


Dry and humid heat acclimation induces similar adaptations and cross-acclimation benefits in trained male cyclists

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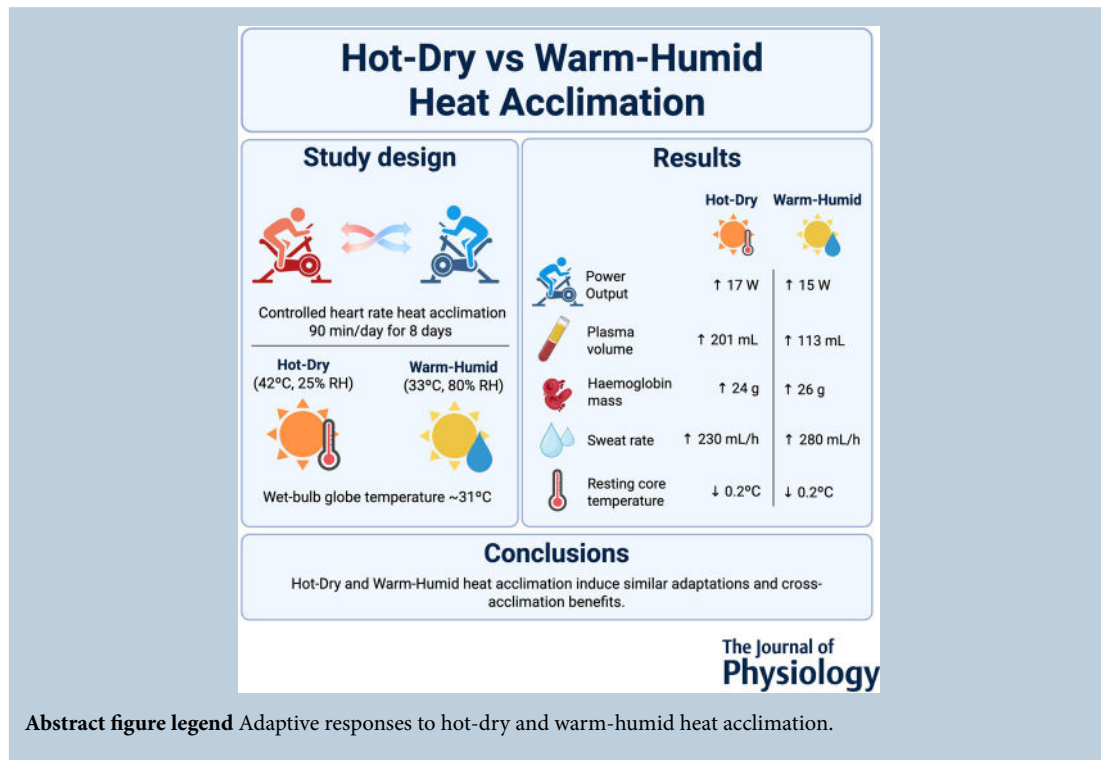
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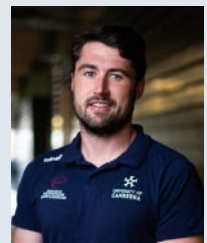
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Peter McDonald is a lecturer in the School of Medical Sciences at the University of Sydney, Australia. He completed his PhD under the supervision of Professor Julien Périard at the University of Canberra Research Institute for Sport and Exercise, where his research investigated the influence of heat acclimation protocol characteristics on the adaptive response. His research interests include human heat adaptation and the underpinning mechanisms, alongside optimising student engagement and academic success in health and medical education.



Abstract This study compared adaptive responses and cross-acclimation between dry and humid heat acclimation (HA). In a cross-over design, trained males completed a heat stress test in hot-dry (Dry-HST: 42°C, 25% relative humidity [RH]) and warm-humid (Humid-HST: 33°C, 80% RH) conditions before and after 8 days of controlled heart rate (HR) HA in hot-dry (Dry-HA, $n = 10$) and warm-humid (Humid-HA, $n = 12$) environments (wet-bulb globe temperature: $\sim 31^\circ\text{C}$). Bayesian multi-level models were used to determine posterior means and 90% credible intervals. Mean power output increased similarly during Dry-HA and Humid-HA but was higher throughout Dry-HA (13 W [6, 20]). Sweat rate increased during both regimens but was higher throughout Dry-HA (100 mL \cdot h $^{-1}$ [20, 180]). Plasma volume expanded with Dry-HA (201 mL [71, 324]) and Humid-HA (113 mL [-5, 232]), as did haemoglobin mass (24 g [2, 46] and 26 g [6, 47]). During the Dry-HST, end-exercise rectal temperature changed by -0.2°C ($-0.3, -0.1$; Dry-HA) and -0.3°C ($-0.4, -0.2$; Humid-HA), and during the Humid-HST by -0.3°C ($-0.4, -0.2$; Dry-HA) and -0.1°C ($-0.2, 0.0$; Humid-HA). HR changed by -2 beats \cdot min $^{-1}$ ($-5, -1$; Dry-HA) and -5 beats \cdot min $^{-1}$ ($-9, -2$; Humid-HA) during the Dry-HST, and by -6 beats \cdot min $^{-1}$ ($-9, -4$; Dry-HA) and -1 beats \cdot min $^{-1}$ ($-4, -2$; Humid-HA) during the Humid-HST. Our data indicate that Dry-HA and Humid-HA induced similar adaptations, despite work rate and sweat rate being higher during Dry-HA. Cross-acclimation benefits were also similar between interventions. The adaptive stimulus to heat stress, whether dry or humid, appears more impactful on the exercise-HA phenotype than the specificity of the environment.

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Key points

- The adaptive response to dry and humid heat remains poorly understood, as are the cross-acclimation benefits between these environments.
- A cross-over design approach was used to compare the adaptive response to hot-dry and warm-humid heat acclimation (HA), and the cross-acclimation provided by each environment.
- The negligible physiological differences observed between dry and humid HA regimens suggest that the specificity of the environmental characteristics was overshadowed by the overall adaptive stimulus (controlled heart rate [HR] HA).
- The greater work rate sustained for a similar HR, rectal temperature, rating of perceived exertion and thermal comfort during dry compared to humid HA highlights that drier conditions may better preserve physical training quality.
- Athletes, soldiers and workers may use dry heat to optimise preparation for competition and work in both dry and humid heat, with the possibility of habituating to humid heat in the final few acclimation sessions if such conditions are anticipated.

Introduction

Dry and humid environmental heat stress exacerbates the development of thermal and cardiovascular strain during exercise and occupational tasks (Périard et al., 2021; Rowell, 1974), which leads to performance impairments and increases the risk of exertional heat illness (Flouris et al., 2018; Mantzios et al., 2022; Roberts et al., 2021). However, heat acclimation (HA) can be undertaken prior to competing or working in the heat to induce adaptations that reduce physiological strain and exertional heat illness

risk (Périard et al., 2015; Racinais et al., 2015; 2023). Heat adaptations are typically characterised by an increased plasma volume (PV) and enhanced sweating and skin blood flow responses that lead to circulatory stability (i.e. lower heart rate [HR]) and reduced thermal strain (i.e. lower core temperature and skin temperature) during exercise at a given work rate (Périard et al., 2015; Sawka, 1996).

To optimise heat adaptations, athletes and military/occupational personnel are generally recommended to acclimate in an environment similar to the one they anti-

cipate competing or working in (Guy et al., 2015; Périard et al., 2015; Racinais et al., 2015). This recommendation is based on the principle of training specificity (Taylor, 2014), along with suggestions that heat adaptations are specific to the environmental characteristics in which they are induced (i.e. dry or humid) (Frye & Kamon, 1983; Shvartz et al., 1973). For example, it has been suggested that the primary adaptative pathway of HA is an enhanced sweating response (i.e. onset threshold and sensitivity) (Bass, 1963; Eichna et al., 1950; Sawka & Coyle, 1999), which benefits evaporative heat loss in dry environments. In contrast, it has been proposed that vascular expansion (i.e. PV) and concomitant circulatory stability (Bass et al., 1955; Senay et al., 1976) are principal adaptations, which under humid heat stress would support dry heat loss. However, few studies have investigated these pathways and most prior investigations comparing dry and humid HA failed to match environmental heat stress between conditions (Fox et al., 1967; Nielsen et al., 1993; Nielsen et al., 1997), and/or employed low exercise intensities (25%–35% peak oxygen uptake: $\dot{V}O_{2\text{peak}}$) (Griefahn, 1997; Shvartz et al., 1973) to drive the adaptive response. Therefore, evidence to support the suggestion that HA adaptations are specific to environmental conditions remains ambiguous, as do the underpinning pathways driving environment-specific adaptations (Sawka & Coyle, 1999).

To the best of our knowledge, only four studies have directly compared the influence of different temperature and humidity combinations on the adaptive response (Fox et al., 1967; Griefahn, 1997; Shvartz et al., 1973; Tebeck et al., 2020), with two others adopting a similar design in high- (Nielsen et al., 1997) and low-humidity environments (Nielsen et al., 1993). Early findings from Fox et al. (1967) indicated similar increases in sweat loss and reductions in aural temperature and HR after exercise in 40°C and 3.5 kPa conditions following dry (45–55°C, 1.9–2.4 kPa) and humid (49°C, wearing water-barrier suit) HA. Conversely, skin temperature was reduced to a greater extent after dry HA. Griefahn (1997) reported similar changes in rectal temperature (T_{re}), HR and sweat loss after 15 days of constant work rate exercise in dry (50°C and 1.9 kPa) and humid (37°C and 5.0 kPa) conditions matched for wet-bulb globe temperature (WBGT: $\sim 34^\circ\text{C}$). In contrast, Shvartz et al. (1973) demonstrated greater reductions in T_{re} and HR during a heat stress test (HST) at 50°C and 3.6 kPa after HA in the same conditions, compared to a more humid regimen (37°C, 5.7 kPa) of similar WBGT ($\sim 35^\circ\text{C}$). More recently, greater reductions in HR and gastrointestinal temperature were reported after humid (32°C and 3.8 kPa) compared to dry (43°C and 1.7 kPa) HA, with both regimens using a matched WBGT of $\sim 31^\circ\text{C}$ (Tebeck et al., 2020). However, only dry HA tended to improve sweat rate (Tebeck et al., 2020). In two separate studies, Nielsen et al.

(1993, 1997) demonstrated a 51% greater improvement in time to exhaustion during 9–12 consecutive days of HA in dry heat (41°C, 0.97 kPa, 34°C WBGT) compared to 8–13 days of HA in humid heat (35°C, 5.0 kPa, 27°C WBGT), despite a larger improvement in sweat rate in the latter (17% vs. 24%). Taken together, it is clear that the specificity of adaptations to dry and humid heat has not been fully elucidated. Moreover, the environment in which adaptations were assessed in previous studies may have influenced the findings, with testing typically undertaken in only one condition (i.e. either dry or humid) (Nielsen et al., 1993; Nielsen et al., 1997; Tebeck et al., 2020), leading to a potential bias in the magnitude of adaptation detected. Therefore, it remains to be determined how adaptations specific to a particular environment carry over to an environment with different heat stress characteristics (i.e. cross-acclimation).

The issue of cross-acclimation (i.e. transfer of beneficial adaptations from a given heat stress condition to another) between dry and humid heat has great importance for sports medicine, military and occupational settings. Indeed, athletes, soldiers and workers may have prior exposure to one of these environments but be required to travel/deploy to compete or work in the other. Therefore, the aim of this study was to evaluate the probability that HA in hot-dry and warm-humid environments produces environment-specific thermoregulatory, cardiovascular, perceptual and haematological adaptations, and the extent to which these adaptations transfer between environments (i.e. cross-acclimation).

Methods

Ethical approval

This study was approved by the University of Canberra Human Research Ethics Committee (project ID: 20229212) and conducted in accordance with the *Declaration of Helsinki* except for registration in a clinical trials database.

Participants

Twelve endurance-trained (tiers 2–3) male cyclists or triathletes (De Pauw et al., 2013; McKay et al., 2022) participated in this study (Table 1), with 10 completing both HA interventions and 2 completing only humid HA due to personal circumstances. Due to our comparison of two HA interventions, rather than to a control condition, a formal *a priori* sample size calculation was not performed. Instead, sample size was based on previous studies comparing HA interventions over a similar time frame (Garrett et al., 2014; Gerrett et al., 2021; Lundby et al., 2021; Tebeck et al., 2020; Travers,

Table 1. Participant characteristics for hot-dry (Dry-HA) and warm-humid (Humid-HA) heat acclimation

	Dry-HA (n = 10)	Humid-HA (n = 12)
Age (year)	43 ± 9	42 ± 10.
Height (cm)	183.1 ± 5.5	181.8 ± 7.2
Body mass (kg)	81.3 ± 6.6	80.2 ± 8.3
$\dot{V}O_{2peak}$ (mL·kg ⁻¹ ·min ⁻¹)	59.2 ± 7.0	60.5 ± 6.1
Peak power output (W)	389 ± 31	396 ± 50
Training volume pre-HA (min·wk ⁻¹)	530 ± 236	476 ± 200
Training volume during HA (min·wk ⁻¹)	565 ± 167	537 ± 247

Note: Data are mean ± SD.

Abbreviations: HA, heat acclimation; training volume during HA, average weekly training volume during the intervention inclusive of pre- and post-testing and HA sessions; training volume pre-HA, average weekly training volume during the 4 weeks prior to the intervention; $\dot{V}O_{2peak}$, peak oxygen uptake.

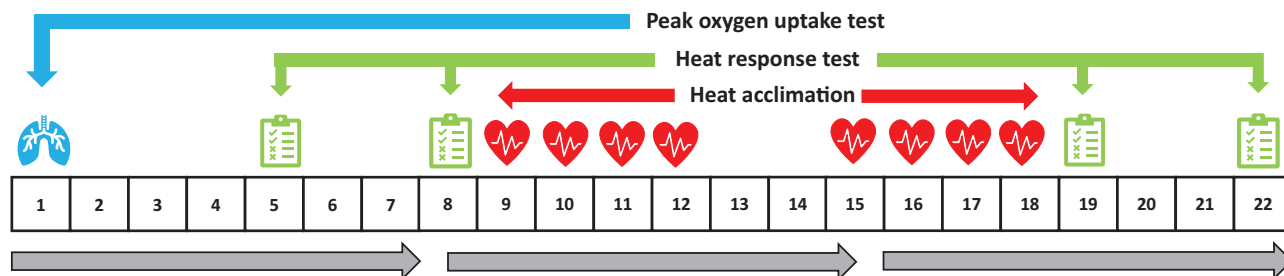
Nichols, et al., 2020). Participants had a minimum of 3-year cycling experience and regularly trained ≥ 4 h per week. Training volume was recorded for the 4 weeks preceding each HA intervention and during the intervention period (Table 1). All participants completed a pre-exercise screening questionnaire (Exercise and Sport Science Australia Adult Pre-Exercise Screening Tool) and provided written informed consent before study commencement. Experimental testing was conducted outside of the summer months between April and November in Canberra (Australia) to minimise the confounding influence of seasonal heat acclimatisation.

Experimental design

Two HA interventions using the controlled HR approach (Périard et al., 2015) were completed in a randomised cross-over design, with a minimum seven-week washout period between interventions (24 ± 17 weeks). Hot-dry HA (Dry-HA) was undertaken at $41.5 \pm 1.2^\circ\text{C}$, $25.4 \pm 1.7\%$ relative humidity (RH; 2.03 ± 0.16 kPa) and warm-humid HA (Humid-HA) at $32.9 \pm 0.4^\circ\text{C}$,

$81.5 \pm 1.1\%$ RH (4.06 ± 0.10 kPa) for a matched WBGT of $\sim 31^\circ\text{C}$. Prior to commencing each HA intervention, participants completed a $\dot{V}O_{2peak}$ test in temperate conditions (22°C , 50% RH; Fig. 1). The $\dot{V}O_{2peak}$ tests consisted of four submaximal stages starting at 80 or 115 W and increasing by 35 W every 4 min. Immediately after the final submaximal stage, work rate increased by $25 \text{ W}\cdot\text{min}^{-1}$ until volitional exhaustion. HR was recorded throughout (RS400, Polar, Kempele, Finland), and expired gases were collected via a one-way valve (Hans Rudolph Inc., Shawnee, KS, USA) and analysed using a stationary metabolic gas analyser (TrueOne, Parvomedics, Sandy, UT, USA). $\dot{V}O_{2peak}$ was calculated as the highest 45-s rolling average, whereas $\dot{V}O_2$ and HR during each submaximal stage were averaged over the final 60 s of each stage. These data were used to calculate the target work rate and HR for the HST and HA sessions via linear regression of the $\dot{V}O_2$ -power and $\dot{V}O_2$ -HR relationships, respectively.

On separate visits, participants completed a HST in hot-dry (Dry-HST: $40.3 \pm 1.3^\circ\text{C}$, $24.5 \pm 2.9\%$ RH, 1.84 ± 0.24 kPa) and warm-humid conditions

**Figure 1.**

Schematic overview of the study design for cross-over heat acclimation (HA) in hot-dry and warm-humid conditions. Peak oxygen uptake testing was conducted in temperate conditions, with a heat stress test (HST) conducted in hot-dry and warm-humid conditions. The HST on day 5 was always conducted in the environment opposite to the HA intervention, with the HST on day 8 taking place under the same environmental conditions as the HA intervention. Post-intervention HSTs on days 19 and 22 were counterbalanced. Days 6, 7, 13, 14, 20 and 21 were intervention-free days.

(Humid-HST: $32.4 \pm 0.8^\circ\text{C}$, $80.5 \pm 0.8\%$ RH, 3.93 ± 0.17 kPa). These tests were repeated after HA. The HA intervention consisted of 4 days of controlled HR exercise followed by 2 days of rest, and then another 4 days of HA. The second HST during pre-testing was conducted in the environmental conditions in which HA was undertaken to ensure 9 days of exposure to that environment during HA. The post-HA HSTs were conducted in a counterbalanced order (Fig. 1). All HA exposures, $\dot{V}\text{O}_{2\text{peak}}$ and HST were completed on a cycle ergometer (SRM, GmbH, Jülich, Germany) with a facing airflow of $\sim 3 \text{ m}\cdot\text{s}^{-1}$ (Dynabreeze, FA-23105, Regency Park, South Australia). The time of day for all experimental trials was held constant within each participant.

Heat stress tests

After having arrived at the laboratory at a similar time of day (± 2 h), participants provided the clothing they were to exercise in, which were weighed. Participants then self-inserted a single-use general-purpose probe (TM400, Covidien, Mansfield, MA, USA) to a depth of 10 cm past the anal sphincter to measure T_{re} (Squirrel SQ2010, Grant Instruments, Cambridge, England) and provided a urine sample to assess urine-specific gravity (USG; PEN-Urine S.G., Atago Co. Ltd, Tokyo, Japan). If USG was > 1.025 , participants were considered hypohydrated (Kenefick & Cheuvront, 2012) and consumed $5 \text{ mL}\cdot\text{kg}^{-1}$ of water. Participants were then weighed on a platform scale (KW Industrial Platform Scales, Atweigh, VIC, Australia) wearing the clothing that had been weighed. Following this, participants sat outside the environmental chamber (22°C , 50% RH) while being fitted with four skin temperature sensors (iButtons, Maximum Integrated Products, San Jose, CA, USA) to determine mean skin temperature (T_{sk}) as per Ramanathan (1964). A HR sensor (Wahoo TICKR, Atlanta, GA, USA) and two absorbent patches (5×7 cm, Tegaderm, 3M, USA) were placed on the forearm (dorsal, 1 cm from the elbow) and upper back (superior to the scapula, ~ 15 cm lateral to the vertebral column) to collect sweat for subsequent measurement of sweat sodium concentration ($[\text{Na}^+]$). Participants were then seated for 5 min to determine baseline HR, T_{re} and T_{sk} .

Participants then entered the environmental chamber and sat on the cycle ergometer, where local sweat rate (LSR) capsules were affixed to the upper back (~ 5 cm above the scapular spine) and forearm (~ 5 cm distal to the antecubital fossa) using surgical tape (Transpore 3M, North Ryde, Australia). Anhydrous air was passed through each capsule at a flow rate of $\sim 500 \text{ mL}\cdot\text{min}^{-1}$, with the temperature and humidity of the outgoing air measured using a factory-calibrated capacitance hygrometer (HMT333, Vaisala, Vantaa, Finland). LSR was

determined by calculating the product of flow rate and the difference in absolute humidity between effluent and influent air, normalised to the skin surface area beneath the capsule (4.0 cm^2).

Participants rested for 5 min in the environmental chamber before commencing the 45-min HST at a work rate equivalent to 65% of $\dot{V}\text{O}_{2\text{peak}}$ measured in cool conditions. HR, T_{re} , T_{sk} and LSR were recorded continuously. Thermal comfort (Bedford, 1936) and sweating sensation (Vokac et al., 1976) were recorded at baseline and every 10 min during exercise from 5 min onwards, whereas rating of perceived exertion (RPE; Borg, 1998) was recorded every 10 min during the exercise. At the end of the HST, the absorbent patches were removed and placed inside 5 mL syringes to squeeze the sweat into a sample tray (4.5×4.5 cm) and left to sit at room temperature as per the manufacturer's instructions. Samples were measured in triplicate using pre-calibrated biosensor strips (MX3 Diagnostics Inc., Melbourne, Australia), with additional samples taken if prompted due to the coefficient of variation being greater than 10%. A recent study of the MX3 system demonstrated a single-trial sweat $[\text{Na}^+]$ coefficient of variation of 5.6% and a standard error of measurement of $3.3 \text{ mmol}\cdot\text{L}^{-1}$ (Brown et al., 2024). Whole-body sweat rate (WBSR) was estimated by measuring the change in body mass from pre- to post-exercise (measured in duplicate), accounting for the sweat trapped in clothing, fluid consumed and exercise time.

Heat acclimation

HA sessions consisted of 90 min of cycling, with each session commencing with an initial 15 min at a power output equivalent to 65% $\dot{V}\text{O}_{2\text{peak}}$ (210 ± 28 W) measured in cool conditions. Thereafter, power output was manually adjusted to elicit a HR equivalent to 65% $\dot{V}\text{O}_{2\text{peak}}$ (final 75 min). Power output was adjusted when HR was ± 2 beats $\cdot\text{min}^{-1}$ from the target HR for > 120 s. Participants were instructed to maintain a steady cadence (≥ 80 rpm) throughout each HA session. Participants were given a volume of water to consume based on replenishing 80% of the previous-session WBSR (adjusted daily) in six aliquots every 15 min. HR, T_{re} , T_{sk} , thermal comfort, sweating sensation and RPE were measured similarly to the HST throughout each 90-min HA session.

Haematological measures

On two occasions before commencing the study, participants attended the laboratory to determine haemoglobin mass (Hb_{mass}) using the optimised carbon monoxide (CO) rebreathing method (Schmidt & Prommer, 2005). The typical error calculated on

all duplicate pre-Hb_{mass} measurements was 1.3%, corresponding to ~13 g (Dry-HA: 1.2% and 12 g; Humid-HA: 1.4% and 15 g). After 15 min of seated rest, participants fully exhaled into a CO gas metre (CO-220 CO Meter, Fluke, Everett, WA, USA) to record baseline CO levels. Finger prick capillary blood samples (200 µL) were then taken and analysed in quintuplicate for baseline carboxyhaemoglobin concentration (OSM3 Hemoximeter, Radiometer, Copenhagen, Denmark) and in quadruplicate for haematocrit (75 µL capillary tubes) using a centrifuge. Participants then fully exhaled residual volume into a spirometer and inhaled a mixture of ~3 L of O₂ and CO (1.0 mL.kg⁻¹), which was held in the lungs for 10 s. Participants then rebreathed the O₂-CO gas mixture for 110 s. At the end of this rebreathing procedure, participants fully exhaled into the spirometer, providing a sample to calculate the amount of CO not absorbed. Participants exhaled again into the CO gas metre after 4 min to assess changes in CO residual volume, followed by a capillary fingertip blood sample taken at 7 min to assess post-carboxyhaemoglobin concentration. Total blood volume (BV), red blood cell volume (RCV) and PV were calculated from Hb_{mass} and haematocrit (Burge & Skinner, 1995).

Data analysis

Bayesian hierarchical generalised additive models (HGAMs) (Pedersen et al., 2019) were employed to compare changes in HR, T_{re} and T_{sk} throughout the 45-min HST. The condition (Dry-HA or Humid-HA), HA time frame (pre or post) and HST timepoint (5–45 min) were entered as predictor variables, with an interaction term placed on condition-by-HA time frame. Smooth terms were placed on time and condition for HR, T_{re} and T_{sk} due to the known non-linear relationship in HA adaptations. This was implemented using penalised smoothing splines to allow the relationship to be informed from the data (Wood, 2004) and prevent overfitting (Mundo et al., 2022). RPE, thermal comfort and sweating sensation were also analysed using a Bayesian HGAM with a β -binomial distribution as the variables were defined as categorical. Bayesian linear hierarchical models (BLHMs) were employed to analyse pre-to-post HST changes in resting T_{re} , resting HR, WBSR, upper-back and forearm LSR and sweat [Na⁺]. Haematological variables were also measured using a BLHM model, with data from the duplicates taken pre-HA averaged. Resting T_{re} and resting HR data from the HST were averaged over the two pre- and post-tests. Upper-back and forearm sweat [Na⁺] were averaged per site and then combined to a single value per participant. Predictors for these models were condition (Dry-HA or Humid-HA) and HA time frame (pre or post), with an interaction term of condition-by-HA time frame.

For the HA sessions, similar to the HST, a Bayesian HGAM was used to compare changes in HR, T_{re} , T_{sk} , power output, RPE, thermal comfort and sweating sensation during the HA sessions, whereas a BLHM was employed to analyse WBSR and fluid consumption. Predictors for these models were condition (Dry-HA or Humid-HA) and HA day (days 1–8), with an interaction term placed on condition-by-HA day. Timepoint (0–90 min) was included as a predictor in the HGAM models, with a smooth term placed on HR, T_{re} , T_{sk} and power output.

A random intercept was included for each participant in all HGAM and BLHM models to account for the individual variability between participants. Models were implemented using 'brms' package (Bürkner, 2017) via R software (Team RDC, 2009) in RStudio (version 4.3.3). Model convergence was assessed using the Rhat statistic and the effective sample size using Markov Chain Monte Carlo sampling (Vehtari et al., 2021). Graphics were developed via the 'ggplot2' package (Wickham, 2016). Descriptive data are presented as mean \pm SD, with data from the models presented as posterior means with 90% credible intervals (CrIs) and probability of direction (Pd) statements. The Pd was calculated as the percentage of the posterior draws that crossed zero, relative to the total number of samples, and represents the probability that the change is positive (i.e. >0) or negative (i.e. <0). Priors were set as normally distributed and intended to be weakly informative for all outcome variables, whereas flat priors were placed on smooth terms (Gelman, 2006). For all statistical analyses, $n = 12$ for Dry-HA and $n = 10$ for Humid-HA.

Results

HA responses

The change in HR after the initial 15 min of constant work rate exercise was -3 beats.min⁻¹ (-7 , 0; Pd = 93%) on day 8 compared to day 1 in Dry-HA and -3 beats.min⁻¹ (-7 , 0; Pd = 94%) with Humid-HA. Mean HR over the final 75 min of exercise across the 8 days of HA averaged 143 beats.min⁻¹ (122, 159) during Dry-HA and 142 beats.min⁻¹ (121, 158) during Humid-HA. Mean T_{re} over the final 75 min of exercise was similar on day 1 during Dry-HA (38.5°C [38.1, 38.9]) and Humid-HA (38.5°C [38.1, 38.9]), remaining similar on day 8 (Dry-HA: 38.4°C [38.1, 38.9]; Humid-HA: 38.4°C [38.1, 38.9]). Mean T_{sk} over the final 75 min of exercise was 2.1°C (1.8, 2.4; Pd > 99%) higher throughout Dry-HA (36.4°C [35.6, 37.2]) compared to Humid-HA (34.3°C [33.5, 35.0]) and did not change in either condition.

Mean power output over the final 75 min of exercise was 13 W (6, 20; Pd = 97%) higher throughout Dry-HA (196 W [132, 234]) compared to Humid-HA (183 W [120,

221]; Fig. 2A). Notwithstanding, power output increased by 17 W (10, 24; Pd > 99%) with Dry-HA and 15 W (9, 22; Pd > 99%) with Humid-HA on day 8 compared to day 1 (Fig. 2A). The change in WBSR on day 8 relative to day 1 was 230 mL·h⁻¹ (140, 320; Pd > 99%) with Dry-HA and 280 mL·h⁻¹ (200, 360; Pd > 99%) with Humid-HA (Fig. 2B), with a difference of 50 mL·h⁻¹ (-70, 170; Pd = 76%) between conditions. WBSR was 100 mL·h⁻¹ (20, 180; Pd = 96%) higher throughout Dry-HA (1730 mL·h⁻¹ [920, 2430]) than Humid-HA (1630 mL·h⁻¹ [830, 2320]). Fluid consumption from days 1 to 8 increased from 2050 mL (520, 2910) to 2480 mL (950, 3350) in Dry-HA, and from 1890 mL (360, 2500) to 2040 L (510, 2900) in Humid-HA.

Mean RPE was similar from day 1 (12.3 [10.3, 13.8]) to day 8 (12.5 [10.5, 14.0]) in Dry-HA and Humid-HA (12.4 [10.4, 13.8] to 12.4 [10.4, 13.8]). Mean thermal comfort during Dry-HA changed by -0.3 (-0.6, -0.0; Pd = 98%) from day 1 (6.1 [4.9, 6.8]) to day 8 (5.8 [4.5, 6.7]) but was similar during Humid-HA (5.9 [4.5, 6.7] to 5.9 [4.6, 6.8]). Mean sweating sensation was similar on days 1 and 8 during Dry-HA (3.7 [2.1, 5.0] to 3.9 [2.3, 5.0]) and Humid-HA (4.2 [2.6, 5.0] to 4.2 [2.6, 5.0]). On days 1 and 8 of HA, mean sweating sensation was 0.5 (0.3, 0.8; Pd > 99%) and 0.3 (0.0, 0.6; Pd = 98%) higher during Humid-HA than Dry-HA, respectively.

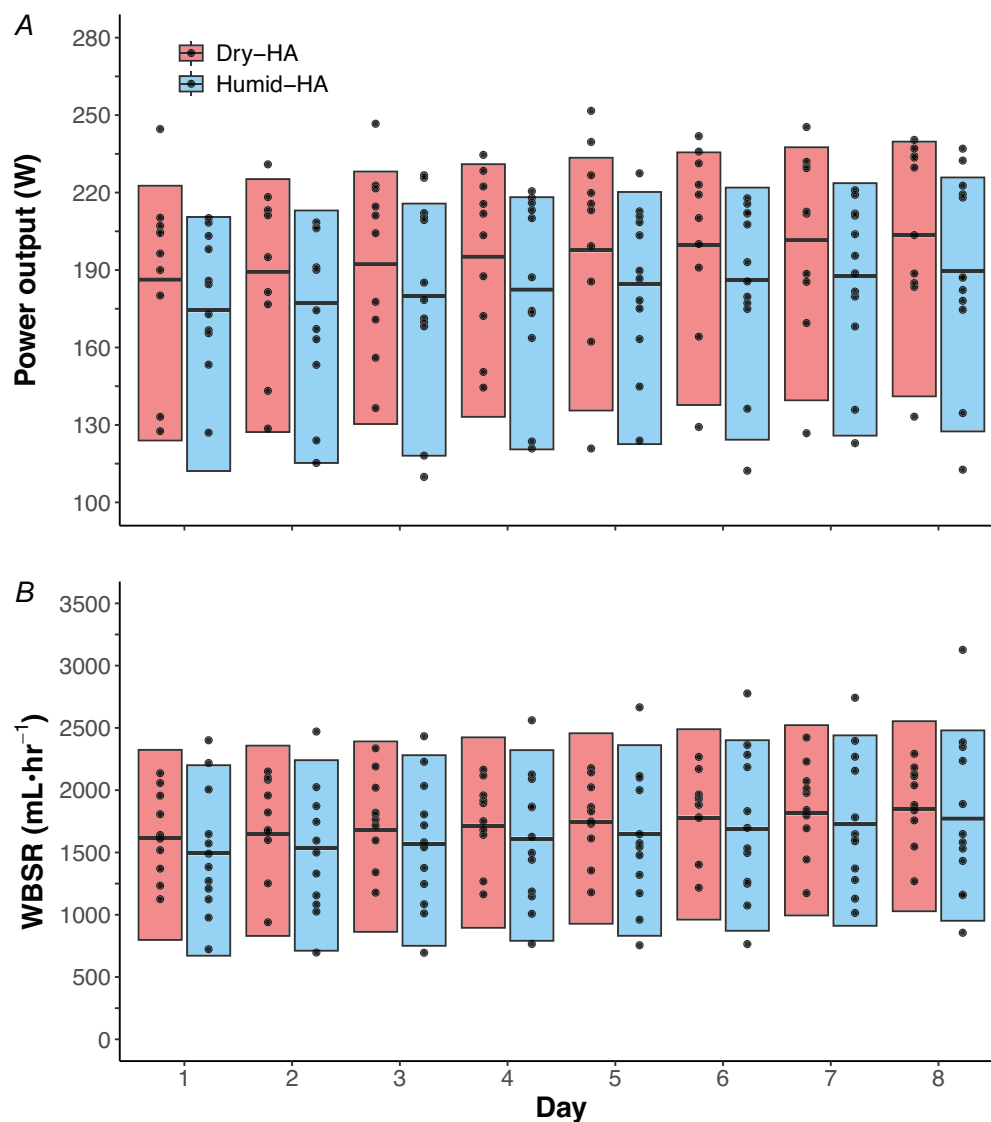


Figure 2.

A, mean 75-min power output and B, whole-body sweat rate (WBSR) during 8 days of controlled heart rate heat acclimation (HA) in a hot-dry (Dry-HA, $n = 10$) and warm-humid (Humid-HA, $n = 12$) environment. Data are presented as posterior mean with 90% credible intervals and individual observations.

Resting responses

Resting T_{re} changed by -0.13°C (-0.22 , -0.05 ; $\text{Pd} > 99\%$) with Dry-HA (37.1°C [36.7 , 37.4] to 36.9°C [36.5 , 37.2]) and by -0.17°C (-0.25 , -0.09 ; $\text{Pd} > 99\%$) with Humid-HA (37.0°C [36.6 , 37.3] to 36.8°C [36.5 , 37.1]). There was a difference of -0.04°C (-0.15 , 0.08 ; $\text{Pd} = 72\%$) between Humid-HA and Dry-HA. Resting HR changed by -3 beats $\cdot\text{min}^{-1}$ (-6 , 1 ; $\text{Pd} = 91\%$) with Dry-HA (62 beats $\cdot\text{min}^{-1}$ [49 , 72] to 59 beats $\cdot\text{min}^{-1}$ [46 , 70]) and by -3 beats $\cdot\text{min}^{-1}$ (-6 , 0 ; $\text{Pd} = 94\%$) with Humid-HA (60 beats $\cdot\text{min}^{-1}$ [47 , 70] to 57 beats $\cdot\text{min}^{-1}$ [44 , 67]), with a difference of 0 beats $\cdot\text{min}^{-1}$ (-5 , 4 ; $\text{Pd} = 54\%$) between conditions.

BV changed by 271 mL (83 , 460 ; $\text{Pd} = 99\%$) with Dry-HA and by 219 mL (43 , 395 ; $\text{Pd} = 98\%$) with Humid-HA, with a difference of 52 mL (-205 , 308 ; $\text{Pd} = 64\%$) between conditions (Fig. 3A). PV changed by 201 mL (71 , 324 ; $\text{Pd} = 99\%$) with Dry-HA and by 114 mL (-5 , 232 ; $\text{Pd} = 94\%$) with Humid-HA, with a difference of 87 mL (-85 , 255 ; $\text{Pd} = 81\%$) between conditions (Fig. 3B). RCV changed by 60 mL (-21 , 140 ; $\text{Pd} = 89\%$) with Dry-HA and by 103 mL (30 , 175 ; $\text{Pd} = 99\%$) with Humid-HA, with a difference of 43 mL (-65 , 151 ; $\text{Pd} = 75\%$) between conditions (Fig. 3C). Hb_{mass} changed by 24 g (2 , 46 ; $\text{Pd} = 96\%$) with Dry-HA and by 26 g (6 , 46 ; $\text{Pd} = 98\%$) with Humid-HA, with a difference of 2 g (-27 , 32 ; $\text{Pd} = 56\%$) between conditions (Fig. 3D).

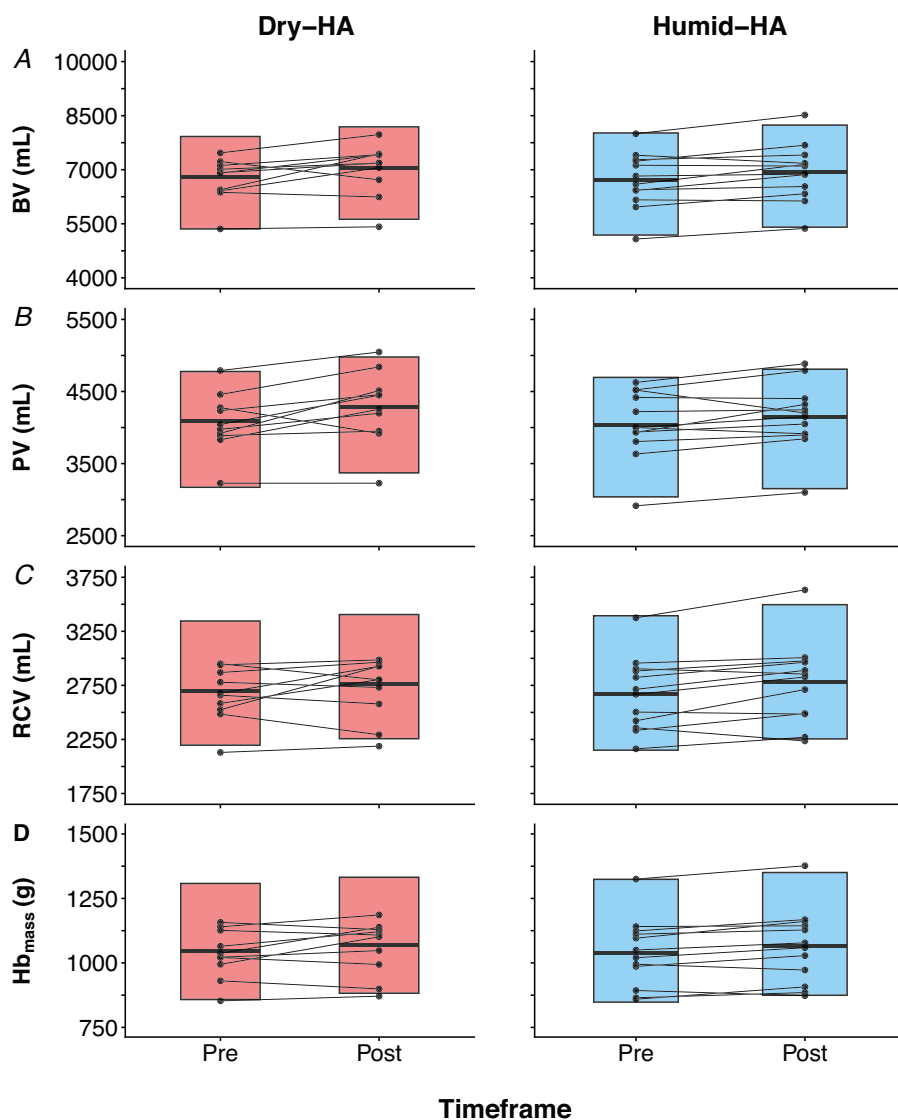


Figure 3.

A, blood volume (BV), B, plasma volume (PV), C, red cell volume (RCV) and D, haemoglobin mass (Hb_{mass}) before (pre) and after (post) heat acclimation (HA) in a hot-dry (Dry-HA, $n = 10$) and warm-humid (Humid-HA, $n = 12$) environment. Data are presented as posterior mean with 90% credible intervals and individual observations.

HSTs and cross-acclimation

Thermal and cardiovascular responses. End-exercise T_{re} during the Dry-HST changed by -0.2°C ($-0.3, -0.1$; Pd > 99%) with Dry-HA and by -0.3°C ($-0.4, -0.2$; Pd > 99%) with Humid-HA (Fig. 4A and B), with a difference of -0.1°C ($-0.2, -0.1$; Pd > 99%) between conditions. The increase in T_{re} during Dry-HST changed by -0.04 ($-0.20, 0.11$; Pd = 68%) with Dry-HA and by -0.05 ($-0.20, 0.10$; Pd = 71%) with Humid-HA. End-exercise T_{re} during the Humid-HST changed by -0.3°C ($-0.4, -0.2$; Pd > 99%) with Dry-HA and by -0.1°C ($-0.2, 0.0$; Pd = 99%) with Humid-HA

(Fig. 4C and D), with a difference of -0.2°C ($-0.2, -0.1$; Pd > 99%) between conditions. The increase in T_{re} during Humid-HST changed by -0.10 ($-0.24, 0.04$; Pd = 89%) with Dry-HA and by -0.13 ($-0.27, 0.00$; Pd = 95%) with Humid-HA.

Mean T_{sk} during the Dry-HST changed by -0.5°C ($-0.8, -0.1$; Pd = 99%) with Dry-HA and by -0.2°C ($-0.4, 0.2$; Pd = 77%) with Humid-HA (Fig. 5A and B), with a difference of 0.3°C ($0.2, 0.5$; Pd > 99%) between conditions. Mean T_{sk} during the Humid-HST changed by -0.2°C ($-0.3, 0.0$; Pd = 96%) with Dry-HA and by 0.0°C ($-0.2, 0.1$; Pd = 68%) with Humid-HA (Fig. 5C and D),

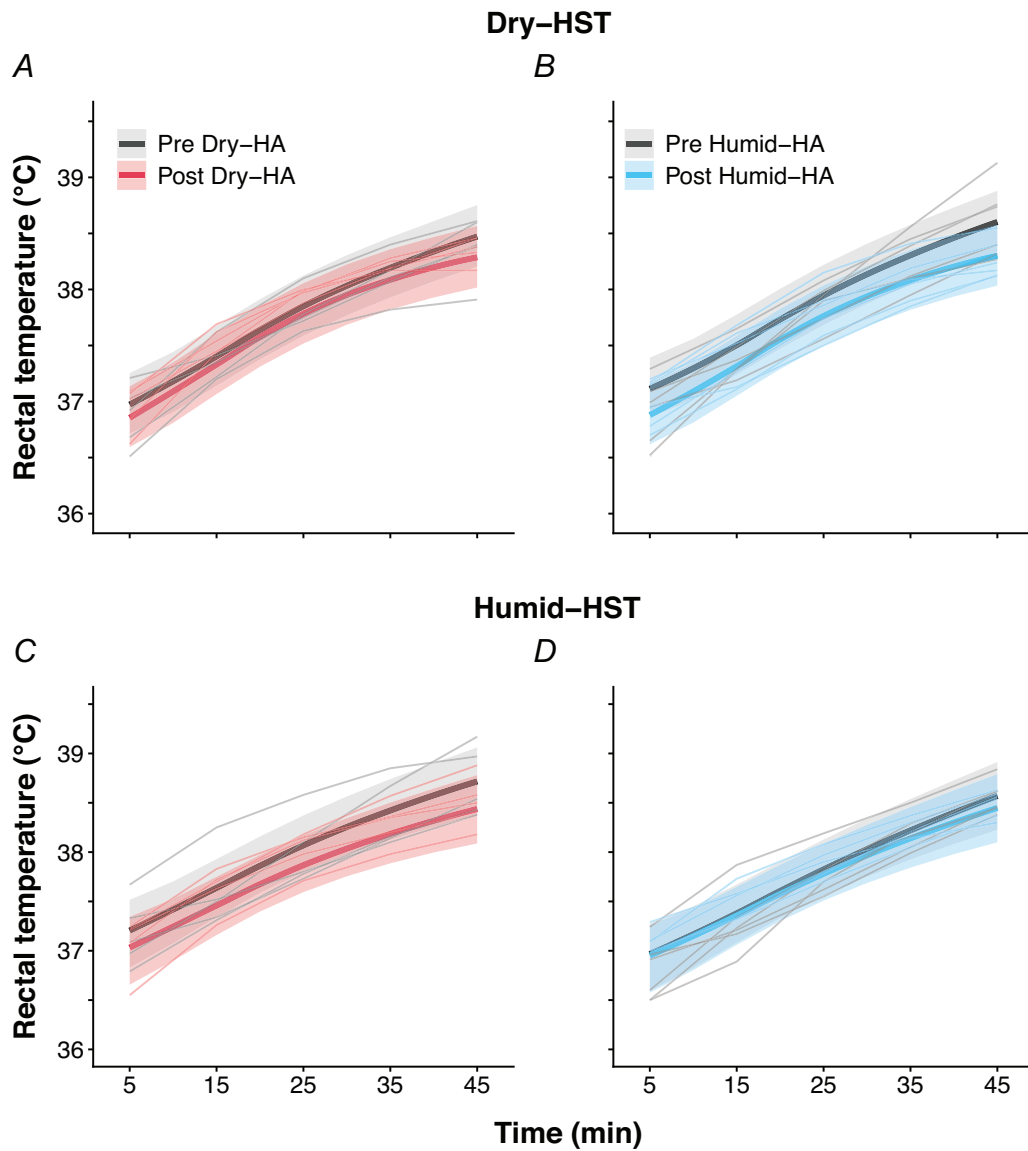


Figure 4.

Rectal temperature during a 45-min heat stress test (HST) in hot-dry (top panel, Dry-HST) and warm-humid (bottom panel, Humid-HST) conditions before (pre) and after (post) heat acclimation (HA) in a A and C, hot-dry (Dry-HA, $n = 10$) and B and D, warm-humid (Humid-HA, $n = 12$) environment. Data are presented as posterior mean with 90% credible intervals and individual observations.

with a difference of 0.1°C (0.0, 0.3; Pd = 95%) between conditions.

Mean HR during the Dry-HST changed by -2 beats $\cdot\text{min}^{-1}$ (-5 , -1 ; Pd = 81%) with Dry-HA and by -5 beats $\cdot\text{min}^{-1}$ (-9 , -2 ; Pd > 99%) with Humid-HA (Fig. 6A and B), with a difference of -3 beats $\cdot\text{min}^{-1}$ (-5 , -2 ; Pd > 99%) between conditions. Mean HR during the Humid-HST changed by -6 beats $\cdot\text{min}^{-1}$ (-9 , -4 ; Pd > 99%) with Dry-HA and by -1 beats $\cdot\text{min}^{-1}$ (-4 , -2 ; Pd = 71%) with Humid-HA (Fig. 6C and D), with a difference of -5 beats $\cdot\text{min}^{-1}$ (-7 , -3 ; Pd > 99%) between conditions.

Sweating responses. WBSR during the Dry-HST changed by 10 mL $\cdot\text{h}^{-1}$ (-90 , 110 ; Pd = 55%) with

Dry-HA and by 80 mL $\cdot\text{h}^{-1}$ (-10 , 170 ; Pd = 92%) with Humid-HA (Fig. 7A), with a difference of 70 mL $\cdot\text{h}^{-1}$ (-60 , 210 ; Pd = 81%) between conditions. WBSR during the Humid-HST changed by 210 mL $\cdot\text{h}^{-1}$ (70 , 340 ; Pd = 99%) with Dry-HA and by 190 mL $\cdot\text{h}^{-1}$ (70 , 320 ; Pd = 99%) with Humid-HA (Fig. 7A), with a difference of 10 mL $\cdot\text{h}^{-1}$ (-160 , 190 ; Pd = 56%) between conditions.

Upper back LSR during the Dry-HST changed by 0.18 mg $\cdot\text{cm}^{-2}\cdot\text{min}^{-1}$ (0.03, 0.34; Pd = 97%) with Dry-HA and by 0.07 mg $\cdot\text{cm}^{-2}\cdot\text{min}^{-1}$ (-0.07 , 0.22 ; Pd = 79%) with Humid-HA (Fig. 7B), with a difference of 0.11 mg $\cdot\text{cm}^{-2}\cdot\text{min}^{-1}$ (-0.10 , 0.32 ; Pd = 82%) between conditions. Upper back LSR during the Humid-HST changed by 0.10 mg $\cdot\text{cm}^{-2}\cdot\text{min}^{-1}$ (-0.03 , 0.23 ; Pd = 89%) with Dry-HA and by 0.17 mg $\cdot\text{cm}^{-2}\cdot\text{min}^{-1}$ (0.03, 0.31;

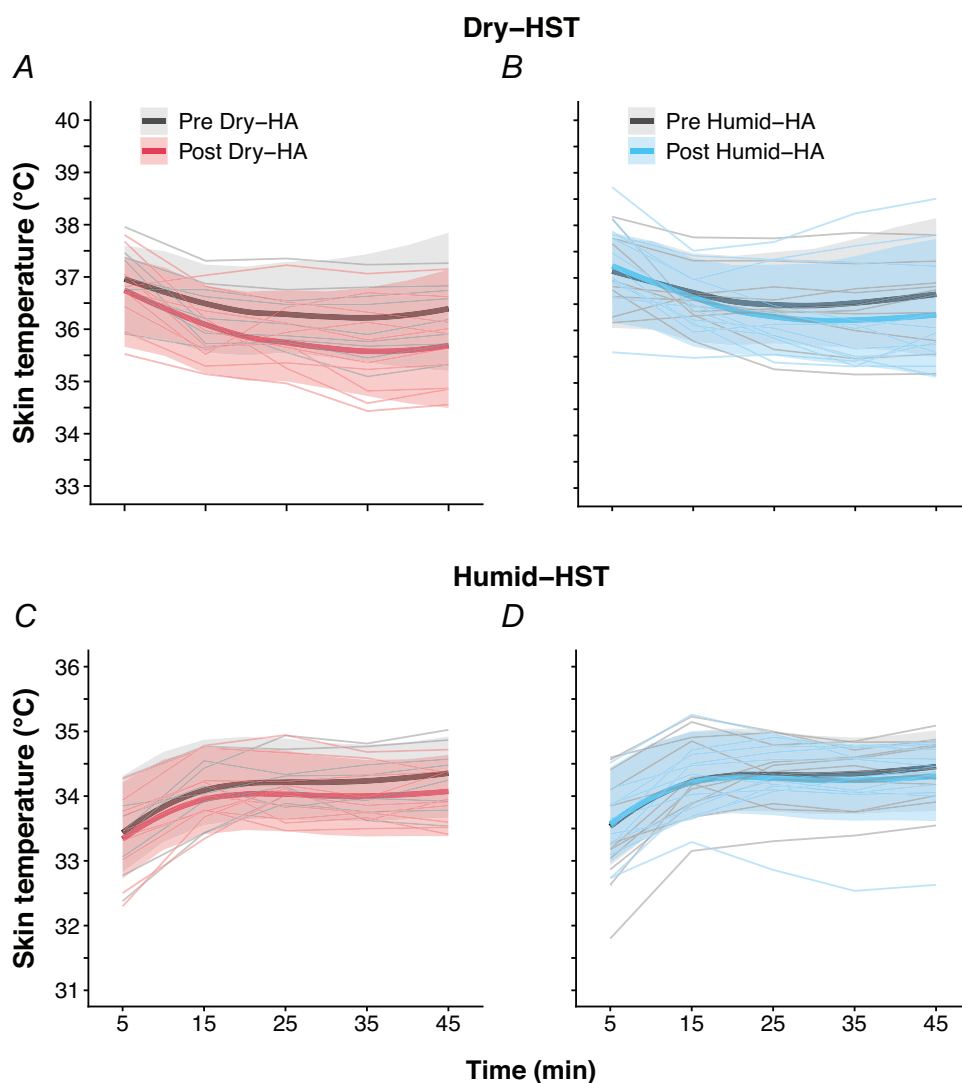


Figure 5.

Mean skin temperature during a 45-min heat stress test (HST) in hot-dry (top panel, Dry-HST) and warm-humid (bottom panel, Humid-HST) conditions before (pre) and after (post) heat acclimation (HA) in a A and C, hot-dry (Dry-HA, $n = 10$) and B and D, warm-humid (Humid-HA, $n = 12$) environment. Data are presented as posterior mean with 90% credible intervals and individual observations.

Pd = 97%) with Humid-HA (Fig. 7B), with a difference of $0.07 \text{ mg}\cdot\text{cm}^{-2}\cdot\text{min}^{-1}$ ($-0.12, 0.26$; Pd = 74%) between conditions. Forearm LSR during the Dry-HST changed by $0.24 \text{ mg}\cdot\text{cm}^{-2}\cdot\text{min}^{-1}$ ($0.10, 0.37$; Pd > 99%) with Dry-HA and by $0.15 \text{ mg}\cdot\text{cm}^{-2}\cdot\text{min}^{-1}$ ($0.03, 0.28$; Pd = 98%) with Humid-HA (Fig. 7C), with a difference of $0.08 \text{ mg}\cdot\text{cm}^{-2}\cdot\text{min}^{-1}$ ($-0.10, 0.26$; Pd = 77%) between conditions. Forearm LSR during the Humid-HST changed by $0.09 \text{ mg}\cdot\text{cm}^{-2}\cdot\text{min}^{-1}$ ($-0.03, 0.21$; Pd = 88%) with Dry-HA and by $0.19 \text{ mg}\cdot\text{cm}^{-2}\cdot\text{min}^{-1}$ ($0.06, 0.32$; Pd = 99%) with Humid-HA (Fig. 7C), with a difference of $0.10 \text{ mg}\cdot\text{cm}^{-2}\cdot\text{min}^{-1}$ ($-0.07, 0.27$; Pd = 84%) between conditions.

Sweat $[\text{Na}^+]$ during the Dry-HST changed by $-12 \text{ mmol}\cdot\text{L}^{-1}$ ($-21, -2$; Pd = 98%) with Dry-HA and

by $-3 \text{ mmol}\cdot\text{L}^{-1}$ ($-12, 7$; Pd = 68%) with Humid-HA (Fig. 7D), with a difference of $-9 \text{ mmol}\cdot\text{L}^{-1}$ ($-21, 3$; Pd = 88%) between conditions. Sweat $[\text{Na}^+]$ during the Humid-HST changed by $-8 \text{ mmol}\cdot\text{L}^{-1}$ ($-17, 1$; Pd = 94%) with Dry-HA and by $-11 \text{ mmol}\cdot\text{L}^{-1}$ ($-19, -2$; Pd = 98%) with Humid-HA (Fig. 7D), with a difference of $-3 \text{ mmol}\cdot\text{L}^{-1}$ ($-14, 9$; Pd = 64%) between conditions.

Perceptual responses. Mean RPE during the Dry-HST changed by -0.8 ($-1.5, -0.2$; Pd = 98%) with Dry-HA (pre: 13.1 [11.1, 15.1]; post: 12.3 [10.3, 14.3]) and by -1.1 ($-1.7, -0.6$; Pd > 99%) with Humid-HA (pre: 13.7 [11.7, 15.6]; post: 12.5 [10.5, 14.5]). Mean RPE during the

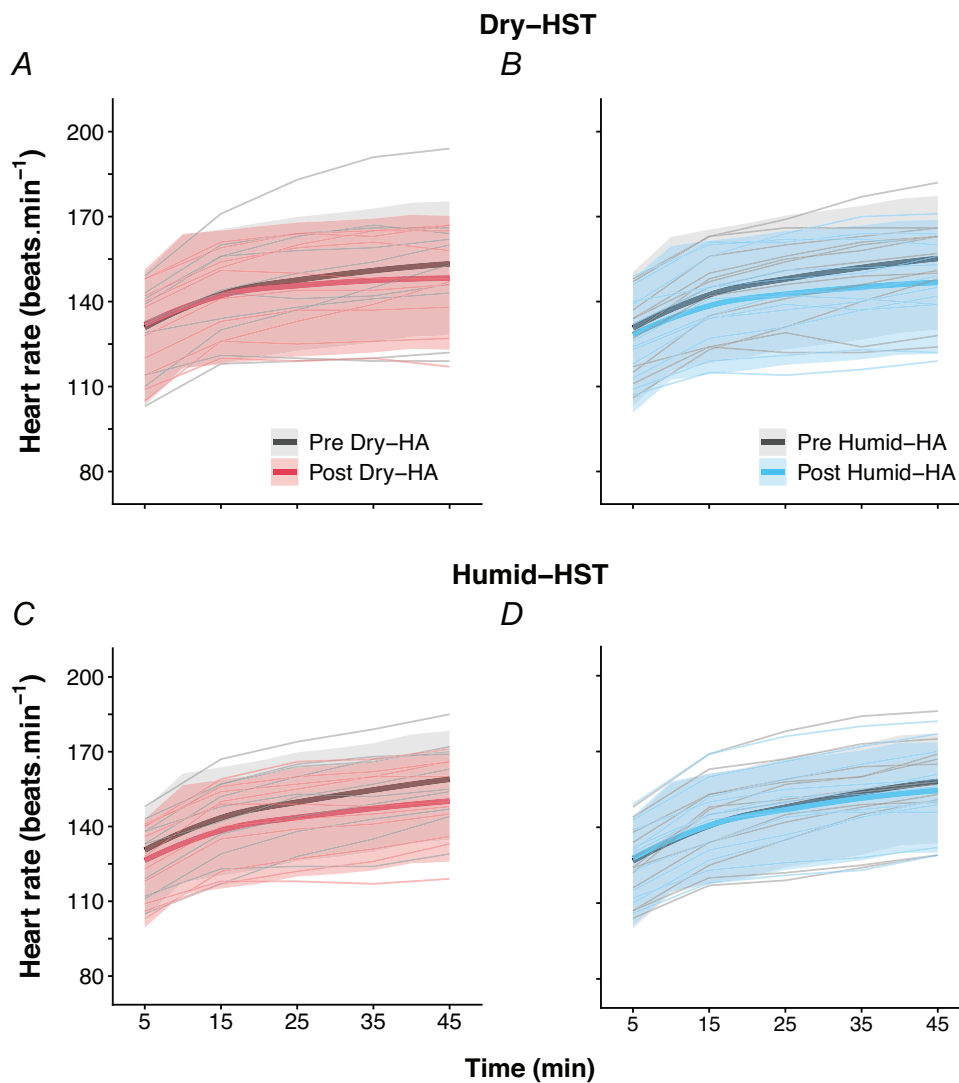


Figure 6.

Heart rate during a 45-min heat stress test (HST) in hot-dry (top panel, Dry-HST) and warm-humid (bottom panel, Humid-HST) conditions before (pre) and after (post) heat acclimation (HA) in A and C, hot-dry (Dry-HA, $n = 10$) and B and D, warm-humid (Humid-HA, $n = 12$) environment. Data are presented as posterior mean with 90% credible intervals and individual observations.

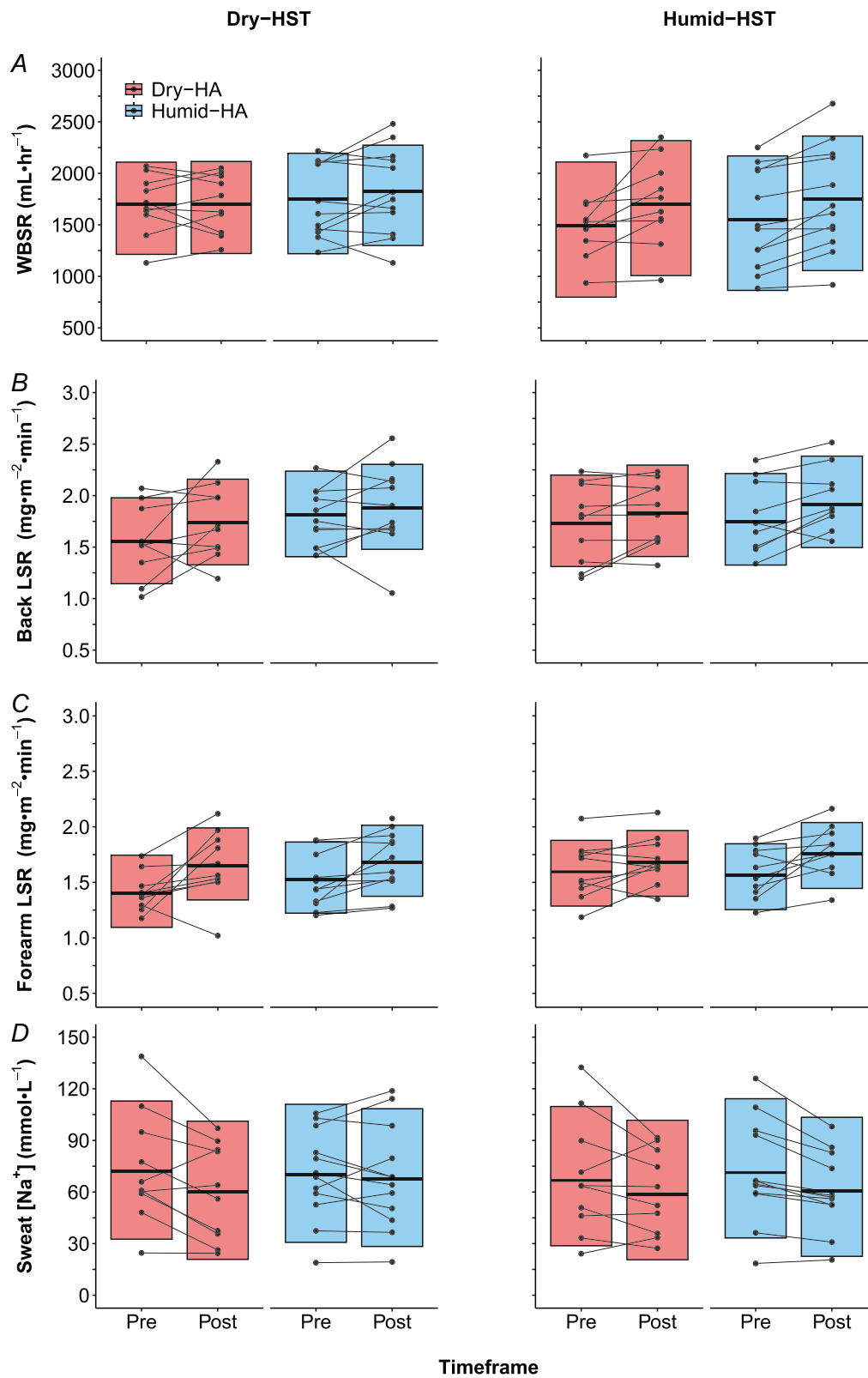


Figure 7. A, whole-body sweat rate (WBSR), B and C, upper back and forearm local sweat rate (LSR) and D, sweat sodium concentration [Na⁺] during a 45-min heat stress test (HST) in hot-dry (left panel, Dry-HST) and warm-humid (right panel, Humid-HST) conditions before (pre) and after (post) heat acclimation (HA) in a hot-dry (Dry-HA; A and C; $n = 10$) and warm-humid (Humid-HA; B and D; $n = 12$) environment. Data are presented as posterior mean with 90% credible intervals and individual observations.

Humid-HST changed by -0.9 ($-1.5, -0.2$; Pd = 99%) with Dry-HA (pre: 13.2 [11.0, 15.2]; post: 12.4 [10.2, 14.4]) and by -0.8 ($-1.4, -0.2$; Pd = 99%) with Humid-HA (pre: 13.5 [11.3, 15.5]; post: 12.7 [10.5, 14.7]). Mean thermal comfort during the Dry-HST changed by -0.4 ($-0.9, -0.1$; Pd = 98%) with Dry-HA (pre: 6.0 [5.0, 6.7]; post: 5.6 [4.4, 6.6]) and by -0.3 ($-0.7, 0.0$; Pd = 96%) with Humid-HA (pre: 6.0 [5.0, 6.7]; post: 5.7 [4.5, 6.6]). Mean thermal comfort during the Humid-HST was similar with Dry-HA (pre: 5.7 [4.2, 6.6]; post: 5.6 [4.0, 6.6]) and changed by -0.4 ($-0.8, 0.0$; Pd = 98%) with Humid-HA (pre: 5.9 [4.6, 6.7]; post: 5.5 [3.9, 6.6]). Mean sweating sensation during the Dry-HST changed by 0.1 ($-0.1, 0.4$; Pd = 77%) with Dry-HA (pre: 3.2 [1.3, 4.6]; post: 3.3 [1.4, 4.7]) and by -0.1 ($-0.4, 0.1$; Pd = 84%) with Humid-HA (pre: 3.2 [1.3, 4.6]; post: 3.1 [1.1, 4.6]). Mean sweating sensation in Humid-HST was similar with Dry-HA (pre: 4.1 [2.0, 5.0]; post: 4.1 [2.0, 5.0]) and Humid-HA (pre: 4.0 [1.8, 5.0]; post: 4.0 [1.7, 5.0]).

Discussion

This study examined the adaptive response to Dry-HA and Humid-HA and compared the extent to which adaptations from one environment transfer to the other. Using a cross-over design, our data demonstrate that power output and WBSR increased similarly throughout Dry-HA and Humid-HA when exercising at a given HR, allowing for a mean T_{re} of $\sim 38.5^\circ\text{C}$ to be maintained across both regimens. Of note, mean power output and WBSR were higher throughout Dry-HA compared to Humid-HA, but for a similar RPE and thermal comfort, while sweating sensation was slightly higher during Humid-HA. Furthermore, both Dry-HA and Humid-HA expanded PV and increased Hb_{mass} to a similar extent. The similarity in physiological adaptations between HA protocols indicates that the specificity of the environmental characteristics was overshadowed by the overall exercise-heat stimulus, failing to drive meaningful environment-specific adaptations. Moreover, the greater work rate sustained for a similar HR, T_{re} , RPE and thermal comfort during Dry-HA compared to Humid-HA indicates that drier HA conditions may better preserve training quality. Therefore, athletes, soldiers and workers may use hot-dry HA to prepare for competition and work in both dry and humid heat, with the possibility of habituating to humid heat in the final few acclimation sessions.

Adaptations to dry and humid heat

Controlled HR HA resulted in a similar mean T_{re} ($\sim 38.5^\circ\text{C}$) over the final 75 min of each exposure throughout both interventions, which is similar to pre-

vious reports using this approach (Traverset al., 2020). However, mean T_{sk} was $\sim 2^\circ\text{C}$ higher during Dry-HA compared to Humid-HA due to the $\sim 9^\circ\text{C}$ higher ambient temperature. Notwithstanding, the increase in mean power output when cycling at a given HR was similar (~ 16 W) after both regimens, despite the maintenance of a ~ 13 W higher power output during Dry-HA (Fig. 2A). This higher power output is likely associated with the greater evaporative potential in the dry compared to humid environment (~ 2 vs. 4 kPa), allowing for greater evaporation of sweat and consequently a higher rate of metabolic heat production (i.e. work rate) for a given HR. This is similar to Tebeck et al. (2020), who reported greater overall work (761 vs. 670 kJ) completed in 5 days of hot-dry (45°C , 1.48 kPa) compared to warm-humid (32°C , 3.98 kPa) HA using the controlled hyperthermia approach. Due to the greater work rate maintained during Dry-HA, in conjunction with a similar mean HR, T_{re} , RPE and thermal comfort to Humid-HA, drier HA conditions appear beneficial for optimising oxygen flux and thus endurance training quality. As the adaptive response between regimens was relatively similar, Dry-HA may be used to prepare for work/competition in both dry and humid heat, with the option to include additional humid exposures to ensure habituation if such environments are anticipated. Of note, participants anecdotally preferred the Dry-HA regimen as it was perceived to be more enjoyable than Humid-HA, which was associated with a slightly higher sweating sensation.

Our data show minimal change in WBSR with Humid-HA ($50\text{ mL}\cdot\text{h}^{-1}$ [$-70, 170$]) compared to Dry-HA (Fig. 2B). In contrast, two separate studies of longer duration (8–13 days) suggest that WBSR is further augmented ($\sim 130\text{ mL}\cdot\text{h}^{-1}$; 7%) after Humid- (Nielsen et al., 1997) compared to Dry-HA (Nielsen et al., 1997), although these were not a direct comparison. In a direct comparison, Griefahn (1997) noted a minimal difference in sweat rate ($\sim 40\text{ mL}\cdot\text{h}^{-1}$) after 15 days of constant work rate HA in humid (37°C and 5.0 kPa) and dry (50°C and 1.9 kPa) conditions, highlighting the variability in responses. Indeed, the day-to-day variability in WBSR has been shown to range from 5% to 7% (Baker et al., 2009; Hayden et al., 2004). Tebeck et al. (2020) noted that 5 days of Dry-HA resulted in a larger increase in WBSR ($\sim 300\text{ mL}\cdot\text{h}^{-1}$) than Humid-HA. In a recent meta-analysis, we reported an additional increase in WBSR of $\sim 37\text{ mL}\cdot\text{h}^{-1}$ for every 1 kPa increase in P_a during HA (McDonald et al., 2025). Therefore, whether elevated humidity during HA confers a greater increase in WBSR remains to be elucidated.

After both Dry-HA and Humid-HA, we noted an expansion in BV (4.1% and 3.3%) and PV (5.0% and 2.9%; Fig. 3A and B). Although increases in BV with repeated heat exposure are well documented (Dawson et al., 1989; Greenleaf et al., 1983; Shapiro et al., 1981), our data

indicate that Dry-HA and Humid-HA do not influence the magnitude of increase. Similarly, the expansion of PV was comparable between Dry-HA and Humid-HA (~4%), which is in line with a recent meta-analysis (6%; range: -8% to 24%; McDonald et al., 2025) and data from Tebeck et al. (2020), ~5%, but lower than previously reported after Dry-HA (13%; Nielsen et al., 1993) and Humid-HA (9%; Nielsen et al., 1997). These discrepancies may relate to the use of different measurement conditions (e.g. arm position, posture, skin temperature; Sawka, 1988), as well as measurement techniques, with the albumin-iodine radioisotope method (Nielsen et al., 1993; Nielsen et al., 1997) having a larger error (~5%) than CO rebreathing (~2%; Gore et al., 2005). Therefore, the difference in PV expansion between HA studies may be more homogenous than reported.

A novel finding of our study is that Dry-HA and Humid-HA rapidly increased RCV (~2.3% and 3.9%) and Hb_{mass} (~2.3% and 2.6%, ~25 g; Fig. 3C and D). This finding adds to more recent long-term (~5 weeks) HA studies demonstrating the ergogenic potential for HA to increase oxygen-carrying capacity (i.e. Hb_{mass} increase of 3%–5%; Cubel et al., 2024; Jenkins, Killick, et al., 2025; Oberholzer et al., 2019; Rønnestad et al., 2022). For example, in a recent study by Cubel et al. (2024), an increase in Hb_{mass} of ~30 g (~4%) was reported after 18 exposures over 3 weeks of exercise while wearing a sweat suit/winter clothing. In contrast, similar-length HA protocols (8–12 exposures) to the current study reported that Hb_{mass} was unchanged (McCleave et al., 2020; McIntyre et al., 2021; Pethick et al., 2019), decreased (Travers, Edgett, et al., 2020) or returned to baseline after a decrease (Racinais et al., 2024). Of note, Lundby et al. (2021) reported a 9 g (~1%) increase in Hb_{mass} after 10 days of HA; however, this increase was statistically supported only when data from three HA regimens were pooled (i.e. exercise HA, exercise while wearing thermal clothing and exercise while wearing thermal clothing followed by hot water immersion). The pathway via which Hb_{mass} increases during HA may relate to the upregulation of heat shock protein expression (McClung et al., 2008) increasing the molecular stability of hypoxia-inducible factor-1 α , which stimulates erythropoiesis (Shein et al., 2005). It may also stem from the expansion of PV and subsequent reduction in haematocrit triggering the kidneys to stimulate erythropoiesis (Donnelly, 2001), and/or from increased activation of blood pressure-regulating hormones (i.e. angiotensin II) via the renin-angiotensin-aldosterone system (Guo & Montero, 2025).

The comparable responses in BV, PV, RCV and Hb_{mass} between HA regimens in the current study indicate that the influence of specific environmental characteristics was overshadowed by the adaptive process, and thus had limited influence on driving haematological adaptations,

as well as the HA phenotype more broadly. This notion contrasts with the contemporary tenet, albeit supported with limited evidence, that heat adaptations are specific to the environmental characteristics in which they are induced (Guy et al., 2015; Périard et al., 2015; Racinais et al., 2015; Taylor, 2014). However, our data may inform the long-standing debate regarding the factors underpinning the HA phenotype (Eichna et al., 1950; Sawka & Coyle, 1999). Historically, arguments focused on whether heat adaptations were primarily driven by PV expansion or by improvements in sweating responses (Bass et al., 1955; Eichna et al., 1950; Senay et al., 1976; Sawka & Coyle, 1999). Evidence challenging PV expansion as the primary driver of heat adaptations includes the timing of expansion (Eichna et al., 1950; Sawka & Coyle, 1999), as well as observations that acute PV expansion via albumin infusion (mechanistic pathway expanding PV with HA) did not confer thermoregulatory benefits (Fortney et al., 1981; Sawka et al., 1989). Moreover, HA adaptations have been shown to occur in the absence of PV expansion (Bass et al., 1958; Neal, Corbett, et al., 2016; Travers, Nichols, et al., 2020). Recently, advances in Hb_{mass} measurement (Siebenmann et al., 2017) and the use of long-term moderate- to high-intensity HA protocols consistently show Hb_{mass} increases (Jenkins et al., 2025; McDonald et al., 2025). Earlier studies relied on complex radioactive tagging for erythrocyte volume measurement (Oddershede & Elizondo, 1980; Sterling & Grey, 1950; Wennesland et al., 1959), so these were largely absent from HA research. Importantly, acute erythrocyte expansion via red blood cell (RBC) infusion improves the sweating response (i.e. rate and sensitivity) and reduces physiological strain (i.e. HR and T_{re}) during exercise in the heat (Patterson et al., 1995; Sawka et al., 1987; Sawka et al., 1988). These effects are greater in heat-acclimated than non-acclimated individuals (Sawka & Young, 1989; Sawka et al., 1989), suggesting that increased circulating RBCs exert an immediate thermoregulatory and concomitant cardiovascular benefit, amplified by HA. The increase in Hb_{mass} during prolonged HA may represent an important factor in inducing the HA phenotype, particularly for improving the sweating response. The underlying mechanism by which an increase in erythrocyte volume, and perhaps Hb_{mass}, improves sweating rate responses remains unclear (Patterson et al., 1995; Sawka & Coyle, 1999).

Dry-HST and cross-acclimation

In the Dry-HST, both Dry-HA and Humid-HA lowered end-exercise T_{re} (range: 0.2–0.3°C) and mean T_{sk} (range: 0.2–0.5°C), with Humid-HA leading to a slightly greater change in WBSR (70 mL·h⁻¹) and mean HR (-3 beats·min⁻¹; Figures 4 to 6). The lack of change in WBSR (10 mL·h⁻¹; -90, 110) after Dry-HA is somewhat

surprising because it increased during HA. However, there was high interindividual variability in WBSR during the Dry-HST (Fig. 7A), with 5 of 10 participants demonstrating an increase (130–210 mL·h⁻¹) and 5 a decrease (–30 to –290 mL·h⁻¹). Further, participants who demonstrated a reduction in WBSR during the Dry-HST had a lower starting T_{re} (~0.2°C) and a lower mean exercising T_{re} (~0.3°C) and T_{sk} (~0.3°C) compared to those exhibiting an increase in WBSR. Furthermore, LSR was lower in participants who exhibited a decrease in WBSR, both at the upper back (~0.37 mg·cm⁻²·min⁻¹) and forearm (~0.19 mg·cm⁻²·min⁻¹). Individual responses to HA differ and are important to highlight (Corbett et al., 2018; Daanen et al., 2018), as these shed light on the adaptive responses (McDonald et al., 2025). After Humid-HA, there was also interindividual variability in WBSR during the Dry-HST. Five of the 12 participants experienced a decrease in WBSR (–50 to –250 mL·h⁻¹), 1 remained unchanged (~10 mL·h⁻¹) and 6 increased (60–390 mL·h⁻¹). As earlier, those demonstrating a reduction in WBSR also exhibited evidence of a lower starting T_{re} (~0.1°C), mean exercising T_{re} (~0.2°C) and T_{sk} (~0.6°C) compared to those who improved WBSR. Taken together, these data confirm that the adaptive response to HA is highly individualised and that the Dry-HST may not have been stressful enough to elicit a higher WBSR, especially after Dry-HA, due to a lower body temperature at rest and during exercise. Moreover, in less-fit/less-trained participants with minimal heat adaptation (Ravanelli et al., 2018), a more robust WBSR adaptation might have been observed.

The change in end-exercise T_{re} during the Dry-HST was similar for both Dry-HA (–0.2°C) and Humid-HA (–0.3°C), and although there was a further estimated reduction of –0.1°C after Humid-HA compared to Dry-HA, this is likely not physiologically meaningful. The changes demonstrated during the Dry-HST after both interventions are consistent with those from the broader HA literature (Kaufman et al., 1988; Watkins et al., 2008), whereby similar reductions in T_{re} (~0.2°C) have been reported after similar-length HA regimens (6–9 days) and HST (30–40 min, 50%–75% $\dot{V}O_{2peak}$, 39–40°C and 1.99–2.10 kPa). Moreover, when directly comparing the change in mean T_{sk} during the Dry-HST after HA, we noted a slightly greater decrease of ~0.3°C with Dry-HA compared to Humid-HA, which is in line with an earlier study (Shvartz et al., 1973). Indeed, a greater reduction in T_{sk} (~0.5°C) was reported during a HST at 50°C and 3.6 kPa after 6 days of constant work rate HA in the same conditions, compared to a HA group exercising in a more humid environment (37°C and 5.7 kPa). Interestingly, the lower T_{sk} after dry HA was not accompanied by a concurrent increase in sweat rate (Shvartz et al., 1973), whereas in the present study only Humid-HA marginally improved WBSR during the Dry-HST. However, upper

back and forearm LSR during the Dry-HST increased to a similar extent after both regimens.

Our data also indicate that sweat [Na⁺] was reduced in the Dry-HST after Dry-HA (~12 mmol·L⁻¹) but not Humid-HA (~–3 mmol·L⁻¹; Fig. 7D). Similar reductions in sweat [Na⁺] to those observed after Dry-HA have been reported after warm-humid HA (40°C, 4.32 kPa), albeit when tested under the same conditions (Patterson et al., 2014). However, because both Dry-HA and Humid-HA elicited a similar reduction in sweat [Na⁺] (~10 mmol·L⁻¹) during the Humid-HST, where both groups demonstrated larger and comparable increases in WBSR (~200 mL·h⁻¹), the changes observed during the Dry-HST might not reflect a meaningful difference between the interventions. The difference in sweat [Na⁺] between Dry-HA and Humid-HA also falls within the limits of agreement of the device used in the current study (Brown et al., 2024). Moreover, studies that demonstrate greater reductions in sweat [Na⁺] (37–40 mmol·L⁻¹) have also shown larger increases in sweat rate (~340 mL·h⁻¹; Keiser et al., 2015; Neal, Massey, et al., 2016), compared to those showing lesser changes (7–10 mmol·L⁻¹ and ~120 mL·h⁻¹; Kaufman et al., 1988; McCleave et al., 2019; Pichan et al., 1985). Therefore, to identify potential differences in thermoregulatory adaptations between HA protocol characteristics, a maximal/near-maximal WBSR may be required, which did not occur during our Dry-HST.

Humid-HST and cross-acclimation

In the Humid-HST both Dry-HA and Humid-HA reduced end-exercise T_{re} (range: 0.1–0.3°C; Fig. 4); increased upper back LSR (range: 0.10–0.17 mg·cm⁻²·min⁻¹), forearm LSR (range: 0.09–0.19 mg·cm⁻²·min⁻¹) and WBSR (range: 190–210 mL·h⁻¹); and lowered sweat [Na⁺] (range: 8–12 mmol·L⁻¹; Fig. 7). Further, mean T_{sk} during the Humid-HST was reduced after Dry-HA (~0.2°C) but not Humid-HA (Fig. 5C and D), whereas mean HR was reduced by a further 5 beats·min⁻¹ after Dry-HA compared with Humid-HA (Fig. 6C and D). Although the reduction in end-exercise T_{re} was slightly larger (0.2°C) after Dry-HA compared to Humid-HA, both fall within the range associated with similar-length (35–50 min) HST protocols (Alkemade et al., 2021; Kaufman et al., 1988; Kuennen et al., 2011; Salgado et al., 2020), with longer duration tests (70–240 min) eliciting larger reductions (–0.6 to 1.3°C) after both dry (Dini et al., 2007; Fein et al., 1975; Rowell et al., 1967) and humid HA (Buono et al., 1998; Senay, 1978; Strydom et al., 1976).

Improvements in WBSR during the Humid-HST were similar (~200 mL·h⁻¹) between Dry-HA and Humid-HA, and in line with the increase from days 1 to 8 during both HA interventions (~250 mL·h⁻¹).

These changes in WBSR are similar to those reported in a recent meta-analysis ($\sim 163 \text{ mL}\cdot\text{h}^{-1}$; McDonald et al., 2025) and larger than those reported in other HA studies ($\sim 100 \text{ mL}\cdot\text{h}^{-1}$) using a similar HST protocol (55%–65% $\dot{V}\text{O}_{2\text{peak}}$, 40–45 min) after 10–12 days of dry HA (33–40°C, 1.5–2.0 kPa; McIntyre et al., 2022; White et al., 2015). In contrast, several studies acclimating in more humid conditions (3.6–3.7 kPa) reported a similar increase in WBSR to that of the current study ($\sim 200 \text{ mL}\cdot\text{h}^{-1}$) after 7 days using a lower-intensity ($\sim 50\%$ $\dot{V}\text{O}_{2\text{peak}}$) but longer (120–180 min) HST (Greenleaf et al., 1981; Shvartz et al., 1979; Shvartz et al., 1977). Notwithstanding, our findings align with studies reporting similar changes in sweat rate when directly comparing dry and humid HA (Fox et al., 1967; Griefahn, 1997; Shvartz et al., 1973), but not all (Tebeck et al., 2020).

During the Humid-HST, mean T_{sk} decreased after Dry-HA ($\sim 0.2^\circ\text{C}$) but not Humid-HA, with a small difference ($\sim 0.1^\circ\text{C}$) when directly comparing interventions (Fig. 5C and D). Although the small difference observed is unlikely to provide a physiological benefit, and the interday variability in mean T_{sk} during exercise-heat stress is $\sim 0.2^\circ\text{C}$ (Peel et al., 2022), mean T_{sk} was also further reduced with Dry-HA during the Dry-HST ($\sim 0.3^\circ\text{C}$). These observations are akin to those of Fox et al. (1967) reporting less of a reduction in T_{sk} ($\sim 0.2^\circ\text{C}$) during a 3-h test (alternating 30 min of passive rest and bench stepping) in hot-humid conditions (40°C and 4.2 kPa) after 12 days of Humid- (49°C, wearing water-barrier suit) compared to Dry-HA (45–55°C, 1.9–2.4 kPa). The explanation for the slightly greater reduction in mean T_{sk} after Dry-HA compared to Humid-HA is unclear, although consistent with previous observations (Fox et al., 1967; Shvartz et al., 1973). Future studies need to explore potential mechanisms that could explain these minimal differences and if they are further amplified under greater levels of thermal strain (e.g. $T_{\text{re}} > 39^\circ\text{C}$, $T_{\text{sk}} > 37^\circ\text{C}$).

Limitations

The HST employed in the current study could have been more stressful to elicit stronger responses, potentially clarifying if any of the small differences observed between HA conditions were physiologically meaningful. Therefore, the lack of difference observed between Dry-HA and Humid-HA in this study may be specific to the short-duration (~ 45 min) and moderate-intensity HSTs ($\sim 65\%$ $\dot{V}\text{O}_{2\text{peak}}$). However, most adaptations were similar with minimal indication that Dry-HA or Humid-HA provided a strong-enough stimulus to elicit a specific adaptive response, which is reinforced by the cross-over design we adopted. Moreover, a potential training effect cannot be disregarded, as there was

no matched group exercising at a similar intensity in cool conditions. To minimise this potential influence, we employed trained male participants in a cross-over design, and no changes in $\dot{V}\text{O}_{2\text{peak}}$ in temperate conditions were observed after either HA protocol. The inclusion of only male participants limits the generalisability of our findings but stems from the contention that exists with regards to the kinetics (i.e. time frame and magnitude) of HA induction between males and females (Giersch et al., 2025; Kirby et al., 2021; Mee et al., 2015), and the study's aim of comparing the adaptive response to dry and humid heat. Nevertheless, our data support the notion that increasing T_{re} and T_{sk} , along with eliciting a strong sweating response, leads to the HA phenotype in hot-dry and warm-humid conditions (Périard et al., 2015; Sawka et al., 2011), which also provides cross-acclimation.

Conclusions

The current study provides several novel findings: (1) both Dry-HA and Humid-HA induced similar physiological adaptations at rest and during exercise; (2) when exercising at a given HR under matched WBGT conditions, Dry-HA was associated with a higher power output; (3) Dry-HA and Humid-HA increased Hb_{mass} despite the brief 8-day protocol (14-heat exposures between Hb_{mass} measures over ~ 3 weeks); and (4) cross-acclimation benefits were similar between interventions. Ultimately, our data indicate that the adaptive process to exercise in the heat is more impactful on the HA phenotype than the specificity of the environment (i.e. dry or humid). Therefore, to optimise training quality (i.e. exercise at a greater work rate), Dry-HA may be used to prepare for competing or working in both dry and humid heat.

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Additional information

Data availability statement

Data are available from the corresponding author (julien.periard@canberra.edu.au) upon reasonable request and signed access agreement.

Competing interests

Authors have no competing interests to declare.

Author contributions

P.M., B.C., M.N.S. and J.D.P. conceptualised and designed the research work. P.M., K.J. and T.H.T. performed data collection. P.M. performed data analyses and prepared the data visualisations. P.M., B.C. and J.D.P. interpreted the results and drafted the manuscript. All authors revised and approved the final version of the manuscript and agree to be accountable for all aspects of the work and qualify for authorship on the submitted manuscript.

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Keywords

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