Direct Effect of a Hot Environment on Ruminal Motility in Sheep

Katsunori Sunagawa*, Yuji Arikawa, Mika Higashi, Hiroshi Matsuda, Hiroshi Takahashi, Zyunichi Kuriwaki Zuikou Kojiya, Syuntoku Uechi and Fujiya Hongo

Faculty of Agriculture, University of the Ryukyus, 1 Senbaru, Nishihara-cho, Okinawa 903-0213, Japan

ABSTRACT : The aim of this research was to clarify the direct effects of a hot environment on ruminal motility in sheep fed twice a day. In the first experiment, in order to equalize variable factors excluding the ambient temperature between the thermoneutral environment (23°C, relative humidity 80%) and the hot environment (32°C, relative humidity 80%), sheep were fed equal amounts of the same quality feed twice a day. The sheep were allowed free access to water for the duration of the two one-hour feeding periods (10:00 am-11:00 am, 5:00 pm-6:00 pm). On the fourth day after exposure to the hot environment, the frequency and strength of ruminal contractions were continuously recorded between 9:30 am and 11:00 pm. Prior to the exposure to a hot environment the frequency and strength of ruminal contractions were recorded in a thermoneutral environment during the period 9:30 am-11:00 pm. In the second experiment, in order to maintain the stomach content of the sheep at equal levels in both environments, the sheep were fed equal amounts of the same quality feed twice a day. Following the completion of the two one-hour feeding periods, a fixed amount of warm water was infused into the rumen. Rumen motility was then recorded during the same period as for the first experiment (9:30 am-11:00 pm). In the first experiment, when the frequency of ruminal contractions prior to (24, 24 frequency/15 min), during (48, 47 frequency/min) and after (22, 19 frequency/min) both the morning and afternoon feeding in a hot environment was compared with the values from the thermoneutral environment (20, 22; 50, 50; 21, 20 frequency/min), there was found to be no difference. However, the strength of ruminal contractions after morning and afternoon feeding (3.7, 3.1 mm Hg) in the hot environment decreased significantly in comparison with the thermoneutral environment (4.3, 3.8 mm Hg). In the second experiment, the frequency of ruminal contractions in the hot environment was not significantly different from that in the thermoneutral environment. The strength of ruminal contractions after ruminal infusion of warm water in the hot environment (morning: 4.6, afternoon: 4.5 mm Hg) was significantly lower than that in the thermoneutral environment (morning: 5.6, afternoon: 5.0 mm Hg). The results suggest that a hot environment acts directly on the strength of ruminal contractions in sheep fed twice a day rather than on the frequency. ***(Asian-Aust. J. Anim. Sci. 2002. Vol 15, No. 6 : 859-865)***

Key Words : Ruminal Motility, Hot Environment, Direct Effect, Fed Sheep

INTRODUCTION

Reticuloruminal motility mixes large amounts of ingested forage with saliva and rumen microorganisms. The churning action of the rumen promotes ruminal fermentation, and increases the contact between the end products of fermentation and the rumen wall, thus aiding absorption. Reticuloruminal motility also propels digesta into the abomasum through the omasum.

Sunagawa et al. (1988) reported that in goats fed the same amount and quality of feed, the net daily absorption of volatile fatty acids (VFA, mg/day) in a hot environment were greater than those in a thermoneutral environment. Sunagawa et al. (1997) also reported that in goats fed with the same feeding system (fed twice a day for 1 h), digestibilities of dry matter, organic matter, crude protein, nitrogen free extract (NFE) and neutral detergent fiber (ADF) of alfalfa hay cubes in a hot environment were significantly greater than those in a thermoneutral environment. Decreases in the frequency of ruminal contractions extends the time that ingested matter is retained in the rumen, thus increasing ruminal digestion (Pharr et al., 1967). Therefore, it is thought that the ruminal production of VFA increased in goats exposed to a hot environment due to the extended ruminal retention of digesta caused by decreases in the frequency of ruminal contractions. The number of ruminal contractions is dependent upon the type of feed (forage, concentrate), feed quality (herbage, rice straw), the form in which feed is ingested (hay, pellets), the amount of feed consumed and rumen wall stimulation (Reid, 1963; Pharr et al., 1967; Church, 1976; Colvin et al., 1978).

In a hot environment, feed intake in ruminants decreases while water intake increases excessively (109%) (Colditz and Kellaway, 1972). Up until now, there has been little research on the effect of a hot environment on ruminal motility. Attebery et al. (1969) reported that both the frequency and strength of ruminal contractions decreased in cows exposed to a hot environment. The measurements for this experiment were conducted 14 h after feeding. Detailed observations of the animals under normal feeding conditions were not made.

In order to clarify the direct effects of a hot environment

* Address reprint request to Katsunori Sunagawa. Tel: +81-98-895-8798, Fax: +81-98-895-8734, E-mail: b986094@agr.u-ryukyu.ac.jp

Received September 6, 2001; Accepted December 20, 2001

on ruminal motility, the frequency and strength of ruminal contractions (internal ruminal pressure) were continuously measured in two experiments. Both experiments were conducted on sheep in two environments: a thermoneutral environment and a hot environment. In the first experiment, the sheep were fed equal amounts of the same quality feed and were given free access to drinking water for the 1 h duration of both the morning and the afternoon feeding periods. The second experiment used the same sheep. In this experiment, the sheep were fed equal amounts of the same quality feed, but warm water was infused into the rumen through a nasal catheter in order to keep water intake levels the same for both environments.

MATERIALS AND METHODS

Animals

Four 4 year old castrated male crossbred sheep (Suffolk ×Southdown), weighing 61-71 kg, with a fleece depth of 1-2 cm were used. All animals were surgically prepared with a rumen fistula (30 mm i.d.) and had a carotid artery exteriorized in a skin loop.

The sheep were introduced to, and maintained in individual metabolic cages in a climatic room under thermoneutral conditions (23°C, 80% relative humidity) 30 days prior to the experiments. Sheep were fed twice daily (10:00 am, 5:00 pm) with equal amounts of alfalfa hay cubes (total digestible nutrient, TDN 61.6%, digestible crude protein, DCP 9.2%; 600 g) and a commercial beef cattle feed (TDN 68.0%, DCP 14.5%; 200 g). Alfalfa hay cubes were roughly crushed by hand. The particles of alfalfa feed measured on average 4×4×0.5 cm after crushing. The animals were trained to consume these rations within 1 h. Animals were allowed to drink water freely during the period of feeding (1 h). The alfalfa hay cubes (84.3% dry matter) contained, on a dry matter basis, 18.7% crude protein, 2.4% crude fat, 29.7% crude fiber, 39.7% NFE, 45.9% NDF and 36.6% ADF.

Experimental procedures

The experiment was first conducted in a thermoneutral environment (23°C, relative humidity 80%). One day before the start of the experiment, a polyvinyl catheter (V-2, Top Ltd, Japan) was inserted into the carotid artery and filled with heparine-saline solution (50 i.u./ml). On the day of the experiment, measurements of respiration frequency and heart rates were taken regularly over a 13.5 h period, beginning 30 mins prior to the morning feeding and continuing until 6 h after the afternoon feeding. At the same time, a total of 22 blood samples (3 ml each) were taken from the carotid artery catheter. During this 13.5 h period, rectal temperature and ruminal motility were continuously recorded. Water intake was measured after the conclusion of both the morning and the afternoon feeding periods and combined to give daily water intake. Fourteen days after the completion of the thermoneutral stage of the experiment, temperature and humidity in the climatic room was reset to 32°C, 80% relative humidity. On the 4th day after resetting the environment, the exact same experiment conducted in the thermoneutral environment, was reconducted in the hot environment. The same treatment was applied to all animals with a time interval of 14 days between treatments. This allowed for animal recovery and minimized the compounding effect of the previous treatments. The respiration frequency, heart rate and rectal temperature were measured everyday before both the morning and the afternoon feeding periods. The values of these physiological parameters indicated whether an individual was in good health and had no measurable carry-over effects from the previous experiments.

The frequency of ruminal contractions and intraruminal pressure, namely the strength of the contraction, were measured to ascertain ruminal motility. An open-tipped polyethylene pipe (2.0 mm i.d., 5.0 cm length, Imamura Ltd. Tokyo) was inserted into the rumen fistula in the dorsal sac of the rumen. The outer end of this pipe was connected via a polyethylene tube to a pressure-transducer (Viggo-Spectramed S Pte Ltd, Singapore). The pipe and the tube were filled with saline. The changes in intraruminal pressure caused by ruminal contraction were passed on via the saline to the pressure-transducer whereby the pressure was converted into electrical signals. These electrical signals were continuously recorded by a Multipurpose monitor and recorder (RM-45, Nihon Koden Ltd. Tokyo) between the hours of 9:30 am. and 11:00 pm. The frequency of ruminal contraction is indicated by the number of waves per 15 min. The strength of ruminal contractions was measured by converting maximum wave height (mm) into intraruminal pressure (mm Hg). In the present research, respiration frequency, heart rate and rectal temperature were also measured frequently to compare physiological responses to feeding in both environments. Respiration frequency and heart rate were determined by listening to and counting both the sounds of respiration (breaths/min) and heart beat (beats/min) with a stethoscope. Heart rate was also measured by taking the pulse rate of the carotid artery loop. Rectal temperature was continuously measured between 9:30 am. and 11:00 pm. by way of a sensor inserted approximately 10 cm into the rectum. Temperature was recorded using a thermistor thermometer (E-688, Ioudenki Ltd, Tokyo). Hematocrit was measured using the capillary tube method. Water intake was measured twice each day following the completion of the morning and the afternoon feeding periods. The daily water intake values shown in figure 2 are an aggregate of the measurement taken in the morning and the afternoon on each day. Water

intake recorded on each day during exposure to a hot environment was compared to a 7 day average compiled from water intake measurements in the thermoneutral environment.

In the second experiment, water intake was maintained at an equal level for both environments so as to keep ruminal content volumes at an equal level. In order to maintain water intake levels, 5 liters of warm water (40°C) were infused into the rumen over a 30 min period via a nasal catheter by a motor-driven pump (Cole-Parmer Instrument Co. PA-21A, Chicago) 1 h after the completion of the feeding period. This process was conducted after both the morning and the afternoon feeding periods. The remainder of the experiment was conducted the same as the first experiment in which sheep were given free access to drinking water during feeding.

Statistical analysis

The experiments in this research were conducted according to a switchback design. A two-way analysis (animal, environment) of variance was performed. The F-test was used to compare the parameters at the same time in the thermoneutral and hot environments. For statistical analysis, GLM procedures (SAS, 1990) were adopted.

RESULTS

Figures 1, 2 and 3 show the results of the first experiment. Respiration frequency (breaths/min) decreased markedly during the morning and the afternoon feeding periods in both the thermoneutral (41±4, 35±2) and the hot environment (54±4, 75±7). However, heart rate (100±2, 115±4; 90±6, 93±4 beats/min) and rectal temperature (39.6±0.2, 39.6±0.2; 40.1±0.3, 40.4±0.3°C) increased during the morning and the afternoon feeding periods in both the thermoneutral and the hot environment. Hematocrit (29.3±1.3, 29.6±1.3; 29.9±1.0, 29.6±0.9%) also increased during feeding in both environments. The frequency of ruminal contractions (50±4, 50±5; 48±4, 47±3 frequency/15 min) increased during feeding, but the strength of ruminal contractions (3.1±0.1, 2.9±0.0; 3.2±0.2, 3.5±0.3 mm Hg) decreased in both environments.

The respiration frequency (179±8, 54±4, 187±7 breaths /min) and rectal temperature (39.7±0.3, 40.1±0.4, 39.9±0.2°C) prior to, during and after feeding in a hot environment were significantly ($p<0.01$) greater than those in a thermoneutral environment (60±7, 40±4, 78±7 breaths / min; 39.2±0.2, 39.6±0.2, 39.1±0.2°C) (figure 1). On the other hand, heart rate (69±1, 90±6, 79±3 beats/min) and hematocrit (23.5±0.3, 29.9±1.0, 22.7±0.6%) in a hot environment remained unchanged from those in a thermoneutral environment (66±2, 100±2, 78±3 beats/min;

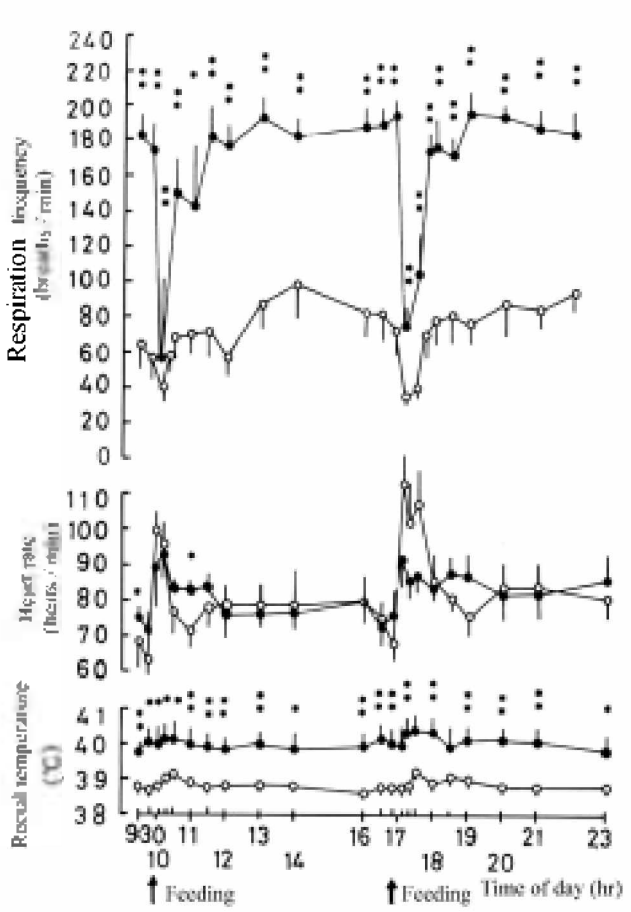

Figure 1. Changes in respiration frequency, heart rate and rectal temperature during exposure to a thermoneutral environment (○) and a hot environment (●). Each point represents the means±SE of 4 sheep. Values that are significantly different from the means in the thermoneutral environment are indicated by * ($p<0.05$) and ** ($p<0.01$).

25.9±0.9, 29.3±1.3, 22.8±0.5%). Water intake on the first, second, third and fourth days (8.1±0.3, 9.3±0.3, 7.6±0.8, 6.9±0.6 l/day) of exposure to a hot environment had increased significantly compared to the thermoneutral environment (4.8±0.6 l/day).

When the frequency of ruminal contractions prior to, during and after both the morning (24±2, 48±3, 22±2 frequency/15 min) and the afternoon (24±2, 46±3, 19±2 frequency/15 min) feeding in the hot environment were compared with the values from the thermoneutral environment (20±2, 50±4, 21±3; 22±3, 50±3, 20±2 frequency/15 min) there was found to be no difference. However, the strength of ruminal contractions after the morning (3.7±0.6 mm Hg) and the afternoon (3.1±0.5 mm Hg) feeding in the hot environment decreased significantly in comparison with the thermoneutral environment (4.3±0.6, 3.8±0.3 mm Hg) (figure 3).

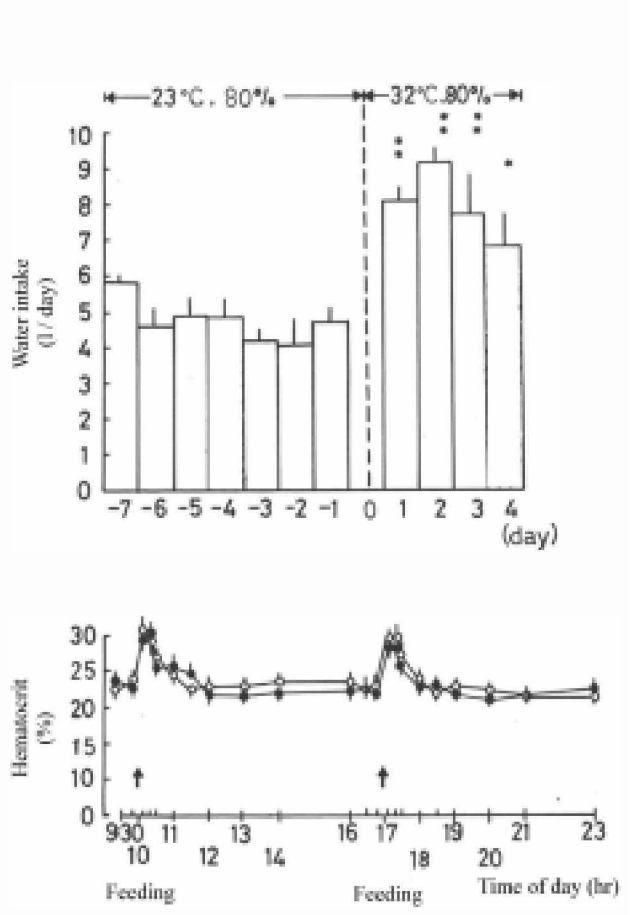

Figure 2. Water intake and hematocrit (means±SE, n=4) when sheep were allowed to drink water freely during the period of feeding (1 h) in a thermoneutral environment (○) and a hot environment (●). Values that are significantly different from the means in the thermoneutral environment are indicated by * ($p<0.05$) and ** ($p<0.01$).

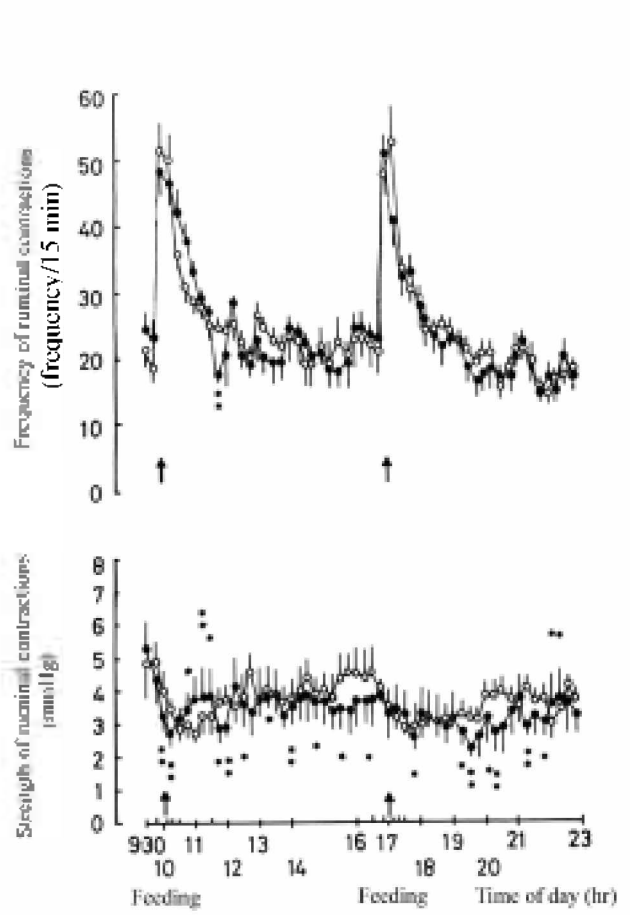

Figure 3. Frequency and strength (means±SE, n=4) of ruminal contractions when sheep were allowed to drink water freely during the period of feeding (1 h) in a thermoneutral environment (○) and a hot environment (●). Values that are significantly different from the means in the thermoneutral environment are indicated by * ($p<0.05$) and ** ($p<0.01$).

Figure 4 shows the results of the second experiment. Changes in respiration frequency, heart rate, rectal temperature and hematocrit in the second experiment were similar to the changes recorded in the first experiment. The frequency of ruminal contractions increased with the infusion of warm water into the rumen in both the thermoneutral (morning: 34±4, afternoon 37±4 frequency/15 min) and the hot (morning: 34±5, afternoon: 40±6 frequency/15 min) environments. However, the difference in ruminal contraction frequency between the two environments after the infusion of warm water was minimal (figure 4). On the other hand, the strength of ruminal contractions after ruminal infusion of warm water in the hot environment (morning: 4.6±0.5, afternoon: 4.5±0.5 mm Hg) was significantly lower than that in the thermoneutral environment (morning: 5.6±0.6, afternoon: 5.0±0.6 mm Hg) (figure 4).

DISCUSSION

In a hot environment, heat dissipation in the animal is unable to keep pace with the body's heat production and thus the body temperature rises. Because of this, the rectal temperature of the sheep used in this experiment was markedly higher in the hot environment as opposed to the thermoneutral environment. When the body temperature in animals increased, the activation of heat loss mechanisms can be observed as the animal actively attempts to dissipate the heat produced in its body (Blaxter et al., 1959). Respiration frequency in the sheep used in this experiment was markedly higher in a hot environment indicating attempts to increase evaporative heat loss via the respiratory tract (figure 1). Cattle in a hot environment lost water through the skin and via the respiratory tract (McDowell,

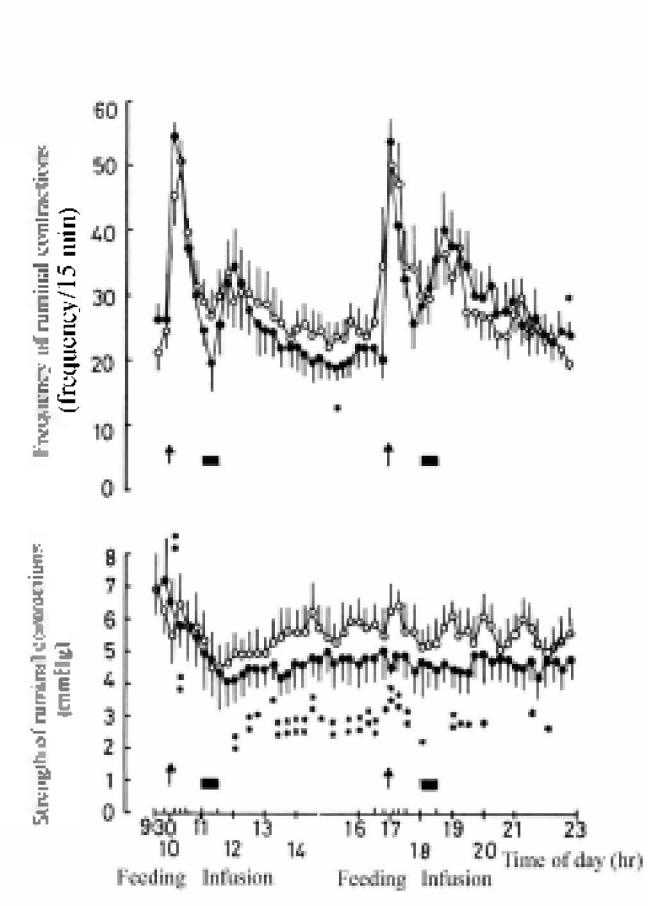

Figure 4. Frequency and strength (means±SE, n=4) of ruminal contractions when warm water was infused into the rumen after the completion of the feeding period in a thermoneutral environment (○) and a hot environment (●). Values that are significantly different from the means in the thermoneutral environment are indicated by * ($p<0.05$) and ** ($p<0.01$).

1969). This water loss caused a temporary body water deficit and consequently a hypertonicity in body fluids, stimulating the thirst center to produce the sensation of thirst and activate a drinking response (Anderson, 1971; Kamal, 1972). Increased extracellular fluid osmolality, decreased extracellular fluid volume, angiotensin II and dryness of the mouth, stimulated the sensation of thirst (Guyton and Hall, 1996). In the first experiment of the present research, in order to equalize all variable conditions except for the ambient temperature between the two environments, sheep in both environments were given water during both the morning and the afternoon one-hour feeding periods. However, water intake on the 4th day of exposure to a hot environment had increased significantly ($p<0.01$) by 2.1 l/day when compared to the thermoneutral environment (figure 2). There was no difference in the arterial blood hematocrit of the sheep between the two environments (figure 2). In this experiment, it is thought that the cause of this was the fact that increases in water intake by sheep in the hot environment were offset largely by the increase in respiratory tract water evaporation. Heart rate between both environments remained unchanged. From the increases in rectal temperature, respiration frequency and water intake in the sheep exposed to a hot environment, it is thought the sheep had experienced ample heat stress during the course of the experiments.

Motility of the reticulo-rumen consists of sequences of primary and secondary contractions. Firstly, the reticulum contracts to approximately half its original size, after which there is a slight relaxation before the reticulum contracts even further (biphasic contractions). The digesta in the reticulum and cranial sac is tipped back and forth across the reticulo-ruminal fold. The second phase of the reticulum contraction begins with the contraction of the rumen. The rumen is separated into two sections (front and rear) by the contraction of the cranial pillar. Following the relaxation of the cranial pillar, contractions in the dorsal sac followed by the ventral sac begin. These contractions progress alternately from front to back (primary contractions). Due to these primary contractions the digesta in the mid-rumen flows caudally. Following the primary contractions, the dorsal sac and the ventral sac each contract again (secondary contractions). At this time the reticulum does not contract. That is, secondary contractions only take place in the rumen and spread from the rear to the front. The secondary contraction sequences cause the digesta in the rumen to divide and flow to the front in two streams, the dorsal stream and the ventral stream. The dorsal stream flows into the dorsal blind sac then turned cranially across the dorsal rumen. The ventral stream moves into the caudal ventral blind sac and the central rumen. Eructation appears in conjunction with secondary contractions (Wyburn, 1980; Tsuda, 1994).

Ruminal contraction frequency is highest during feeding (2.7 frequency/min). Second highest frequency is recorded during rumination (2.3 frequency/min), while the lowest frequency is recorded during rest periods (2.0 frequency/min) (Tsuda, 1994). In the present experiment, the frequency of ruminal contraction increased during feeding (figures 3 and 4). The strength of the contractions, however, decreased during feeding in both the thermoneutral and hot environments (figures 3 and 4). Increases in heart rate during feeding in the thermoneutral and hot environments indicated an increase in the activity of the sympathetic nervous system (figure 1). All of the motility of the gastrointestinal tract necessary for digestion including reticulo-rumen motility, saliva secretion, eructation and rumination are carried out by vago-vagal reflexes (Leek and Harding, 1974). From this report, it is thought that the increases in frequency of ruminal

contractions during feeding was caused by the activation of the para-sympathetic nervous system including the vagus nerves (figures 3 and 4). In the first experiment of the present research, sheep were fed equal amounts of the same quality of feed twice a day in both environments. In the second experiment, sheep were fed equal amounts of the same quality of feed twice a day, and a fixed amount of warm water was infused into the rumen in both environments. The activation of tension receptors in the reticulo-rumen caused by ruminal distension promotes ruminal contraction (Gregory, 1984). The increases in frequency of ruminal contractions due to intraruminal infusion of warm water were caused by the activation of tension receptors in the rumen in both environments (figure 4). Ruminal contractions in both environments in experiment 1 were not significantly different and thus it is thought that due to the equal volumes of feed consumed, ruminal distension in the sheep was also similar. Sunagawa et al. (1988) reported that in goats fed the same amount and quality of feed, the net daily absorption of volatile fatty acids (VFA, mg/day, arterio-portal venous concentration difference of VFA×portal blood flow) in a hot environment was greater than that in a thermoneutral environment. The activation of epithelial receptors in response to volatile fatty acids sends an inhibitory afferent signal to the gastric centers, which inhibits ruminal contraction (Leek and Harding, 1974). It is thought that the significant decrease in the strength of ruminal contractions by exposure to a hot environment in experiments 1 and 2 was due to the increased concentrations of ruminal volatile fatty acids. Attebery et al. (1969) reported that both frequency and strength of ruminal contractions decreased in cows exposed to a hot environment. The difference in results of the present experiment and that of Attebery et al. arises from the feeding system employed. The Attebery et al. (1969) experiment employed a voluntary feeding system which resulted in a significant decrease the amount of feed consumed by the cows when exposed to a hot environment. Other experiments have confirmed the phenomenon of decreased feed intake due to a hot environment (Colditz and Kellaway, 1972). Therefore, the decreases in both frequency and strength of ruminal contractions in cows exposed to a hot environment were due to the differences of ruminal distension and ruminal volatile fatty acid levels caused by decreases in voluntary feed intake in a hot environment.

From the results of the first experiment, it is suggested that the changes in ruminal motility in a hot environment were the effect of not only the hot environment itself, but also the increase in water intake. In the second experiment, in order to clarify the direct effects of a hot environment on ruminal motility, a fixed amount of warm water was infused into the rumen so as to keep water intake levels equal between the two environments. As previously stated the transient increases in the frequency of ruminal contractions following the infusion of warm water were caused by extension stimulus of the rumen wall (Gregory, 1984). When compared with the thermoneutral environment, the frequency of ruminal contractions in the hot environment was unchanged. The strength of the contractions however, decreased significantly in virtually all time periods (figure 4). However, in the second experiment whereby warm water was infused into the rumen, the extent of the decrease (18%) in the strength of ruminal contractions was larger than the extent of the decrease in the first experiment (14%). The intraruminal infusion of warm water employed in the second experiment not only kept water intake levels equal but also kept stomach content at an equal level in both environments. This is a direct reflection of the effect of a hot environment on ruminal motility. It is thought that the effect of a hot environment appears more readily in the strength of ruminal contractions than in the frequency of ruminal contractions in sheep fed twice a day.

In their 1988 experiment in which goats were kept in hot and thermoneutral environments, fed equal amounts and quality of feed, and allowed to drink for one hour twice a day, Sunagawa et al. found that the net daily absorption of volatile fatty acids increased in a hot environment. Sunagawa et al. (1997) also reported that in goats fed with the same feeding system, digestibilities of dry matter, organic matter, crude protein, nitrogen-free extracts (NFE) and neutral detergent fiber (NDF) of alfalfa hay cubes in a hot environment were significantly greater than those in a thermoneutral environment. In addition, Sunagawa et al. (1996) indicated that water consumption has an inhibitory influence on the increase of ruminal absorption of VFA due to heat exposure in goats. Sunagawa et al. (1989) reported that the disappearance rate of dry matter, organic matter, neutral detergent solubles (NDS) and NDF from nylon bags incubated in the rumen of the sheep exposed to a hot environment were the same as those of the animals exposed to a thermoneutral environment. The results indicated that the rates of ruminal digestion of alfalfa feed components in the hot environment were the same as those in the thermoneutral environment when the retention time of each component in the rumen was equal in both environments. Warren et al. (1974) reported that the mean retention time of digesta in the digestive tract of steers given forage was increased from 36.6 h to 43.2 h when the temperature was increased from 18°C to 32°C. In the present experiment, the strength of ruminal contractions after feeding in the hot environment decreased in comparison with the thermoneutral environment. From these reports, it is thought that in ruminants exposed to a hot environment, the decrease in the strength of ruminal contractions caused an extension in the retention time of digesta in the rumen, thus increasing ruminal digestion of crude protein, NFE and

crude fiber.

The results suggest that a hot environment acts directly on the strength of ruminal contractions in sheep fed twice a day rather than on the frequency.

ACKNOWLEDGMENTS

We thank G. McIlvride and I. Nagamine for help in preparing the manuscript.

REFFERENCES

Anderson, B. 1971. Thirst- and brain control of water balance. Am. Scient. 59:408-415.

Attebery, J. T. and H. D. Johnson. 1969. Effects of environmental temperature, controlled feeding and fasting on rumen motility. J. Anim. Sci. 29:734-737.

Blaxter, K. L., N. McC. Graham, F. W. Wainman and D. G. Armstrong. 1959. Environmental temperature, energy metabolism and heat regulation in sheep. II. The partition of heat losses in closely clipped sheep. J. Agric. Sci. (Cambridge) 52:25-40.

Church, D. C. 1976. Motility of the gastro-intestinal tract. In: Digestive Physiology and Nutrition of Ruminants. Vol. 1 (Ed. D. C. Church). New York, O and B Books, Inc. pp. 69-98.

Colditz, P. J. and R. C. Kellaway. 1972. The effect of diet and heat stress on feed intake, growth, and nitrogen metabolism in Friesian, F_1 Brahman×Friesian, and Brahman heifers. Aust. J. Agric. Res. 23:715-725.

Colvin, H. W., R. D. Digesti and J. A. Louvier. 1978. Effect of succulent and nonsucculent diets on rumen motility and pressure before, during and after eating. J. Dairy Sci. 61:1414-1421.

Gregory, P. C. 1984. Control of intrinsic reticulo-ruminal motility in the vagotomized sheep. J. Physiology. 225:309-338.

Guyton, A. C. and J. E. Hall. 1996. Central nervous system centers for thirst. In: Textbook of Medical Physiology. 9th Ed. W.B. Saunders Company, Philadelphia, Pennsylvania, p. 361.

Kamal, T. H., O. Shehata and I. M. Elbanna. 1972. Effect of heat and water restriction on water metabolism and body fluid compartments in farm animals. In: Isotope Studies on the Physiology of Domestic Animals. International Atomic Energy Agency, Vienna, pp. 95-102.

Leek, B. F. and R. H. Harding. 1974. Sensory nervous receptors in the ruminant stomach and the reflex control of reticulo-ruminal motility. In: Digestion and Metabolism in the Ruminant (Ed. I. W. McDonald and A. C. I. Warner). The University of New England Press, Armidale, Australia pp. 60-76.

McDowell, R. E., E. G. Moody, F. J. Van Soest, R. P. Lehmann and G. L. Ford. 1969. Effect of heat stress on energy and water utilization of lactating cows. J. Dairy Sci. 52:188-194.

Pharr, L. D., H. W. Jr. Colvin and P. R. Noland. 1967. Rumen motility of sheep as affected by the physical form of oat hay. J. Anim. Sci. 26:414-417.

Tsuda, T. 1994. Digestion and absorption. In: Animal Physiology. (Ed. T. Tsuda). Youkendo, Tokyo, pp. 161-162.

Reid, C. S. W. 1963. Diet and the motility of the forestomachs of the sheep. Proc. NZ Soc. Anim. Prod. 23:169-188.

Sunagawa, K., H. Takahashi, Z. Kojiya and F. Hongo. 1988. Net absorption amounts of volatile fatty acids in goats exposed to a heat environment. Jpn. J. Zootech. Sci. 59:787-792.

Sunagawa, K., T. Senshu, H. Matsuda. H. Takahashi, Z. Kojiya and F. Hongo. 1989. Effects of a heat environment on the disappearance of feed fractions from nylon bags incubated in the rumen of sheep. Asian-Aus. J. Anim. Sci. 2:384-385.

Sunagawa, K., H. Takahashi, Y. Iseki, M. Higashi, S. Umeda, H. Yamashiro, F. Nakamatsu, H. Akutsu, F. Hongo, A. Shinjo, S. Shiroma and Y. Kawashima. 1996. Effects of excessive water intake on net absorption of volatile fatty acids in goats exposed to hot environment. Anim. Sci. Technol. (Jpn.) 67:893-899.

Sunagawa, K., M. Sakurada, H. Takahashi, F. Hongo, A. Shinjo and S. Shiroma. 1997. The ruminal concentrations of volatile fatty acids and digestibility of the feed fractions in goats exposed to a hot environment. Anim. Sci. Technol. (Jpn). 68:156-162.

Warren, W. P., F. A. Martz, K. H. Assay, E. S. Hilderbrand, C. G. Payne and J. R. Vogt. 1974. Digestibility and rate of passage by steers fed tall fescue, alfalfa and orchardgrass hay in 18 and 32 C ambient temperature. J. Anim. Sci. 39:93-96.

Wyburn, R. S. 1980. The mixing and propulsion of the stomach contents of ruminants. In: Digestive Physiology and Metabolism in Ruminants (Ed. Y. Ruckebusch and P. Thivend). MTP Press, Lancaster, UK, pp. 35-51.