Effects of Solar Radiation, Dietary Energy, and Time of Feeding on Thermoregulatory Responses and Energy Balance in Cattle in a Hot Environment[1]

A. Brosh*,[2], Y. Aharoni*, A. A. Degen† D. Wright‡, and B. A. Young§

*Department of Beef Cattle, Agricultural Research Organization, Institute of Animal Science, Newe Ya'ar Research Center, P.O. Box 1021, Ramat Yishay, 30095, Israel; †Desert Animal Adaptations and Husbandry, Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Beer Sheva 84105, Israel; ‡Department of Companion Animal Medicine and Surgery, University of Queensland, St. Lucia, 4067 Australia; §Department of Animal Production, University of Queensland, Gatton College 4343, Australia

ABSTRACT: Ten growing heifers were either exposed to or protected from solar radiation, offered a diet of either high (H) or low (L) ME, and fed either in the morning or afternoon during a hot summer. Heifers that consumed the H diet had a greater water intake, DMI, metabolizable energy intake, energy expenditure, and retained energy than heifers that consumed the L diet. Solar radiation did not have an effect on any of these variables. Furthermore, dietary energy and time of measurement had an effect on rectal temperature (Tr), respiration rate (RR), heart rate (HR), and rate of oxygen uptake (VO_2); solar radiation had an effect on Tr and RR but not on HR and VO_2; and time of feeding had an effect only on VO_2. Heifers coped with greater heat loads by increasing RR and the difference in Tr between morning and afternoon. It seems that a lowered body temperature in the morning is a physiological mechanism used by animals to prepare for the heat load that develops during the day. Heat production (HP) and HR throughout the day were affected mainly by the time of feeding and not by the environmental heat load. Feeding in the afternoon increased HP in the cooler hours of the day when heat losses from the animal through conduction and radiation were more efficient. With a pending high heat load situation, reducing feed quality and(or) changing the time of feeding to the late afternoon could be beneficial to the animals in reducing their heat loads.

Key Words: Cattle, Solar Radiation, Time of Feeding, Thermoregulation, Energy Balance

 J. Anim. Sci. 1998. 76:2671–2677

Introduction

The performance of livestock raised in tropical and subtropical areas is generally poorer than that in temperate climates (Payne, 1981). Summer heat load causes a reduction in feed and energy intakes (Young and Hall, 1993) and consequently in productivity (Blackshaw and Blackshaw, 1994). In cattle, this can result in decreased growth rate (Turner, 1984), lower milk production (Wolfenson et al., 1988), and reduced reproductive rate (Brown, 1974).

Beef cattle maintain body temperature within a narrow range (Bligh and Lampkin, 1965). Apparently, this allows for maximum production. Body temperature is determined by heat input from metabolic heat production (HP) and solar radiation and by heat output through evaporative and nonevaporative avenues. When heat loss does not attain heat gain, heat is stored, with a resultant increase in body temperature. Although some large animals use thermolability as an adaptive strategy to tolerate heat stress, this does not seem to be so with cattle.

Beede and Collier (1986) discussed three approaches that can improve productivity in cattle raised in hot climates: 1) protection from solar radiation (Buffington et al., 1983); 2) use and genetic development of heat-resistant breeds (Finch, 1986); and 3) improvement of nutritional management. In addition, the timing of feeding can affect heat production and heat balance. Cattle are generally fed in the morning; the provision of feed to the trough is the greatest stimulus to feeding (Fell and Clark, 1993). The

[1]Contribution from the Agric. Res. Organization, the Volcani Center, Bet Dagan, Israel, No. 302/98. The authors wish to thank S. Fennell, G. Beneke, B. Hall, A. Goodwin, K. Rowan, J. McCosker, M. Josey, F. Gorbacz, R. Englebright, I. Williams, and T. Schoorl for their contributions.

[2]To whom correspondence should be addressed: phone: 972-4-9539523; fax: 04-9836936; E-mail: beefny@netvision.net.il.

Received February 6, 1998.
Accepted June 23, 1998.

Table 1. Proximate analysis (% of dry matter) and metabolizable energy of the low- (L) and high- (H) energy diets consumed by the heifers

Diet	OM	CP	EE[a]	CF[b]	NDF	ME, MJ/kg
L	89.77	7.68	1.31	52.93	68.53	7.2
H	93.56	16.92	2.23	18.12	29.53	10.6

[a]Ether extract.
[b]Crude fiber.

consumption and digestion of feed increase heat production (Young and Webster, 1963; West, 1994), and this internal heat production, combined with high air temperatures, can result in heat stress in the animal. This study was designed to determine the effects of dietary quality, solar radiation, and time of feeding on thermoregulatory responses and energy balance in feedlot beef cattle during summer in a subtropical region.

Materials and Methods

Animals and Treatments. Ten growing 12-mo-old Hereford heifers (345 ± 10.8 kg BW) were used. The heifers were healthy and grazing before the experiment, and their condition was judged as good. They were observed frequently during the study, and no ovarian cyclic behavior was noted. Heart rate radio transmitters (Telonics, Mesa, AZ) were implanted in six of them, approximately 1 mo before commencement of measurements. Animals were kept individually in open feedlot pens, each 40 m^2. Shade was provided over approximately half the area of each pen: galvanized-iron sheets, at a height of 2.2 m, covering 11.5 m^2, and 70% shade cloth, at a height of 4 m, covering 12 m^2. The study was conducted during the summer (January–March) of 1993 in southeast Queensland, Australia, a subtropical region with summer temperatures commonly over 30°C.

During the study, animals were either exposed (**EXP**; not offered shade) to or protected (**PRO**; offered shade) from solar radiation. They were offered either a high-ME diet (**H**) of 10.6 MJ/kg of DM, which consisted of a concentrate:sorghum hay ratio of 80:20 on a DM basis, or a low-ME roughage diet (**L**) of 7.2 MJ/kg of DM, which consisted only of sorghum hay. Composition of the diets is presented in Table 1. The amount of feed given was adjusted so that refusals would be less than 5% of that offered. On each treatment of diet quality or solar radiation, feed was offered either at 0800 or 1630, and the animals had free access to the feed at all times thereafter. Refusals were collected and weighed once weekly. Water consumption was measured volumetrically and recorded daily.

The experimental design consisted of four periods as follows: 1) 2-wk adaptation; 2) 5-wk first experimental; 3) 2-wk adaptation; and 4) 5-wk second experimental. Half the heifers were assigned to the H diet and half to the L diet in Periods 1 and 2, and the diets were switched in Periods 3 and 4. In each 5-wk period, two 2-wk periods were assigned to each of the two solar radiation treatments with a 1-wk adaptation period between them.

Measurements. Heart rate (**HR**) for each of the six implanted heifers was measured for 5 min every .5 h throughout every day. The O_2 uptake measurements were made on seven heifers, which included the six heifers implanted with HR transmitters, by the use of a face mask, open-circuit respiratory system (Taylor et al., 1982). The accuracy was checked gravimetrically by injecting nitrogen into the mask (McLean and Tobin, 1990). Energy expenditure (**EE**) was calculated assuming 20.47 kJ/L of O_2 (Nicol and Young, 1990).

Simultaneous HR and O_2 uptake measurements were made for each of the implanted animals on each treatment during two consecutive days when at rest. Each measurement was made over 15 to 20 min between 0700 and 0830 before the morning feed and between 1400 and 1530 in the afternoon. Data were averaged every 5 s, recorded on a data logger (Mini-Logger™, Mini-Mitter Co., Sunriver, OR), and transferred to a laptop computer for processing. For analysis, the data were pooled over 30-s intervals. For each such simultaneous measurement of HR and O_2 uptake, the O_2 pulse was calculated as the O_2 uptake per heart beat.

Respiration rate (**RR**) was measured by counting the rate of flank movement, and rectal temperature (**Tr**) was measured with an electronic thermometer (accuracy to .1°C) in all 10 heifers.

Daily EE of the heifers for each trial combination was calculated from multiplication of the total daily heart beats by EE of one pulse. The relationship of HR to EE was established for each individual animal for each dietary regimen (Brosh et al., 1994, 1998).

Meteorological data, including air temperature (**Ta**), black globe temperature (**BG**), and relative humidity (**RH**), were collected between 0700 and 0830 before feeding and between 1400 and 1530. Black globe humidity indices (**BGHI**) were calculated (Buffington et al., 1981).

Calculations and Statistical Analyses. Dry matter intake, metabolizable energy intake, and water consumption were measured in the 10 heifers, whereas

EE and retained energy were determined for only the six heifers that were equipped with heart rate radio transmitters. These variables were calculated for each 2-wk subperiod of diet and solar radiation treatment and were analyzed by ANOVA random block design, with animals as blocks, for the effects of diet, solar radiation, and their interaction. Respiration rate and rectal temperature were available for 10 heifers, HR for six heifers, and O_2 uptake for seven heifers. For each of these variables, 32 measurements were made for each heifer: two replicates in the morning and two replicates in the afternoon, during two consecutive days, in each treatment of diet, solar radiation, and time of feeding. These variables were analyzed by ANOVA of a random block design, with animals as blocks, for the effects of diet, solar radiation, time of feeding, time of measurement, and their interactions. Because the interaction of all four variables was not available by this design, a paired *t*-test within animals was used where applicable to analyze for differences between measurements (i.e., between morning and afternoon measurements within a treatment). All analyses were made using Genstat 5 Release 3.2 (Lawes Agricultural Trust, 1995).

Results and Discussion

Meteorological data are presented in Table 2. The greatest environmental heat load was recorded during the afternoon in the EXP pens.

The actual ratios of concentrate to sorghum hay DMI on the H diet were 80.0 ± .17 : 20.0 ± .17 for the PRO heifers and 80.6 ± .36 : 19.4 ± .36 for the EXP heifers. Dietary ME was 10.63 MJ/kg of DM and 10.65 MJ/kg of DM for the PRO and EXP heifers, respectively.

Heifers on the H diet consumed 1.38 times the water, 1.76 times the DM, and 2.59 times the ME consumed by the heifers on the L diet. Differences between diets were all significant (Table 3). In contrast, solar radiation did not have an effect on any of these three measurements. The interaction between dietary ME and radiation, however, did have an effect on water consumption. Results in this study were similar to those for Merino sheep, as obtained in a study in which shade was not related to patterns of drinking or feeding (Johnson and Strack, 1992). However, they were unlike results reported for Jersey and Holstein cows in lactation because shaded cows consumed more total feed than cows not shaded (Mallonee et al., 1985).

Table 2. Meteorological data during the study (mean ± SE, n = 16)

	Morning	Afternoon	Mean 24 h ± SD
Ambient temperature, °C	23.7 ± .8	30.4 ± .7	25.2 ± 6.07
Relative humidity, %	64.2 ± 2.4	43.6 ± 2.7	
Black globe temperature, °C			
Protected pens	25.3 ± .8	33.1 ± .7	
Exposed pens	36.6 ± 1.2	43.6 ± 1.2	
Black globe humidity indices, °C			
Protected pens	72.6 ± 1.0	80.4 ± .7	
Exposed pens	83.9 ± 1.2	90.9 ± 1.5	

Dietary energy and time of measurement had an effect on Tr, RR, HR, and rate of oxygen uptake (VO_2), and solar radiation had an effect on Tr and RR but not on HR and VO_2. Time of feeding had an effect only on VO_2, but there were significant interactions between time of feeding and diet on VO_2; time of feeding × diet × radiation on HR; and time of feeding × diet × time of measurement on Tr, HR, and VO_2 (Table 4). Thus, time of feeding exerts an effect on the animal mainly in conjunction with other factors. Measurements of Tr, RR, HR, and VO_2 are presented in Figure 1, and the corresponding statistical analysis is summarized in Table 4.

The percentage change between morning and afternoon RR, Tr, HR, and VO_2 and the effect of diet, solar radiation, time of feeding, and their interactions are

Table 3. Water intake (WI, mL/[$kg^{.75}$·d]), DMI, g/($kg^{.75}$·d), and energy balance data, metabolizable energy intake (MEI), energy expenditure (EE), and energy retained (RE, (kJ/[$kg^{.75}$·d]) of the heifers on the two diets when either exposed (EXP) or protected (PRO) from solar radiation

	Diet L		Diet H					
Item	EXP	PRO	EXP	PRO	SE	P^a Diet	P Radiation	P Interaction
WI	335	368	508	461	19.3	***	NS	*
DMI	63.2	61.5	111.0	108.5	2.6	***	NS	NS
MEI	447	448	1,155	1,167	25.0	***	NS	NS
EE	388	373	666	642	11.5	***	NS	NS
RE	59	74	489	525	21.5	***	NS	NS

[a]NS, not significant, $*P < .05$, $***P < .001$.

Table 4. The effects of diet, solar radiation, time of feeding, and time of measurement and its interactions, on the rectal temperature (Tr, df = 319), respiration rate (RR, df = 319), heart rate (HR, df = 191), and oxygen consumption (VO_2, df = 222) in heifers

Item	Tr	RR	HR	VO_2
Effects				
Diet (D)	***	***	***	***
Radiation (R)	***	***	NS	NS
Time feeding (Tf)	NS	NS	NS	***
Time measured (Tm)	***	***	***	***
Interactions				
D × R	**	**	**	NS
D × Tf	NS	NS	NS	**
R × Tf	NS	NS	NS	NS
D × Tm	*	***	***	*
R × Tm	***	***	*	NS
Tf × Tm	**	†	***	***
D × R × Tf	NS	NS	*	NS
D × R × Tm	*	*	NS	NS
D × Tf × Tm	**	†	***	**
R × Tf × Tm	NS	NS	NS	NS

NS, not significant, †$P < .1$, *$P < .05$, **$P < .01$, ***$P < .001$.

presented in Table 5. The main effect that caused an increase in HR and VO_2 from morning to afternoon was the time of feeding (Table 5, Figure 1). In addition, the interaction of either diet or radiation and time of feeding was significant. The RR and Tr increased greatly in the afternoon owing to the heat load; it increased more so when the heifers were exposed to solar radiation and to even a greater extent when combined with feeding the higher ME diet. Because eating caused an increase in the intrinsic heat load, feeding in the morning increased the heat load during the late morning to early afternoon, when there was much solar radiation, to a greater extent than did eating in the afternoon, when there was less solar radiation in the late afternoon to evening. Consequently, the increase of RR and Tr from morning to afternoon was greater when the feed was given in the morning rather than in the afternoon.

Despite the larger heat load induced by solar radiation, the morning Tr of the EXP heifers was significantly ($P < .05$) lower than that of the PRO heifers, under all feeding regimens. The largest difference between morning and afternoon Tr was 1.5°C, which was recorded under the highest heat load conditions (i.e., the morning-fed H diet regimen). This fluctuation in Tr is similar or slightly less than the nyctothemeral variation in deep body temperature of Hereford and Zebu cows and of three breeds of African cattle under conditions that did not produce heat stress (Bligh and Harthoorn, 1965; Bligh and Lampkin, 1965). Body temperature responses in this study are unlike those reported for nonlactating Holstein cows in which body temperature was not affected by changes in air temperature, regardless of shade availability (Lefcourt and Schmidtmann, 1989). The results also differ for those in sheep, a thermostabile animal (Johnson, 1971). There was no difference in minimum, maximum, or daily body temperature fluctuation between Merino sheep that were inclined to stay in the sun and those inclined to stay in the shade. However, maximum and minimum body temperatures occurred 1 to 2 h later in the shade sheep (Johnson, 1991).

Even though some large animals use thermolability as an adaptive strategy to tolerate heat stress (Schmidt-Nielsen et al., 1957; Taylor, 1970), this does not seem to be so with cattle, although there may be some differences among breeds. Two alternate possibilities exist that may explain the results in this study: 1) that the EXP heifers were less tolerant of the environmental conditions than were the PRO heifers; or 2) that the lower morning Tr of the EXP heifers was an adaptive mechanism that allows an animal to cope with an upcoming heat load; that is, maintaining a lower Tr would require a lower heat production than maintaining a higher Tr.

The HR and VO_2 uptake on the H diet were 2.05 and 1.75 times those on the L diet, respectively. The HR and the VO_2 were significantly affected by the time of measurement, which also interacted with time of feeding, and both interacted with the dietary ME. The HR and VO_2 uptake during the hotter afternoon hours were higher ($P < .05$) than in the morning only when the feed was given in the morning, and the difference between the morning and afternoon measurements were larger in the H diet than in the L diet. Solar radiation did not affect HR and VO_2 despite the heat load induced by the radiation and the significant increase in RR and Tr. The afternoon measurement of the morning-fed heifers was taken 4 to 6 h after feeding, whereas, in all the other measurements, a long time elapsed from the feeding time to the measurement. We suggest, therefore, that the HR and the VO_2 of the heifers were affected only by metabolizable energy intake and the intrinsic heat load that was induced following eating.

The effect of time of feed presentation on HR of the heifers during the day is presented in Figure 2A; the ambient temperatures during these measurements is presented in Figure 2B. Because solar radiation did not affect HR and VO_2, the EXP and PRO heifers on each feeding regimen were combined into one group of six. On both diets, HR started to increase following the provision of feed to the trough. On the H diet, HR and HP were different ($P < .05$) between the two feeding regimens during most of the day (except between 0800 to 1000 and between 1800 to 2000). Thus, HP of morning-fed animals was highest when the heat load from the environment was highest. This pattern was reversed when the feed was given in the afternoon. Then, the highest HP occurred during the cooler hours and permitted easier nonevaporative heat loss from the body to the environment. The same pattern was found on the L diet, but differences were significant only between 1000 and 1600. The daily EE and the HP on the L diet was lower than those on the H diet (Table 3), and, as a result, the intrinsic heat load on the L diet was also lower. Consequently, the relief of heat load induced by the afternoon feeding was less on the L diet than on the H diet.

Daily EE was calculated from the product between average daily HR and the EE per one heart beat, and retained energy (**RE**) was calculated from the difference between MEI and EE. Heifers on the H diet had a higher EE and a higher RE than heifers on the L diet (Table 3).

As found for HR and VO_2, EE and RE were affected by dietary ME and not by solar radiation. Heifers on the L diet increased RE by 59 to 74 KJ $kg^{-.75}$/d, whereas those on the H diet increased RE by 489 to 525 $kg^{-.75}$/d ($P < .05$). However, RR was affected by solar radiation, increasing during the hot part of the day, and, therefore, there was an increase in RR without a concomitant increase in energy expenditure. The increase in RR with little change in energy heat production was also found in panting sheep (Hales and Brown, 1974) and oxen (Hales and Findlay, 1968). This apparent anomaly has possible explanations. A panting rate at the resonant frequency of the respiratory system allows an animal to pant with little

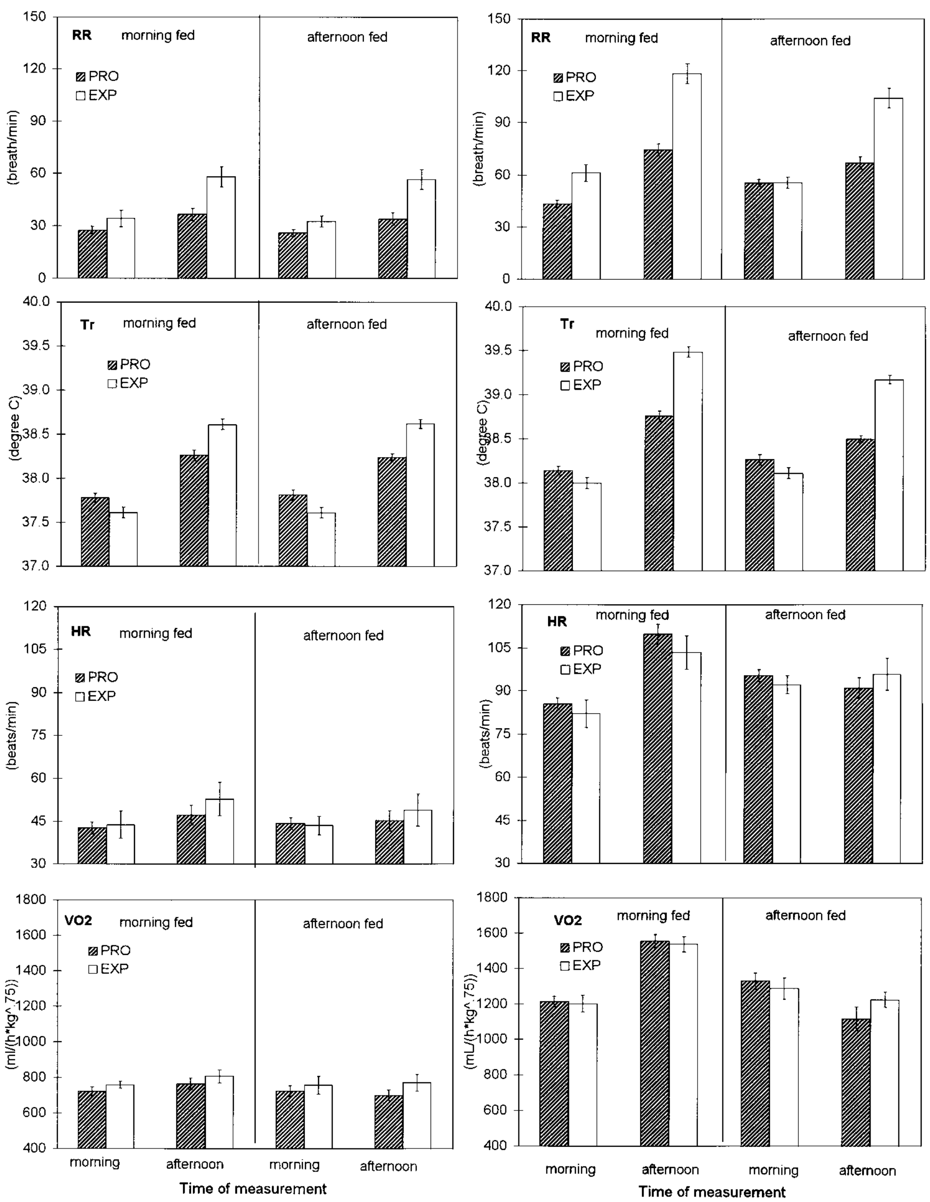

Figure 1. Respiration rate (RR), rectal temperature (Tr), heart rate (HR), and oxygen uptake (VO_2) of heifers (mean ± SE, n = 10, 10, 6 and 7, respectively), in the morning and in the afternoon when animals were protected (striped area) or exposed (clear area) to solar radiation and were fed in the morning and in the afternoon. Heifers were fed low-ME diet (the graph pairs on the left) and high-ME diet (the graph pairs on the right).

Table 5. Effect of dietary ME (D), solar radiation (R; exposed vs protected), and time of feeding (Tf; morning, fm and afternoon, fa) on the magnitude of change of respiration rate (RR), rectal temperature (Tr), heart rate (HR), and of oxygen uptake (VO_2) between morning and afternoon (percentage of morning measurement)

	Exposed		Protected				Main effects, *P*			Interactions, *P*			
Diet	fm	fa	fm	fa	SE	df	D	R	Tf	D × R	D × Tf	R × Tf	D × R × Tf
L, RR	90.9	90.7	39.5	33.3									
H, RR	110.7	118.7	85.2	29.2	10.89	159	*	**	NS	NS	NS	†	NS
L, Tr	2.67	2.70	1.28	1.16									
H, Tr	3.94	2.82	1.61	.64	.22	159	*	***	***	*	***	NS	NS
L, HR	21.10	13.45	10.93	2.34									
H, HR	26.94	4.30	28.63	−4.44	2.27	95	NS	***	***	*	***	**	†
L, VO_2	8.0	3.9	6.2	−2.0									
H, VO_2	30.2	−2.3	29.6	−15.8	3.76	110	*	*	***	NS	***	†	NS

NS, not significant, †$P < .1$, *$P < .05$, **$P < .01$, ***$P < .001$.

effect on the internal heat production. Also, any increase in energy expenditure needed by respiratory muscles could be accompanied by a decrease in metabolism of other tissues. There is an increase in blood flow to the respiratory system and a decrease to some other tissues during heat stress (Hales, 1973).

When the morning-fed heifers were offered the H diet, the daily EE of the EXP heifers was 4.7% less than that of the PRO heifers ($P < .05$). Similar results were obtained on Bedouin goats that were either exposed to or protected from solar radiation in the summer and were fed alfalfa hay and deprived of water for 4 d (Brosh, 1985). The VO_2 consumption of protected goats was 15% higher than that of exposed goats. We suggest that under heat load conditions, acclimated ruminants reduce HP despite an elevated RR. This could be due to an animal's ability to reduce alimentary activity. The splanchnic tissues in growing

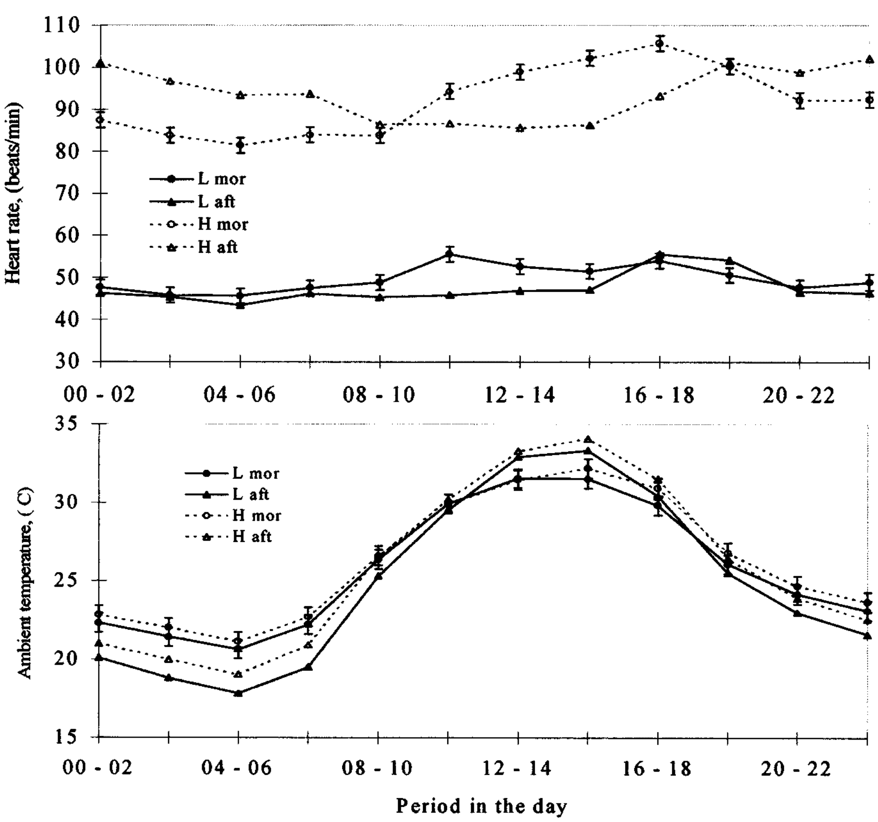

Figure 2. Heart rate during the day of heifers (mean ± SE) fed low-ME diet (L) and high-ME diet (H); feed was given in the morning (mor) or in the afternoon (aft) (top). Ambient temperature during the days of the HR measurements (bottom).

cattle account for about 45% of the total body HP (Reynolds et al., 1991), and any reduction in the activity of this system could compensate for an increase in energy of the respiratory system.

We conclude that a high-energy intake, required for a high level of production, is the main cause for heat load in growing cattle and that solar radiation has a minor effect. In fact, high-producing cattle in a hot environment tend to reduce HP under solar radiation.

Implications

Feed quality and not solar radiation had the major effect on heat production. In addition, heat production increased during and after feeding. Feeding in the cooler hours of the day allows easier nonevaporative heat loss from the body to the environment. With a pending high heat load situation, reducing feed quality and(or) providing feed in the late afternoon would be beneficial to animals in reducing their heat loads.

Literature Cited

Beede, D. K., and R. J. Collier. 1986. Potential nutritional strategies for intensively managed cattle during thermal stress. J. Anim. Sci. 62:543–554.

Blackshaw, J. K., and A. W. Blackshaw. 1994. Heat stress in cattle and the effect of shade on production and behaviour: A review. Aust. J. Exp. Agric. 34:285–295.

Bligh, J., and A. M. Harthoorn. 1965. Continuous radiotelemetric records of the deep body temperature of some unrestrained African mammals under near-natural conditions. J. Physiol. 176:145–162.

Bligh, J., and G. H. Lampkin. 1965. A comparison of the deep-body temperature of Hereford and Zebu cows recorded continuously by radio-telemetry under similar field conditions. J. Agric. Sci. 64:221–227.

Brosh, A. 1985. Metabolic effect of infrequent drinking and low-quality feed on Bedouin goats. Ph.D. dissertation. Tel-Aviv Univ., Tel Aviv, Israel (in Hebrew).

Brosh, A., Y. Aharoni, A. A. Degen, D. Wright, and B. Young. 1998. Estimation of energy expenditure from heart rate measurements in cattle maintained under different conditions. J. Anim. Sci. (In press).

Brosh, A., G. Beneke, S. Fennell, D. Wright, Y. Aharoni, and B. A. Young. 1994. Prediction of energy expenditure by heart rate measurements in cattle, the effect of exercise, diet, and sun radiation. 13th Symp. on Energy Metabolism of Farm Animals, Mojacar, Spain. EAAP Publ. No. 76.

Brown, G. D. 1974. Heat tolerance and animal productivity in the Australian zone. In: A. D. Wilson (Ed.) Studies of the Australian Arid Zone. II. Animal Production. pp 23–36. CSIRO, Melbourne, Australia.

Buffington, D. E., A. Collazo-Arocho, G. H. Canton, D. Pitt, W. W. Thatcher, and R. J. Collier. 1981. Black globe-humidity index (BGHI) as comfort equation for dairy cows. Trans. Am. Soc. Agric. Eng. 24:711–714.

Buffington, D., R. J. Collier, and G. H. Canton. 1983. Shade management systems to reduce heat stress for dairy cows in hot, humid climates. Trans. Am. Soc. Agric. Eng. 26:1798–1802.

Fell, L. R., and M. R. Clarke. 1993. Behaviour of lot-fed cattle. In: D. J. Farrell (Ed.) Recent Advances in Animal Nutrition in Australia. pp 107–116. Univ. of New England, Armidale, NSW, Australia.

Finch, V. A. 1986. Body temperature in beef cattle: Its control and relevance to production in the tropics. J. Anim. Sci. 62:531–542.

Hales, J.R.S. 1973. Effects of heat stress on blood flow in respiratory and non-respiratory muscles in sheep. Pfluegers Arch. 345: 123–130.

Hales, J.R.S., and G. D. Brown. 1974. Net energetic and thermoregulatory efficiency during panting in the sheep. Comp. Biochem. Physiol. 49A:413–422.

Hales, J.R.S., and J. D. Findlay. 1968. The oxygen cost of thermally-induced and CO_2-induced hyperventilation in the ox. Respir. Physiol. 4:353–362.

Johnson, K. G. 1971. Body temperature lability in sheep and goats during short-term exposures to heat and cold. J. Agric. Sci. 77: 267–273.

Johnson, K. G. 1991. Body temperature and respiratory rates of free-ranging Merino sheep in and out of shade during summer. Aust. J. Agric. Res. 42:1347–1357.

Johnson, K. G., and R. Strack. 1992. Effects of shade use on grazing, drinking, ruminating and postural patterns of Merino sheep. Aust. J. Agric. Res. 43:261–464.

Lawes Agricultural Trust. 1995. Genstat 5 Release 3.2 (PC/Windows/Win32s). Rothamsted Experimental Station, Harpenden, Hertfordshire, U.K.

Lefcourt, A. M., and E. T. Schmidtmann. 1989. Body temperature of dry cows on pasture: Environmental and behavioral effects. J. Dairy Sci. 72:3040–3049.

Mallonee, P. G., D. K. Beede, R. J. Collier, and C. J. Wilcox. 1985. Production and physiological responses of dairy cows to varying dietary potassium during heat stress. J. Dairy Sci. 68: 1479–1487.

McLean, J. A., and G. Tobin. 1990. Animal and Human Calorimetry. Cambridge University Press, Cambridge.

Nicol, A. M., and B. A. Young. 1990. Short-term thermal and metabolic responses of sheep to ruminal cooling: Effects of level of cooling and physiological state. Can. J. Anim. Sci. 70:833–843.

Payne, W.J.A. 1981. The desirability and implications of encouraging intensive animal production enterprises in developing countries. In: A. J. Smith and R. G. Gunn (Ed.) Intensive Animal Production in Developing Countries. p 1. British Society of Animal Production, Penicuik, U.K.

Reynolds, C. K., H. F. Tyrrell, and P. I. Reynolds. 1991. Effect of diet forage-to-concentrate ratio and intake on energy metabolism in growing beef heifers: Whole body energy and nitrogen balance and visceral heat production. J. Nutr. 121:994–1003.

Schmidt-Nielsen, K., B. Schmidt-N, S. A. Jarnum, and T. R. Houpt. 1957. Body temperature of the camel and its relation to water economy. Am. J. Physiol. 188:103–112.

Taylor, C. R. 1970. Dehydration and heat: Effects on temperature regulation of East African ungulates. Am. J. Physiol. 219: 1136–1139.

Taylor, C. R., N. C Heglund, and G.M.O. Maloiy. 1982. Energetics and mechanics of terrestrial locomotion as a function of speed and body size in birds and mammals. J. Exp. Biol. 97:1–21.

Turner, H. G. 1984. Variation of rectal temperature of cattle in a tropical environment and its relation to growth rate. Anim. Prod. 38:417–427.

West, J. W. 1994. Interactions of energy and bovine somatotropin with heat stress. J. Dairy Sci. 77:2091–2102.

Wolfenson, D., I. Flamenbaum, and A. Berman. 1988. Dry period heat stress relief effects on prepartum progesterone, calf birth weight, and milk production. J. Dairy Sci. 71:809–818.

Young, B. A., and A. B. Hall. 1993. Heat load in cattle in the Australian environment. In: B. Coombs (Ed.) Australian Beef. pp 143–148. Morescope Pty Ltd., Melbourne, Victoria, Australia.

Young, B. A., and M.E.D. Webster. 1963. A technique for the estimation of energy expenditure in sheep. Aust. J. Agric. Res. 14: 867–873.