Physiological responses of *Bos taurus* and *Bos indicus* cattle to prolonged, continuous heat and humidity[1]

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ABSTRACT: Two experiments were conducted to investigate the physiological responses of *Bos taurus* (Angus cross, n = 6) and *Bos indicus* (Brahman, n = 6) cattle to prolonged heat and humidity, as can occur during live export by sea. Each experiment was carried out in climate-controlled rooms, where heifers were exposed to 15 d of sustained heat and humidity. The treatment was designed to be representative of a long-haul, live-export voyage leaving a southern Australian winter and traveling to a Middle Eastern summer. Wet bulb temperature (WBT) was used to give a combined measure of dry bulb temperature and relative humidity and was increased over several days, culminating in 5 d at 32°C WBT between d 7 and 11. By d 11, the respiratory rate and core body temperature increased ($P < 0.001$) compared with values at lower ambient temperature on d 1 and 2 when climate-controlled rooms were not operating. Feed intake of *Bos taurus* was reduced ($P < 0.001$) by d 11, whereas that of *Bos indicus* did not change ($P = 0.14$). Despite no diurnal variation in climatic conditions, core body temperature of both *Bos taurus* and *Bos indicus* continued to show a circadian amplitude of approximately 1°C throughout the hottest period. This amplitude increased during the recovery period after heat was removed (up to 1.8°C for Bos indicus and 1.6°C for Bos taurus). Water intake for both *Bos taurus* and *Bos indicus* increased when WBT increased ($P < 0.01$ on d 11). Significant acid-base and blood electrolyte imbalances occurred in both *Bos taurus* and *Bos indicus,* with changes in *Bos taurus* being more substantial and prolonged. The increase in respiratory rate coincided with a decrease in the partial pressures of carbon dioxide and bicarbonate in venous blood. However, during the hottest period, average daily venous blood pH remained unchanged. When the heat load was reduced after d 11, the blood pH decreased, indicating metabolic acidosis. Blood pH declined from 7.44 to 7.36 for *Bos taurus* ($P < 0.001$) and from 7.44 to 7.38 for *Bos indicus* ($P < 0.001$). Other parameters measured include heart rate; packed cell volume; plasma and urine Na, K, and Cl; urine pH; and specific gravity. Our results suggest that *Bos taurus* cattle experience significant physiological changes during exposure to prolonged and continuous high heat and humidity, with alterations persisting for some days after the heat-stress conditions subside. *Bos indicus* experience similar but less pronounced physiological changes.

Key words: acid-base, *Bos indicus*, *Bos taurus*, electrolyte, heat stress, temperature

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INTRODUCTION

The effects of excessive heat on the health and welfare of cattle shipped live from Australia to the Middle East is of major concern, with heat stroke, trauma, and respiratory disease being the most common causes of mortality (Norris et al., 2003). Information about animal husbandry and environmental conditions on board livestock vessels is largely anecdotal. Heat stress is of greatest concern when unacclimatized animals are transported from winter in southern Australia into the northern hemisphere summer where environmental conditions can be extreme and diurnal fluctuations minimal. Maximum wet bulb temperature (**WBT**) on voyages between Australia and the Middle East ranges from 32 to 34°C with little or no diurnal variation, meaning that animals have no nocturnal respite from heat-stress conditions (MLA, 2000a,b). Both *Bos taurus*

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and *Bos indicus* breeds are shipped live to the Middle East from southern Australian ports (ports south of latitude 31°S); *Bos indicus* appear to cope better with hot, humid conditions on ships than *Bos taurus* (Norris et al., 2003).

Excessive heat load has been used to describe heat stress in cattle and occurs when a combination of local environmental conditions and animal factors leads to an increase in body heat content beyond the animals' normal physiological range (Young, 1993). The physiological responses of cattle to acute periods of excessive heat load have been well described (Blackshaw and Blackshaw, 1994; Sanchez et al., 1994; Gaughan et al., 1999) and include increased respiratory rate (**RR**), decreased feed intake, increased water intake, and imbalances in blood gases and plasma electrolytes. However, previous studies on cattle under conditions of high heat load have not examined the effects of continuous heat load. The experiments described here were undertaken to characterize the physiological response of both *Bos taurus* and *Bos indicus* animals to continuous and prolonged high temperature and humidity such as might be experienced during live export.

MATERIALS AND METHODS

Environmental Rooms

Two experiments were conducted in 2 climate-controlled rooms (**CCR**) at Murdoch University, Perth, Australia. Each room had an electric duct heater and a humidifier capable of maintaining air temperature and moisture content as high as 60°C and 40 g of moisture/kg of dry air. The system was controlled by independent electronic temperature and absolute moisture controls, with one sensor in each room providing feedback control.

Three animals were individually penned in each room. Each animal had a pen space of 2.3 m^2, with additional space in each pen occupied by a galvanized iron feeder (200 × 530 × 390 mm) and a water bucket (25 L), both bolted to the wall below head height. The animals could not take feed or water from their neighbors, and the design of the feed and water containers minimized wastage. The animals had room to turn around and lie down.

Experimental Design

The length of the experiments and the environmental conditions were based on reports collated from voyages to the Middle East during summer in the northern hemisphere (MLA, 2000a,b). The animals spent 15 d in the CCR, with an additional 2 d of data collection after they exited the rooms. Upon entry on d 1, the animals had 2 d at ambient conditions (CCR turned off), then 4 d of gradually increasing temperature, followed by a hot period of 5 d at 32°C WBT or above, and then a cool-down and recovery period of 4 d (Table 1). Each day ran from midnight to midnight, and the overhead lights remained on for the duration of both experiments. Both experiments were conducted during winter in the southern hemisphere, with the *Bos taurus* experiment (Exp. 1) conducted in June, and the *Bos indicus* experiment (Exp. 2) in August.

Table 1. Set wet bulb temperature (WBT) of climate-controlled rooms for *Bos taurus* and *Bos indicus* experiments[1]

Day of experiment	WBT, °C	
	Bos taurus	*Bos indicus*
1–2	Ambient	Ambient
3–4	26	26
5	28	28
6	30	30
7–10	32	32
11	32	33
12	28	28
13	26	26
14–15	Ambient	Ambient

[1]26°C WBT = 30°C and 75% relative humidity (RH); 28°C WBT = 32°C and 75% RH; 30°C WBT = 33°C and 80% RH; 32°C WBT = 35°C and 80%; and 33°C WBT = 36°C and 80% RH.

Animals and Management

All experimental procedures were reviewed and approved by the animal ethics committee at Murdoch University (Perth, Australia).

Six 18-mo-old *Bos taurus* heifers (Angus cross, 331 ± 10 kg of BW) were used in Exp. 1, and six 18-mo-old *Bos indicus* heifers (Brahman, 339 ± 14 kg of BW) were used for Exp. 2. These animals were typical of cattle shipped to the Middle East. All animals were considered winter-acclimatized, because they were sourced locally.

Each animal was fitted with a temperature telemeter (Datamet, Potchefstroom, South Africa) implanted into the peritoneal cavity 2 wk before experimentation (see below). Each telemeter operated at a separate frequency in the 150 to 152 MHz range, and produced radio signals of short duration (100 ms) at a rate proportional to the temperature of the unit. Radio signals from the temperature telemeters were received on an AR8000 receiver (AOC, Tokyo, Japan) interfaced with a personal computer running dedicated software. The software ran continuously, scanned each frequency sequentially, measured the time taken to receive 30 pulses from the telemeter (to millisecond resolution), converted the pulse period to temperature using individual calibration coefficients determined before implantation, and stored the temperature data to disk in real time. *Bos indicus* heifers were also implanted with temperature loggers (Stowaway XTI, Onset Computer Corp, Pocasset, MA) specially modified with a range of 32 to 46°C and a resolution of 0.04°C. The accuracy after individual calibration was equal to 0.04°C. The scan interval was set to 10 min.

When covered in an inert polymer (Sasolwax EXP987, Sasolburg, South Africa), all units had external dimensions of approximately 50 × 45 × 20 mm and a mass of 40 g. All units were surgically implanted into the peritoneal cavity, in the region of the right paralumbar fossa, 2 wk before the experiment. Surgery was performed on the animals while they were standing. Epidural nerve block provided sedation; 0.04 mg/kg of xylazine (Ilium/Troy Laboratories, NSW, Australia) made up to 2 mL with 2% plain lignocaine (Ilium/Troy Laboratories); and lumbar paravertebral nerve block provided anesthesia (Cakala, 1961).

A 20-cm skin incision was made, and the muscle layers were blunt-dissected down to the level of the peritoneum. An incision was made in the peritoneum large enough for the units to fit through. Each unit was suspended close to the peritoneal wall with a short length of 0.40-mm heavy nonabsorbable suture (Vetafil, Bengen, Germany), which was incorporated into the wax coating of the unit and sutured in place as part of the muscle layer. Ethicon Vicryl (Johnson and Johnson Medical, NSW, Australia) was used to close the peritoneum and muscle layers, and 0.40-mm heavy nonabsorbable suture material (Vetafil) was used to close the skin incision. The animals were treated at the time of surgery with 30 mL of oxytet-200 LA (Ilium/Troy Laboratories) and 10 mL of Flunixin (Ilium/Troy Laboratories), and monitored for any postoperative problems. After the experiments, the same technique was used to retrieve the units.

Jugular catheters were sutured in place on the day before the experiments began. An epidural (as used for telemeter implantation) was used for sedation, and local anesthetic (2% plain lignocaine; Ilium/Troy Laboratories) was infused around the venipuncture site. A 12-gauge catheter (Dwellcaths, Western Biomedical, WA, Australia) was inserted into a jugular vein, and then a 90-cm length of Teflon tubing (polytetrafluorethane, 1.2-mm i.d., 1.8-mm o.d., Jepson Bolton, UK), was run 20 cm caudally into the vein. The catheter was then removed and a tab of Elastoplast (Smith and Nephew, Victoria, Australia) was attached to the Teflon tubing and sutured to the skin. The 70 cm of Teflon tubing remaining was covered with 70 cm of Nylex clear vinyl tubing (Nylex Plastics, Sale, Australia), and an 18-gauge needle was glued onto the end of the Teflon tubing with methacrylate (Selleys Superglue, NSW, Australia) and capped. The 70 cm of covered Teflon tubing was then sutured to the side of the neck every 20 cm so that the capped needle hub was situated at the top of the neck for easy sampling access.

The heifers were fed a commercial dietary cube (8.6 MJ of ME, 11.9% CP, and 39.9% NDF/kg of DM) offered at 2.25% of BW on a DM basis in 2 feedings (0700 and 1300 daily), which was comparable to the feeding regimen on board livestock vessels (M. McCarthy, unpublished data). The heifers were given 1 wk to adapt to the feed before being randomly assigned to a pen in the CCR on d 1. Feed residues were removed and weighed daily before the morning feeding. Water was always available in 25-L metal buckets that could not be tipped over, and refilled as required with water that did not exceed 26°C; once in the buckets, the water heated up to approximately room temperature. This was comparable with water in the troughs on livestock export ships (M. McCarthy, unpublished data). The total volume of water consumed was calculated once daily by subtracting the weighed residue of water each morning from the total amount of water provided during the past 24 h.

Sample Collection

Body weights were recorded on d 0, 12, 16, and 21 (after 18 h off feed but not off water). Dry bulb temperature and relative humidity were measured using a Testo 445 electronic meter (Testo, Victoria, Australia). Measurements were taken 4 times daily at 0600, 1200, 1800, and 2200. Wet bulb temperature was calculated from the dry bulb temperature and relative humidity, and the results were averaged over each day to get a mean daily WBT for each experiment.

For both experiments, core body temperature (**T_c**) data recording began on d –3, which was 4 d before the heifers entered the CCR. For the *Bos taurus* experiment, 30-min averages of T_c were calculated from the stored telemetry recordings. For the *Bos indicus* experiment, the data loggers logged the T_c every 10 min, and 30-min averages were calculated. In both experiments, 30-min averages of T_c were used for statistical analyses.

Heart rate (**HR**) and RR were measured and recorded 4 times daily at 0600, 1200, 1800, and 2200. The HR was measured by manual palpation of the coccygeal artery; the number of pulses over 20 s was counted and was converted to beats/min. The RR was calculated by counting the number of breaths a heifer took over 30 s. A single daily average was calculated from the measurements from each day.

Jugular venous blood and voided urine samples were collected at 0600, 1200, and 2200 on d 7 to 11, and once daily at 1200 on all other days. On d 7 to 11, a single daily average was calculated from the 3 samples. Blood was collected into tubes containing lithium heparin (Becton Dickinson Pty. Ltd., NSW, Australia) for plasma electrolyte analysis and into a heparin-coated syringe for blood gas analysis. The lithium heparin tubes were centrifuged at 900 × *g* for 15 min, and the plasma was removed, and stored at –20°C within 2 h of collection for later analysis. Blood gas syringes were capped and placed on ice, and the analysis was performed within 30 min of collection.

Urine samples were collected into 50-mL plain urine pots (Sarstedt Australia, Technology Park, SA, Australia) and immediately placed on ice. Urine pH and specific gravity (**SG**) were measured within 1 h of collection (ISFET pH meter KS723, IQ Scientific Instruments, Carlsbad, CA; and Leica 10436 Veterinary Refractometer, Kernco Instruments Co., El Paso, TX). An aliquot

of urine was removed from each sample and stored at –20°C for later analysis of urine electrolytes.

Measurements

The pH, partial pressure of carbon dioxide (**pCO_2**), partial pressure of oxygen, and bicarbonate (**HCO_3^-**) of venous blood were measured on the heparinized samples using a blood gas analyzer (Pacific ABL 5 Blood Gas System, Radiometer, Copenhagen, Denmark). Plasma and urine concentrations of Na, K, and Cl were measured using the diluted ion-selective electrode method on an Olympus AU400 Automated Chemistry Analyzer (Olympus Analyzers, Tokyo, Japan). The concentration of Cr in plasma and urine was measured using Cr liquid reagent (Integrated Sciences, Melbourne, Australia) on an Olympus AU400 Automated Chemistry Analyzer. Packed cell volume (**PCV**) was measured by micro hematocrit from the heparinized samples.

The fractional excretion ratio (**FER**) for each urinary electrolyte was calculated from the following equation (King, 1994):

$$FER_x = \{([x]_{urine} \times [Cr]_{serum}) / ([x]_{serum} \times [Cr]_{urine})\} \times 100,$$

where x = electrolyte under investigation; $[x]_{urine}$ = urinary concentration of the electrolyte; and $[x]_{serum}$ = plasma concentration of the electrolyte.

Statistical Analyses

A 5% level of significance was used throughout and all analyses were carried out using SPSS 11.0 for Windows (SPSS Inc., Chicago, IL).

For each separate experiment, a 2-way ANOVA with animal and day as fixed factors was used to test for an overall change over days. When the overall effect of days was significant, the Dunnett *t*-test was used to compare each day with a control day. Except for T_c, the control day for each variable was the average of d 1 and 2. For T_c, the control day was the average of d –3 to 0.

The relationship between elevations in T_c and feed intake, water intake, RR, and HR rate were analyzed by regressing the mean daily value for each species on the mean daily T_c for each species. The strength of each relationship was tested with linear regression (Zar, 1996).

RESULTS

Differences in WBT between *Bos taurus* and *Bos indicus* experiments were seen on d 1 and 2 when the CCR were not operating; therefore, the climatic conditions were the same as ambient conditions (Figure 1, a and b). Days 7 to 11 represent the hottest period of each experiment and conditions were controlled at these times. The maximum WBT measured was on d 11 (33.3°C for the *Bos taurus* and 34.2°C for the *Bos indicus*). On average, *Bos indicus* animals were subjected to slightly higher WBT than *Bos taurus* animals. In general, climatic conditions were comparable with voyage conditions recorded on livestock vessels during the northern hemisphere summer (MLA, 2000a,b).

The overall effect of days was significant for every variable measured in the *Bos taurus* experiment except plasma K concentration. For the *Bos indicus* experiment, the overall effect of days was significant for all variables except feed intake and urine pH.

For both experiments, associated with the increase in WBT was a rise in T_c (Figure 1, c and d), indicating that animals were storing heat when WBT increased. The overall effect of days on mean T_c was significant for both *Bos taurus* and *Bos indicus* ($P < 0.001$). Mean T_c for *Bos taurus* was greater on d 5 to 13 ($P < 0.01$) compared with control days. The mean T_c for *Bos indicus* was greater on d 7 to 12 ($P < 0.01$) compared with control days. The mean maximum T_c reached for the *Bos taurus* was 41.2°C (d 10 at 0330) and for *Bos indicus* was 40.4°C (d 10 at 1600). The maximum individual T_c for *Bos taurus* was 41.9°C (d 10 at 2200) and for *Bos indicus* was 41.2°C (d 11 at 1430). The overall effect of days on minimum T_c was significant for both *Bos taurus* and *Bos indicus* ($P < 0.001$). The minimum mean T_c was increased on d 5 to 13 ($P < 0.01$) for *Bos taurus* and d 8 to 11 ($P < 0.001$) for *Bos indicus* (Figure 1, e and f). The overall effect of days on mean maximum T_c was significant for both *Bos taurus* and *Bos indicus* ($P < 0.001$). Compared with the control days, the maximum T_c for *Bos taurus* was increased on d 5 to 14 and d 17 ($P < 0.01$) and d 8 to 13 ($P < 0.01$) for *Bos indicus* (Figure 1, g and h). In general, the daily circadian rhythm of T_c was maintained throughout the hot period and increased when WBT decreased (Figure 1, i and j). The overall effect of days on the daily range of T_c was significant for both *Bos taurus* and *Bos indicus* ($P < 0.001$). The daily range of T_c was increased on d 12 ($P = 0.03$) and d 17 ($P = 0.02$) for *Bos taurus*, and d 12 to 14 and d 17 ($P < 0.01$) for *Bos indicus*. A maximum circadian amplitude of 1.7°C (d 17) and 1.9°C (d 13) was reached for *Bos taurus* and *Bos indicus*, respectively.

The overall effect of days on mean daily feed intake was significant for *Bos taurus* ($P < 0.001$) but not *Bos indicus*. The mean daily feed intake, expressed as a percentage of beginning weight, of the *Bos taurus* was reduced on d 6 to 14 ($P < 0.01$) compared with control days (Figure 2a). There was no significant change in feed intake for *Bos indicus* (Figure 2b).

The overall effect of days on mean daily water intake was significant for both *Bos taurus* and *Bos indicus* ($P < 0.001$). Water intake increased in both species as WBT increased (Figure 2, c and d). *Bos taurus* animals showed increases in daily water consumption on d 8 to 11 ($P < 0.05$), and *Bos indicus* animals showed increases on d 5 to 12 ($P < 0.05$).

The overall effect of days on mean daily RR was significant for both *Bos taurus* and *Bos indicus* ($P < 0.001$).

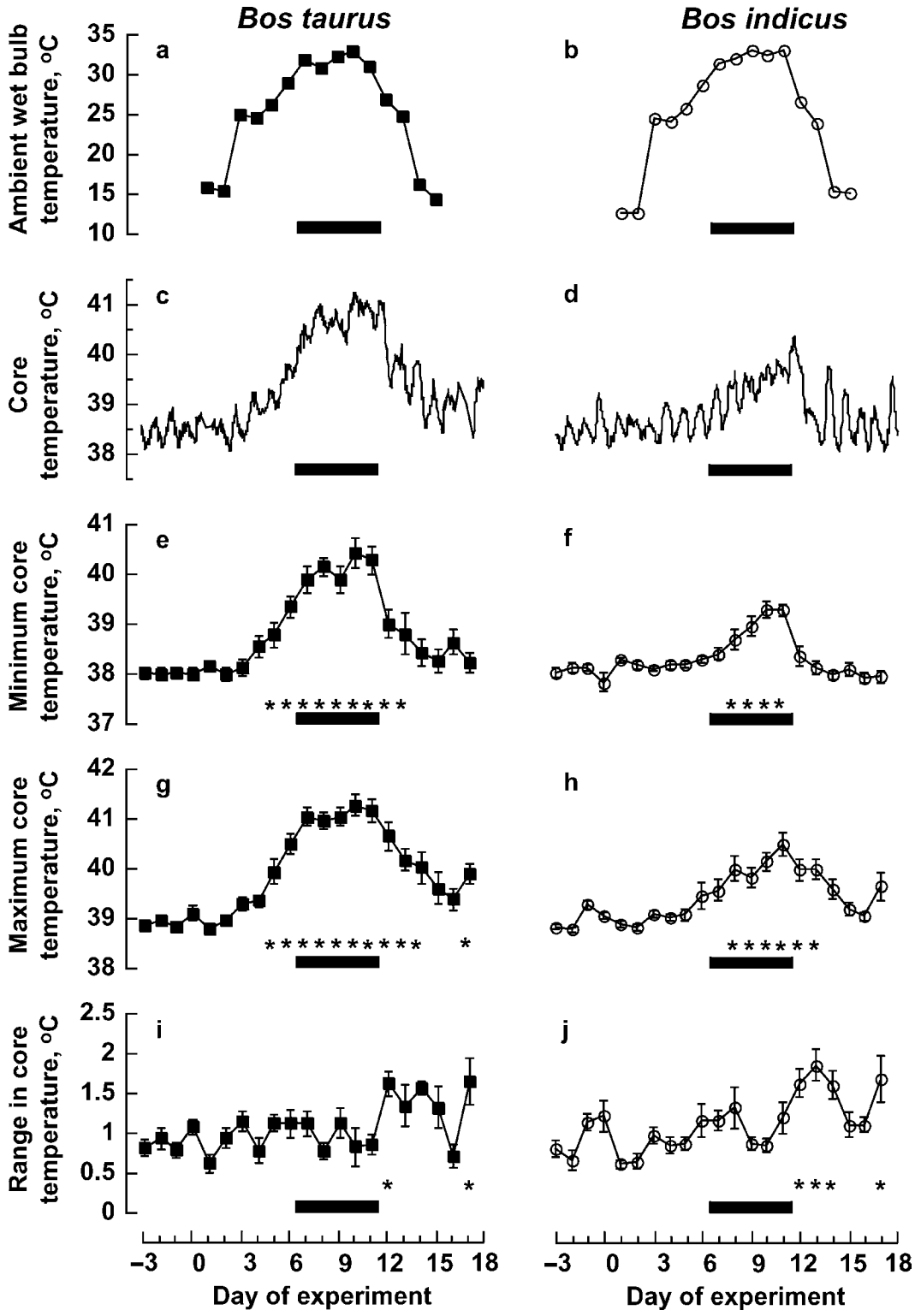

Figure 1. Mean daily wet bulb temperature (a and b), 10-min average core body temperature (c and d), mean minimum daily core temperature (e and f), mean maximum daily core temperature (g and h), and mean daily range in core body temperature (i and j) in climate-controlled rooms for the duration of each experiment in *Bos taurus* (left) and *Bos indicus* (right) heifers. Points show the mean ± SEM for each of 6 animals. The horizontal bar under each figure indicates the hottest 5 d of the experiment. Asterisks under the data denote $P < 0.05$ for the day marked vs. the control days (d –3 to 0).

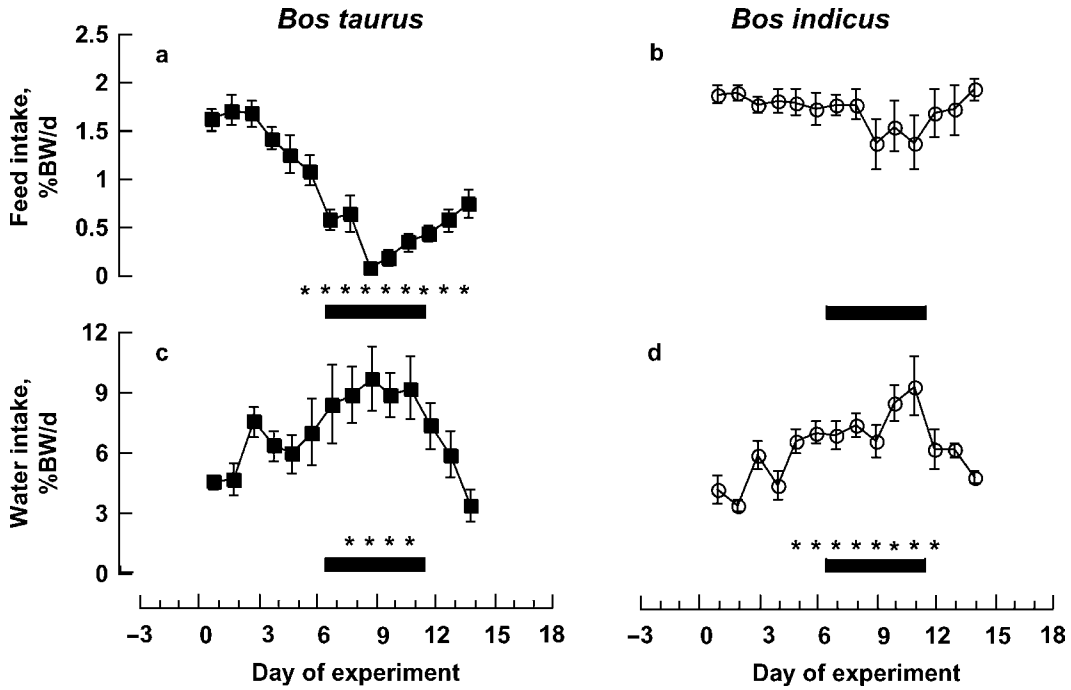

Figure 2. Mean daily feed intake (a and b) and water intake (c and d) for *Bos taurus* and *Bos indicus* heifers. Points show the mean ± SEM for each of 6 animals. The horizontal bar under each figure indicates the hottest 5 d of the experiment. Asterisks under the data denote $P < 0.05$ for the day marked vs. the control days (d 1 and 2).

As WBT increased, the RR of both *Bos taurus* and *Bos indicus* increased (Figure 3, a and b). There appeared to be a linear increase in mean RR for *Bos taurus* as WBT rose from 26°C (d 3, 75 breaths/min) to 32°C (d 7, 127 breaths/min). The RR increase for *Bos indicus* was also linear; however, the initial response of the *Bos taurus* occurred at a lower WBT than that of the *Bos indicus*. By the end of the hottest period, all animals

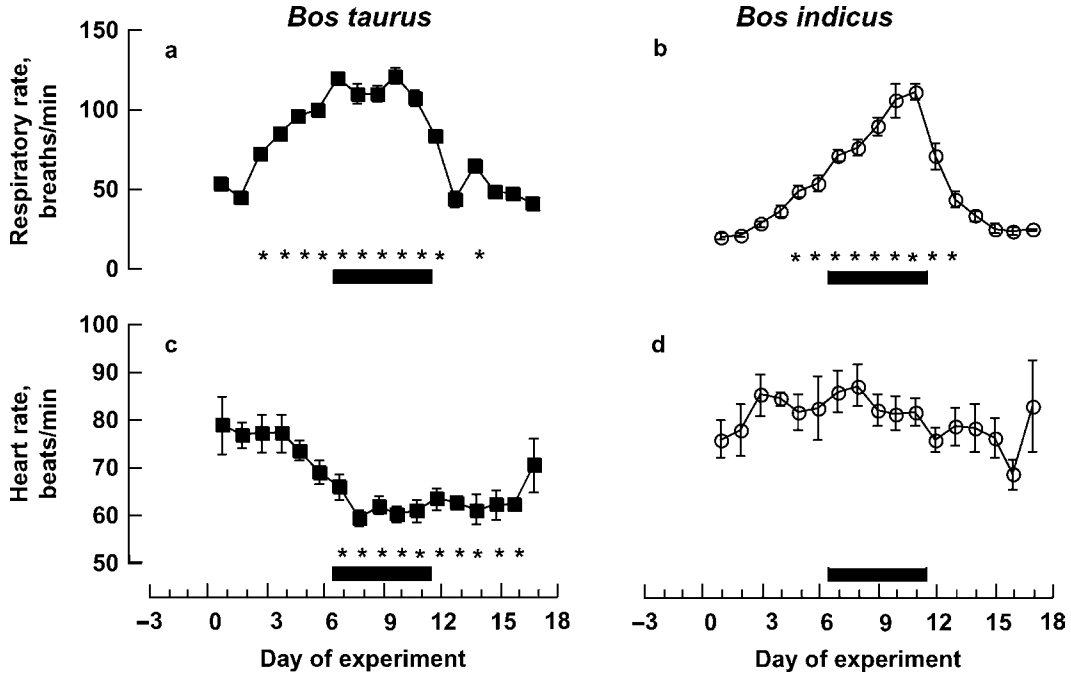

Figure 3. Mean daily respiratory rate (a and b) and heart rate (c and d) for *Bos taurus* and *Bos indicus* heifers. Points show the mean ± SEM for each of 6 animals. The horizontal bar under each figure indicates the hottest 5 d of the experiment. Asterisks under the data denote $P < 0.05$ for the day marked vs. the control days (d 1 and 2).

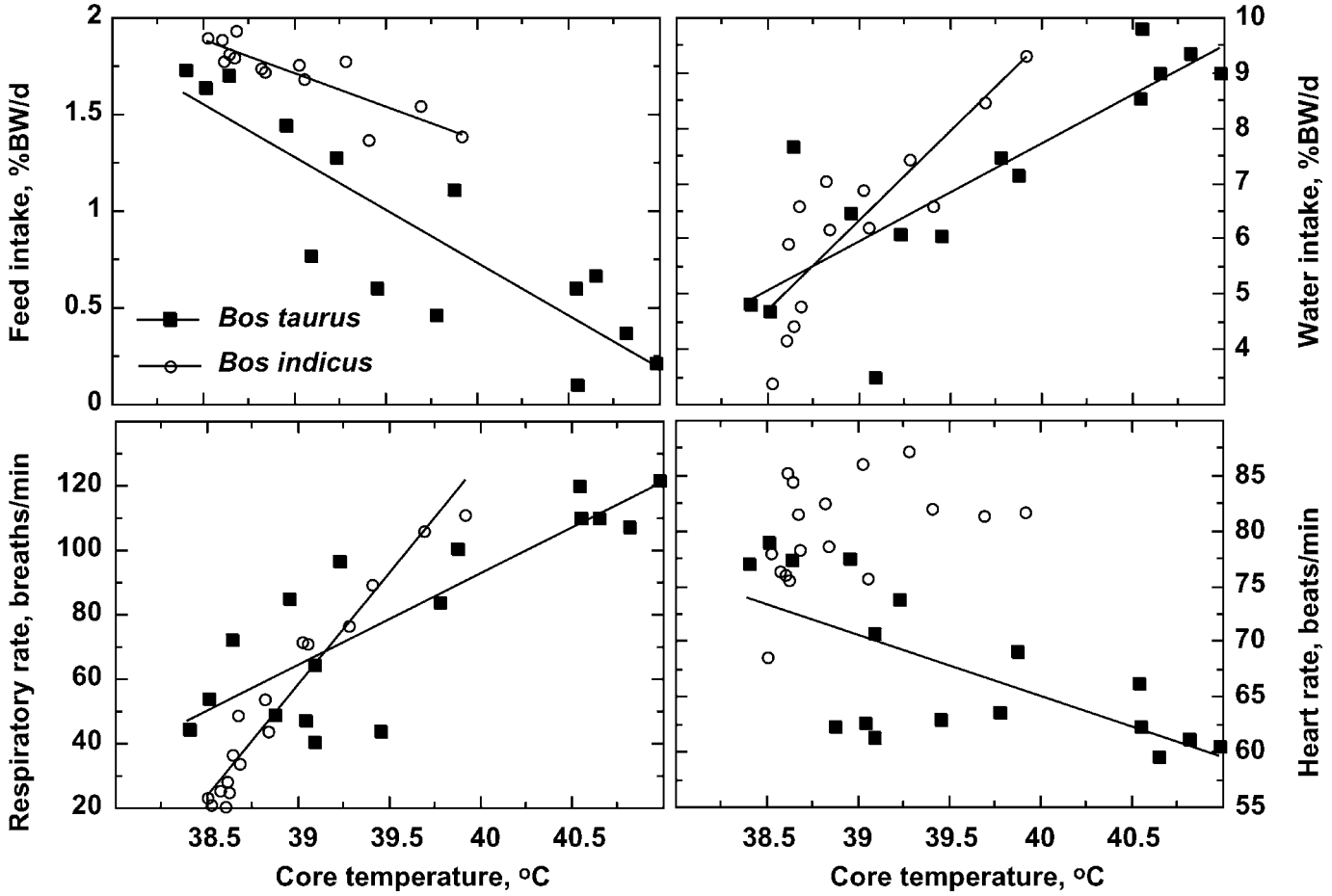

Figure 4. Daily average feed intake, water intake, respiratory rate, and heart rate plotted against daily averages of core body temperature for *Bos taurus* and *Bos indicus* heifers (n = 6 per type). Significant regressions ($P < 0.05$) are indicated by lines in each panel (the thicker line indicates *Bos taurus*).

had similarly high respiratory rates (126 and 125 breaths/min, respectively).

Heart rates were variable and there was only a significant overall effect of days for *Bos taurus* ($P < 0.001$). In *Bos taurus*, HR decreased on d 7 to 16 ($P < 0.01$; Figure 3c). No significant change of HR was detected on any day during the *Bos indicus* experiment (Figure 3d).

Both species showed significant decreases in feed intake as T_c increased (Figure 4, $P < 0.001$, $R^2 = 0.76$ and $P < 0.001$, $R^2 = 0.75$ for *Bos taurus* and *Bos indicus*, respectively). Both species showed significant elevations in water intake as T_c increased ($P < 0.001$, $R^2 = 0.69$ and $P < 0.001$, $R^2 = 0.74$ for *Bos taurus* and *Bos indicus*, respectively). Both species showed significant elevations in RR with increases in T_c ($P < 0.001$, $R^2 = 0.70$ and $P < 0.001$, $R^2 = 0.95$ for *Bos taurus* and *Bos indicus*, respectively). *Bos taurus* showed a significant decrease in HR with increases in T_c ($P = 0.002$, $R^2 = 0.47$), but there was no relationship between T_c and HR for *Bos indicus*.

In general, blood gas responses were similar in *Bos taurus* and *Bos indicus* but the latter had less severe changes. The overall effect of days on mean pCO_2 and HCO_3^- were significant for both *Bos taurus* and *Bos indicus* ($P < 0.001$). Blood pCO_2 (Figure 5, a and b) and HCO_3^- (Figure 5, c and d) concentrations were significantly reduced during and after the hot period, with the changes in *Bos taurus* being more prolonged than those in *Bos indicus*. *Bos taurus* and *Bos indicus* pCO_2 concentrations were reduced on d 6 to 13 ($P < 0.01$) and d 6 to 12 ($P < 0.05$), respectively. Bicarbonate concentration took longer than pCO_2 to return to baseline concentrations in both species (d 16 for *Bos taurus* and d 14 for *Bos indicus*). The overall effect of days on venous blood pH was significant for both *Bos taurus* and *Bos indicus* ($P < 0.001$). Average daily blood pH was maintained in the lead up to and during the heat period but was significantly reduced after the heating period ended for both *Bos taurus* and *Bos indicus* (Figure 5, e and f).

The overall effect of days on mean plasma Na concentration was significant for both *Bos taurus* and *Bos indicus* ($P < 0.001$). Significant decreases in plasma Na concentrations were observed for both *Bos taurus* and *Bos indicus* (Figure 6, a and b). For *Bos taurus*, decreases were measured during and after the hottest period on d 10 to 15 ($P < 0.05$). For *Bos indicus*, decreases in plasma Na concentration were measured on

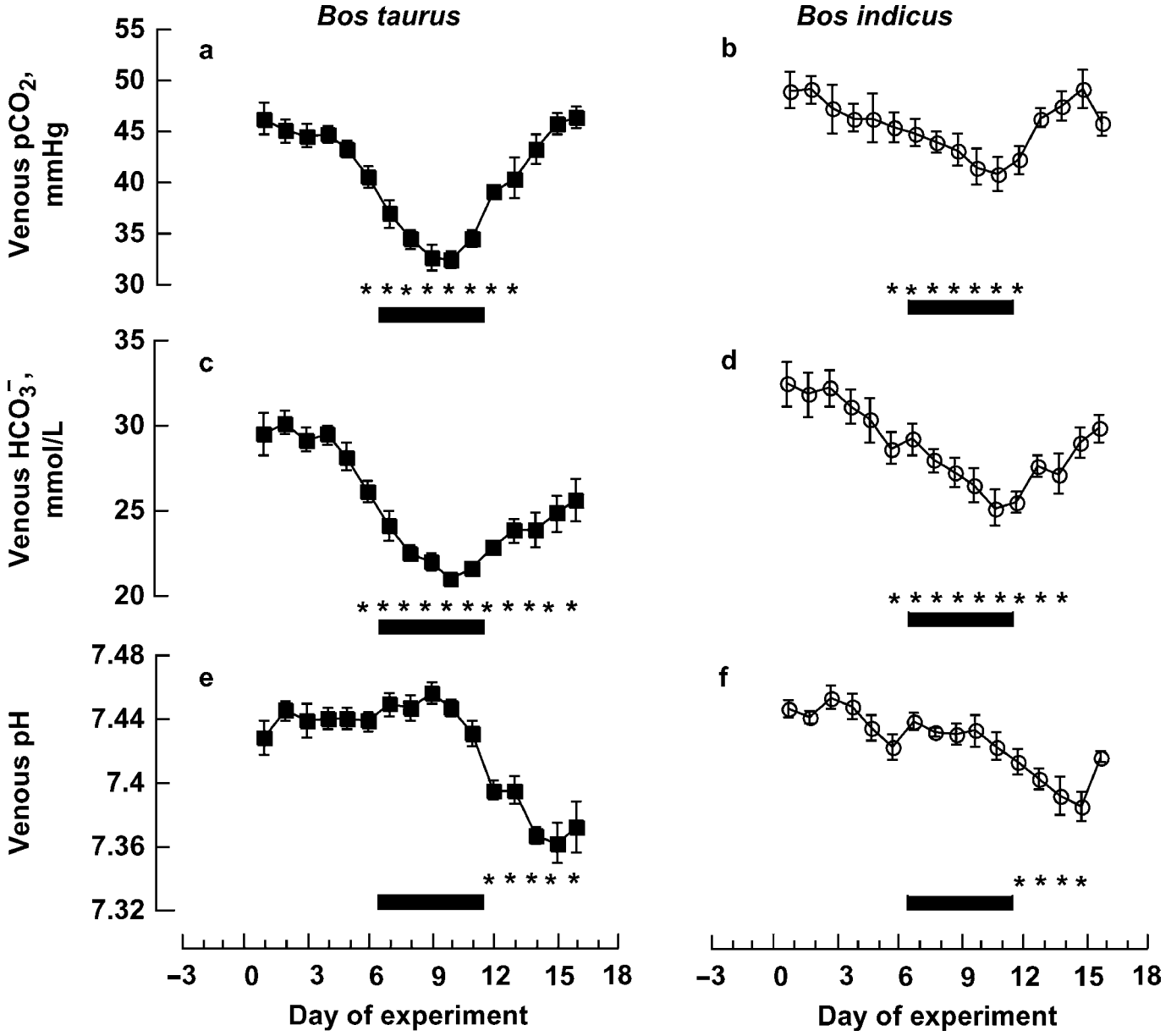

Figure 5. Mean daily venous blood partial pressure of CO_2 (pCO_2; a and b), bicarbonate (HCO_3^-) concentration (c and d), and pH (e and f) for *Bos taurus* and *Bos indicus* heifers. Points show the mean ± SEM for each of 6 animals. The horizontal bar under each figure indicates the hottest 5 d of the experiment. Asterisks under the data denote $P < 0.05$ for the day marked vs. the control days (d 1 and 2).

d 4 to 11 and d 16 ($P < 0.05$). The overall effect of days on mean plasma K concentration was significant for *Bos indicus* ($P = 0.001$) but not *Bos taurus*. However, there was no significant change in plasma K concentration in either *Bos taurus* or *Bos indicus* compared with control days (Figure 6, e and f). The FER of Na was variable during the hottest period in both experiments, increasing in *Bos taurus* and decreasing in *Bos indicus* during that time. The FER of Na was decreased and very low after the hot period for both species (Figure 6, c and d). The FER of K decreased during and after the hot period for both *Bos taurus* and *Bos indicus* (Figure 6, g and h). This change was less marked for the *Bos indicus* animals. Plasma Cl concentration was variable for both *Bos taurus* and *Bos indicus*. There was an overall effect of days on plasma Cl concentration for both *Bos taurus* and *Bos indicus* ($P < 0.001$). Increases were seen on d 10, 15, 17, and 18 ($P < 0.05$) for *Bos taurus*; no significant changes were detected in *Bos indicus* (data not presented).

There was an overall effect of days on urine SG and PCV for both *Bos taurus* and *Bos indicus* ($P < 0.001$). Urine SG was decreased on d 9 to 13 ($P < 0.01$) and 10 to 12 ($P < 0.05$) for *Bos taurus* and *Bos indicus*, respectively, indicating that the animals were producing dilute urine (Figure 7, a and b). Packed cell volume was reduced after the heating period in *Bos taurus* on d 12 to 16 ($P < 0.06$) and during and after the heating

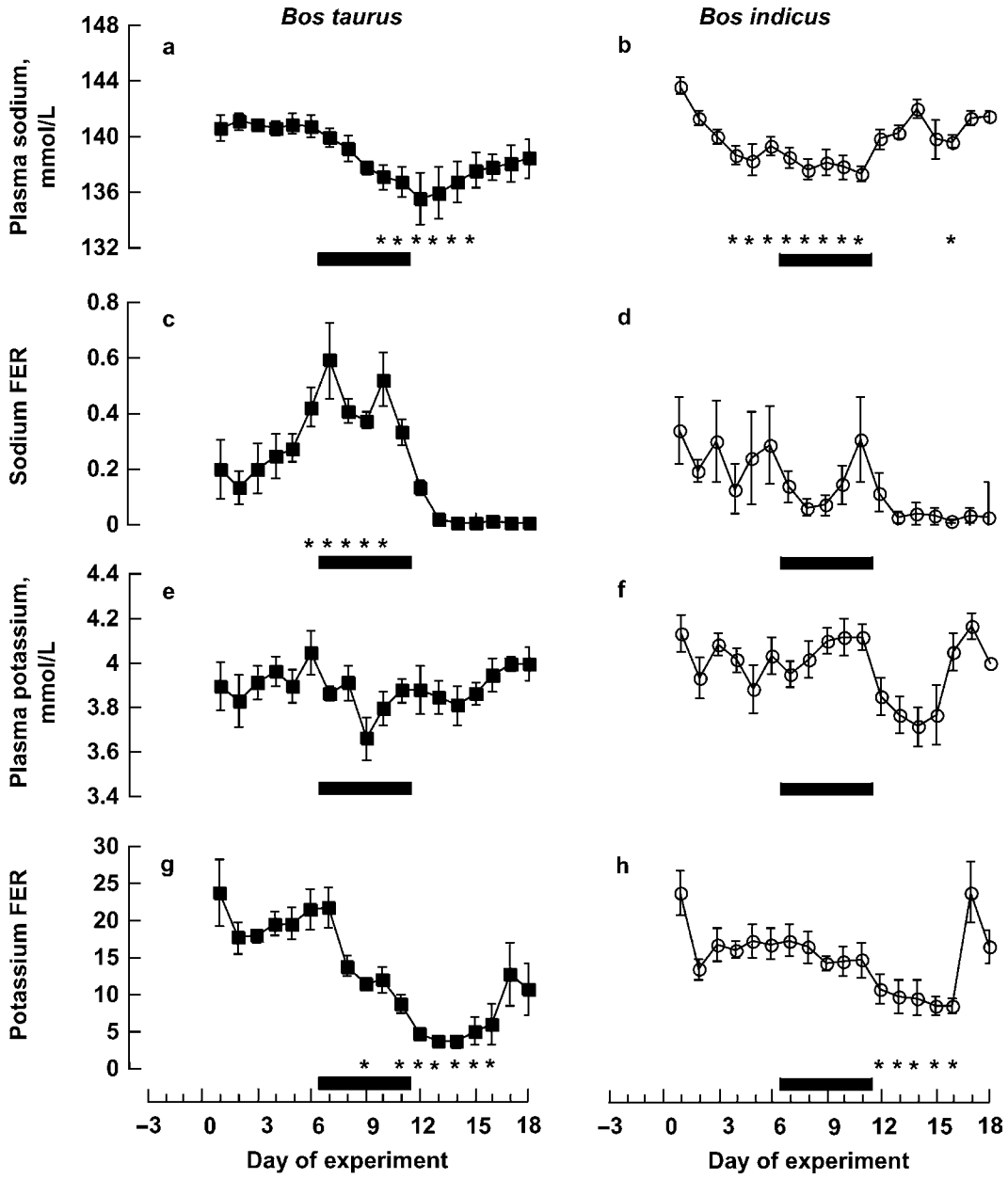

Figure 6. Mean daily plasma sodium concentration (a and b), fractional excretion ratio (FER) of sodium (c and d), plasma potassium concentration (e and f), and FER of potassium (g and h) for *Bos taurus* and *Bos indicus* heifers. Points show the mean ± SEM for each of 6 animals. The horizontal bar under each figure indicates the hottest 5 d of the experiment. Asterisks under the data denote $P < 0.05$ for the day marked vs. the control days (d 1 and 2).

period in *Bos indicus* on d 6 to 15 ($P < 0.01$) (Figure 7, c and d). There was an overall effect of days on urine pH for *Bos taurus* ($P < 0.001$) but not *Bos indicus*. For *Bos taurus*, urine pH followed a similar pattern to blood pH, becoming acidic after the heat period (Figure 7e), whereas for *Bos indicus*, urine pH did not change (Figure 7f).

DISCUSSION

The results of these experiments highlight the ability of *Bos taurus* and *Bos indicus* to maintain blood pH and acid-base homeostasis as well as a circadian rhythm of T_c during prolonged periods of heat stress without diurnal variation in environmental conditions. The apparent consequences of this ability to maintain homeostasis in continuous heat appeared after environmental conditions returned to thermoneutrality, when the animals experienced a profound metabolic acidosis as seen by the reduction in blood pH, and an increase in the amplitude of the circadian rhythm of T_c.

The prolonged exposure to heat and humidity caused a significant increase in T_c for both *Bos taurus* and *Bos indicus* indicating that the animals' heat-loss mechanisms could not compensate fully for the excessive heat load. Many other studies have confirmed an increase

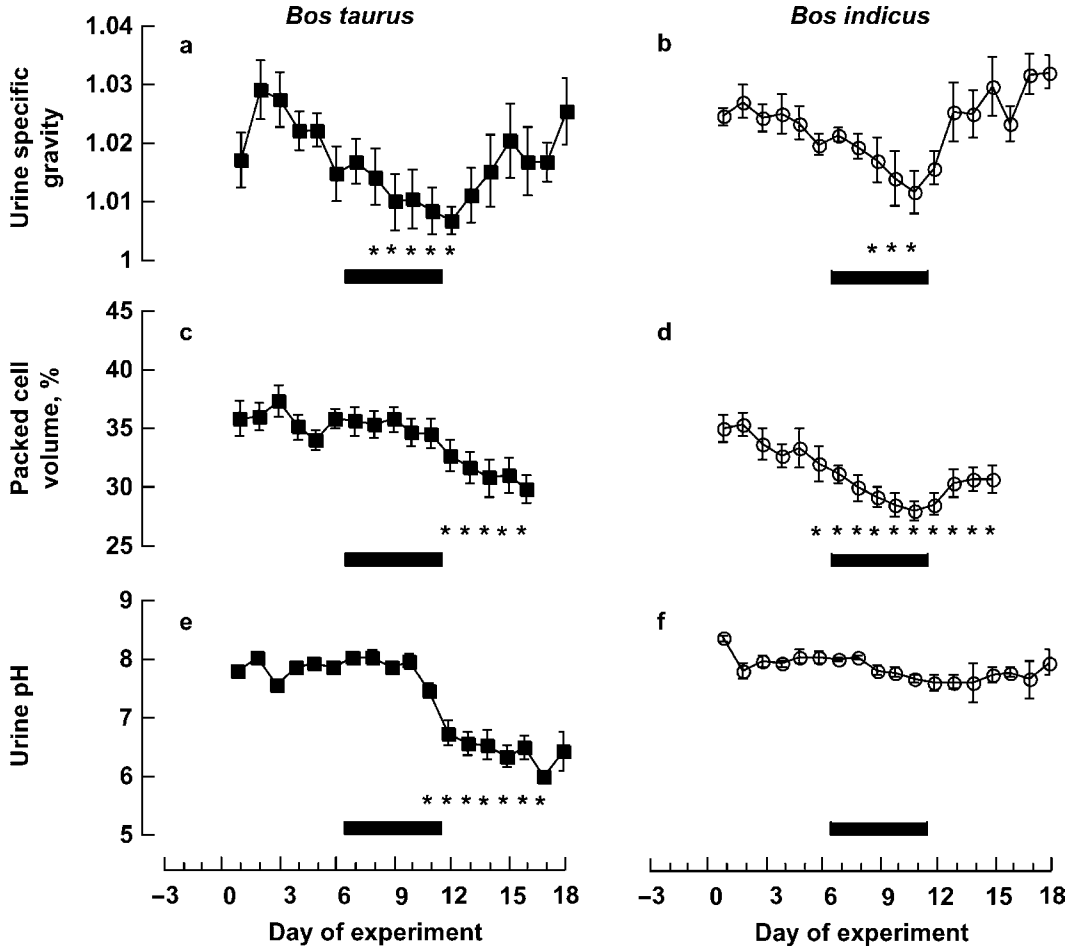

Figure 7. Mean daily urine specific gravity (a and b), packed cell volume (c and d), and urine pH (e and f) for *Bos taurus* and *Bos indicus* heifers. Points show the mean ± SEM for each of 6 animals. The horizontal bar under each figure indicates the hottest 5 d of the experiment. Asterisks under the data denote $P < 0.05$ for the day marked vs. the control days (d 1 and 2).

in T_c when cattle are exposed to hot conditions both in natural environments (Kabuga, 1992; Gaughan et al., 1999) and in climate-controlled rooms (Zhang et al., 1994; Gaughan et al., 1999), but no other study has assessed the physiological responses of cattle to continuous and prolonged high heat and humidity. In *Bos taurus*, mean T_c became elevated on d 5 (WBT 28°C) and remained elevated until d 13 when WBT decreased to 26°C. Associated with the rise in WBT and T_c were clinical signs of heat stress in *Bos taurus* animals. These clinical signs included open-mouthed panting, drooling, reluctance or inability to rise, increased licking of coat, and general dullness including neurological signs with staring and glazed eyes. For *Bos indicus* animals, the prolonged exposure to heat and humidity caused an increase in mean daily T_c between d 7 and 12 of the experiment; however, clinical signs of heat stress were not observed.

Gaughan et al. (1999) observed an increase of 1.2°C in mean rectal temperature over 10 h when *Bos indicus* were subjected to extremely hot conditions in a climate-controlled room. The *Bos indicus* animals in our experiment were exposed to conditions of continuous high heat and humidity resulting in a mean increase of 2.3°C from the lowest recorded mean T_c during ambient conditions (38.1°C at 0900 on d –3) to the highest recorded mean T_c (40.4°C at 1600 on d 11). A cumulative effect of the heat-stress conditions was also evident in that the mean daily T_c did not become elevated until d 7 of the experiment when WBT was 32°C. However, on d 12, T_c was still elevated and WBT was only 28°C. By d 12, animals had been exposed to 10 d of continuous heat and humidity.

The mean daily T_c of *Bos indicus* animals increased steadily when WBT increased. This would suggest that the maximum tolerable T_c for *Bos indicus* was not reached, because the mean T_c for *Bos taurus* animals appeared to plateau by d 7 at the beginning of the hottest period.

The nychthemeral amplitude of T_c (mean daily maximum T_c – mean daily minimum T_c) remained approximately 1°C in both species during the hottest period. This was in spite of mean daily T_c increasing (from 38.4 to 41.0°C for *Bos taurus* and 38.5 to 39.9°C for *Bos*

indicus), the daily feed intake of *Bos taurus* animals falling significantly, and the lack of diurnal variation in environmental conditions and 24-h artificial lighting. A nychthemeral amplitude of 1°C is consistent with some previous studies (Zhang et al., 1994). However, others (e.g., Berman and Morag, 1971; Gaughan et al., 1999; Mader et al., 1999) found differences in nychthemeral amplitude in natural environments to be dependent on climatic conditions. Berman and Morag (1971) found that the range in rectal temperature in dairy cows was 0.4°C in winter but 1.2°C in summer. Similarly, Mader et al. (1999), working with Hereford steers fed high-energy feedlot diets in climate chambers, reported daily ranges in rectal temperatures of 0.7 and 1.3°C under thermoneutral and hot environmental conditions, respectively.

It is likely that the increases in nychthemeral amplitude observed by others involved an increase in diurnal maximum of T_c under heat stress, whereas the nocturnal minimum remained unaffected when nocturnal respite from heat stress was provided. No nocturnal respite was provided in our experiments. We did observe an increase in nychthemeral amplitude after the hottest period when WBT was reduced. This was because of an increase in maximum daily T_c for both *Bos taurus* and *Bos indicus* animals. The reason for this is unclear. It would appear that the heat increment of feeding had little impact on the amplitude of T_c because the amplitude was maintained in the absence of feed intake in *Bos taurus* animals. Furthermore, the daily maximum and minimum T_c for both species occurred between 2100 to 2200 and 0700 to 0800, respectively, despite the lack of nighttime cooling and variations in feed intake. Finch (1986) suggested that an increase in the amplitude of T_c in *Bos indicus* was in response to food deficits and was due to a decrease in the lower range of body temperature during the cooler night hours. In our *Bos indicus* experiment, there was no voluntary reduction in feed intake, no nighttime cooling, and no decrease in nocturnal T_c.

Elevated respiratory rates are part of the repertoire of responses used by cattle to increase heat loss in situations of elevated heat load (Hales and Findlay, 1968; Hales, 1976). Initially, the elevated rate is associated with a decreased tidal volume and increases in alveolar ventilation are limited (Hales, 1976). In extreme conditions, however, tidal volume increases, which increases respiratory evaporative water loss, but also leads to elevated alveolar ventilation, elevated CO_2 excretion, and alkalosis (discussed further below). *Bos indicus* apparently have a number of anatomical and physiological features that improve heat loss from the skin, including greater blood flow to the skin facilitating heat transfer to the surface (Finch, 1986), lower resistance to internal heat transfer thus allowing heat to be removed via the skin (Finch, 1985), and shorter hair coats (Finch, 1986). However, for both species, there were significant increases in RR with increases in T_c, and the maximum RR was similar for both species. There was also an indication of reduced RR in the middle of the hottest period for the *Bos taurus*, with a shift in RR dynamics from rapid open-mouth panting to deep open-mouth panting at a reduced rate (Gaughan et al., 2000), which was associated with further blood gas changes (discussed below).

An increase in RR is an important thermoregulatory response to heat stress, and aids in heat dissipation via evaporative cooling (West et al., 1991, 1992; Blackshaw and Blackshaw, 1994). However, increased alveolar ventilation results in the excretion of CO_2 at a rate exceeding its production (Sanchez et al., 1994), shifting bicarbonate equilibrium toward H_2CO_3 from H^+ and HCO_3^-. The net result of these processes is respiratory alkalosis in which pCO_2 decreases, pH increases, and the concentration of HCO_3^- decreases and is replaced by other buffers (Cunningham, 2002). When RR increased in our experiments, pCO_2 and HCO_3^- decreased, but there was no increase in blood pH. This finding is in contrast with other studies that assessed acute heat stress in cows and calves (Dale and Brody, 1952; Bianca and Findlay, 1962). Although there was no significant increase in blood pH during the heat-stress period, the reduced pCO_2 and HCO_3^- suggest that the animals were experiencing respiratory alkalosis, but buffering mechanisms effectively countered this alkalosis and maintained blood pH. To counter alkalosis, the kidney can excrete HCO_3^-, and there is a compensatory decrease in renal H^+ ion secretion within 2 h of heat exposure, but it is not complete for 2 to 3 d (Cunningham, 2002). It was hypothesized that this further decreases blood HCO_3^- concentration and increases urine pH (Schneider et al., 1988). The evidence suggests that renal adjustments helped to maintain blood pH within a normal range during the hottest part of our experiments.

Schneider et al. (1988) characterized the nychthemeral patterns of acid-base balance in cattle exposed to heat-stress conditions during the day, and cool conditions at night. Respiratory alkalosis occurred only when heat stress was present during the day. During the cooler hours at night, lower urine pH and greater urine ammonium concentration were recorded, suggesting excretion of H^+ in a compensatory urinary acidosis. This pattern of responses was similar to our observations, but the respite only occurred when WBT was decreased. Then, the animals were no longer panting and so expired less CO_2. Without adequate HCO_3^- buffering, a reduced blood pH and acidic urine resulted. Blood HCO_3^- concentration remained less than control values at the end of the experiments for many days after WBT had been reduced.

The changes in blood gases we observed in both species agree with Schneider et al. (1988) and indicate that there is a large turnover of HCO_3^- to maintain blood pH after a heating period, especially after such a prolonged and continuous heat-stress period. However, unlike the findings of Schneider et al. (1988), an increase in urine pH during the continuous heat period was not observed.

If the kidneys were excreting HCO_3^-, an increase in urine pH would be expected. The ratio between plasma HCO_3^- and plasma pCO_2 was maintained throughout the heating period in our experiment, although the values of both were reduced. After the heating period, this ratio was reduced, indicating a total body deficit of HCO_3^- and metabolic acidosis. Total body stores of HCO_3^- were depleted because it was used as a blood buffer to counter the loss of CO_2 (for both species) and not being replaced due to inappetence (in *Bos taurus* only).

Cattle reduce feed intake in response to heat stress (Yousef, 1985; Blackshaw and Blackshaw, 1994). A reduction in feed intake is followed by a decline in metabolic rate and, therefore, reduced heat production, which helps to maintain heat balance (Turner and Taylor, 1983). The decrease in feed intake in *Bos taurus* with increasing WBT was more pronounced than has previously been reported. Bianca (1965) reported that intakes began to decline at 21, 24, and 27°C dry bulb for Holstein, Jersey, and Brown Swiss cows, respectively. At 32°C dry bulb, feed consumption of lactating Holstein cows was depressed by 20%, and at 40°C dry bulb, feed intake of Holstein and Jersey cows virtually stopped. Other studies report that at 15 to 25°C dry bulb, normal feed intake occurs (Conrad, 1985; Blackshaw and Blackshaw, 1994), whereas temperatures above 35°C dry bulb result in a 10 to 35% reduction in feed intake (Conrad, 1985). These figures contrast markedly with our results. After d 6 in the *Bos taurus* experiment, when WBT was 32°C, the average feed intake was reduced by 78%. A WBT of 32°C was achieved with a relative humidity of 80% and dry bulb of 36°C. The major reason for the difference in results probably was that the animals in our experiments were exposed to continuous high WBT with no nocturnal "cooling off" period.

The etiology of the decreased feed intake for the *Bos taurus* is unknown, but it was significantly associated with the elevation in T_c. Whether it was a direct effect of heat or hormonally mediated cannot be determined in these experiments. However, heating of the preoptic area and rostral hypothalamus of hungry goats caused them to stop eating within 1 min (Bianca, 1965). The cumulative effect of prolonged heat load was also evident on feed intake, whereby postheat feed intake did not return quickly to preheat intake, even at similar room WBT, with T_c still elevated on d 13. It has been previously documented that animals exposed to high diurnal heat loads shift feeding to the cooler hours of the day (Blackshaw and Blackshaw, 1994). We did not observe any such change in behavior, probably because, unlike previous studies, our animals had no nocturnal respite from the heat.

Maximum water intakes during the hot period were at least doubled from the control period, from 4.8 to 9.8% of beginning weight for *Bos taurus*, and from 3.8 to 9.3% of beginning weight for *Bos indicus*, agreeing with previous studies (Winchester and Morris, 1956; Phillips, 1960; Colditz and Kellaway, 1972; Beede and Collier, 1986). However, in *Bos taurus*, this increase could not be linked to a greater requirement per unit of feed ingested, as Winchester and Morris (1956) proposed, because of the drastic decrease in feed intake by *Bos taurus*. The mechanism for the increase in water consumption may, like feed intake, involve direct effects of the heat, because directly warming the preoptic area and rostral hypothalamus of the goat caused a large increase in water consumption (Andersson et al., 1960). Additionally, although depleted water stores due to evaporative demands could induce increased water intake via hypovolemia or hyperosmolarity, neither of these changes occurred in this study, suggesting the direct effect of heat.

There was no attempt made to cool the drinking water in our experiments beyond that considered average for live-export vessels traveling in the Middle East (D. T. Beatty, unpublished data). Water temperature can influence intake, and several studies have reported that dairy cows exposed to hot conditions drank less chilled water (around 10°C) than warmer water (around 26°C), but that there can be a cooling effect of drinking chilled water (Lanham et al., 1986; Baker et al., 1988; Wilks et al., 1990). Heat-stressed lactating goats also drank more warm (35°C) than cool (15°C) water (Olsson and Hydbring, 1996). It would seem that the water temperature in the experiments reported here may have encouraged the animals to drink more than if the water was cooled, although in cattle there is a suggestion that if the water is too hot (greater than 30°C), there is a negative effect on water intake (Rouda et al., 1994).

The increased water consumption was accompanied by more dilute urine formation, as indicated by the very low urine SG. Although total urine output could not be measured, subjective assessment of the bedding indicated there was greater urine output. However, there were some indications that not all the extra water was lost and there may have been an increase in total blood volume as indicated by a decrease in PCV. This would agree with other reports (El-Nouty et al., 1980) that, although there were increases in both water intake and urine output of cattle in hot environments, the ratio of water intake to urine output also increased, along with a 2-fold increase in vasopressin. Theoretically, reduced plasma osmolality should inhibit water intake, but in pregnant goats heat stress also induced a primary polydipsia (Olsson et al., 1995). It was suggested that stimulating signals from warm receptors override inhibiting influences from receptors signaling hyponatremia or hypoosmolality at the "thirst center" in the hypothalamus, leading to polydipsia. A similar mechanism may have operated in our cattle. Furthermore, an expanded blood volume, and therefore a greater preload and stroke volume, could also explain the decrease in heart rate of the *Bos taurus*, which is contrary to other reports of increased heart rate during heat stress (Terui et al., 1979).

The reduction in plasma Na concentration during heat stress has been described by El-Nouty et al. (1980), and may be caused by an increase in urinary Na excretion due to increased total urinary output. Low plasma aldosterone during heat exposure may be responsible for the increase in urinary Na excretion and decrease in plasma Na concentration. An expanded blood volume could also result in a reduced plasma Na concentration. It has also been suggested that renal excretion of HCO_3^- must be accompanied by a cation (Sanchez et al., 1994). Sodium and K are possibilities, but Na is more likely. After the heating period, the Na FER was reduced indicating conservation of Na. For the *Bos taurus* animals, inappetence meant that Na stores were not being replenished; this is probably why they had larger and more prolonged reductions in plasma Na concentrations than those observed in *Bos indicus*.

Plasma K concentration was well maintained throughout the heating period during both experiments. El-Nouty et al. (1980) found that both Na and K serum concentrations were reduced in Holstein cows during prolonged heat stress. It is possible that the plasma K did not reflect total body K stores because the majority of K is maintained in the intracellular compartment and we do not know what happened to the volume of this compartment. However, the fractional excretion ratio for K was decreased for both *Bos taurus* and *Bos indicus* after the heating period, indicating renal conservation of K and presumably a replenishment of body stores. El-Nouty et al. (1980) suggested that reductions in serum and urinary K during heat exposure were due to loss of K in sweat. It was also suggested that decreased plasma K was the main factor inhibiting aldosterone release during heat exposure. Because plasma K did not change in the cattle in our experiments, if aldosterone changes were mediating the naturiesis, then another mechanism must be involved, such as greater extracellular fluid volume or greater plasma concentrations of vasopressin.

In conclusion, both *Bos taurus* and *Bos indicus* showed a remarkable ability to maintain blood gas homeostasis during prolonged and continuous high heat and humidity. It would appear that after the heating period the animals were not able to maintain homeostasis and a metabolic acidosis developed. The qualitative changes in blood gas parameters were the same for both species, but *Bos taurus* were more severely affected for longer duration. It appears that *Bos indicus* are better adapted to cope with continuous periods of high heat and humidity because the changes in feed intake, core body temperature, respiratory rate, and blood gas parameters were not as marked as in *Bos taurus*. Inappetence would appear to be of major concern for *Bos taurus* animals experiencing continuous periods of high heat and humidity. Further research is required to evaluate methods of alleviating or modifying the physiological responses and imbalances that occur when *Bos taurus* animals in particular are subjected to prolonged and continuous periods of high heat and humidity.

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