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Interactions between heat stress and nutrition in sheep fed roughage diets

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SUMMARY

Intake, digestion and growth were examined in young Merino × Border Leicester wether sheep held for 44 days in either cool (13–15 °C, thermal humidity index 56–58) or hot (32–40 °C, 50–70 % relative humidity, thermal humidity index minimum 83–84, maximum 83–88) environments. The sheep were offered diets of medium quality hay *ad libitum* alone (Con) or supplemented with either 22 g air-dry/kg metabolic liveweight ($W^{0·75}$) of barley grain fortified with urea and sulphur (Bar/N) or 10 g air-dry/kg $W^{0·75}$ of fishmeal (FM). Intake of the Con diet by the sheep in the cool environment was high at 79 g DM/kg $W^{0·75}$ per day. Sheep in the hot environment had higher rectal temperatures and higher respiration rates (40·1 °C *v.* 39·2 °C, 196 *v.* 56 respirations/min respectively, $P < 0·01$). The hot environment reduced ($P < 0·05$) total dry matter (DM) intake, estimated metabolizable energy (ME) intake, liveweight (LW) gain and nitrogen (N) balance. The provision of supplements did not change total DM intake, but increased ($P < 0·05$) organic matter digestibility, estimated ME intake, LW gain and N balance. Wool growth was increased much more by the FM than by the Bar/N supplement, indicating that the supply of absorbed amino acids was increased substantially by the FM supplement. Neither voluntary intake nor productivity were influenced by any interactions between the thermal environments and the balance of nutrients provided by the diets. In conclusion, in these young sheep consuming a high intake of a medium quality roughage diet, moderate heat stress reduced intake and growth but did not affect the relative responses of the sheep to supplements providing principally fermentable ME or a similar amount of fermentable ME and additional metabolizable protein.

INTRODUCTION

The productivity of ruminants often declines when high ambient temperature and humidity lead to heat stress, primarily due to reduced voluntary intake of feed and metabolizable energy (ME) (Bianca 1965; NRC 1981; Beede & Collier 1986). The general inverse relationship between ambient temperature and intake is influenced by a number of factors, including environmental humidity, genotype, physiological state, thermal susceptibility, acclimation and diet (Colditz & Kellaway 1972; Young 1987). The decline in feed intake is generally lower for concentrate diets than for roughage diets, particularly when the concentrate contains fat (Bhattacharya & Hussain 1974; Beede & Collier 1986). This has been attributed to the lower endogenous heat production of diets containing starch and fat.

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The requirements of ruminants for absorbed amino acids and ME may also be modified by heat stress. As the body temperature of an animal increases above that normal for thermoneutral conditions, metabolic rate, maintenance energy requirements and protein catabolism may increase (Blaxter 1962). However the importance of these changes for the balance of various nutrients required by the ruminant are not well understood. It has been argued that the increased maintenance energy requirements and reduced voluntary feed intake will reduce the required ratio of metabolizable protein to metabolizable energy (Ames 1979; Ames *et al.* 1980; NRC 1981). Conversely, in recent studies heat stress has been associated with increased requirements for absorbed amino acids for growth in sheep and cattle fed concentrate diets (Bunting *et al.* 1992, 1996; White *et al.* 1992) and in lactating dairy cows (Higginbotham *et al.* 1989; Taylor *et al.* 1991). This is consistent with increased protein catabolism. However, it may also be at least partly due to reduced supply of amino acids to the small intestine since heat stress is associated with

increased retention times of feed residues in the rumen and increased degradation of dietary proteins (Christopherson & Kennedy 1983). It has also been suggested (Leng 1990) that the low feed intakes and the large responses to protein supplements often observed in ruminants in tropical conditions is because animals in these circumstances use less ME to maintain thermoneutrality, thus decreasing the ratio of absorbed amino acids to ME available for productive purposes. Hence there is evidence that interactions between diet and heat stress could change the requirements for ME and absorbed amino acids. This has obvious implications for predicting the energy and protein requirements of ruminants in tropical environments.

The objective of the following experiment was to examine whether interactions between heat stress and nutrient supply influenced the responses of young sheep fed a roughage diet to supplements. Sheep were fed oat hay *ad libitum* and a restricted amount of lucerne hay to provide a roughage diet of moderate digestibility and nitrogen (N) content. Some sheep were fed supplements based on either barley grain or fishmeal (FM) which were respectively intended to provide primarily additional fermentable ME, or additional amounts of both fermentable ME and metabolizable protein. Sheep were held in environments which were expected to be either thermoneutral or to induce moderate heat stress.

MATERIALS AND METHODS

Sheep, treatments and procedures

The experiment was conducted in three consecutive phases. During Phase 1 (days 1–12) the sheep were held indoors in individual pens in an animal house without temperature control. During Phase 2 (days 13–57) the sheep were held in metabolism crates in rooms in which cool or hot environments were maintained. During Phase 3 (days 58–67) the sheep were returned to individual pens in the animal house without temperature control.

Thirty-six Merino × Border Leicester wether sheep (initially *c*. 8 months of age, liveweight (LW) mean 33 ± S.D. 2·4 kg) were used in the experiment, and were allocated at random to the six treatments. The control diet (Con) consisted of chopped oat hay offered at *c*. 20 % in excess of intake, and a restricted amount of chopped lucerne hay (14 g air-dry/kg metabolic liveweight ($W^{0.75}$) per day). The other two diets consisted of the same roughage and supplements of 22 g air-dry/kg $W^{0.75}$ of whole barley grain fortified with urea and sulphur (Bar/N), or 10 g air-dry/kg $W^{0.75}$ of fishmeal (FM) per day. The Bar/N supplement was prepared by mixing whole barley grain with a solution of urea and sodium sulphate (27 g N and 2·7 g S in 180 ml solution per kg air-dry barley grain) immediately before feeding. The supplements were fed daily at 08.00 h mixed with the allocation of lucerne hay and 20 g mineral mixture, and were offered in a separate feeder. Water was freely available. The mineral mixture contained (g/kg) NaCl 270, Ca_2HPO_4 270, Na_2SO_4 200, KCl 108, $CaCO_3$ 80, $MgSO_4.7H_2O$ 68, $FeSO_4.7H_2O$ 2·74, and (mg/kg) $MnSO_4.4H_2O$ 547, $ZnCO_3.2ZnO.3H_2O$ 465, $CuSO_4.5H_2O$ 110, $CoSO_4.7H_2O$ 54, K_2MoO_4 48 and Na_2SeO_4 14.

During Phase 1, the intake of feed was measured daily. Midside patches (100 × 100 mm) of wool were clipped on day 5, and the sheep were shorn on day 6. The sheep were weighed before feeding on days 5, 7 and 9.

At the commencement of Phase 2, the sheep were moved to cool or hot environments in metabolism rooms. In the cool environment (COOL), the temperature was maintained at 13–15 °C. In the hot environment (HOT), temperature was maintained at 30–32 °C from 16.00 to 08.00 h. From 08.00 to 16.00 h heat input was increased so that the average maximum temperature was 33 °C during week 1, 36 °C during week 2 and 37 °C during weeks 3–6. This gradational increase in the maximum temperature was to allow some acclimatization of the sheep and to meet animal welfare requirements by avoiding excessive heat stress. Humidity was not controlled.

Intakes of feed and water were measured daily. A total collection of faeces and urine was carried out between days 41 and 48. Urine was collected into containers containing sufficient hydrochloric acid to acidify the urine to $pH < 4$. Faeces were sampled daily for DM analysis, and subsamples of urine and faeces were stored frozen pending laboratory analysis. Sheep were weighed weekly. Rectal temperature and respiration rates were measured at 13.00 h on 3 days each week. These measurements were also made five times (at 07.00, 10.00, 13.00, 16.00 and 22.00 h) on day 35 and at 07.00 h on day 36. On day 55 or 56, samples of rumen fluid were obtained by gentle suction through a tube inserted into the rumen before feeding and *c*. 6 h after feeding, precautions being taken to avoid saliva contamination. Rumen fluid pH was determined immediately using a glass electrode, and samples of rumen fluid were acidified (0·2 ml 5 M sulphuric acid per 20 ml) and stored frozen. Wool growth was measured by closely clipping 100 × 100 mm midside patches on days 29 and 59.

For Phase 3, which lasted for 10 days, all of the sheep were moved from the temperature-controlled rooms to an animal house without temperature control where the sheep were held in individual pens. Dietary treatments were continued. Sheep were weighed on days 65, 66 and 67 to establish LW at a common ambient temperature following any changes in water content of the sheep due to the thermal environments (MacFarlane *et al*. 1956; Silanikove 1987) imposed during Phase 2.

Measurements and laboratory analysis

Temperature and humidity were recorded in the controlled environment rooms using thermohydrographs (Casella, London, UK). Rectal temperature was measured using a calibrated clinical thermometer, and respiration rate from the time required for 50 breaths. Samples of feed offered, feed refused and faeces were dried at 95 °C to determine DM content, and were ignited at 550 °C for 6 h to determine organic matter (OM) content. Neutral detergent fibre (NDF) and acid detergent fibre (ADF) were analysed as described by Goering & Van Soest (1970). Lignin was determined as the ash-free residue after treatment of ADF with 72% sulphuric acid by the method of Van Soest (1963). Total N was determined by Kjeldahl procedures and ether extract by Soxlet apparatus (AOAC 1970). Concentration of ammonia in rumen fluid was determined using an ammonia electrode (Model 5941-00, Cole Palmer, Chicago, IL, USA) attached to a pH meter (Model 701, Orion Research Laboratories, Cambridge, MA, USA). Concentrations of individual volatile fatty acids (VFA) were determined using the procedure described by Erwin *et al*. (1961). Wool was washed with hexane and then dried (Chapman 1960) to determine clean dry wool yield.

Calculations and statistical procedures

Thermal humidity index (THI) was calculated as described by Kelly & Bond (1971). LW change of the sheep was calculated by two procedures. For the first procedure, LW gain during the entire experiment was calculated from the difference in LW measured during Phase 1 (mean of measurements on days 5, 7 and 9) and the LW measured at the end of Phase 3 (mean of measurements on days 65, 66 and 67). For the second procedure, LW gain during Phase 2 was calculated as the linear regression of sheep liveweight with time during this phase. The estimated ME content of each diet in each environment was calculated as $M/D = 0{\cdot}16\ OMD\% - 1{\cdot}8$, where M/D was the MJ of ME per kg feed DM and OMD% was the percentage OM digestibility measured by total collection (SCA 1990).

Data were analysed by analysis of variance for a 2×3 factorial experimental design. Wool growth measured before the experiment commenced was used as a covariate for analysis of wool growth. Least significant differences (L.S.D.) were used to compare between means when the *F*-test was significant.

RESULTS

Thermal environments and diet composition

In the COOL environment, temperature fluctuated through the intended range (13–15 °C) both within and between days. Relative humidity was usually within the range 75–90%, and the weekly average THI ranged from 56 to 58. In the HOT environment, relative humidity fluctuated within the range 45–70%. The weekly average minimum THI ranged from 83 to 84, and the weekly average maximum THI was 84 in week 1, and 86–88 during weeks 2–6. During Phase 3, ambient temperature was usually within the range 15–30 °C, while the average minimum THI was 65 and the average maximum THI 74.

Table 1. *Composition (g/kg dry matter) of diet components*

Measurement	Oat hay	Lucerne hay	Barley grain	Fishmeal
Dry matter*	883	883	913	911
Organic matter	921	898	978	852
Total nitrogen	10·3	31·9	16·7	115·2
Neutral detergent fibre	710	432	313	150
Acid detergent fibre	407	308	66	3
Lignin	40	54	12	—
Hemicellulose	303	124	247	—
Cellulose	367	254	54	—
Ether extract	—	—	24	98

* Dry matter content is on an 'as fed' basis.

The composition of the feeds is shown in Table 1. Since the ratio of lucerne to oat hay ranged from 0·18 to 0·31, the combinations of lucerne and oat hays ingested were equivalent to roughage containing 13·4–15·5 g N/kg DM. The fortification of the barley grain with the urea and sodium sulphate solution resulted in a supplement with a N content of 46·3 g N/kg DM. Since on average 297 g Bar/N DM and 134 g fishmeal DM were fed, these supplements provided 13·8 and 15·4 g N/day, respectively.

Rectal temperature and respiration rate

The HOT environment, on average, increased ($P < 0{\cdot}01$) rectal temperature measured at 13.00 h throughout Phase 2 from 39·2 to 40·1 °C (Table 2). The measurements at intervals throughout the 24 h cycle indicated that the increase in rectal temperature in the HOT environment ranged from 0·6 to 0·9 °C during the diurnal cycle, the greatest difference occurring at 13.00 h. Rectal temperature was not affected ($P > 0{\cdot}05$) by the provision of supplements. Respiration rate measured at 13.00 h was on average increased ($P < 0{\cdot}01$) by the HOT environment from 56 to 196 respirations per min (Table 2). Within the HOT environment, the sheep fed the Bar/N supplement had a higher ($P < 0{\cdot}05$) respiration rate (208 respirations/min) than the sheep fed the Con or FM

Table 2. *Means of rectal temperature and respiration rates measured at 13.00 h, and intake, excretion and balance of water and nitrogen in sheep fed three diets in two environments. The three diets consisted of roughage alone (Con), or roughage supplemented with barley grain, urea and sulphur (Bar/N) or fishmeal (FM). The two environments consisted of cool conditions (COOL) or moderate heat stress (HOT)*

Measurement	COOL			HOT			S.E.	
	Con	Bar/N	FM	Con	Bar/N	FM	Between environments	Between diets
n	5	5	5	7	7	7	(D.F. = 30)	
Rectal temperature (°C)	39·2	39·3	39·2	40·1	40·0	40·2	0·04	0·05
Respiration rate (breaths/min)	49	52	68	194	208	186	4·1	4·9
Water (g/day)								
Ingested	2177	2571	2637	4407	5830	6614	454	549
Feed	170	178	179	115	126	118	4	4
Total intake	2347	2749	2816	4522	5955	6732	456	550
Urine	997	1111	1290	1806	3214	3616	400	483
Faeces	975	1163	873	974	819	755	49	59
Evaporative loss	376	475	653	1742	1923	2360	84	101
n	5	4	5	7	7	7	(D.F. = 29)	
Nitrogen								
Intake (g/day)	14·1	27·0	29·7	12·5	26·3	29·7	0·52	0·63
Faeces (g/day)	6·4	8·8	7·5	6·1	7·1	6·6	0·26	0·31
Urine (g/day)	5·7	12·7	13·0	6·8	18·7	20·1	1·14	1·37
Digestibility (g/kg)	536	676	749	487	731	778	17	21
Balance (g/day)	2·0	5·5	9·2	−0·4	0·5	3·0	1·23	1·46

diets (194 and 186 respirations/min, respectively). The measurements throughout the diurnal cycle indicated that at 07.00 h the respiration rate was increased by the HOT environment to a lesser extent (from 56 to 120 respirations/min).

Intake, digestibility and pathways of excretion

Oat hay intake did not appear to change during Phase 2, as the sheep had the opportunity to acclimatize to the COOL or HOT environments. Total DM intake during Phase 2, whether expressed as g/d or as g/kg $W^{0.75}$ per day, was not affected by the Bar/N or FM supplements, but was decreased by *c.* 9% ($P < 0.01$) by the HOT environment (Table 3). The Bar/N supplement constituted 25–28% of total DM intake, and FM supplement 11–13% of total DM intake. Intake of oat hay was decreased ($P < 0.05$) by both supplements, with substitution ratios in the range 0·8–1·0.

DM digestibility was significantly higher (589 *v.* 613 g/kg; $P < 0.05$) and OM digestibility tended to be higher ($P = 0.05$) for sheep in the HOT environment. Also digestibility of both NDF and ADF components was higher ($P < 0.01$ and < 0.05, respectively) in sheep in the HOT environment. Estimated ME intake was on average increased ($P < 0.01$) by 26% by the supplements, and tended ($P = 0.06$) to be reduced by 6% in the HOT environment. Both supplements increased the apparent digestibility in the gastrointestinal tract of DM and OM ($P < 0.01$); OM digestibility was increased from 558 g/kg for the Con diet to 635 and 645 g/kg for the Bar/N and FM diets, respectively (Table 3). Digestibilities of NDF and ADF were not changed by provision of the Bar/N supplement, but were increased ($P < 0.01$) by the FM supplement.

Sheep in the HOT environment consumed more water ($P < 0.01$; 5617 *v.* 2462 ml/day respectively) and excreted more water in urine ($P < 0.01$; 2879 *v.* 1133 ml/day respectively) (Table 2). Evaporative losses of water were generally increased by both the HOT environment ($P < 0.01$; 501 *v.* 2008 g/day) and by the FM supplement ($P < 0.05$; 1059, 1199 and 1507 g/day for the Con, Bar/N and FM diets, respectively).

In association with the lower total DM intake described above, faecal N excretion was reduced ($P < 0.05$) in the HOT environment (Table 2). However, averaged across all diets, urine N excretion was increased ($P < 0.01$) and N balance was reduced ($P < 0.05$) from 5·6 to 1·0 g N/day by the HOT environment. The FM supplement tended ($P = 0.05$) to increase N balance. This was associated with a large increase in N intake from 13·3 to 26·7 and 29·7 g N/day, and concomitant increases in digestibility of N and excretion of N in faeces and in urine ($P < 0.01$).

LW gain, feed conversion efficiency and wool growth

LW gain measured during Phase 2 was reduced ($P < 0.05$) from 61 g/day in the COOL environment

Table 3. *Intake, digestibility of dietary components, liveweight (LW) gain, wool production (mg clean wool/patch per day) and feed conversion efficiency (g liveweight gain/kg fed DM) in sheep fed three diets in two environments. The three diets consisted of roughage alone (Con) or roughage supplemented with barley grain, urea and sulphur (Bar/N) or fishmeal (FM), while the two environments consisted of cool conditions (COOL) or moderate heat stress (HOT)*

Measurement	COOL			HOT			S.E. (D.F. = 30)	
	Con	Bar/N	FM	Con	Bar/N	FM	Between environments	Between diets
n	5	5	5	7	7	7	—	—
Dry matter (DM) intake (g/day)								
Oat hay	922	690	855	795	578	690	19·9	24·1
Lucerne hay	170	167	171	176	181	184	—	—
Supplement	0	286	129	0	308	138	—	—
Total	1110	1161	1174	989	1085	1030	21·8	26·3
DM intake (g/$W^{0·75}$ per day)								
Oat hay	65·7	48·3	59·1	58·2	40·6	48·2	1·22	1·47
Lucerne hay	12·1	11·7	11·8	12·8	12·8	12·8	—	—
Supplement	0	20·1	8·9	0	21·7	9·6	—	—
Total	79·1	81·4	81·1	72·3	76·5	71·9	1·17	1·41
Digestibility (g/kg)								
DM	550	605	612	551	639	648	7	8
Organic matter (OM)	559	620	627	557	649	663	7	9
Neutral detergent fibre (NDF)	514	506	561	521	538	611	7	8
Acid detergent fibre (ADF)	412	372	446	421	404	507	9	11
Intake								
Digestible organic matter (DOM) (g/day)	557	661	657	495	644	607	14	16
Estimated metabolizable energy (ME) (MJ/day)	7·93	9·44	9·66	7·03	9·27	9·06	0·200	0·241
Initial LW (kg)	32·4	31·8	32·5	32·6	33·4	34·0	0·34	0·41
LW gain (phase 2) (g/day)	42	59	81	35	38	34	7·6	9·2
LW gain (phase 2 and 3) (g/day)	51	96	93	29	50	51	5·1	6·1
Feed conversion	38	50	70	36	34	31	7·0	8·4
Wool growth	90	103	160	76	95	132	3·8	4·6

to 36 g/day in the HOT environment (Table 3), while LW gain measured during both Phases 2 and 3 was reduced ($P < 0·01$) similarly. Supplements increased ($P < 0·01$) LW gain measured during Phases 2 and 3 from 40 g/day for the Con diet to 72–73 g/day for the Bar/N and the FM diets.

Clean wool growth was reduced ($P < 0·05$) from 118 to 101 mg/patch per day by the HOT environment. Wool growth was also increased ($P < 0·01$) from 83 mg/patch per day in sheep fed the Con diet to 99 and 146 mg/patch per day for sheep fed the Bar/N and FM supplements, respectively, but there was no significant interaction between the environmental conditions and the diet. Feed conversion efficiency tended ($P = 0·07$) to be lower in the HOT environment.

Rumen pH, NH_3 concentration, VFA concentrations and proportions

Rumen pH measured before feeding was not affected by supplements, but 6 h after feeding was decreased ($P < 0·01$) by the Bar/N supplement (Table 4). Thermal environment did not affect rumen pH ($P > 0·05$). Rumen ammonia concentrations were similar in sheep offered the Con and Bar/N diets, but were increased ($P < 0·01$) by FM supplement both before feeding and 6 h after feeding.

The HOT environment reduced ($P < 0·01$) the concentration of total VFA, increased the proportion of acetate and decreased the proportion of butyrate both before and 6 h after feeding (Table 4). Diet influenced the concentration of total VFA and the

Table 4. *Means of pH, the concentrations of ammonia and total volatile fatty acids (VFA), and the proportions of the individual VFA in rumen fluid measured shortly before feeding and 6 h after feeding in sheep fed three diets in two environments. The three diets consisted of roughage alone (Con) or roughage supplemented with barley grain, urea and sulphur (Bar/N) or fishmeal (FM), while the two environments consisted of cool conditions (COOL) or moderate heat stress (HOT)*

Measurements	COOL			HOT			S.E. (D.F. = 29)	
	Con	Bar/N	FM	Con	Bar/N	FM	Between environments	Between diets
n	5	5	5	7	7	7	—	—
pH								
Before feeding	6·54	6·60	6·60	6·50	6·60	6·53	0·028	0·034
After feeding	6·34	5·88	6·50	6·21	6·04	6·37	0·044	0·053
NH_3 (mg/l)								
Before feeding	92	111	182	81	88	169	6·3	7·7
After feeding	96	117	213	67	105	165	9·8	11·9
VFA								
Before feeding								
Total (mmol/l)	63·1	63·0	59·1	55·0	40·2	39·5	2·58	3·10
Acetate (mmol/M)	748	683	709	771	727	724	7·4	8·9
Propionate (mmol/M)	153	180	164	152	164	152	4·4	5·3
Butyrate (mmol/M)	91	129	99	70	87	87	5·0	6·0
Iso-valerate (mmol/M)	9	9	24	7	18	33	3·2	3·8
Valerate (mmol/M)	0	0	0	0	0	0	—	—
Iso-butyrate (mmol/M)	0	0	4	0	5	4	2·0	2·4
After feeding								
Total (mmol/l)	87·0	107·4	79·7	77·6	82·3	59·2	2·95	3·57
Acetate (mmol/M)	715	640	677	773	694	734	6·2	7·5
Propionate (mmol/M)	191	257	200	160	228	179	6·5	7·9
Butyrate (mmol/M)	91	94	105	66	74	80	3·8	4·5
Iso-valerate (mmol/M)	2	2	13	0	0	6	0·9	1·0
Valerate (mmol/M)	0	8	5	1	4	0	0·7	0·9
Iso-butyrate (mmol/M)	0	0	0	0	0	0	—	—

proportions of individual VFA. Before feeding the proportion of acetate was reduced ($P < 0{\cdot}01$), and the proportions of propionate and butyrate were increased ($P < 0{\cdot}05$ and $P < 0{\cdot}01$ respectively) by Bar/N supplement. FM supplement decreased ($P < 0{\cdot}01$) the proportion of acetate. After feeding both supplements decreased ($P < 0{\cdot}01$) the proportion of acetate and Bar/N supplement increased ($P < 0{\cdot}01$) the proportion of propionate, these changes being greater than before feeding.

DISCUSSION

It was intended that the mixture of oat and lucerne hays fed should provide just sufficient absorbed amino acids to meet the requirements of the sheep for the ME intake. In sheep offered the Con diet or the barley supplemented diet (Bar/N) in the COOL environment, according to AFRC (1993) and SCA (1990) calculations, intake of absorbed amino acids was 102–108 % or 95–99 %, respectively, of the amounts expected to be required for the measured growth rates. Fishmeal supplement increased the absorbed amino acid supply to *c.* 130 % of expected requirements. Although oat hay intake was reduced and therefore the proportion of supplement in the total diet was increased in the HOT environment, the intake of total N per MJ ME intake did not change markedly due to the HOT environment because of the increases in digestibility. In the HOT environment this ratio was similar for the Con and Bar/N diets and was increased by only 7 % for the FM diet. Thus if the optimal ratio of absorbed amino acids to ME required by the sheep was changed appreciably by the hot environmental conditions imposed in the experiment, it is likely that intake and productivity of the sheep would indeed have been affected by the interaction between the diets and the environment.

Effects of diet and thermal environment

Both supplements increased ME intake of the sheep by *c.* 25 %, and the changes were associated with increases in OM digestibility rather than total intake. The similar increases in OM digestibility were associated with the ingestion of much larger amounts

of the Bar/N than of the FM supplement, but increases in the digestion of fibrous components of the diet with the latter supplement. Fishmeal supplements have also been observed to increase digestion of the fibrous components of the diet in previous studies (Hussein *et al.* 1991; McAllan 1991; Stritzler *et al.* 1992; R. M. Dixon, unpublished), presumably due to the provision of microbial substrates by the fishmeal. In the sheep offered the Bar/N supplement, the magnitude of the reduction of the rumen pH was such that fibre digestion in the rumen would probably have been adversely affected (Mould *et al.* 1983; Dixon 1986). The large increase in wool growth with the FM supplement indicated that a substantial proportion of the fishmeal protein escaped rumen digestion and increased the amino acid supply to the small intestine (Reis 1979). This is supported by observations that this fishmeal disappeared only slowly from synthetic fibre bags incubated in the rumen (R. M. Dixon, unpublished). The similarity of the LW gains, ME intakes and feed conversion efficiencies of sheep fed the two supplements within each environment in the present experiment provides direct evidence that the ratio of absorbed amino acids to ME approached the optimal for LW gain of young sheep when the Bar/N supplement was fed; there was no benefit to further increasing the supply of absorbed amino acids.

The increases in rectal temperature and in respiration rate indicated that the sheep in the HOT environment were subjected to a moderate degree of heat stress. The increases in these measurements were similar to those reported for sheep without shade during the middle of the day in summer in the arid tropics (Macfarlane *et al.* 1956, 1958). It therefore appears that the degree of heat stress imposed during the present studies was comparable with that often encountered by grazing sheep in the tropics. The decreases in voluntary intake of DM and ME and the increases in the digestibility of OM and of fibrous components due to heat stress are in agreement with previous reports of such changes (Lippke 1975; Christopherson & Kennedy 1983; Beede & Collier 1986). However, the decreases in LW gain, N retention and wool growth in the HOT environment were only partly due to the lower ME intake, since the decreases due to environment were still significant, or approached significance ($P < 0{\cdot}01$, $P = 0{\cdot}06$ and $P < 0{\cdot}05$, respectively) when the effects of differences in ME intake were removed by inclusion of ME intake as a covariate in the analysis of variance. This is in agreement with previous reports of increased maintenance energy requirements, increased catabolism of protein and reduced N retention during heat stress (Graham *et al.* 1959; Vercoe 1969; Colditz & Kellaway 1972). Maintenance energy requirements would be expected to be higher in the HOT environment. Firstly, maintenance energy requirements are expected to increase by 7% per °C increase in mean body temperature (Graham *et al.* 1959). If the temperature of the peripheral tissues increased more than rectal temperature, as may occur during heat stress (Macfarlane *et al.* 1958), the increase in maintenance energy requirements of the sheep may have been greater than that expected from the 0·9 °C increase in rectal temperature. Secondly, other changes such as increased protein catabolism and activities to increase heat loss may have increased maintenance energy requirements.

Interactions between diet and thermal environment

The absence of any interaction between the effects of the diets and the environment on voluntary intake, LW gain, N balance or wool growth suggests that, in young sheep fed a medium quality roughage diet, moderate heat stress does not change the required ratio of metabolizable protein to ME. Also the supply of additional metabolizable protein did not alleviate the adverse effects of heat stress on voluntary intake. Similarly, von Keyserlingk & Mathison (1993) reported that cold stress did not change the response of sheep to additional dietary metabolizable protein.

The results of the present study contrast with evidence that hot environmental conditions increase the requirements of growing ruminants for absorbed amino acids. Bunting *et al.* (1992) reported that fishmeal containing a substantial proportion of escape protein increased N retention in sheep in a hot environment, but not in a thermoneutral environment. Also White *et al.* (1992) and Bunting *et al.* (1996) reported increased liveweight gains of young cattle under summer, but not winter, conditions when the proportion of escape protein in the diet was increased. However, the diets used in these studies were based on grain and ME intakes and growth rates were high compared with the present study. Furthermore, in the studies with cattle, thermal environment was confounded with the season of the year, and in the experiment of White *et al.* (1992) also with the age of the animals. Hence the differences between the present study and these previous studies may have been due to the differences in the diets and the growth rates, but may also have been associated with the limitations of the previous experiments.

In conclusion, a number of factors are likely to determine whether the thermal environment changes the optimal ratio of absorbed amino acids to ME for ruminants. Firstly, an increase due to heat stress in requirements for both energy and absorbed amino acids for maintenance purposes may result in only a small change in their required ratio. Secondly, a lower intake of feed, and therefore of ME, in a hot environment, and any changes in the composition of tissue gain due to either the reduced ME intake or heat stress *per se*, will alter the required ratios of

specific nutrients. Thirdly, a response to additional absorbed amino acids will only occur when the animal is deficient in specific amino acid(s) and these are provided. In the present experiment where the roughage diet apparently provided a ratio of metabolizable protein to ME which was satisfactory for slow growth of these sheep, although providing additional absorbed amino acids with a fishmeal supplement increased wool growth, it did not change LW gain or the response of the sheep to hot environmental conditions.

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