Differences in nitrogen and urea metabolism between goats bred for fibre production (Angora goat) or meat production (Boer goat)

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This experiment was conducted to determine whether selection for fleece weight is accompanied by changes in the efficiency of nitrogen utilization, using Angora and Boer goats as models of animals bred for fleece or meat production respectively. A diet, containing a protein: energy ratio of 12 g CP/MJ ME, was fed at either 77, 88.5, 100, 111.5 or 123% of estimated maintenance energy requirements. Mean N digestibility was 5% lower in Angora goats ($P < 0.01$), but Angoras retained 33% more N ($P < 0.01$). N retention increased quadratically ($P < 0.01$) with level of feed, but there was no interaction between diet and breed ($P > 0.05$). When expressed on a metabolic weight basis, urea N plasma flux rate was 14% higher in Angoras ($P < 0.05$), but 18% less urea N was excreted in the urine ($P < 0.01$). Urea N recycling was 48% higher in Angoras ($P < 0.01$). Angoras partitioned 62% of flux to recycling and 38% to excretion; in Boer goats proportionately less was recycled (48%) and more was excreted (52%) ($P < 0.01$). Urea N flux and recycling rates (g N/d) increased ($P < 0.05$) as the amount of diet fed was increased. It is suggested that higher N retention and urea recycling could be an adaptative mechanism consequent to increasing the demand for amino acids via selection for fleece production.

Hierdie proef is uitgevoer om te bepaal of seleksie vir vagmassa met veranderings in die doeltreffendheid van stikstofbenutting gepaard gaan. Die Angorabok en die Boerbok is gebruik as modelle van diere wat vir vag- of vleisproduksie onderskeidelik geteel is. 'n Dieet met 'n proteien: energie-verhouding van 12 g RP/MJ ME is teen peile van 77, 88.5, 100, 111.5 of 123% van beraamde onderhoudsenergiebehoefte gevoer. Gemiddelde N-verteerbaarheid was 5% laer by die Angora ($P < 0.01$), maar N-retensie was 33% hoër ($P < 0.01$). N-retensie het kwadraties verhoog ($P < 0.01$) met dieetvlak, maar geen interaksie tussen dieet en ras ($P > 0.05$) is gevind nie. Plasma-ureumomsettempo (uitgedruk op 'n metaboliese massabasis) was 14% hoër by Angoras ($P < 0.05$), maar 18% minder ureum-N is in die uriene uitgeskei ($P < 0.01$). Hersirkulering van ureum-N was 48% hoër by die Angora ($P < 0.01$). By die Angora is 62% van die gesintetiseerde ureum hergesirkuleer en 38% uitgeskei; by die Boerbok is minder hergesirkuleer (48%) en meer uitgeskei (52%) ($P < 0.01$). Ureum-N-omset- en hersirkuleringstempo's (g N/d) het toegeneem ($P < 0.05$) namate die dieetvlak toegeneem het. Daar word voorgestel dat hoër N-retensie en ureumhersirkulasie moontlik 'n aanpassingsmeganisme kan wees in reaksie op 'n verhoogde aminosuurbehoefte geassosieer met seleksie vir vagproduksie.

Keywords: Angora, goat, metabolism, nitrogen, nutrition, recycling, retention, ruminant, urea.

Although techniques for accelerating the rate of genetic change in livestock breeds have advanced considerably in recent years, knowledge of the metabolic implications of different selection criteria has not kept pace. Reports of differences in nutrient partitioning and efficiency of utilization of individual nutrients between and within sheep and goat breeds (Gallagher & Shelton, 1972; Williams *et al.*, 1972; McGraham & Searle, 1982) have stimulated research on blood profiles of sheep selected for fleece weight. Several authors have shown blood urea and cystine concentrations to be lower in sheep selected for fleece weight (Williams *et al.*, 1972; McCutcheon *et al.*, 1987; Hough *et al.*, 1988; Clark *et al.*, 1989). Lower blood urea concentrations are generally interpreted as being indicative of more efficient amino acid utilization (McCutcheon *et al.*, 1987), but this needs to be verified.

This experiment was conducted to provide more detailed information on the metabolism of urea in two breeds of ruminants which represent extremes in respect of genetic potential for fibre production. Although both breeds are descended from a common ancestor, the South African Angora goat has been selected exclusively for mohair production, while the Boer goat has been selected for meat production. There are few breeds of livestock which produce as much fibre per unit of body mass as the Angora goat, which makes it an excellent model for studying the metabolic effects of selection for fibre production in ruminants.

The incidence of abortions, stress-induced mortalities and slow growth rates is remarkably higher among Angoras when compared with other goat breeds in South Africa (Wentzel, 1986). This may be a metabolic consequence of extreme selection for fibre production, but it may also simply be related to a quantitative or qualitative deficiency in nutrient supply relative to requirements. By comparing responses of key metabolites to levels of nutrition which varied from deficient to surplus in the Angora vs. Boer goat, this experiment was planned to shed some light as to the possible origin of these phenomena.

Procedure

Five Angora goat ewes (mean live mass 24 kg, $SE = 1$) and five Boer goat ewes (mean live mass 57 kg, $SE = 2.8$), 12—18 months of age, were fed each of five levels of a pelleted diet in a cross-over design with five periods. The Angora goats were selected from a flock bred at the Grootfontein Agricultural Research Station, Middelburg. The diet was formulated to contain 12 g crude protein (CP)/MJ metabolizable energy (ME) (9.9 MJ ME/kg; 119 g CP/kg) and was fed to provide 77, 88.5, 100, 111.5, or 123% of maintenance energy requirements (0.424 MJ/kg $W^{0.75}$/d; NRC, 1981). Animals were housed indoors in metabolism crates and fed at two-hourly intervals with automated feeders. Animals were allowed to adapt to new diets for a minimum period of 10 days before commencement of measurement periods which lasted for five days.

Urine and faeces collections were begun on the first day of the measurement period and continued for the following four days. Glacial acetic acid (40 ml/d) was added to urine collection vessels to minimize bacterial decomposition. Urine and faeces were collected daily, weighed and 10% sub-samples were added to a bulk sample which was then frozen until analysis. Nitrogen (N) content of feed, faeces and urine and organic matter (OM) content of faeces and feed were determined using standard (AOAC, 1984) methods.

Catheters (1 mm ID / 2 mm OD; Dural Plastics, Australia) were inserted into both jugular veins on the second day. On the third day, a single intravenous injection of D-[2-^{3}H]-glucose was administered for estimation of glucose kinetics which are reported elsewhere (Cronjé, 1992). On the fourth day, a single intravenous injection of [^{14}C]-urea [73 μCi plus 31 mg carrier in 5 ml sterile saline solution (9 g NaCl/l)] was administered for determination of urea kinetics. Urine was collected for the following 24 h, sub-sampled and frozen until analysis. Urea concentration was determined using the Berthelot method (Faulkner & King, 1982). For counting radioactivity, 100 μl of urine was mixed with 100 μl of glacial acetic acid and dried over H_2SO_4 and soda lime to remove radioactivity associated with $^{14}CO_2$ and any ^3H_2O which may have been present as a result of the D-[2-^{3}H]-glucose injection. The dried sample was reconstituted with 1 ml distilled H_2O and beta emission was counted in 10 ml scintillation fluid (Ready Value; Beckman Instruments). All samples were corrected for counting efficiency using an external standard and quench curve.

Urea flux rate was calculated on the assumption that the proportion of flux excreted as urea in the urine is equal to the proportion of injected radioactivity recovered in the urine:

$$\text{Flux} = \frac{\text{urea N excretion rate (g/d)} \times {}^{14}\text{C urea excreted (DPM)}}{{}^{14}\text{C urea injected (DPM)}}$$

Recycled urea was calculated as the difference between urea flux and excretion, and was assumed to represent that fraction which left the plasma, entered the gut and underwent hydrolysis catalysed by microbial urease (Ford & Milligan, 1970).

Statistical analysis

Results were analysed as for a cross-over design and polinomial effects were tested using a mixed model least-squares and maximum likelihood computer program (Harvey, 1988). Regression equations were computed using Genstat 5 (Genstat, 1987).

Results

Significance levels of effects and mean values are shown in Tables 1 (unscaled values) and 2 (scaled to $W^{0.75}$).

N digestion differed ($P < 0.01$) between breeds (Table 1). Mean N digestion was 5% lower in Angora goats, but Angoras retained 33% more N than Boer goats (Table 1). N retention (Figure 1) differed significantly ($P < 0.01$) between breeds, and increased quadratically with level of diet fed ($P < 0.01$) until a level of feed equivalent to 113% of maintenance energy was reached in Angoras (approximate standard error = 31%), and 120% in Boer goats (approximate standard error = 55%). There was no significant interaction found between breed and level of diet ($P > 0.05$). The regression equations are:

Angora goats: $Y = -1.657 + 0.03528.D - 0.0001555.D^2$

(se) (0.418) (0.00852) (0.0000425)

R^2: 94%

Boer goats: $Y = -1.064 + 0.02210.D - 0.0000918.D^2$

(se) (0.413) (0.00842) (0.0000420)

R^2: 92%

(Y = proportion of dietary N retained; D = percentage of maintenance energy requirements)

When expressed on a metabolic weight basis (Table 2), there were significant differences between breeds for the flux

Table 1 Influence of level of feed intake on nitrogen and urea metabolism in Angora vs. Boer goats

		Feed intake (% of maintenance energy)								Significance of effect[1]		
	Breed	77.0	88.5	100.0	111.5	123.0	Mean	n	SEM^2	Breed	Diet	Inter-action
N digestion	Angora	72.00	73.20	73.00	75.40	76.40	74.00	25	0.5521	**	*	NS
(%)	Boer	75.80	78.80	79.20	78.00	77.00	77.80	25	0.5521			
N retention	Angora	12.60	26.80	29.80	33.60	33.00	27.16	25	1.6179	**	**	NS
(% of intake)	Boer	9.00	17.40	24.40	23.60	27.40	20.36	25	1.6179			
Urea flux	Angora	9.494	9.298	7.598	10.87	10.47	9.547	25	0.3998	*	*	NS
(g N/d)	Boer	14.07	15.27	14.44	17.46	17.35	15.72	24	0.4161			
Urea excreted	Angora	3.388	3.370	3.376	3.612	3.868	3.523	25	0.2208	**	*	NS
(g N/d)	Boer	7.154	7.237	8.220	9.056	8.778	8.089	24	0.2298			
Urea recycled	Angora	6.106	5.926	4.222	7.260	6.608	6.024	25	0.2893	**	*	NS
(g N/d)	Boer	6.910	8.035	6.218	8.402	8.578	7.629	24	0.3011			
Urea recycled	Angora	62.52	63.48	56.68	65.66	61.36	61.90	25	1.3110	**	NS	NS
(% of flux)	Boer	48.34	52.80	42.10	47.88	49.88	48.20	24	1.3640			

[1] ** $P < 0.01$; * $P < 0.05$; NS = not significant ($P > 0.05$).

[2] SEM = Standard error of the mean.

Table 2 Responses of urea kinetics to changes in level of diet fed in Angora vs. Boer goats, expressed per kilogram metabolic mass

		Level of diet fed (% of maintenance energy)								Significance of effect[1]		
	Breed	77.0	88.5	100.0	111.5	123.0	Mean	*n*	*SEM*[2]	Breed	Diet	Inter-action
Urea flux	Angora	0.8694	0.8590	0.6908	0.9980	0.9488	0.8732	25	0.02803	*	*	NS
(g N/kg$^{0.75}$/d)	Boer	0.6892	0.7408	0.7006	0.8512	0.8442	0.7652	24	0.02918			
Urea excreted	Angora	0.3088	0.3130	0.3038	0.3292	0.3544	0.3218	25	0.01441	**	*	NS
(g N/kg$^{0.75}$/d)	Boer	0.3492	0.3506	0.3988	0.4454	0.4240	0.3936	24	0.01410			
Urea recycled	Angora	0.5606	0.5462	0.3874	0.6688	0.5946	0.5515	25	0.02113	**	NS	NS
(g N/kg$^{0.75}$/d)	Boer	0.3404	0.3904	0.3016	0.4058	0.4198	0.3716	24	0.02199			
Urine excreted	Angora	91.07	75.71	106.70	115.20	80.60	93.87	25	6.211	**	NS	NS
(g N/kg$^{0.75}$/d)	Boer	39.13	46.41	43.26	59.32	50.95	47.81	24	6.464			

[1] ** $P < 0.01$; * $P < 0.05$; NS = not significant ($P > 0.05$).

[2] *SEM* = Standard error of the mean.

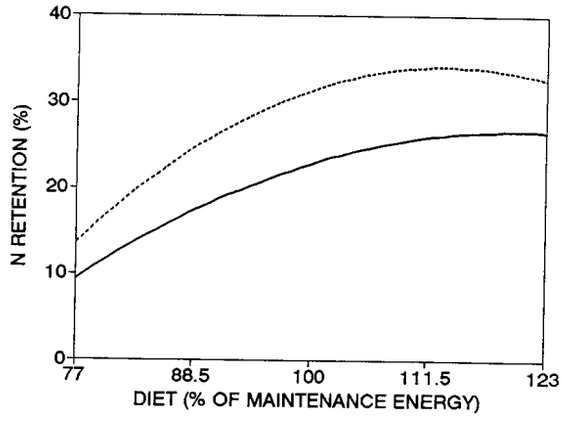

Figure 1 Quadratic regressions describing the responses of nitrogen retention to changes in the level of diet fed to Angora goats (------) or to Boer goats (——). For details see text.

rate ($P < 0.05$), excretion rate ($P < 0.01$) and recycling rate ($P < 0.01$) of urea N. Mean urea flux rate per kilogram metabolic body weight was 14% higher in Angoras (Table 2). Despite the fact that urine excretion rate in Angoras was nearly double that of Boer goats (Table 2), 18% less urea N was excreted in the urine, with the result that the amount of urea N recycled to the gut was 48% higher in Angoras. Urea flux and recycling rate (g N/d) increased as the level of diet fed was increased ($P < 0.05$).

Discussion

The diet fed was formulated to contain a protein:energy ratio of 12 g CP/MJ ME. Using a mean coefficient of N digestion of 0.74 for the Angora (Table 1), it can be calculated that the ratio of digestible crude protein (DP) to metabolizable energy was 9:1. Although this figure is higher than that required for maintenance alone (6.4 g DP/MJ ME; NRC, 1981), it is equivalent to the ratio recommended by NRC (1981) for maintenance plus maximum mohair growth (9.2 g DP/MJ ME), but lower than that recommended by Kempton (1979) for maximum rates of wool growth and liveweight gain in lambs (12 g DP/MJ ME). The crude protein in the diets supplying 77, 88.5, 100, 111.5 and 123% of maintenance energy requirements was equivalent to (% of maintenance CP requirements) 100, 114, 129, 144 and 159 respectively. The amount of protein and energy supplied by these treatments is expressed relative to requirements for maintenance and fleece production for Angoras in Figure 2. One of the anticipated effects of reducing the relative supply of nutrients as shown in Figure 2 would be to exert pressure on metabolic control mechanisms to divert increasing amounts of amino acids away from protein synthesis towards gluconeogenesis. Thus, the object of these treatments was to determine whether an energy deficit would change the partitioning of nitrogen away from fleece production to energy production (gluconeogenesis) in the Angora using the Boer goat as reference.

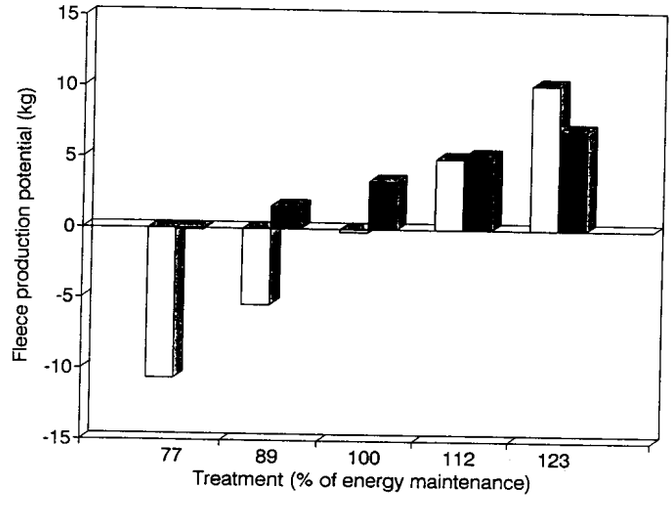

Figure 2 Theoretical fleece production potential of the dietary constituents (ME □ ; CP ■) supplied by the diets fed in the experiment. [Values were calculated according to NRC (1981) feeding standards, assuming that nutrients in excess of maintenance requirements will be used only for fleece production.]

The existence of a curvilinear decrease in the efficiency of N retention, at all levels of diet below those which supplied energy in excess of maintenance requirements (cf. Figures 1 and 2), suggests that the partitioning of nitrogen utilization may have been affected by the energy deficit. The most likely explanation for this is that amino acids were catabolized to produce glucose. This, together with the fact that there was no difference in the pattern of response between the Boer and Angora goats, suggest that the Angora goat will adapt to a deficit of energy by changing nutrient partitioning, presumably by reducing the amount of amino acids partitioned to fibre production.

The fact that N retention was 33% higher in the Angora than in the Boer goat suggests that nitrogen metabolism is comparatively more efficient in the Angora. This conclusion is supported by data recorded for urea kinetics which indicate that less urea is excreted and more is recycled in the Angora. Although these measures of protein metabolism are analytically independent, the higher nitrogen retention of the Angora is probably due to a slower urea excretion rate, as urea N constitutes 83% of urinary Kjeldahl N (Ford & Milligan, 1970).

A generalized model of urea metabolism in the ruminant is shown in Figure 3. Urea is synthesized in the liver from ammonia carried via the portal blood system from the rumen (11—41%), caecum (9%), from deamination of amino acids (30—58%) and from ammonia arising from nitrogenous bases (Nolan *et al.*, 1972; Nolan & Rowe, 1976; Lindsay, 1982; Dixon & Nolan, 1986). Mean urea N flux rates recorded in this study were 0.873 g N/d/kg$^{0.75}$ (9.5 g N/d) for Angoras and 0.765 g N/d/kg$^{0.75}$ (15.7 g N/d) for Boer goats. These values fall within the range of previously reported data for sheep (0.141—1.757 g N/d/kg$^{0.75}$) (Cocimano & Leng, 1967; Ford & Milligan, 1970; Nolan & Stachiw, 1979), but comparison is complicated by the influence of diet on urea flux. As shown in this study, several authors have noted an increase in urea flux with increasing dietary nitrogen content (Cocimano & Leng, 1967; Ford & Milligan, 1970). The higher flux rate per unit metabolic body mass in Angoras could be due either to a higher contribution of NH_4^+ from the gut or to a higher rate of tissue protein breakdown.

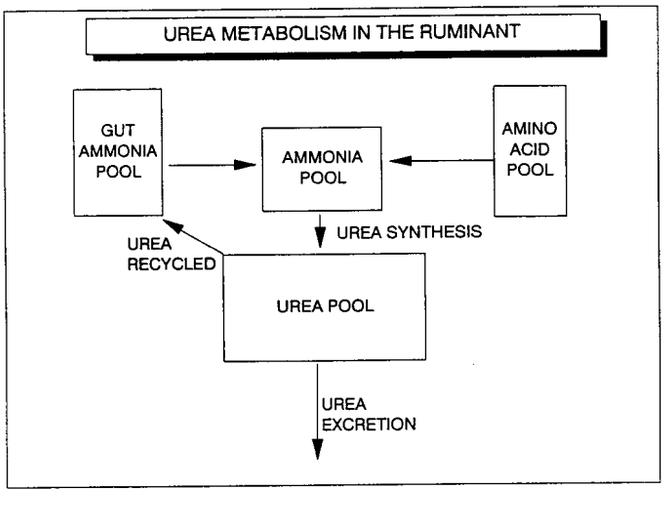

Figure 3 Urea metabolism in the ruminant.

Because mammals do not synthesize endogenous ureases, urea irreversibly lost from the body pool is either excreted via the urine or recycled to the gut and hydrolized to ammonia by bacterial ureases. Losses of urea by routes other than these (e.g. by sweat) are thought to be negligible (Nolan *et al.*, 1972). Only 2.5% of faecal N is derived from plasma urea (Nolan & Leng, 1972). Urea enters the gut by diffusion through the gut wall and in secretions such as saliva, gastric juice and bile. The extent of urea recycling was found to be 0.552 g N/d/kg$^{0.75}$ in the Angora (6 g N/d), and 0.372 g N/d/kg$^{0.75}$ in the Boer goat (7.6 g N/d). Recycling rates in sheep vary between 0.133 and 0.923 g N/d/kg$^{0.75}$ (Cocimano & Leng 1967; Nolan & Leng, 1972). Recycling rate per unit metabolic weight was increased (P = 0.08) by diet, but there was no interaction between breed and diet (P > 0.05). Ford & Milligan (1970) reported that recycling was positively correlated with urea flux rate and plasma concentration which was increased by adding urea to the diet. In the present experiment, however, the dietary protein:energy ratio was kept constant, and urea flux rate was increased in response to the amount of feed consumed. There are several site-specific mechanisms which may be involved in regulating the extent of recycling or excretion. The rate of recycling to the gut will be influenced by factors such as rumen ammonia concentration, volatile fatty acid production, partial pressure of CO_2, pH, ureolytic activity, blood flow to the gut, rate of saliva flow and plasma urea concentration (Nikolic *et al.*, 1980). It is not possible to ascertain whether any of these factors were responsible for the breed differences observed in this study, but the fact that urea excretion rate in Angoras was lower despite a substantially higher urine excretion rate suggests that differences in renal function could be responsible for the higher recycling of urea. Angoras excreted 0.322 g N/d/kg$^{0.75}$ as urea (3.5 g N/d), and Boer goats excreted 0.394 g N/d/kg$^{0.75}$ (8.1 g N/d). Depending on diet, values for sheep reported by other researchers vary from 0.087 to 0.734 g N/d/kg$^{0.75}$ (Packett & Groves, 1965; Nolan & Stachiw, 1979; Dixon & Nolan, 1986). Urinary excretion of urea will be influenced by glomerular filtration rate and kidney reabsorption of urea (Ford & Milligan, 1970), which provides a possible explanation for the differences in urea recycling and excretion observed in this study.

Not only was the quantitative excretion of urea lower in the Angora, but the proportion of flux partitioned towards excretion was also lower, despite a higher flux rate (Figure 4). In Angoras, 38% of urea flux was lost by excretion in the urine and 62% was retained by recycling to the gut; in Boer goats, proportionately more was excreted (52%) and less was recycled (48%). While site-specific mechanisms such as those mentioned above could be responsible for differences in the amount of urea recycled, they would not alter the proportion of urea secretion partitioned between the gut and urine. It has been proposed that the large variation in partitioning of urea between these two routes seen within and between species could be explained by differences in the partitioning of blood flow between the gut and the kidneys, which would conceivably influence the diffusion of urea to urine or digesta water (Oldham & Lindsay, 1983).

Urea recycling to the gut can be substantial. In sheep, recycling may provide 30—57% as much N as is available

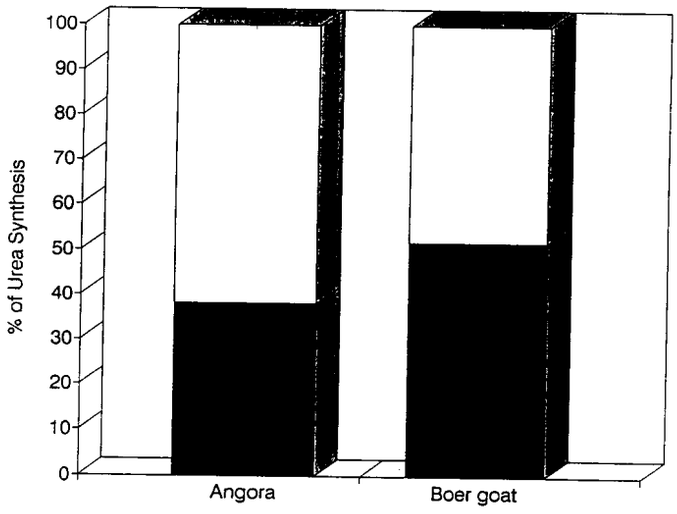

Figure 4 The proportional contribution of urea recycling (□) and excretion (■) to total flux rate in the Angora goat or Boer goat.

from the diet (Cocimano & Leng, 1967; Ford & Milligan, 1970). The data from the current experiment indicate that urea recycling for a 30kg Boer goat fed at maintenance would be equivalent to 58% of dietary N, and 87% for an Angora goat of equivalent mass. The physiological significance of increased rates of urea recycling is uncertain. Although earlier researchers hypothesized that urea recycling to the rumen could stimulate microbial protein synthesis and VFA production (Houpt, 1959), the quantitative significance of this is open to question. In this experiment, the higher recycling rate did not seem to confer any advantage on rumen fermentation as judged by digestion coefficients; in fact, N digestion was slightly lower in the Angora. Various authors have shown that recycling to the rumen constitutes only 19—58% of total recycling to the gut (Nolan & Leng, 1972; Nolan & Stachiw, 1979), the majority of recycling being post-ruminal. A more likely tenet is that recycling and degradation in the gut may be a mechanism for maintaining a constant supply of ammonia to the liver for synthesis of non-essential amino acids without maintaining a high concentration of ammonia in the plasma (Nolan *et al.*, 1972). Nolan & Leng (1972) showed that only 38% of the urea N that entered the gut and was degraded reappeared in the plasma urea pool. It was proposed that the remaining ammonia derived from recycled urea could be synthesized into amides or non-essential amino acids in the gut wall or liver and be passed into slowly equilibrating N pools such as body protein. A mechanism of this nature would be an advantage in the case of the Angora where hair production would make a substantial drain on the available amino acid supply. In the present study, the difference in urea N recycling between a 30kg Angora and a Boer goat of equal live mass would be equivalent to an extra supply of 14.4 g CP/d; this would be sufficient for the production of 3.3 kg of fleece per anum.

The proportion of urea flux diverted to recycling appears to be actively controlled, as is evident from the study of Cocimano & Leng (1967), in which recycling rate in sheep was increased from 30% of urea flux on a high protein diet to 92% on a maintenance diet. This study and other studies with sheep (Ford & Milligan, 1970) where similar results were obtained, suggest that recycling rate will be increased in situations where the supply of amino acids is low relative to the demand or capacity for utilization (Oldham & Lindsay, 1983). Similar trends are apparent in studies of lambs compared with mature sheep, and of malnourished children compared with mature adults (see Oldham & Lindsay, 1983). In this context, the higher recycling rate in Angora goats may be interpreted as an adaptive mechanism consequent to increasing the demand for amino acids via selection for increased fleece production. Conversely, the already high efficiency of N metabolism in this animal could leave little room for adaptation when nutrient supply suddenly falls below demand, predisposing the Angora to abortions and cold-stress mortalities in such situations.

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References

AOAC, 1984. Official methods of analysis (14th edn.). Association of Official Analytical Chemists, Inc. Arlington, Virginia.

CLARK, C.M., MACKENZIE, D.D.S., McCUTCHEON, S.N. & BLAIR, H.T., 1989. Physiological responses to selection for greasy fleeceweight in Romney sheep. *N.Z. J. Agric. Res.* 32, 29.

COCIMANO, M.R. & LENG, R.A., 1967. Metabolism of urea in sheep. *Br. J. Nutr.* 21, 535.

CRONJÉ, P.B., 1992. Glucose metabolism and adrenal function in goats bred for fibre production (Angora goat) or meat production (Boer goat). *S. Afr. J. Anim. Sci.* 22, 149.

DIXON, R.M. & NOLAN, J.V., 1986. Nitrogen and carbon flows between the caecum, blood and rumen in sheep given chopped lucerne (*Medicago sativa*) hay. *Br. J. Nutr.* 55, 313.

FAULKNER, W.R. & KING, J.W., 1982. Renal function. In: Fundamentals of clinical chemistry. Ed. Teitz, N.W., W.B. Saunders Co., Philadelphia. p. 991.

FORD, A.L. & MILLIGAN, L.P., 1970. Tracer studies of urea recycling in sheep. *Can. J. Anim. Sci.* 50, 129.

GALLAGHER, J.R. & SHELTON, M., 1972. Efficiencies of conversion of feed to fibre of Angora goats and Rambouillet sheep. *J. Anim. Sci.* 34, 319.

GENSTAT 1987. Genstat 5 Release 1.2. Lawes Agricultural Trust, Rothamsted Experimental Station.

HARVEY, W.R., 1988. Mixed model least-squares and maximum likelihood computer program. PC-1 Version. Ohio State University, Columbus, Ohio.

HOUGH, G.M., WILLIAMS, A.J., McDOWELL, G.H. & ANNISON, E.F., 1988. Blood metabolites in ewes selectively bred for high or low clean fleece weights: possible use for selection of superior animals. *Proc. Aust. Soc. Anim. Prod.* 17, 422.

HOUPT, T.R., 1959. Utilization of blood urea in ruminants. *Am. J. Physiol.* 197, 115.

KEMPTON, T.J., 1979. Protein to energy ratio of absorbed nutrients in relation to wool growth. In: Physiological and environmental limitations to wool growth. Eds. Black, J.L. & Reis, P.J., University of New England Publishing Unit, Armidale, Australia. p. 209.

LINDSAY, D.B., 1982. Relationships between amino acid catabolism and protein anabolism in the ruminant. *Federation Proc.* 41, 2550.

McCUTCHEON, S.N., MACKENZIE, D.D.S. & BLAIR, H.T., 1987. Nitrogen metabolism and plasma urea concentrations in fleeceweight-selected and control Romney rams. *Aust. J. Agric. Res.* 38, 917.

McGRAHAM, N. & SEARLE, T.W., 1982. Energy and nitrogen utilization for body growth in young sheep from two breeds with differing capacities for wool growth. *Aust. J. Agric. Res.* 33, 607.

NIKOLIC, J.A., PAVLICEVIC, A., ZEREMSKI, D. & NEGOVANOVIC, D., 1980. Adaptation to diets containing significant amounts of non-protein nitrogen. In: Digestive physiology and metabolism in ruminants. Eds. Ruckebush, Y. & Thivend, P., MTP Press, Lancaster. p. 603.

NOLAN, J.V. & LENG, R.A., 1972. Dynamic aspects of ammonia and urea metabolism in sheep. *Br. J. Nutr.* 27, 177.

NOLAN, J.V., NORTON, W.B. & LENG, R.A., 1972. Dynamic aspects of nitrogen metabolism in sheep. In: Tracer studies on non-protein nitrogen for ruminants. IAEA, Vienna. p. 13.

NOLAN, J.V. & ROWE, J.B., 1976. Models of nitrogen metabolism in sheep. In: Reviews in rural science (2). Eds. Sutherland, T.M., McWilliam, J.R. & Leng, R.A., University of New England Publishing Unit, Armidale, Australia. p.151.

NOLAN, J.V. & STACHIW, S., 1979. Fermentation and nitrogen dynamics in Merino sheep given a low-quality roughage diet. *Br. J. Nutr.* 42, 63.

NRC, 1981. Nutrient requirements of domestic animals No 15. Nutrient requirements of goats: Angora, Dairy and Meat goats in temperate and tropical countries. National Academy Press, Washington, DC.

OLDHAM, J.D. & LINDSAY, D.B., 1983. Interrelationships between protein-yielding and energy-yielding nutrients. In: Proc. 4th Int. Symp. Protein metabolism and nutrition, Clermont-Ferrand (les Colloques de l'INRA no 16). Eds. Amal, M., Pion, R. & Bonin, D., INRA, Versailles. p. 183.

PACKETT, L.V. & GROVES, T.D.D., 1965. Urea recycling in the ovine. *J. Anim. Sci.* 24, 341.

WENTZEL, D., 1986. Improved small stock production – collaboration between scientist and producer. *S. Afr. J. Anim. Sci.* 16, 123.

WILLIAMS, A.J., LENG, R.A. & STEPHENSON, S.K., 1972. Metabolism of cystine by Merino sheep genetically different in wool production. 1. Comparison of the entry rates of cystine in sheep from flocks selectively bred for high and low fleece weight. *Aust. J. biol. Sci.* 25, 1259.