CHAPTER 10

10. THE IMPORTANCE OF MICROBIAL YIELD FROM THE RUMEN IN ACCOUNTING FOR DIFFERENCES IN THE RATE OF WOOL GROWTH BETWEEN SHEEP SELECTED EITHER FOR OR AGAINST CLEAN FLEECE WEIGHT

10.1 Introduction

Over the last 30 years many studies have been undertaken in an attempt to determine the biological mechanisms that are responsible for genetic differences in clean fleece weight (Williams 1987). The majority of these studies have used animals from the Trangie (Dun 1958) and Cunnamulla (Turner 1958) fleece selection lines. The Trangie fleece selection lines were established in 1951 by N.S.W Department of Agriculture and resulted from a divergent selection program in which Merino sheep were either selected for (fleece plus, F_p) or against (fleece minus, F_m) clean fleece weight at 15–16 months. A third group was selected at random. Selection of Merino sheep either for clean wool weight or at random was also conducted by the C.S.I.R.O at Cunnamulla. In brief, animals in the selected line (S) were chosen for greatest clean wool weight at 15–16 months of age after initial culling for excessive wrinkling and high fibre diameter.

The rate of wool growth is potentially controlled by the availability of sulphur amino acids to the wool follicle and the efficiency with which the wool follicle uses these materials for the synthesis of fibre. With most diets, the sulphur amino acids available to the wool follicle are microbial in origin. Alterations to the availability of sulphur amino acids to the wool follicle (see Chapter 2) may arise from changes to external factors such as feed intake, intestinal supply of microbial protein and digestion and absorption of protein, or from changes to internal factors such as blood flow to the skin and the use of sulphur amino acids by other protein pools within the body (Black and Reis 1979).

In one of the earliest studies with F_p and F_m sheep, Ahmed *et al.* (1963) reported that F_p animals had a higher voluntary feed intake and also produced more wool per unit feed intake. These findings supported the earlier work of Schinckel (1960), who observed that sheep which

had higher levels of wool product on per unit body weight also had higher feed intakes and were more efficient at converting feed to wool. In contrast to this, Piper and Dolling (1969a) reported that the voluntary feed intake of Cunnamulla fleece weight selected and random mating lines did not differ and Williams and Winston (1965) found no differences in feed intake between F_p and F_m animals. However, Williams and Winston (1965) reported a significant interaction between selection line and level of nutrition. The form of this interaction was that the F_m flock had the greatest feed intake when animals were maintained at low body weights (*c.* 30 kg) but had the least feed intake when animals were maintained at the greatest body weights (*c.* 45 kg).

Determination of apparent whole-tract digestibility in the sheep has been used to elucidate whether the digestion and absorption of nutrients is related to phenotypic and genetic differences in wool growth rate. The results from a number of studies indicate that variation in the apparent whole-tract digestibility of DM (Hutchinson 1961; Piper and Dolling 1969b), OM (Weston 1959; Piper and Dolling 1969b), N (Hutchinson 1961; Piper and Dolling 1969b) and S (Piper and Dolling 1969b) is not related to variation within and between selection lines in the rate of wool growth.

Whilst estimates of apparent digestibility give an indication of the proportion of the dietary constituents that are absorbed into the body, they do not give any information on the site of digestion nor on the types of nutrients arising from rumen fermentation that are available to the animal. In this respect, Lush *et al.* (1991) were able to demonstrate that the net portal absorption of α-amino-nitrogen was consistently higher (although not statistically) in F_p as compared to F_m sheep across a range of feed intakes (0.7 to 1.3 x maintenance).

There are very few reports indicating whether differences in wool growth rate at constant feed intake are related to variation in the intestinal supply of protein. With most diets, a large fraction of the dietary protein is fermented in the rumen as a result of microbial proteolysis. Consequently, little dietary protein is available for digestion and absorption and the majority of amino acids and peptides that are absorbed from the digestive tract of ruminants are of microbial origin. The amino acid composition of microbial protein is relatively constant and little affected by diet (see Chapter 3), and on average sulphur amino acids are 3–4% of total bacterial amino acids. Thus in many instances it is the yield of microbial protein that governs the rate of growth and composition of wool. Consequently, it seems plausible that some of the genetic and phenotypic variation in wool growth rate, at constant feed intake, may reflect differences in the yield of microbial protein.

The studies reported here were designed to examine whether divergent selection for clean fleece weight has produced animals that differ in the yield of microbial protein from the rumen and to calculate whether such differences were important in determining the difference between the selection lines in the rate of wool growth. As the concentration of ammonia in rumen fluid is an important factor in determining the yield of microbial cells per unit intake (see Chapter 5), it was decided to examine the relationship between feed intake, yield of microbial protein from the rumen and wool production when animals were fed a roughage diet low in dietary N, and when supplemented with varying levels of urea. In the studies reported in this Chapter, microbial yield from the rumen was estimated from the urinary excretion of purine derivatives.

10.2 Materials and Methods

10.2.1 Animals and conditions

Forty Merino ewes born in 1988 and 6 years old at the start of the experiment were obtained from the F_p (n = 20)and F_m (n = 20) selection lines maintained by N.S.W Agriculture (Table 10.1). These lines have been selected either for or against clean fleece weight and were described by Dun (1958). These animals represented the entire female 1988 drop. Animals were treated for internal and external parasites before delivery to the animal house and on arrival were drenched with *Ivermectin* and a coccidiostat. Throughout the experiment, animals had unrestricted access to water and were housed in individual pens with natural lighting.

10.2.2 Experimental design, feeding and sequence of events

Within each selection line, animals were ranked on greasy fleece weight (GFW) from the previous shearing and the highest wool producers (4 ewes/selection line) were then allocated to block 1 (n = 8) and the lowest producers to block 5. Within blocks, ewes were stratified on live weight and average feed intake (determined from the pre-experimental period) and were then randomly allocated to experimental diets. There were no significant differences between blocks or experimental diets in the previous year's reproductive performance (lambs born per ewe joined for blocks 1-5: 1.7, 1.5. 1.1, 1.3, 0.9; and for diets 1-4: 0.8, 1.4, 1.7, 1.3). Animals were randomly allocated to pens within blocks and blocks were randomised throughout the animal house. During the trial, animals were re-randomised within blocks to ensure against any unidentifiable effect of pen location.

Table 10.1. Live weight and greasy fleece weight of 6 year old ewes from the F_m and F_p flocks. (live weight measured upon entry to animal house and greasy fleece weight was from shearing at 5 years of age).

Selection line	Live weight[A] (kg)		Greasy fleece weight (kg)	
	mean	s.d.	mean	s.d.
Fleece minus	43.0	5.10	1.9	0.67
Fleece plus	39.5	4.76	5.6	0.75
	n = 20		n = 20	
	P < 0.05		P < 0.01	

[A] Live weight is fleece-free.

Feed was offered daily at 9.00 am after refusals had been collected and weighed. This feeding protocol continued throughout the trial. Initially, animals were offered 800 g/d (as fed) of oaten chaff (*Avena sativa* and 1.2% N) sprayed with urea at 1% (w/w) and supplemented with a mineral mix (Table 10.3) at 2% (w/w) of intake. Animals were kept on this pre-experimental diet for 7 weeks in order to minimise previous differences between the lines and to determine individual feed intake. Following this period, animals were allocated to experimental diets which were offered *ad libitum* + 10% (based on a two-day rolling average). The experimental diets are summarised below:

T1. Basal diet (oaten chaff)

T2. Basal diet sprayed with urea (1 kg urea / 100 kg chaff)

T3. Basal diet sprayed with urea (3 kg urea / 100 kg chaff)

T4. Basal diet sprayed with urea (3 kg urea / 100 kg chaff) plus 100 g/d of CSM pellets (the CSM was fed as a fixed amount).

The required quantity of urea was dissolved in a volume of water equivalent to 2.5% of the mass of the oaten chaff. The oaten chaff was sprayed with this solution whilst being constantly mixed in a commercial 'auger type' feed mixer. A sufficient quantity of oaten chaff was prepared to satisfy the feeding requirements for two weeks and over this period the N content of the chaff did not change The sequence of experimental events is outlined in Table 10.2.

10.2.3 Wool parameters

Animals were kept on the experimental diets for 5 wk prior to the start of the wool growth period (WGP) to allow for the lag in the response of wool growth to a change in diet (Nagorcka 1977). To determine wool growth, a 15 cm dyeband (Chapman and Wheeler 1963) was placed horizontally on the shoulder position on both sides of the animal on the first day of the wool growth period. A second dyeband was placed on the animals after 76 days and the dyebands were removed (Oster clippers No 40) 2 months later. Calculation of wool growth followed the procedure of Langlands and Wheeler (1968). Average fibre diameter and its standard deviation were determined on 2000 wool snippets using the Sirolan-Laserscan (Charlton 1995). Washing yield (includes 16% regain) was determined according to A.W.T.A standards (New England Fibre Testing, Walcha N.S.W)

10.2.4 Collection of rumen fluid

Rumen fluid was sampled (using an oesophageal tube) 4 h after feeding on days 1, 34 and 69 and 2 h after feeding on day 86. Rumen pH was measured immediately and a subsample (15 ml) was acidified (4 drops of conc. sulphuric acid) and stored at –20°C for later analysis.

10.2.5 Ammonia-N

Rumen fluid was centrifuged (1500 *g*) for 5 min and a subsample from the supernatant was diluted (40 fold) with 0.2% sulphuric acid. Ammonia concentrations were then determined using a Technicon Auto-analyser (Technicon Instruments Comp. New Jersey, U.S.A) according to the method of Crook and Simpson (1971) and modified by Beitz (1974).

Table 10.2. The sequence and duration of experimental events

Experimental event	start date	time period[A] (weeks)
1.Allocation to individual pens in animal house	17–12–93	
2.Initial feeding period for standard sation	17–12–93	7
3.First estimate of body composition	26–1–94	
4.Allocation to experimental diets for fibre equilibration	3–2–94	5
5.Start of wool growth period (WGP)	7–3–94	11
6.End of wool growth period	20–5–94	
7.Second estimate of body composition	23–5–94	
8.Enter metabolism crates, blocks 3, 4 and 5	3–6–94	
9.Total collection	17–6–94	1
10.Enter metabolism crates blocks, 1 and 2	27–6–94	
11.Total collection	8–7–94	1

[A] Time period rounded up to the closest whole week.

10.2.6 Volatile fatty acids

The concentrations of acetic, propionic, butyric, valeric, isobutyric and isovaleric acids in the rumen fluid supernatant were determined using a gas chromatograph (Model 427, Packard Instrument Comp. Illinois, U.S.A) according to the method of (Erwin *et al.* 1961) with isocaproic acid as the internal standard (Geissler *et al.* 1976).

10.2.7 Plasma ammonia concentration

Two hours after feeding on day 86, blood (10 ml) was sampled from the jugular vein into lithium heparin tubes and immediately placed on ice. Blood samples were then centrifuged (3000 *g* for 10 min) and the plasma was separated and immediately stored at 4° C. Plasma ammonia concentrations were determined (Kodak Ektachem 1986) on the day of sampling.

10.2.8 Live weight

Animals were weighed at monthly intervals prior to the morning feed. The estimated mass of wool at each weighing was subtracted from live weight values.

10.2.9 Computer-aided tomography

Differences in body composition may indicate differences between lines in the partitioning of protein between wool and other tissues. In order to explore this hypothesis, the body composition of F_p and F_m ewes was estimated using computer-aided tomography. Before animals were allocated to experimental diets (Table 10.2), three animals per selection line were selected from treatments 1 and 4 (N=12) and were used as representative animals for estimation of body composition by computer-aided tomography (CAT) (Thompson and Kinghorn 1992). The selected animals were chosen on the basis that they covered the range of condition scores that were present X-ray imaging started at the distal end of the femur and continued sequentially at 45 mm intervals until the 6 th cervical vertebra. Whole-body scanning was performed prior to and at the completion of the trial (110d period). From the scan, the areas of bone, muscle, viscera, protein (muscle plus viscera), fat and total (sum of the components) were determined. The mass of each component in each image was subsequently calculated by multiplying area measurements by the density of each tissue. Total mass of bone, muscle, viscera, protein, fat and total fleece and digesta free carcass were calculated as the sum of all X-ray images (*c.* 20 per animal).

10.2.10 Total collection for in vivo digestibility and N retention

At the conclusion of the 76 day WGP, experimental animals were placed in metabolism crates (Table 10.2). During this period the metabolism rooms were continuously illuminated and feeding procedures remained the same as described for the pen trial. Fourteen days was allowed for the animals to become accustomed to the new conditions after which a 7 day total collection of urine and faeces was performed in order to determine the apparent digestibility of DM and N in the whole tract, N retention and urinary purine excretion.

Urine was collected into 1 l of tap water containing (10 ml of glacial acetic acid and 5 ml of 50% v/v sulphuric acid). A daily subsample (5%) was taken, pooled over 7 days, and stored at –20° C. Total daily faecal output was well mixed, subsampled (10%), pooled over 7 days and stored at –20° C. Feed offered and that refused were subsampled daily (25%), pooled and stored at –20° C until later analysis.

10.2.11 Determination of dry matter and total-N

Dry matter (DM) of experimental diets, feed refusals and faeces was determined by drying a subsample at 60° C in a forced draught oven to a constant weight. Total-N in ground (1 mm sieve) and dry feed and faecal samples and in urine was determined using an automated Organic Nitrogen Determinator (FP-228, Leco Corporation, U.S.A).

10.2.12 Urinary purine concentrations

The concentrations of purine derivatives; allantoin, uric acid, hypoxanthine and xanthine were determined according to the procedure described in Chapter 8.

10.2.13 Calculation of the yield of microbial nitrogen

The yield of total microbial nitrogen (including nucleic acids) from the rumen was calculated from the urinary excretion of purine derivatives using the predictive equations of Chen *et al.* (1992a).

10.2.14 Statistical analysis

The experiment was established as a randomised complete block design. Multiple measurements were analysed using a repeated measures analysis of variance. Where interactions with time were not statistically significant, the overall means are presented and analysis of variance was used to test the significance of all main effects and interactions. Differences between least squares means (l.s.mean) were tested using multiple t-tests. To

reduce the probability of finding spurious differences, only means where the F statistic was significant ($P < 0.05$) were compared. The computer programs SAS (SAS Institute Inc) and Minitab (Ryan *et al.* 1985) were used for all analyses.

Hutchinson (1961) suggested that the physiological components of wool production can be expressed in the multiplicative model

$$W = W/I \,.\, I/B \,.\, B \qquad (1)$$

where W = clean wool weight

I = feed intake

B = live weight

W/I = wool produced per unit intake

I/B = intake per unit live weight

To easily partition the variance in *W* between these components Hutchinson (1961) transformed the multiplicative expression (1) into an additive form (2) by using logarithms (Henderson and Hayman 1960). The additive model then becomes

$$\log(W) = \log(W/I) + \log(I/B) + \log B \qquad (2)$$

Biological interpretation of the efficiency term (W/I) is difficult because gross conversion includes a contribution from both digestion and utilisation of dietary material. Hutchinson (1961) suggested that these components could be separated by the expression

$$W/I = W/I_D \,.\, D \qquad (3)$$

where W/I_D = Wool produced per unit digestible intake

D = Apparent whole-tract digestibility.

The primary concern with the approach in (2) and (3), was that intake and apparent digestion in the whole-tract give little information on the nutrients that are available for utilisation at the tissue level and it is these nutrients that are most relevant in determining the rate of wool growth. Wool growth is primarily limited by the intestinal-supply of sulphur amino acids (Reis and Schinckel 1963; Reis *et al.* 1990), and for ruminants consuming low quality roughage diets, it is the yield of microbial protein from the rumen that provides the vast

majority of the amino acid supply to the animal (see Chapter 3). Hence in the studies reported here, wool growth was partitioned by

$$\log(W) = \log(W/MN) + \log(MN/I) + \log (I/B) + \log(B) \qquad (4)$$

where W/MN = wool produced per unit microbial-N yield

MN/I = yield of microbial-N per unit intake

I = dry matter intake

Similarly, the yield of microbial-N from the rumen was partitioned by

$$\log(MN) = \log(MN/I) + \log(I/B) + \log(B) \qquad (5)$$

Henderson and Hayman (1960) suggested that the variation in Y (in log measure) can be partitioned among its components ($C_1....C_n$) (also in log measure) by the regression coefficient b_i, where

$$b_i = \text{cov}(Y, C_i) / \text{var } Y$$

b_i represents the proportion of variation in Y attributable to variation in C_i and 100 b_i is the percentage contribution. The analysis of variance divides the variation in Y into several categories, each of which can be partitioned among the physiological components by this regression. The computer program Harvey (1988) was used for this purpose.

10.3 Results

The analysis of the experimental diets is described in Table 10.3.

10.3.1 Differences between selection lines averaged across experimental diets

Three ewes from the F_m and 1 ewe from the F_p flock were removed from all analyses on the basis of low and irregular feed intake.

Average dry matter intake (DMI) did not differ between the selection lines during the WGP, but ewes from the F_p flock had a greater DMI ($P < 0.05$) during the total collection period (Table 10.4). When intakes were scaled for metabolic wool-free body weight, F_p ewes consumed approximately 12 and 19% more than their F_m counterparts during both the WGP

($P < 0.05$) and total collection period ($P < 0.01$) respectively. Apparent digestibility of DM in the whole tract (ADMD) did not differ statistically between the two selection lines but there was a small advantage to F_m ewes (1.6%). Ewes from the F_p flock had a greater digestible dry matter intake (DDMI/$kg^{0.75}$) ($P < 0.05$) during the period of total collection. In contrast DDMI/$kg^{0.75}$ did not differ between the selection lines during the WGP. Ewes from the F_p flock ate their feed at a faster rate and by 4 h after feeding had consumed *c.* 23% more feed (Table 10.4).

Table 10.3. Analysis of the experimental diets.

Diet	Dry matter[A] (%)	Urea-N (%)	Total-N (%)
T1	89.3	0	1.19
T2	88.7	0.48	1.67
T3	89.0	1.35	2.54
CSM pellets	90.3	0.47	5.51

Mineral and vitamin/micromineral premix: sodium chloride (0.2), sodium sulphate (0.2), dicalcium phosphate (0.4), vitamin/micromineral premix (0.2). The premix was Pfizer 422 supplied by Pfizer Pty. Ltd. North Ryde and contained (g/kg) 150 Ca, 106 Mg, 60 P, 18 Fe, 18 Zn, 4 Cu, 0.4 I, 0.1 Co, 4.4 x 10^6 i.u. vitamin A and 1.76 x 10^6 i.u vitamin D_3.

[A] DM determined 48 h after urea application.

There were no differences between the selection lines in rumen ammonia concentration (230 mg NH_3-N/l; s.e. 12.9), pH (6.7; s.e. 0.04), total volatile fatty acid (VFA) concentration (80 mM; s.e. 2.8) or the ratio of propionate:(acetate + butyrate) (0.25; s.e. 0.008) in rumen fluid taken 4 h after feeding on three separate occasions throughout the 76 day WGP. Similarly, the ammonia concentration (74.8 µM; s.e. 6.35) in jugular blood taken 2 h after feeding did not differ between the selection lines. The concentration of isovaleric and isobutyric acid was greater ($P < 0.01$) in F_m ewes (F_m 0.68 mM; s.e. 0.050: F_p 0.44 mM; s.e. 0.047) and in these ewes the isoacids made a greater proportional contribution to the total VFA concentration (F_m 0.009; s.e. 0.0007: F_p 0.005; s.e. 0.0006: $P < 0.01$). Both the yield of

microbial nitrogen (MN; g/d) from the rumen and the yield of MN per unit DMI (MN/DMI), and nitrogen intake were greater in ewes from the F_p flock (Table 10.5).

Table 10.4. Intake and apparent digestibility of DM in the whole-tract of ewes selected for or against clean fleece weight (main effect of selection line is averaged across diets).

	Fleece minus		Fleece plus		P value
	l.s.mean	s.e.	l.s.mean	s.e.	
DMI[A] (g/d)	735		795		NS
DMI[B] (g/d)	674	37.3	790	34.9	$P < 0.05$
DMI[AE] (g/$W^{0.75}$/d)	42.7	1.68	47.6	1.57	$P < 0.05$
DMI[BF] (g/$W^{0.75}$/d)	38.5	1.65	46.0	1.55	$P < 0.01$
N intake[AE] (g/$W^{0.75}$/d)	0.9	0.03	1.0	0.03	$P < 0.05$
ADMD[B] (%)	56.3		54.7		NS
DDMI[ACE] g/$W^{0.75}$/d)	24.0	0.94	26.1	0.88	NS
DDMI[BF] (g/$W^{0.75}$/d)	21.6	0.92	25.1	0.86	$P < 0.05$
4h / 24h intake[AD] (%)	57		65		

[A] Data from WGP, [B] Data from 7 d total collection period, [C] Calculated from DMI during WGP and ADMD from total collection, [D] Mean of three measurements, [E] Live weight from the mid-point of the WGP were used to adjust values, [F] Live weight measured immediately prior to entering metabolism crates used to adjust values.

Table 10.5. Yield of microbial nitrogen from the rumen (calculated from urinary excretion of purine derivatives) of ewes selected for or against clean fleece weight.

	Fleece minus		Fleece plus		P value
	l.s.mean	s.e.	l.s.mean	s.e.	
Microbial-N (g/d)	7.0	0.47	8.9	0.45	$P < 0.01$
MN/DMI (g/kg)	10.3	0.31	11.2	0.29	$P < 0.05$
MN/N intake (g/g)	0.55	0.021	0.61	0.020	$P < 0.05$

Ewes from the F_p flock had a greater ($P < 0.01$) rate of clean wool growth during the WGP (Table 10.6). Concomitant with this change, F_p ewes had a greater average fibre

diameter (AVFD), standard deviation of AVFD (SD) and a higher washing yield. The increased wool growth of ewes from the F_p flock was associated with an increase in wool growth efficiency as measured by g clean wool /kg DDMI.

Table 10.6. Response of wool growth rate and fibre characteristics to divergent selection for clean fleece weight

	Fleece minus		Fleece plus		P value
	l.s.mean	s.e.	l.s.mean	s.e.	
Clean wool (g/d)	2.9	0.34	9.2	0.32	P < 0.01
AVFD (μm)	18.8	0.39	23.3	0.37	P < 0.01
Standard deviation	3.2	0.12	4.7	0.12	P < 0.01
Washing yield (%)	59	1.6	81	1.5	P < 0.01
Cwool[A] / DDMI (g/kg)	7.2	0.66	21.4	0.62	P < 0.01
Cwool[A] / N intake (g/g)	0.12	0.023	0.62	0.021	P < 0.01

[A] Cwool represents clean wool growth.

There was no difference between the selection lines in wool-free body weight change during the 117 day period between the first and second CAT scan. However, N retention (estimated from the 7 day total collection) was greater in ewes from the F_p flock (Table 10.7). When the N associated with the increased wool growth of F_p ewes (*c.* 1.0 g/d) was removed from this calculation the N retention of the 2 selection lines became similar. Similarly, the difference between the selection lines in the proportion of N intake that was retained in the body was entirely due to the more efficient wool growth of ewes from the F_p flock.

Table 10.7. Nitrogen utilisation of Merino ewes selected for or against clean fleece weight.

	Fleece minus		Fleece plus		P value
	l.s.mean	s.e.	l.s.mean	s.e.	
N retention (g/d)	2.4	0.30	3.7	0.28	P < 0.01
N ret / N intake (g/g)	0.17	0.018	0.22	0.017	NS

N ret represents N retention.

10.3.2 Treatment effects averaged across selection lines

Increasing both the non-protein nitrogen (NPN) (T2, T3) and the protein content (T4) of the basal diet tended to stimulate DMI beyond that of the control animals (T1). This trend was apparent during both the WGP and the total collection period: in the latter period the differences were statistically significant (Table 10.8). Addition of urea and CSM pellets to the basal diet did not increase ADMD (Table 10.8) and consequently any trends for DDMI mirrored those previously discussed for DMI.

Table 10.8. DMI of Merino ewes as affected by addition of urea and CSM pellets to a basal diet of oaten chaff. (oaten chaff (T1), +1% urea (T2), +3% urea (T3), +3% urea and 100 g CSM pellets (T4)).

Variable	T1		T2		T3		T4		P value
	l.s.mean	s.e.	l.s.mean	s.e.	l.s.mean	s.e.	l.s.mean	s.e.	
DMI[A] (g/d)	680	50.2	782	46.9	733	54.2	864	50.2	NS
DMI[B] (g/d)	617[a]	51.1	726[ab]	47.7	737[ab]	55.1	847[b]	51.1	$P < 0.05$
DMI[AE] ($g/W^{0.75}/d$)	40.6[a]	2.30	45.4[ab]	2.14	44.2[ab]	2.48	50.3[b]	2.30	$P < 0.05$
DMI[BF] ($g/W^{0.75}/d$)	36.4[a]	2.26	41.1[ab]	2.11	43.7[bc]	2.44	47.7[c]	2.26	$P < 0.05$
N intake[AE] (g/d)	8.2[a]	1.02	13.3[b]	0.96	18.3[c]	1.11	24.6[d]	1.02	$P < 0.01$
ADMD[B] (%)	55	1.1	54	1.0	56	1.0	57	1.0	NS
DDMI[AC] (g/d)	372[a]	28.0	424[ab]	26.1	412[ab]	30.2	490[b]	28.0	$P < 0.05$
DDMI[B] (g/d)	337[a]	28.3	394[a]	26.4	414[ab]	30.6	480[b]	28.3	$P < 0.05$
4/24h intake[AD] (%)	64		75		47		58		

[A] Data from WGP, [B] Data from 7 d total collection period, [C] Calculated from DMI during WGP, and ADMD from total collection, [D] Mean of three measurements, [E] Live weight from the mid-point of the WGP were used to adjust values, [F] Live weight measured immediately prior to animals entering metabolism crates used to adjust values. Within rows, means with a common suffix do not differ significantly ($P > 0.05$).

Addition of urea at 1% (w/v) (T2) to the basal diet increased the rate of intake so that by 4 h after feeding, ewes in the T2 group had consumed 11% more of their daily intake relative to animals in the T1 group (Table 10.8). Further additions of urea (T3) suppressed the rate of intake below that of the T1 group. Addition of 100 g CSM pellets to the 3% urea diet

(T4) increased the rate of intake to a value that was not significantly different from that recorded for ewes in the T1 group.

Incremental additions of urea resulted in a stepwise increase in rumen ammonia concentrations. Addition of CSM pellets to the diet (T4) further increased rumen ammonia concentrations (Table 10.9). Plasma ammonia (μmol/l) increased with additional dietary NPN ($P < 0.05$) (Table 10.9) and was well correlated with the concentration of ammonia in rumen fluid. However, this correlation did not hold for ewes in the T4 group. The pH of rumen fluid sampled at 2 and 4 h after feeding was increased by the addition of 3% (w/w) urea (T3) to the diet. Total VFA concentration in rumen fluid sampled 4 h after feeding was unaffected by dietary treatment, however, the ratio of propionate:(acetate + butyrate) was significantly lowered by the addition of urea and CSM to the diet (table 10.9).

Table 10.9. The effect of adding urea and CSM pellets to a basal diet of oaten chaff on rumen and jugular ammonia concentrations, rumen pH and volatile fatty acid concentration and proportions. (oaten chaff (T1), +1% urea (T2), +3% urea (T3), +3% urea and 100 g CSM pellets (T4)).

Variable	T1		T2		T3		T4		P value
	l.s.mean	s.e.	l.s.mean	s.e.	l.s.mean	s.e.	l.s.mean	s.e.	
R-NH_3 (mg NH_3-N/l)[A]	16[a]	17.6	142[b]	17.6	322[c]	20.3	441[d]	17.6	$P < 0.01$
R-NH_3 (mg NH_3-N/l)[B]	66[a]	25.2	230[b]	22.3	339[c]	22.3	482[d]	22.3	$P < 0.01$
P-NH_3 (μmol/l)	54.8[a]	10.09	68.4[ab]	8.58	87.6[b]	8.58	88.5[b]	8.58	$P < 0.05$
Rumen -pH[A]	6.5[a]	0.06	6.5[a]	0.06	6.8[b]	0.07	6.7[b]	0.06	$P < 0.01$
Rumen -pH[B]	6.8[a]	0.05	6.8[a]	0.04	7.0[b]	0.04	6.9[a]	0.04	$P < 0.01$
Total VFA (mM)	79	4.0	83	3.7	74	4.3	84	4.0	NS
C3/(C2+C4)[C] (%)	28[a]	1.1	24[b]	1.0	22[b]	1.2	24[b]	1.1	$P < 0.01$

[A] Values for mean of 3 samples taken 4 h after feeding, [B] Values from a single sample taken 2 h after feeding, [C] propionate/(acetate + butyrate). Within rows, means with a common suffix do not differ significantly ($P > 0.05$).

Addition of 1% urea (T2) to the basal diet of oaten chaff increased the yield of MN (g/d) and MN /kg DMI ($P < 0.05$). Additional inputs of urea (T3) or urea and CSM (T4) did not increase further the yield of MN nor MN /kg DMI (Table 10.10). Increasing N intake

beyond that of the basal diet (T1) resulted in a lesser fraction of the dietary N being assimilated into microbial cells (Table 10.10).

The diet by selection line interaction was significant for the traits of clean wool growth and AVFD ($P < 0.05$). The clean wool growth of ewes in the F_m flock did not increase in response to increasing amounts of urea and CSM pellets in the diet (Figure 10.1). Correspondingly, the AVFD of these animals was also unresponsive to the experimental diets. In contrast, clean wool growth and AVFD of ewes from the F_p flock did increase in response to an increase in the supply of urea and CSM pellets (Figure 10.1). The incorporation of dietary-N into wool-N declined with increasing N intake ($P < 0.01$). The means and s.e. for this trait (g wool-N /g N-intake) were: T1 0.082^a, 0.0042; T2 0.062^b, 0.0039; T3 0.043^c, 0.0044; and T4 0.039^c, 0.0042.

Table 10.10. Yield of microbial-N from the rumen of ewes from the F_p and F_m flocks when fed a basal diet of oaten chaff (T1) and either 1% (T2) or 3% (T3) urea or 3% urea+100 g CSM pellets (T4).

Variable	T1		T2		T3		T4		P value
	l.s.mean	s.e.	l.s.mean	s.e.	l.s.mean	s.e.	l.s.mean	s.e.	
Microbial-N (g/d)	6.1^a	0.65	8.4^b	0.61	7.8^{ab}	0.70	9.6^b	0.65	$P < 0.05$
MN/DMI (g/kg)	9.7^a	0.42	11.5^b	0.39	10.6^{ab}	0.46	11.3^b	0.42	$P < 0.05$
MN/N intake (g/g)	0.81^a	0.029	0.67^b	0.027	0.42^c	0.031	0.40^c	0.029	$P < 0.01$

Within rows, means with a common suffix do not differ significantly ($P > 0.05$).

Wool-free weight gain (g/d) was increased by the addition of CSM to the diet (Table 10.11). The food conversion ratio (FCR: g feed /g live weight gain) was unaffected by diet but addition of CSM pellets tended to greatly reduce the FCR.

Table 10.11. Weight gain and nitrogen retention of ewes from the F_p and F_m flocks

Variable	T1		T2		T3		T4		P value
	l.s.mean	s.e	l.s.mean	s.e.	l.s.mean	s.e.	l.s.mean	s.e.	
Weight gain [A] (g/d)	8^a	5.4	10^a	5.0	7^a	5.8	29^b	5.4	$P < 0.05$
N retention (g/d)	1.5^a	0.41	2.6^{ab}	0.39	3.0^b	0.45	5.0^c	0.41	$P < 0.01$

[A] wool-free weight gain (WFWG) over 117 d period. Within rows, means with a common suffix do not differ significantly ($P > 0.05$).

10.3.3 Physiological components of wool production

Variation in the amount of wool produced per unit microbial-N yield was responsible for 80.6% of the differences in wool growth between the selection lines. The yield of microbial-N per unit DMI accounted for a further 8.3% of the difference in wool production between the selection lines. The remainder of the variation between the selection lines in wool production was attributable to variation in intake (DMI) which was a composite of I/B and *B*.

The yield of MN per unit DMI and DMI (a composite of DMI/B and B) each accounted for approximately half of the difference between the selection lines in the yield of MN from the rumen (Table 10.12). Dry matter intake accounted for *c.* 61% of the between-diet differences in the yield of MN from the rumen. The efficiency term, MN/DMI accounting for the remainder (Table 10.12).

Table 10.12. Percentage of the variation (100 b_i) in MN attributable to the physiological components

Source of variation	Physiological components		
	MN/DMI	DMI/B	B
Selection lines	45.3	101.2	–46.4
Experimental diets	38.9	48.4	12.8

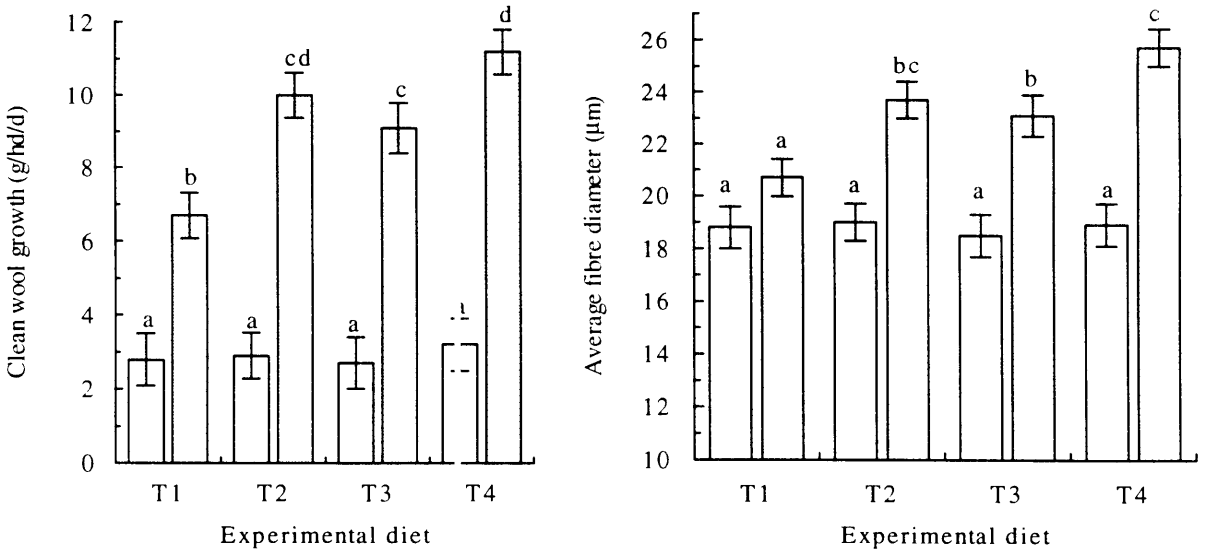

Figure 10.1. Clean wool growth and average fibre diameter (means ± s.e) of ewes from the F_m (unfilled histogram) and F_p (hatched histogram) flocks fed either, oaten chaff (T1), +1% urea (T2), +3% urea (T3) or +3% urea + 100g CSM pellets (T4). Means with a common letter do not differ significantly ($P > 0.05$).

10.3.4 Body composition

The first estimate of body composition was made 41 days after the animals entered the animal house and 7 days before experimental diets were offered. The second estimate was completed 117 days later, that is, after 110 days on the experimental diets.

The mass of muscle in the wool-free and digesta-free body of ewes from the 2 selection lines did not differ statistically at either estimate of body composition (Figure 10.2). At the beginning of the experimental period, muscle mass represented a similar proportion of the wool-free and digesta-free body mass in ewes from the 2 selection lines. At the end of the experimental period, muscle mass represented a greater proportion of the wool-free and digesta-free body mass ($P < 0.05$) (Table 10.13) in ewes from the F_p flock. The proportional increase of muscle mass in F_p ewes was a result of a greater rate of muscle deposition, as compared to ewes from the F_m flock, over the 110 day experimental period (Figure 10.3).

At the beginning of the experimental period, ewes from the F_p flock had a greater mass of viscera ($P < 0.05$) and visceral mass represented a greater proportion of their wool-free and digesta-free body mass (Table 10.13). However, F_p ewes tended to lose a greater amount of viscera over the experimental period (Figure 10.3). There were no statistical differences between the selection lines for the amount of muscle plus viscera (total protein; t.protein) present at either estimate of body composition (Figure 10.2). The mass of total protein in F_p ewes represented a greater proportion of wool-free and digesta-free body mass than that in ewes from the F_m flock (Table 10.13).

Ewes from the F_m flock had a greater mass of fat both at the start and end of the experimental period ($P < 0.05$) (Figure 10.2). Fat represented over 30% of the wool-free and digesta-free body mass of F_m ewes as compared to less than 20% for ewes from the F_p flock (Table 10.13).

During the 110 day experimental period, ewes that were provided with 3% urea and 100 g/d CSM pellets (T4) in addition to the basal oaten chaff diet (T1) had a greater rate of muscle deposition ($P < 0.01$). In contrast to this, ewes from the T4 group tended to have a greater rate of visceral loss (Figure 10.4). Irrespective of this, total protein deposition of ewes from the T4 group tended to be greater than that of ewes from the T1 but the differences were not statistically significant. Ewes in the T4 group also tended to gain more fat. The net result of these changes was that ewes in the T4 group tended to gain more wool-free and digesta-free body mass over the experimental period (Figure 10.4). The proportional contribution of viscera to wool-free and digesta-free body mass of ewes in the T4 group decreased over the

experimental period ($P < 0.01$) whereas this proportion remained constant for ewes in the T1 group (estimate 1: T1 0.20, T4 0.22, s.e. 0.009; estimate 2: T1 0.19, T4 0.17, s.e. 0.006).

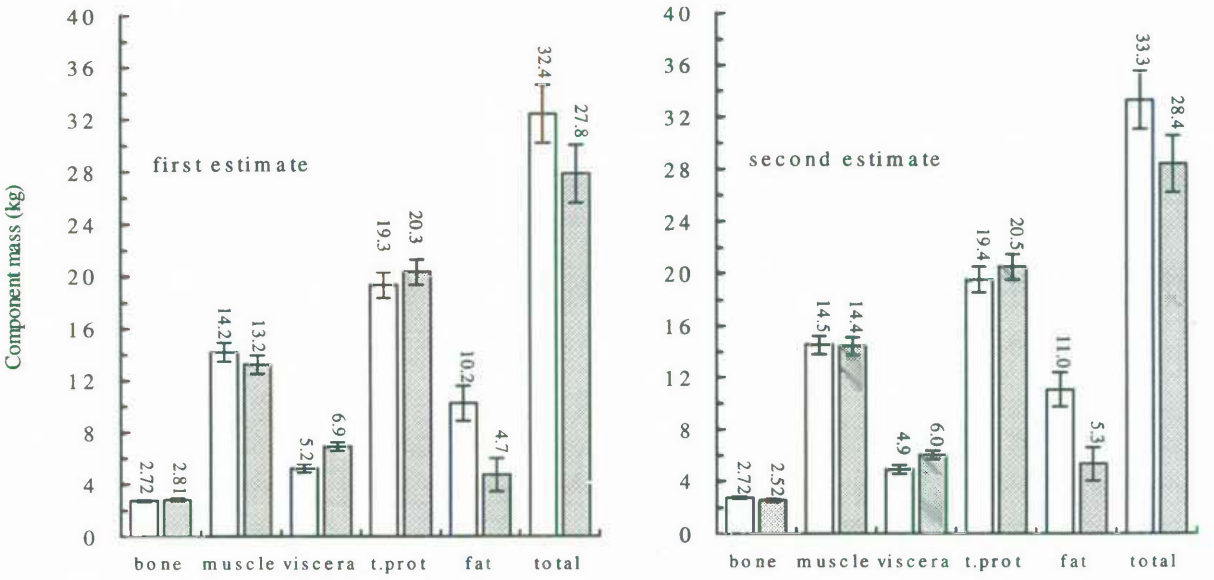

Figure 10.2. Estimate of body composition (mean ± s.e.) of F_p (hatched histogram) and F_m (unfilled histogram) ewes before introduction to (estimate 1) and after 110 days (estimate 2) on the experimental diets. (t.prot represents total protein).

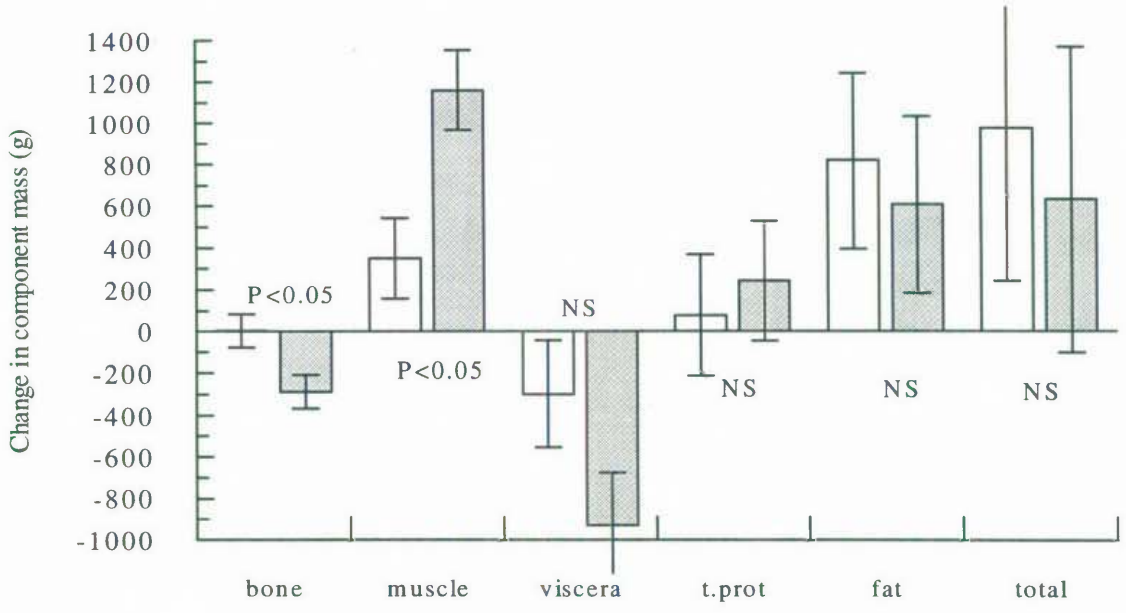

Figure 10.3. Change in the mass of body components (mean ± s.e.) of F_p (hatched histogram) and F_m (unfilled histogram) ewes over 110 days (t.prot represents total protein).

Table 10.13. The proportion of wool-free and digesta-free body mass occupied by the body components at the start (estimate 1) and end (estimate 2) of the experimental period.

Body component	estimate 1 l.s.mean		s.e.		estimate 2 l.s.mean		s.e.	
	F_m	F_p		P value	F_m	F_p		P value
bone	0.09	0.10	0.006	NS	0.08	0.09	0.005	NS
muscle	0.44	0.48	0.017	NS	0.44	0.51	0.017	$P < 0.05$
viscera	0.16	0.25	0.009	$P < 0.01$	0.15	0.21	0.006	$P < 0.01$
t. protein[A]	0.60	0.74	0.023	$P < 0.01$	0.59	0.73	0.018	$P < 0.01$
fat	0.31	0.16	0.028	$P < 0.01$	0.32	0.18	0.022	$P < 0.01$

[A] t. protein (total protein) is the sum of muscle and visceral mass.

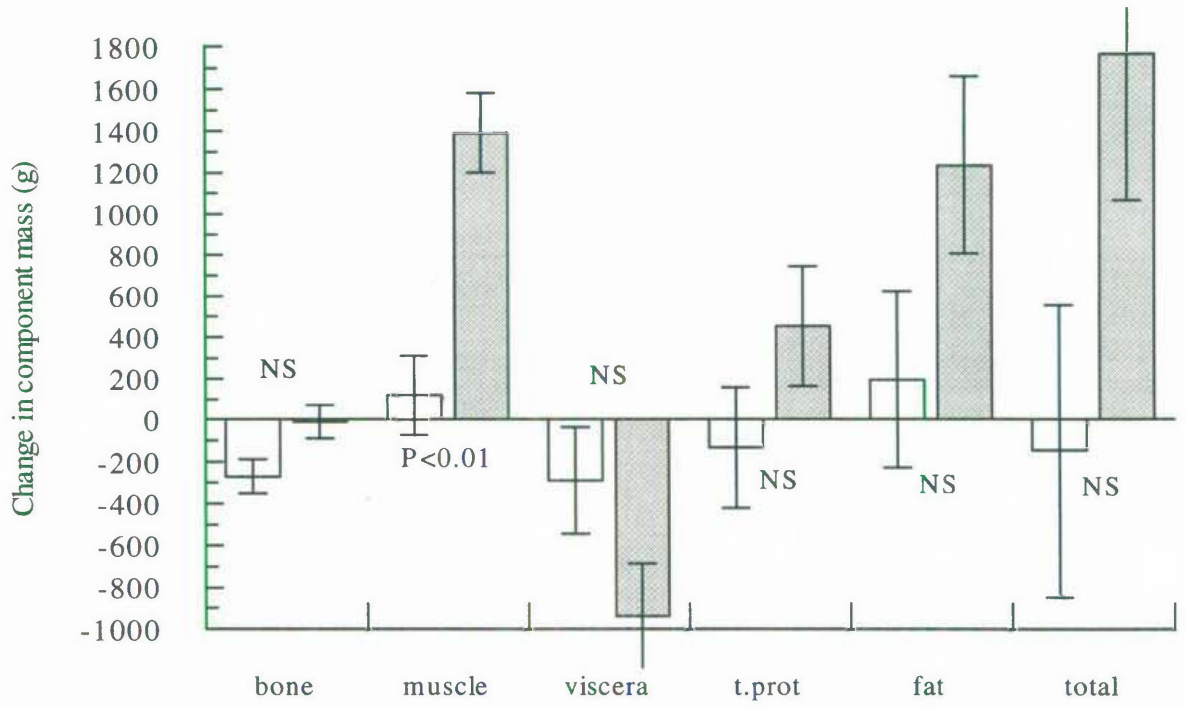

Figure 10.4. Change in the mass of body components (means ± s.e.) in sheep consuming a basal diet of oaten chaff (T1) (unfilled histogram) and supplemented with 3% urea and 100 g/d CSM pellets (T4) (hatched histogram). (t.prot represents total protein).

10.4 DISCUSSION

Divergent selection for clean fleece weight has produced changes in voluntary feed intake $/W^{0.75}$; F_p ewes consumed approximately 12 and 19% more feed when compared to F_m ewes

during the WGP and total collection period respectively. Ahmed *et al.* (1963) also reported that the voluntary feed intake of 2 year old ewes from the F_p flock was greater than that of the same age ewes from the F_m flock, but when their data were adjusted for differences in live weight no effect was obvious. In the experiment of Williams and Winston (1965) there were no differences in feed intake between 2 year old F_p and F_m ewes. However, these authors did report a significant interaction between selection line and level of diet for both feed intake (g/d) and intake scaled for metabolic weight ($g/kg^{0.75}/d$). In that interaction, ewes from the F_m flock had the greatest intake of lucerne pellets when all ewes were maintained at low body weights (*c.* 30 kg) but had the least feed intake when all ewes were maintained at the greatest body weights (*c.* 45 kg). In the study conducted by Williams and Winston (1965) the level of feed offered to the ewes was adjusted weekly in an attempt to keep the body weight of each ewe constant. In doing this, ewes would have, at times, had restricted access to the diet of lucerne pellets and hence it is difficult to relate these results to the present findings.

Estimates of apparent digestibility of DM in the whole-tract did not differ between the selection lines and supports the findings of Piper and Dolling (1969b) that sheep with genetic differences in clean wool production have the same capacity to digest DM. Whilst estimates of ADMD give an indication of the quantity of dietary nutrients that are available for utilisation, in ruminants, dietary nutrients often bear little resemblance to the nutrients made available to the animal as a result of ruminal fermentation. With regards to wool growth, the most important nutrient that arises from ruminal fermentation of dietary material is microbial protein. In contrast, digestion in the lower tract will increase the availability to the animal of VFA's but not microbial protein.

The increased yield of microbial-N from the rumen of ewes from the F_p flock was not simply the result of a greater DMI (Kahn 1991; Chen *et al.* 1992a). The efficiency term, yield of MN/DMI, accounted for approximately half of the difference between the selection lines in the yield of microbial-N. Differences between the selection lines for DM disappearance from the rumen may explain these results but whole-tract estimates suggest that any differences are likely to be small. Another possible explanation for the greater yield of MN and MN/DMI of ewes from the F_p flock is that divergent selection for clean fleece weight has produced F_p ewes that possess a rumen environment that utilises an increased proportion of dietary organic matter for microbial synthesis at the expense of VFA production (Leng 1982b; Preston and Leng 1987). Alternatively, the greater yield of MN and MN/DMI of ewes from the F_p flock may have been associated with a lower rate of turnover of microbial protein within the rumen.

Bacterial protein turnover is predominately caused by predation of microbes by protozoa (Abe and Kandatsu 1969 in Leng and Nolan 1984; Cottle 1980; Wallace and McPherson 1987). During this process, protozoa retain about half of the N ingested (Coleman 1975). The presence of protozoa greatly reduces the flow of bacterial-N into the duodenum (Ivan *et al.* 1991, 1992) and in addition, protozoa-N contributes little to the flow of nitrogen to the duodenum (Weller and Pilgrim 1974; Ivan *et al.* 1992). In the studies reported here, no measurements were made of protozoal concentrations in rumen fluid or the rate of turnover of microbial protein. However, the lower concentration of isovaleric and isobutyric acid (branched chain volatile fatty acids) in rumen fluid and the lower proportional contribution of these acids to the total concentration of VFA's in ewes from the F_p flock, indicates that microbial protein turnover was relatively lower in ewes from the F_p as compared to the F_m flock.

The concentration of a metabolite is a function of the volume of distribution and the rate of entry and removal (flux) of the metabolite from its metabolic pool. With reference to the branched chain volatile fatty acids (BCVFA), isobutyric and isovaleric acid, the volume of distribution is defined by rumen volume. No estimates were made to determine if rumen volume differences between the selection lines could account for the differences in the concentration of BCVFA but the magnitude of the difference between the selection lines in the concentration of the BCVFA was too great to be totally explained in this way. In support of this, the proportional contribution of isobutyric and isovaleric acid to total VFA concentration was also less in F_p ewes. Hence a change to the flux rate seems the more probable explanation for differences between the selection lines in BCVFA concentrations.

The BCVFA are important growth factors for many strains of cellulolytic and noncellulolytic micro-organisms (Dehority *et al.* 1967; Bryant 1973). Preferences for the choice of BCVFA differ between organisms with all strains of *Bacteroides succinogenes* requiring either isobutyric or 2-methylbutyric acid but not isovaleric acid for growth (Dehority *et al.* 1967). *Ruminococcus flavefaciens* appear to require 2 BCVFA for growth and in decreasing order of effectiveness these are isobutyric, 2-methylbutyric and isovaleric acid (Dehority *et al.* 1967). Many rumen bacteria utilise BCVFA for synthesis of longer chain fatty acids (Bryant 1973) and also for biosynthesis of valine, leucine and isoleucine via reductive carboxylation reactions (Allison 1969; Bryant 1973). Conversely, BCVFA are also produced from valine, leucine and isoleucine via oxidative deamination and decarboxylation (Van Den Hende *et al.* 1963).

Substrate for synthesis (entry) of BCVFA is dependent on the availability of precursor compounds (valine and leucine) derived either from the diet as protein or from turnover of microbial protein (Bryant 1973). In this study, the BCVFA would have been derived predominately from microbial protein given the low protein content of the basal diet. Clearance of BCVFA from rumen fluid will be governed by the rate of microbial uptake and hence the size and species composition of the bacterial population and also by absorption across the rumen epithelium and outflow in rumen digesta. Greater yields of microbial-N leaving the rumen of F_p ewes as estimated from the urinary excretion of purine derivatives provides support for both a reduction in the turnover of microbial protein and for increased bacterial population size (Topps and Elliot 1965). These alternatives are not mutually exclusive and coincide following the elimination of protozoa from the rumen (Bryant and Small 1960; Eadie and Hobson 1962; Coelle 1980).

Estimation of the yield of microbial-N from the rumen (Chen *et al.* 1992a) is based on the relationship between intestinal purine absorption and urinary excretion of purine derivatives, predominately allantoin (Chen *et al.* 1990b; Balcells *et al.* 1991). The calculation also involves an estimate of 1) the endogenous contribution to urinary purine excretion, 2) true intestinal digestibility of microbial purines and 3) the purine:total-N ratio of microbes in rumen outflow. The endogenous purine contribution derives from obligatory cellular loss from the gut and from degradation of tissue nucleic acids and is known to be sensitive to cumulative nitrogen retention and protein supply (Chen *et al.* 1992b).

Given the apparent sensitivity of endogenous purine excretion to cellular turnover it is conceivable that the greater viscera mass, increased loss of viscera and a greater net accretion rate of muscle in ewes from the F_p flock may have resulted in the endogenous purine excretion of F_p ewes being greater than that for ewes from the F_m flock. If this was so, then the calculated differences in the yield of microbial-N may not be truly representative of intestinal digesta contents.

In order to explore this notion more fully, linear models relating both DMI and DDMI with purine derivative excretion were developed with either, separate intercepts and a common slope or separate intercepts and slopes for the 2 selection lines. In these models the intercept and slope represented endogenous purine excretion in urine and the yield of microbial-N per unit intake respectively. The results from these analyses indicated that the 2 selection lines did not differ in either intercept or slope when urinary purine excretion was a function of DMI. That is, the endogenous purine excretion in urine was similar for ewes from both selection

lines. However, when DDMI was substituted for DMI, the analysis indicated that ewes from the F_p flock had a greater endogenous purine excretion in urine ($P = 0.05$) but that the yield of microbial-N per unit DDMI did not differ between the selection lines.

A criticism of this approach, is that a linear relationship between both DMI, DDMI and urinary purine excretion does not account for allosteric inhibition of *de novo* synthesis of adenylate or guanylate (Lehninger 1977) which is hypothesised to be active at low levels of exogenous purine absorption (Chen *et al.* 1990b) and consequently feed intake. Nevertheless, the analyses discussed above do suggest the possibility that ewes from the F_p flock may have a greater endogenous excretion of purine derivatives. This may in part, contribute to the differences between the selection line in urinary purine excretion and consequently estimates of microbial yield from the rumen.

The failure of ewes from the F_m flock to increase wool growth in response to an increase in protein supply (Figure 10.5), in this instance microbial in origin, has not been previously reported. Most reports of wool growth with these and other selection flocks have been from animals considerably younger than those used in the current experiment. Whether this is evidence for an interaction of selection line * age or even physiological status in determining the responsiveness of the wool follicle to increased protein supply is difficult to assess. An alternative but highly speculative explanation for these results would be that divergent selection for clean fleece weight has targeted different genes and it is invalid to assume that the wool growth potential of ewes from the F_p and F_m flocks lie on the same continuum.

To explain this hypothesis further, some of the sheep that were originally selected from the foundation flock on the basis of a low clean fleece weight may have had low rates of wool growth because they possessed a major gene that limited the synthesis of fibre regardless of the availability of sulphur amino acids: this major gene was absent from the genome of sheep that were selected for a high clean fleece weight. Other sheep that were selected to enter the F_m flock may have been poor wool producers but not possessed a major gene limiting wool production. Following the initial selection, single trait selection for low clean fleece weight over many generations would have increased the frequency of the major gene within the F_m population and eventually it would have become fixed. As a consequence, comparisons made between sheep from the F_p and F_m flocks may not be examining the outcome of divergent selection on the same genes.

The superior clean wool production of F_p ewes was associated with a large increase in the efficiency of wool growth (g clean wool /kg DDMI). The apparent correlation between efficiency and wool growth has previously been reported for the Trangie fleece selection lines (Ahmed *et al.* 1963; Williams and Winston 1965), Cunnamulla selection lines (Dolling and Moore 1960; Schinckel 1960; Dolling and Piper 1968; Piper and Dolling 1969a), South Australian strong-woolled Merino flock (Hutchinson 1961) and the multiple bloodline Merino flock (Lee and Williams 1994).

Wool growth is primarily limited by the intestinal-supply of sulphur amino acids (Reis and Schinckel 1963; Reis *et al.* 1990), and for ruminants consuming low quality roughage diets, such as that fed in the studies reported here, it is the ruminal outflow of microbial protein that provides the vast majority of the amino acid supply to the animal. Hence it was reasoned that, in this experiment, the yield of MN, although biologically confounded with intake, was a more suitable correlate for wool growth. Accordingly, the wool growth efficiency term (W/I) as proposed by Hutchinson (1961) was replaced with the relationship between clean wool growth and the yield of microbial-N (W/MN).

Component analysis (Henderson and Hayman 1960) indicated that the efficiency term (W/MN) accounted for *c.* 81% of the difference between the selection lines in wool production. This result supports previous findings (Weston 1959; Hutchinson 1961; Piper and Dolling 1969a) which concluded that variation in the gross conversion efficiency term (W/I) accounted for most of the between sheep/strain variation in wool production. While the selection lines differed in the yield of MN/DMI, this only accounted for *c.* 8% of the difference in wool production between the selection lines. Thus it can be concluded, that while divergent selection for clean fleece weight has produced changes in the protein supply to the animal, these changes only account for a small fraction of the differences in wool production.

For four of the five sheep in the F_p flock consuming CSM pellets (T4) the rate of clean wool growth was greater than that predicted from the regression of clean wool growth and the yield of MN calculated for F_p animals allocated to diets T1-T3 (Figure 10.5B). This was expected because in these animals T4) the supply of dietary protein would be unaccounted. Clean wool growth for these 4 animals was on average 1.8 g/d (s.d. = 0.47) greater than that predicted from the regression equation relating clean wool growth with the yield of MN. This represents a fractional wool growth response (FWGR) to CSM of 0.357 g clean wool /g CSM-N intake (1.8/5.04 = 0.357, where 100 g CSM pellets contains 5.04 g CSM-N). For CSM to have an equivalent FWGR as MN (0.626 as predicted from linear regression (Figure

10.5B)) 0.57 of the CSM-N (0.357/0.626) must avoid ruminal degradation and become available for intestinal absorption (ignoring any potential differences in digestibility and biological value). If greater than 0 57 of the CSM avoids ruminal degradation, the FWGR to CSM will be lower than that for MN.

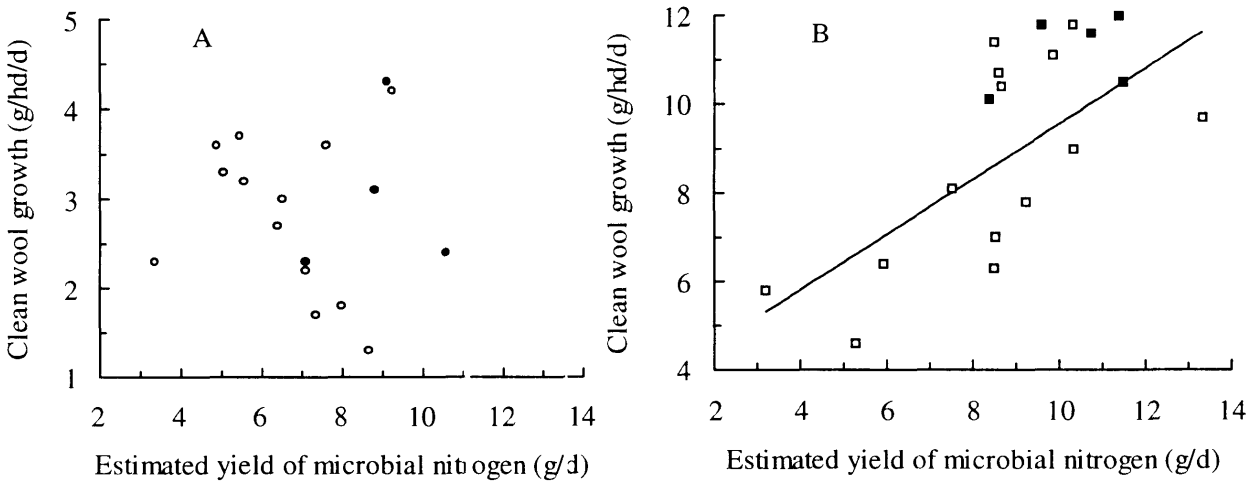

Figure 10.5. Response in wool growth to the estimated yield of microbial-N by F_m (Figure A, circle) and F_p (Figure B, square) ewes consuming diets T1-T3 (open symbols) and T4 (shaded symbols). The line of best fit (Figure B, Y = 3.3 (s.d. = 1.81) + 0.63 (s.d. = 0.207) X; r^2 = 0.43) describes the relationship for F_p ewes consuming diets without CSM (T1-T3)

The published estimates of the genetic correlation between clean fleece weight and live weight range from +0.384 (Davis and Kinghorn 1986) to 0 (Mortimer and Atkins 1989). Some of the variation between published estimates arises from live weight being measured at different ages and presumably also because live weight measurements are made with and without a contribution from the fleece. However, the general consensus is that the 2 traits are genetically unrelated (Williams 1987). Given this, the greater live weight (fleece-free) of the F_m flock (Table 10.2) at the start of the trial was most likely a result of environmental influences and other previous differences between the selection lines even though the F_m and F_p flocks were grazed in the same paddock and experienced identical management (S.Mortimer 1993 personnel communication).

10.4.1 Body composition

It has been suggested that selection for wool production may produce animals that are more efficient at producing wool but may not be more efficient in overall terms (e.g. live weight and weaning mass) (Cronjé and Smuts 1994). This notion is supported by the findings that the basal metabolic rate of rams (MJ/d/$kg^{0.75}$) selected for clean fleece weight was 13% greater than that of rams selected against clean fleece weight (Graham 1968). The extension of this hypothesis is that selection which favours one organ (wool follicles) will result in the partitioning of nutrients away from other organs (e.g mammary gland for milk production, and muscle deposition) (Cronjé and Smuts 1994). The data collected from this experiment do not support the notion that divergent selection for clean wool growth is at the expense of muscle or visceral mass. However, ewes from the F_p flock were significantly less fat than those from the F_m flock and this lowers the energy demand for fat synthesis. This tendency is supported by the findings of Graham (1968) who reported that fat occupied a lesser proportion of fleece-free body weight in Merino rams selected for as opposed to against clean fleece weight.

Ewes from the F_p flock deposited more muscle but tended to lose more viscera than ewes from the F_m flock. Regardless of the greater fluctuation in the mass of muscle and viscera, total body protein was similar between the selection lines at the start and end of the experimental period. A hypothesis to account for these results is to suggest that the increased mobilisation of muscle and viscera in ewes from the F_p flock may be a mechanism for buffering the amino acid supply to the follicle bulb and might also be used as a mobilisable protein pool.

The nitrogen and energy cost to F_p ewes of having a proportionally leaner body with muscle and viscera mass prone to greater fluctuation may have contributed to the greater feed intake in these animals. To explore this idea further, linear regression was used to calculate the intake of digestible DM and digestible energy (DE; assuming the gross energy content of the experimental diets, T1 and T4 was 18.0 and 18.2 MJ/kg respectively) that was required to achieve both weight (wool-free and digesta-free) and energy stasis in the animals used for estimation of body composition. The conclusions from these analyses were firstly, that energy stasis required less DDMI and DE (*c.* 4%) than weight maintenance for both selection lines. Secondly, ewes from the F_p flock required a greater intake of digestible DM and DE relative to F_m ewes to achieve weight (F_p: 450 g/d, 8.1 MJ/d; F_m 395 g/d, 7.1 MJ/d) and energy (F_p 430 g/d, 7.8 MJ/d; F_m 383 g/d, 6.9 MJ/d) stasis.

This approach ignores the energy cost of wool growth but this is relatively minor in relation to the energy requirements of the animal. Nevertheless, the calculations discussed

above do provide a basis to account for the greater voluntary feed intake of ewes from the F_p flock.