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Seasonal changes in physiological responses and energy expenditure of sheep maintained on semi-arid pasture

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SUMMARY

A study on the energy expenditure of sheep was carried out at the Central Sheep and Wool Research Institute, India during August 1995 to July 1996 by conducting two experiments: one on tracheal cannulated rams maintained on stall-feeding in autumn 1995 (Expt 1) followed by year-round grazing on silvipasture (*Cenchrus ciliaris* pasture interspersed with fodder trees) over three seasons: monsoon, winter and summer, 1995/96 (Expt 2). Physiological responses and energy expenditure measurement of housed and grazing sheep were recorded at 06.00, 14.00 and 22.00 h for 5 consecutive days in each season. Tracheostomized sheep harness with meteorological balloon were used for collection of expired air and measurement of energy expenditure. Rectal temperature (RT) of sheep at 06.00 h was similar in all the seasons except for a significant ($P < 0{\cdot}05$) lower value in monsoon. The rise of RT from 06.00 to 14.00 h in grazing animals was 1·6 °C, higher than that in housed sheep (0·9 °C). Skin temperature (ST) was least in winter and highest at 14.00 h in the monsoon and autumn seasons. Respiration rate (RR) showed a marked rise at 14.00 h in all the seasons. The heart rate (HR) of grazing sheep was higher, irrespective of season, at 14.00 h. At 06.00 and 22.00 h, the heart rate was higher in winter and summer than in the monsoon season. Overall energy expenditure (EE) was 4·85 MJ/24 h during winter which increased to 5·85 MJ/24 h in summer and 6·70 MJ/24 h in the monsoon. The mean rise in energy expenditure per °C rectal temperature in all the seasons was 338 kJ/kg $W^{0{\cdot}75}$. Comparable mean values per 10 °C ambient temperature and 10 °C black globe temperature were 404 and 173. The increase in energy expenditure of grazing compared to housed sheep in monsoon, winter and summer was 78, 15 and 33 % respectively. The mean value was +43 %.

INTRODUCTION

The energy requirements of stall-fed sheep have been studied extensively. In contrast, few studies have been made of grazing sheep. The energy expenditure of animals on pasture while grazing is the sum of several components (basal metabolism; the heat increment of feeding; activities associated with free grazing; and thermoregulation) (White 1993). It has been estimated that sheep on pasture have a maintenance requirement that is 60–70 % greater than that of stall-fed animals (Young & Corbett 1972). In semi-arid regions, sheep are exposed to a wide variation in radiation exposure. It is well recognized that sheep require a high respiratory ventilation and cutaneous evaporation to control their body temperature when exposed to intense radiation. Even with efficient thermal control, with an increase of 10–20 % in metabolic rate, there is 1–2 °C rise in core temperature (Graham *et al.* 1959). In addition the progressive deterioration of forage availability in the summer obliges animals to spend more energy walking in search of food and water. These factors may be expected to result in increased energy expenditure for sheep on tropical pastures. Without information on the energy costs of grazing and its variation with season, it is not possible to develop quantitative management aids. This study was planned to make such a determination.

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MATERIALS AND METHODS

Two experiments were done on tracheal cannulated adult Malpura rams. In Expt 1 they were fed on a maintenance ration in an open-sided, asbestos-roofed animal shed and in Expt 2 the same animals grazed freely on silvipasture (*Cenchrus ciliaris* pasture interspersed with fodder trees). The studies were conducted at the Central Sheep and Wool Research Institute, Avikanagar, India from August 1995 to July 1996 (75° 28′ E, 26° 17′ N, 320 m above mean sea level). The climate is typically semi-arid with yearly mean minimum and maximum temperatures of 8·0 and 41·5 °C and with 275 mm of annual precipitation, with 93% of annual rainfall being distributed between June and September and the remaining 7% taking the form of short winter showers from January to March.

Experiment 1

The experiment was conducted in the autumn (October). Four adult Malpura rams (3–4 years old) with a mean body weight of 34·0 kg were taken from the Institute flock and fitted with tracheal cannulae by surgical techniques perfected by Karim *et al.* (1997). The animals were housed in the animal shed and individually fed on the amount of ration (300 g concentrate and 400 g cenchrus hay) calculated to meet 100% of their maintenance requirements (ICAR 1985). After 15 days of feeding on the maintenance ration, measurement of energy expenditure (EE) was carried out. Meteorological observations: ambient temperature (AT), black globe temperature (BGT) (with thermometer in the centre of 150 mm diameter hollow copper spheres) and relative humidity (RH); and physiological responses such as respiration rate (RR), heart rate (HR), rectal temperature (RT), skin temperature (ST) and energy expenditure (EE) measurements were recorded at 06.00, 14.00 and 22.00 h for 5 consecutive days.

Experiment 2

Fourteen intact Malpura rams of similar body weight and age to the fistulated animals were maintained all year on pasture alone, while the fistulated rams were maintained under stall-feeding with 300 g concentrate and cenchrus hay *ad libitum* per day. The fistulated rams were taken to pasture 15 days before the measurement of EE in each season to get them acclimatized to the prevailing pasture and ambient conditions and during this period they were maintained on grazing alone. The animals were allowed 9 h of grazing (08.00–17.00 h) following a continuous grazing system under the supervision of a shepherd.

The grazing experiment was initiated in August 1995 and continued until July 1996, encompassing one each of monsoon, winter and summer seasons. Field research was conducted on 3·5 ha plots of silvipasture dominated by perennial grass (*Cenchrus ciliaris*), native grasses and forbs (*Commelina forskaeli*, *Eleusine aegyptiaca* and *Crotalaria burhia*) and fodder trees (*Ailanthus excelsa*, *Azadirachta indica*, *Albizia lebbek* and *Prosopis cineraria*). Pasture vegetation was lush green and dense in the monsoon, long and stalky in the winter, and dry and patchily distributed in the summer. Average forage yield of pasture in monsoon, winter and summer was 1·68, 3·24 and 1·89 t DM/ha respectively. Although the green yield of pasture in the monsoon was higher than in the winter and summer, the much greater moisture content of the vegetation resulted in a lower DM yield.

Meteorological observations (AT, BGT and RH), physiological responses (RR, HR, RT and ST) and EE measurements were recorded at 06.00 (in shed), 14.00 (in field) and 22.00 h (in shed) for 5 consecutive days during the monsoon, winter and summer seasons. All the tracheostomized sheep were trained and accustomed to measurement procedures. Each sheep was successively held in the field without chasing them, so that it was possible to obtain a satisfactory recording of expired air that was not affected by extreme activity such as running. Collections of expired air and measurements of physiological responses in individual animals were all of 5–7 min duration in each recording period.

EXPERIMENTAL METHODS

Meteorological observations

Dry and wet bulb temperatures were recorded using suitable thermometers, and net radiation impinging on the animals was measured using a black globe thermometer placed at the height of animals in the shed and field. Relative humidity was calculated from dry and wet bulb temperatures.

Physiological measurements

Respiration rate (RR) was recorded by counting thoracic and flank movements, heart rate (HR) by using a stethoscope placed on the ventro-lateral thorax and rectal (RT) and skin (ST) temperatures using an Aplab multichannel telethermometer. Sweating rate was recorded in the field (Expt 2) during the peak hot period (14.00 h) by the method of Schleger & Turner (1965), which determined the total amount of moisture available on the skin surface of the animals per unit time.

Collection of expired air

An L-shaped tracheal cannula was fabricated and surgically fitted in the lumen of the trachea by a technique perfected in the laboratory. The cannula was open at both ends in the trachea and the end facing outside was normally kept closed by a screw cap, allowing breathing through the nasopharynx. During gaseous exchange measurements, the outside screw cap was removed and a balloon with a tubular lead was introduced into the L-shaped tracheal cannula facing towards the upper respiratory tract. On inflating the balloon in the cannula-L, the respiratory air movement through the nasopharynx was blocked and the animal breathed through the cannula. The balloon in the trachea was maintained

Fig. 1. Malpura ram with L-shaped tracheal cannula and balloon for the collection of expired air *in situ*.

in an inflated condition by tying. The inlet and outlet one-way air valve was screwed to the outer end of the cannula-L. The inflated balloon inside the tracheal cannula was maintained in place till the breathing pattern of the animals stabilized. A meteorological balloon of 30–35 litre capacity was then connected to the expiratory end of the cannula with 30 cm non-collapsible polyethylene tubing (Fig. 1). Expired air was collected in the balloon for 5–10 min in each recording period until the balloon was completely filled but not distended. The volume of air collected in the balloon per unit time was determined and corrected for standard temperature and pressure. The O_2 content of the expired air was determined using a Haldane gas analyser.

Energy expenditure was calculated according to the formula of Young & Webster (1963), excluding the CO_2 and CH_4 factors.

$$EE(kJ) = [20{\cdot}28 \times VO_2(1\ STP)]$$

where VO_2 = volume of O_2 consumed, STP = standard temperature and pressure.

Statistical analyses

Periodic measurements made on variables for four animals were averaged over 5 consecutive days in each season. The data were evaluated by analysis of variance (Harvey 1990), resulting in sources of variation designated season, period, season × period interaction and within season error. The relationships between ambient conditions, physiological responses and energy expenditure were described by use of linear correlation analysis only for values recorded at 14.00 h in the field.

RESULTS AND DISCUSSION

Meteorological observations during the experimental recording are presented in Table 1.

Rectal temperature

Rectal temperature (RT) of both groups of sheep at 06.00 h was similar throughout the seasons (Tables 2 and 3) except for a significantly ($P < 0{\cdot}05$) lower value in the monsoon season, perhaps caused by hyperventilation in the humid conditions. The peak rectal temperature at 14.00 h was 40·7 °C. The mean rise in RT from 06.00 to 14.00 h in grazing sheep was 1·6 °C, appreciably greater than for the housed sheep (0·9 °C). The rise is thus substantially greater than for animals grazing temperate pasture (Bligh *et al.* 1965) and may be a consequence of the greater ambient temperature or solar radiation exposure. Since the response per 10 °C rise in ambient temperature was

Table 1. *Meteorological observations during recording of physiological responses and energy expenditure of sheep in India*

	Expt 1	Expt 2		
Time of recording	Autumn	Monsoon	Winter	Summer
Dry bulb temperature (°C)				
06.00 h	17·5	23·6	9·0	26·9
14.00 h	29·2	34·9	23·8	41·3
22.00 h	22·2	28·7	16·2	33·7
Mean	22·9	28·7	16·2	33·7
Black globe temperature (°C)				
06.00 h	17·6	22·2	9·6	26·8
14.00 h	28·5	44·1	39·8	57·8
22.00 h	22·5	24·7	16·4	33·3
Mean	22·8	30·4	21·9	39·3
Relative humidity (%)				
06.00 h	69·3	90·3	71·1	38·0
14.00 h	28·0	48·3	42·3	24·0
22.00 h	53·0	76·0	43·5	33·8
Mean	50·1	71·5	52·3	31·9

Table 2. *Physiological responses and energy expenditure of stall-fed rams in India*

	06.00 h	14.00 h	22.00 h	S.E. (59 D.F.)
Rectal temperature (°C)	39·4	40·3	39·6	0·137
Skin temperature (°C)	36·3	38·1	36·8	0·047
Gradient of body temperature (°C)	3·03	2·18	2·83	0·112
Respiration rate (respiration/min)	18	25	18	1·11
Heart rate (beat/min)	78	78	71	2·50
EE (kJ/h)	118·10	213·81	188·57	23·251
EE (MJ/day)	2·83	5·13	4·52	0·558
EE (kJ/kg BW)	83·28	152·08	130·74	17·409
EE (kJ/kg $W^{0·75}$)	201·21	366·44	318·52	38·167

Table 3. *Seasonal changes in physiological responses of rams on silvipasture in India*

	Monsoon	Winter	Summer	S.E. (103 D.F.)
Rectal temperature (°C)				
06.00 h	38·4	39·3	39·2	0·17
14.00 h	40·4	40·8	40·7	0·16
22.00 h	39·3	39·8	39·0	0·13
Mean	39·4	39·9	39·6	0·11
Increase Δ 10 °C AT	1·74	1·08	1·01	0·177
Increase Δ 10 °C BGT	0·84	0·52	0·50	0·096
Skin temperature (°C)				
06.00 h	35·8	30·3	36·0	0·62
14.00 h	40·0	36·2	38·5	0·69
22.00 h	36·4	32·9	36·2	0·39
Mean	37·4	33·2	36·9	0·39
Gradient body temperature (°C) (core temperature − skin temperature)				
06.00 h	2·5	8·9	3·3	0·67
14.00 h	0·5	4·6	2·3	0·59
22.00 h	2·7	6·9	2·8	0·41
Mean	1·9	6·8	2·8	0·41
Sweating rate (g/m²/h)	163	58	243	25·9
Respiration rate (respiration/min)				
06.00 h	16	14	21	3·5
14.00 h	66	62	76	3·0
22.00 h	29	23	23	2·9
Mean	37	33	40	2·1
Increase Δ °C RT	36	32	31	7·1
Increase Δ 10 °C AT	48	35	41	4·3
Increase Δ 10 °C BGT	21	15	18	2·1
Heart rate (beat/min)				
06.00 h	62	73	67	3·9
14.00 h	97	97	102	3·4
22.00 h	69	86	75	4·0
Mean	76	85	81	2·3
Increase Δ °C RT	32	20	33	6·9
Increase Δ 10 °C AT	30	17	20	4·6
Increase Δ 10 °C BGT	17	8	11	2·3

almost twice that per 10 °C BGT, it seems likely that the effect is more affected by increases in ambient temperature.

Skin temperature

Skin temperature (ST) was lowest in the winter, at all measurement times, and highest at 14.00 h in the

Table 4. *Seasonal changes in energy expenditure* (*EE*) *of rams on silvipasture in India*

	Monsoon	Winter	Summer	S.E. (103 D.F.)
		EE (kJ/h)		
06.00 h	137·81	146·05	116·76	11·486
14·00 h	493·99	286·50	417·85	21·669
22.00 h	208·20	173·76	196·98	19·965
Mean	279·97	202·09	243·90	16·145
		EE (MJ/day)		
06.00 h	3·30	3·50	2·79	0·243
14.00 h	11·85	6·87	10·02	0·533
22.00 h	4·99	4·16	4·72	0·239
Mean	6·71	4·85	5·85	0·283
		EE (kJ/kg BW)		
06.00 h	108·93	99·18	77·71	7·375
14.00 h	396·40	193·34	275·54	16·299
22.00 h	164·51	117·80	129·98	5·936
Mean	233·26	136·76	161·08	9·998
		EE (kJ/kg $W^{0·75}$)		
06.00 h	267·46	261·93	190·45	21·487
14.00 h	927·31	459·09	676·92	46·399
22.00 h	386·31	301·33	319·27	26·018
Mean	527·01	340·78	395·52	30·021
Increase Δ °C RT	438·00	172·92	402·38	12·695
Increase Δ 10 °C AT	650·97	185·89	374·43	11·585
Increase Δ 10 °C BGT	256·79	86·25	175·39	6·794

summer and monsoon periods. The values probably reflect ambient and black globe temperature and humidity.

Gradient (*rectal – skin temperature*)

The gradient at 14.00 h was much higher in winter, while it was much lower in the monsoon probably due to the combination of high temperature and humidity, which made evaporative cooling very inefficient (Monty *et al*. 1991). This is clearly shown in the lower sweating rate in the monsoon compared to the summer period (Table 3).

Respiration rate

Respiration rate (RR) at 06.00 h showed no significant variation with season although the mean value shifted from 14 to 21 between winter and summer. There was a marked rise in ambient temperature by 14.00 h and a rise of RR, in the grazing sheep in all the seasons. The incremental rise in RR per degree rise in RT, AT and BGT was quite similar in grazed sheep and much greater than was seen in the stall-fed animals. Hence it seems more likely that the difference was a consequence of the additional exercise cost than due to a thermal component of solar radiation (Ahmed & Abdelatif 1992).

Heart rate

Heart rate (HR) at both 06.00 and 22.00 h, when sheep were housed, was higher in winter and summer than in the monsoon season. At 14.00 h heart rate in grazing sheep was invariably high, irrespective of season, and substantially higher than in housed animals. The increment in heart rate per °C RT or per 10 °C AT was similar for all three seasons and substantially greater than per 10 °C BGT. These findings might suggest that heart rate responds more to a rise in rectal or ambient temperature than to a rise in solar radiation (black globe temperature). Higher HR in winter facilitates the increased need for energy (Sleiman & Sabb 1995) and in summer contributes to an increased blood flow to the skin to encourage evaporative cooling (Hales 1974).

Energy expenditure

Overall energy expenditure (EE) of grazing sheep was 4·85 MJ/24 h during winter, which increased to 5·85 MJ/24 h in summer and 6·7 MJ/24 h in the monsoon (Table 4). Energy expenditure of housed sheep was 4·16 MJ/24 h. There was a marked increase in energy expenditure of housed and grazing sheep during the day (14.00 h), which may be explained, in part at least, by the increment caused by feeding

Table 5. *Correlation of energy expenditure (EE kJ/h) of rams with ambient condition and physiological responses* (n = *60*)

	Correlation coefficient
Ambient condition	
AT (°C)	0·47
BGT (°C)	0·67
Physiological responses	
RR (respiration/min)	0·68
HR (beats/min)	0·51
RT (°C)	0·50
ST (°C)	0·45

Table 6. *Comparison of energy expenditure (EE) of stall-fed and grazing rams in India*

	Stall-feeding ($n = 60$)	Grazing ($n = 180$)
EE (kJ/h)	173·46 ± 9·520	241·97 ± 15·567
EE (MJ/day)	4·16 ± 0·170	5·80 ± 0·220
EE (kJ/kg BW)	122·28 ± 7·227	173·67 ± 9·499
EE (kJ/kg $W^{0·75}$)	295·37 ± 17·668	421·09 ± 53·736

(Osuji 1974). However, the increase was substantially greater in all grazing sheep, and was very much greater in the summer and even more in the monsoon than in the winter. Although the temperature in the monsoon was less than in the summer, the much greater humidity would result in a greater heat stress. Even so, in the monsoon sheep walked shorter distances on pasture to meet their food requirements due to lush vegetation coverage.

Energy expenditure per °C RT was also substantially greater in monsoon and summer than in the winter. The mean value was 338 kJ/$kg^{0·75}$. Comparable mean values per 10 °C AT were 404 and per 10 °C BGT 173. The van't Hoff coefficients calculated by the formulae of Graham *et al.* (1959) for the seasons: monsoon, winter and summer, were 0·067, 0·042 and 0·081 (mean 0·063), which implies that EE would double with increases in rectal temperature of 8·6, 5·4 and 10·4 °C respectively. In housed sheep the value was 0·066, as in the monsoon. The mean value is very similar to that reported by Graham *et al.* (1959) for sheep.

Energy expenditure was significantly ($P < 0·01$) correlated with AT, BGT, RR, HR and ST (Table 5), the highest correlation coefficients being obtained for RR (0·68) and BGT (0·64). The mean EE of housed sheep was 295 kJ/kg $W^{0·75}$, which increased to 421 kJ/kg $W^{0·75}$ under grazing conditions (Table 6). The mean increase in energy expenditure of grazed compared to housed sheep was +43%, which is similar to values reported by Young & Corbett (1972). The seasonal increases were 78, 15 and 33% in monsoon, winter and summer, respectively.

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