Effect of fat supplementation on voluntary food intake and rumen metabolism in sheep

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1. In an experiment in which a high-fat supplement was given in the dry form to lambs offered dried grass ad lib., both the voluntary intake and digestibility of the dried grass were reduced. When the high-fat supplement was given in a liquid suspension so that the rumen was by-passed, the voluntary intake and digestibility of the dried grass were not significantly altered.

2. The effect of injecting an emulsion of tallow into the rumen of sheep on rumen metabolism was studied in another experiment. Increasing the fat supplementation lowered the rate of digestion of both dried grass and cotton thread, lowered markedly the concentration of rumen ammonia, and raised the proportion of propionic acid in the rumen.

Feeds with a high lipid content for ruminants are of interest for several reasons. Firstly, their high-energy density makes them an attractive supplement. Secondly, they afford a means of producing animal products containing fat with a composition which coincides with current consumer preferences, hence recent interest in increasing the polyunsaturated fatty acids in milk fat (Storry, Brumby, Hall & Johnson, 1974).

On the other hand, lipids have been reported to inhibit some rumen microbes, in particular the cellulolytic bacteria, thus producing a low acetate fermentation (Henderson, 1973). Therefore an increase in the proportion of propionic acid in the rumen fluid has been noted when ruminant diets were supplemented with fat (Shaw & Ensor, 1959). Also the digestibility of cellulose and protein has been reduced (Brooks, Garner, Gehrke, Muhrer & Pfander, 1954), and the rate of voluntary food intake depressed (Bull, 1971).

The development of a method whereby the rumen could be by-passed in the functioning ruminant (Ørskov & Benzie, 1969) led us to examine the voluntary intake and digestibility of dried grass when it was supplemented with fat entering or by-passing the rumen. On the basis of the results obtained, a second experiment was carried out to test the effect of fat supplementation on rumen metabolism. A short account of the first experiment has been published (Bailey, 1972; Bailey & Ørskov, 1974).

MATERIALS AND METHODS

Experiment 1

Animals. Two entire male and three female Suffolk × (Finnish Landrace × Dorset Horn) lambs were used. They were about 8 weeks of age and weighed on average

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16 kg live weight at the start of the experiment. They had been weaned from their dams at 2–3 d of age and given milk from a bottle fitted with a teat and allowed to consume dried grass \textit{ad lib.}

\textit{Design and treatment}. At the start of the experiment the lambs were allocated to five treatments according to a latin-square design. The lambs were fed on dried grass \textit{ad lib.} and the treatments consisted of no supplement, or either 7 or 14 \% of estimated voluntary intake given as a high-fat supplement in the dry form or in a liquid suspension. Each period lasted 18 d, during the last 8 d of which the faeces were collected. The faeces were analysed for acid detergent fibre (ADF) by the method of Van Soest (1963), ash by ashing to constant weight at 550° and fat by the chloroform–methanol method of Atkinson, Fowler, Garton & Lough, (1972).

\textit{Composition of diets}. The dried grass, which was chopped into approximately 2.5 cm lengths, contained 28 g nitrogen using the method described by Davidson, Mathieson & Boyne (1970) and 290 gADF/kg DM. The high-fat supplement contained 660 g beef tallow, 320 g spray dried skimmed milk and 20 g lecithin.

\textit{Management}. The lambs were kept in metabolism cages. Dried grass was offered twice daily in quantities allowing a daily amount of uneaten food of about 200 g. The high fat supplement was given three times daily at 08.00, 13.00 and 17.00 hours, in equal amounts. When it was given in the dry form it was offered in a small trough separately from the dried grass. In the liquid form it was suspended in approximately 250 ml of water and fed from a bottle. With both dry and liquid feeding the supplements were consumed readily within a few minutes.

\textit{Experiment 2}

\textit{Animals}. Four castrated Finnish Landrace $\times$ Dorset Horn sheep were fitted with large rumen cannulae (3 cm diameter). They weighed about 50 kg live weight and were about 1 year of age.

\textit{Diets}. The sheep were given 800 g/d (736 g DM) of dried grass in two equal feeds at 08.00 and 17.00 hours. The DM of the dried grass contained per kg, 25 g N, 48 g lipids, 277 g ADF and 205 g of cellulose (Updegraff, 1969).

\textit{Design and treatments}. The four treatments consisted of four different amounts of tallow injected into the rumen, and were given according to a latin-square design to the sheep, each for periods of 8 d. Prior to the experiment it was shown that the effect of injecting the fat on the modification of rumen metabolism was established very quickly; for instance, it was shown that the difference in digestion of dried grass incubated in the rumen of sheep receiving no supplement and those receiving the highest level of tallow supplementation was 190 g/kg after 1 week, while after 4 weeks it was 230 g/kg. The tallow was suspended in water with glycerol monostearate (9:1, v/v) to give a fat concentration of 300 g/l. It was injected into the rumen via the cannulae in two equal quantities immediately after giving the dried grass. The quantities injected were 0, 40, 80 or 120 g/d of fat. On the last day of each treatment period four Dacron bags (10 $\times$ 17 cm) (see Mehrez & Œrskov, 1976), were incubated in the rumen with 5 g of dried grass which was prepared by shattering it through a laboratory hammer mill.
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Table 1. Expt 1. The effect of supplementing lambs with low and high levels of a high-fat supplement in dry or liquid form on the daily voluntary intake and fibre digestibility of dried grass

(Each value is the mean of five observations)

<table>
<thead>
<tr>
<th>Amount and form of supplement</th>
<th>Intake of dry matter from grass (g/kg body-weight)</th>
<th>Consumption of dry matter from supplement (g/kg body-weight)</th>
<th>Intake of digestible energy (MJ/kg body-weight)</th>
<th>Digestibility of ADF (g/kg)</th>
<th>Digestibility of supplementary fat (g/kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>55.1</td>
<td>0</td>
<td>0.68</td>
<td>725</td>
<td>884</td>
</tr>
<tr>
<td>Low Dry</td>
<td>48.8</td>
<td>3.9</td>
<td>0.68</td>
<td>686</td>
<td>882</td>
</tr>
<tr>
<td>High Dry</td>
<td>45.1</td>
<td>6.9</td>
<td>0.72</td>
<td>675</td>
<td>828</td>
</tr>
<tr>
<td>Low Liquid</td>
<td>54.3</td>
<td>3.9</td>
<td>0.75</td>
<td>728</td>
<td>828</td>
</tr>
<tr>
<td>High Liquid</td>
<td>51.2</td>
<td>7.6</td>
<td>0.81</td>
<td>703</td>
<td>752</td>
</tr>
<tr>
<td>str of treatment differences</td>
<td>3.0</td>
<td>---</td>
<td>0.05</td>
<td>34</td>
<td>60</td>
</tr>
</tbody>
</table>

Calculated from increment in fat intake and increments in faecal excretion.

without a screen. The bags were suspended in the rumen by nylon strings, attached to the cap of the cannula, and were withdrawn after either 6, 12, 18 or 24 h of incubation.

The pH of the rumen liquor was determined at each sampling time. A composite sample, made from the rumen contents from the four sheep, was analysed for free fatty acids (FFA not including volatile fatty acids) by the method of Itaya & Ui (1965), for ammonia by a modification of the method of Whitehead, Cooke & Chapman (1967), and for volatile fatty acids by gas liquid chromatography (Whitelaw, Hylgaard-Jensen, Reid & Kay, 1970).

After withdrawal, the bags were rinsed in cold water until the rinse water was colourless. The bags with contents were subsequently dried for 48 h at 60° and the weight loss calculated. The contents of the bags were subsequently analysed for cellulose by the method of Updegraff (1969).

Separate Dacron bags were used to incubate dewaxed cotton threads in the rumen. The threads (total weight about 300 mg) were incubated in the rumen for 24 h and washed by the method of Halliwell (1957); the loss in weight was determined after drying to constant weight at 37°. The cotton (Egyptian Menoufi, J. and P. Coates, Paisley, Renfrewshire) had a stated cellulose content of over 98%, so the weight losses were taken to represent cellulose degradation.

RESULTS

Experiment 1

The results of Expt 1 are given in Table 1. When the high fat supplement was given in the dry form there was a significant linear decrease in intake of dried grass ($P < 0.01$) though the greatest reduction appeared after the first increment, while the small decline in intake with liquid feeding was not significant. The total intake of digestible energy increased with increasing fat supplementation when it was given in the liquid form ($P < 0.05$) but not when it was given in the dry form. Supplementation
Table 2. Effect on rate of digestion of dry matter from dried grass, cotton threads and cellulose of infusing increasing levels of tallow into the rumen of sheep receiving dried grass

(Each value is the mean of five observations)

<table>
<thead>
<tr>
<th>Amount of tallow supplementation (g/kg grass)</th>
<th>Percentage disappearance of dry matter after 6h</th>
<th>Percentage disappearance of dry matter after 12h</th>
<th>Percentage disappearance of dry matter after 18h</th>
<th>Percentage disappearance of dry matter after 24h</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>39.4</td>
<td>55.0</td>
<td>65.1</td>
<td>72.1</td>
</tr>
<tr>
<td>50</td>
<td>38.1</td>
<td>53.5</td>
<td>64.7</td>
<td>71.0</td>
</tr>
<tr>
<td>100</td>
<td>36.3</td>
<td>50.5</td>
<td>60.3</td>
<td>67.7</td>
</tr>
<tr>
<td>150</td>
<td>34.5</td>
<td>45.0</td>
<td>52.3</td>
<td>60.0</td>
</tr>
<tr>
<td>se of treatment differences</td>
<td>1.5</td>
<td>3.1</td>
<td>3.7</td>
<td>3.9</td>
</tr>
</tbody>
</table>

Table 3. Effect on rumen pH and concentration of ammonia and free fatty acids of infusing increasing amounts of tallow into the rumen of sheep receiving dried grass

(Each value is the mean of four observations)

<table>
<thead>
<tr>
<th>Amount of tallow supplementation (g/kg grass)</th>
<th>Rumen pH</th>
<th>NH₃ (mmol/l)</th>
<th>Free fatty acids (mmol/l)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>6.4</td>
<td>13.8</td>
<td>2.2</td>
</tr>
<tr>
<td>50</td>
<td>6.4</td>
<td>12.9</td>
<td>2.6</td>
</tr>
<tr>
<td>100</td>
<td>6.5</td>
<td>7.1</td>
<td>1.5</td>
</tr>
<tr>
<td>150</td>
<td>6.6</td>
<td>4.2</td>
<td>17.6</td>
</tr>
<tr>
<td>se of treatment differences</td>
<td>0.1</td>
<td>1.8</td>
<td>1.5</td>
</tr>
</tbody>
</table>

in the dry form decreased the digestibility of ADF more than when it was given in the liquid form though these differences were not significant. None of the differences in digestibility of the fat increment reached significance.

Experiment 2

The animals consumed their feeds regularly though occasionally some dried grass was left uneaten, particularly with the high amount of injected lipid.

The effect of the amount of injected fat on the weight loss from the Dacron bags after various incubation intervals and the weight loss of cellulose and cotton threads after 24 h of incubation in the rumen are given in Table 2. With each incubation interval there was a linear decrease ($P < 0.05$) in the weight loss of dried grass with increase in amount of tallow. Also the weight loss of cotton thread and cellulose decreased with increase in amount of tallow ($P < 0.001$).

The effects of injected tallow on the pH, the concentration of FFA and the ammonia concentration of the rumen liquor are given in Table 3. Rumen pH tended to increase with increase in amount of tallow; the differences approached significance ($P < 0.1$). The concentration of FFA in the rumen liquor increased linearly ($P < 0.001$) with amount of tallow and the NH₃ concentration decreased linearly with amount of
Table 4. Effect on volatile fatty acid (VFA) proportions (mmol/100 mmol) of infusing increasing amounts of tallow into the rumen of sheep receiving dried grass

(Each value is the mean of four observations)

<table>
<thead>
<tr>
<th>Amount of tallow supplementation (g/kg grass)</th>
<th>Acetic acid</th>
<th>Propionic acid</th>
<th>Isobutyric acid</th>
<th>Butyric acid</th>
<th>Isovaleric acid</th>
<th>Valeric acid</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>69.6</td>
<td>19.8</td>
<td>1.3</td>
<td>7.0</td>
<td>1.7</td>
<td>0.5</td>
</tr>
<tr>
<td>50</td>
<td>68.2</td>
<td>20.3</td>
<td>1.5</td>
<td>7.7</td>
<td>1.6</td>
<td>0.8</td>
</tr>
<tr>
<td>100</td>
<td>66.8</td>
<td>22.9</td>
<td>1.3</td>
<td>7.5</td>
<td>1.4</td>
<td>0.8</td>
</tr>
<tr>
<td>150</td>
<td>64.5</td>
<td>26.2</td>
<td>0.8</td>
<td>6.9</td>
<td>1.4</td>
<td>0.5</td>
</tr>
<tr>
<td>SE of treatment differences</td>
<td>1.6</td>
<td>1.3</td>
<td>0.3</td>
<td>0.8</td>
<td>0.6</td>
<td>0.1</td>
</tr>
</tbody>
</table>

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tallow \((P < 0.001)\). The effect on the molar proportion of VFA in the rumen are given in Table 4. There was a linear decrease in the proportion of acetic acid \((P < 0.05)\) and a linear increase in the proportion of propionic acid \((P < 0.01)\) with increasing fat supplementation.

**DISCUSSION**

**Effect of ruminal or postruminal fat supplementation**

The results of Expt 1 indicate that the problems associated with fat supplementation in ruminants are due to problems of rumen fermentation and not to a limited capacity for absorption by the host animal. When the liquid suspension was given so that the rumen was by-passed, there was no reduction in voluntary food intake and digestibility. On the other hand, where fat entered the rumen both intake and digestibility of dried grass fell. Bailey (1972) showed that lambs weighing about 20 kg were able to absorb about 100 g lipid daily from the small intestine.
Effect of fat supplementation on rumen metabolism

The effect observed in Expt 2 agrees fairly well with the trends reported in the literature, namely a reduction in cellulose digestibility and a small increase in the proportion of propionic acid. What is more important, however, is the reduction in rate of digestion which was observed with the dried grass, since this can have a profound effect on the retention time of food in the rumen and consequently on voluntary food intake.

The mechanism of the effect of fatty acids on rumen metabolism is not fully understood. Henderson (1973) showed that the growth of some strains of important rumen bacteria (Butyrivibrio, Ruminococcus and Methanobrevibacter) could be strongly inhibited by the presence of long-chain fatty acids. Adverse effects of fatty acids on rumen protozoa have also been noted (Czerkawski, 1973). It is of interest to note that in the present experiment there was a rapid fall in NH₃ concentration as the fat supplementation increased. The NH₃ concentration on the high-fat treatment was well below that found by Mehrez & Ørskov (1976) to give the maximum rate of digestion of barley, although it is not lower than earlier estimates (Mercer & Annison, 1976) reported to give maximum yield of microbial N.

The simultaneous reduction in NH₃ concentration with increasing concentration of FFA is illustrated in Fig. 1. This has interesting implications and raises the important question as to whether or not the over-all inhibition observed in the present study may be the result of the low rumen NH₃ concentration. If so, then it may be possible to limit the adverse effect of fatty acid supplementation by addition of a source of NH₃. This will be the subject of a further investigation.

While the composition of the FFA will no doubt affect the level at which inhibition occurs (see Henderson, 1973), an attempt was made to group the results of FFA concentration and rate of digestion. From the analysis of these limited data it would appear that if, with tallow supplementation, the FFA in the rumen liquor was in excess of about 5 mmol/l then a rapid fall in rate of digestion can be expected.

The authors wish to acknowledge the contribution by Miss P. C. Bailey in Expt 1. We are grateful to Mr I. McDonald for help with the statistical analysis of the results.

REFERENCES