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Allostasis as a consequence of high heat load in grain-fed feedlot cattle

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ABSTRACT

Heat wave intensity, frequency, and duration are increasing in many regions of the world, including locations where highly productive livestock are raised. There are animal health and welfare, as well as economic impacts from these events. In this study, the physiological responses of grain-fed steers during a high heat load challenge through to recovery in climate-controlled rooms (**CCR**) were intensively evaluated. Two cohorts of 12 Black Angus steers (BW, 615.4 ± 40.1 kg) sequentially underwent a simulated heatwave event that consisted of 3 phases in the CCR: PreChallenge (5 d duration and temperature humidity index (**THI**) range of 65 to 71), Challenge (7-d duration and THI 66 to 95 with diurnal cycling), and Recovery (5 d duration and THI 65 to 70). The Challenge period was modeled on a severe heat wave, characterized by 3 very hot days. Individual rumen temperature (**RumT**, °C) was collected every 10 min, and respiration rate (**RR**, breaths per minute), panting score (**PS**), and water usage ($L{\cdot}steer^{-1}{\cdot}day^{-1}$) were obtained at multiple time points daily, by trained observers. Individual animal daily DMI was also determined. Morning (0700 hours) rectal temperature (**RecT**, °C) was measured on days 3, 5, 7 to 13, 15, and 17. Not unexpectedly, RumT, RecT, RR, and PS rose during Challenge and fell rapidly as conditions eased. Conversely, DMI was reduced during Challenge. During the transition between PreChallenge and Challenge, there were abrupt increases in RumT, and RR. It was also very apparent that during Recovery the steers did not return to the baseline PreChallenge state. Compared to PreChallenge, Recovery was characterized by persistent lowered daily mean RumT ($P = 0.0010$), RecT ($P = 0.0922$), RR ($P = 0.0257$), PS ($P \leq 0.0001$), and DMI ($P \leq 0.0001$). These results provide evidence that these steers have undergone an allostatic response in response to high heat load, and the new adjusted physiological state post-heat event may not be transient.

LAY SUMMARY

Extreme weather events such as severe heat waves are more frequently affecting cattle production globally. This study aimed to understand the differences in the physiological responses of cattle undergoing exposure to a high heat load challenge, as compared to a moderate heat load. A previous study highlighted that during moderate heat load, grain-fed cattle easily adjusted core body temperature, respiration rate (**RR**), panting score (**PS**), and dry matter intake (**DMI**) but were able to reverse these changes during recovery to return to the PreChallenge (pre-heatwave) state. This reversal did not happen under the high heat load scenario presented here. Changes to body temperature, RR, PS, and DMI were abrupt, and there was rapid readjustment after the heat wave had peaked. In Recovery, the cattle overcorrected the PreChallenge state to become persistently hypothermic, with low RR and PS, while DMI only partially recovered. This suggests that the cattle underwent an allostatic response that resulted in a new state of reduced appetence, metabolism, and growth post-exposure to the high heat load event. These results indicate that the expectations of the future performance of cattle that have experienced severe heat waves need to be adjusted accordingly.

Key words: climate-controlled rooms, feedlot cattle, high heat load, recovery, rumen temperature

INTRODUCTION

Regions of Australia, particularly those where high numbers of cattle feedlots are located, are typically frequented by 3 to 5 heat wave events of moderate to strong intensity each summer (Howden and Turnpenny, 1997; Trancoso et al., 2020). Nienaber et al. (2007) and Mader et al. (2008) defined a heat wave event as a number of successive days, typically 3 to 5, where maximum ambient conditions are above a specific threshold, i.e., heat load index (**HLI**) above 86 for an unshaded black Angus steer (Gaughan et al., 2008). Heat waves are well documented to compromise animal welfare and productivity (Brown-Brandl et al., 2006; Mader, 2014); however, the effects observed are influenced by the intensity and duration of the heat wave event (Gaughan et al., 2013). A significant volume of research has been undertaken to provide mitigation solutions for the feedlot industry, predominantly around the benefits of providing shade (Gaughan et al., 2010; Sullivan et al., 2011; Edwards-Callaway et al., 2021; Maia et al., 2023). Despite the increasing knowledge available in mitigation strategies and the impacts of heat load on the production and wellbeing of cattle, the impact of these conditions continues to be of major significance globally. Understanding the underlying biological impacts of heat load on behavior, performance, and physiological responses has the potential to provide novel insights toward improved management of cattle during exposure to heat load events,

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including heat wave conditions. Previously, the impact of the moderate heat load challenge found that the steers evoked homeorhetic mechanisms highlighting linear responses between daily means of rumen temperature to ambient temperature (**TA**) and the temperature humidity index (**THI**; Sullivan et al., 2022). Furthermore, daily means of respiration rate (**RR**), panting scores (**PS**), and water usage (**WU**) maintained a linear relationship with rumen temperature, whereas dry matter intake (**DMI**) showed an elliptical relationship with rumen temperature (Sullivan et al., 2022). In the current study, the primary objective was to document the physiological responses of feedlot steers during a high heat load challenge and to generate foundational knowledge of animal responses during recovery from the high heat load challenge. A secondary objective of this study was to compare the responses of the feedlot steers during and after high heat load with those of the moderate heat load challenge as reported by Sullivan et al. (2022). The hypothesis of the second objective was that the behavior, performance, and physiological response during and after the moderate and high heat load challenges would be different, highlighting that the means enlisted to cope with sudden high heat load is not a continuum of the responses observed during moderate heat load.

MATERIALS AND METHODS

The study was undertaken during a Southern Hemisphere mid-summer to mid-autumn period (January to May) at the large animal research facility within the Queensland Animal Science Precinct (**QASP**), located at The University of Queensland (**UQ**), Gatton, Australia. The location (27.54°S,152.34°E; 90-m height above sea level) is characterized by hot/humid subtropical weather conditions across the summer and autumn months. The study was approved by the UQ Production and Companion Animals ethics committee (SAFS/460/16) in accordance with the guidelines described by the National Health and Medical Research Council (2013) and Queensland Government (2001) in Australia. Following a similar regimen to that implemented by Sullivan et al. (2022), for this study, a total of 24 purebred Black Angus yearling steers underwent 4 phases: 1) an induction and backgrounding phase, 2) a 60-d feedlot phase, 3) the 17-d controlled climate rooms (**CCR**) phase, and finally 4) a 20-d feedlot finishing phase. The detail of each phase is provided below. The CCR phase was conducted on 2 cohorts (n = 2) of 12 animals per cohort (n = 24). Each cohort of 12 steers was maintained as a group of 12 through the feedlot, CCR, and finishing phases. The cohorts were balanced by BW, temperament, and age. Cohort 2 entered the feedlot 21 d after cohort 1. This was done so that the 2 cohorts entered the CCR with the same number of days on feed (60 d). Only data from the CCR phase are presented here.

Animal Management

The steers were purchased from a commercial property approximately 300 km from QASP and transported by road. The duration of the journey was approximately 4 h. The property was located in a tick-free zone, in the Northern Tablelands of NSW. The district has a temperate climate and the weather in the 3 months prior to transport was characterized by a maximum TA range of 20.3 to 26.0 °C, and a minimum TA range of 4.5 to 13.0 °C. Thus, the steers were not adapted to hot conditions on arrival at QASP. For the study, the 24 steers were selected based on breed (Black Angus). Steers were purchased as young animals with an estimated age of 16 to 18 months. Cattle selections also incorporated evaluating animals for temperament using flight distance and ease of sorting/movements modified from the protocol described by Kilgour et al. (2006). Where flight distance considers the distance that individual animals allowed human proximity without moving away (Kilgour et al. 2006). Ease of sorting/movement was considered as the ability to relocate an individual animal into an adjacent pen from a group of conspecifics (Kilgour et al. 2006).

Induction and Backgrounding Phase

Upon arrival at QASP, the cattle were unloaded into a shaded holding yard (12 m × 12 m). They were visually assessed to ensure that there were no injuries and that they were in good health. While in the holding yard, they had ad libitum access to water and grass hay. Two days after arrival all cattle were vaccinated with a 5-in-1 vaccine for clostridial diseases (Pfizer Animal Health, Australia), trivalent tick fever (*Babesia bovis*, *B. bigemina*, and *Anaplasma centrale*; Department of Agriculture, Fisheries and Forestry, Biosecurity Queensland, Australia), bovine ephemeral fever (**BEF**) vaccine (Webster's live BEF vaccine, Fort Dodge Australia P/L, Baulkham Hills, NSW, Australia), and against bovine respiratory disease (**BRD**, Bovillis MH, Coopers Animal Health, Australia). On the same day, they were treated for endo- and ectoparasites (Cydectin: 5 g·L^{-1} moxidectin solvent, 150 g·L^{-1} hydrocarbon liquid; Fort Dodge Australia, Australia). Following these treatments, the cattle were retained in a nearby 10-ha paddock to graze on predominately Rhodes grass (*Chloris gayana*) pasture without any feed supplements. Steers had access to shade from native trees (*Eucalyptus spp.*) and access to water via a concrete water trough (2.2 m long × 0.45 m wide). The cattle remained in this paddock until feedlot entry.

The cattle were given a second vaccination against BRD and BEF 23 d after the first vaccination, and each steer had a management ear tag with an individual number (1 to 24) inserted in random allocation. Cohort 1 steers (n = 12) were then implanted with a hormonal growth promotant (HGP: Synovex Plus, 200 mg trenbolone acetate + 28 mg estradiol benzoate, Zoetis Australia, Siliverwater, Australia) and were orally administered with an active RFID transmitting rumen temperature bolus (model SSL001-60, Smartstock, Pawnee, OK) using the specified bolus application device (SmartStock). Technical specifications and temperature validation of the boluses have been described previously by Sullivan et al. (2022). Cohort 1 steers were then relocated to feedlot pens. Cohort 2 steers (n = 12) remained on pasture for another 21 d. Upon feedlot induction, these steers were implanted with an HGP, and the rumen boluses were administered.

The weather conditions for the duration of the study were recorded by an automated weather station (GRWS100 Weather Station, Campbell Scientific, Logan, UT) situated at the feedlot pens. The grazing paddock, feedlot pens, and CCR were located within 1 km of each other at QASP. During the induction and backgrounding phase, the overall daily mean (± SD) minimum and maximum TA were 21.4 ± 2.0 °C and 33.0 ± 3.9 °C °C, respectively; and the corresponding daily mean minimum and maximum temperature humidity index (**THI**) were 69.4 ± 3.2 and 81.4 ± 4.0. Information on the specific weather conditions for each cohort during this phase can be found in Supplementary Table S1.

Feedlot Phase

The feedlot phase (60 d) allowed a transition from a pasture-based diet to a feedlot finisher diet. Cattle commenced on a starter diet on entry to the feedlot, transitioning to an intermediate diet between days 6 and 15, and then transitioned to a finisher diet over a 10-d period (Table 1). Cattle were fed twice daily at 0900 and 1300 hours with 50% of the ration fed at each feed. Refusals were removed once daily (0830 hours) and consumption per pen was recorded.

The feedlot pens were described in detail by Sullivan et al. (2022). Briefly, each 27 m × 6 m pen was furnished with a single 3-m concrete feed bunk and a water trough, and the pen was partially shaded (14.4 m^2). With 12 steers·pen^{-1}, the stocking density was 13.5 m^2·$animal^{-1}$. During the final 10 d of the feedlot phase, the steers were moved from the feedlot pen and individually housed in shaded pens (30 m^2, 1 steer·pen^{-1}). The individual pens had a concrete floor, a feed bunk, and a water bowl. This allowed for individual feed intake to be assessed and helped with the habituation of the cattle to the routines they would experience in the CCR. The cattle were weighed every 7 d using the procedure outlined in Sullivan et al. (2022).

The mean nonfasted BW (±SD) on feedlot entry for cohorts 1 and 2 were 490.8 ± 32.3 and 495.4 ± 35.9 kg, respectively (P = 0.7456). Cohort 1 cattle entered the feedlot in early January and cohort 2 entered the feedlot 21 d later, thus the second cohort remained in the backgrounding paddock. The average daily maximum THIs for the 17 d (cohort 1) and final 21 d (cohort 2) in the paddock prior to entry to the feedlot pens fell into the "Alert" THI category (USDC-ESSA, 1970). Cohort 2 experienced slightly warmer conditions (Supplementary Table S1). The average daily minimum THIs for both cohorts were in the "Normal" category during these intervals. In maintaining the chronological separation of the 2 cohorts, cohort 2 entered the CCR 21 days after cohort 1. The weather conditions for both cohorts in the 21 d prior to CCR entry (and while in feedlot pens) is given in Supplementary Table S1. The average daily maximum and minimum THIs for both cohorts fell into "Alert" and Normal THI categories (USDC-ESSA, 1970). Cohort 2 experienced slightly cooler conditions relative to cohort 1 in the 21 d interval prior to CCR entry (Supplementary Table S1).

When housed in the individual pens RR and PS for each animal were obtained at 2-h intervals from 0600 to 1800 hours, by trained personnel. Rumen temperature (**RumT,** °C) data were recorded at 10-min intervals from feedlot induction. These data were used to determine a baseline measure of the cattle prior to entry to CCR.

Climate-Controlled Room Phase

The configuration of the climate-controlled room (CCR) is described in detail by Sullivan et al. (2022). The facility had

Table 1. Diet formulations and nutrient compositions of the rations fed

Ration	Starter[1]	Intermediate[2]	Finisher[3]	Heat load[4]
Ingredient, %				
Sub-batch grain mix[*]	62.1	74.5	86.8	78.7
Whole cottonseed	9.0	9.0	9.0	9.0
Lucerne hay	28.9	16.5	4.2	12.3
Nutrient composition, DM basis				
DM, %	90.1	90.9	90.0	88.3
ADF, %	14.7	16.8	12.1	18.9
NDF, %	24.1	28.0	22.7	29.2
NE_g, MJ/kg	3.0	3.0	3.0	3.0
Fat, %	4.2	5.1	5.2	4.9
Protein, %	16.9	17.1	15.4	14.7
Crude fiber, %	11.5	14.0	9.2	15.4
Nitrogen-free extract, %	61.5	57.9	65.3	59.5
ME, MJ/kg[†]	12.5	12.4	13.0	12.4
DE, MJ/kg	15.4	15.3	16.0	15.3
Feed digestibility, %	83.0	81.6	85.0	82.0
Total digestible nutrient, %	82.5	82.0	86.3	82.7
Digestible protein %	14.1	14.0	13.1	12.1
Starch, %	32.7	27.1	35.4	29.2

[1]Starter ration was offered to cohorts 1 and 2 between days 0 and 5.
[2]Intermetdiate ration was offered to cohorts 1 and 2 between days 6 and 15.
[3]Steers were transitioned to a complete finisher ration over 10 d between days 16 and 25, then were offered to a complete finisher ration from day 26 for the duration of the study.
[4]Due to the withdrawal of steers from cohort 1 during the heat wave Challenge, steers in cohort 2 were offered a heat load ration from the second day of the heat wave challenge for 5 d until cattle entered the Recovery phase when they returned to a complete finisher ration.
[*]Sub-batch grain mix: feedlot pellet[#] 9.2%, steam rolled barley 89.2%, vegetable oil 1.6%.
[#]Feedlot pellet: millrun wheat 55.9%, ammonium sulfate 2.6%, dry rolled wheat 12.5%, calcium carbonate (limestone) 15.6%, Rumensin 100 0.3%, magnesium oxide 0.7%, Availa zinc 100 0.34 %, vegetable oil 3.1 %, salt (NaCl) 2.8%, urea 5.7%, vitamin A 500 0.009%, vitamin E 0.057%, XFE-Select L 0.385.
[†]ME (MJ/kg DM) = 0.12 × CP + 0.31 × EE + 0.05 × CF + 0.14 × NFE. Where CP = crude protein; EE = ether extract; CF = crude fiber; NFE = nitrogen-free extract. The diets were analyzed by a commercial analytical laboratory (Symbio Laboratories Pty Ltd, QLD, Australia).

4 rooms and with 3 pens per room. Individual steers were allocated to steel framed pens (2.5 m × 2.5 m per pen) which were fitted with a water bowl and a feed trough. Water was available ad libitum via easily accessible self-filling water bowls located in each pen throughout the study. The lighting schedule delivered 100% lighting from 0501 to 1859 hours and 10% lighting from 1900 to 0500 hours daily.

Each cohort ($n = 12$ steers) was housed in CCR for this 17-d phase. The CCR entry day mean BW (±SD) for cohorts 1 and 2 were 616.3 ± 37.3 and 614.5 ± 44.4 kg·steer^{-1}, respectively ($P = 0.9138$). The mean DMI of the final 3 d in individual pens were 12.0 ± 1.2 and 12.5 ± 1.4 kg·steer^{-1}·d^{-1} for cohorts 1 and 2, respectively ($P = 0.6495$). Upon entry to the CCR, cohort 1 remained on the finisher diet throughout the 17 d. Following the approved animal ethics protocol, 2 steers in the first cohort were deemed as not coping with the Challenge conditions and were removed from the CCR on days 6 and 7 (the first days of Challenge). To avoid a similar outcome with cohort 2 during Challenge, the cohort 2 steers were offered a heat load ration on day 7 (the second day of Challenge) to assist the steers in coping with the conditions. The heat load ration is included as a remedial action in the animal ethics protocol. The composition of the diets is provided in Table 1. The daily ration was provided once daily at 0700 hours after the prior day's residual feed (refusals) was removed from the feed trough.

Thermal Conditions

The CCR was programmed to deliver diurnal cycling of TA and RH for 3 successive periods of varying conditions (see below). Monitoring of actual conditions was conducted on a 10-min basis throughout using TA and RH data loggers (HOBO UX100-011, Onset, MA). The THI was calculated using the following formula (NOAA, 1976): THI = (0.8 × TA) + {[(RH/100) × (TA − 14.3)] + 46.3}. This THI formula is used by the U.S. National Weather Service for the classification of heat stress conditions (USDC-ESSA, 1970): Normal, ≤74; alert, 75 to 78; danger, 79 to 83; emergency, ≥84.

In the CCR, all animals in both cohorts were subjected 3 sequential periods over 17 d (Figure 1): PreChallenge (days 1 to 5, 5 d), Challenge (days 6 to 12, 7 d), and Recovery (days 13 to 17, 5 d). The evening of day 5 was the start of the transition from PreChallenge to Challenge conditions, and the transition between Challenge to Recovery occurred on the evening of day 12. During PreChallenge and Recovery, the cattle were exposed to thermoneutral conditions within a very narrow range of TA. The overall average daily minimum and maximum TA (±SD) experienced by cohorts 1 and 2 in PreChallenge were 19.4 ± 0.2 and 22.0 ± 1.8 °C, respectively, with corresponding average daily minimum and maximum THI (±SD) of 65.1 ± 0.4 and 70.5 ± 1.8 (Figure 1; Supplementary Table S2). Recovery conditions were similar with the overall average minimum and maximum TA (±SD) at 19.4 ± 0.3 and 21.5 ± 0.8 °C, respectively, and associated mean minimum and maximum THI (±SD) at 65.1 ± 0.1 and 69.6 ± 1.0. Thus, the steers were maintained under the "Normal" THI category during these 2 periods.

The Challenge period was modeled on a sudden onset of a 7-d heatwave that occurred at Dalby Queensland, Australia between January 3 and 9, 2014. This year was notable for heatwaves and other extreme events (http://www.bom.gov.au/climate/current/annual/qld/archive/2014.summary.shtml). The meteorological data were obtained from the Bureau of Meteorology (Australia) site 041522 (Dalby Airport). The event was characterized by respective maximum TA of 41.4 and 42.3 °C on days 1 and 2; 37.4 and 36.1 °C on days 3 and 4, and 29.2 to 32.3 °C on days 5 to 7. Daily minimum TA was 24. 6 °C on days 1 and 2 and ranged between 18.7 and 21.5 °C on days 3 to 7. This event falls under the "Strong" category of heatwave using the heatwave schedule developed by Hahn et al. (2009).

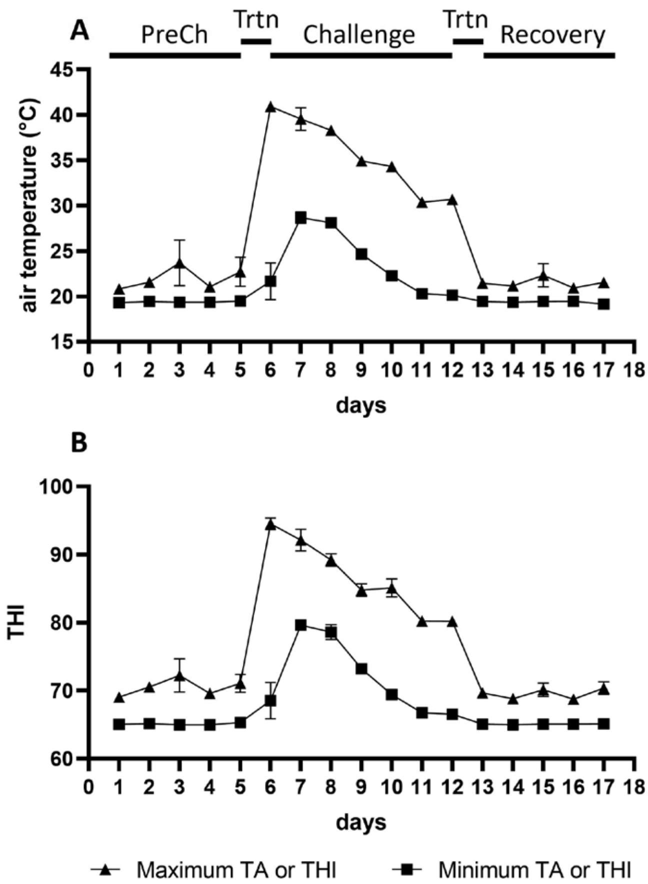

Figure 1. Thermal conditions imposed on 2 sequential cohorts of steers during PreChallenge (days 1 to 5), Challenge (days 6 to 12), and Recovery (days 13 to 17) phases of the climate-controlled conditions highlighting the daily means of maximum and minimum. (A) Ambient temperature (TA, °C). (B) Temperature humidity index (THI).

The simulated heatwave implemented during Challenge consisted of 3 d of very hot (days 6 to 8) and then 2 steps down of 2 d each in TA and THI over the subsequent 4 d (days 9 and 10, and days 11 and 12; Figure 1; Supplementary Table S2). Days 6 to 10 were in the Emergency THI category (where maximum daily THI ≥ 84), and days 11 and 12 were in the Danger category (where maximum daily THI lies between 79 and 83). The overnight minimum THI for days 7 and 8 ranged between 77.5 and 79.8; for days 9 and 10, the overnight minimum THI ranged between 69.0 and 73.4; and the overnight minimum for days 11 and 12 was between 66.4 and 67.1 (Figure 1; Supplementary Table S2).

Diurnal cycling of TA and RH was implemented during Challenge to simulate a circadian cycle. To achieve this, the CCR was set to deliver hourly incremental increases in TA from 0700 hours, arriving at the daily maximum at 1200 hours which was maintained till 1600 hours, from whence the TA underwent hourly reductions to reach the daily minimum at 2200 hours.

The RH profile was the inverse of the TA profile, so RH was greatest when TA was at its minimum. The simulated heatwave applied to cohorts 1 and 2 during Challenge applied a morning TA rise and afternoon temperature fall of 2.0 °C·h^{-1}. For comparison, the morning rate of TA rise for the 2014 heatwave described above was 2.3 °C·h^{-1} untill the daytime maximum and then fell at 3.0 °C·h^{-1} untill the evening plateau.

The thermal conditions for cohorts 1 and 2 slightly differed during Challenge (Supplementary Figure S1 and Tables S2 and S3). Adjustments were made to the regime applied to cohort 2 in response to 2 animals having been withdrawn from cohort 1 during Challenge. The main differences in climate schedules between the 2 cohorts were in the daytime conditions on days 6 to 8, and the nighttime conditions on days 5 to 7. Cohort 1 experienced daily maximum TA of 41.0, 40.8, and 38.0 °C on days 6 to 8, respectively (with daily maximum THI ranging over 94 to 95), whereas cohort 2 experienced slightly cooler daily maximum TA of 40.8, 38.4, and 38.6 °C, respectively, on those days (with daily maximum THI in the range of 88 to 94). Furthermore, cohort 1 experienced an abrupt transition into Challenge conditions in the nighttime so that the daily minimum TA for days 5 to 7 were 19.3, 19.7, and 28.0, respectively (with corresponding daily minimum THI of 65.0, 65.8, and 78.8). The rise in daily minimum TA and THI was more gradual for cohort 2; the daily minimum TA were 19.7, 23.7, and 28.8 °C for days 5 to 7, respectively (corresponding daily minimum THI were 65.7, 71.2, and 79.5; Supplementary Figure S1 and Tables S2 and S3).

Physiological Data Collection

Physiological data were collected from days 3 to 17 of the CCR phase; however, the frequency of observations for data collection varied according to the day and period (Supplementary Table S4). All data collection timepoint recorded RR, PS, and WU. For the PreChallenge period, day 4 was selected as the exemplar PreChallenge day as the steers had 4 full days in the CCR to adjust to changed housing conditions and routine. On day 4, hourly observations were conducted from 0600 to 0500 hours (into day 5). On days 3 and 5, observations were performed during the daytime only, i.e., at 0600 hours, at 1000 hours, and then every 2 h till 1800 hours. During Challenge, hourly observations were conducted from 0000 to 2300 hours (except for 0800 hours) on days 7 to 12. On day 6, the first day of Challenge, observations commenced from 0600 hours and proceeded hourly till 2300 hours. During the Recovery period, day 15 was selected as the exemplar Recovery day since the steers had been returned to thermoneutral conditions for over 48 h. Similar to day 3 (PreChallenge), hourly observations were conducted on day 15 from 0600 to 0500 hours (on day 16). On the remaining Recovery days (days 13, 14, 16, and 17), observations were performed during the day only, i.e., at 0600 hours, at 1000 hours, and then every 2 h till 1800 hours. On day 17, the steers were being prepared to exit the CCR and thus the 1800 hours observations were brought forward to 1700 hours.

Prior to the 0700 hour feed allocation, refusals were collected for weighing and calculation of the prior day's intake (i.e., weight of feed allocated – weight of refusals). Daily feed intake was then converted to DMI based on DM percentage (DM, %) obtained from dietary analysis (Table 1). Due to malfunction of the scales located at the CCR facility at the commencement of that phase, BW was not obtained. The methodologies for determining the RR, PS, and WU are given in Sullivan et al. (2022). Rectal temperatures (**RecT, °C**) were obtained on days 3, 5, 7 to 13, 15, and 17 at 0700 hours by insertion of a digital thermometer (Becton, Dickinson and Company, NJ) into the rectal cavity.

The rumen boluses recorded rumen temperature every 10 min, and each new reading alongside the previous 10 readings was radio transmitted (via yagi antenna) to a base station and uploaded to a database (TechTrol Inc., Pawnee, OK). The influence of recent WU on the analysis and interpretation of RumT data was minimized by removing values of ≤35 °C. As discussed by Sullivan et al. (2022), currently there is no standardized methodology to deal with this issue.

Statistical Analysis

Two steers from each cohort were withdrawn from the CCR during Challenge. These steers were withdrawn from the study due to an adverse response to the prevailing heat load conditions, specifically, steers exhibited a combination of highly agitated/distressed behaviors (sunken eyes and increased vocalizations); rapid increases to RumT over a 30- to 90-min period, where RumT exceeded 42 °C; markers of respiratory distress including elevated RR > 160 bpm, PS ≥ 3.5 and hypersalivation; signs of acute acidosis symptoms (rumen pH > 5.0); and a significant reduction or termination or water intake. All data collected on these animals from any time point was excluded from the analyses; thus, the analyses are based on the data collected on 10 steers per cohort. Individual 10-min RumT were converted to individual hourly means. Individual animal maximum, mean, and minimum RumT were calculated from the hourly means over the 0600 to 0559 hours of the following day to coincide with observational data collection times. RR and PS were measured on all steers at multiple timepoints during most days in the CCR. As shown in Supplementary Table S4, on days 4, 6 to 12, and 15, RR and PS were taken between 22 and 24 times daily (intended hourly schedule). On days 3, 5,13, 14, 16, and 17, measures were taken during daytime hours on a 2-h schedule. Individual animal daily maximum, mean, and minimum RR and PS were calculated from these data and were used to determine daily maximum, mean, and minimum RR and PS for all animals ($n = 20$). To compare periods, overall period averages were calculated. Individual animal DMI, WU, and RecT were measured only once daily and were used to calculate a daily means for all animals ($n = 20$). As above, period means of these variables were also determined.

Prism 9.0 (GraphPad Software, San Diego, CA) was used to determine and describe a simple linear relationship amongst variables (Pearson correlation coefficient, r) and the level of statistical significance (P value). This analysis was applied to discover relationships among the physiological variables with THI, TA, and RumT. Initially, the analysis was conducted with the data across all 17 d in the CCR. When it became evident that, in most cases, there was no simple relationship across the 3 periods, the analysis then focused on behavior within each period, especially during the Challenge period. The Student's t-test was used to find and determine levels of significant difference between period means. P values below 0.05 were considered significant whereas when P values ranging between 0.05 and 0.08 was described as a trend toward significance.

Analysis of Cohorts 1 and 2 Rumen Temperatures

Slight changes were made to the thermal conditions applied to cohort 2 in response to 2 animals having been withdrawn from cohort 1 during Challenge (see above and Supplementary Figure S1 and Tables S1 and S2). Also, cohort 2 was offered the heat load diet from day 7 (the second day of Challenge), whereas cohort 1 completed Challenge on the finisher ration. The slight differences in the treatments imposed on the 2 cohorts may have led to different physiological responses, especially during Challenge.

Body temperature is the overall measure of the integration of well-known mechanisms to reduce exogenous and endogenous heat load (e.g., respiration/panting, sweating, shunting of blood supply to the peripheral tissues, reduced feed intake to decrease endogenous heat load, reduced movement, shade seeking, and increased water consumption). As individual animals may invoke or place emphasis on differing subsets of these mechanisms at different times of the day, or over days of Challenge, we chose to focus on body temperature (RumT) as the variable to assess any differences in the responses of the 2 cohorts. A generalized linear model (GLM) of analysis of variance in SAS program (version 9.4 TS1M1, SAS Institute Inc., Cary, NC) was performed on the hourly RumT data of the 2 cohorts. For comparison purposes, the analysis was performed for 3 metrices, daily maximum, mean, and minimum RumT, respectively. For each metric, e.g., daily maximum RumT, the GLM model contained mean RumT, cohort, period, day cohort nested within climate control chamber, cohort nested within period, cohort nested within day, in addition to linear and quadratic terms accounting for day across cohorts and as fixed effects and individual animal id as the random term. The model aimed to examine whether individual fixed effects had significant impacts on maximum RumT, mean RumT, and minimum RumT. These include testing: 1) cohort difference across all periods, subsequently referred to as cohort; 2) room difference within individual cohort across periods, using room nested within cohort; 3) period difference across cohorts, as per the previously described periods; 4) the interactions between period and cohort, including period within cohort as a nested term; 5) linear and quadratic terms of the day across cohorts and periods; and 6) linear and quadratic terms of day nested within each cohort. The linear and quadratic day terms were included as these terms are able to elucidate daily RumT change rate, specifically, a regression slope, followed linear and nonlinear curves. Similarly, the inclusion of linear and quadratic day terms within the cohort provides an evaluation of daily RumT change rate between the cohorts, identifying if 2 cohorts followed a similar daily RumT change rate.

When comparing the cohort rumen temperatures across the 3 experimental periods, results from the ANOVA and from the GLM clearly highlighted that there were no differences between the 2 cohorts, as indicated by the Cohort term in the model, for maximum ($P = 0.8641$), minimum ($P = 0.5352$), or mean ($P = 0.7190$) RumT. No differences between the two cohorts were observed for maximum, minimum, or mean RumT, in the linear ($P \geq 0.5116$) or quadratic ($P \geq 0.7365$) comparisons of RumT change rate across 3 phases. In addition, there was no interaction between period or cohort, nested within period, for maximum ($P = 0.2008$), minimum ($P = 0.6642$), and mean RumT ($P = 0.7365$). However, the daily change of RumT did impact maximum, minimum, and mean RumT ($P < 0.0001$).

For maximum RumT, P values of 0.6936 and 0.9843 were obtained for the difference between the 2 cohorts, within Challenge and Recovery periods, respectively. A significance of $P = 0.0164$ indicated a difference between the 2 cohorts in PreChallenge mostly likely reflecting the inadvertent transient increase in maximum TA, to 26.2 °C, on day 3 and greater maximum TA on day 5 (24.3 °C) in cohort 2. Furthermore, $P = 0.1466$ and $P = 0.6416$ were observed with mean RumT for Challenge and Recovery periods, respectively. A significance of $P = 0.0509$ indicated a trend toward a difference in mean RumT between the 2 cohorts during PreChallenge. There were no differences between the 2 cohorts for minimum RumT for any period (PreChallenge, $P = 0.2781$; Challenge, $P = 0.2413$; Recovery, $P = 0.1411$). As a result, the RumT data from 2 cohorts were combined.

Daily mean RR of the 2 cohorts was assessed also for differences. The overall daily mean RR across the 17 days in the CCR was not different (cohort 1 vs. cohort 2: 81.1 ± 3.2 bpm vs. 87.8 ± 2.8 bpm; $P = 0.6045$). A difference in daily mean RR was detected for PreChallenge (cohort 1 vs. cohort 2: 55.2 ± 1.2 bpm vs. 70.2 ± 2.6 bpm; $P = 0.0039$). As noted above, the difference during PreChallenge was a consequence of greater maximum TA unintentionally delivered to cohort 2 on days 3 and 5 (Supplementary Figure S1 and Tables S2 and S3). Similarly, there were no differences in overall daily maximum RR (cohort 1 vs. cohort 2: 112.5 ± 4.0 bpm vs. 117.4 ± 3.5 bpm; $P = 0.7685$) and overall daily minimum RR (cohort 1 vs. cohort 2: 53.1 ± 2.3 bpm vs. 60.9 ± 2.3 bpm; $P = 0.4357$). In each case, differences were detected for the PreChallenge period, with P values of 0.0287 and 0.0132 obtained for daily maximum and minimum RR, respectively.

RESULTS

Behavior of Physiological and Performance Measures During Thermal Challenge and Recovery

Rumen and rectal temperatures.

As anticipated, RumT closely followed TA and THI over the PreChallenge, Challenge, and Recovery phases (Figure 2A). The greatest daily mean RumT (±SEM), 40.47 ± 0.11 °C, was observed on day 7; an elevation of 1.71 °C above the PreChallenge mean (38.76 ± 0.036 °C, Table 2). The greatest daily minimum RumT, 39.80 ± 0.13 °C, occurred also on day 7, whereas the greatest daily maximum RumT, 41.35 ± 0.13 °C, was recorded on day 6 which was the first day of Challenge (Figure 2A). Following this, RumT gradually declined as conditions eased. On day 12, the lowest daily mean RumT, 38.29 ± 0.28 °C, was observed. The lowest daily minimum RumT, 37.47 ± 0.13 °C, occurred on day 13, and the lowest maximum RumT occurred on day 14 (38.85 ± 0.08 °C, Figure 2A). With the exception of day 6 (transition day), the mean difference between daily maximum and minimum RumT was 1.41 ± 0.03 °C, during the 17 d in the CCR. In all cases, the overall means for RumT during Recovery were stable and less than the overall means of PreChallenge RumT (Table 2). The overall daily mean RumT in Recovery was 0.33 °C less than the corresponding PreChallenge mean ($P < 0.0001$, Table 2).

The time course of daily rectal temperature (RecT, taken at 0700 hours) was like that of RumT (Figure 2B). Note that RecT was obtained on 11 d only. The greatest daily mean RecT was recorded on day 7 (40.21 ± 0.12 °C) and the lowest occurred on day 13 (38.22 ± 0.05 °C). The overall mean RecT during Recovery was less (0.26 °C) than the overall PreChallenge mean ($P < 0.0001$, Table 2).

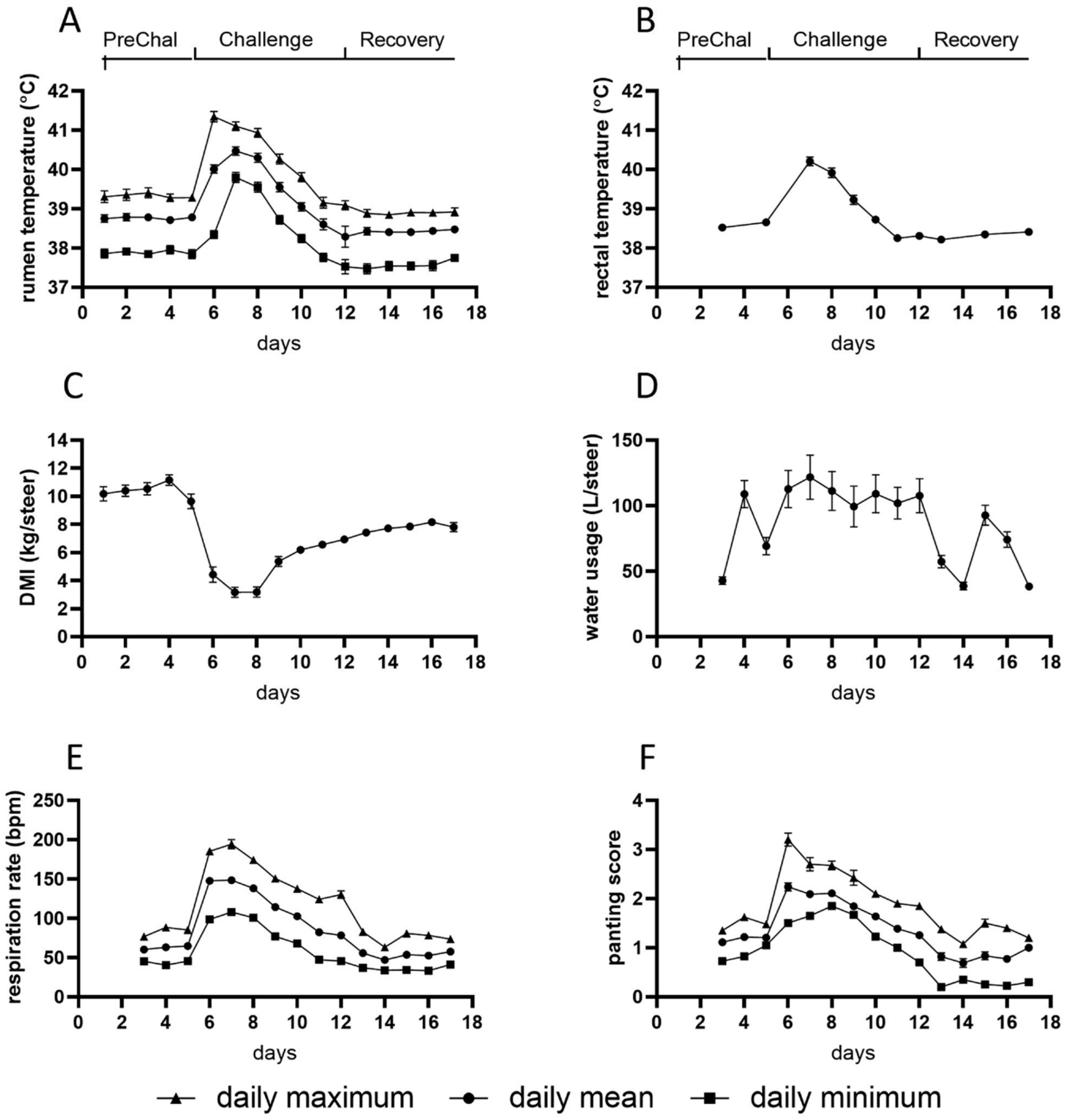

Figure 2. Daily maximum, mean, and minimum. (A) Rumen temperature (RumT, °C ± SEM); (B) 0700 hours rectal temperature (RecT, °C ± SEM; recorded on days 3, 5, 7 to 13, 15, and 17); (C) daily mean dry matter intake (DMI, kg·steer^{-1}·day^{-1} ± SEM); (D) daily mean water usage (WU, L·steer^{-1}·day^{-1} ± SEM); (E) daily maximum, mean and minimum respiration rate (RR, breaths per minute ± SEM); and (F) daily maximum, mean, and minimum panting scores (±SEM).

DMI and WU.

Daily DMI declined from day 6. The overall PreChallenge daily DMI (± SEM) of 10.4 ± 0.20 was reduced to 3.2 ± 0.36 kg·steer^{-1}·d^{-1} on days 7 and 8 (Challenge, Figure 2C). There was a large increase in daily mean DMI on day 9, but this rate of increased DMI was not sustained despite the easing conditions through days 10 to 12 (Challenge) and into the Recovery phase. The rate of increase in DMI between days 10 and 16 was approximately 0.33 kg·steer^{-1}·d^{-1}. The overall daily mean DMI (± SEM) in Recovery was 7.8 ± 0.11 kg·steer^{-1}·d^{-1}, which was less that DMI during PreChallenge (10.4 ± 0.20 kg·steer^{-1}·d^{-1}, $P < 0.0001$; Table 2).

WU was highly variable during PreChallenge and Recovery (Figure 2D). Daily mean WU was more consistent during Challenge increasing to between 99 and 122 L·steer^{-1}·d^{-1} and the overall Challenge mean WU was 109.l ± 5.4 L·steer^{-1}·d^{-1}. The greatest WU was achieved on day 7 (121.8 ± 16.9 L·steer^{-1}·d^{-1}) and even though conditions were cooling between days 10 and 12, daily mean WU remained elevated (> 100 L·steer^{-1}·d^{-1}).

Table 2. Pooled maximum means and minimum for RumT (°C), RR (breaths per minute), RecT (°C), PS, DMI ($kg\cdot steer^{-1}\cdot day^{-1}$), and WU ($L\cdot steer^{-1}\cdot day^{-1}$) during the PreChallenge (days 1 to 5) and Recovery (days 13 to 17) periods and significance (*P* value) between these periods

Parameter	Period	Overall daily maximum		Overall daily mean		Overall daily minimum	
		PreChallenge	Recovery	PreChallenge	Recovery	PreChallenge	Recovery
RumT, °C	Mean	39.33	38.89	38.76	38.43	37.88	37.57
	SEM	0.05	0.04	0.04	0.03	0.05	0.05
	**P* value	—	0.0002	—	0.0010	—	0.0084
RR, bpm	Mean	83.4	75.7	62.7	53.4	43.6	35.9
	SEM	2.30	1.74	1.72	1.20	1.66	1.04
	**P* value	—	0.147	—	0.0257	—	0.0544
RecT, °C	Mean	—	—	38.59	38.33	—	—
	SEM	—	—	0.04	0.03	—	—
	**P* value	—	—	—	0.092	—	—
PS	Average	1.48	1.31	1.18	0.82	0.88	0.27
	SEM	0.03	0.03	0.02	0.03	0.05	0.05
	**P* value	—	0.087	—	<0.0001	—	<0.0001
DMI, $kg\cdot steer^{-1}\cdot day^{-1}$	Mean	—	—	10.39	7.80	—	—
	SEM	—	—	0.20	0.11	—	—
	**P* value	—	—	—	<0.0001	—	—
WU, $L\cdot steer^{-1}\cdot day^{-1}$	Mean	—	—	67.1	53.4	—	—
	SEM	—	—	5.9	3.3	—	—
	**P* value	—	—	—	0.240	—	—

Abbreviations: DMI, dry matter intake; PS, panting score; RecT, rectal temperature; RR, respiration rate; RumT, rumen temperature; WU, water usage.

RR and PS.

There were similarities between RumT and RR responses over the 3 phases, the exception being on day 12 when the decline in daily maximum RR stalled (Figure 2E). The greatest daily maximum RR (±SEM) occurred on day 7 (194.3 ± 5.9 bpm), and on days 6 and 7 the steers experienced the largest difference (86.4 bpm) between maximum and minimum RR. The lowest daily minimum RR (±SEM) was observed on day 16 (33.3 ± 2.6 bpm). Daily mean RR during Recovery was stable and less than the overall PreChallenge mean RR (Figure 2E). The overall daily mean RR (±SEM) during Recovery was 53.4 ± 1.2 bpm as compared to the PreChallenge overall mean of 62.7 ± 1.7 bpm ($P < 0.0001$; Table 2), a difference of 9.3 bpm and 15% less than the PreChallenge overall mean RR. The same comparisons for overall daily minimum and maximum RR revealed differences between PreChallenge and Recovery RR.

Daily mean and maximum PS generally followed the trajectories observed for RR. The greatest PS occurred on day 6 with the respective daily mean and maximum PS (±SEM) determined to be 2.2 ± 0.08 and 3.2 ± 0.13 (Figure 2F). In contrast, daily minimum PS rose steadily so that it peaked on day 8 at 1.86 ± 0.05; and then fell so that the lowest daily mean minimum PS occurred on day 13 (first day of Recovery; 0.20 ± 0.09). In Recovery, the overall daily maximum, mean, and minimum PS were less ($P < 0.0001$) than the corresponding PreChallenge means (Table 2).

Relationships of physiological and performance measures with climatic conditions.

Rectal temperature, RumT, DMI, and WU were all characterized by differing behaviors in response to altered daily mean THI or TA in each of the 3 periods (Figures 3 and 4; Supplementary Figure S4). Preliminary exploration of the relationships of mean RumT, RecT, and DMI with mean TA and mean THI across the 3 phases revealed the relationships were nonlinear. The results obtained during the PreChallenge and Recovery phases manifest into distinct clusters, whereas results from the Challenge present as a linear relationship.

To better describe and quantify the responses of mean RumT, RecT, and DMI with mean TA and mean THI, the rate of transition was determined between PreChallenge and the peak Challenge conditions (days 6 and 7). The transition rate was taken as the slope (m) of the linear equation ($y = mx + c$) obtained when applied to all PreChallenge values and the early Challenge values (days 6 and/or 7). The transition rate differs from the rate of change during Challenge, the latter representing the decline in core body temperature or rise in DMI, as the peak of the heatwave simulated in Challenge passes and conditions start to ease.

In response to the sudden onset of heat load, the transition rate in daily mean RumT was 0.094 °C per unit increase in daily mean THI (Figure 3A). The corresponding transition rate relative to daily mean RumT was 0.123 °C for each 1 °C rise in TA (Figure 4A). During Challenge, daily mean RumT showed a linear relationship and strong positive correlation with daily mean THI ($r = 0.988$, $P < 0.0001$; Figure 3A). As conditions cooled during Challenge, the rate of change of mean RumT was 0.173 °C for each unit mean THI^{-1}, which is almost 2-fold greater than the transition rate. The daily mean RumT from the PreChallenge and Recovery periods were not contiguous with Challenge RumT and thus did not contribute to the linear relationship (Figure 3A). Daily mean RumT strongly correlated with daily mean TA during Challenge ($r = 0.992$, $P < 0.0001$, Figure 4A). The linear relationship described a rate of change of mean daily RumT of

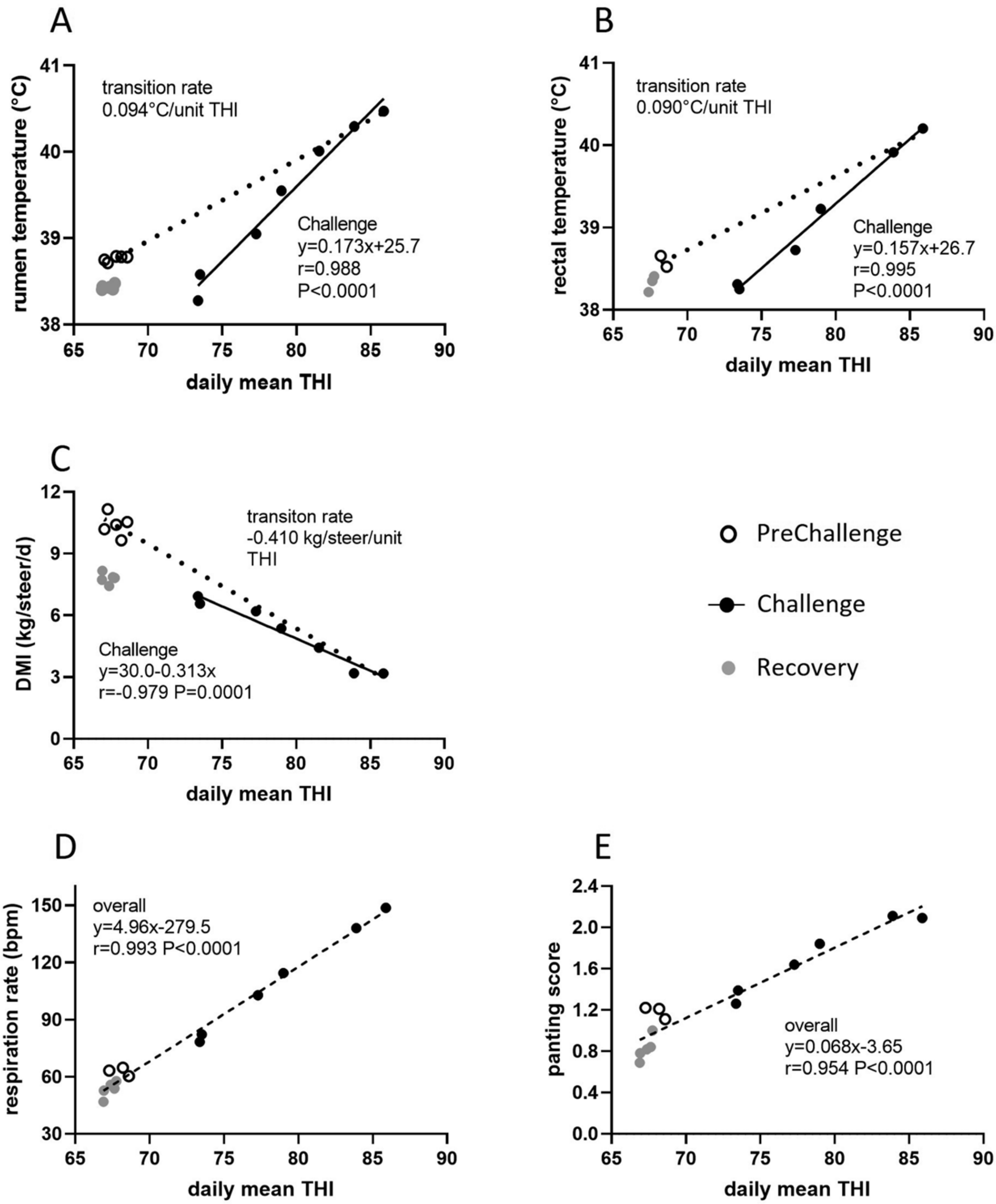

Figure 3. Relationships between daily mean temperature humidity index (THI) during PreChallenge (days 1 to 5), Challenge (days 6 to 12), and Recovery (days 13 to 17) phases of the controlled climate study. (A) Rumen temperature (RumT, °C); (B) 0700 hours rectal temperature (RecT, °C ± SEM; recorded on days 3, 5, 7 to 13, 15, and 17); (C) daily mean dry matter intake (DMI, kg·steer^{-1}·day^{-1}); (D) respiration rate (RR, breaths per minute); and (E) panting score. The equations describing the linear relationships with THI during Challenge (continuous line) or overall (dashed line) are given along with the Pearson correlation coefficient (*r*). The dotted line represents the transition from PreChallenge (days 1 to 5) to Challenge (days 6 to 12) conditions that occurred between days 5 and 6, and the transition rate is given.

0.237 °C per °C change in mean TA, noting that this is also double that of the transition rate. As with THI, the linear relationship between mean daily RumT and mean daily TA was restricted to the Challenge period, with no contribution from the PreChallenge and Recovery daily mean RumT (Figure 4A).

The above relationships that occurred for extremes of the day were evaluated. Firstly, the relationships between daily minimum, mean and maximum RumT with daily THI and TA consistently returned the linear relationships during the Challenge period which were independent of PreChallenge and Recovery (Supplementary Figures S2 and S3). Daily

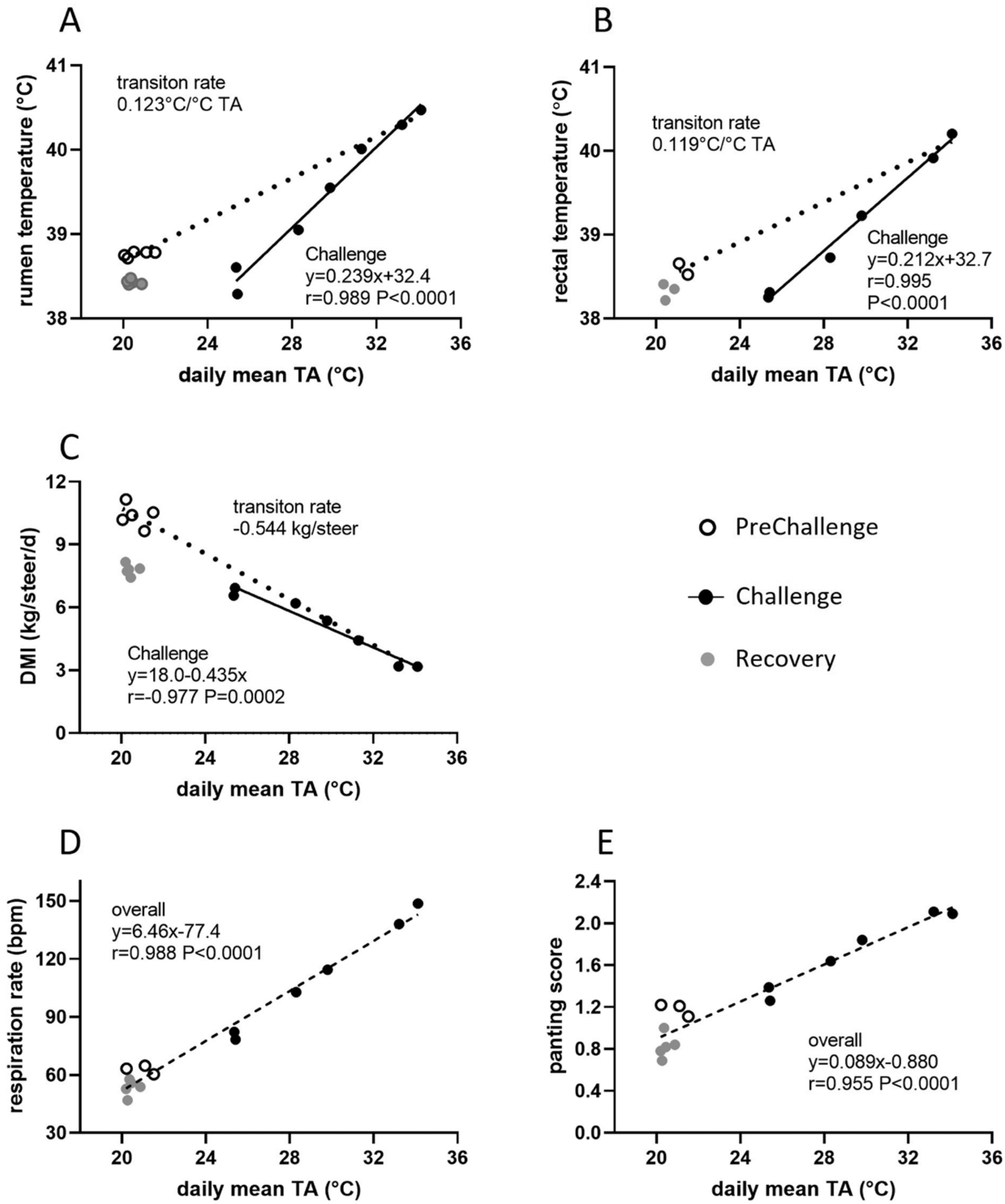

Figure 4. Relationships between daily mean ambient temperature (TA, °C) during PreChallenge (days 1 to 5), Challenge (days 6 to 12), and Recovery (days 13 to 17) phases of the controlled climate study. (A) Rumen temperature (RumT, °C); (B) 0700 hours rectal temperature (RecT, °C ± SEM; recorded on days 3, 5, 7 to 13, 15, and 17); (C) daily mean dry matter intake (DMI, kg·steer^{-1}·day^{-1}); (D) respiration rate (RR, breaths per minute); and (E) panting score. The equations describing the linear relationships with THI during Challenge (continuous line) or overall (dashed line) are given along with the Pearson correlation coefficient (*r*). The dotted line represents the transition from PreChallenge (days 1 to 5) to Challenge (days 6 to 12) conditions that occurred between days 5 and 6, and the transition rate is given.

mean RumT had greatest correlation with daily minimum THI ($r = 0.992$, $P < 0.0001$) but was least sensitive to it (rate of change: 0.154 °C per unit change in daily minimum THI; Supplementary Figure S2A). The least robust relationships during Challenge were between daily maximum THI and daily minimum, mean, and maximum RumT; Pearson correlation coefficients (r) ranged between 0.966 and 0.973 (Supplementary Figure S2C).

The mean RumT transition rates relative to maximum and minimum THI were 0.080 and 0.116 °C·unit THI^{-1}, respectively (Supplementary Figure S2A and C), and relative to maximum and minimum TA were 0.095 and 0.180 °C per 1 °C rise

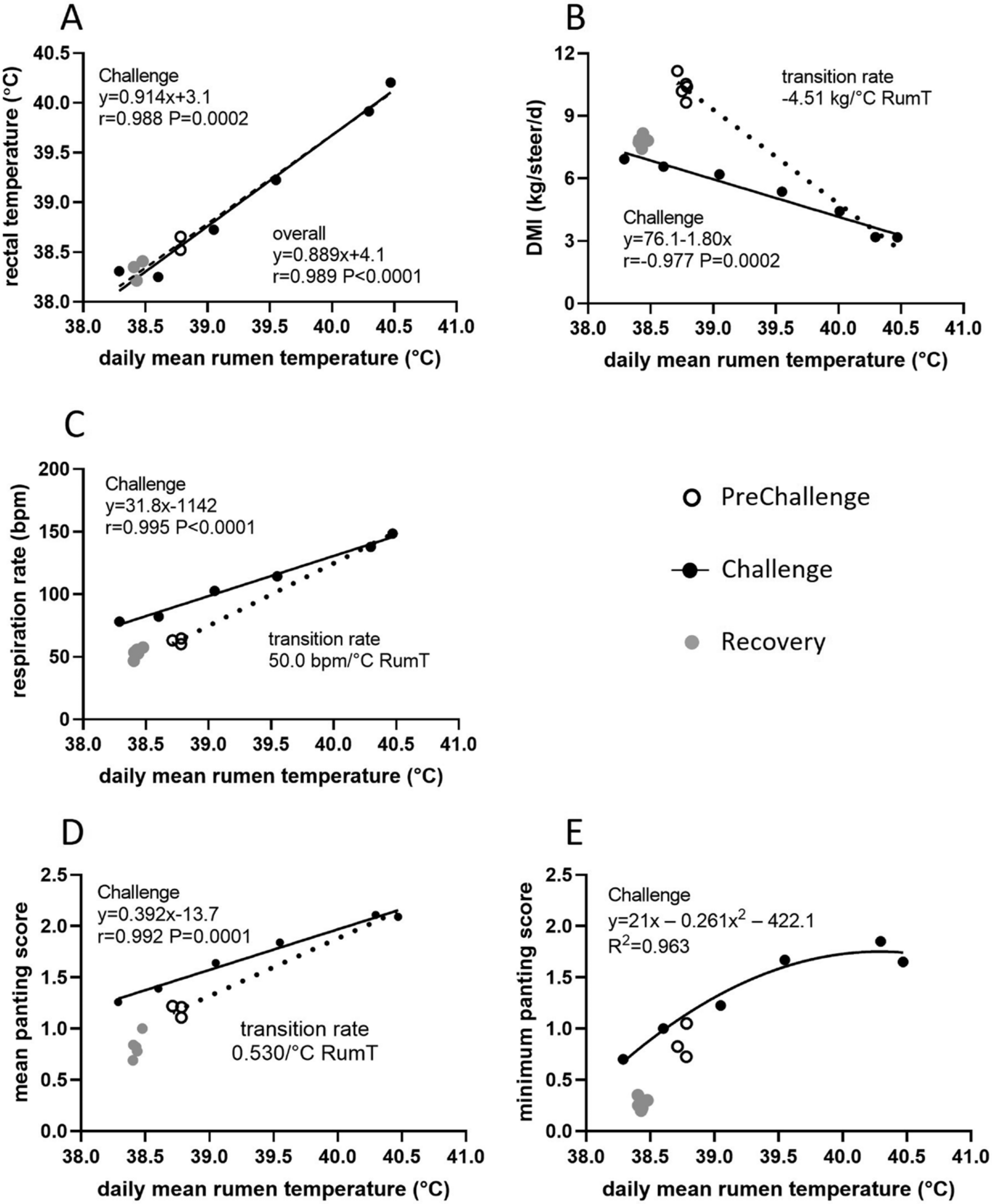

Figure 5. Relationships between daily mean rumen temperature (RumT, °C) during PreChallenge (days 1 to 5), Challenge (days 6 to 12) and Recovery (days 13 to 17) phases of the controlled climate study. (A) 0700 hours rectal temperature (RecT, °C ± SEM; recorded on days 3, 5, 7 to 13, 15, and 17); (B) daily mean dry matter intake (DMI, kg·steer^{-1}·day^{-1}); (C) daily mean respiration rate (RR, breaths per minute); (D) daily mean panting score (PS); and (E) daily minimum PS. The equations describing the linear relationships with THI during Challenge (continuous line) or overall (dashed line) are given along with the Pearson correlation coefficient (*r*). The polynomial equation and coefficient of determination (R^2) are represented in (E) for daily minimum PS. The dotted line represents the transition from PreChallenge (days 1 to 5) to Challenge (days 6 to 12) conditions that occurred between days 5 and 6, and the transition rate is given.

in TA, respectively (Supplementary Figure S3A and C). The most rapid transition rates were for daily minimum RumT responding to rises in minimum THI and TA at rates of 0.132 and 0.199 °C per unit increment, respectively (Supplementary Figures S2A and S3A). Interestingly, under the conditions of this experiment, linear relationships during Challenge between daily minimum, mean and maximum RumT with daily TA returned superior correlation coefficients ($r \geq 0.982$) and levels of significance ($P \leq 0.0005$) than the relationships with THI (Supplementary Figures S2 and S3).

The transition rates for mean RecT were 0.090 °C per unit daily mean THI (Figure 3B) and 0.119 °C per 1 °C increase in daily mean TA (Figure 4B). These rates of increase were 0.0040 °C mean TA^{-1} less than mean RumT transition rates. RecT during Challenge displayed very similar behavior as daily mean RumT (Figures 3B and 4B). RecT showed a strong positive linear relationship with mean THI during Challenge ($r = 0.995$, $P < 0.0001$) with a rate of increment of 0.157 °C per unit change in mean THI, and 0.212 °C·°C mean TA^{-1}. These rates of response are less than those observed for mean RumT.

The transition rate for daily mean DMI (kg·steer^{-1}·d^{-1}) were −0.41 kg·THI unit^{-1} and −0.54 kg·°C TA^{-1}, respectively (Figures 3C and 4C). During Challenge, daily mean DMI showed a strong negative linear relationship with daily mean THI ($r = -0.979$, $P = 0.0001$) with a rate of reduction of DMI at 0.31 kg·steer^{-1} (Figure 3C). If Challenge and Recovery DMI were considered contiguous, the negative linear relationship with daily mean THI yields a rate of change of −0.245 kg·steer^{-1}·unit mean THI^{-1} ($r = -0.986$, $P < 0.0001$). It was notable that the DMI transition rate was greater compared to the rate during Challenge (−0.41 vs. −0.31 kg·steer^{-1}·unit THI^{-1}). There was a strong negative linear relationship between daily mean DMI and daily mean TA ($r = -0.977$, $P = 0.0002$) which prescribed a rate of decrease in DMI of 0.44 kg·steer^{-1}·°C mean TA^{-1} (Figure 4C). By comparison, the DMI transition rate was −0.54 kg·steer^{-1}·°C TA^{-1}.

Unfortunately, the high variability of daily mean WU in the PreChallenge and Recovery periods precluded confident discovery of relationships between WU and the climatic conditions across the 3 phases (Supplementary Figures S4A and B). This did not allow for credible determination of transition rates for WU.

RR and PS.

In contrast to the body temperature measures, DMI, and WU, it was evident that the linear relationships between daily mean RR and daily mean THI or TA extended across PreChallenge, Challenge, and Recovery (Figures 3D and 4D). The overall linear equation with mean daily THI predicted a constant rate of increase in mean daily RR of 4.96 bpm·unit THI^{-1} over the entire daily mean THI range of 66.9 to 85.9 ($r = 0.993$, $P < 0.0001$; Figure 3D). The rate of rise of daily RR is predicted to be 6.46 bpm·°C mean TA^{-1} over the range of 20.01 to 34.12 °C ($r = 0.988$, $P < 0.0001$; Figure 4D).

The PS had a similar pattern to RR (Figures 3E and 4E). In respect of mean daily THI, mean daily PS maintained a linear relationship during Challenge ($r = 0.997$, $P = 0.0002$) and could be extended to the PreChallenge and Recovery periods (overall: $r = 0.954$, $P < 0.0001$; Figure 3E). The overall rate of increment of mean daily PS was 0.068 per unit mean THI^{-1}. For mean daily mean TA, the respective rate of change was 0.089 PS units per °C mean TA (Figure 4E).

Relationships of Rumen Temperature with Physiological and Performance Measures

Not unexpectedly, the daily means of RecT and RumT were highly correlated for all days in the CCR ($r = 0.989$, $P < 0.0001$; Figure 5A). The linear relationship indicated that RecT increased at the rate of 0.889 °C per degree increase in mean RumT. Daily mean DMI, mean RR, and mean and minimum PS, the 3 phases possessed apparently independent relationships with RumT (Figures 5B–E). Transition rates, the change relative to mean RumT between PreChallenge and peak Challenge conditions, were determined for these variables. During the PreChallenge DMI clustered independently of Challenge and Recovery results, but there was a strong negative linear relationship between DMI and daily mean RumT during Challenge ($r = -0.976$, $P = 0.0002$; Figure 5B). The Challenge rate of reduction in DMI was 1.78 kg·steer^{-1} for each 1 °C rise in daily mean RumT; much less than the transition rate of −4.5 kg·steer^{-1}·°C mean RumT^{-1} (Figure 5B). In the case of WU, a moderately correlated linear relationship ($r = 0.632$) was detected between WU and RumT, but it was not significant ($P = 0.1279$; Supplementary Figure S4C).

A linear relationship was evident between daily mean RumT and daily mean RR during Challenge ($r = 0.995$, $P < 0.0001$; Figure 5C). The Challenge rate of increase of mean RR in response to increasing mean RumT was 31.8 bpm per 1 °C increase in mean RumT. The transition rate as the steers underwent the sudden impost of high heat load was 50 bpm·°C RumT^{-1} which is a greater rate than seen during Challenge. The daily mean RR observed during PreChallenge and Recovery are below Challenge daily mean RR, reiterating their distinction from the response during Challenge and each other (Figure 5C). Maximum RR showed the greatest rates of increase between 55 and 65 bpm·°C^{-1} in daily minimum, mean, and maximum RumT (Supplementary Figure S5).

Daily mean PS displayed a linear relationship with mean daily RumT during Challenge ($r = 0.992$, $P = 0.0001$; Figure 5D). The Challenge rate of change in daily mean PS relative to daily mean RumT was 0.39 PS unit·°C mean RumT^{-1}, while the transition rate was 0.53 PS unit·°C RumT^{-1}. The daily mean PS obtained during PreChallenge and Recovery showed no relationship with mean RumT. Daily maximum PS maintained linear relationships with mean RumT as well as daily minimum and maximum RumT during Challenge (Supplementary Figure S6A–C). However, minimum PS plateaued at high RumT, such that over a mean RumT range of 39.5 to 40.5 °C, minimum PS constrained to 1.65 to 1.85 PS units (Figure 5E). The relationships of minimum PS and RumT were best described by polynomial equations (Figure 5E and Supplementary Figure S6A–C).

DISCUSSION

Interactions of Core Temperatures with THI and TA

One of the goals of biometeorologists working with production animals is to provide robust predictive models of the behavior of core body temperature, DMI, and WU in relation to ambient conditions, especially during and after heatwave events. It is well understood through decades of research that when heat stress thresholds, largely described by TA and/or THI, are exceeded there is a consequential elevation of core body temperature. The TA threshold for *Bos taurus* feeder cattle, regardless of breed, housing, diet, and body weight appears to be when conditions exceed TA of 25 °C and/or THI of 76 (Hahn et al.., 1992; Lefcourt and Adams, 1996; Scharf et al., 2011a; Curtis et al., 2017). Previous studies have highlighted that when core body temperature was recorded over a TA range between 20 and 36 °C, quadratic relationships were described (Scharf et al., 2011a; Curtis et al., 2017). Beyond the TA threshold till 40 °C, the responses of core body temperature to TA were linear although the strength of correlation coefficient values varies (Lefcourt and Adams, 1996; Mundia and Yamato 1997; Brown-Brandl et al., 2005; Curtis et al., 2017; Sullivan et al., 2022). The linear equations give a measure of the rates of change of core temperature to TA or THI, and these rates of rise in core body temperature fall into a range of 0.75 to 0.10 °C per increment of THI or per °C mean TA (Lefcourt and Adams, 1996; Brown-Brandl et al., 2005; O'Brien et al., 2010; Scharf et al., 2011b; Curtis et al., 2017; Sullivan et al., 2022). Collectively, the restricted range in rates of elevation in core body temperature due to increasing heat load may point to a controlled rise in core temperature in healthy animals.

In the current study, the linear relationship of proxies for core temperature with TA and THI was not observed. Examination of the interactions of RumT and climatic conditions showed there were no contiguous linear relationships between the PreChallenge state, the trajectory during Challenge, and Recovery, which differ from those described by Sullivan et al. (2022), when cattle were exposed to moderate heat load conditions. The transition rate of increment in mean daily RumT was 0.094 °C·unit THI^{-1} and 0.12 °C·°C TA^{-1}. The values for mean daily RecT were 0.090 °C·unit THI^{-1} and 0.12 °C·°C TA^{-1}; very close to those mentioned above. However, during Challenge, the rates of change in RumT relative to THI or TA are approximately 2-fold faster than the transition rate, highlighting that these steers were able to dissipate the accumulated heat load twice as rapidly than it was accumulated. This dissipation of accumulated heat showed strongly correlated linearity with THI or TA during the Challenge.

The rate of change in RecT was similar to that of RumT although the responsivity of RecT to varying THI and TA was reduced when compared with RumT. During the transition, the rate of increment of RecT was 0.004 °C·unit THI^{-1} less than that of RumT, and 0.016 °C·unit THI^{-1} slower during Challenge. In Recovery, steers experienced their lowest RumT and RecT. This slight hypothermia persisted throughout the 6-d duration of the Recovery period and is further discussed below.

The Interactions of Physiological Measures with THI and TA, and RumT

DMI.

The TA threshold which prompts a rise in core body temperature in feeder cattle coincides with the threshold where feed intake declines (Hahn et al., 1992). While reduction in feed intake with rising TA has been observed in many species, the link to core body temperature and regulation of feed intake by the hypothalamus has only recently been unraveled (Vicent et al., 2018; Qian et al., 2022). However, predictive relationships between DMI and ambient conditions exceeding the TA threshold have been difficult to identify. In a comprehensive analysis of variants of TA and THI, Curtis et al. (2017) failed to find creditable relationships with DMI. Reduction of feed intake is influenced by the rate of increasing TA and THI, the level of intake at onset of increased heat load, and the maximum TA and THI and its persistence. Examples of varying rates of reduction of DMI of feeder cattle subjected to high TA and THI have been reported in several studies (Brown-Brandl et al., 2003; Beatty et al., 2006; Gaughan et al., 2010; Curtis et al., 2017; Sullivan et al., 2022). Furthermore, the resumption of feed intake following high heat loads is not the mirror reverse of the decline of intake, tending to be significantly more gradual despite the return to cool conditions (Beatty et al., 2006; Sullivan et al., 2022). In the current experiment, the transition rate of reduction of DMI with a sudden elevation of TA and THI was at least 30% more rapid than the rate of increase of DMI in Challenge reported by Sullivan et al. (2022), when cattle were exposed to moderate conditions.

Using core body temperature as a predictor of DMI shows mixed findings. Curtis et al. (2017) found RumT was not useful in determining DMI, whereas Beatty et al. (2006) reported a linear relationship between RumT and DMI (R^2 = 0.76). Sullivan et al. (2022) described a rotated elliptical relationship (R^2 = 0.96) showing an initial slow return of feed intake in cattle subjected to moderate heat load for 5 d and recovery in thermoneutral conditions. The current study is an example of the difficulty in understanding the relationships between DMI and core body temperature. The rate of fall in DMI in transition was approximately 4.5 kg·steer^{-1}·°C RumT^{-1} and its linear trajectory as conditions cooled was ~1.8 kg·steer^{-1}·°C RumT^{-1}. Once RumT was stabilized in thermoneutral conditions, DMI was also stabilized, however, both were significantly less than PreChallenge.

Water Usage.

WU during Challenge was reasonably stable at ~110 L·steer^{-1}·day^{-1}, which is 2- to 3-fold greater than WU reported in earlier studies for feeder cattle under various heat loads (Beatty et al., 2006; Gaughan et al., 2010; Sullivan et al., 2011, 2022; Ahlberg et al., 2018). In clement conditions, DMI has a major influence on WU (West, 2003). As thermal indices rise, WU rises in parallel and its relationship with DMI is less influential (Arias and Mader, 2011). The "inflection" point at which DMI or thermal conditions predominates in this relationship is underexplored and likely to very case specific. For example, in the current experiment, WU remained high despite conditions exhibiting a declining TA and THI but coinciding with some incremental increase in DMI. A similar response was observed by Beatty et al. (2006).

RR and PS.

RR has been shown to correlate well with a linear relationship with TA and THI in both climate-controlled facilities and outdoor pens, shaded and unshaded (Brown-Brandl et al., 2005; Scharf et al., 2011b). The current study concurs with these findings although the rates of change per unit THI or °C TA were greater than previously reported (~5 bpm·THI unit^{-1} and ~6.5 bpm·°C TA^{-1} vs. 3.0 to 4.6 bpm·°C TA^{-1}; Hahn, 1999; Brown-Brandl et al., 2005; Sullivan et al., 2022). Combined with earlier findings of the linear relationships between core temperatures and ambient conditions, beyond the TA threshold, it should not be surprising to find strongly correlated linear relationships between RumT and RR (Beatty et al., 2006; Sullivan et al., 2022). Even so, a quadratic equation (R^2 = 0.68) best described the interaction between core body temperature and RR during a heatwave in outdoor pen conditions (Gaughan and Mader, 2014). The steers in the current experiment displayed very different respiratory response to high heat load. There was a rapid rise in RR (50 bpm·°C RumT^{-1}) but as TA and THI moderated there was a linear rate of change in RR of 30 bpm·°C RumT^{-1} until RumT was

38.3 °C. In Recovery when RumT stabilized at 38.4 °C; RR steadied at 53.3 bpm.

The PS has been developed as a proxy for RR although it captures postural and behavioral changes that cannot be reported by counting exhalations (Gaughan et al., 2010). Across the 3 phases, mean daily PS of the steers in this study was found to correlate strongly and in a linear fashion with TA and THI ($r \sim 0.95$) with overall rates of change of 0.068 and 0.089 units per increment in THI or °C TA, respectively. Under the moderate heat load described by Sullivan et al. (2022), PS responded linearly with TA and THI, at 0.068 and 0.076 units per increment THI or °C TA, respectively (unpublished data). Most studies of PS have focused on its validation as an indicator of RR or core body temperature. Gaughan and Mader (2014) working with feedlot steers housed in outdoor pens, determined an overall linear relationship between PS and core body temperature ($R^2 = 0.68$) which predicted a change of 0.38 units per °C core body temperature. In climate-controlled rooms, the overall linear rate of change for PS and RumT under moderate heat load and thermoneutral conditions was 0.60 °C RumT^{-1} (Sullivan et al., 2022). In the high heat load experiment here, like RR, there was a linear relationship between daily mean PS and daily mean RumT during Challenge only, with the transition rate much greater than that of Challenge (0.53 vs 0.39 units·°C RumT^{-1}).

Maximum PS also showed linear relationships with RumT during Challenge, but minimum PS returned a polynomial relationship. Gaughan and Mader (2014) reported a polynomial (quadratic) relationship with early morning assessment of PS and core body temperature. In feedlot cattle, minimum PS coincides with the daily minima of core body temperature and RR which occurs in the early morning (0600 to 0800 hours; Brown-Brandl et al., 2005; Scharf et al., 2011a; Gaughan and Mader, 2014; Curtis et al., 2017; Lees et al., 2019). The quadratic relationship is dependent on greater values of minimum PS for a given RumT than would be observed in a linear relationship. Gaughan and Mader (2014) suggested that this was a response in cattle attempting to dissipate accumulated heat load in the early morning and prior to the warming conditions of the day ahead.

Differences in responses and recovery from moderate and high heat loads: homeorhesis vs. allostasis?

In the moderate heat load study by Sullivan et al. (2022), there were strong linear relationships between RumT and THI (or TA) and between RumT and RR, PS and WU across the 3 periods, PreChallenge, Challenge, and Recovery. We speculated that these relationships reflected homeorhetic adjustments to changing conditions and demonstrated the capacity of the steers to cope with moderate thermal challenges with no lasting effects. In the current study, these relationships are no longer held across the 3 periods. Each period appeared to produce a different and apparently independent physiological state in these steers. Interestingly, the transition rates for RumT, RR and PS with THI, and RR and PS with RumT are very similar to those previously reported for the moderate heat load study and elsewhere (Lefcourt and Adams, 1996; Brown-Brandl et al., 2005; O'Brien et al., 2010; Scharf et al., 2011b; Curtis et al., 2017). A key feature of the altered relationships became evident as the simulated heatwave abated, and conditions cooled in the later days of Challenge. Daily mean RumT declined rapidly and linearly with THI (0.173 °C. unit THI^{-1}), and at almost twice the transition rate. However, RR and PS maintained or were constrained to a linear relationship with THI (or TA), and no longer possessed a linear relationship with RumT as seen under moderate heat load. The altered interaction between RumT and RR ensured that RR declined more slowly relative to RumT than seen in recovery from moderate heat load (31.8 vs 46.1 bpm^{-1}·°C RumT). This reduced rate of decline in RR is likely to be one of the mechanisms that enabled the rapid dissipation of heat load, as observed by decreasing RumT. A second major contributor to the rapid reduction of core body temperature was the very low and then, very gradual but linear increase in DMI as RumT rose. In the moderate heat load study, as conditions cooled, increments in DMI were initially very small but accelerated so that as RumT returned to PreChallenge values, feed intake was completely restored. This did not occur in the current experiment. In fact, the steers required a further 4 wk in outdoor pens to return to PreChallenge levels of DMI (data not shown here).

In Recovery, the steers were characterized by persistent hypothermia, as evidenced by lower RumT and RecT, reduced RR, PS, and DMI, and possibly WU, relative to their PreChallenge. While post-heat stress hypothermia has been described in rodent models of heat stroke, it can be difficult to relate the extreme thermal loads and short timeframes (hours) of these models to large production animals (Lambert et al., 2002; Leon et al., 2006). However, Renaudeau (2020), in an elegant experiment of single or repeated bouts of thermal challenge in swine, was also able to show hypothermia and reduced feed intake during the recovery phase. The recovery state may be representative of an allostatic response to the strong systemic perturbation of physiology in these steers by the high heat load challenge.

The concepts of homeorhesis and allostasis and their differentiation remain under development with much discussion and debate (Sterling and Eyer, 1988; McEwan, 2006; Ramsay and Woods, 2014; Colditz, 2020; Word et al., 2022). Colditz (2020) described homeorhesis as a coordination of processes that enable appropriate adjustments to "support" ongoing functions appropriate to the animal's life stage, in this case, growth. Allostasis, on the other hand, coordinates adjustments at the "expense" of these functions. As such, allostasis is a pathway to adaptation (Sterling and Eyer, 1988; McEwan, 2006; Colditz, 2020). Ramsay and Woods (2014) attributed regulatory features such as altered set points, defense of the altered set point, learned responses, and overcorrection to allostasis. Furthermore, in extreme cases of ongoing or repeated perturbations, allostatic adaptation may lead to pathology (Sterling and Eyer, 1988; McEwan, 2006). The concept and potential implications of allostasis have not been widely applied to animals in general, especially in production animal species or with regard to animal welfare outcomes (Korte et al., 2007; Romero et al., 2015; Seeley et al., 2022; Colditz et al., 2023).

In this study, an attempt to draw out the homeorhetic and allostatic features of the responses of the steers subjected to 2 differing levels of thermal challenge has been presented (Figure 6). Here evidence has been provided that shows the high heat load challenge evoked very different responses in feedlot cattle compared to the moderate heat load reported previously by Sullivan et al. (2022). The steers subjected to moderate heat load rapidly and straightforwardly moved from PreChallenge to Challenge state and back again. The physiological adjustments were linear and bidirectional. The recovered post-challenge animal was very similar to the

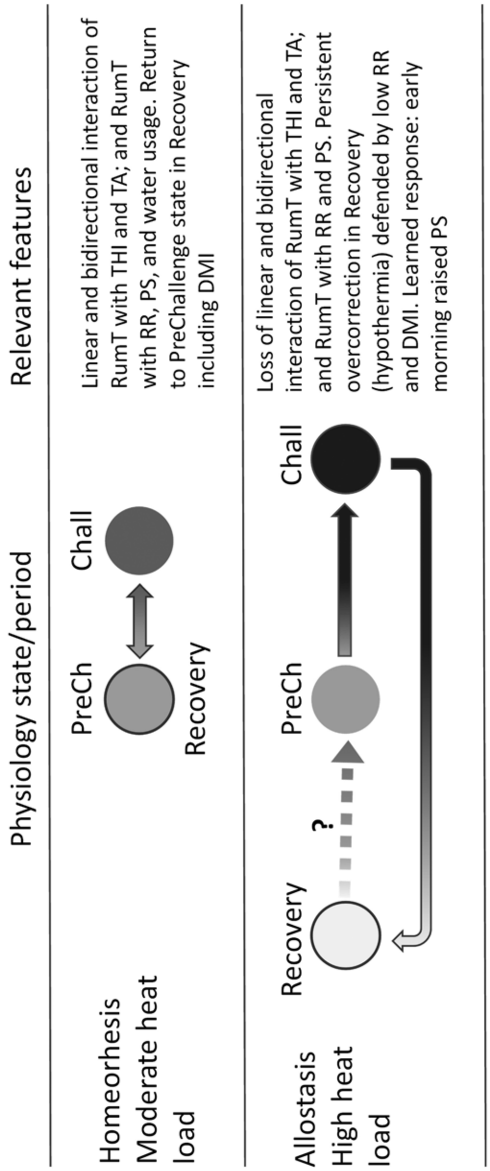

Figure 6. A schematic interpretation and differentiation of the changes in the physiological state of feedlot steers as they transitioned between PreChallenge (PreCh, days 1 to 5), to Challenge (Chall, days 6 to 12) and then through the Recovery (days 13 to 17) phase in moderate and high heat load trials. Moderate heat load elicited a homeorhetic response whereas it is proposed that the high head load evoked an allostatic response and return to the PreChallenge state was not achieved within the timeframe investigated here.

PreChallenge animal. However, when evaluating the high heat load challenge reported here, the steers showed no continuity between the PreChallenge, Challenge, and Recovery states; they did not return to the PreChallenge state within the timeframe of the experiment. The Recovery state was characterized by RumT and RR implying an "overcorrection" occured. The linear relationships of RumT with RR, PS, and WU evident during responses to moderate heat load and recovery were longer evident. The physiological and performance responses to the 2 levels of heat load were distinctive; one was not an extension of the other. It can be argued that steers subjected to high heat load displayed an allostatic response, especially in Recovery that may persist and reflect altered set points for body temperature, appetence, and growth rate, which are reduced when compared to the pre-heat wave status of these animals. The presumed allostasis persisted over a prolonged period of time; the animals in this study required an additional 28-day period to return to baseline DMI.

CONCLUSION

This study has provided novel evidence that feedlot cattle exhibit an allostatic response to periods of high heat load. This allostatic response resulted primarily in hypothermia and ongoing reduction in DMI during the recovery phase. These findings have implications for managing feedlot cattle after high heat wave events and expectations of future performance of growing grain-fed cattle in both short- and long-term feeding programs.

Supplementary Data

Supplementary data are available at *Translational Animal Science* online.

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Conflict of Interest Statement

None declared.

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