring (1957). This time, the scientists were the controls, with one of them sleeping (or failing to sleep) on the ground (naked) next to each Aboriginal man, now with rectal and skin temperatures recorded throughout; "*silly bugger white man*" (Scholander 1978 [P. 10]).

To test for seasonal variations, Hammel returned with a second group of scientists for Summer trials (December 1957 to January 1958). From those projects, it appeared that the Aborigines did not show seasonal variations in their cold responses, and nor did the coastal tropical- and

desert-dwelling groups differ (Scholander et al. 1958a, b; Hammel et al. 1959). Furthermore, their strong insulative response appeared to be retained years after adopting European lifestyles (Scholander et al. 1958a, b). In his contribution to the *Handbook of Physiology*, Hammel (1964) interpreted those observations to reflect a genotypic difference (also see: Moskowitz 1996).

The possibility that those differences were of a genotypic nature was questioned 40 years later (Taylor 2006a, b). When archival resources were subsequently found (2017: Hicks 1974), it became clear that Hicks also believed the responses of the Aborigines were phenotypic adaptations to the combination of their unique lifestyle and thermal environment. He described being led towards that interpretation by a lay person who had experienced a very similar adaptation (Hicks 1974 [P. 99]). One might therefore ask (albeit rhetorically): why seek a genetic explanation if such outcomes can adequately be explained on a phenotypic basis? Indeed, it is now generally accepted that even artificially induced cold adaptation desensitises the metabolic response (LeBlanc, 1956b, 1978; Davis 1961; Keatinge 1961; Golden and Tipton, 1988; Stocks et al. 2001; Tipton et al. 2013). Therefore, we believe that those adaptations were a function of unique adaptation opportunities (Taylor 2006a, b), but without adequate experimental controls, any interpretation could be tenuous.

Other thermal physiologists were hot on the heels of Hicks, Scholander and Hammel, diverging down various paths, always with a thermal agendum, but sometimes with occupational athletes in mind. Their stories are reported in Blatteis et al. (2022). For example, interests in Canada were driven by possible adaptations of the *Inuit* people, and by cold exposures experienced by fishermen (*e.g.*, Jacques LeBlanc [1921–2010]; Tikuisis 2022). The first-nations population of Finland and the *Sámi* (previously called *Lapps*), who live in Norway, Sweden and Russia, were studied (Blix et al. 2022; Leppäluoto et al. 2022). Many *Sámi* are reindeer farmers living above the Arctic Circle, and just like the *Inuit*, they too experience very cold weather. The scientists of Japan and South Korea took a special interest in their women of the sea (breath-hold divers): the Japanese *ama* and the Korean *haenyeo* (*e.g.*, Suk Ki Hong [1928–1999]; Blatteis and Schneider 2022). The Japanese also have an old, first-nations people (the *Ainu*), who live on Hokkaido Island (*e.g.*, Shinji Itoh [1912–2003; also spelt "Ito"]; Nagasaka 2022). Down in South Africa (the hottest continent), Cyril Wyndham took an interest in the *Bushmen* of the Kalahari Desert (Wyndham and Morrison 1958). Space will not allow examinations of those interesting and diverse populations. Instead, we have grouped the classical papers under loose thematic topics, whilst including many others within the recommended readings.

Hypothermic adaptation The immediate responses of non-adapted individuals to an acute and unprotected cold exposure involve cutaneous vasoconstriction, plus shivering and non-shivering thermogenesis (Notley et al. 2023c). The commonly reported pattern of human cold adaptation is an attenuation of the metabolic response, a rapid fall in deep-body temperature and increased thermal comfort, but without a powerful cutaneous vasoconstrictor response. Whilst that has been described as an hypothermic adaptation (Hammel 1964; LeBlanc 1978), that description does not imply an unregulated decline in body temperature. Instead, it is a permissive reduction. Shivering still occurs, but it is attenuated. That response seems to be temperature specific, and possibly related to the body temperatures experienced during adaptation (Rees et al. 2002). Thus, when a subsequent cold stress induces cooling beyond that previously encountered, the metabolic response appears to be restored towards that observed in the non-adapted state.

Perhaps the most common observation of cold-exposed indigenes was their thermal comfort. They were tested under the conditions in which they lived, although their greater comfort, relative to their European counterparts, was maintained even though they often experienced greater reductions in deep-body temperature. In addition to the *Walpiri* people of Central Australia (Hicks and Matters 1933), it has been reported for the *Sámi* people of Norway (Andersen et al. 1960), and for the *Gwich'in* (Irving et al. 1960) and *Inuit* people of Canada (Hart et al. 1962). The frequently cited exception comes from the *Kawésqar* people of Chilean Patagonia (previously known as the *Alacaluf* people), who defended deep-body temperatures closer to its normothermic level (Hammel 1960).

The metabolic responses of those groups highlight the difficulty of trying to put people and their adaptation responses into tidy boxes (such as our headings). For instance, unlike the *Walpiri* (Goldby et al. 1938), the *Kawésqar* people elevated their metabolic heat production during resting cold exposures (Hammel 1960). To further highlight this complexity, consider the investigation of Elsner (1963), who studied the high-altitude *Quechua* people (Andean Mountains, Peru). Relative to those of European ancestry, they displayed a similar metabolic response during cold exposure, but did not appear to defend their deep-body temperatures through equally strong, cutaneous vasoconstrictor activity, as estimated from hand and foot skin temperatures. Another complication of such classifications stems from the apparently simultaneously reduced metabolic response and a more powerful cutaneous vasoconstrictor response, as evidenced by reductions in skin temperatures, vasomotor activity and thermal conductance (Goldby et al. 1938; Hammel et al. 1959). Whilst such vascular responses support heat conservation, reconciling how adaptation might reduce the sensitivity of one thermoeffector whilst concurrently elevating

that of another, requires the existence of separate controllers for thermogenesis and cutaneous vasomotor activity. We now believe that separate controllers do exist (Taylor and Gordon 2019; Notley et al. 2023a [Fig. 22]).

We commenced this sub-section by looking at the first-nations people of Australia. In closing, we return to the birthplace of *Homo sapiens* (Africa). As often happens in science, a flurry of thematic research activity attracts the attention of others. Re-enter Cyril Wyndham, who was interested in the *Bushmen* of the Kalahari Desert, whose thermal environment was then similar to the Australian Aborigines, but they used different behavioural strategies (skin cloaks and grass shelters). As with the studies of Hicks, their first field study was exploratory (Wyndham and Morrison 1958). In their second investigation (Ward et al. 1960), they compared the metabolic responses of *Bushmen* and individuals of European ancestry during the cold nights of the Kalahari winter. Both groups were almost naked. Their metabolic responses were almost identical, as were their deep-body (rectal) temperatures (Wyndham 1965). The only physical difference was their subcutaneous adiposity, which was higher in the Europeans. The authors concluded that traditional *Bushmen* had adopted behavioural strategies to maintain a comfortable microclimate, and, in so doing, did not require pronounced autonomic adaptations to sustain their lifestyle.

Experimental controls were limited in most, but not all, of those field studies, which were often performed under inhospitable conditions using samples of convenience and without the support of contemporary laboratories, so we should not try too hard to apply matching physiological explanations to those observations. From a pragmatic perspective, cold-adapted workers may benefit from this so-called hypothermic response, but when body temperatures decrease far enough, vigorous shivering will be activated, which, when combined with heat production from exercise, can support thermal homeostasis. However, evidence from some of these indigenous groups seems to indicate stronger cutaneous vascular responses. In some workplaces, such responses will not be protective, but may instead lead to local tissue damage.

Adaptation to localised cooling—occupational physiology For this final sub-section on acclimatisation, we enter the realm of cold injuries which accompany protracted local-tissue temperatures < 5 ℃ (Notley et al. 2023c). When we think of localised cold exposures, images of fishermen working in very cold water and cold-room workers handling refrigerated, often frozen, fish and meat come to mind. From an exercise perspective, we might think of kayakers, whose hands are always wet and continually moving through the air, thereby ensuring that the skin temperatures of inadequately protected hands will approach the winter water and air temperatures.

Competitive kayakers undertaking twilight endurance training in the winter will generate significant metabolic heat, so few will wear upper-body thermal protective clothing, to avoid overheating and thermal discomfort. Deep-body temperatures will remain close to the normothermic state, and may even be elevated, and accompanied by cutaneous vasodilatation. When training stops, heat loss is both rapid and dramatic, even in temperate climates, because the control of blood flow to the hands and feet in resting states is primarily dictated by changes in deep-body temperature. That influence is about ten times more powerful than an equivalent change in local skin temperature (Caldwell et al. 2014). Therefore, during recovery, segmental blood flows will remain high and heat loss is rapid. The resulting protracted and frequently repeated tissue cooling may stimulate cold adaptation, but excessive tissue cooling creates opportunities for tissue damage. Almost 25% of paddle-sport athletes report symptoms consistent with non-freezing cold injuries (Oakley et al. 2022).

High-latitude ocean fishermen intermittently expose their hands, often unprotected, to cold seawater for several hours each day. Much of the research into the impact of that exposure was undertaken during the middle of the twentieth Century, and we will focus on studies of Canadian (Gaspé region and Southampton Island) and Norwegian fishermen (Lofoten Islands). In the first group, LeBlanc et al. (1960) compared fisherman with other local workers (labourers, woodsmen, farmers, truck drivers), using cold-pressor tests (2.5 °C water immersion), with hand heat loss estimated using immersion calorimetry. The fishermen maintained higher finger temperatures and had less pronounced elevations in blood pressure during sudden hand immersions. They also lost more heat from their hands, which are superior heat-exchangers (Taylor et al. 2014).

In a subsequent study, LeBlanc (1962) repeated those tests, this time comparing the hand and foot responses of the Gaspé fishermen with control subjects during summer and winter. He again observed a reduced pressor response in the fishermen, regardless of which limb segment was treated or the time of year. LeBlanc suggested that response reflected a generalised cutaneous vasomotor adaptation, although he recognised that the feet, and perhaps even the whole body, might also have been regularly cold exposed. Collectively, those observations were interpreted to reflect the maintenance of higher local perfusion rates by the fishermen during cold exposure (LeBlanc 1962). That adaptation would reduce the risk of cold injury, and he described it as an habituation of the vasoconstrictor response (LeBlanc 1978), which Glaser et al. (1959) suggested was centrally mediated (also see: Yurkevicius et al. 2021), although that habituation has not been unequivocally observed.

For the Norwegian study, Krog et al. (1960) recruited fisherman, *Sámi* participants from the mainland and

European, non-fisherman controls. They measured hand blood flows (displacement plethysmography) across a range of steady-state water temperatures (5–40 ℃), as well as segmental tissue temperatures and heat loss (ice-water immersion; 0–1 ℃). They did not observe significant differences in blood flow among the groups at any water temperature, although the *Sámi* displayed slightly higher blood flows at the lowest temperature. They also examined cold-induced vasodilatation, which occurs in the anastomoses of the hands (palms) and feet (soles), and follows extended, cold-induced under-perfusion (Lewis 1930; Fox and Wyatt 1962; Notley et al. 2023c). The anastomoses intermittently open, with each surge of blood acting to protect the local tissues from cold damage. Krog et al. (1960) observed an earlier onset of that vasomotor pattern in both the *Sámi* and the fishermen. That would also be a protective adaptation. A difficulty with that study, as recognised by the authors, was determining the extent to which either local or whole-body cold adaptation might have occurred. Both Brown and Page (1952) and Brown et al. (1953) reported consistently higher hand and forearm blood flows in the *Inuit* (Southampton Island, Canada), relative to those of European ancestry, across immersion temperatures from 5 to 45 °C. Notwithstanding some differences among the observations, those studies collectively reinforced the development of a protective, adaptation-induced habituation of the vasoconstrictor response of the hands following repeated, localised cold exposure.

An ideal population sample for further exploring that possibility would be those in whom repetitive and protracted hand cooling is an occupational requirement, such as those who fillet fish for a living, as that occurs in ice-cold water. Nelms and Soper (1962, England) recognised that opportunity, and studied workers exposed to seasonal variations in ambient conditions and to water temperatures < 10 ℃, with the left hand almost continually immersed. Over 36 consecutive days, water temperatures varied between − 1 and 3 ℃. "*It is hard to envisage a local cold stimulus of greater intensity acting for prolonged periods in any other trade*" (Nelms and Soper 1962 [P. 448]). To evaluate cold-induced vasodilatation of that hand, they measured finger skin temperatures during hand immersion in ice water (0 ℃). Relative to control subjects, the filleters displayed a more rapid onset of cold-induced vasodilatation and their hand temperatures were consistently higher. If finger temperatures reflected local blood flows, those observations were consistent with the observations of LeBlanc et al. (1960) and LeBlanc (1962). Collectively, they demonstrated improved stress tolerance, reduced local soft-tissue injury risk and less physiological strain. Those habituated vascular responses are the hallmarks of a more complete phenotypic adaptation to the cold.

Postscript As with the early research into ancestral differences in thermoregulation in the heat, observations made when investigating the indigenous inhabitants of, or workers from, colder climates, sparked the interests of scientists interested in the mechanisms of cold adaptation. Those responses to whole-body exposures frequently involved increasing thermal insulation at the periphery and turning down the "*fire of life*" (metabolic habituation). When repeatedly exposed to localised cooling, a protective response seems to have been induced, such that cold-induced vasodilatation occurred more quickly in individuals who had adapted to repeatedly applied localised cooling. Those adaptations represent phenotypic variations induced by lifestyles, as well as occupational and recreational opportunities to experience natural climates. Adaptations are, in fact, specific to the nature of the homeostatic disturbance, and whilst some of those changes afford other benefits, they are adventitious, and not pre-ordained. Given these relationships, we now move to examine how artificially applied thermal stimuli might induce adaptations that provide ergogenic benefits for recreational and occupational athletes.

Artificially induced adaptation: the principles of thermal acclimation

Humans can, and will adapt to unfamiliar and thermally challenging climates and working environments. During the Krogh-Hill epoch, most research was directed towards learning from acclimatised first-nations people or workers. We have now reached the point where we must bring this topic into the modern epoch, so our emphasis turns towards artificially induced thermal adaptation (thermal acclimation), motivated by the desire to achieve thermal adaptation more rapidly than it occurs during acclimatisation. Such ergogenic thermal acclimation has its roots with Marcus S. Pembrey (1868–1934, England), who knew that exercise could elevate deep-body temperature (Pembrey 1902) even without ambient heat, that such changes were beneficial (Pembrey 1904) and that those benefits might be obtained by "*training on hot as well as on cold days*" (Pembrey 1902 [P. 269]). Similarly, Theodore Hough (1909, U.S.A.) noted that "*Muscular activity also affords important training to the heat-regulating mechanism of the body*" (Hough 1909 [P. 486]). In the next section, we describe the principles of thermal acclimation, and re-introduce the concepts of a thermal impulse and the cumulative adaptation impulse. We examine how our physiological responses might vary across different treatments, and how those observations might influence our understanding of the physiology of thermal adaptation. We begin with practical considerations concerning thermal adaptation.

How should one artificially induce a thermal impulse?

Elite endurance athletes, factory workers and soldiers are vastly different individuals, so whilst thermal-adaptation interventions that work for an athlete will also be beneficial to workers and soldiers, they may be unnecessarily stressful. The best interventions will be those that are specific to the intended beneficiaries, and the various methods through which thermal adaptation might be induced have been described by others (*e.g.*, Hellon et al. 1956; Davis 1961; Edholm et al. 1963; Gisolfi and Robinson 1969; Strydom et al. 1971; Shvartz et al. 1973b; Janský et al. 1996; Savourey et al. 1996; Taylor 2000; Taylor and Cotter 2006; Brazaitis et al. 2014; Taylor 2014; Schmit et al. 2017; Duvnjak-Zaknich et al. 2019). Elite endurance athletes constitute a special case, as they require sufficiently strong stimuli to induce adaptation across several physiological systems. Heat or cold adapting non-elite athletes may improve their welfare, but it will not transform them into elite athletes. Thermal adaptation represents a supplementary modification, but its acquisition must not interfere with the primary objective, which is elite endurance performance. Let us consider another analogy.

High-altitude exposures have been used in attempts to increase the oxygen-carrying capacity of the blood, primarily through erythropoiesis (Lundby et al. 2008), and thereby provide a possible endurance advantage. However, the hypoxic stress required to stimulate erythropoiesis, when residing at simulated or actual altitudes, would restrict endurance-training quality and physiological adaptations. Realising that conflict, Levine and Stray-Gundersen (1997) introduced the practice of living high, and training at lower altitudes. The application of that practice to heat adaptation would involve completing high-quality endurance training in the cool, whilst living, training and rehearsing race strategies in the heat (Taylor and Cotter 2006).

In applied scenarios, quantifying the thermal impulse (Eq. 1) is often difficult, which has prompted the use of surrogate variables of thermal strain (*e.g.*, heart rate). For research purposes, that approach cannot be supported. Whether investigating the mechanisms behind physiological responses, comparing the utility of various adaptation methods or differentiating among the responses of individuals, there is no valid alternative to quantifying the stimulus to which adaptation occurs (thermal strain), other than through changes in body temperature. That quantification is the cornerstone of the controlled-hyperthermia technique developed by Ronald Fox (Fox et al. 1961, 1963a), and its subsequent modifications (Taylor et al. 2020).

During the traditional (classical) methods of thermal acclimation (Dreosti 1935; Bean and Eichna 1943; Robinson et al. 1943; Horvath and Shelley 1946; Wyndham et al. 1953), the ambient conditions and the external workloads, but not body temperatures, were kept constant before, during and after adaptation. That is a constant-stress method, which differs in two aspects from the controlled-hyperthermia technique recommended by Fox et al. (1963b), which uses a constant-strain approach. Firstly, for constant-strain designs, the pre- and post-acclimation (uniformity) tests, which are used to identify treatment-induced adaptations, are performed under thermal and exercise forcing functions that elicit the same body temperatures. That is not achieved with the constant-stress design, so, if adaptation occurs, constant-stress uniformity tests will impose different levels of physiological strain. Secondly, throughout the acclimation exposures, the constant-strain method induces equivalent body temperatures during each treatment. That is, the stimulus to adapt (thermal impulse: Eq. 1) is kept stable. The process is similar to thermal clamping, and it might actually provide a closer reflection of heat acclimatisation, during which people modify their work and exercise intensities based upon perceived levels of physical strain (effort sense), and possibly thermal discomfort. Indeed, it is well known that perceived exertion is elevated in more stressful environments (e.g., Maw et al. 1993; Simmons et al. 2008; Levine and Buono 2019), even when the external work rate remains constant.

There is nothing wrong with coaches setting work rates relative to other indices of strain (*e.g.*, heart rate), as originally conceived by Banister and Calvert (1980), but that practice is not appropriate for research (Taylor et al. 2020). For instance, the heart is an effector organ for regulating blood pressure. It is also a secondary effector for any regulated variable that relies upon modifications to blood volume or flow (Notley et al. 2023a [Table 1]). Consequently, heart rates may reflect disturbances other than thermal loading, increasing artefactual effects, although those influences get smaller at higher exercise loads. Because of the need to service the cutaneous blood flow required for heat dissipation during heat exposure, heart rates will also be elevated in the heat, even if the work rate is unaltered, with that affect being more pronounced at lighter work rates and when hypohydrated. During ambulatory (mass-dependent) exercise performed at the same speed, heart rates will generally be higher in smaller than larger individuals (Taylor et al. 1980). Finally, when comparing the adaptation responses of treatment groups using different forms of mass-supported ergometry (*e.g.*, cycling and wheel-chair ergometry), the chronotropic response to upper-limb exercise will be greater than to lower-limb exercise conducted at the same absolute work rate (Louhevaara et al. 1990; Notley et al. 2014).

We must also recognise that the vast majority of the heat adaptation experiments were focussed only upon thermoregulation. For elite endurance athletes, that represents just one of the regulated variables that will be disturbed during their event. What about the others? It seems that a superior level of thermal adaptation might be achieved if one or more of the other regulated variables is simultaneously

modified during adaptation training, but again, that must not compromise more critical, activity-specific physiological adaptations.

The thermal adaptation continuum

All forms of physiological adaptation fall along continua from a complete absence of adaptation through to some indeterminable maximally adapted state. Adaptations are not on–off mechanisms. Instead, they are time-dependent, continuous phenomena, and, as with physical endurance, thermal adaptation will be acquired non-linearly, with ever-decreasing improvements as maximal adaptation is approached. The factors that influence that time course, but also the extent to which adaptation is achievable, include the genotype and phenotype of each individual (high versus low responders), their situational status (*e.g.*, nutritional, hydration and health states) and the nature of the thermal stress used (*e.g.*, intensity, duration, frequency, variability). There are also transfer (cross-adaptation) benefits that may occur across different physiological adaptations (*e.g.*, Hale 1969; Sridharan et al. 1986; Mäkinen 2007; Gibson et al. 2017; Ciuha et al. 2021). Whilst the breadth of that topic is beyond our current scope, endurance training in temperate environments has long been recognised as facilitating thermal tolerance (Pembrey 1902; Hough 1909; Robinson et al. 1941; Piwonka and Robinson 1967; Gisolfi and Robinson 1969; Baum et al. 1976; Bittel and Buguet 1980; Fortney and Vroman 1985; Armstrong et al. 1987; Andres et al. 2000; Taylor 2014), although optimal thermal tolerance requires exercise in the heat (Strydom et al. 1966, 1969; Cheung and McLellan 1998).

Because heat and cold adaptation are both time-dependent processes, complete thermal adaptation occurs only after years of living, working and training within thermally stressful conditions. Since thermal adaptations are often specific to the types of stress imposed (Adolph 1956; Gelineo 1964; Radomski and Boutelier 1982; Rees et al. 2002; Patterson et al. 2004b, 2014), and since recreational and occupational athletes have varying attributes and levels of adaptation, then it would be wrong to assume that any one adaptation regimen might suit all requirements, just as we cannot train sprint and marathon athletes using the same programme. Moreover, it is impossible to determine precisely when adaptation plateaux have been reached. It is also possible that some adaptations are related not just to the change in body temperature relative to its basal level, but to the size of that change relative to each of the thermoeffector thresholds. To our knowledge, experimental designs incorporating that possibility have not yet been used. Finally, as adaptation progresses, we are moved from a state of physiological accommodation through to short-term, super-compensation (short-term adaptations) and eventually to a more efficient state in which thermoeffector habituation might be observed following years of exposure (Sundstroem 1927). Adaptation may become optimal when, and only when, thermal compensation and self-protection can be achieved with minimal physiological costs. Therefore, one must remain cautious about assuming that any artificially induced adaptation might reflect either ideal or complete adaptation, and the literature contains many such misinterpretations. With these

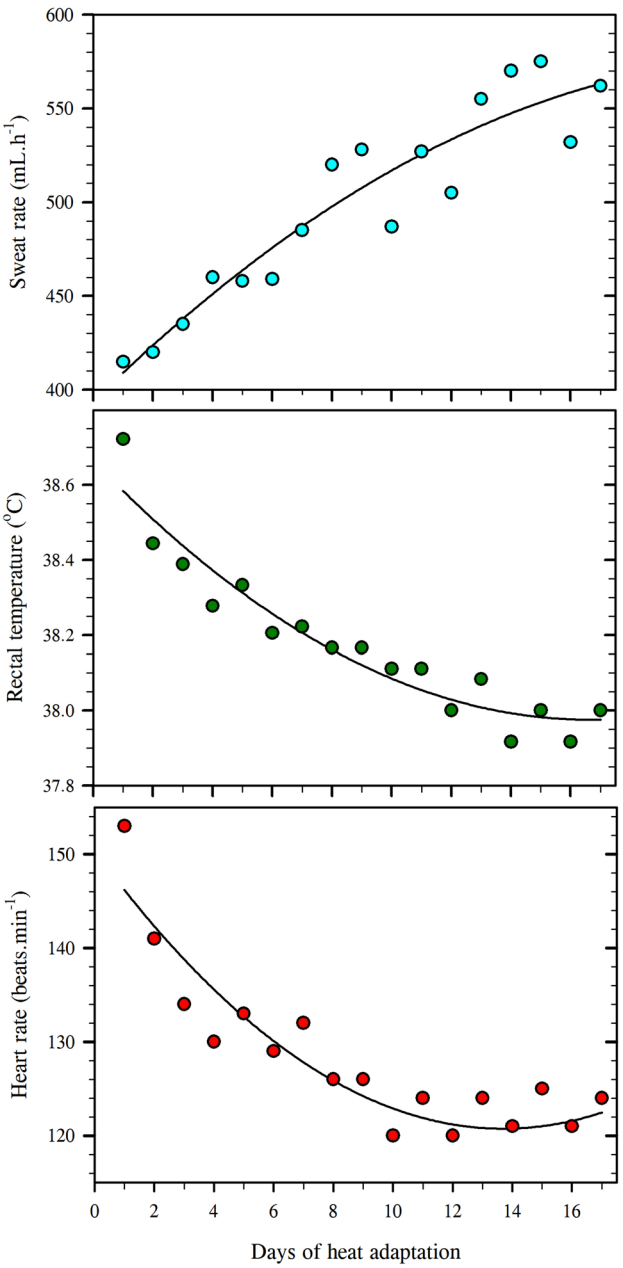


Fig. 9 Average sweat rates, post-exercise deep-body (rectal) temperatures and heart rates of young men ($N=6$) during 17 days of heat acclimation using a fixed external work rate (box stepping 12 steps min^{-1}, 4 h) and a constant thermal load (34 ℃ dry bulb, ~ 80% relative humidity; 31 ℃ wet bulb). Data extracted and redrawn from Wyndham et al. (1968)

qualifications in mind, we move to our last topics, in which we summarise the physiological changes that accompany artificially induced heat and cold adaptation (acclimation).

Physiological acclimation to elevate heat tolerance

Classical definitions of human heat adaptation were based upon the "*maintenance of lower body temperature, lower pulse rate, and readier sweating*" when next exposed to heat (Adolph 1947d [Pp. 329–331]). With few exceptions, that response triad (Fig. 9) applies to short-term observations made when identical pre- and post-acclimation heat-stress (or uniformity) tests were administered; the constant-stress method ("How should one artificially induce a thermal impulse?"). Such observations are relevant for occupational physiologists, whose objectives are to increase worker health and safety within jobs for which both the workloads and the climatic conditions are known and somewhat constant. That pragmatic approach is appropriate, and perhaps even necessary, as it replicates known stresses, reduces physiological strain and elevates worker productivity.

That constant-stress approach can be ill-suited to mechanistic research, during which one is primarily interested in how and why the body responds to exercise and ambient stresses that exert the same relative strain (homeostatic disturbance) before, during and following heat acclimation. Constant-stress designs do not allow one to distinguish between the effects of reduced physiological strain, which occurs because the relative (but not the absolute) intensity is reduced as adaptation progresses, and the phenotypic adaptations that occur during the course of those exposures. The decision as to which heat-acclimation protocol one might use must be dictated by the reason for thermal adaptation or the nature of each research question, and not by past practices.

Since the predominant (traditional) past practice has been to use the constant-stress model throughout heat adaptation, then we must be aware of the type of questions for which the measured responses can provide, or cannot provide, appropriate answers. That method certainly allows one to evaluate changes in the ability of individuals to tolerate a fixed set of working conditions. It also allows one to determine thermoeffector thresholds, providing the uniformity tests elicit similar rates of body temperature change, since participants are taken from a basal state to some point beyond which the thermoeffectors have been activated. However, deep-body temperatures will always be lower when an identical absolute stress is applied before and after a successful adaptation intervention (Fig. 9). Since the thermoeffectors are driven by both a body temperature deviation and its rate of change, then an elevation in sweat rate following heat acclimation (Fig. 9) reveals a change in the relationship between sudomotor function and body temperature. They do not, however, reveal the nature of that change. Discovering that requires elevating body temperature to the same pre-acclimation (strain) level. That experimental procedure has rarely been used.

Investigators who used constant-strain designs have reported heat acclimation to enhance cutaneous vasomotor function (Notley et al. 2018), whilst those who used constant-stress method have reported either unchanged (Whitney 1954; Nielsen et al. 1993) or reduced vasomotor responses (Wyndham 1951; Rowell et al. 1967). With regard to body-fluid, and more specifically, blood-volume regulation (Notley et al. 2023a [Table 1]), the perceived wisdom arising from traditional (constant-stress) designs was that the plasma volume initially expanded during heat adaptation, and then contracted (Bass et al. 1955; Wyndham et al. 1968; Fortney and Senay 1979; Senay 1979; Shapiro et al. 1981; Aoyagi et al. 1995). However, when passive (Bonner et al. 1976; Harrison et al. 1981) and exercise-induced, whole-body heating (Patterson et al. 2004b, 2014) were applied using constant-strain protocols, the plasma volume did not contract, but remained stable and elevated. Whilst we are not challenging previous observations, we believe they are more related to the experimental design than to physiological adaptation. Accordingly, we do not accept that those observations are both unequivocally interpretable and universally applicable, and with that caution in mind, we will endeavour to summarise the principal physiological changes accompanying artificially induced heat adaptation. For more information on contemporary topics (*e.g.*, molecular, genetic and cellular adaptation), we direct readers to Horowitz (2016), Schneider (2016) and Murray et al. (2022).

Sudomotor adaptations

Sudomotor adaptations to repeated heat exposures occur over at least three stages ("Sudomotor responses"; Candas 1987), the last of which is a response habituation. That last stage neither involves nor implies an active sweat suppression. Instead, sudomotor habituation simply means that less prolific sweating is observed when someone is exposed to an equally stressful set of conditions, following long-term heat adaptation.

We have known about habituated autonomic responses throughout our century of exercise physiology, with research from three continents providing descriptions of sudomotor habituation following long-term heat adaptation: Asia (Eijkman 1895, 1924), Australia (Sunstroem 1927) and Africa (Dreosti 1935). Such responses are also described as negative phenotypic adaptations (Taylor 2014). In the modern epoch, few embraced the concept of thermoeffector habituation (Burton et al. 1940; Glaser and Whittow 1953; Yoshimura 1964; Hori et al. 1976; Candas 1987), which differs from, but does not conflict with, observations of hypersecretion following short-term adaptation. Since heat acclimation occurs over much shorter durations than acclimatisation, then responses to the former represent a transitional phase that precedes sudomotor habituation.

Heat adaptation can modify sudomotor function through changes within the regulatory centre or at the sweat glands themselves. Adaptations within the regulatory centre have two forms. Firstly, there may be an increase in the sympathetic (thermoefferent) flow from the regulatory centre to the sweat glands for a given change in body temperature. That is, the central thermosensitivity may have changed. Whilst we are unaware of conclusive evidence for that mechanism, it is possible that we now have the tools with which one might test that hypothesis, and Barry et al. (2020) have suggested that such a change does not occur.

Secondly, the regulatory centre temperature threshold for sudomotor activation might be reduced, so that sweating is activated earlier. Whilst we cannot measure an integrated body temperature that reflects the overall thermoafferent flow to the regulatory centre, reductions of 0.2–0.5 °C in the threshold for the deep-body contribution to that signal are frequently observed following heat adaptation (Ladell 1951; Fox et al. 1963b, 1967a; Wyndham 1967; Nadel et al. 1974b, 1978; Hessemer et al. 1986; Armstrong and Kenney 1993; Cotter et al. 1997; Yamazaki and Hamasaki 2003; Patterson et al. 2004a; Barry et al. 2020). Patterson et al. (2004a) noticed a similarity between the size of the post-acclimation reduction in the deep-body temperature threshold for sweating and the reduction in the pre-exposure (baseline) deep-body temperature, which was being regulated at a lower level (also see: Barry et al. 2020). That equivalence raised the possibility that the critical determinant for sudomotor activation was not attaining some absolute body temperature, but a change in that temperature from it pre-exposure level (also see: Booth et al. 2004).

At the glandular level, two adaptations can occur, both of which yield more prolific sweating for a given thermoeffector drive. That outcome can result from sweat-gland hypertrophy or from an elevation in the cholinergic sensitivity of those glands. Joseph Weiner (1945) was possibly the first to hypothesise that the sweat glands could be enlarged if repeatedly stimulated, with Kenzo Sato providing the morphological proof. With his wife (Fusako Sato), he found a correlation between endurance-exercise behaviours and eccrine-gland size in humans (Sato and Sato 1983). To explore a possible mechanistic connection, Sato et al. (1990) heat adapted (9 months) patas monkeys; our speedy, hairy, eccrine sweaters (" Thermoeffector evolution: vascular networks, homeothermy, sweating and hairlessness"). They proved that glandular hypertrophy could accompany heat adaptation. Moreover, those heat-adapted glands secreted almost three times more sweat in response to a subcutaneous methacholine injection (1% methacholine in saline; Sato and Sato 1983).

English scientists had earlier shown sweat-gland training to be a predominantly localised (glandular) phenomenon (Fox et al. 1964, 1967b; Collins et al. 1965, 1966). The underlying mechanism for that effect seemed to be either the separate, or combined, results of sweat-gland hypertrophy and an elevated sensitivity of their muscarinic receptors (subtype M_3; Sato and Sato 1983; Sato et al. 1990). Those studies established that the thermal sensitivities (mg cm^{-2} min^{-1} $^{o}C^{-1}$) of sweat glands were not fixed, but increased during heat acclimation. Since those responses verified the prevailing dogma of hypersecretion following acclimation, then it appears those adaptations were not further explored. However, one wonders whether the eccrine glands of heat-acclimatised and habituated sweaters, who have lived and worked for many years in a tropical climate, might also be hypertrophied and more responsive to cholinergic stimulation, or whether those characteristics might revert back to their pre-adapted phenotype as their sudorific responses to heat stress became less pronounced (habituated). In that regard, Inoue et al. (2009) reported a reduced sensitivity to acetylcholine iontophoresis in long-term, heat-acclimatised indigenes from a hot-humid climate, which one might anticipate in those with an habituated sudomotor response. That hypothesis requires testing.

Elevated sudomotor thermosensitivities are consistently observed within heat-adapted individuals (Ladell 1951; Fox et al. 1963b, 1967a, 1967b; Wyndham et al. 1966; Wyndham 1967; Stolwijk et al. 1977; Armstrong and Kenney 1993; Patterson et al. 2004a; Goto et al. 2010; Lorenzo and Minson 2010), and it appears that sensitivity change can be induced within the first week of acclimation (Mitchell et al. 1976; Cotter et al. 1997; Patterson et al. 2004a). It is interesting to see that larger people, with lower mass-specific surface areas, show stronger sudomotor responses during passive heat acclimation than do smaller people (Alkemade et al. 2021). Those responses are consistent with larger individuals relying more heavily upon evaporative cooling than do smaller individuals (Notley et al. 2016).

When heat acclimation was combined with the simultaneous cooling of one forearm (water immersion), less pronounced sweating was observed from that forearm when thermal stimuli were applied after acclimation (Fox et al. 1964). Those changes reflected localised, glandular-training affects, and were reinforced by the observations of Chen and Elizondo (1974, U.S.A.) and Ogawa et al. (1982, Japan). Collectively, those investigations gave rise to the view that enhanced sudomotor sensitivity during heat acclimation was primarily a peripheral phenomenon.

If sudomotor heat acclimation is predominately a peripheral phenomenon, how might we explain the lower, rather than higher, cholinergic sensitivity reported by Inoue et al. (2009) in acclimatised Thai nationals? One possibility, for which we have only indirect evidence, would be reduced sudomotor drive from the regulatory centre, although Barry et al. (2020) suggested that does not occur. We know that short-term heat acclimation elevates the sudomotor response,

whilst long-term heat acclimatisation leads to an habituation. Is it possible that both hypersecretion and sudomotor habituation are centrally, but not peripherally, mediated? Is it also possible that those changes are expressed locally, with sudomotor habituation being a form of desensitisation?

Others have advanced the possibility that autonomic habituation might be determined centrally (*e.g.*, Glaser and Whittow 1953; Glaser and Griffin 1962; Teichner and Youngling 1962; Yoshimura 1964; Henane 1980; Smith et al. 2008; Simpson et al. 2018; Yurkevicius et al. 2021). In support of that concept, we hypothesise that both sudomotor hypersecretion and habituation result from localised and time-dependent changes in the sweat glands, brought about by changes in the intensity of the thermoefferent drive, which might vary during the course of long-term heat adaptation. During the early adaptation phase, it is possible that the regulatory centre is more sensitive to increases in body temperature, with the resulting thermoefferent flow being of greater intensity. The urgency of those early signals might cause the sweat glands to move away from their pre-adapted size and sensitivity. It might also be possible that, as the regulatory centre becomes accustomed, and perhaps desensitised, to those increases in body temperature, the intensity of the thermoefferent flow might be reduced, with the sweat glands regressing towards their pre-adapted size and sensitivity.

Consistent with that central hypothesis are the observations of a group led by Tokuo Ogawa (1929-present, Japan; Nagasaka 2022). For instance, Ohnishi et al. (1986) and Sugenoya et al. (1986) used the constant-strain model of heat acclimation, in combination with a surrogate index of sympathetic drive (sweat-expulsion frequency). They found that both the sympathetic drive and whole-body sweat rate were elevated at the same body temperature following short-term heat acclimation. If those changes also resulted in glandular hypertrophy or an increased cholinergic sensitivity, then one might hypothesise that sudomotor habituation results from a gradual reduction in central thermosensitivity, as reflected in sympathetic drive, with those influences being expressed locally.

Against that background, we will now examine how sweating is modified across different skin surfaces during heat adaptation. Could there be a redistribution of segmental secretion to maximise evaporative efficiency and heat loss? Short-term heat acclimation usually results in elevated sweat secretion from most skin surfaces (Kuno 1934, 1956; Robinson et al. 1941, 1943; Bean and Eichna 1943; Horvath and Shelley 1946; Ladell 1951; Bass et al. 1955; Fox et al. 1963a, 1963b; Strydom et al. 1966), although that is not always observed (Burton et al. 1940; Fox et al. 1967b; Dasler and Hardenberg 1971; Havenith and van Middendorp 1986; Hessemer et al. 1986). It also results in a more homogeneous distribution of sweat (Collins et al. 1965; Cotter et al. 1997; Patterson et al. 2004a), relative to the non-adapted state (Taylor and Machado-Moreira 2013). It appears that less productive skin sites before heat acclimation, tended to exhibit greater increases in sweat secretion following acclimation (Fox et al. 1964; Patterson et al. 2004a). Those short-term changes elevate the wetted skin-surface area and optimise evaporative cooling (Candas 1987), but sometimes with an elevation in superfluous (dripping) sweat (Mitchell et al. 1976), which occurs before local skin wettedness reaches 50% (supine posture; Candas et al. 1979b, 1980).

Ken Collins and his colleagues (1965) reported a disproportionate elevation in sweating from the arm following heat acclimation, and interpreted that to reflect a greater potential of that site for hypersecretion. Indeed, others observed greater sweat drippage from the limbs during heat acclimation (Candas et al. 1980). However, Höfler (1968, Germany), who also found the limbs produced more sweat following acclimation, suggested that it might be part of the adaptation process, during which a "*distribution toward the limbs during acclimatization utilizes these large surface areas with particularly favorable evaporation conditions*" (Höfler 1968 [P. 506]). Such an effect might enhance evaporative efficiency, but he did not report local sweat rates. Instead, data were averaged across sites and used to determine responses for the trunk, head, arms and legs, with the only significant increase being for the arm, with its contribution to the overall sweat production increasing from 17 to 20%. Shvartz et al. (1979, U.S.A.) supported that proposition, although they collected data from only three sites using a single sweat capsule that was moved around those sites within each trial. They did not compare inter-site sweat-rate changes. Nevertheless, a sweat redistribution towards the limbs during heat adaptation represented a plausible hypothesis, which became broadly accepted (Taylor 1986; Wenger 1988; Sawka et al. 1996), and was reinforced by ourselves (Regan et al. 1996; forehead and forearm) and others (Smith and Havenith 2019; torso and upper limbs), although neither of those experiments provided a sufficiently robust test of that hypothesis.

With hindsight gained from subsequent experiments (Cotter et al. 1997; Patterson et al. 2004a; Australia and New Zealand), we recognised our misinterpretation ("… *we have all been wrong often*" Hill 1965 [P. 167]). In an extensive heat-acclimation experiment, Patterson et al. (2004a) tracked five local sweating responses over 21 consecutive days (Fig. 10), which included 17 days of exercise in the heat (constant-strain model). The sudomotor responses from five, commonly used sites were measured. The absolute sweat rate of the forehead was always the highest, with all local sweat rates increasing throughout heat acclimation. The biggest relative increase was observed at the forearm, with similar changes at the chest and scapula, and smaller increases at the forehead and thigh. Those outcomes are inconsistent

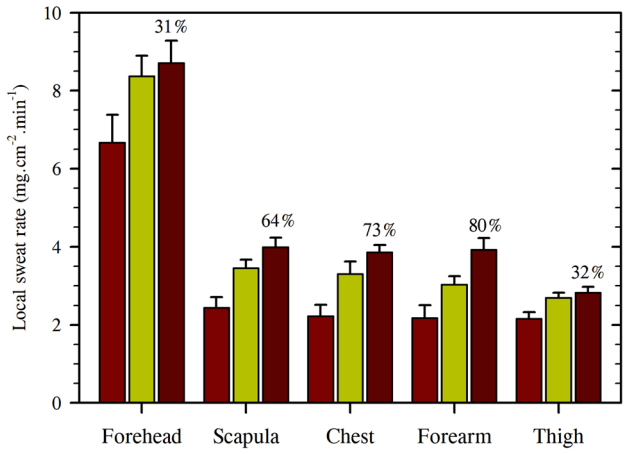


Fig. 10 Local sweat rates during 21 days of heat acclimation (90 min, 40 ℃ dry bulb, 60% relative humidity, 33 ℃ wet bulb). The experiment was based on the constant-strain (controlled hyperthermia) model, with alternately exercise and rest periods used to clamp deep-body (insulated auditory canal) temperature at 38.5 ℃ during the acclimation exposures. Data are means, with standard errors of the means ($N=11$), taken from exercising heat-stress tests conducted before (day 1 [control]: left bars), during (day 8: middle bars) and immediately after the experiment (day 22: right bars). Changes in the sweat rates for day 22, relative to the corresponding values for day 1, are shown as percentages. Modified from Patterson et al. (2004a)

with a systematic peripheral redistribution, so we should revert to the interpretation of Collins et al. (1965). During short-term heat acclimation, local variations in the strength of the sudomotor response might simply reflect differences between the pre-acclimated state and the genetically determined maximal sweat rate of each site, with greater sweating being elicited from sites with lower pre-acclimation sweat rates.

Before moving to the vasomotor responses, we will examine the process of evaporation and changes in sweat composition following heat acclimation. Evaporation depends upon the water vapour-pressure gradient between the skin and its boundary layer, as well as the speed with which air moves across the body surface, due either to wind or body movements accompanying exercise (Notley et al. 2023a). The primary determinant of the cutaneous water-vapour pressure is the skin temperature, and that relationship is non-linear and steep. Thus, providing the sweat rate is adequate, evaporative cooling can be elevated simply by increasing skin temperature, even if the sweat rate remains constant. Evaporation will decrease if the skin temperature falls. If a reduced vapour pressure gradient results in evaporation being impaired, the skin temperature will rise. When acclimating to exercise in hot-dry conditions, there is a reduction in skin temperature which is not observed in hot-humid environments (Shvartz et al. 1973a, b). Those effects were perhaps first described by Dreosti et al. (1936), who reported increases in evaporative cooling and efficiency in dry heat, without an increase in sweat rate.

Since elevated sweat rates commonly accompany heat acclimation, then details concerning intra-glandular water turnover become important (Schwartz and Thaysen 1956; Slegers 1966; Ohara et al. 1974). Indeed, since sodium reabsorption is inversely linked to the ductal transit time of primary sweat, higher sweat rates will yield more concentrated discharged sweat, regardless of one's level of heat adaptation (Dill et al. 1938; Kuno 1956; Sato and Dobson 1969). However, heat adaptation, independently of changes in transit time, will increase electrolyte reabsorption (Dill et al. 1938; Conn 1949; Bass et al. 1955; Kuno 1956; Allan and Wilson 1971; Ogawa et al. 1982; Kirby and Convertino 1986; Chinevere et al. 2008). Therefore, at the same sweat rate, a lower sweat electrolyte concentration will be observed following heat acclimation (Allan and Wilson 1971; England). That flow dependency means that reporting electrolyte concentrations without quantifying sweat rates merely provides descriptive information of minimal physiological relevance. Readers are directed elsewhere for sources dealing with the composition of sweat for non-adapted individuals (Patterson et al. 2000; Taylor and Machado-Moreira 2013) and for interactions between our endocrine responses and electrolyte conservation during heat adaptation (*e.g.*, Ladell 1945; Moreira et al. 1945; Conn 1949; Taylor et al. 1943b; Ladell and Shephard 1961; Collins and Weiner 1968; Sato and Dobson 1969; Finberg and Berlyne 1977; Davies et al. 1981; Kirby and Convertino 1986).

As described in Part 2 of this review series (Notley et al. 2023b), high ambient water-vapour pressures, when combined with high skin temperatures and prolific sweating, can result in sweat suppression (hidromeiosis: Randall and Peiss 1957; Collins and Weiner, 1962; Brown and Sargent, 1965; Candas et al. 1979a). That effect was incorrectly assumed to reflect sweat-gland fatigue (Fox et al. 1967b), and it appeared uniquely linked to hot-humid conditions (Fox et al. 1967b). Henane (1980) noted that, within 35 of the 55 papers he reviewed, elevated sweat rates accompanied heat adaptation. Among those studies, hypersecretion occurred more commonly during hot-humid adaptation, whilst the 20 studies that revealed minimal sudomotor effects involved hot-dry conditions (also see: Griefahn 1997). For those 55 investigations, Adolph's (1947a, b, c, d) acclimation triad applied only to humid heat, but became a dyad in dry heat. Neither Nielsen (1998) nor Tebeck and colleagues (2020) agreed. They reported sweat-rate increases during both dry- and humid-heat acclimation, with the former being greater (Tebeck et al. 2020).

Concerning heat adaptation in recreational and occupational athletes, two questions arise. Firstly, is exercise on its own sufficient to induce adaptation? Endurance exercise in both cool and temperate environments can elevate body

temperatures, so frequent endurance training will induce some level of thermal adaptation. Those changes are intensity dependent, so unless the exercise intensity is sufficiently high, it is not an adequate substitute for heat adaptation (Strydom et al. 1966; Strydom and Williams 1969; Roberts et al. 1977). For example, the regular physical training undertaken by soldiers did not prevent a substantial minority failing heat-tolerance tests (Mitchell et al. 2021). Conversely, heat acclimating highly trained endurance athletes may appear ineffectual, depending upon the index used to make that assessment, due to their repeatedly experienced, and often protracted, elevations in deep-body temperature.

Our second question relates to the ambient conditions. Should we use dry or humid heat? As with most adaptations, specificity is important, so exercise in humid heat should be used if those conditions are expected at places of work or competition. Indeed, dry-heat acclimation appears inadequate for subsequent exercise in hot-humid conditions (Armstrong and Maresh 1991; Tipton et al. 2008). It also seems that acclimation to exercise in humid heat might be achieved better through harder physical work in moderate heat than by lighter work in more severe heat (Wyndham et al. 1973). Also of relevance is the rate at which acclimation benefits decay, for which readers are directed to Wyndham and Jacobs (1957) Fox et al. (1960), Pandolf et al. (1977), Weller et al. (2007), Tipton et al. (2008) and Périard et al. (2015).

Vasomotor adaptations

Exercise requires increased muscle blood flow, as well as increased cutaneous blood flow to convey excess metabolic heat to the skin. The high skin temperatures associated with hot environments (Werner and Reents 1980), and especially humid heat, reduce the temperature gradient between the muscles and skin, making that heat transfer more difficult. Therefore, during heat adaptation, one might expect elevated peripheral heat delivery, in the form of enhanced cutaneous blood flow, especially during adaptation to hot-humid environments. Adaptations to cutaneous vasomotor function that might accompany chronic heat exposure, were first described by Burton et al. (1940), although few investigators followed that lead. Furthermore, since "*every adaptation is an integration*" (Barcroft 1934 [P. 187]), we must also consider the possibility of regulatory conflicts between thermoregulation and the regulation of blood volume and pressure (Notley et al. 2023a [Table 1]). When exercising in the heat, uncompensated cutaneous vasodilatation, in combination with elevated sweating and intramuscular vasodilatation, can compromise those homeostatic processes.

Heat-acclimatised indigenes from the tropics have typically demonstrated habituated (attenuated), but not elevated, sudomotor responses (Eijkman 1924; Dreosti 1935; Burton et al. 1940; Glaser and Whittow 1953; Hori et al. 1976; Candas 1987) along with elevated skin temperatures (Thompson 1954; Saat et al. 2005). One might expect those indigenes to also show higher cutaneous blood flows, but that was not necessarily the case, with Fox et al. (1974) and Katsuura et al. (1993) not observing blood-flow elevations. Indeed, they described peripheral blood-flow reductions in tropical indigenes (hand) and long-term residents (forearm). Such responses resembled sudomotor habituation, but what happens during artificial heat acclimation?

Evidence from studies of cutaneous vasomotor function during short-term heat acclimation is currently inconclusive. Some have reported acclimation to elicit greater cutaneous vasodilatation (Fox et al. 1963b; Roberts et al. 1977; Lorenzo and Minson 2010; Fujii et al. 2012), others found no significant changes (Whitney 1954; Nielsen et al. 1993), whilst still others reported reduced cutaneous blood flow (Wyndham 1951; Rowell et al. 1967; Havenith and van Middendorp 1986). The current authors revisited that topic (Notley et al. 2018), using constant-strain heat adaptation, and with the pre- and post-acclimation (uniformity) tests undertaken during both mild (37.5 °C) and moderate hyperthermia (38.4 °C). Vascular conductance for both the forearm (strain-gauge plethysmography) and local cutaneous tissues (laser-Dopler flowmetry) increased during both mild (21% and 23%, respectively) and moderate hyperthermia (11% and 25%, respectively). Therefore, if verifiable, it seems that short-term heat acclimation, when carried out using the constant-strain method, can induce adaptations that increase convective heat delivery to the periphery, as well as an elevated sudomotor response to dissipate that heat. For those adaptations to occur without compromising other homeostatic functions or exercise itself, compensatory vasoconstriction must occur within other vascular beds, and presumably within the splanchnic network. Unfortunately, little is known of such mechanisms. What also remains to be seen is whether or not long-term heat adaptation might lead to an habituated vasomotor response. On the basis of studies by Fox et al. (1974) and Katsuura et al. (1993), that seems probable.

Body-fluid adaptations in the heat

Both heat exposure (Diaz et al. 1979; Harrison et al. 1983; Maw et al. 2000) and exercise (Senay 1972; Diaz et al. 1979; Edwards and Harrison 1984; Maw et al. 1998) will independently modify the blood volume. The underlying mechanisms for those changes were identified by Ernest H. Starling (1866–1927, England), who was twice nominated for the Nobel Prize in Physiology (Colp 1952; Ahlqvist 2003; Henriksen 2005). Starling (1896) observed that, following acute blood loss, the blood volume was restored, but it became more dilute (isovolaemic haemodilution), at least in the short term. He described a mechanism involving

fluid redistribution into the vascular space, with transcapillary forces that act across capillary walls driving that fluid shift. Those transcapillary influences are now known as the Starling forces. Since our blood volume and pressure are regulated using feedback from the low-pressure baroreceptors (Notley et al. 2023a [Table 1]), then any blood volume reduction, whether accompanying blood removal (Morimoto et al. 1981) or hypohydration (Nose et al. 1988a), will be corrected. That occurs via transcapillary fluid movements, as determined by local hydrostatic, as well as colloid and crystalloid osmotic pressures (Pappenheimer 1953; Länne and Lundvall 1989).

During the Krogh-Hill epoch, Joseph Barcroft (1872–1947, England; Roughton 1949; Longo 2016), who was studying the affects of altitude exposure in the Peruvian Andes (South America), found that basal blood volumes were constantly varying (Barcroft et al. 1923). Indeed, those fluctuations were temperature dependent, with blood volume increasing in the heat (Fig. 11), primarily due to an expanded plasma volume (hypervolaemic haemodilution), and contracting in cooler conditions. The highly responsive nature of the plasma volume was eventually linked with exercise, and the pieces for another puzzle were starting to be assembled.

We now know that during the first 10 min of aerobic exercise, a reduction in the plasma volume occurs (Greenleaf et al. 1977; Maw et al. 1998). That change is intensity dependent (Morimoto et al. 1978; Senay et al. 1980; Gagnon and Kenny 2012), it is related to the redistribution of the cardiac output to the active muscles (Senay 1972; Harrison 1985) and it occurs because the Starling forces

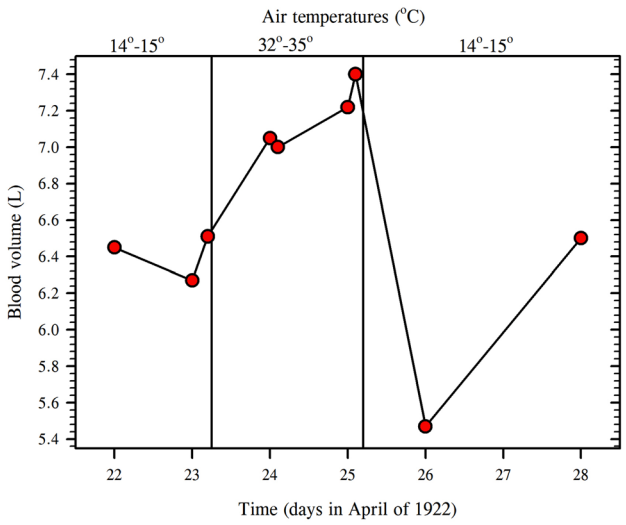


Fig. 11 Changes in the blood volume of one man during consecutive days of exposure to cool-cold air (2 days), warm-hot air (2 days) and back to cool-cold air (3 days). Data extracted and redrawn from Barcroft et al. (1923)

now favour a fluid shift from the blood into the active muscles. Those same mechanisms cause fluid shifts during heat exposure. Not surprisingly, when exercise and heat stress are combined, the overall effect is larger, and it may even challenge the regulation of body fluids and blood pressure. We believe that fluid shift is dictated by transmural protein movements out of the vascular space, since each gram of albumin can osmotically attract 15 mL of fluid (Scatchard et al. 1944). Indeed, Patterson et al. (2014, Australia) could explain > 90% of the exercise-related plasma losses on days 8 and 22 of heat acclimation on the basis of protein lost from the blood. Whilst protein movements could explain the acute reductions in the plasma volume, they were unable to account for the rapid restoration of the resting plasma volume during a 30-min recovery when water was withheld. The mechanism for that seemed to be related to a greater plasma osmolality, which was associated with increased plasma-sodium content (Patterson et al. 2014). Details concerning the physiological mechanisms underlying those changes may be found elsewhere (*e.g.*, Kjellmer 1964; Senay 1972; Guyton et al. 1975; Röcker et al. 1976; Morimoto et al. 1978; Greenleaf et al. 1979; Harrison et al. 1981; Sawka et al. 1984; Harrison 1985; Nielsen et al. 1986; Sejersted et al. 1986; Horowitz and Samueloff 1988; Björnberg 1990; Haddad and Horowitz 1994; Maw et al. 1998).

For a long time, one of the tenets of heat-adaptation research within the modern epoch was that the rapid plasma-volume restoration acted as an essential, precursor step when adapting to exercise in the heat. Such restoration occurred during the initial phase of heat adaptation and it reduced cardiovascular strain during subsequent heat exposures, but it represented only a transient phase of heat adaptation (Taylor et al. 1943a; Ladell 1951; Bass et al. 1955, 1958; Bass 1963; Robinson 1963; Wyndham et al. 1968, 1976; Senay et al. 1976; Fortney and Senay 1979; Senay 1979; Shapiro et al. 1981; Sawka et al. 1983; Brück and Zeisberger 1990; Aoyagi et al. 1995; Mack and Nadel 1996). Indeed, when several regulated variables are disturbed simultaneously during exercise in the heat, even small blood-volume changes can make the difference between stress accommodation and cardiovascular insufficiency (Machle and Hatch 1947; Bass 1963). With some exceptions (*e.g.*, Rowell 1978, 1993; Harrison et al. 1981), that initial plasma-volume expansion has been observed regularly during heat acclimation, both at rest (Bazett et al. 1940) and during exercise (Wyndham et al. 1968; Senay et al. 1976; Nielsen et al. 1993, 1997; Patterson et al. 2004b; Goto et al. 2010; Lorenzo et al. 2010). It seem to have been the result of an isotonic expansion of the plasma volume (Bass et al. 1955; Wyndham et al. 1968; Convertino et al. 1980; Patterson et al. 2014).

The apparently short-term nature of that plasma-volume expansion became part of a mechanistic theory that linked its early expansion, and then its contraction, to supporting

the other processes that underpinned heat adaptation, but which responded more gradually. That hypothesis prevailed throughout most of twentieth Century (Harrison 1985; Senay 1986; Mack and Nadel 1996). Although contradictory evidence already existed (Harrison et al. 1981; England), the domestication of that hypothesis came through the research of Patterson et al. (2004b, 2014), and it now seems that gradual plasma-volume reduction may simply have been a consequence (artefact) of the experimental design. Indeed, that decrease may have been an habituated response created by using the constant-stress experimental design (Taylor 2014).

Furthermore, those earlier observations were generally interpreted to show that the intravascular compartment was preferentially expanded during the early phase of heat acclimation (Harrison et al. 1981; Mack and Nadel 1996). There were two reasons for that presumption. The first was methodological, since measuring volume changes beyond the vascular space was not easy. Secondly, since the body mass seemed to remain stable during heat acclimation (Bass et al. 1955; Senay et al. 1976; Harrison 1985), it was presumed that the total body water also remained stable, with that plasma expansion being facilitated by a reciprocal interstitial-fluid contraction. However, those body-mass and body-fluid compartment variations are only loosely linked (Costill et al. 1976).

Two groups attempted to measure total body water during heat acclimation (Bass et al. 1955; Wyndham et al. 1968). Bass et al. (1955 [$N=5$], U.S.A.) reported a non-significant elevation in total body water after heat acclimation, with three participants experiencing an expansion. Subsequently, Wyndham et al. (1968 [$N=3$], South Africa) described a significant increase in total body water. Both groups used constant-stress designs, and their methods were not equally sensitive (Bass et al. 1955 [antipyrine dilution; less sensitive]; Wyndham et al. 1968 [tritiated water]), so the nett result was inconclusive.

More recently, Patterson et al. (2004b, 2014) simultaneously tracked the volumes of six body-fluid compartments using three radioisotopes and Evans-blue dye (Maw et al. 1996; Australia). Constant-strain forcing functions were used during both the adaptation exposures (controlled hyperthermia; deep-body temperature clamped at 38.5 °C) and the uniformity tests (same relative exercise intensity) across 22 consecutive days. Those methods provided a more robust evaluation of physiological adaptation, with total body water expanding significantly when measured on days 8 and 22 of acclimation (Fig. 12; upper panel), supporting the observations of Wyndham et al. (1968). Moreover, both the extracellular and interstitial fluid volumes increased significantly, but without a selective expansion of the intravascular space, and without those compartmental increases occurring at the expense of other fluid compartments. Those outcomes challenged the notion of a nett fluid exchange between the interstitium and the blood during heat acclimation.

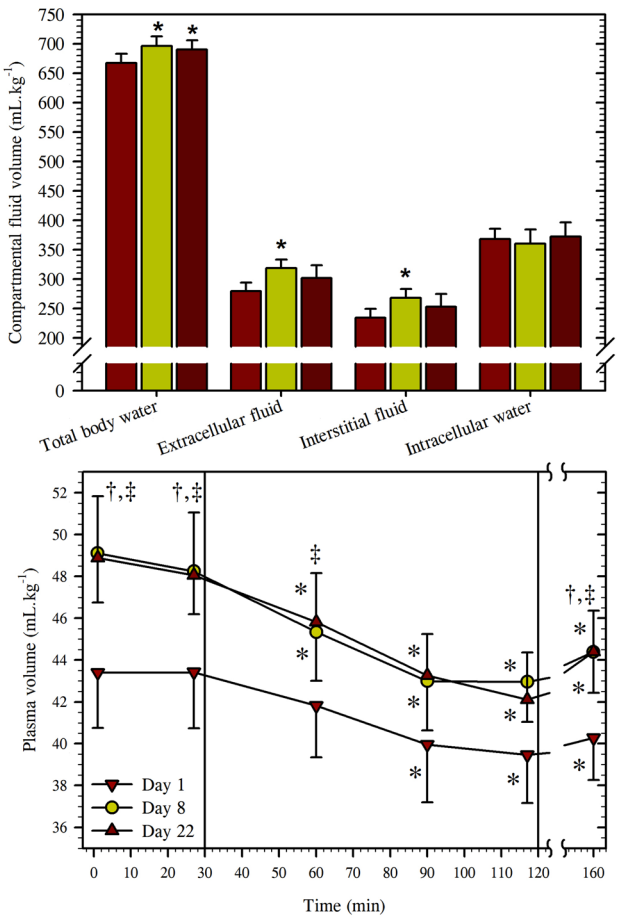


Fig. 12 Mass-specific, body-fluid volumes during the course of heat acclimation. Upper panel: baseline (pre-exposure) fluid-compartment volumes before (day 1 [control]: left bars), during (day 8: middle bars) and immediately after completing acclimation (day 22: right bars). Data are means with standard errors of the means extracted from Patterson et al. (2004b), with each asterisk indicating a significant change relative to day 1. Lower panel: mass-specific plasma volumes at rest (0–30 min; baseline), during an exercising, constant-strain stress test (30% peak aerobic power, 30–120 min: 39.8 ℃ dry bulb, water-vapour pressure 4.32 kPa) administered before (day 1), during (day 8) and following (day 22) heat acclimation. Data are means with standard errors of the means extracted from Patterson et al. (2014). Significant differences are indicated ($P<0.05$): *differences from pre-heating baselines; †differences between days 1 and 8; ‡differences between days 1 and 22

The lower panel of Fig. 12 shows the plasma-volume responses during exercise in the heat (30–90 min), following an initial resting exposure (0–30 min), on three days during 22 days of heat acclimation (Patterson et al. 2014). The baseline plasma volumes (0 min), once elevated (day 8) during heat acclimation, did not contract, but remained elevated and equivalent from day 8 to day 22. At the end of exercise (120 min), the plasma volumes of days 8 and 22

were equivalent to the baseline volumes observed prior to heat exposure (day 1), whilst the absolute plasma-volume reductions at 120 min were larger on days 8 and 20 than on day 1. Patterson et al. (2014) hypothesised that an elevated fluid loss from the intravascular compartment during exercise was advantageous, since it supported an elevated sudomotor response without compromising either fluid homeostasis or blood-pressure regulation, and it facilitated the plasma-volume recovery following exercise.

We believe that the difference between the observations of plasma-volume stability during constant-strain heat acclimation, and a plasma-volume reduction during the course of a constant-stress protocol, can be attributed to the forcing functions used in those studies. The earlier studies almost invariably used the constant-stress method, whilst Patterson et al. (2004b, 2014) used the constant-strain design (controlled hyperthermia) to maintain a constant homeostatic disturbance. It is also our belief that gradual reductions in plasma volume reported by others, following an initial expansion, represent physiological habituation. That is, if the strength of the adaptation impulse is not sustained, then the gradual reduction in physiological strain must modify both the nature of the adaptation itself, and the causal mechanisms underlying adaptation. A detailed discussion of that topic is presented elsewhere (Taylor 2014).

Before moving to cold acclimation, we return to one of our opening questions. Will sitting in a hot bath or a sauna with a good book be advantageous for a marathon runner preparing to race in the heat? Heathcote and colleagues (2018) suggest that passive exposures can achieve the hallmarks of acclimation: decreased resting and exercising deep-body temperatures, increased sweat rate, decreased heart rate and increased plasma volume. Thus, our triad becomes a quartet, which can lead to improved exercise performance, but sport-specific adaptations obtained during exercise in the heat may still be superior (Heathcote et al. 2018). Garrett and colleagues (2009, 2011) also identified those benefits, but cautioned that they were short lived. Earlier still, Wyndham (1973) provided a much stronger view, suggesting that exercise in the heat was essential because workers, and therefore athletes, required both cardiovascular and sudomotor adaptations. Since highly trained endurance athletes repeatedly experience elevated deep-body temperatures, even when training in cooler conditions, then heat acclimation may offer minimal physiological, but very important psychological, preparation for racing in the heat.

Postscript

From these observations, the following interpretations may be drawn. When short-term, constant-stress protocols are used to induce heat acclimation, we can expect to see lower deep-body temperatures and heart rates, as well as a greater sweat production, following acclimation. The plasma volume would increase transiently, but then revert to its pre-adapted state. Whilst those adaptations are beneficial to heat tolerance, that form of heat acclimation does not elicit the same level of physiological (homeostatic) strain across the full duration of those exposures, which can make mechanistic interpretations of the underlying physiological processes difficult to reach. Therefore, it is our view that the constant-strain (controlled hyperthermia) heat-acclimation method developed by Ronald Fox will elicit slightly different, yet mechanistically more interpretable outcomes, that are a function of the size and duration of those body-temperature disturbances. Of course, we do not adapt to changes in controlled variables (*e.g.*, heart rate); they are merely indices of physiological strain. During constant-strain heat adaptation, sweat rates will increase, and possibly more rapidly, but the available evidence does not support a redistribution of sweat towards the limbs. The plasma volume will be elevated, and will remain so, as long as the physiological strain is sustained. Since long-term heat adaptation results in an habituated sudomotor response, one might hypothesise that both the size and cholinergic sensitivity of the sweat glands will return towards their pre-adapted states during the course of long-term heat adaptation. Those changes might result from reduced thermoefferent drive from the regulatory centre. However, the degree to which passively induced (constant-strain) heat adaptation can prepare recreational athletes to exercise in the heat remains untested (Casadio et al. 2017).

Physiological acclimation to increase cold tolerance

Readers of Part 3 of this historical series will know of an imbalance between the number of heat- and cold-related papers (Notley et al. 2023c). That does not reflect their importance, yet the imbalance continues as we narrow our focus to thermal adaptation. From research conducted across different ethnic groups, we can characterise and define human cold adaptation as responses that increase peripheral thermal insulation and reduce (habituate) metabolic heat production when again confronted with similar ambient conditions. Repeated localised cooling also seems to elicit more frequent cold-induced vasodilatation.

Cold acclimation is infrequently considered within the athletic context, even for swimmers, despite it having been demonstrated > 70 years ago that reductions in the body temperatures of lightly clothed men exposed to air temperatures close to zero, are attenuated following 72 h of continuous exposure (Glaser 1949; England). It is also rarely considered within most occupational scenarios, although there are some exceptions, and so this final section is directed at those exceptions. Whilst it might be possible to adapt to cold-water shock, we have restricted our discussion to more protracted cold exposures.

Before commencing, we make an early qualification regarding the available research evidence, and that relates to differences between experiments that use resting exposures and those that involve exercise, even though exercise might be essential from an applied perspective. During heat exposure, the metabolic heat of exercise and environmental heat combine to drive body temperatures in the same direction. But during cold exposures, exercise removes the protective thermal boundary layers and can dramatically elevate heat loss, but that effect can be offset by heat produced during that exercise, depending upon the temperature and nature of the ambient medium. Indeed, within the short term, and with the proviso that one can tolerate the initial cold shock, heat loss during resting immersions can temporarily be balanced by elevating metabolic heat production (shivering) and non-shivering thermogenesis. Those mechanisms also supplement heat production during exercise in cold water (Notley et al. 2023c). Nevertheless, when exploring physiological mechanisms, exercise can complicate data interpretation, due to its activation of processes that share one or more of the controlled (effector) variables used during thermoregulation. For instance, when we swim, muscle blood flow to the limbs is necessarily elevated, which reduces physiological insulation and increases heat loss (Cannon and Keatinge 1960; Nadel et al. 1974a; Veicsteinas et al. 1982), making it more difficult to identify cold-induced adaptations within the cardiovascular system. These complications require the readers of cold-acclimation papers to closely examine how the experimental evidence from such studies has been interpreted.

Turning down the metabolic heaters

Following cold adaptation, and regardless of whether one studies acclimatised first-nations populations or artificially acclimated individuals, the commonly observed outcome over the past century has been an habituation of the metabolic response (Hicks and Matters 1933; LeBlanc 1956, 1978; Davis 1961; Keatinge 1961; Golden and Tipton, 1988; Janský et al. 1996; Stocks et al. 2001; Mäkinen 2010; Tipton et al. 2013; Brazaitis et al. 2014; Yurkevicius et al. 2021). Just like sudomotor habituation (" Sudomotor adaptations"), a metabolic habituation means a less powerful shivering response to subsequent body cooling. In achieving that habituated state, we may tolerate some degree of hypothermia and we might also modify the anatomical and physiological insulation provided by our cutaneous and subcutaneous tissues. Due to differences in the intensity of the cold stress and the resulting homeostatic disturbances, metabolic habituation would be more pronounced following protracted cold-water immersion than cold-air exposures of the same temperature and duration. Since we can still achieve heat balance during subsequent cold exposures, even though shivering has been reduced, then we assume that cold acclimation led to a reduced transcutaneous heat loss (Stocks et al. 2001), or that the non-shivering contribution to heat production was elevated (Janský, 1973; Blondin et al. 2014; Gordon et al. 2019).

In Part 3 of this series (Notley et al. 2023c), we introduced non-shivering thermogenesis, noting that significant gaps exist within our understanding of its role in humans, and especially within exercising adults. Similar gaps exist with regard to the role of the brown adipocytes during the cold adaptation, although Hassi (1977) found that about 10% of the adipocytes of adults from northern Finland, when examined *post mortem*, were brown adipocytes. Huttunen et al. (1981) confirmed that observation, and suggested that people living in cold climates (*e.g.*, 65° North) might have a greater volume of brown adipose tissue than the residents of temperate and tropical climates (also see: Leppäluoto et al. 2022). Those changes were thought to have resulted from regular cold exposures during occupational activities. That possibility was supported experimentally by Davis (1961), Blondin et al. (2017) and Gordon et al. (2019), and it appears that the metabolic adaptations that accompany repeated whole-body cooling (water 14 °C) result in a partial shift from shivering to non-shivering thermogenesis, but without a change in overall heat production (Gordon et al. 2019; Canada).

There might also be a desensitisation of the peripheral thermoreceptors to repeated cold exposures. Such a change would improve thermal comfort, a benefit that has been consistently observed during adaptation (Brück et al. 1976; Golden and Tipton, 1988; Leppäluoto et al. 2001). Earlier in this review, we suggested that the sudomotor, and possibly also vasomotor, habituation that accompanies long-term heat adaptation might be centrally mediated, and result from reduced thermoefferent drive for a fixed homeostatic disturbance. It is possible that mechanism might also explain metabolic habituation following cold adaptation.

Indirect support of that possibility comes from the experiment of Tipton et al. (2013, England; also see: O'Brien et al. 2000). They compared both the acute ventilatory (cold-shock) and metabolic responses (respirometry) of three groups of subjects during cold-water immersion: a non-immersed control group, a group exposed to repeated whole-body (cold) immersions and a group that was cold immersed for only 5 min. The last group only experienced cooling of the superficial tissues, and they demonstrated an habituation of the ventilatory, cold-shock response, but not the metabolic habituation observed in the second group. Thus, the peripheral thermoreceptors appear to participate in aspects of both heat (Fox et al. 1964; Regan et al. 1996) and cold adaptation (Tipton et al. 2013). It also appeared that deep-body cooling was

essential for metabolic habituation to be expressed, which may have resulted from reduced, centrally mediated thermoefferent drive. Indeed, that is consistent with the observations of Mäkinen et al. (2008, Finland), who examined changes in heart-rate variability to estimate sympathetic and parasympathetic cardiac drive, before and after cold-air acclimation. They found a reduction in sympathetic drive during cold exposure following acclimation, along with elevated parasympathetic drive. Nevertheless, whilst the deep-body thermoreceptors seem to be responsible for metabolic habituation in the cold, the full suite of processes involved in cold acclimation requires activation of both deep and peripheral thermoreceptors, similar to their role during heat acclimation.

Direct support for centrally mediated metabolic habituation comes from human and other animal studies. For example, Brück et al. (1970, Germany [guinea pigs]) found that cold acclimation reduced the threshold temperature at which shivering commenced. They subsequently found a reduction of 0.5 °C in the mean body temperature threshold for shivering in humans following cold acclimation (Brück et al. 1976). Of relevance to recreational and occupational athletes are the observations of the thermal physiologists, Frank St. C. Golden (1936–2014, Ireland and England; Tipton 2014) and Mike J. Tipton (1959-present). They reported that metabolic habituation was evident only in resting, cold-acclimated subjects (Golden and Tipton 1988). In similarly cold-exposed individuals who exercised, that response was not observed, presumably due to metabolic heat production preventing the deep-body hypothermia necessary to induce adaptation. That group found that the relationship between the size of metabolic response and the change in deep-body temperature was the same before and after cold acclimation (Rees et al. 2002). Janský et al. (1996, Czech Republic) described cold acclimation in humans that induced both metabolic habituation and a reduction in the thermogenic threshold, although the latter is not always observed (Stocks et al. 2001; Australia). It is possible that the thermosensitivity of the thermogenic response might be reduced, although such a change seems not to have been observed following cold acclimation (Janský et al. 1996; Rees et al. 2002). Whatever the mechanism of cold habituation, it appears to be surprisingly long-lasting, even after returning to a temperate climate (Shephard 1985).

Finally, we draw attention to the specific nature of the metabolic responses seen during cold acclimation. That specificity can relate to the site of cold stimulus, with deep-body and peripheral cooling differing in their physiological affects (Tipton et al. 2013; O'Brien et al. 2000). It can also relate to the size of the deep-body temperature reduction (Rees et al. 2002; Tipton et al. 2008). Thus, cold acclimation to one set of conditions does not necessarily bestow the same effect when one is exposed to conditions that elicit a greater decline in deep-body temperature, wherein the metabolic response might revert to that seen in the non-adapted state (Tipton et al. 2008). That reversion was seen when the habituated metabolic response of cold-acclimated individuals, observed during the resting phase of cold-water immersion, disappeared 10 min after commencing exercise (cycling). In fact, their whole-body oxygen consumption returned to that observed prior to acclimation, yet deep-body (oesophageal) temperatures remained almost identical (Stocks et al. 2001).

Turning up physiological insulation

Our emphasis now returns to variations in anatomical and physiological insulation between the skeletal muscles and the skin. The cutaneous thermal insulation depends mainly on changes in cutaneous blood flow (conductance), and not on changes in the thermal properties of less perfused tissues. Unfortunately, there is a shortage of experimental evidence from cold-acclimation studies concerning cutaneous vasomotor adaptations. Whilst that may open a door for some, and we hope that gap might ignite some interest, it leaves an obvious hole in this commentary. Fortunately, our forebears have assisted, with Goldby et al. (1938) describing an earlier and more powerful cutaneous vasoconstrictor response during the whole-body cooling of cold-acclimatised Australian Aborigines. That was confirmed by Hammel et al. (1959, U.S.A), who reported reductions in both skin temperatures and thermal conductance.

Conversely, from observations of workers who regularly immersed their hands in cold water, there is evidence for an habituation of the local vasoconstrictor response, resulting in the maintenance of higher perfusion rates (Glaser et al. 1959; LeBlanc et al. 1960; Nelms and Soper 1962; LeBlanc 1978). That outcome was reflected in a more rapid onset of cold-induced vasodilatation (Krog et al. 1960 [Norway and England]; also see: Wakabayashi et al. 2012 [Japan]). Those observations presumably reflect adaptations specific to the conditions to which those individuals were exposed, and will be beneficial to workers who regularly immerse their hands in cold water. Curiously, it seems that the active heat acclimation of people who are not regularly exposed to cold-water immersion, also seems to enhance their cold-induced vasodilatation response (Ciuha et al. 2021).

Apart from the research just described, it seems that few have investigated the cutaneous vascular responses that accompany either whole-body or localised cold acclimation, and we are unaware of experiments in which the cutaneous vasomotor responses have been studied during acclimation to exercise in the cold. Amongst those few who have investigated cutaneous vasomotion during rest are Young et al. (1986, U.S.A.), who suggested they had provided the first evidence of a generalised

insulative response (cutaneous vasoconstriction), although they measured skin temperatures and not vasomotor activity, which were lower following cold adaptation. Hicks and O'Connor (1938a) had similarly reported lower skin temperatures for Australian Aborigines during cold exposures. Subsequently, Leftheriotis et al. (1990, France) measured forearm and finger blood flows (strain-gauge plethysmography) following cold-water adaptation of the forearm and hand. They examined reactive hyperaemia following local ischaemia, and found blood flows to both regions were significantly reduced, indicating an elevation of basal vasomotor tone following cold acclimation. Whilst those observations are consistent with an elevated cutaneous insulation, the treatments were localised, and that experiment was designed to address other research questions.

Subsequently, Budd et al. (1993, Australia) estimated changes in finger blood flow (photoelectric pulsimetry) following cold acclimation. They also found increased vasomotor tone, but suggested that it did not occur within the cutaneous tissues, but within the deeper tissues of the finger. At the same time, Naidu and Sachdeva (1993, India) measured finger blood flow (laser-Doppler flowmetry) in members of an Antarctic expedition (8 weeks), and reported an opposite effect. Their baseline blood flows were elevated. When the hands were repeatedly cold immersed, there was a gradual reduction in the strength of the vasoconstrictor response, such that, after 8 weeks, vasoconstriction was completely abolished. Those observations are consistent with an habituation of the constrictor tone as their participants adapted to the local climate, but they conflict with the results of both Leftheriotis et al. (1990) and Budd et al. (1993). Indeed, despite the interpretations and conclusions of others who have reviewed the experimental evidence, this topic requires further investigation to unravel these uncertainties.

Postscript

From the evidence presented above, turning down our metabolic heaters would not appear to offer a significant advantage during subsequent cold exposures, except perhaps within the workplace. On the other hand, reduced shivering can increase thermal comfort and allow fine-motor tasks to be performed more easily during subsequent cold exposures. However, during cold-weather military and civilian operations, it is the learned behavioural responses that contribute more to thermal tolerance than the acquired physiological responses (Shephard 1985; Castellani and Young 2016; Nindl et al. 2018). Those behaviours relate to the recognition of the early warning signs of hypothermia, and the correct use and maintenance of thermal protective clothing and shelter. For swimmers, cold adaptation may provide psychological preparation, which is acquired through increased familiarity with the stresses to be encountered. Therefore, it seems that, apart from the protective advantage for the hands and feet gained from adaptations of the cold-induced vasodilatation response, there seem to be few physiological benefits that accompany cold adaptation for those who exercise in the cold.

Conclusions: Part 4

In this final contribution to our four-part historical series, we aimed to accomplish two objectives. Firstly, we endeavoured to describe the evolutionary steps that endowed each of us with the potential to be both fast endurance mammals and sweating specialists. Secondly, we examined the enhancement of those genetic attributes by acquiring, either naturally or artificially, the physiological (phenotypic) adaptations necessary for us to tolerate endurance exercise and work in both hot and cold environments.

From the evolutionary evidence, we might draw the following conclusions.

- The first of our ancestors to qualify as an athlete was probably *Homo erectus*.
- Whilst they could carry water, they were at risk of hypohydration because the thermoregulatory capability that distinguished them most from other large mammals was their very effective evaporative cooling ability.
- They had become sweating specialists (*Homo sudomotor*) with eccrine sweat glands covering almost their entire body surfaces, replacing the apocrine glands and their partnered hair follicles, as they lost most of their dense body hair.
- When *Homo sapiens* left Africa, they required thermoregulatory competence for exercise in both hot and cold environments. That required behavioural thermoregulation to buffer physiological shortcomings, including the development of thermal protective clothing (> 3000 years B.C.E.).
- Humans had not speciated. Instead, we all remained *Homo sapiens*, but we acquired different sizes, shapes and behaviours, which endowed us with subtle differences in thermal tolerance. Some of those differences appeared as though they might be linked to our ancestral origins, which ignited the interests of scientists.

Research directed towards understanding the naturally occurring thermal adaptation (acclimatisation) of people of varying ancestry was undertaken across several continents, from which we offer the following conclusions and recommendations.

- In Africa, the thermoregulatory capabilities of the small-bodied and nomadic people of the Kalahari differed little from those of people with a European ancestry.
- In tropical Asia, recent European immigrants were found to secrete more unevaporated sweat than the indigenes, yet they had similar sweat-gland densities.
- Long-term heat acclimatisation is now known to lead to an habituation of the sweating response, with more efficient rather than exaggerated sweating.
- A similar adaptation might occur with our cutaneous vasomotor responses, but we currently lack the evidence that allows that possibility to be resolved.
- In Australia, cold acclimatisation of the traditional-living, first-nations people revealed that their thermogenic metabolic responses were not elevated during cold stress. Instead, thermogenesis also became habituated.
- Those examples of physiological habituation may well occur because neural drive from the thermoregulatory centre had been turned down.
- One might anticipate sustained and powerful vasoconstriction in the hands of workers when they are repeatedly exposed to near-freezing water. Those responses also seem to habituate, which reduces their risk of local cold injuries.

Those observations, in combination with a growing awareness of heat illness and cold injuries, ignited interest in the possibility that the rapidly and artificially induced thermal adaptation (acclimation) of occupational and recreational athletes might provide both protective and ergogenic benefits. From that research, we have arrived at the following conclusions and recommendations.

- Those practices elicit rapid improvements in our thermoregulatory capabilities, with the strongest responses seen in those least adapted to those stresses.
- The most common outcome is an exaggeration of our thermoeffector responses. Those states are only a transitional phase of thermal adaptation, because long-term protection arises from mechanisms that place less demand upon our resources.
- Habituated effector responses satisfy that requirement. They impose less strain and make it less likely that our regulated variables might come into conflict.
- Acclimation-induced physiological changes are thermally protective.
- When evaluating the literature, we should examine how experimental designs and methods might introduce interpretative bias. Was the design a constant-strain or a constant-stress model? Were the pre- and post-adaptation responses evaluated at equivalent levels of the primary regulated variable (body temperature)?
- Adaptation responses are not a generalised panacea to impending strain. Instead, they are targeted to coping better with specific threats, and are exercise-intensity and climate specific.
- Improved heat tolerance can be achieved passively, but those responses may be inadequate for those who must exercise or work hard in hot environments. It remains unknown whether passively induced, constant-strain heat adaptation might provide a substitute for exercise in the heat.
- The metabolic habituation that follows cold-acclimation may not offer a significant advantage during subsequent cold exposures, except perhaps within the workplace, with reduced shivering increasing thermal comfort and facilitating fine-motor tasks.
- For cold-exposed occupational athletes, we believe more can be gained from learned behavioural responses than from autonomic adaptations, although protective advantages exist for the hands and feet following adaptation of the cold-induced vasodilatation response.

Series overview: closing remarks and concepts that did not withstand the tests of time

Our mandate within this review series was not just to record research in thermoregulation over our century of exercise physiology, but to assess whether concepts and hypotheses that arose from historical research remained valid in the light of contemporary research. Recent research has reinforced and amplified many early developments, but it has also domesticated some of those theories, just as our interpretations will be revised and corrected by future generations. Our ultimate emphasis was thermoregulation within recreational and occupational pursuits, but before evaluating and discussing the relevant basic and applied research, we reminded ourselves of the scientific foundations upon which sound research must sit. Strong foundations are associated with longevity.

Across this series, we have endeavoured to build an historical treatment founded upon first principles, since those principles govern all heat exchanges and the tools we use to quantify physiological responses to thermal and exercise stresses. Those responses determine our stress tolerance. To provide a background from which to explore thermal adaptation, we examined the possible evolutionary sequence that gave rise to *Homo sapiens* as fast endurance, sweating specialists. To bring all of those topics to life, we went beyond the science, and into the social and political climates within which our predecessors lived and worked. As one part of the antidote to scientific parochialism, we

identified and incorporated research from > 25 countries across all seven continents. Our depth of coverage was aimed at revealing the significance that thermal physiology plays as a core discipline of physiology within the basic and applied sciences, and it is hoped that we have identified some shoulders upon which younger researchers may choose to stand.

We close this series with a reminder of how far we have come today, through revisiting concepts and hypotheses that did not withstand the tests of time. We also provide some thoughts on how younger researchers might, with a view from those shoulders, develop testable hypotheses and experimental designs that will sit on strong scientific foundations.

Concepts of exercise thermoregulation that did not withstand the tests of time

Scientific progression requires the constant interrogation of past ideas, regardless of who developed those concepts and how many might still support them. Astute readers may realise that applications of thermal physiology to recreational and occupational interests often lack the scientific rigour needed to unambiguously reveal the underlying physiological mechanisms. Many of us contributed to that shortfall as we developed our skills. In concluding this series, we have identified some of the hypotheses, observations and interpretations that did not withstand the tests of time (Tables 1 and 2). Those concepts have been described within our four reviews.

How did the concepts and hypotheses of Tables 1 and 2 succumb to scientific scrutiny? Their validity was tested and re-evaluated, sometimes repeatedly, by successive generations. Scientific progression has always been contingent upon the passion and commitment of inquisitive minds. It starts with well-developed research questions and testable hypotheses driven by observational, applied or mechanistic outcomes. There is nothing wrong with observational research (*e.g.*, case reports), which can be extremely important. Many scientific breakthroughs followed on the heels of unexpected, sometimes serendipitous, observations that prompted the question: "*I wonder why that happened?*".

Much research is driven from applied perspectives, with the objective being to solve problems of practical relevance. The provision of practical solutions that can save lives must surely be as, if not more, important than the acquisition of new knowledge. However, reliable solutions will be revealed only if we investigate and understand causes and effects. If mechanistic research is the emphasis, then which aspect of physiology is of primary interest? Will the emphasis be upon physiological regulation (homeostasis) or effector control? Both are important, and from a thermoregulatory perspective, that will determine whether the focus is upon thermoreceptor function, thermoafferent signals and neural pathways, the central integration and interpretation of those messages, thermoefferent signals or thermoeffector function.

Applied and mechanistic research is best directed by experimental hypotheses that arise from research questions. In turn, those questions determine the experimental design, the measurement techniques and how the results should be analysed. No measurement should infringe first principles. We must be able to justify each measurement and how it allows us to test our hypotheses. Are those methods relevant to the application of interest? Are the experimental subjects representative of the occupational or athletic population of interest? Is that population made up of elite or average performers? For circumstances in which physiological measurements can be extremely difficult, we must dispel the notion that "*any measurement is better than no measurement*", unless that measurement can provide dynamically appropriate and valid observations of the target physiological function.

The following questions are often helpful during the development of research questions and hypotheses. What is currently known about the topic? Are there gaps within our knowledge? Do those gaps spark a research interest? Why it is important to discover that information, and how does it adds to our existing knowledge? Can we develop valid research questions that will lead to the acquisition of that knowledge? Since experimental science is generally, but not always, driven by research hypotheses, then we must determine whether logical and novel research hypotheses can be developed. Are those hypotheses testable? Testability has several aspects: appropriate experimental treatments, the right measurements, the most relevant population sample, adequate statistical power and appropriate analytical methods. Do we have the tools and expertise that will allow our hypotheses to be tested?

In the modern epoch, readers must exercise great caution when filtering contemporary publications, since "*All that glisters* [glitters] *is not gold*" (Shakespeare 1823 [P. 171]). Indeed, in the twenty first Century, the publication of one's research can now be easily achieved by those with enough money (open access) or by those whose nominated reviewers (scientific cliques) will accept, but rarely challenge, submitted manuscripts. A similar caveat applies to the overuse and misuse of systematic reviews and meta-analyses, which the current journal does not generally favour, due largely to the absence of "*an intellectual evaluation of the experimental methods and subsequent data interpretation*" (Instructions for Authors). Furthermore, sample sizes are often too small for those analyses (Dechartres et al. 2013; Cook and Hatala 2015; Møller and Myles 2016), with Yavchitz et al. (2016) finding 39 different types of author spin (over or understatements of experimental evidence) that have distorted interpretation. Accordingly, we have avoided the inclusion of

Table 1 An overview of hypotheses, concepts and interpretations concerning human thermoregulation, made before 1930, that have not withstood the tests of time

Historical concept	Origin	Implication	Modern concept
Europeans are heat intolerant	Lind (1771) [Part 4]	Europeans cannot live in the tropics	Ancestry plays little or no role in heat tolerance
All body temperature increases are pathological	de Haen (1776) [Part 2]	Elevated body temperatures during exercise are dangerous	Sustained elevations are necessary for continuous heat-loss effector activation
Exercise did not increase deep-body temperature	Davy (1844) [Part 2]	Increases in body temperature are caused by other influences	Exercise absolutely increases deep-body temperatures
Thermoregulation operates like a thermostat	Liebermeister (1860) [Part 1]	Human have fixed body temperatures for effector activation	There are no reference signals that resemble thermostat settings
Rectal temperature is the highest deep-body temperature	Bernard (1876) [Part 1]	During heat strain, all tissues have a lower temperature than the rectum	The rectum is cooler than arterial blood temperature and can be much lower than working muscle temperatures
Control centre for sweating is in the spinal cord	Luchsinger (1877) [Part 3]	The brain plays no role in thermoregulatory sweating	The centre for thermoregulation is in the hypothalamus
Exercise will not induce hyperthermia	Flint (1877) [Part 3]	Cellular metabolism does not release thermal energy	Exercise can elicit hyperthermia even in cool conditions
Control centre for cutaneous vasomotion is in the spinal cord	Ott (1879) [Part 1]	The brain has no role in thermoregulatory vasomotion	The centre for thermoregulation is in the hypothalamus
Excitatory and inhibitory neurons modulate sweating	Ott (1879) [Part 1]	Increased and reduced sweating are controlled by different neurons	Sweat glands have only excitatory neurons
Lethal sunburn and heat stroke have the same symptoms	Fayrer (1879) [Part 3]	Sunburn and heat-stroke casualties were treated similarly	Sunburn is a toxic condition, unrelated to body temperature
Darker skin loses heat more slowly	Woodruff (1900) [Part 4]	People of African ancestry lose less heat via radiation	Human skin colour has no effect on its thermal emissivity
Wet-bulb temperature predicts thermal strain	Haldane (1905) [Part 3]	Conditions with the same wet-bulb temperature are physiologically equivalent	Ignores radiant heat and air movement. It underestimates strain in very dry environments
Ice-water enemata and ice rubbing are effective treatments for exertional heat stroke	Beamish (1907) and Pattison (1920) [Part 3]	Treat heat-stroke casualties with ice and ice-cold water	Not justified on first principles, possibly dangerous and sometimes lethal
Hyperthermia especially affects brain tissue	Pembrey (1914) [Part 3]	Direct cooling of the brain should be attempted	Brain function, but not brain tissue, is especially sensitive to high temperature
Dry skin is a hallmark of heat stroke	Pembrey (1914) [Part 3]	Sweating casualties were not treated for heat stroke	Sweating may be profuse in casualties with exertional heat stroke
Tropical neurasthenia is climate induced	Taylor (1916) [Part 4]	Europeans are vulnerable to climate-induced psychological disorders	This condition does not exist
Metabolic heat production scales linearly with body mass	Harris and Benedict (1919) [Part 2]	Metabolic heat production expressed per unit body mass is size independent	Metabolic heat production scales allometrically, not linearly, with body mass
Human thermoregulation operates on an on–off basis	Barbour (1921) [Part 1]	Precise body temperature regulation would be impossible	Thermoregulation operates under proportional and rate control
Hypohydration does not affect thermoregulation	Adolph (1921) [Part 3]	Fluid replacement is not required until a significant water deficit occurs	Hypohydration does alter the relationship between body temperature and the thermoeffectors
Effective temperature is a heat-stress index	Houghten and Yagloglou (1923) [Part 3]	It has been used as an occupational heat-stress index	It is not a stress index, but an index of thermal sensation

Table 1 (continued)

Historical concept	Origin	Implication	Modern concept
Rectal temperature is equal to that of aortic blood	Bazett (1927) [Part 1]	Rectal temperature reflects temperatures of tissues well perfused by arterial blood	Rectal temperature neither equals nor correlates with arterial temperatures
Deep-body temperature is the regulated body temperature because it is more stable	Various authors [Part 1]	Deep-body thermoreceptors provide the only input to the regulatory centre	All thermosensitive tissues contribute to the regulated temperature

Part numbers identify the manuscripts from this historical series (Notley et al. 2023a [Part 1], 2023b [Part 2], 2023c [Part 3]) within which each of those concepts was first described and discussed

systematic reviews that suffer such limitations within this historical series.

Closing remarks in our changing world

The world of the twenty first Century would have been beyond the imaginations of even the most clairvoyant of those who studied thermoregulation during exercise in our first two epochs. They could not foresee our future climate. Whilst John Tyndall (Ireland) warned, in the nineteenth Century, that greenhouse gases coated the earth like a blanket, Henry G. Barbour (1921, U.S.A.) suggested that "… *man's chief enemy is the cold, and must become more so with the passing of time if the physical fate of the world be correctly predicted*" (P. 320). Within our century of exercise physiology, grave concerns were voiced for worker welfare, not from cold exposure, but because the world is warming out of control (Kjellstrom et al. 2009; Lucas et al. 2014). Athletic events are being cancelled due to the heat. Heat waves like those that caused so many deaths during the nineteenth Century are occurring, and are becoming commonplace, even in countries with temperate climates (Perčič et al. 2018; Zhang et al. 2018; Oudin et al. 2020; Schneider and Mücke 2021). Thermal physiology is becoming the physiology of extremes (Kenney et al. 2004), and our best indices of heat stress are proving unreliable in hot-dry conditions.

Outdoor competitions, when conducted in summer, may become night events, and winter events may be abandoned as it becomes impossible to maintain snow slopes. Totally foreign to our predecessors would have been the prospect of medical tents prepared for the treatment of heat stroke during contemporary marathons. The possibly clairvoyant physiologist, Marcus Pembrey, would have welcomed support from physiologists as he fought to persuade the British Army to provide adequate drinking water to soldiers in the heat (Pembrey 1914). But neither Pembrey nor Edward Adolph (U.S.A.) would have foreseen that, within the next century, there would be thermal physiologists debating the degree to which hypohydration affected human thermoregulation, how it affected exercise performance independently of the effects on body temperature, and how hypohydration could be combatted without compromising either thermoregulation or body-fluid regulation.

T. Clifford Allbutt (1836–1925, England) invented the clinical thermometer, yet 150 years later, contemporary thermal physiologists cannot reliably detect hyperthermia and hypothermia in occupational and recreational athletes in the field unless they are hard-wired. During maximal exercise and all non-steady states, rectal temperature is of very limited value as an index of human deep-body temperatures. Remote measurements of deep-body temperature in exercising humans are confined to ingestible devices that traverse

Table 2 Some hypotheses, concepts and interpretations relating to exercise in thermally stressful conditions, published after 1930, that have not withstood the tests of time

Historical concept	Origin	Implication	Modern concept
High deep-body temperatures set limits for exercise	Christensen (1931) [Part 2]	There was a fatigue-related critical body temperature	There is no self-protective, thermal barrier to exercise
High salt intakes may prevent heat illness when working in the heat	Bock and Dill (1933) [Part 3]	Salt supplementation improves performance during exercise in the heat	Standard (dietary) sodium intakes are sufficient in most instances
Heat storage can be estimated from a weighted summation of tissue temperatures	Burton (1935) [Part 2]	Thermometry can be used to estimate whole-body heat storage	Whole-body heat storage cannot be calculated from any combination of body temperatures
Evaporative cooling rate is proportional to the rate of body-mass loss	Gagge (1936) [Part 2]	One can quantify evaporative heat loss from body-mass changes	To determine evaporative heat loss, unevaporated sweat must be quantified
Biophysical modelling can be used to estimate heat exchange	Gagge et al. (1938) [Part 2]	Dry, evaporative and respiratory heat exchanges can be estimated using heat-transfer equations	Biophysical modelling has significant limitations and cannot (yet) replace calorimetry
Skin temperatures are independent of the external work rate	Nielsen (1938) [Part 2]	Thermal responses of deep-body and skin tissues are independent	Skin temperatures track changes in work rate until the skin is fully wet
Exercising deep-body temperatures are independent of the thermal loads between 5 and 30 °C	Nielsen (1938) [Part 2]	Exercise intensity alone dictates the deep-body temperature	Deep-body temperature is determined by both exercise intensity and the ambient thermal load
Women sweat less than men during heat exposure	Hardy and Dubois (1940) [Part 3]	Women have a thermoregulatory disadvantage during heat stress	Sex differences in thermoregulation are predominantly morphologically related
Plasma volume expansion represents a transient phase of heat adaptation	Taylor et al. (1943a) [Part 4]	Plasma volume always decreases as heat acclimation continues	Plasma volume does not decrease when constant-strain heat acclimation is used
The wind-chill index can be used to predict the risk of hypothermia	Siple and Passel (1945) [Part 3]	Wind-chill equivalent temperatures can be used to guide safe work and exercise in the cold	The wind-chill index should be used only to predict the risk of a frostbite
Deep-body temperature is lower following upper- than lower-body exercise	Asmussen and Nielsen (1947) [Part 2]	Less heat is generated from upper-body exercise	Deep-body thermal responses are mode specific, but work-rate dependent
Arctic hysteria is climate induced	Aberle (1952) [Part 4]	Arctic hysteria is a climate-induced psychological disorder	This condition does not exist
The Wet-Bulb Globe Temperature index can predict heat-casualties risks	Yaglou and Minard (1957) [Part 3]	The index has been widely endorsed and must therefore be valid	The WBGT index is an unvalidated index of thermal stress
Thermoeffector activation in the heat can be modulated by skin sensors, but only by our cold receptors	Benzinger (1961) [Part 1]	Heat-sensitive thermoreceptors do not modify effector activity in the heat	Both heat- and cold-sensitive receptors modify thermoeffector activity
Non-shivering thermogenesis does not occur in adults	Dawkins and Hull (1965) [Part 3]	Adults produce heat only through skeletal-muscle activation	Non-shivering thermogenesis does occur in adults
Thresholds for thermoeffector activation imply that reference signals (*set-points*) exist	Hardy (1965) [Part 1]	Thermally insensitive neurones in the hypothalamus generate a neural *set-point*	There are no neural *set-point* generators
Deep-body temperature is more tightly linked to the relative than to the absolute exercise intensity	Saltin and Hermansen (1966) [Part 2]	One can standardise exercise intensities across individuals using relative intensities	Metabolic heat production is dictated by the absolute work rate. Heat loss is determined by its relative intensity
Heat acclimation is accompanied by a redistribution of sweat secretion	Höfler (1968) [Part 4]	Redistribution is to the limbs due to their anatomical potential for evaporative cooling	Heat acclimation is accompanied by greater sweating at sites with lower initial sweat rates
Humans can cool their brains selectively	Cabanac and Caputa (1979) [Part 1]	Human hypothalamic temperature can be cooler than arterial-blood temperature	Humans do not have selective brain cooling

Table 2 (continued)

Historical concept	Origin	Implication	Modern concept
Cutaneous vasodilatation is maximal when the skin is heated to 42 ℃	Taylor et al. (1984) [Part 2]	Skin heating alone can induce maximal cutaneous blood flow	Maximal cutaneous vasodilatation cannot occur unless the deep-body temperature is elevated
The effect of ice-water immersion on cutaneous vasomotor function during hyperthermia is relatively negligible	Noakes (1986) [Part 3]	Body cooling of hyperthermic individuals is achieved best by ice-cold water immersion	Even cool-water immersion causes vasoconstriction. There is no evidence that a practically meaningful reduction in cooling occurs in ice water
Whole-body pre-cooling delays elevations in tissue temperatures	Various authors [Part 1]	Pre-cooling delays hyperthermia-related performance decrements	Pre-cooled tissues reach the same temperatures at about the same time as tissues that are not cooled
Local sweat rates reflect whole-body sweating	Various authors [Part 2]	Single-site measurements can provide valid whole-body information	Extrapolation of local sweat rates rarely gives an accurate estimate of whole-body sweat rate
Sweat-electrolyte concentrations on their own are physiologically useful	Various authors [Part 2]	Electrolyte concentrations provide interpretable and actionable information	Sweat-electrolyte concentrations are meaningful only if reported with sweat rates

Part numbers identify the manuscripts from this historical series (Notley et al. 2023a [Part 1], 2023b [Part 2], 2023c [Part 3]) within which each of those concepts was first described and discussed

the gastrointestinal tract, and provide data which not everyone considers useful.

Our forebears experienced the infection pandemic which still holds the record for causing the greatest number of deaths; the Spanish (American) Flu of 1918. They would have been astounded that so little had been learned from pandemics over the ensuing century that the world would be devastated by a coronavirus pandemic in 2020. They would be stupefied to see thermal physiologists reminding medical practitioners and politicians that forehead skin temperature have minimal, if any, usefulness as screening tools for fevers (Mercer and Ring 2009; Fuller and Mitchell 2020; Mekjavic and Tipton 2021; Fisher et al. 2022).

Blessed with a similar lack clairvoyance, not to mention our other limitations, the authors will be sorry to miss the scientific discoveries that will occur over the next century of exercise physiology. Unfortunately, our World is rapidly warming towards an increasingly less tolerable, and eventually intolerable habitat. Despite our current efforts, or perhaps because of their inadequacy, our descendants can expect to experience continued increases in the frequency and severity of extreme weather, which will create increasing economic and health burdens that will have an adverse impact on the quality of all life. We can be certain, therefore, that the work of thermal physiologists will be more important than ever, and we hope that importance will be reflected in the priorities of governments and funding agencies.

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Declarations

Conflict of interest There are no conflicts of interest.

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