Effects upon glucose metabolism of feeding a low- or high-roughage diet at two levels of intake to sheep

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(*Received* 12 *February* 1974 – *Accepted* 23 *April* 1974)

1. To determine the effect of diet and level of energy intake on glucose metabolism in sheep, four dietary treatments consisting of feeding a low-roughage (LR) and a high-roughage (HR) diet at each of two intake levels estimated to provide 586 and 1172 kJ (140 and 280 kcal) digestible energy (DE)/kg body-weight$^{0.75}$ per d were given to each of eight yearling rams in four different time periods each of 4 weeks duration. Both diets contained 140 g crude protein/kg using ground maize, mixed hay and soya-bean meal and were given in two meals/d. Estimated DE values of food were verified during the study and actual intakes of DE were within 9·5 % of the estimated values.

2. To study glucose metabolism, a single intravenous injection of [2-^{3}H]glucose and subsequent withdrawal of nine venous blood samples within 3 h were made in each experiment. Two experiments were conducted on consecutive days for each sheep on each dietary treatment.

3. Coefficients of determination (r^2) for linear regressions to measure the effect of time after a single injection of [2-^{3}H]glucose on log specific radioactivity of plasma glucose were calculated for fifty-eight experiments. In fifty-six of the experiments, r^2 values exceeding 0·95 were obtained.

4. Compared to the HR diet, the LR diet increased ($P < 0·05$) the pool size and decreased ($P < 0·05$) the half-life of glucose. At both intake levels, the LR diet increased ($P < 0·05$) the plasma concentration and the entry rate of glucose compared to the HR diet but interaction ($P < 0·05$) between diet and intake level was attributed to a greater difference obtained between diets at the higher compared to the lower level of food intake. Increasing the level of intake caused a greater ($P < 0·05$) pool size and space, and a shorter ($P < 0·05$) half-life of glucose.

5. It was concluded that substitution of roughage by concentrate in a ruminant's diet may increase the rate of glucose entry during a short time period after eating.

Under most circumstances, ruminants do not absorb sufficient glucose from the gut to meet their requirements (Lindsay, 1970). Their requirement is supplied by endogenous synthesis and propionate is a primary contributor. Replacement of roughage by concentrate in a ruminant's diet increases the concentration and rate of production of propionate in the rumen (Bauman, Davis & Bucholtz, 1971; Blaxter, 1967). Increased intake of concentrate may also augment the amount of glucose absorbed direct from the small intestine (Armstrong & Beever, 1969; Sutton, 1971). For these two reasons, replacement of roughage by concentrate in a ruminant's diet might be expected to increase the glucose entry rate. In one study of glucose metabolism, diets containing different proportions of lucerne chaff and maize were fed to sheep (Judson, Anderson, Luick & Leng, 1968) and in another, pelleted diets of dried grass, hay or bruised barley were also fed to sheep (Ulyatt, Whitelaw & Watson, 1970). Glucose entry rates were not significantly affected by the different diets in either study. These results are unexpected.

Increased glucose entry rate could be an important factor in explaining the observation that replacement of roughage by concentrate in the diet increases deposition of fat in the carcass and depresses milk-fat secretion of ruminants (Van Soest, 1963). In a recent study, the effects of a zero- or high-roughage diet for cattle on lipogenic metabolism in adipose tissue and carcass fat were determined (Buchanan-Smith, Horney, Usborne & Burgess, 1973). Increased availability of glucose in cattle fed the zero-roughage as opposed to high-roughage diet was a logical explanation of why the zero-roughage diet increased the amount of fat in the carcass. The purpose of the present study was to examine further the effects on glucose metabolism of replacing roughage by concentrate in a ruminant's diet. Because the glucose entry rate in ruminants may be increased by a higher intake of digestible energy (DE) (Lindsay, 1970), it was decided to feed isoenergetic amounts of the different diets at two different levels of energy intake. This enabled the interaction between diet and intake level to be studied. [2-^{3}H]glucose was found to have advantages over [U-^{14}C]glucose as a tracer for studies of glucose metabolism in sheep (Judson & Leng, 1972). Therefore a single-injection technique using [2-^{3}H]glucose was used to estimate pool size, space, half-life, and entry rate of glucose in the present study. In the experiments of Judson & Leng (1972), sheep were fed hourly to minimize fluctuations in the rate of glucose entry. It was decided to feed sheep in the present study with two meals daily, so preliminary experiments were done and results are presented to validate this procedure.

EXPERIMENTAL

Animals and diets

Initially, two yearling rams were used to establish the technique to study glucose metabolism and validate the procedure for giving the diets. The rams were fed on grass–legume haylage to appetite in two daily meals. They were housed in metabolism crates and offered water at all times.

To determine effects of diet and level of food intake on glucose metabolism, eight other yearling rams which weighed 31–42 kg (mean 34·4) were divided into two equal groups. Within groups, a latin-square design was used to assign four dietary treatments to each ram during four successive time periods of 4 weeks duration. Both groups were studied simultaneously. The dietary treatments consisted of feeding a low-roughage (LR) or high-roughage (HR) diet at both one and two times the estimated maintenance requirement. Ground maize and mixed grass–legume hay were basic constituents of both diets. Soya-bean meal was added to the LR diet to provide 140 g crude protein/kg in both diets. Composition of diets, the crude protein content, and particle sizes of the feeds used are given in Table 1. Maintenance intakes of these diets were estimated as 586 kJ (140 kcal) DE/kg body-weight$^{0·75}$ per d and tabulated values for DE content of the feeds were used to determine the daily rations ((US) National Academy of Sciences/National Research Council, 1968). The sheep were fasted and the body-weight of each determined prior to each period. Each animal received its daily ration in two equal portions at 08.00 and 16.00 hours. Water and cobalt-iodized salt were available at all times. The sheep were individually penned on concrete floors with

Table 1. *Composition and crude protein content (g/kg) and particle size distribution of the ingredients of diets given to yearling rams*

Ingredient	Diet		Crude protein	Particle size distribution†							
	Low-roughage	High-roughage		0·15	0·3	0·6	1·2	2·4	4·8	9·6	>9·6
Ground, shelled maize	626	118	88·6	—	1·2	20·5	40·4	32·3	5·6	—	—
Ground, mixed hay‡	244	—	91·7	3·0	5·9	5·9	14·7	22·1	30·9	17·7	—
Chopped, mixed hay‡	—	882	147·5	—	—	—	2·0	2·0	6·0	14·0	76·0
Soya-bean meal	130	—	447·3	—	—	2·2	12·3	39·1	45·2	1·1	—

† Percentage of ingredient passing through a mesh screen with the diameter of the holes ranging from 0·15 to 9·6 mm as indicated.
‡ Each hay contained legume and grass species.

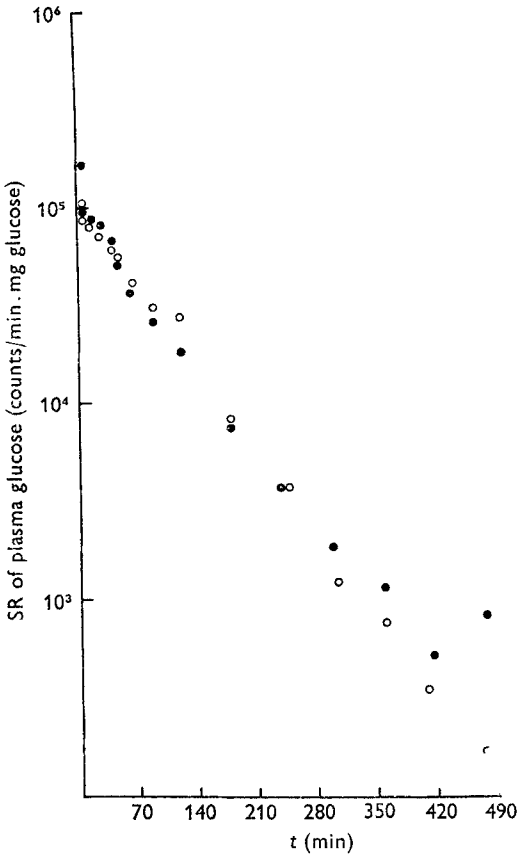

Fig. 1. Relationship between specific radioactivity (SR) of plasma glucose and the time (t) after a single injection of 500 μCi [2-^{3}H]glucose for each of two experiments using two sheep consuming a haylage diet. Linear regression line in one experiment (○) was: SR = 4·953 − 0·00434t, where SR is expressed as log counts/min per mg plasma glucose and t is in min. The corresponding line in the second experiment (●) was: SR = 4·970 − 0·00511t; SE of the estimates were 0·0853 and 0·1636 respectively; coefficients of determination (r^2) were 0·965 and 0·987 respectively.

sawdust bedding during the first 2 weeks of each period. For the last 2 weeks, sheep were in metabolism crates in which faeces and urine could be collected separately. Faeces were retained from the last week of the period.

Measurements of glucose metabolism and collection of blood samples

The technique selected to measure glucose metabolism was single injection of [2-^{3}H]glucose followed by withdrawal of blood samples to determine isotope dilution. Sheep were prepared by inserting 16 gauge catheters, 82·5 mm in length (Angiocath, Deseret Pharmaceutical Co., Sandy, Utah, USA), into the jugular vein on the day before experiments. [2-^{3}H]glucose (specific activity 540 mCi/mmol; New England Nuclear, Boston, Mass., USA) was administered to the sheep dissolved in 10 ml isotonic saline. For two initial experiments using two rams consuming a haylage diet,

500 μCi [2-^{3}H]glucose was administered to each sheep 1 h after the morning meal had been offered. For each subsequent experiment with rams in the diet study, 150 μCi [2-^{3}H]glucose was administered at 09.00 hours. To ensure that specified quantities of labelled glucose were given, three washings of 2–4 ml isotonic saline each, two of which had been used to rinse the container and syringe and one which was used to rinse the catheter itself, were also administered to the sheep. For the two initial experiments, fifteen samples of blood were taken within 8 h of injection of labelled glucose at times that are indicated in Fig. 1. For each experiment in the main diet study, nine blood samples were taken, to measure isotope dilution, at 20 min intervals for 180 min after injection. Additional blood samples were taken 30 min pre- and post-feeding and at 220, 280, 340 and 400 min post-injection.

In the main diet study, two experiments were completed for each ram fed on each diet, on 2 consecutive days prior to the last week of the period during which the sheep were given each dietary treatment. Blood samples of 5–10 ml were taken and immediately placed in tubes containing heparin. Within 6 h of sample collection, plasma was removed by centrifugation of blood at 5000 *g* for 20 min. Blood and plasma were held at $-10°$ to $-20°$ until analysed.

Chemical and radioassay techniques

Crude protein and gross energy contents of foodstuffs and faeces were determined by the Kjeldahl method and bomb calorimetry (Association of Official Analytical Chemists, 1970) respectively. Plasma concentrations of glucose were determined by the glucose-oxidase method (Raabo & Terkildsen, 1960) using commercially available test kits (Sigma Laboratories Inc., St Louis, Missouri, USA).

To isolate glucose from plasma to determine specific radioactivity (SR), the penta-acetate derivative was synthesized (Jones, 1965). To determine radioactivity, 100 mg glucose pentaacetate were dissolved in 10 ml of a scintillation fluid consisting of 5 g 2,5-diphenyl oxazole and 0·1 g 1,4-bis-2-(5-phenyl oxazoyl)benzene/l toluene. Radioactivity was counted using a liquid scintillation spectrometer (Model 3375, Packard Instrument Co. Inc., Downers Grove, Illinois, USA). Solutions for counting were kept in darkness for at least 3 h before being placed in the spectrometer so as to avoid interference from absorbed fluorescent light. To standardize results and correct for tritium exchange with hydrogen in the labelled glucose solutions injected, two 10 μl standards of injected glucose were retained from each experiment and the glucose from these samples was also converted into the pentaacetate derivative. Standards and samples from each experiment were counted simultaneously, using automatic external standardization to correct for differences in quenching. Blood glucose determinations and preparation of glucose pentaacetate from samples and standards were completed within 1 week of collection of blood.

Calculations

Linear regressions to measure the effect of time after the injection of labelled glucose *v.* log SR of plasma glucose were obtained for individual experiments. Total glucose entry rate and body pool size of glucose were calculated by monoexponential analyses

of these regressions (Judson & Leng, 1972). To correct for variation in body-weight of rams, pool sizes and entry rate of glucose were expressed per kg body-weight and per kg body-weight$^{0.75}$ respectively. The half-life of glucose was calculated by the method of Ginochia & Evans (1973). Glucose space was calculated by dividing the pool size of glucose by the corresponding plasma concentration and expressing the value obtained as a percentage of body-weight. The value for plasma concentration used in these calculations was the mean from determinations made in every sample of blood collected.

Fifty-eight experiments out of a possible sixty-four were completed in the main diet study. Because of the missing results, treatment effects were analysed using the least-squares method with a model in which animal, period and treatment effects were included (Searle, 1971). Differences between the two days were not significant ($P > 0.05$), therefore values obtained from two experiments performed on each sheep in each period were averaged before the least-squares analysis was done. Period and animal effects were not significant ($P > 0.05$). Results are therefore shown in Table 4 as the means and standard deviations of values obtained from all the experiments done with sheep given each dietary treatment. When a significant interaction ($P < 0.05$) between diet and energy level was analysed by the least-squares method, then the individual treatment means were compared using the *t* test.

RESULTS

Single-injection technique to administer [2-^{3}H]glucose

Results for regressions to measure the effect of time after a single injection of [2-^{3}H]-glucose *v.* log SR of plasma glucose obtained in the two initial experiments are presented in Fig. 1. The linearity of these regression lines was indicated by coefficients of determination (r^2) of 0·987 and 0·965. Similar r^2 values were calculated for results obtained in all experiments with the rams used in the diet study; these values are shown in Table 2. An r^2 value of less than 0·95 was obtained in only two of fifty-eight experiments. Treatment did not affect ($P > 0.05$) the r^2 values. Coefficients of variation about the linear regressions averaged 1·17% and were never above 3·0%.

Food intake

With the exception of the HR diet given at twice maintenance level, diets were consumed completely by the sheep. The mean value for weigh-back of feed for sheep on the HR diet fed at twice maintenance level was 7·4% of the estimated DE intake above maintenance. The actual intake of DE from the LR diet was slightly less than estimated whereas the reverse was true for the HR diet given at the low level of intake (Table 3). The actual intake of the HR diet given at the high level was approximately equal to the estimated intake.

Both LR diets and the HR diet given at the low level of intake were generally consumed by the sheep within 1 h after the meals were given. The HR diet given at the high level of intake was largely consumed within this period of time but some eating also occurred during the remaining time between meals.

Table 2. *Coefficients of determination* (r^2) *calculated for linear regressions of the effect of time after a single injection of* [2-^{3}*H*]*glucose* v. *specific activity of plasma glucose in yearling rams given low-* (*LR*) *or high-roughage* (*HR*) *diets at each of two levels of intake*

(In each experiment, 150 μCi [2^3-H]glucose was injected intravenously and blood was taken every 20 min for 3 h after injection)

Sheep	Expt	LR–1 ×	LR–2 ×	HR–1 ×	HR–2 ×
R	1	0·971	0·994	0·993	0·990
	2	0·910	0·993	0·964	0·984
L	1	0·985	0·990	0·987	0·995
	2	0·984	0·958	0·992	0·962
J	1	0·956	0·981	0·983	0·991
	2	0·992	0·998	0·991	—
G	1	0·946	—	0·995	0·997
	2	0·996	—	0·976	0·987
C	1	0·995	0·987	0·996	0·973
	2	0·997	0·993	—	0·996
M	1	0·993	—	0·998	0·994
	2	0·981	—	0·994	0·992
S	1	0·989	0·987	0·987	0·981
	2	0·976	0·955	0·995	0·983
D	1	0·996	0·982	0·989	0·962
	2	0·991	0·995	0·985	0·977

1 ×, fed at level equivalent to maintenance requirement (taken as 568 kJ (140 kcal) digestible energy (DE)/kg body-weight$^{0·75}$ (National Academy of Sciences/National Research Council, 1968)); 2 ×, fed at level equivalent to twice maintenance requirement (DE basis).

Table 3. *Actual and estimated energy digestibility ratios and intakes of digestible energy* (DE) *of low-* (*LR*) *and high-roughage* (*HR*) *diets given at each of two levels of intake to yearling rams*

	Energy digestibility		DE intake (percentage of maintenance requirement†)	
Dietary treatment	Estimated	Actual	Estimated	Actual
LR–1 ×	0·816	0·782	100	95·9
LR–2 ×	0·816	0·718	200	183·0
HR–1 ×	0·556	0·600	100	107·8
HR–2 ×	0·556	0·644	200	201·2‡

1 ×, fed at a level equivalent to the maintenance requirement (DE basis); 2 ×, fed at a level equivalent to twice the maintenance requirement (DE basis).

† Maintenance requirement taken as 586 kJ (140 kcal) DE/kg body-weight$^{0·75}$ (National Academy of Sciences/National Research Council, 1968).

‡ This value partially reflects food refusal equivalent to 7·4 % of the estimated DE intake above maintenance.

Plasma glucose concentration

At both levels of feeding, plasma glucose concentration was increased ($P < 0·05$) by the LR compared to the HR diet (Table 4). A main effect interaction ($P < 0·05$) was attributed to the response to diet being greater at the higher rather than lower level of food intake. Coefficients of variation for plasma glucose values determined

Table 4. *Effects of low- (LR) and high-roughage (HR) diets given at each of two levels of intake to yearling rams on plasma concentration, pool size, space, half-life and entry rate of glucose*

(Mean values and standard deviations. In each experiment, 150 μCi [2-^{3}H]glucose was given by a single injection intravenously and nine blood samples were taken within 180 min of injection to determine the specific radioactivity of plasma glucose. Values for concentration of glucose only, include six other values for blood taken before and after eating)

Dietary treatment	No. of experiments	Plasma glucose concentration (mmol/l)		Body pool size of glucose (mg/kg body-wt)		Body glucose space (% body-wt)		Half-life of glucose (min)		Glucose entry rate (mg/kg body-wt$^{0.75}$ per min)	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
LR–1 ×	16	3·40	0·34	118·8	21·8	19·0	2·2	40·4	9·7	4·91	0·92
LR–2 ×	12	4·27	0·57	151·8	12·6	19·8	2·1	34·8	2·4	7·66	0·67
HR–1 ×	15	2·86	0·15	97·8	23·5	19·0	2·1	44·2	4·5	3·87	0·91
HR–2 ×	15	3·07	0·19	107·6	25·0	19·5	2·9	38·3	3·4	4·92	1·16
Statistical significance											
Diet		*		*		NS		*		*	
Intake level		*		*		NS		*		*	
Diet and intake level interaction		*		NS		NS		NS		*	

1 ×, fed at a level equivalent to the maintenance requirement (taken as 568 kJ (140 kcal) digestible energy (DE)/kg body-weight$^{0.75}$ (National Academy of Sciences/National Research Council, 1968)); 2 ×, fed at a level equivalent to twice the maintenance requirement (DE basis).

NS, not significant.

* $P < 0.05$.

during 3 h after a single injection of [2-^{3}H]glucose ranged from 3·8 to 20·5 % (mean 9·2) for different experiments. Significant increases ($P < 0·05$) in plasma glucose concentration occurred with all dietary treatments 3 h after the injection of [2-^{3}H]-glucose into the sheep.

Pool sizes

Greater values ($P < 0·05$) were obtained from feeding the LR compared to the HR diet (Table 4). Interaction between diet and level of intake was not significant. Increasing intake of these diets raised ($P < 0·05$) the pool size.

Glucose space

Glucose space was not significantly affected by either diet or the level of dietary intake.

Half-life of glucose

There were no significant interactions between diets and intake levels on the half-life of glucose (Table 4). Half-life was decreased ($P < 0·05$) from 41·2 min to 37·9 min by feeding the LR compared to HR diet and was also decreased ($P > 0·05$) by increasing intakes of the diets.

Glucose entry rates

The LR diet increased the glucose entry rates compared to the HR diet ($P < 0·05$) at both levels of food intake. At the feeding level of twice maintenance, the LR diet increased the entry rate by 56 % above the value obtained for the HR diet whereas the corresponding increase at the maintenance feeding level was only 27 %. This caused a significant ($P < 0·05$) interaction between the main effects for this measurement.

DISCUSSION

Judson & Leng (1972) evaluated the technique of a single injection of [2-^{3}H]glucose to measure glucose entry rate in sheep. A linear decline in log SR of plasma glucose *v.* time after injection was demonstrated and attributed to the absence of recycling of labelled glucose into the unlabelled glucose pool. On this basis, Judson & Leng (1972) proposed the technique for estimation of total glucose entry rate. In the present studies, results obtained for the estimation of total entry rate were also used to estimate other measures of glucose metabolism. Sheep were given their daily ration in two equal meals, which was different from the hourly feeding technique used by Judson & Leng (1972). Since the feeding of two daily meals only, as opposed to hourly feeding, could cause the rate of glucose entry to fluctuate, preliminary experiments were conducted to evaluate the relationship between log SR of plasma glucose and time after a single injection of [2-^{3}H]glucose into sheep given their diet in two daily meals. High r^2 values and low standard errors of the estimates determined for regressions describing this relationship suggest that glucose entry rates did not fluctuate. It is conceivable that an error caused by an accelerating rate of glucose entry could nullify an opposite error caused by recycling of the radioactivity. The absence of recycling of radioactivity from [2-^{3}H]glucose shown by Judson & Leng (1972) is

indicative that this situation would not have existed. It was unlikely that any of the treatments used in the main diet study caused the rate of glucose entry to fluctuate, because r^2 values were generally very close to 1·0 in all experiments and were not affected by treatment. For this reason, it is also unlikely that the increases found in plasma glucose concentrations greatly affected the measurements of glucose metabolism. Therefore, the estimates of glucose metabolism are meaningful representations of the period during which blood samples were collected to determine the SR of blood glucose. However, it cannot be assumed that the estimates apply to the entire day period.

The LR and HR diets were fed to sheep to provide equivalent estimated DE intakes. Since a higher intake of DE is correlated with a higher rate of entry (Lindsay, 1970; table 4), body pool size and plasma concentration of glucose as well as a lower half-life (Table 4), actual DE intakes of the diets were determined during the studies to verify estimates made initially. The actual intakes of DE from the LR diet were generally slightly less than those from the HR diet. Substitution of roughage by concentrate raised the observed plasma concentration, pool size and entry rate of glucose, and depressed the half-life. If the actual DE intakes of the diets studied had been exactly equivalent, the substitution of roughage by concentrate might have caused slightly greater differences than those observed in the measurements of glucose metabolism that were affected.

In a study on glucose metabolism in sheep, substitution of lucerne chaff by cracked maize did not increase the glucose entry rate although the plasma glucose concentration was increased slightly (Judson *et al.* 1968). In a different study, bruised barley, dried grass or hay were each fed as pellets to sheep (Ulyatt *et al.* 1970). The plasma concentration, body pool size and entry rate of glucose were not affected by diet in the latter study. It would be useful to examine why the results of the former studies might have differed from those of the present study. In contrast with the present study, [U-^{14}C]glucose was administered by continuous-infusion and primed-infusion techniques in the studies reported by Judson *et al.* (1968) and Ulyatt *et al.* (1970) respectively. It would be expected that [2-^{3}H]glucose would cause higher estimates of glucose entry rates compared to [U-^{14}C]glucose in ruminants, because contributions from recycled glucose carbon would be included in the former estimates but not in the latter (Judson & Leng, 1972). The general effects of substitution of roughage by concentrate in a ruminant's diet on the extent of recycling of glucose carbon are not presently known. Lactate and glycerol are primary contributors of recycled glucose carbon but have been found to contribute generally less than 30% to the glucose entry rate in fed ruminants (Lindsay, 1970). Therefore, recycling of glucose carbon could partially explain the different results obtained between the present study and the former studies. It is conceivable that different feeding techniques used were also responsible. Judson *et al.* (1968) gave the diets in twelve equal amounts from 07.00 to 18.00 hours and Ulyatt *et al.* (1970) used an automatic device to supply the diets continuously. These techniques would have minimized fluctuations in the rate of glucose entry over a 24 h period. As the present experiments were conducted within a 3 h period following one meal when the animals consumed half their daily ration,

it is conceivable that total entry of glucose in 24 h would not have been affected by diet. The feeding technique used presently simulates practical conditions. Animals offered substantially less food than their maximum voluntary food intake consume their rations quickly. Animals fed at intake levels approaching their maximum voluntary food intake (levels as high, or higher than, the high level used in the present experiment) will eat in a few quick meals if so trained (Leveille, 1970). Ruminants offered food continuously develop cyclical patterns of eating activity (Ray & Roubicek, 1971). Therefore, under practical conditions, it is probable that substitution of roughage with concentrate may increase the plasma concentration, pool size and entry rate of glucose and depress the half-life for short periods of time after eating, if not continuously.

There is evidence to support a conclusion that the proportion of concentrate and roughage in the diet might affect glucose metabolism in ruminants. Substitution of roughage with concentrate increased plasma glucose concentration in sheep (Trenkle, 1970) and dairy cows (Jorgenson, Schultz & Barr, 1965; Storry & Rook, 1966). Greater rates of glucose entry could probably be reflected by increased clearances of glucose loads injected intravenously. Substitution of roughage with concentrate in the diet of lambs has produced this response (Hale & King, 1958; Reid, 1958). Propionate is an important precursor of glucose in fed ruminants (Lindsay, 1970) and propionate infusions into the rumen increase plasma glucose concentration in these animals (Ash, Pennington & Reid, 1964). Substitution of roughage with concentrate in diets for ruminants increases propionate concentration in the rumen (Blaxter, 1967) and the production rate of the acid (Bauman *et al.* 1971). Increased production rates of propionate in the rumen may increase glucose entry rate, although only when the increase in production rate of propionate is relatively substantial (Judson & Leng, 1973*a*). In addition to the effect on rumen propionate production, substitution of roughage by concentrate in diets for ruminants may cause significant quantities of glucose to be absorbed direct from the small intestine (Armstrong & Beever, 1969; Sutton, 1971). The absorbed glucose would probably effect higher glucose entry rates since intravenous infusions of glucose consistently increased the irreversible loss of glucose in sheep (Judson & Leng, 1973*b*).

Glucogenic effects of concentrate feeding have been used to explain why increasing the proportion of concentrates in the diet can cause greater fat deposition in the body and depressed milk-fat production in cattle (Van Soest, 1963). Evidence that greater glucose availability may be an important mediating cause of greater fatness in beef cattle fed zero-roughage compared to high-roughage diets was recently obtained (Buchanan-Smith *et al.* 1973). Ballard, Hanson & Kronfeld (1969) provided evidence that glucose concentration is an important regulator of lipogenesis in ruminant adipose tissue in vitro. Experimental evidence that substitution of roughage with concentrates in a ruminant's diet may increase the glucose entry rate was lacking. The present study provides this evidence. For reasons discussed, it is obvious that this phenomenon depends on several circumstances concerning the diets and feeding technique used. Physical processing of concentrates affects the pattern of their digestion, particularly ruminal bypass of starch and absorption of glucose from the small

intestine (Armstrong & Beever, 1969; Sutton, 1971; Burt, 1973). It would be useful to know the importance of physical processing of foods on glucose metabolism in ruminants. Studies on the effects of continuous *v.* meal feeding and the significance of food intake level applied to different types of diets are also warranted.

The authors thank Miss Joanne Lansbargen and Mr Y. T. Yao for technical assistance, M. G. Freeman for advice on statistical analyses of the data and the Ontario Ministry of Agriculture and Food and the National Research Council of Canada (Grant A5934) for financial assistance.

REFERENCES

Armstrong, D. G. & Beever, D. E. (1969). *Proc. Nutr. Soc.* **28**, 121.
Ash, R. W., Pennington, R. J. & Reid, R. S. (1964). *Biochem. J.* **90**, 353.
Association of Official Analytical Chemists (1970). *Official Methods of Analysis* 11th ed. Washington, DC: Association of Official Analytical Chemists.
Ballard, F. J., Hanson, R. W. & Kronfeld, D. S. (1969). *Fedn Proc. Fedn Am. Socs exp. Biol.* **28**, 218.
Bauman, D. E., Davis, C. L. & Bucholtz, H. F. (1971). *J. Dairy Sci.* **54**, 1282.
Blaxter, K. L. (1967). *The Energy Metabolism of Ruminants* 2nd ed., p. 185. London: Hutchinson Scientific and Technical.
Buchanan-Smith, J. G., Horney, F. D., Usborne, W. R. & Burgess, T. D. (1973). *Can. J. Physiol. Pharmac.* **51**, 532.
Burt, A. W. A. (1973). *Proc. Nutr. Soc.* **32**, 31.
Ginochia, R. J. & Evans, J. W. (1973). *J. Anim. Sci.* **37**, 484.
Hale, W. H. & King, R. P. (1958). *Proc. Iowa Acad. Sci.* **65**, 224.
Jones, G. B. (1965). *Analyt. Biochem.* **12**, 249.
Jorgenson, N. A., Schultz, L. H. & Barr, G. R. (1965). *J. Dairy Sci.* **48**, 1031.
Judson, G. J., Anderson, E., Luick, J. R. & Leng, R. A. (1968). *Br. J. Nutr.* **22**, 69.
Judson, G. J. & Leng, R. A. (1972). *Aust. J. biol. Sci.* **25**, 1313.
Judson, G. J. & Leng, R. A. (1973*a*). *Br. J. Nutr.* **29**, 175.
Judson, G. J. & Leng, R. A. (1973*b*). *Br. J. Nutr.* **29**, 159.
Leveille, G. A. (1970). *Fedn Proc. Fedn Am. Socs exp. Biol.* **29**, 1294.
Lindsay, D. B. (1970). In *Physiology of Digestion and Metabolism in the Ruminant* p. 438 [A. T. Phillipson, editor]. Newcastle upon Tyne: Oriel Press.
National Academy of Sciences/National Research Council (1968). *Nutrient Requirements of Domestic Animals* No. 5, *Nutrient Requirements of Sheep* 4th ed. Washington, DC: National Academy of Sciences.
Raabo, E. & Terkildsen, T. C. (1960). *Scand. J. clin. Lab. Invest.* **12**, 402.
Ray, D. E. & Roubicek, C. B. (1971). *J. Anim. Sci.* **33**, 72.
Reid, R. L. (1958). *Aust. J. agric. Res.* **9**, 788.
Searle, S. R. (1971). *Linear Models.* New York: John Wiley & Sons.
Storry, J. E. & Rook, J. A. F. (1966). *Br. J. Nutr.* **20**, 217.
Sutton, J. D. (1971). *Proc. Nutr. Soc.* **30**, 243.
Trenkle, A. (1970). *J. Nutr.* **100**, 1323.
Ulyatt, M. J., Whitelaw, F. G. & Watson, F. G. (1970). *J. agric. Sci., Camb.* **75**, 565.
Van Soest, P. J. (1963). *J. Dairy Sci.* **46**, 204.

Printed in Great Britain