

Rumen temperature is a reliable proxy of core body temperature in sheep (*Ovis aries*)

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Handling Editor:

John Gaughan

Received: 23 September 2021

Accepted: 3 June 2022

Published: 8 July 2022

Cite this:

Vesterdorf K *et al.* (2022)
Animal Production Science, **62**(17),
1671–1682.
doi:[10.1071/AN21490](https://doi.org/10.1071/AN21490)

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ABSTRACT

Context. In ruminant animals, such as sheep, the maintenance of a stable core body temperature is achieved through the controlled process of thermoregulation. The live export of sheep from Australia can expose sheep to heat stress, especially when vessels near, or cross, the equator, that can impact on animal welfare by causing hyperthermia. **Aim.** The use of thermologgers located in the rumen of sheep could provide a direct, real-time method to monitor the thermal status of sheep during live export without the need to handle animals during shipping. We determined the relationship between core temperature and rumen temperature during changes in various factors that impact on an animal's heat balance. **Methods.** Sixteen wethers were implanted with thermologgers in the rumen to measure rumen temperature and in the abdominal cavity to measure core temperature. The sheep were exposed to environmental conditions similar to those experienced by sheep on live export vessels. The environment was assessed using the wet-bulb temperature. In the first trial, eight Merinos were shorn while the remaining eight retained their fleece. In the second trial all sheep were shorn, and eight sheep were offered a chaff diet and eight a pelletised diet while the wet bulb temperature increased. The rumen and core temperatures were compared. **Key results.** We show that when core temperature increased during exposure to heat load, so did rumen temperature and, despite relatively large changes in overall body temperature, the difference between these temperatures remained stable. The daily average relationship between rumen and core temperatures was $0.5 \pm 0.1^\circ\text{C}$ and that difference was not affected by water ingestion, length of fleece, diet composition, or exposure to hot and humid conditions similar to those reported on live export vessels. **Conclusion and implications.** By subtraction of 0.5°C from the measured rumen temperature in live export sheep, the use of rumen thermologgers would provide a reliable measure of core temperature and hence an indication of the thermal status of the sheep throughout the export journey.

Keywords: animal welfare, biologging, heat stress, live sheep export, nutrition, rumen temperature, thermoregulation, wool.

Introduction

In mammals, the maintenance of a stable core body temperature (T_{core}) is achieved through the homeostatically controlled process of thermoregulation. The T_{core} varies with time of day in a circadian rhythm, and variations in the characteristics of that rhythm can provide an indication of pathology (Maloney *et al.* 2013, 2017, 2019). Variations in the circadian rhythm can occur during heat exposure, malnutrition, pregnancy, or infection (Hales 1973; Marai *et al.* 2007, 2008; Maloney *et al.* 2019).

Sheep that are being exported live from Australia can be exposed to thermal stress, especially when they cross the equator (Stockman *et al.* 2011). When the environmental conditions exceed the prescriptive zone for sheep (Mitchell *et al.* 2018), they cannot achieve heat balance and the T_{core} increases (Marai *et al.* 2007; Beatty *et al.* 2008b; Stockman *et al.* 2011; Koltes *et al.* 2018). Welfare in an animal can be defined by alterations in body temperature, hormone levels and animal behaviour. If an animal has

difficulties coping in a challenging environment, poor welfare will ensue (Silanikove 2000). Monitoring the T_{core} of live export sheep could therefore provide a useful indicator of the physiological responses of the animals during transport, as an indication of their welfare.

The measurement of T_{core} over long periods of time in live sheep is, however, not a straightforward task. The gold standard measurement of body core temperature is the temperature of the blood in the pulmonary artery, but the placement of a sensor into a patent artery involves complex surgery (Lim et al. 2008; Fuller et al. 2011; Vesterdorf et al. 2011). Other sites within the body are easier to access and can correlate reasonably well with the arterial blood temperature, such as within the abdominal cavity (Beatty et al. 2008a, 2008b; Adam et al. 2016). The insertion of a sensor into an artery or into the abdominal cavity requires general anaesthesia and surgery for implantation. If the sensor is connected to a telemetry unit, data can be read in real-time with the appropriate infrastructure (Beatty et al. 2006). More commonly the sensor is connected to a logger that has to be retrieved to access the stored data (Beatty et al. 2008a, 2008b; Fuller et al. 2011; Vesterdorf et al. 2011). Directly measuring T_{core} is therefore difficult and impractical when large numbers of animals are involved. The handling of an animal for recording of rectal temperature (T_{rec}) using handheld devices may increase body temperature, thus confounding the results. True body temperature must be collected in unrestrained animals at frequent intervals (Sherwin and Johnson 1990). An alternative is to measure at a site that is more easily accessible, such as the gastrointestinal tract. In monogastric animals, including humans, a device can be swallowed. That device passes through the gastrointestinal tract, and can provide one to 4 days of temperature recordings (Byrne and Lim 2007). In ruminants, such as sheep and cattle, devices inserted into the esophagus will settle in the rumen and can provide long-term recordings of rumen temperature (T_{rum}) (Crock et al. 1992; Beatty et al. 2008a, 2008b; Cooper-Prado et al. 2011; Gonzales-Rivas et al. 2018; Lees et al. 2018, 2019, 2020). If the animals are destined for market, the loggers can be retrieved at slaughter, eliminating the need for surgery to retrieve the data.

The technique of measuring T_{rum} involves the insertion of a rumen capsule that is fitted either with a thermologger that records, logs, and stores measurements (Beatty et al. 2008a, 2008b; Cooper-Prado et al. 2011), or a thermo-transmitter that senses temperature and sends a signal to a data receiving unit outside the animal in real time (Beatty et al. 2006; Signer et al. 2010; AlZahal et al. 2011; Turbill et al. 2011; Lees et al. 2018, 2019, 2020). As opposed to about an hour per animal for surgery to implant thermologgers into the abdominal cavity, the use of rumen capsules makes it possible to orally insert thermologgers into ~30 sheep per hour using an applicator. As a non-invasive approach, the technique is time- and cost-effective, as well as imposing considerably less stress on the animal.

However, to be useful as a proxy for T_{core} , T_{rum} should vary in a consistent fashion with T_{core} , regardless of changes in the various environmental factors that impact on an animal's heat balance. Lees et al. (2018) found a distinct effect of time of day in the T_{rum} of steers. Because variation in T_{core} across the day/night cycle is important, it needs to be established whether the parameters of the circadian rhythm of T_{core} are reflected in measures of T_{rum} .

The heat of fermentation in the rumen accounts for approximately 8% of the total heat production in a ruminant (Czerkawski 1980). Due to that local heat production in the rumen, T_{rum} has been reported to be approximately 1.0°C higher than T_{core} or T_{rec} in cattle (Beatty et al. 2008b), and approximately 0.5°C higher than T_{core} in sheep (Beatty et al. 2008a). The difference between T_{core} and T_{rum} depends on the rate of local heat production in the rumen, and the rate of heat loss from the rumen, which will depend on the perfusion of the rumen and therefore on the rate of blood flow to the rumen. Beatty et al. (2008a) showed that the difference between T_{core} and T_{rum} remained quite consistent in sheep that were exposed to thermoneutrality and moderate heat (33°C dry-bulb temperature [T_{db} , °C] and 25°C wet-bulb temperature [T_{wb} , °C]). But whether the relationship remains the same at higher heat load, or when the composition of the diet changes, is unknown. Under heat load, an increase in peripheral blood flow is important for heat loss, and so any compensatory changes in rumen blood flow would be expected to impact on the heat balance of the rumen, and so on the rumen to core temperature difference.

We here test the hypothesis that, in sheep, the rumen to core temperature difference (designated $T_{\text{rum-core}}$) is consistent when sheep are exposed to conditions that induce an increase in peripheral blood flow (Trial 1) or rumen heat production (Trial 2). We use data from 15 sheep that were fitted with loggers in the abdominal cavity (T_{core}) and in the rumen (T_{rum}) that measured temperature simultaneously, every 12 min. The sheep were exposed to T_{wb} up to 26.8°C with a T_{db} that exceeded the body temperature of the sheep (~38.0°C; Lee 1950). In the first part of the experiment the sheep were either fleeced or recently shorn to determine the effect of fleece when ambient temperature (T_{a} ; °C) is higher than body temperature. Being fleeced should insulate the sheep against heat gain from the environment under such conditions (Thwaites 1966), and so it might be expected that fleeced sheep would achieve heat balance with smaller redistribution of blood flow than shorn sheep.

In the second part of the experiment all of the sheep were shorn, and half received a change in diet from chaff to concentrated pellets, which will change the fermentation time and bacterial activity of the rumen, and thereby potentially change rumen heat production.

Materials and methods

The present work consisted of two separate trials, using the same animals in the two trials.

Animals

All experimental procedures were conducted in accordance with the guidelines in the Australian Code for the Care and Use of Animals for Scientific Purposes (National Health and Medical Research Council 2013) and were reviewed and approved by the animal ethics committee at Murdoch University (AEC approval number R2004/06).

Sixteen 2-year old Australia Merino-cross wethers (64.1 ± 6.7 kg; fleece length: ~ 85 mm) were used. Most sheep exported from Australia are wethers. The use of wethers also removed any confounding effect of hormonal cycles. The sheep were obtained in the Southern Hemisphere spring, and all animals had spent the winter in the southern part of Western Australia. One week before the start of the experiments, eight of the sheep were randomly selected and shorn at the Murdoch University farm, Perth, Australia according to Australian industry standards using mechanical shears. The remaining eight sheep were kept with their fleece intact. The animals were then trucked (1 h drive) to the large animal facility at Murdoch University where they were housed for the duration of the experiment.

During the first part of the experiment (termed 'Trial 1'; see below) the sheep were fed a commercial cube offered at 3% of body mass per day (on a dry matter basis) twice daily at 08:00 hours and 13:00 hours. The dietary regimen was chosen because it is similar to the diet that sheep consume on livestock vessels. The sheep were given one week on the diet prior to experimentation. A description of the feed administered during the second part of the experiment (termed 'Trial 2') is given below. Water was available *ad libitum* throughout both trials, and the water temperature never exceeded 26°C, which was comparable to water in troughs on livestock vessels (Beatty *et al.* 2007).

Climate control chambers

The 16 sheep were individually penned, with four shorn and four fleeced sheep in each of two climate chambers. The sheep had individual feed and water buckets and had room to turn around and lie down in the pens. Each pen was 0.88 m^2 , which is equal to the space per head on the livestock vessels. The sheep could not take food or water from neighbouring animals. Sawdust was used as bedding in all pens and was replaced or topped up as necessary.

The temperature and humidity in each chamber was controlled and adjusted to expose the sheep to gradually hotter conditions over each of the trials. The relative humidity (RH) was maintained at 55–60% and the T_{db} was adjusted to achieve a given T_{wb} in the rooms. The settings

were adjusted at 08:00 hours each morning, and so for statistical purposes, each experimental day began at 08:00 hours and ended the next day at 07:59 hours. A low level of artificial lighting remained on for the duration of the experiment, as occurs on board livestock vessels (Beatty *et al.* 2007).

Environmental data loggers

An environmental data logger (HOBO Pro H08-032-08, Onset Computer Corp, Pocasset, MA, USA) was suspended in the centre of each climate chamber that measured T_{db} and RH. The data loggers were set to log at 10 min intervals. At the end of the experiment, the data were downloaded from the two data loggers onto a personal computer (PC).

The T_{wb} can be measured directly with a sling psychrometer, but can also be derived from electronic measures of T_{db} and RH. The standard formulae that are available to derive T_{wb} from T_{db} and RH come with caveats that the formulae provide approximations only, and therefore are inaccurate under some conditions. The RH is easily derived from measures of T_{db} and T_{wb} , but working back the other way from T_{db} and RH to T_{wb} is not possible algebraically, and so deriving T_{wb} from T_{db} and RH requires an iterative process. We developed a macro in Excel using the 'Solver' function to perform this process. The iterative approach uses the following formulae, each taken from Barenbrug (1974):

The saturation water vapour pressure in kPa (e_{sat}) is calculated as

$$e_{\text{sat}} = 0.6106 \times \exp \left[\left(\frac{17.27 \times T_{\text{db}}}{237.3 + T_{\text{db}}} \right) \right], \quad (1)$$

where exp is the base of natural logarithms (e) to the power of the number in the square brackets.

The water vapour pressure in an unsaturated atmosphere in kPa (e) is therefore (where RH is expressed as a proportion)

$$e = e_{\text{sat}} \times \text{RH}. \quad (2)$$

The relationship between e and the T_{db} and T_{wb} is given by

$$e = \frac{[e_{\text{sat}} \times (371.4 + 0.24 \times T_{\text{db}} - 0.6 \times T_{\text{wb}}) - 0.24 \times (T_{\text{db}} - T_{\text{wb}}) \times \text{BP}]}{371.4 + 0.04 \times T_{\text{db}} - 0.4 \times T_{\text{wb}}}, \quad (3)$$

where BP is the barometric pressure in kPa. In the iterative process, e is obtained using formulae (1) and (2), and then formula (3) is solved iteratively to obtain T_{wb} .

Body temperature loggers

Temperature loggers (iButton, DS1922L, Maximum Dallas, CA, USA) were implanted into the rumen and abdomen of all 16 sheep, one week before the start of the experiment.

The temperature loggers remained in place until they were retrieved at slaughter.

Rumen temperature loggers

To measure rumen temperature, an iButton temperature logger was coated in biologically inert wax (EXP987, Sasol Wax Pty Ltd., South Africa) and inserted into an emptied control release capsule (CAPTEC, Nufarm Health and Sciences, NZ). The rumen temperature loggers were orally administered.

Abdominal temperature loggers

To measure abdominal temperature, an iButton temperature logger was coated in biologically inert wax. The loggers were surgically implanted into the peritoneal cavity via an incision in the region of the right paralumbar fossa. Each temperature logger was suspended proximal to the peritoneal wall with a short length of 0.40 mm non-absorbable suture (Vetafil, Bengen, Germany) that was incorporated into the outer layers of the wax coating of the logger and sutured into the peritoneal muscle layer. Details of the surgery, post-operative care and medication are given in [Beatty et al. \(2008a\)](#). Upon retrieval of the abdominal temperature loggers, it was noted that no scar tissue had formed around any of the loggers.

All of the body, rumen and abdominal temperature loggers were calibrated before, and again after, the experiment against a certified mercury-in-glass thermometer (certified by the National Association of Testing Authorities, Australia) with a resolution of 0.05°C in an insulated water bath at five temperatures over the range of 34–45°C. The loggers were programmed to log the temperature every 12 min. After retrieval from the sheep and calibration, data from the temperature loggers were downloaded onto a PC and each was adjusted according to its unique calibration. No drift between the initial and final calibration was observed in any of the loggers.

Experimental design

The aim of the experiment was to determine the relationship between T_{core} and T_{rum} under thermoneutral and hot and humid environmental conditions (high heat load, as may be experienced on board live export vessels; [Stockman et al. 2011](#)) in sheep that were shorn versus fleeced ('Trial 1'), and in sheep that received a diet of either chaff or of pellets, with the same ME ('Trial 2').

Trial 1

The climate chambers were set to the prevailing ambient conditions for the first 3 days of the trial (thermoneutral; Day 1–3). During this time, the average daily T_{wb} in each room was $14.9 \pm 1.1^\circ\text{C}$. The T_{wb} was then gradually increased from Days 4–7 (moderate heat load), and was then maintained at an average daily T_{wb} of $25.4 \pm 0.3^\circ\text{C}$ from Day 8 to the end of the trial on Day 13 (high heat

load). One shorn sheep was removed before the experiment began due to illness. On Day 11, all of the sheep were loaded onto a truck in the morning and driven 1 h to the University farm for shearing. The sheep that had been shorn prior to the start of the experiment were sham shorn to mimic the effect of shearing, while the remaining sheep were shorn. All of the sheep were then returned to their pens in the climate chambers where they were exposed to T_{wb} of $\sim 25^\circ\text{C}$ on Days 12 and 13. After Day 13 the sheep were brought back to the University farm where they remained from Day 14–16. During this time the sheep were exposed to the prevailing environmental conditions. The sheep were then returned to the climate chambers for Trial 2 early on the morning of Day 17.

Trial 2

Each sheep was returned to the same pen as Trial 1 in the climate chamber for the second trial, and randomly assigned to receive either a chaff based diet or a pellet based diet, irrespective of their treatment in the first trial. Because one sheep had been removed prior to the start of the experiment, eight sheep were fed pellets and the remaining seven sheep were fed chaff, twice daily at 08:00 hours and 13:00 hours. The diets did not differ in ME content and were offered at 3% of body mass on a dry matter basis per day. The diets were offered from Day 17.

For the initial 3 days of the trial (Day 17–19) the climate chambers were set to the prevailing ambient conditions. During this time, the average daily T_{wb} was $12.9 \pm 0.1^\circ\text{C}$. Then the T_{wb} was increased gradually, from Day 20–23, to reach a maximum on Day 24 and Day 25 of $26.8 \pm 0.1^\circ\text{C}$. The animals were brought back to the University farm on the morning of Day 26.

Analyses

Smoothing T_{rum}

The difference between T_{rum} and T_{core} measured from the first part of the experiment was reported by [Beatty et al. \(2008a\)](#). Rapid, but transient, decreases in T_{rum} were observed in all of the sheep and were directly related to water intake ([Beatty et al. 2008a](#)), as was previously found in cows ([Cantor et al. 2018](#)), potentially confounding the use of T_{rum} to predict T_{core} . We therefore tested whether the removal of the effect of water intake on the T_{rum} made a difference to the analysis of T_{rum} . The raw T_{rum} for each individual sheep was run through a custom-written macro to identify rapid decreases in T_{rum} that were associated with drinking. We looked initially at the distribution of changes in T_{rum} between two subsequent measurements. The vast majority ($95.2 \pm 1.9\%$; average \pm s.d.) were between -0.3 and $+0.3^\circ\text{C}$. Changes larger than 0.4°C were always associated with a characteristic rapid decrease and then a logarithmic increase back to an asymptote over the subsequent ~ 96 min. In the 15 experimental sheep, a decrease of

more than 0.4°C in T_{rum} was observed in $3.1 \pm 0.8\%$ of the collected data points, corresponding to a drinking bout on average every ~ 6.5 h. A macro was then written to identify each incidence of a point-to-point decrease in T_{rum} of $>0.4^{\circ}\text{C}$, and the data points on either side of the rapid decrease, and gradual increase back to the prevailing T_{rum} over the subsequent ~ 96 min, were smoothed by interpolation. The smoothed T_{rum} was termed $T_{\text{rum,smooth}}$ ($^{\circ}\text{C}$) in further data analyses. The difference between $T_{\text{rum,smooth}}$ and T_{core} was termed the $T_{\text{rum,smooth-core}}$ ($^{\circ}\text{C}$).

Cosinor analyses over periods

We used a cosinor model (Nelson *et al.* 1979) to derive the parameters of the circadian rhythm (daily mesor, amplitude, and acrophase) of T_{core} , T_{rum} , $T_{\text{rum,smooth}}$, $T_{\text{rum-core}}$, and the $T_{\text{rum,smooth-core}}$ on selected days during each trial. The cosinor function was used to quantify the circadian temperature rhythm and remove the undue influence of single points that can occur when alternative approaches are used, such as analysing the 'range' of daily temperatures (Piccione and Caola 2003). For both trials the periods were: (1) thermoneutral, (2) moderate heat load, (3) high heat load.

Statistics

Daily means \pm s.d. of the mesor, the amplitude of the T_{core} , T_{rum} , $T_{\text{rum,smooth}}$, and the differences between the T_{rum} and the T_{core} and between $T_{\text{rum,smooth}}$ and the T_{core} were calculated for each individual in each of the two trials. To test whether the mesor or the amplitude of the T_{rum} changed with smoothing, two-way repeated measures (RM) ANOVAs were performed to compare the mesor and the amplitude, respectively, of the T_{rum} against the $T_{\text{rum,smooth}}$ within individuals, regardless of treatment. Because there was no significant effect of smoothing on the mesor or on the amplitude of the T_{rum} (see Results), all subsequent analyses were performed on the T_{rum} . The means of the mesor and the amplitude of the T_{core} and of the difference between T_{rum} and T_{core} were compared separately for Trial 1, using two-way RM ANOVAs with heat load in Periods 1, 2, and 3 (as defined above) as the repeated measure, and with the Greenhouse–Geisser correction. We used 'shorn' versus 'fleeced' as a fixed variable in the two-way RM ANOVAs.

Data from Trial 2 were separated and analysed in a similar way to those of Trial 1, except that we used repeated measures MANCOVA with 'chaff' versus 'pellets' as the fixed variable, and Periods 1, 2, and 3 as repeated measures.

Because the same sheep were used in the two trials we also tested for any carry-over effect of having been shorn early or late in Trial 1, using 'shorn' and 'fleeced' as variables in the RM MANCOVA.

For a detailed analysis of the relationship between T_{core} and T_{rum} , we took each simultaneous measurement of the two temperatures for each sheep, calculated the difference between the two temperatures (i.e. $T_{\text{rum}} - T_{\text{core}}$) and

binned those differences into 0.1°C categories of T_{core} . For each animal we then calculated the number at each category of T_{core} , and the average \pm s.d., minimum, and maximum of $T_{\text{rum}} - T_{\text{core}}$ at each category of T_{core} . We then did the same across sheep to determine if the difference between the temperatures remained constant across T_{core} , and how common were differences that deviated from the general relationship. A Broken-Stick analysis was used to determine inflection points in the relationship between $T_{\text{rum-core}}$ and T_{core} .

Statistical analyses for Trial 1 were performed using InStat Prism (7.0, GraphPad Software Inc., CA, USA), while analyses for Trial 2 were performed using Statistica (9.0, StatSoft Inc., Tulsa, OK, USA). Where appropriate, *post hoc* tests were performed using Tukey's HSD test. Results were considered statistically significant when $P < 0.05$.

Results

The effect of correcting data for water intake

The effect of water intake on the circadian rhythm of T_{rum} was obvious (Fig. 1, upper panel), and the macro that averaged out rapid decreases successfully removed those episodes (Fig. 1, lower panel). Nevertheless, correcting T_{rum} for the effect of water intake had no effect on the parameters of the circadian rhythm of T_{rum} . The average difference between the mesor of T_{rum} and that of $T_{\text{rum,smooth}}$ was $-0.07 \pm 0.02^{\circ}\text{C}$ ($F_{1,28} = 0.5$; $P = 0.50$), while the average difference between the daily amplitude of T_{rum} and the daily amplitude of $T_{\text{rum,smooth}}$ was $0.01 \pm 0.02^{\circ}\text{C}$ ($F_{1,28} = 0.8$; $P = 0.376$). Similarly, there was no effect of smoothing on the estimate of the difference between T_{rum} and T_{core} , with the difference in mesor being $-0.07 \pm 0.03^{\circ}\text{C}$ ($F_{1,28} = 4.1$; $P = 0.053$) and the difference in amplitude being $0.02 \pm 0.01^{\circ}\text{C}$ ($F_{1,28} = 3.8$; $P = 0.060$). Further analyses were therefore run using the original T_{rum} .

Trial 1

In both treatment groups the mesor of T_{core} increased with the increase in T_{wb} (Fig. 2 – upper panel; $F_{1.7,22.0} = 60.8$, $P < 0.0001$), and the mesor of T_{core} of the fleeced sheep was $0.6 \pm 0.1^{\circ}\text{C}$ higher than that of the shorn sheep during Periods 1 and 2 ($F_{1,13} = 21.9$, $P = 0.0004$). When the sheep were exposed to the maximum heat load conditions during Period 3, however, there was no effect of fleece on the T_{core} of the animals. As such, while the T_{core} of the fleeced animals did not increase from Period 2 to Period 3, the T_{core} in the shorn sheep did ($P = 0.04$). The daily amplitude of the T_{core} was not different between periods ($F_{1.8,23.6} = 2.0$, $P = 0.16$) and was not different between the fleeced and shorn animals at any period ($F_{1,13} = 2.5$, $P = 0.14$).

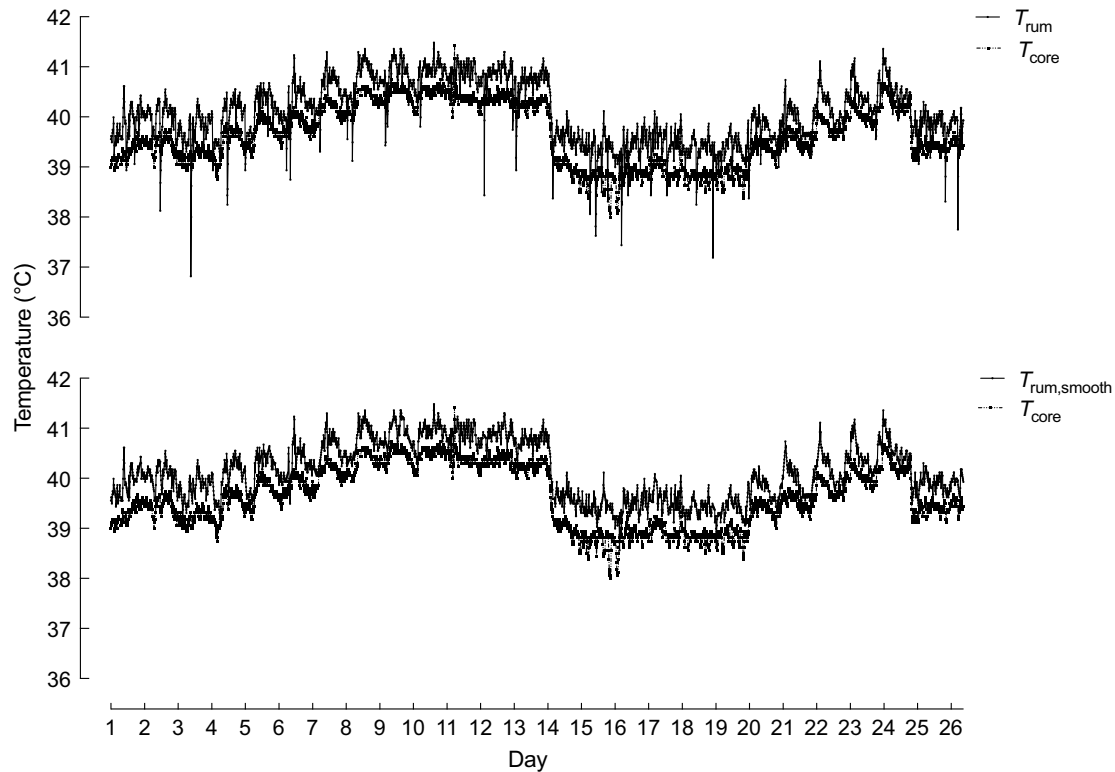


Fig. 1. Upper panel: original core (T_{core} , lower broken line in each panel) and rumen temperature (T_{rum} , higher solid line in each panel) from a randomly selected sheep during the 26 days of experimentation. Lower panel: smoothed T_{rum} ($T_{\text{rum,smooth}}$) was calculated by interpolation to remove decreases in T_{rum} that were larger than 0.4°C .

Like T_{core} , the mesor of T_{rum} also increased in both groups with each increase in T_{wb} (data not shown; $F_{1.7,21.5} = 55.4$, $P < 0.0001$). The average mesor of T_{rum} of the fleeced sheep was $0.6 \pm 0.1^{\circ}\text{C}$ higher than that of the shorn sheep ($F_{1,13} = 15.8$, $P = 0.0016$). The amplitude of the circadian rhythm of the T_{rum} was not different between periods ($F_{2.0,25.8} = 0.27$, $P = 0.77$) or affected by fleece ($F_{1,13} = 0.54$, $P = 0.48$).

The increase in heat load between the periods had no effect on the difference between T_{rum} and T_{core} , despite the increase in T_{core} with increasing heat load (Fig. 2 – lower panel; mesor $T_{\text{rum-core}}$: $F_{1.2,14.6} = 0.44$, $P = 0.54$; amplitude: $F_{1.5,19.5} = 0.80$, $P = 0.43$). Being fleeced or shorn also had no effect on the difference between T_{rum} and T_{core} (Fig. 2 – lower panel; mesor $T_{\text{rum-core}}$: $F_{1,13} = 3.95$, $P = 0.07$; amplitude: $F_{1,13} = 0.04$, $P = 0.84$). The $T_{\text{rum-core}}$ remained stable despite increasing heat load. The grand mean of the mesor of the $T_{\text{rum-core}}$ in the sheep was $0.5 \pm 0.1^{\circ}\text{C}$.

Trial 2

The mesor of the T_{core} was different across the periods (Fig. 3; $F_{2,22} = 79.3$, $P < 0.0001$), but was not affected by diet ($F_{1,11} = 1.6$, $P = 0.23$) or by the treatment in Trial 1 ($F_{1,11} = 0.22$, $P = 0.65$). The mesor of T_{core} was higher

during Period 2 than during Period 1 ($P = 0.0001$), and was lower in Period 3 than during Period 2 ($P = 0.0002$).

The amplitude of the circadian rhythm of T_{core} also increased with increased heat load (data not shown; $F_{2,22} = 4.9$, $P = 0.02$), and was affected by diet ($F_{1,11} = 11.3$; $P = 0.006$), but not by previous wool treatment ($F_{1,11} = 0.23$, $P = 0.64$). Although the ANOVA detected an effect of diet on the amplitude of T_{core} , *post hoc* Tukey's HSD testing failed to detect any difference in the amplitude of T_{core} between the diets within any of the three periods ($F_{2,22} = 2.5$; $P = 0.1$).

The mesor of T_{rum} was affected by period ($F_{1.7,22.3} = 35.3$, $P < 0.0001$), and was not affected by diet ($F_{1,13} = 3.70$, $P = 0.08$). The amplitude of the circadian rhythm of T_{rum} also increased with increased heat load ($F_{1.9,25.2} = 7.72$, $P = 0.003$), and was not affected by diet ($F_{1,13} = 0.021$, $P = 0.88$).

The difference between T_{rum} and T_{core} was different between the periods (Fig. 3 – lower panel; $F_{1.8,23.6} = 9.7$, $P = 0.001$), but there was no effect of diet ($F_{1,13} = 1.3$, $P = 0.28$) or previous wool treatment ($F_{1,11} = 2.4$, $P = 0.16$). A *post hoc* Tukey's HSD test revealed that the difference between the T_{rum} and the T_{core} was higher during Period 1 than during Period 2 by $0.2 \pm 0.03^{\circ}\text{C}$.

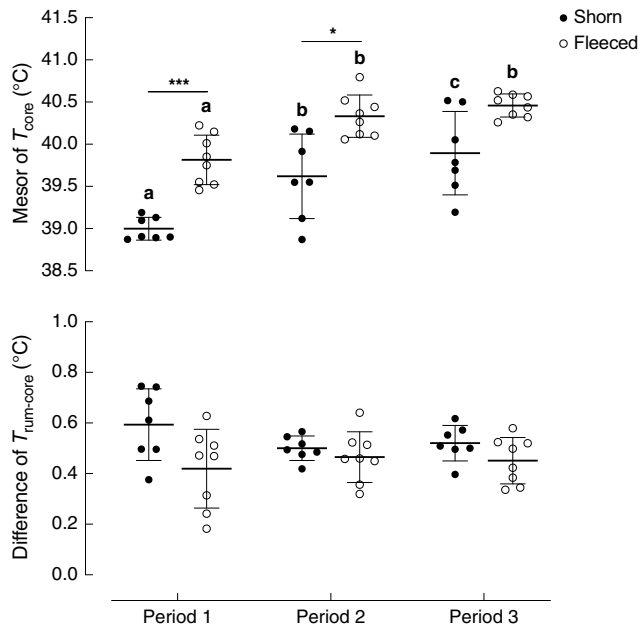


Fig. 2. Trial 1: mesor of the core temperature (T_{core} – upper panel) and the difference between the temperature of the rumen and the core ($T_{rum-core}$ – lower panel) in sheep that were either shorn or fleeced, and exposed to thermoneutral (Period 1), moderate heat load (Period 2), and high heat load (Period 3) in a climate chamber. Different superscripts indicate statistical difference ($P < 0.05$) between periods within each treatment, and bars denote statistical difference between treatment groups within a period, where * = $P < 0.05$, *** = $P < 0.001$. Error bars indicate s.d.

($P = 0.0002$). The difference between T_{rum} and T_{core} during Period 3 was not different from Period 1 or Period 2.

There was no effect of increasing heat load on the amplitude of $T_{rum-core}$ ($F_{1,6,21.0} = 1.118$, $P = 0.33$), or of diet ($F_{1,13} = 4.730$, $P = 0.05$).

The range of the difference between T_{rum} and T_{core} during the Trial 2 was 0.3–1.0 $^{\circ}\text{C}$, with a grand mean of $0.5 \pm 0.2^{\circ}\text{C}$, irrespective of the effect of diet or previous wool treatment.

The $T_{rum-core}$ difference during the entire experiment

Because there was no effect of either the fleece or diet on the difference between the T_{rum} and the T_{core} in the sheep, we then calculated the overall average and standard deviation for each individual sheep during the duration of the entire experimental period (25 days; Fig. 4). The grand average $T_{rum-core}$ difference in all sheep was $0.5 \pm 0.1^{\circ}\text{C}$ during the entire experimental period.

The $T_{rum-core}$ difference at categories of T_{core}

A general relationship emerged with the difference between T_{rum} and T_{core} being higher at the lower T_{core} ($P < 0.05$; Fig. 5), decreasing to a plateau of a difference of $0.5 \pm 0.1^{\circ}\text{C}$ in the range of T_{core} higher than 38.5 $^{\circ}\text{C}$ and

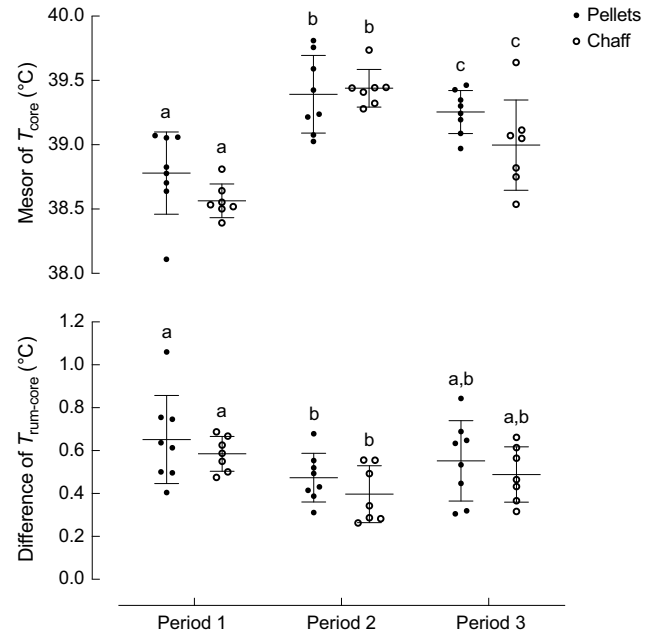


Fig. 3. Trial 2: Mesor of the core temperature (T_{core} – upper panel) and the difference between the temperature of the rumen and the T_{core} ($T_{rum-core}$ – lower panel) in sheep that were fed either pellets or chaff, at thermoneutral (Period 1), moderate heat load (Period 2), and high heat load (Period 3) in a climate chamber. A two-way RM MANOVA revealed an effect of increasing heat load and different superscripts indicate statistical difference ($P < 0.05$) between periods within each treatment. There was no effect of diet on the mesor of T_{core} or of $T_{rum-core}$. Error bars indicate s.d.

lower than 41.1 $^{\circ}\text{C}$. The vast majority of observations (92%) occurred when T_{core} was between 38.5 $^{\circ}\text{C}$ and 41.1 $^{\circ}\text{C}$, with 7.9% below 38.4 $^{\circ}\text{C}$, and 0.03% above 41.1 $^{\circ}\text{C}$. The T_{rum} was therefore consistently 0.5 $^{\circ}\text{C}$ higher than the T_{core} across the normal range of T_{core} . The $T_{rum-core}$ difference was smaller than 0.5 $^{\circ}\text{C}$ when T_{core} exceeded 41.1 $^{\circ}\text{C}$ ($P < 0.05$; Fig. 5).

Discussion

This study was conducted to determine the relationship between T_{core} and T_{rum} in sheep. Because the measurement of T_{rum} is less invasive than the measurement of T_{core} , which requires surgery for the placement of a logger in the abdominal cavity or an artery, there are advantages to using T_{rum} . The live export of sheep from Australia to destinations around the world can expose sheep to heat stress when vessels near or cross the equator (Stockman *et al.* 2011). The routine measurement of T_{rum} is a feasible strategy to monitor the physiological/thermal responses of sheep during voyages, while the measurement of T_{core} would require surgery on each animal. However, before the measurement of T_{rum} is acceptable, we need to assess if T_{rum} can be used as a proxy for T_{core} in sheep.

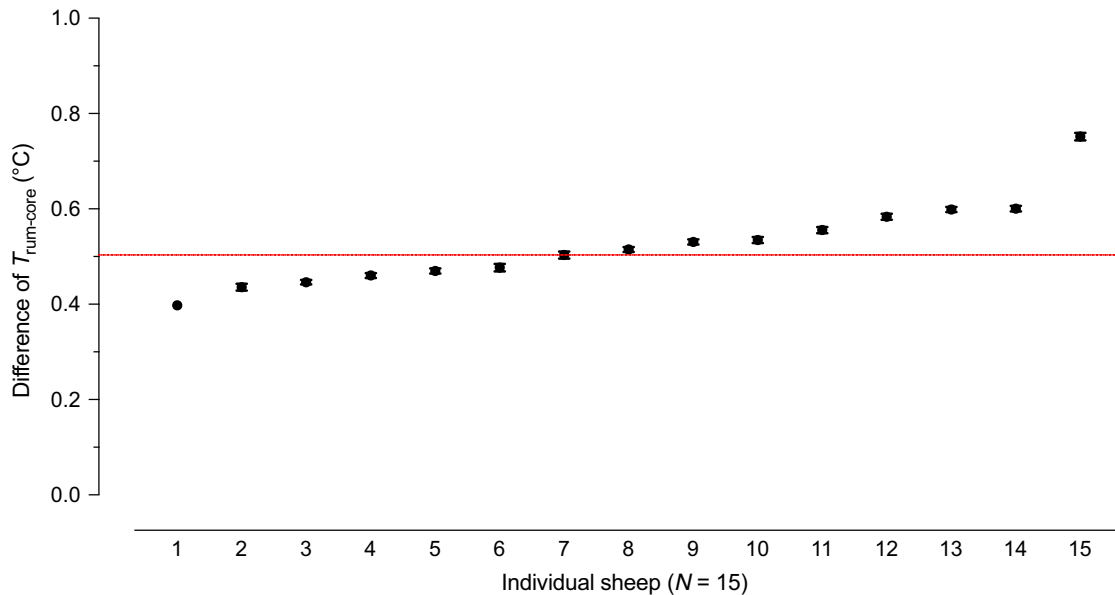


Fig. 4. Average and standard error of the mean of the difference between the T_{rum} and T_{core} in each individual sheep during the entire experimental period. The stippled line denotes the grand average $T_{\text{rum-core}}$ difference in all sheep (0.5°C) during the entire experimental period.

There are some studies in cattle suggesting that T_{rum} is a useful proxy for T_{rec} (Lees *et al.* 2018, 2019, 2020). Presumably the temperature in the rectum will be subject to most of the same factors as will temperature in the rumen, especially changes in the distribution of blood flow to the gastrointestinal tract when blood is diverted to the periphery during exposure to high T_{a} , and so while the temperature measured in those two locations might be well correlated, it does not mean that they will be correlated with T_{core} . For example, the use of T_{rec} as a proxy for T_{core} in sheep can result in an overestimation of the use of selective brain cooling because T_{rec} always exceeded arterial blood temperature (Maloney *et al.* 2001).

We show here that when T_{core} increased during exposure to heat load, so did the T_{rum} and so, despite relatively large changes in overall body temperature, the $T_{\text{rum-core}}$ difference did not change. The grand mean of the difference between T_{rum} and T_{core} was $0.5 \pm 0.1^{\circ}\text{C}$ across a range of individuals and environmental conditions similar to those experienced by sheep on live export vessels, and irrespective of length of wool or different diet composition.

The T_{wb} that our sheep were exposed to was higher than the 25.5°C threshold for an increase in morbidity and mortality identified during live export but lower than the T_{wb} that is often experienced near the Equator (Maunsell Australia 2003). During the days of high heat load the body temperature of the sheep increased relative to thermoneutral conditions, indicating that the conditions exceeded the thermoneutral zone (Mitchell *et al.* 2018). The central question in this study is whether the state of the animal's body temperature can be inferred from measurements of T_{rum} .

The applicability of T_{rum} as a proxy for T_{core}

To establish T_{rum} as a valid proxy for T_{core} in sheep, the relationship between the two needed to be validated over a range of conditions. Any change in T_{a} stimulates various physiological responses that allow mammals to maintain thermal homeostasis in the altered environment. These responses include changes in circulatory (Hales 1973; Von Engelhardt and Hales 1977) and respiratory (Hales 1973; Vesterdorf *et al.* 2011) function in ruminants. As such, rumen pH and T_{rum} changes have been observed in response to heat stress in cattle (e.g. Beatty *et al.* 2006, 2008b; Baumgard and Rhoads 2013), goats (e.g. Salama *et al.* 2014; Castro-Costa *et al.* 2015), and sheep (e.g. Hales 1973; Von Engelhardt and Hales 1977; Beatty *et al.* 2008a; Vesterdorf *et al.* 2011).

The effect of drinking

The drinking of water at room temperature by our sheep resulted in a sharp but transient decrease in T_{rum} . These decreases in T_{rum} were always larger than 0.4°C and of approximately 90 min duration, from the initial rapid decrease and back to an asymptote. The T_{rum} in heat stressed goats that were provided with water for only for 30 min per day decreased rapidly when water was provided and then increased back to the normal range over the subsequent 2 h (Castro-Costa *et al.* 2015). The logical explanation for the temperature decrease is that, because the water was cooler than the body and rumen, heat was transferred from the rumen contents to the ingested water, resulting in the rapid decrease in temperature. Because the

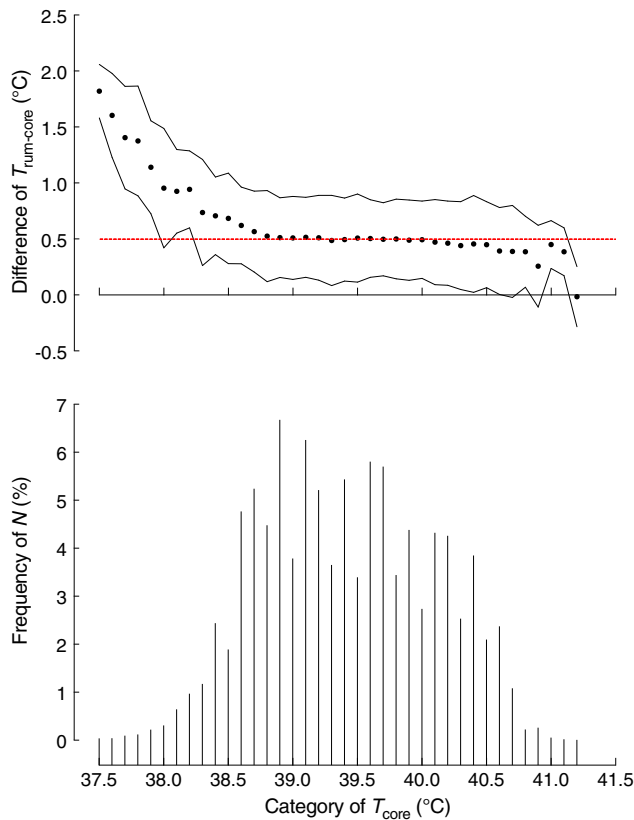


Fig. 5. Observations of the difference between T_{rum} and T_{core} (°C) in all sheep during the entire experimental period: (upper panel) The $T_{rum-core}$ difference (solid circle) surrounded by the average maximum and minimum (solid lines) at categories of T_{core} ; (Lower panel) The percentage of the total sample size (N ; 46 785 observations) at each of those categories of T_{core} during the two experiments. The T_{rum} was consistently $0.5 \pm 0.1^\circ\text{C}$ higher than T_{core} when T_{core} was between 38.5°C and 41.1°C (upper panel: stippled line; $P < 0.05$; 92.03%).

T_{rum} would then have been lower than temperature in the surrounding body, heat would diffuse into the rumen and cause the gradual asymptote as the ruminal contents re-established a thermal steady state with the body. Similar observations have been reported in previous studies in cattle (Bianca 1964; Beatty *et al.* 2008b; Cooper-Prado *et al.* 2011) and goats (Castro-Costa *et al.* 2015).

While there was a clear effect on T_{rum} when a sheep consumed water, the transient nature of the temperature change had no impact on the estimate of any of the parameters of the circadian rhythm of T_{rum} . Beatty *et al.* (2008a) found 'spike-like' decreases in average hourly T_{rum} that explained 10–20% of the variability in hourly T_{core} in sheep. By analysis of T_{rum} collected at 12-min intervals, instead of hourly averages, we discerned more clearly the timing, length, and range of these 'spike-like' decreases. We compared the effect on the circadian rhythm of T_{rum} of 'smoothing' the T_{rum} , by eliminating those spike-like decreases from the data set, against that of the raw,

'unsmoothed', T_{rum} . We found that there was no effect of drinking on the circadian rhythm of T_{rum} or indeed on the difference between T_{rum} and T_{core} .

Rumen heat balance

Exposure to heat stress affects rumen function in sheep through changes in rumen blood flow and T_{rum} (Hales 1973; Von Engelhardt and Hales 1977; Beatty *et al.* 2008a; Lees *et al.* 2020), as well as decreases in digestibility, motility, bacterial activity, and pH (Bernabucci *et al.* 2009). In cattle, exposure to heat load conditions resulted in increased T_{rum} and lower feed intake, which is often interpreted as a thermoregulatory adaptation that reduces the heat increment of feeding (Mendel and Raghavan 1964; Beatty *et al.* 2006, 2008b; Gonzales-Rivas *et al.* 2018; Lees *et al.* 2018, 2019). In our study, however, increased heat load did not affect feed intake in the sheep during either of the trials. Similar observations were made in goats, also fed to maintenance level and exposed to a similar heat load as that used in our study (Castro-Costa *et al.* 2015).

Exposure to heat load initiates a series of thermoregulatory responses, including a redistribution of blood flow to the periphery that facilitates heat loss across the skin and mucosal membranes (Hales 1973; Von Engelhardt and Hales 1977) and increased respiratory frequency that facilitates respiratory evaporative heat loss (Vesterdorf *et al.* 2011). Rumen temperature likely depends on the rate of local heat production in the rumen by fermentation and the rate of heat loss from the rumen. With a change in ruminal blood flow during heat exposure, heat produced from fermentation is less readily removed from the rumen, resulting in higher T_{rum} . The temperature of the rumen therefore depends on the level of blood flow to and from the rumen relative to the heat production (Maloney *et al.* 2001). When blood flow is redirected away from the rumen during heat exposure, the T_{rum} should increase because heat exchange between the rumen and the surrounding body will decrease. That increase in T_{rum} will then affect the relationship between T_{rum} and T_{core} .

Effect of fleece

When T_a is lower than the body temperature (T_b ; °C) the presence of fleece will reduce heat flow from the skin to the environment, but when T_a exceeds T_b that fleece will reduce heat flow from the environment into the skin (Robertshaw 1968; Von Engelhardt and Hales 1977). A fully fleeced sheep should therefore rely more on respiratory evaporative heat loss (REHL) at thermoneutrality than a shorn sheep (Hales 1973; Vesterdorf *et al.* 2011). But when the T_a is higher than T_b , a fleeced sheep should have a lower heat load than a shorn sheep, and thus require smaller REHL to achieve heat balance. Comparing the $T_{rum-core}$ difference in fleeced versus shorn sheep when they are exposed to heat stress should reveal whether differences

in blood flow to the rumen result in changes in T_{rum} relative to T_{core} . In our study, the T_{core} of shorn sheep was $0.6 \pm 0.1^\circ\text{C}$ lower than that of fleeced sheep during the thermoneutral Period 1 and the moderate heat load in Period 2, reflecting a relatively higher degree of heat loss from the body of the shorn sheep that clearly was not compensated for by higher REHL in the fleeced sheep. During exposure to high heat load, the T_{core} of shorn and fleeced sheep was the same, and there was no difference in the $T_{\text{rum-core}}$.

Effect of diet

Different composition of a diet has the potential to affect the capacity to cope with heat stress. Particle size can affect the extent of rumen fermentation and retention time in the rumen (Kaske et al. 1992). As such, changes in particle size in the diet may cause changes to the bacterial activity of the rumen, along with fermentation, digestibility, and ruminal flow-through rate, which in turn would affect the heat production of the rumen and hence rumen heat balance (Silanikove 1985). There was, however, no effect of a change in dietary composition on the T_{rum} or indeed the difference between the T_{rum} and the T_{core} in the sheep in the present study. Our findings are corroborated by studies in goats kept on either high or low roughage diets (Castro-Costa et al. 2015) and in cattle kept on either completely pelleted or mixed roughage diets (Bonfante et al. 2016) where no change in T_{rum} was detected.

The $T_{\text{rum-core}}$ difference

The difference between T_{rum} and T_{core} remained constant at 0.5°C despite increasing heat load in sheep during the fleece experiment in Trial 1. During Trial 2, while there was no effect of diet on the $T_{\text{rum-core}}$ difference, that difference decreased by 0.2°C from Period 1 to Period 2, and then did not change into Period 3. Because the $T_{\text{rum-core}}$ difference in Period 2 and 3 of Trial 2 was similar to the $T_{\text{rum-core}}$ measured during all of Trial 1, it seems that the anomaly was the larger $T_{\text{rum-core}}$ difference in Period 1 of Trial 2. During Period 1 of Trial 2 the T_{core} was lower than it had been in Trial 1 and was in the other periods of Trial 2. As a result the data from Period 1 of Trial 2 were all toward the left side of Fig. 5, and we do not think that the data reflect any impact of the diet, *per se*, on the $T_{\text{rum-core}}$ difference, but rather reflect the relatively low T_{core} .

It was apparent that sheep in both Trial 1 and 2 adjusted to the high heat load with the onset of thermoregulatory mechanisms, including increased respiratory frequency that allowed the sheep to lose heat via REHL (Vesterdorf et al. 2011). That the sheep were affected by heat load was evident from the higher T_{core} and T_{rum} , and the increased daily amplitude of both, irrespective of fleece length or diet.

For the vast majority of simultaneous observations of T_{rum} and T_{core} when T_{core} was within the normal range for sheep (that is, in 92% of observations when T_{core} was between

38.5°C and 41.1°C) in our study, the difference between T_{rum} and T_{core} was within the $0.45\text{--}0.55^\circ\text{C}$ range. At the few observations of high T_{core} (0.03%; higher than 41.1°C), the $T_{\text{rum-core}}$ difference was smaller than 0.5°C . Similarly, for the few observations at low T_{core} (8%; lower than 38.5°C), the $T_{\text{rum-core}}$ difference was higher than 0.5°C . The low and the high T_{core} observations were associated with exposure to low and high T_{wb} exposure, respectively.

Above a T_{core} of 41.1°C , the average $T_{\text{rum-core}}$ decreased, suggesting either that heat production in the rumen decreased or heat loss from the rumen to the general body increased. The use of T_{rum} to infer T_{core} at these high body temperatures would lead to an overestimation of T_{core} . While a small proportion of our data (0.03%) were in that category, the T_{wb} onboard livestock vessels can exceed 27°C when ships are near the equator (Maunsell Australia 2003), and we do not know whether the $T_{\text{rum-core}}$ difference continues to decline as T_{wb} increases further. Conversely, at T_{core} lower than 38.5°C , the $T_{\text{rum-core}}$ difference increased, suggesting either that heat production in the rumen increased or that heat loss from the rumen to the general body decreased. The use of T_{rum} to infer T_{core} at these low body temperatures would lead to underestimation of T_{core} .

Because the major welfare concern during live export is heat stress (Stockman et al. 2011), and the associated high body temperatures, it is unlikely that the underestimation of T_{core} at low body temperature would be an important issue with the use of T_{rum} during live export.

Conclusion

The use of thermo-transmitters located in the rumen of sheep would provide a direct, real-time method for the continuous monitoring of sheep during transport onboard live export vessels. We show here that the daily average relationship between T_{rum} and T_{core} is not affected by water ingestion, length of fleece, diet composition, or heat load. Management could directly monitor values of the T_{rum} and could, by subtraction of the 0.5°C difference shown in this study, obtain a reliable measure of the T_{core} of the sheep at all times of day, providing a live and reliable indication of the thermal status of the animals.

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

Conflicts of interest. The authors declare no conflicts of interest.

Declaration of funding. This research did not receive any specific funding.

Acknowledgements. The authors wish to thank Malcolm Boyce, Donald Hook, Eric Taylor, and Kim Thomas for their assistance during the experimental work in the laboratory and on the Murdoch University farm.

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