METABOLISM IN COMPENSATORY GROWTH: V. EFFECT OF UNDEGRADED PROTEIN IN COMPENSATORY GROWTH

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ABSTRAK

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Suatu percobaan dirancang untuk mempelajari pengaruh pertambahan asam amino yang tersedia, pada temak yang sedang tumbuh yang diberi pakan basal dan yang telah mengalami kurang pakan.Dua belas domba jantan dibagi dalam 3 group perlakuan yang masing-masing diberi lucerne *(Medicago sativa)* pellet. Perlakuan tersebut adalah: pemberian pakan pada tingkat energi dasar (M), M + 60 g casein yang diperlakukan dengan formaldehid (M + HCHO-casein) dan *ad libitum.* Kenaikan konsumsi protein menaikkan retensi nitrogen (N), meskipun efisiensi dari retensi N tertinggi pada ternak yang mengkonsumsi N terendah yaitu perlakuan M (0.36, dibanding 0.31 dan 0.2 pada ternak M + HCHO-casein dan ad libitum).Penambahan'asam amino dengan HCHO-casein menyebabkan kenaikan 19 g glukosa/hari atau 30 g glukosa/l00 g protein. Laju pemasukan glukosa (GER) naik dengan naiknya protein kasar yang tercerna. Meskipun GER berbeda antara ternak yang diberi pakan M dan M + HCHO-casein, pemasukan glukosa dalam otot kaki pada perlakuan M + HCHO-casein 2 kali (0,18 mM) lebih banyak dari pada perlakuan M (0,08 mM). Ada pengaruh yang signifikan pada pemasukan dan pengeluaran asam amino essensial, leucine, isoleucine, lysine dan threonine, juga asam amino non-essensial, tyrosin dan glutamine dengan naiknya kadar protein ransum. Penambahan HCHHO-casein menaikkan konsentrasi asam amino yang bercabang (BCAA) dalam darah arteri sebanyak 76 % dan phenylalanine sebanyak 61 %. Secara umum, ada kenaikan asam amino dalam darah arteri pada ternak yang diberi pakan M + HCHO-casein atau *ad libitum.* Tetapi kenaikan itu diikuti oleh naiknya oksidasi asam amino yang ditunjukkan dengan naiknya eskresi urea. Ada korelasi yang positif antara urea dalam urin dan konsumsi N, menunjukkan bahwa asam-asam amino itu tidak terpakai semuanya untuk sintesa protein atau deposisi protein.

Kata kunci: Pertumbuhan kompensatori, asam amino, retensi N

ABTRACT

MAHYUDDIN, P. 2001. Metabolism in compensatory growth. V. Effect of undegraded protein in compensatory growth. *Jurnal Ilmu Tenak dan Veteriner* 6(3): 195-204.

An experiment was designed to study the effect of increasing availability of amino acids in growing animal fed maintenance diet and which previously subjected to underfeeding. Twelve wether Iambs were divided into 3 treatment groups, each was fed pelleted lucerne *(Medicago sativa).* The treatments were: diet at maintenance energy level (M), M + 60 g formaldehyde treated-casein (M + HCHO-casein) and *ad libitum.* The increase in protein consumption increased nitrogen (N) retention, although the highest efficiency of N retention occurred in animal fed M diet (0.36) compared to those fed M + HCHO-casein (0.31) or *ad libitum* diet (0.2). Provision of amino acids by supplementation of 60 g HCHO-casein resulted in an increment of 19 g glucose/d or 32 g glucose/lOO g protein. Glucose entry rate (GER) increased with increasing digestible crude protein. Although GER was not different between animals on M and M + HCHO-casein diet, the uptake of glucose in the hind-limb muscles of animals on the M + HCHO-casein was twice (0. 18mM) than that of animals on the M diet (0.08 mM). There was a significant effect on the uptake and output of essential amino acids, leucine, isoleucine, lysine and threonine and non-essential amino acids, tyrosine and glutamine as levels of protein in the diet increased. Supplementation with HCHO-casein increased the arterial blood concentration of branch chain amino acids (BCAA) by 76 % and phenylalanine by 61 %. In general there was an increase in the arterial concentration of amino acids in animals fed either M + HCHO-casein or *ad libitum.* However, this increase was followed by increased amino acids oxidation, which showed in increased urea excretion. There was a positive correlation between urinary urea and N intake, suggesting that amino acids were not fully utilized for protein synthesis or protein deposition.

Key words: Compensatory growth, amino acid, N retension

INTRODUCTION

In the previous paper (MAHYUDDIN and TELENI, 1996), Iambs which resumed *ad libitum* feeding after a period of underfeeding showed a marked increase in their metabolic rates and uptake of glucose by their hid-limb muscles as results of increased feed intake. The estimated rates of protein deposition in these animals

were also higher than those in animal, which grew normally.

Under extended draught conditions feeding at maintenance is normally recommended since it is considered to be more economical. If, during a draught, the animals have been on sub-maintenance feeding, a response in growth may be expected if they were subsequently fed at maintenance level. Additional responses in growth may be anticipated if these animals were supplemented with protein, which is not degraded in the rumen but degraded to amino acids and absorbed from the small intestine (KEMPTON and LENG, 1979). However, the efficiency of utilization of absorbed amino acids depends on the metabolic pathways in which they were utilized. If the energy supply in the body is adequate, the absorbed amino acids are mainly used for protein synthesis. Beyond an optimum protein:energy ratio the animal most likely use amino acids as energy-yielding substrates directly by deamination and decarboxylation or indirectly via their conversion to glucose.

The experiment described below was undertaken to determine the effect of increasing the availability of amino acid in growing animals fed a basal lucerne diet at maintenance energy level and which have been previously subjected to underfeeding.

MATERIALS AND METHODS

Experimental design

The experimental design was a randomised block design. Twelve Merino wether Iambs were stratified into 4 liveweight categories and the animals from each category were randomly allocated to 3 treatment groups.

The treatments were:

- lucerne pellets fed at maintenance energy level (M)
- M + 60 g HCHO-casein
- lucerne pellets fed *ad libitum*

Experimental procedure

Animal, feeding and surgery

The lambs were kept in individual pens and fed lucerne pellets *ad libitum* for 6 weeks after which they were restrictively fed to calculated (MAFF, 1975) half-maintenance energy level for 9 weeks. Following the period of sub-maintenance feeding, the animals were transferred to metabolism cages where they were fed their respective treatment diets, continuously through automatic feeders for 28 days (experimental period).

The HCHO-casein supplement was prepared as described by HEMSLEY *et al.* (1973). Common salt was added to the supplement at 1 % (w/w) to improve the latter's palatability. Measurements were undertaken on these animals from Day 18 of feeding of experimental diets, over a period of 10 days. Before the measurement period each animal was surgically prepared with a chronic indwelling catheter in the left and right external jugular veins and a femoral artery. A day before glucose biokinetics measurements were undertaken, a catheter was inserted into a lateral saphenous vein of each animal. These catheters facilitate the simultaneous use of the isotope dilution and A V difference techniques.

Digestibility and N balance

Feed residues, faeces, and urine were collected and treated daily from Day 18 over a period of 7 days for the determination of feed digestibility and N balance.

Isotope infusion and blood sampling

On Days 25, 26, and 28 of the experimental period, urea, glucose and CO2 entry rates were estimated respectively by isotope dilution using continuous infusion technique. Approximately 1.85 MBq of [14C] urea was infused into a jugular vein for 9 h for the determination of urea entry rate. Arterial blood samples were collected at half-hourly intervals from the femoral artery over the last 3 hours of infusion.

For the determination of glucose entry rate (GER) approximately 2.59 MBq of [U-14C] glucose were infused continuously at a constant rate. During isotope infusion, blood flow across the hind-limb muscle bed, was estimated, between the 8th and 9th h of isotope infusion, using the TOH technique described by ODDY *et al.* (1980). Blood samples collected during blood flow estimation were also used for the determination of _Iucose kinetics. Blood samples for blood gas and 4C02 determination were collected at 15 minutes intervals, half an hour before and half and hour after blood flow estimation.

Carbon dioxide entry rate was determined by infusion of 3.33 MBq of NaHI4C03 continuously at a constant rate for 12 h. Blood samples were. collected at half-hourly intervals over the last 3 h and treated as described in MAHYUDDIN and TELENI (1996).

Sample preparation and laboratory analyses

Measurements conducted on plasma included glucose, urea, FF A, lactate, amino acids, growth hormone, and insulin concentrations. Blood concentrations of CO2 and O2 and radioactivities of glucose, urea and CO2 were also determined. The samples were prepared and analysed according to procedures described in MAHYUDDIN and TELENI (1996).

Calculation *of* results

Calculation *of* entry rates *of* metabolites and oxidation *of* glucose were carried out according to procedures described in MAHYUDDIN and TELENI (1996).

Statistical analysis

Data were subjected to the analysis *of* variance based on a Randomised Block Design. Differences between treatment means were examined using the LSD test (STEEL and TORRIE, 1980). All data were computed using the Statistix 3.0 program (NH Analytical Software, USA)

RESULTS AND DISCUSSION

Intake, digestibility and N retention

In this study, all the animals had undergone feed restriction (half-M) before being subjected to the three different dietary treatments. The diets fed, supplied different levels *of* energy and protein (Tables 1 and 2). The group *of* animals, which had resumed *ad libitum* had the highest level *of* feed DM intake (approximately 4.2% *of* live weight). The highest DM intake in this group was related to the significant reduction in DM digestibility. This result is in consistent with the results *of* the study reported by MAHYUDDIN and TELENI (1995). It was suggested in that study that the higher level *of* intake associated with lower digestibility value might have been due to an increased rate *of* the disappearance *of* feed from the rumen.

The estimated ME content of the diet fed *ad libitum* was lower than those *of* the other *two* diets. The ME intake, however, was highest in animal fed *ad libitum* (Table 1). The ME consumed by animals on the M diet was 2.52 MJ/d, which is equivalent to approximately 281 kjl"gO",. This is lower than the calculated value *of* energy maintenance for N equilibrium (306 kj/kgO,7s)suggested bls ARC (1980). But higher than the value (162 kj/kgo. *s)* observed by HOVELL *et al.* (1983) since at 281 kj/kgo.7s, animals had a positive N retention *of* 3.4 g/d or 375 mg N/kgo.7s/d (Table 2). It is possible that in this experiment the energy requirement *for* maintenance was reduced during underfeeding as was discussed in MAHYUDDIN and TELENI (1995).

Tabell. The intake of dry matter and organic matter and estimated metabolisable energy (ME),' the digestibility of dry matter, organic matter and crude protein in Iambs fed pelleted lucerne at maintenance energy level (M), M + *60* gI hd/ d HCHO-casein or pelleted lucerne ad *libitum.*

	Dietary treatments				
	M	M+HCHO-casein	*Ad libitum*	SE	P
Liveweight (kg):					
Before treatment	18.4	18.4	19.3		
After treatment	18.6	19.4	27.8		
Intake (gld):					
Dry matter	312"	367b	1174e	*10.3*	*<0.05*
Organic matter	269"	322b	1O0ge	9.2	*<0.05*
Digestible organic matter	168"	199b	510e	9.86	*<0.05*
ME (MJ/ d)	2.52"	3.00b	7.65e	1.3	*<0.05*
Digestibility (%)					
Dry Matter	63.2b	62.9b	51.0"	1.6	*<0.05*
Organic matter	53.8b	54.3b	43.5"	1.4	, *<0.05*
Crude protein	74.5b	74.5b	62.2"	1.2	*<0.05*
ME . (MJ/ kg DM)	8. lOb	8.15b	6.53"	0.1	*<0.05*

Values (in each row) with different superscripts differ significantly (P<0,05)
*ME (MJ/ kg) = 0.15 x Organic matter digestibility (%DM) (MAFF (1975)

Therefore, underfed animals would probably respond to additional intake of energy or protein, by depositing more protein. In this experiment particularly, provision of protein increased N retention and there was a strong relationship between N intake and N retention (Figure 4.). However, there was an overall tendency for a reduction in efficiency of N retention as N intake increased although the difference between the M and M + HCHO-casein diet was not significant (Table 2).

The N:DOM ratios of the diets (range 0.05-0.08) were higher than the optimum value (0.04) for microbial growth (HOGAN and WESTON, 1970). There was a high probability that a significant proportion of amino acids might have been utilized in gluconeogenesis. This is particularly so in animals fed the M + HCHO-casein diet in which the increase in N:DOM ratio would have been due to the increase in rumen-undegradable protein. The significant relationship between digestible crude protein intake and GER (Figure 3) observed in this study is consistent with the above suggestion.

Urea and glucose biokinetics

Plasma urea concentrations was lower in Iambs on the M diet than in Iambs on the other two dietary treatments. Urea entry rate was also lowest in animals on the M diet and highest in Iambs fed *ad libitum.* The differences in urea entry rates among animal groups were also reflected in differences in urinary urea excretion rates by these animals.

Across dietary treatments, the relationship between N intake and urea entry rates or plasma urea concentrations, and between urea entry rate and urea excretion are shown in Figures I and 2 respectively. As N intake increased, both the urea entry rate and plasma urea concentration were increased. Similarly, urinary urea excretion rate was increased as urea entry rate increased.

Tabel 2. Nitrogen balance and urea biokinetics in lambs fed pelleted lucerne at maintenance energy level (M), M + 60 glhd/d HCHO-casein or pelleted lucerne ad libitum

	Dietary treatments				
	M	M+HCHO-casein	*Ad libitum*	SE	P
Nitrogen (N) balance (g/d):					
Nitrogen intake	9.4"	16.7b	39.7c	0.4	<0.05
Faecal N	2.4"	4.5b	13.4c	0.4	<0.05
Urine N	3.6"	7.9b	14.6c	0.5	<0.05
Nitrogen retention	3.4"	5.9b	11.7c	0.4	<0.05
Efficiency ofN retention	0.36b	0.31b	0.2"	0.02	<0.05
Urea biokinetics (g/d)					
Plasma urea (mg/dl)	49a	51.2ab	57.4b	2.6	<0.05
Urea entry rate	25.lb	47.5b	62.8c	4.1	<0.05
Urinary urea	4.9b	13.7b	21.4c	1.9	<0.05
Urea transferred to					
The gut"	23.7"	33.8b	41.5b	3.7	<0.05

Values (in each row) with different superscripts differ significantly (P<O.O5)

.*Calculated as N retention! N intake

**Calculated by the defference between urea entry rate and urinary urea excretion rate

Dietary treatments did not significantly affect arterial plasma glucose concentrations. There was a tendency for glucose entry rate (GER), in animal fed the M + HCHO-casein diet, to increase but the value was not significantly different from that in animals on the M diet. Animals on ad libitum feeding had the highest GER. Glocose oxidation and its contribution to CO2 production in the whole body were similar in animals fed M + HCHO-casein and ad libitum and were higher in these two groups of animals than corresponding values in animals fed the M diet.

The CO2 entry rate was highest in animal fed ad libitum and lowest in animals fed the M diet.

The dietary treatments did not sisgnificantly affected blood flow across the hind-limb mucles but they did sisgnificantly increase glucose AV concentration difference and uptake by muscle of lambs fed the M + HCHO-casein diet than those fed lucerne pellets ad libitum (Table 3.)

Table 3. Glucose biokinetics in whole body and hind-limb muscles of lambs fed pelleted lucerne at maintenance energy level (M), M + HCHO-casein and pelleted lucerne *ad libitum*

	Dietary treatments				
	M	M+HCHO-casein	*Ad libitum*	SE	P
Whole body					
Plasma glucose (mM)	3.5	3.7	3.5	0.3	NS
Glucose entry rate (mmole/h)	20.0'	30.2'	38.3b	2.3	<0.05
Glucose entry rate (mmole.h/kg LW)	1.4'	1.5ab	1.7b	0.08	<0.05
Glucose oxidised (%)	15.7'	31.3b	32.7b	2.1	<0.05
CO2 entry rate (mmole/h)	695'	1276b	1612c	54.9	<0.05
Hind-limb muscle					
Blood flow (ml/min/kg)	94.7	82.1	100.7	17.4	NS
Glucose A V conon difference (mM)	0.08'	0.18b	O.13'b	0.04	<0.05
Glucose extraction (%)	2.4	4.8	' 3.9	0.7	<0.05
Glucose uptake (umole/min/kg muscle)	7.6'	14.8b	13.1b	1.7	<0.05
O2 A V concn difference (mM)	2.15	2.68	1.93	0.37	NS
Potential glucose oxidation (%)	23.2'	40.2b	40.9b	4.13	<0.05

Values (in each row) with different superscripts differ significantly (P<0.05)

.*calculated from (6 x A-V gluc)/A-V (02) x 100, assuming that complete oxidation of I mole glucose will ylield 6 moles of oxygen.

If it is assumed that the digestible crude protein was absorbed as amino acids, and every 100 g of protein digested can potentially produce 55 g of glucose and 35 g of urea (KREBS, 1964) the animals fed M, M+HCHOcasein and *ad libitum* could potentially produce 24, 43 and 85 gld, respectively, of glucose from the digestible crude protein which they consumed. The potential glucose production represents about 21, 32, and 51 % respectively of GER in those groups of animals.The 60 g HCHO-casein which pass through the rumen largely undegraded and which would be anticipated to be almost totally absorbed in the small intestine as amino acids, resulted in an incremental increase of 199 glucose/d or 32 g glucosell 00 g HCHO-casein consumed. This value is similar to the 30 g glucose 11 00 g protein suggested by LINDSAY (1982) but lower than the potential value of 55 g glucosellOO g protein reported by KREBS (1964).

Glucose production may also be estimated from urea excretion rate. In this study urinary urea of 4.9, 13.7 and 21.4 g per day could be associated with glucose production of7.7, 21.5 and 36.8 gld in animals fed M, M+ HCHO-casein and *ad libitum* respectively. The supplementation of 60 gld HCHO-casein resulted in an increment of 13.8 g glucose/d or 32 g glucose/IOO g protein intake above. However, the two estimates of the contribution of absorbed amino acids (HCHOcasein) to glucose production were still in the range of values estimated by LINDSAY (1982) or BARRY *et al*. (1982).

Although GER was not different between animals on the M and M+HCHO-casein diets, the uptake of glucose by the hind-limb muscles of animals on the latter diet was twice the value observed in animals on the M diet. The higher uptake of glucose could conceivably be due to the higher amino acids availability in the blood due to the casein supplement (Table 5). The increased absorption of dietary amino acids was reflected in increased A V concentration difference across the hind-limb muscles, particularly the A V concentration difference of essential amino acids. An increased amino acids uptake by muscles would probably result in increased protein synthesis in this tissue. It is probable in this situation that metabolic regulation would stimulate the uptake of glucose to meet the increased demand for energy by protein synthesis and net protein deposition in muscles. If this was the case in this experiment, glucose oxidation in the muscles would have increased. It is unfortunate that data on glucose oxidation in the hind-limb muscles are not available from this experiment to support this. However, it is almost certain that glucose oxidation in the hind-limb muscles was increased as the whole body metabolic rate as well as glucose oxidation were markedly increased (Table 3)

Table 5.Arterial blood concentration of amino acids and their respective arteriovenous (A V) concentration differences across the hind-limb muscles of lambs fed either pelleted lucerne diet at maintenance energy level (M), M + HCHO-casein or the pelleted lucerne *ad libitum*

	Dietary treatments				
	M	M+HCHO-casein	*Ad libitum*	SE	P
Arterial concentration (jlM)					
Essential					
Valine	120"	220b	267b	27.6	<0.05
Leucine	69"	126b	157b	10.8	<0.05
Isoleucine	49"	74"b	101b	10.4	<0.05
Phenylalanine	28"	45b	60c	3.8	<0.05
Histidine	64	60	77	8.0	NS
Lysine	210"	173"	296b	25.1	<0.05
Threonine	105	155	129	22.7	NS
Non-essential					
Thyrosine	34"	56"	84b	8.5	<0.05
Alanine	74"	93"b	1l0b	13.2	<0.1
Glutamate	123"	135ab	163b	15.0	<0.1
Glutamine	88	59	81	21.9	NS
Glycine	406	342	391	48.3	NS
Aspartate	10"	14"b	81b	1.7	<0.05
Serine	71"b	77b	51"	9.5	<0.1
Asparagine	25"	37"b	42b	4.3	<0.05
A V Concentration difference (jlM)					
Essential					
Valine	-1.2	7.9	25.6	17.12	NS
Leucine	-1.9"	7.6"b	25.0b	7.96	<0.05
Isoleucine	-0.3"	4.3"	17.8b	4.67	<0.05
Phenylalanine	-2.9	-.18	4.1	3.79	NS
Histidine	304	-9.4	11.4	9.64	NS
Lysine	24.7"b	-31.9"	4Ub	37.95	<0.05
Threonine	2.6"b	-10.0"	39.0b	15.03	<0.05
Non-esential					
Thyrosine	-5.0"	4.8"b	10Ab	6.2	<0.05
Alanine	-31. 7	-11.3	-4.2	17.9	NS
Glutamate	-9.0"b	-15.9	-22.4	31.02	NS
Glutamine	-25.5"	-27.7a	6.8b	12.91	<0.05
Glycine	-15.4	-17.7	-26.0	47.9	NS
Aspartate	-1.3	-2.0	-1.6	1.80	NS
Serine	5.7	-2.9	14.8	8.22	NS
Asparagine	4.3	1.2	6.8	2.37	NS

Values (in each row) with different superscripts differ significantly (P<O.O5), * Negative values indicate net output from muscles

Among the essential amino acids, histidine, and lysine concentration did change in animals fed the threonine were not significantly affected by the dietary HCHO-casein supplement but increased in animals on treatments. In relation to values in lambs on the M diet, *ad libitum* feeding. The concentrations of the BCAA:

valine, leucine, and isoleucine increased with casein supplementation but did not differe significantly from values in animals on *ad libitum* feeding. Supplementation with HCHO-casein increased the arterial blood concentration of BCAA by approximately 76%. Phenylalanine was also increased (approximately 61%) by HCHO-casein supplementation. While lysine concentrations were increased significantly by *ad libitum* feeding, they were not changed by the feeding ofHCHO-casein supplement.

The dietary treatments did not appear to have a significant effect on the net uptake or output by muscles of essential amino acids, except leucine, isoleucine, lysine and threonine which were taken up in the greatest amount by muscles of lambs fed lucerne *ad libitum.*

Figure 5. The relationship between urinary urea excretion rate and nitrogen intake in Iambs fed M (.), M + HCHO-casein (-<» and lucerne *ad libitum* (+)

Figure 5. The relationship between urinary urea excretion rate and nitrogen intake lambss fed M (●), M + HCHO-casein (♣) and lucerne ad libitum(♦)

Non-essential amino acids

There were no significant differences in the blood concentrations of non-essential amino acids between lambs fed the HCHO-casein supplement than those fed the M diet. However, except in the case of glutamine and glycine, the non-essential amino acid concentrations tended to be higher in lambs fed the HCHO-casein supplement than in those on the M diet. Except for the concentration of glutamine, which did differ significantly and serine which was lower, the other non-essential amino acids were higher in concentration in the lambs fed *ad libitum* than those in either of the two groups animals.

There were no significant differences (in the case of glutamine) in the uptake or output by muscles, of non-essential amino acids between animals in the three dietary treatment groups.

In general there was an increase in the arterial concentration of amino acids in animals fed either the M+ HCHO-casein or *ad libitum.* This probably reflected the initial imbalance between the rate of influx of amino acids into the circulation and their rates of utilization (for protein synthesis and as energy yielding substrates). The rate of amino acid oxidation in the body could be reflected in the excretion rate of urea via the urine. In the present experiment, urinary urea excretion rate was observed to increase with increasing protein intake (Figure 5). This waste of amino acids may be reduced by supplying more non-amino energy-yielding substrate, particularly glucose (MAHYUDDIN, 1997).

CONCLUSION AND RECOMMENDATION

The effects of increasing availability of amino acids in animals undergoing compensatory growth were to increase nitrogen retention, glucose entry rate, uptake of glucose, uptake, and output of some essential and non-essential amino acids, arterial concentration of amino acids particularly essential amino acids and urea excretion. Increased essential amino acids together with increased urea excretion indicating that there was less protein deposition than anticipated. Provision of energy-yielding substrates to reduce N waste should be considered for further study.

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