# THE EFFECT OF FEEDING AND DUODENAL INFUSION OF OLEIC AND LINOLEIC ACIDS ON LIPID DIGESTION IN SHEEP

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# ABSTRACT

The present experiments were conducted to determine the ruminal and intestinal effects on crude fat when no supplemental fat was fed and when oleic and linoleic acids were fed and continuously infused into the duodenum of sheep. The effect of method of administration of the two fatty acids on the fatty acid composition of the jugular plasma was determined as well as the effect on the digestibility of ration components.

During the control period, when no supplemental fat was administered, considerable synthesis of fat occurred within the rumen which was assumed to result from microbial synthesis. Further, on the basis of fatty acid concentration of the fat entering the intestine, it appeared that the $C_{18}$ and $C_{16}$ acids were the main fatty acids synthesized. The addition of oleic or linoleic acids to the daily ration did not result in a corresponding increase in the crude fat which entered the duodenum. It is suggested that this was due to a decrease in the synthesis of crude fat when the two fatty acids were fed.

A significantly higher digestibility of crude fat occurred when oleic and linoleic acids were infused as compared to when the same acids were fed. From analysis of the crude fat entering the duodenum it was found that considerable

hydrogenation of the long chain unsaturated fatty acids occurred in the rumen when oleic and linoleic acids were mixed with the daily ration. It is suggested that such hydrogenation caused the lower digestibility of oleic and linoleic acids when these fatty acids were fed as compared to the infusion of the same acids.

In general, the feeding of oleic and linoleic acids depressed ration digestibility as compared to the infusion of the same acids into the duodenum or the control period.

It was found that the fatty acid composition of the jugular plasma reflected the fatty acid composition of the crude fat available for digestion in the intestine.

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# INTRODUCTION

The process of fat digestion in ruminants differs quite markedly from that which occurs in monogastric animals. This difference is due to the effect of the rumen microorganisms on the ingested fat, within the rumen. In monogastric animals, on the other hand, the ingested fat is subject to little change during the interval between ingestion and digestion in the small intestine.

Ingested fat in ruminants is subjected to considerable chemical changes involving hydrolysis and subsequent hydrogenation of unsaturated fatty acids. The free glycerol is metabolised to volatile fatty acids, in particular, propionic acid. Furthermore, there is synthesis of fat by the rumen microorganisms. As a result the fat entering the small intestine may bear relatively little resemblance to the ingested fat, either in quality or quantity. It may be a result of these changes that ruminants cannot tolerate high levels of dietary fat as well as monogastric animals.

Microbial attack on ingested food in ruminants provides a method whereby such animals can digest and utilize highly fibrous feeds. There is evidence which suggests that added dietary fat results in decreased ration digestibility, particularly when there is a high fibre intake.

The purpose of the present experiments was to determine the effect of the rumen on added dietary oleic and linoleic acid and to estimate the quantity and quality of the fat synthesized by the rumen microorganisms. Further, to determine the intestinal digestibility of individual long chain fatty acids when oleic and linoleic acids were fed and infused into the duodenum. Observations were also made on the effects of method of administration of the two fatty acids on the apparent digestibilities of ration components.

# LITERATURE REVIEW

## Effect of Fat Upon the Digestibility of Ration Components.

The ruminant animal depends to a great degree upon the microbiological degradation of ingested food, within the rumen, to meet its energy requirements. Since all food ingested enters this unique anatomical structure, it is most desirable to know what effect the added fat will have on the utilization of other ration components.

Brethour *et al.* (1958) reported a significant decrease in the dry matter and organic matter digestibilities when 15% animal fat was added to a cotton seed hull ration and fed to sheep. A significant drop in weight gains was also noted. Davison and Woods (1963) found a significant decrease in dry matter and organic matter digestibility, but no effect upon protein digestibility, when 35 grams of corn oil was fed to sheep receiving 700 grams per day of a corn cob ration. In the same paper a decrease in organic matter and cellulose digestibility was noted when 5% corn oil was added to a basal alfalfa ration. The amount of protein absorbed was again unaffected. Esplin *et al.* (1963) added 4% tallow and 4% hydrolyzed vegetable and animal fat to a ration containing 30% alfalfa and 57% grain. No difference in ration digestibility was found between fats or between fat and no fat. It should be noted, however, that the ration in this case had a considerably lower fibre content than

the rations used by other workers. Erwin et al. (1963) reported no change in the digestibility of fibre and nitrogen when 60 grams of methyl myristate or 60 grams of safflower oil were injected into the duodenum or rumen of sheep receiving 800 grams per day of a high fibre ration. Differences were found in the dry matter digestibility but these were accounted for by the differences in fatty acid digestion.

The possibility exists that the method of administration of the fat has an effect on the subsequent digestibility of the ration components. To study this effect, Pfander and Verma (1957) fed a 90% cottonseed hull ration to sheep. The treatments consisted of a control period and either feeding corn oil mixed with the hulls or pouring the same quantity of oil into the rumen via a permanent cannula. The digestibility coefficients reported are as follows:

| | basal | corn oil fed | corn oil poured |
|---|---|---|---|
| organic matter | 50 | 35 | 50 |
| cellulose | 52 | 29 | 49 |
| nitrogen | 51 | 35 | 50 |

The decreased digestibility of the ration when supplemental fat was mixed with the ration appears to be dependent upon the level of fat which was fed. The higher the level of fat the more pronounced was the decrease in digestibility. The causative effect of the fat is still somewhat vague. It has been suggested that ration digestibility is decreased due to

the fat forming a film over the food particles thus rendering them less available to microbiological degradation. Ward et al. (1957) fed corn oil mixed with the concentrate portion of the ration, and fed the same quantity of oil mixed with the roughage portion of the ration. The latter method of feeding resulted in a greater decrease in fibre digestibility. Brooks et al. (1954) used a similar ration but heated the corn oil prior to pouring it over the roughage portion of the ration. The depression in fibre and nitrogen digestibility was greater than that recorded by Ward et al. (1957). The hypothesis put forward by Ward et al. (1957) is that heating the corn oil resulted in a greater dispersion of the oil in the feed causing a greater masking effect. However, Brethour, Sirny and Tillman (1958), found that when the corn oil was mixed with the concentrate portion and fed separately, as compared to mixing the corn oil with the roughage portion and fed separately, little change in fibre digestibility occurred.

There is a well established interrelationship between calcium and fat in ruminant nutrition. Brooks et al. (1954), using an artificial rumen innoculated with rumen microorganisms taken from sheep, found that the depression of ration digestibility following administration of corn oil could be partially ameliorated by the addition of alfalfa ash. Grainger et al. (1957) reported a depression in organic matter, cellulose, and protein digestibility in sheep fed a 5% and 6% level of corn

oil. When a trace mineral mix was given, equal to the amount present in the added alfalfa ash, a reversal in protein digestibility was noted, but organic matter and cellulose digestibility remained unaltered. In a subsequent trial the depressed digestibility of organic matter and cellulose, using a 5% corn oil ration, was alleviated by administering alfalfa ash and calcium, or calcium and phosphorus equal to the amount found in the alfalfa ash. Furthermore, the calcium and phosphorus did not increase the digestibility of the basal ration containing no fat. Davison and Woods (1963) reported that calcium chloride and calcium carbonate were equally effective in alleviating the depression in ration digestibility following addition of corn oil. Magnesium carbonate, on the other hand, was found to be ineffective. Hence it was concluded that the calcium ion alone was responsible for ameliorating the depressed ration digestibility.

White et al. (1958), suggested that the calcium fat interrelationship could be explained on the basis of calcium soap formation. Several research workers have reported a decrease in the calcium digestibility following administration of fat to ruminants (Grainger and Stroud (1959); Grainger et al. (1961); Tillman and Brethour (1958)). It was suggested by Camien and Dunn (1957), that fatty acids can act as antimetabolites to the rumen bacteria. Since neutral fats are hydrolysed within the rumen, to fatty acids and glycerol, (Garton

et al. (1958), Davison and Woods (1963) suggested that the calcium ions form insoluble soaps by combining with the fatty acids and thereby ameliorate the antimetabolite effect. Further, the calcium soaps formed are subsequently hydrolysed in the abomasum and arrive at the duodenum in the undissociated form. These same workers found no increase in the excretion of calcium following addition of the corn oil, but did report an increase in digestible energy when calcium was added to the ration containing corn oil. Furthermore, since magnesium did not produce the same effect as calcium in alleviating depressed ration digestibility, it was concluded that the calcium fat relationship was not simply due to the formation and excretion of soaps.

## The Effect of the Rumen Upon Ingested Fat

In monogastric animals the composition of the dietary fat can appreciably affect that of the depot fat. This, however, is not the case in ruminants. Generally speaking, fat deposition in ruminants is characterized by a high melting point and a high ratio of saturated to unsaturated fatty acids, regardless of the type of fat ingested. Garton (1960) demonstrated that the lipid fraction of forages ingested by ruminants contains high levels of unsaturated fatty acids.

| | Fatty Acid | Mixed Pasture Grasses % | Perinephric Fat |
|---|---|---|---|
| | | Garton (1960) | Hilditch & Pedelty (1941) |
| Saturated | C-12 | 2.9 | |
| | C-14 | 3.3 | 3 |
| | C-16 | 9.4 | 25 |
| | C-18 | 1.5 | 28 |
| | C-18 + | 0.7 | |
| Unsaturated | C-12:1 | 0.3 | |
| | C-14:1 | 0.4 | |
| | C-16:1 | 3.0 | 1 |
| | C-18:1:2:3 | 78.5 | 40 |

The fatty acids occur as esters of galactosyl glycerol and as triglycerides. Further, Garton (1960) reported that the concentrate portion of a ruminant ration has a high level of unsaturated fatty acids in the lipid fraction.

Hilditch and Pedelty (1941) determined the fatty acid composition of sheep perinephric fat. Comparison of the fatty acid composition of the depot fat with dietary fat indicates a considerable shift to saturated fatty acids. In particular, a large increase in palmitic (C-16) and stearic (C-18) acids. Hoflund *et al.* (1956) fed linseed oil to young dairy calves in which the rumen of each animal had not yet achieved an active state. The high levels of unsaturated fatty acids present in the linseed oil were reflected in the depot fat of the animals. Ogilvie and McClymont (1961) reported a large increase in linoleic and linolenic fatty acids of perinephric depot fat when linseed oil was infused into the duodenum of an ewe. It appears then, that the functioning rumen is associated with lack of effect of highly unsaturated dietary

fat on the level of unsaturated fatty acids found in depot fat.

Garton et al. (1961) demonstrated that triglycerides are hydrolysed by sheep rumen contents. Incubation of 1 gram of linseed oil with 100 mls of whole rumen contents resulted in 60-90% hydrolysis of the oil within 24 hours. Following the complete hydrolysis of linseed oil no glycerol could be detected in the rumen contents. Further, no glycerol was detectable after 24 hours when glycerol alone was incubated with the whole rumen contents. The disappearance of glycerol was so rapid that within 4 hours following administration less than 50% of the added glycerol could be detected. It was concluded by Garton that glycerol is largely metabolized within the rumen to propionic acid. During lipolysis no monoglycerides or diglycerides were detected and it was assumed that hydrolysis was complete. In this same paper, it was noted in preliminary experiments by Garton that galactolipids are also readily hydrolysed by rumen microorganisms. Dawson (1959) further reported that the rumen microorganisms are capable of hydrolysing phospholipids. Hence, fat which is ingested by ruminants is subjected to considerable hydrolysis before entering the small intestine where absorption of the long chain fatty acids occurs.

Reiser (1951) was among the first to publish data which indicated that the rumen microorganisms are capable of hydrogenating unsaturated fatty acids. Shorland et al. (1957) incubated oleic, linoleic and linolenic acids with rumen con-

tents of sheep and found that stearic acid as well as positional isomers of the unsaturated acids were formed. Using sheep with ligatures at the reticular-omasal junction, Wood et al. (1963) placed labelled linolenic-1-C-14 acid within the rumen. Tagged compounds of ten or more carbon atoms appeared in the jugular blood 4 hours after administration. However, 85-96% of the original test dose was recovered from the rumen, but, only 3-6% was as linolenic acid. Forty-five per cent of the test dose had been hydrogenated to saturated acids and 33-50% hydrogenated to oleic or elaidic acids. Garton et al. (1961) reported that glycerol esters of unsaturated fatty acids were hydrogenated, but the hydrogenation of the free fatty acids occurred more rapidly. Furthermore, the trienoic C-18 fatty acid was the most effectively hydrogenated. Wright (1960) further substantiates the rapid rate of hydrogenation of trienoic acids as compared to the dienoic and monoenoic acids.

It is generally assumed that the rumen bacteria play the predominant role in the hydrogenation of poly-unsaturated fatty acids. Wright (1960) demonstrated the ability of rumen bacteria to hydrogenate the unsaturated lipid components of chloroplasts by centrifuging rumen contents to remove the protozoa. Garton (1964) reported the hydrogenation of linoleic to stearic acid by mixed rumen bacteria. However, a strain of the organism Butyrivibrio fibrisolvens, was found to be capable of hydrogenating only one of the two double bonds present in

linoleic acid. It was concluded that two systems were required in the conversion of linoleic to stearic acid. One system to convert the dienoic acid to the monoenoic form, and a separate system to convert the monoenoic acid to the saturated form, namely stearic acid. In this same review, Garton reported that protozoa are also capable of hydrogenating poly unsaturated fatty acids. Hoflund et al. (1956) reported that rumen fungi are not an important factor in hydrogenation of the unsaturated fatty acids.

Ingested fat, following hydrolysis and hydrogenation within the rumen, then enters the small intestine where further hydrolysis and absorption occurs. It has been established by Garton (1964) and Wood et al. (1963) that little absorption of fatty acids, of ten or more carbon atoms, occurs within the rumen. Short chain, water soluble fatty acids, on the other hand, are readily absorbed through the rumen wall. Hence the longer chain fatty acids arrive at the small intestine in toto, but are in a more saturated form than when ingestion occurred. Some conversion of stearic acid to palmitic acid was reported by Garton et al. (1961), but such conversion did not represent significant proportions. There is little known concerning the digestion and absorption of lipids in the ruminant small intestine (Garton (1960)). However, it is generally assumed that the process is similar to that which occurs in monogastric animals.

Tove (1964) reports that, in ruminants, the long chain fatty acids enter the circulatory system via the thoracic duct as chylomicra. One-third of the chylomicra, mainly in triglyceride combination, are absorbed by the liver, one-third by the adipose tissue and one-third by the other tissues. In the liver the triglycerides are hydrolyzed by the parenchymal cells and the released fatty acids are re-esterified to glycerol, which arises from endogenous sources. Most of the triglycerides then re-enter the circulatory system as low density lipoproteins.

According to Deuel (1955) the excretion of lipids remains quite constant, under ordinary conditions, and is little influenced by the nature of the fat ingested by monogastric animals. Further, on a fat free ration the fecal fat content is little affected. Deuel (1955) suggests that the fecal fat in monogastric animals arises from dietary lipid residues, cellular debris, lipids secreted into the small intestine caudal to the fat absorptive areas, bile and lipids synthesized by the intestinal bacteria. Of these sources, lipid intestinal secretion and bacterial synthesis comprise the major proportion of the fecal fat. On a fat free diet approximately 40% of the fecal fat results from bacterial synthesis in the intestine. However, Deuel reports that the dietary fat residue of fecal fat can increase appreciably when fats of high melting points are fed.

Differences in the digestibility of fatty acids have been established. Carroll (1958) determined the digestibilities

of various fatty acids fed individually to the rats. The metabolic excretion of the fatty acids was determined in separate experiments by replacing the added fatty acids with glucose, thereby expressing the disappearance of a given fatty acid as a true digestibility coefficient.

| Fatty Acid | % Digestibility |
|---|---|
| Caprylic C-8 | 100 |
| Palmitic C-16 | 48 (45-53) |
| Stearic C-18 | 12 ( 0-22) |
| Oleic C-18:1 | 84 (82-87) |

It is evident that the long chain saturated fatty acids, especially stearic acid, are poorly digested in the rat. The long chain, unsaturated fatty acid, oleic, on the other hand, has a comparatively high digestibility coefficient. The possibility exists that a similar situation exists in ruminants.

Evidence has been published by Young and Garrett (1963) that the low digestibility of stearic and palmitic acids in chicks, can be increased by concomitantly feeding oleic and linoleic acid. Increasing the amount of oleic acid, in relation to palmitic acid, resulted in a linear increase in the absorption of the palmitic acid. The absorption of palmitic acid was 85-90% when the oleic to palmitic ratio was 1.34:1. There was little effect of linoleic acid on the absorption of palmitic acid which remained at about 20%, regardless of the level of

linoleic acid added. The absorption of palmitic and stearic acid was depressed when the two acids were fed together. Mixtures of stearic and palmitic acid required high levels of oleic acid to result in 50% absorption. But, when oleic and linoleic acids were fed with the mixture of palmitic and stearic acid, maximum absorption was obtained with lower levels of both the unsaturated fatty acids. It was concluded by Young and Garrett (1963) that oleic acid appears to play a direct role in facilitating the absorption of saturated fatty acids.

There is little known regarding intestinal digestion of individual fatty acids in ruminants, because of the lack of information on the quantities and types of fatty acids available for digestion. This is due to the still ill-defined effects which the rumen microorganisms exert upon the ingested fat and also because of lack of information on the fat which is synthesized within the rumen. The present experiments were designed to elucidate some of these general phenomena and, in particular, to determine digestibilities of individual long chain fatty acids in the intestine and the quantities and types of these same fatty acids synthesized in the rumen.

# EXPERIMENTAL

## Preliminary Experiment

Roberts and McKirdy (1964) reported a significantly lower crude fat digestibility for sunflower oil as compared to rapeseed oil when fed to beef cattle, this difference was attributed to a greater excretion of fecal soaps from sunflower oil over rapeseed oil. A preliminary experiment was conducted to determine whether this difference occurred when the two oils were duodenally infused into sheep.

The animals were placed in metabolism cages and adjusted to a brome-alfalfa hay ration for ten days, following which, four day total fecal collections were made for each animal. The animals were then allotted into two groups. Sunflower oil was infused into two of the animals and the other two animals received rapeseed oil throughout the experiment. The levels infused in three successive periods were; 22 grams, 39.60 grams, and 61.60 grams per day respectively. The animals were equilibrated to each infusion level for four days followed by four day total fecal collections. The fecal excretion of crude fat was determined as well as the fecal soap excretion.

The fatty acid composition of rapeseed oil, sunflower oil and the basal ration crude fat is shown in Table I.

TABLE I

% FATTY ACID COMPOSITION OF RAPESEED OIL, SUNFLOWER OIL AND BASAL RATION CRUDE FAT

| | $C_{14}$ | $C_{16}$ | $C_{18}$ | $C_{18:1}$ | $C_{18:2}$ | $C_{18:3}$ | $C_{20:1}$ | $C_{22:1}$ | x |
|---|---|---|---|---|---|---|---|---|---|
| Rapeseed Oil | - | 3.4 | 1.5 | 29.10 | 22.80 | 10.60 | 11.60 | 20.70 | 3.40 |
| Sunflower Oil | 0.28 | 12.09 | 6.83 | 21.91 | 58.89 | - | - | - | - |
| Brome-Alfalfa Hay | 1.85 | 25.40 | 2.12 | 9.79 | 20.37 | 32.28 | - | - | 8.20 |

## Experimental Animals

Four crossbred wethers with duodenal cannulae were used in the experiments. The animals weighed 43.1 Kgs, 43.1 Kgs, 61.3 Kgs, and 81.7 Kgs respectively. All animals had been surgically fitted with the cannulae at least four months prior to the initiation of the experiments. The duodenal cannulae were made of machined nylon and were placed 2-3 inches distal to the pylorus.

## Duodenal Infusion Technique

In ruminants, ingested dietary fat is likely to be intimately mixed with the digesta in the rumen. Flow of digesta from the rumen is more or less continuous throughout the day and night. Therefore, a continuous infusion technique was employed since this procedure would most closely approximate the normal passage of lipids from the stomach to the intestine.

The pumping assembly consisted of an electrically driven syringe pump. The 1/8 H.P. motor upon output was decreased by means of an Holroyd worm-gear reducer and a Zero Max variable speed reducer. Four, 50 cc, syringes were placed in the syringe pump cradle and connected with the duodenal cannulae by 1/16 inch ID tygon tubing.

## Sampling Procedure

Feces:

Feces were collected by means of a canvas feces bag

attached to a harness on each animal. The feces were removed each morning, weighed and stored in polyethylene bags at 45°F until the completion of the collection period. The total daily collections were then thoroughly mixed and samples taken for analysis.

Duodenal Contents:

Harris and Phillipson (1962) reported variation in both volume and composition of the flow of duodenal contents within and between days for sheep. Therefore, in order to obtain representative samples, 60 mls of duodenal contents were collected from each sheep, on each of six days during collection periods. On the first day the samples were collected at 7:00 a.m.; the second day at 10:00 a.m. and the third day at 3:00 p.m.; this cycle was repeated on the 4th-6th days. The samples were collected in 30 ml, plastic, screw cap bottles and stored under refrigeration.

Plasma:

Heparinized blood samples of 50 mls were taken from the jugular vein of each sheep on the 8th day of each collection period. The whole blood was centrifuged at 2000 rpm for 15 minutes following which the plasma layer was removed and stored under refrigeration.

## Analytical Methods

The dry matter content of feces and rations were determined by placing 200 gram samples in a forced air oven at

60°C for 48 hours. The samples were subsequently exposed to air for 36 hours, weighed and ground using a 1 mm mesh screen. The samples were stored in screw cap jars at room temperature until subjected to analysis.

Plasma and duodenal samples were dried by lyophilization. The samples were shell frozen in freeze drying bulbs by rotating in an alcohol-dry ice freezing mixture, then placed on the freeze dryer under a pressure of 50μ, or less. The duodenal samples were subsequently equilibrated in air for 36 hours.

Total nitrogen, ether extract, crude fibre and organic matter were determined according to the methods described by Association of Official Agricultural Chemists (1960).

In the preliminary experiment feed and feces samples were analysed for crude fat by the method of Bohman and Lesperance (1962). This consisted of soaking the sample, in a porous alundum thimble, in 0.5N HCl for 6 hours. The samples were then washed with distilled water and dried overnight in a vacuum oven at 60°C followed by ether extraction. Lipids in the form of soaps were calculated by difference between the crude fat and ether extract.

In the main experiment feed, feces and duodenal contents were subjected to acid hydrolysis subsequent to the usual ether extraction in a modification of the method of Bohman and Lesperance (1962). This technique gave direct determinations of the soaps and crude fat was the sum of ether extract plus soaps.

Plasma samples were analysed for ether extract only and constituted the only samples which were not subjected to duplicate analysis.

Free fatty acid content of the samples was determined by the method outlined by Peters and Van Slyke (1932). The method consisted of titrating the free fatty acids with standardized 0.1N sodium ethylate, using a 0.4% alcoholic solution of phenophthalein as the indicator. This analysis was conducted on one each of the duplicate ether extractions of feed, feces and duodenal contents. The remaining duplicate was dissolved in 5 ml of benzene and stored at 45°F in 30 ml air tight, screw cap vials. The lipids obtained from ether extraction of plasma and following acid hydrolysis of the various samples were stored in the same manner.

Methyl esters of fatty acids were prepared from the solutions of lipids in benzene according to the method of Feldman et al. (1962). The constituent fatty acids were determined by gas-liquid chromatography using a Burrell Kromo-Tog gas chromatograph. Helium was used as the carrier gas and diethyl succinyl propionate as the column packing. The constituent fatty acids were identified on the basis of retention times using animal tallow and mixtures of known fatty acids as reference standards. Duplicate analyses were conducted on the basal ration, the infused acids and on one sample each of plasma, duodenal and fecal ether extracts as well as duodenal and fecal soap.

The statistical methods used were the analysis of variance and Duncans Multiple Range Test as outlined in Steel and Torrie (1960).

Experimental Design of the Main Experiment

The basal ration was designed to contain a minimum of lipid and was based on dried, plain sugar beet pulp (Table II and III). The animals were fed a total of 800 gm a day in two equal portions given at 9:00 a.m. and 5:00 p.m. The level of feed intake was kept low due to the anorexic effect of the infused fat encountered in the preliminary experiment. The animals were adjusted to the basal ration for 20 days and then placed in the metabolism cages.

A control period was conducted followed by an infusion trial and a feeding trial. The animals were equilibrated for 4 days at the initiation of each infusion period and equilibrated for 10 days at the initiation of each feeding period. Following equilibration 8 day total fecal collections were made for each period. Duodenal samples were taken, as previously outlined, during the control period and the two periods of the feeding trial. Jugular blood samples were taken for each period on the 8th day of fecal collection.

In the first period of the infusion trial, two animals received 35 grams each of linoleic acid and two animals received 35 grams each of oleic acid per day. In the second period the

treatments were reversed and the animals which previously received linoleic acid, were infused with oleic acid.

In the feeding trial the same procedure was used with the exception that the two acids, oleic and linoleic, were administered in the ration. Thirty-five grams of each acid was mixed into the ration each day and half of the daily ration was given at 9:00 a.m. and the remainder at 5:00 p.m.

The fatty acid composition of the basal ration, oleic acid and linoleic acid is shown in Table IV. The fatty acids, oleic and linoleic, were of commercial origin and were not pure acids. As shown in Table IV oleic acid contained 72.84% as the $C_{18:1}$ acid and linoleic acid contained 65.02% as the $C_{18:2}$ acid.

TABLE II

BASAL RATION COMPOSITION %

| | |
|---|---|
| Plain Beet Pulp | 48 |
| Corn Starch | 16 |
| Molasses | 10 |
| Wheat Straw | 10 |
| Solka Floc | 10 |
| Soybean Protein | 3 |
| Dehydrated Alfalfa | 1 |
| Tricalcium Phosphate | 1 |
| Salt | 1 |
| | 100 |

TABLE III

BASAL RATION CHEMICAL ANALYSIS %

| | |
|---|---|
| Crude Protein | 9.63 |
| Crude Fibre | 25.04 |
| Ash | 6.35 |
| Crude Fat | 0.87 |

TABLE IV

FATTY ACID COMPOSITION OF BASAL RATION CRUDE FAT,

AND OLEIC AND LINOLEIC ACIDS %

| | $C_{14}$ | $C_{16}$ | $C_{16:1}$ | $C_{18}$ | $C_{18:1}$ | $C_{18:2}$ | $C_{18:3}$ | x* |
|---|---|---|---|---|---|---|---|---|
| Basal Ration | 1.41 | 28.77 | 1.52 | 8.48 | 16.12 | 33.65 | 7.41 | 2.64 |
| Oleic Acid | 3.09 | 3.73 | 13.51 | 0.19 | 72.84 | 2.00 | - | 4.64 |
| Linoleic Acid | 0.51 | 4.10 | 0.34 | 0.26 | 24.06 | 65.02 | 5.55 | 0.16 |

*Unidentified lipid components.

# RESULTS AND DISCUSSION

## Preliminary Experiment

The daily fecal excretion of ether extract, crude fat and soaps is shown in Table V.

The infusion of sunflower oil resulted in an increase in the fecal excretion of crude fat over that of rapeseed oil at equal levels of fat intake. Little difference was apparent in the fecal excretion of the ether fraction between the two oils when infused. The increased excretion of crude fat from sunflower oil infusion appears to result from the excretion of fecal soaps. Similar results were reported by Roberts and McKirdy (1964) when rapeseed oil and sunflower oil were fed to beef cattle.

The fatty acid composition of sunflower oil was quite different from that of rapeseed oil. In particular, rapeseed oil was characterized by nearly equal amounts of oleic, linoleic and erucic acids. Sunflower oil, on the other hand was composed primarily of linoleic acid; with an oleic acid content of approximately 20%. Roberts and McKirdy (1964) suggested that the linoleic acid in sunflower oil may be complexed within the rumen to form poorly digested salts. However, on the basis of the infusion experiment it appears that the rumen is not the deciding factor for the decreased crude fat digestibility of sunflower oil.

TABLE V

FECAL EXCRETION OF ETHER EXTRACT, CRUDE FAT AND SOAPS

(GRAMS/DAY)

| | Rapeseed Oil | | | Sunflower Oil | | |
|---|---|---|---|---|---|---|
| Treatment | Ether Extract | Crude Fat | Soap | Ether Extract | Crude Fat | Soap |
| Control | 12.92 | 15.56 | 2.64 | 13.37 | 17.16 | 3.79 |
| 22 gms/day Infused | 11.88 | 16.67 | 4.79 | 14.90 | 21.90 | 7.00 |
| 39.60 gs/day Infused | 12.97 | 19.43 | 6.46 | 15.11 | 27.64 | 12.53 |
| 61.60 gs/day Infused | 18.80 | 31.13 | 12.33 | 20.86 | 41.98 | 21.12 |

The possibility exists that the high level of linoleic acid introduced as sunflower oil resulted in a decreased fat absorption due to unfavorable fatty acid concentration. However, the possibility cannot be excluded that sunflower oil contains an unidentified factor which causes the decreased crude fat digestibility. On the basis of the preliminary experiment no conclusions can be made.

Main Experiment

When linoleic acid was infused it was found that the two smaller animals could not tolerate the infusion of this fatty acid as evidenced by the development of severe anorexia. As a result data were collected for the two larger animals only for the linoleic acid infusion treatment. When oleic and linoleic acids were fed one of the smaller animals completely refused both fatty acids when mixed with the basal ration. Due to the poor condition of this animal it was removed from the feeding experiment. As a result only three observations each were obtained for the feeding of oleic acid and the feeding of linoleic acid.

The reason for the adverse effect of linoleic acid on the smaller animals was not determined. A post-experimental trial was conducted with the two animals to determine if the lack of glycerol was the causative factor when linoleic acid was infused. Linoleic acid was concommittantly infused with glycerol in a ratio of 3:1, respectively. However, the anorexic

condition prevailed.

The main experiment illustrates an attempt to determine if two different fatty acids, oleic and linoleic, result in differences in crude fat excretion when infused or fed. The linoleic acid used in the main experiment was of commercial origin with a fatty acid composition similar to that of sunflower oil.

Digestibility of Proximate Constituents

The apparent digestibility coefficients for dry matter, crude fibre, nitrogen and organic matter are shown in Table VI.

The disappearance of dry matter from the digestive tract was significantly decreased ($P < 0.05$) when linoleic acid was fed as compared to the control period, the infusion of linoleic acid and the infusion of oleic acid. On the other hand, the feeding of oleic acid mixed with the ration did not significantly depress dry matter digestibility.

The independent feeding of oleic and linoleic acid significantly depressed ($P < 0.05$) crude fibre digestibility as compared to feeding no fatty acid or when the same two acids were independently infused. There was no significant difference in crude fibre digestibility between oleic and linoleic acid when the two acids were fed or when the two acids were infused into the duodenum.

The apparent digestibility of organic matter was significantly depressed ($P < 0.05$) when oleic and linoleic acids were independently fed as compared to the control period or when the same two acids were infused. Again no differences were found between acids when fed or between acids when infused in the organic matter digestibility.

The apparent digestibility of nitrogen was found to be significantly depressed ($P < 0.05$) when the acids, oleic and linoleic, were independently fed as compared to the control. No differences were found between acids when fed or between acids when infused.

In general, the two fatty acids, oleic and linoleic, appeared to exert their depressing influence upon ration digestibility when mixed with the ration and fed. The independent infusion of the same two acids appears to have had little effect upon the digestibility of ration components other than nitrogen. Other workers have reported a decreased ration digestibility following the addition of fat to the ration (Brethour et al., 1958, Davison and Woods 1963). Further, Camien and Dunn (1957) reported that fatty acids can act as antimetabolites and thereby depress the enzymatic breakdown of cellulose by the rumen microorganisms.

The apparent digestibility of crude fat was markedly affected by the route of administration of oleic and linoleic acids. A significantly higher ($P < 0.05$) digestibility of crude

fat was found when oleic and linoleic acids were infused as compared to when the same fatty acids were fed. Further, a highly significant increase ($P < 0.05$) in crude fat digestibility was found when the fatty acids were infused or fed as compared to the control period. No significant differences in crude fat digestibility were found between the two fatty acids when infused or when fed.

The possible factors which may have caused these differences in the crude fat digestibility will be discussed in later sections of the thesis.

TABLE VI

APPARENT DIGESTIBILITY OF RATION COMPONENTS %

| | Treatments | | | | |
|---|---|---|---|---|---|
| | | Infused | | Fed | |
| Component | Control | Oleic | Linoleic | Oleic | Linoleic |
| Dry Matter | 82.98[a] | 81.98[a] | 83.57[a] | 79.12[ab] | 75.79[b] |
| Crude Fibre | 74.14[a] | 73.65[a] | 79.25[a] | 52.45[b] | 50.71[b] |
| Organic Matter | 84.14[a] | 83.78[a] | 85.36[a] | 76.35[b] | 76.57[b] |
| Nitrogen | 75.88[a] | 68.82[c] | 72.64[ac] | 65.71[b] | 64.38[b] |
| Crude Fat | 14.61[c] | 79.75[a] | 82.44[a] | 75.22[b] | 76.11[b] |

Treatments with different subscripts indicate significance ($P < .05$).

## The Effect of the Rumen on Lipids

Qualitative analyses of duodenal contents can only partially indicate the effects of the rumen on ingested lipids. However, estimates of the actual amounts of lipids leaving the forestomach and then being made available for digestion in the small intestine require an assumption in respect to the amount of digesta passing into the duodenum. Therefore, an estimated duodenal dry matter flow of 20 grams per hour or 480 grams per day has been assumed in the present experiments. This value was used in conjunction with chemical analysis to calculate amounts of lipids entering the duodenum.

### Lipid Synthesis in the Rumen

In the control period the amount of lipid entering the duodenum was calculated to be 32.37 grams per day which is very considerably greater than the 6.37 grams being consumed in the ration. This indicates that there was a considerable synthesis of crude fat in the rumen, presumably by the rumen microorganisms. Dyck (1963) also found net synthesis of ether extract in the forestomach of sheep. The difference between the amounts entering and leaving the rumen could not be reasonably accounted for by assuming a lower duodenal dry matter flow.

Further analysis showed that 11.31% of the crude fat which entered the duodenum was present as soap and the balance in the form of ether extractable lipids. The free fatty acid

content of the crude fat entering the duodenum was 45.54%.

The fatty acid compositions of the crude fat and the soaps which entered the duodenum during the control period are shown in Table VII.

Stearic acid was the major fatty acid of the crude fat which entered the duodenum during the control period and constituted approximately 50% of the total duodenal crude fat. However, considerable amounts of $C_{16}$ and $C_{18:1}$ acids were also present. Erwin (1963) suggested that the rumen bacteria may synthesize linoleic acid since the high level of linoleic acid present in rumen bacterial fat could not be explained on the basis of linoleic acid intake. However, in the present experiment little linoleic acid was present in duodenal digesta and the principal lipid synthesis was of $C_{16}$ and $C_{18}$ acids.

The fatty acid composition of the soaps which entered the small intestine reveals that the $C_{16}$ acid accounts for approximately 45% of the total soaps. The $C_{18}$ acid constitutes approximately 20% and the $C_{18:1}$ acid approximately 12% of the total soaps entering the small intestine. This high proportion of $C_{16}$ acid in the soaps is surprising, since this acid comprised only about 23% of the acids in the crude fat entering the duodenum. The possibility exists that the soap of the $C_{16}$ acid is less readily hydrolyzed by the acid pH of the abomasum than soaps of the other fatty acids.

TABLE VII

FATTY ACID COMPOSITION OF CRUDE FAT AND SOAP ENTERING THE DUODENUM DURING THE CONTROL PERIOD

| | Gms/day | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Component | $C_{14}$ | $C_{16}$ | $C_{16:1}$ | $C_{18}$ | $C_{18:1}$ | $C_{18:2}$ | $C_{18:3}$ | x* | Total |
| Basal Ration | 0.09 | 1.83 | 0.10 | 0.54 | 1.03 | 2.14 | 0.47 | 0.17 | 6.37 |
| Crude Fat | 0.71 | 7.57 | 0.42 | 15.83 | 3.17 | 0.87 | - | 3.80 | 32.37 |
| Soap | 0.14 | 1.37 | 0.11 | 0.75 | 0.48 | 0.17 | - | 0.64 | 3.66 |

*Represents unidentified fatty acids.

Rumen Effect on Ingested Fatty Acids

The amounts of crude fat, ether extract, soaps and free fatty acids which entered the duodenum when oleic and linoleic were fed in the ration are shown in Table VIII.

Garton (1964) and Wood et al. (1963) established that there was little or no disappearance of dietary long chain fatty acids from the rumen. However, the addition of 35 grams of oleic acid or 35 grams of linoleic acid to the basal ration did not result in corresponding increases in the amount of crude fat entering the duodenum. It is possible that the dry matter flow in this treatment was greater than when there were no supplementary lipids in the ration. A larger dry matter flow would give a larger quantity of crude fat entering the duodenum than is shown in Table VIII. In support of this, reference is made to the previous ration digestibility data, where it was shown that the feeding of oleic and linoleic acid resulted in decreased fibre digestibility which would likely result in increased duodenal dry matter flow. However, Phillips and Roberts (unpublished) found a decrease in the rumen fermentation rate in the presence of added fat. This suggests a decrease in microbial activity which could result in a reduced amount of fat synthesis.

In spite of the limitation in the present experiment the amounts of crude fat entering the duodenum when oleic and linoleic acids were fed suggest that considerable microbial

TABLE VIII

THE AMOUNT OF CRUDE FAT, ETHER EXTRACT, SOAPS AND FFS's ENTERING THE DUODENUM DURING THE CONTROL PERIOD AND WHEN OLEIC AND LINOLEIC ACID WERE FED

| | Grams/Day | | | |
|---|---|---|---|---|
| | Crude Fat | Soaps | Ether Extract | Free Fatty Acids |
| Control | 32.37 | 3.66 | 28.71 | 14.74 |
| Oleic Acid Fed | 52.43 | 3.70 | 48.73 | 38.26 |
| Linoleic Acid Fed | 51.42 | 3.95 | 47.47 | 31.92 |

synthesis of fat occurs when fat is added to the ration. This may be the reason why ruminants, in general, cannot tolerate high fat rations. For, not only is there synthesis of lipid in the rumen but also, due to the digestion of other ration components, the quantity of dry matter leaving the rumen is reduced, thus resulting in a marked increase in the fat content of the digesta entering the duodenum. Thus in the present experiment when oleic and linoleic acid were fed the crude fat content of the ingested dry matter was 4.7%, but, the fat content of the dry matter entering the duodenum was 10-11%.

The addition of oleic or linoleic acid did not result in a significant increase in the amount of soaps entering the small intestine as compared to the control period. The amount of soaps which may have been formed within the rumen was not determined. However, if soap formation within the rumen was appreciable, as was suggested by Davison and Woods (1963), such complexes must have been hydrolysed by the acid in the abomasum.

The amount of free fatty acids which entered the duodenum when oleic and linoleic acid were fed was greater than that which occurred in the control period. However as in the case of crude fat the effect was not additive in that only 38.26 gms and 31.92 gms of free fatty acid entered the duodenum when 35 grams of oleic and linoleic acid were fed respectively. The discrepancy may be due to having assumed too low a dry

matter flow for this treatment as was discussed previously.

The fatty acid composition of the crude fat which entered the duodenum when oleic and linoleic acid were fed is shown in Table IX.

Comparison of the fatty acid composition of ingested fat with the fatty acid composition of the crude fat which subsequently entered the duodenum when oleic acid was fed indicates a considerable change in the fatty acids. The amount of the $C_{16}$ acid which entered the duodenum was 10.24 grams but only 3.14 grams were ingested. During the control period 7.57 grams of the $C_{16}$ acid entered the duodenum, however when oleic acid was fed a decrease in rumen synthesis may have occurred as explained above and this could decrease the amount of the $C_{16}$ acid synthesized. Hence the $C_{16}$ acid in the crude fat entering the duodenum when oleic acid was fed probably resulted from the hydrogenation of the 4.83 grams of the $C_{16:1}$ acid and from the 3.14 grams of the $C_{16}$ acid ingested with the balance being synthesized in the rumen. A considerable increase occurred in the $C_{18}$ acid content of the crude fat entering the duodenum when oleic acid was ingested. Shorland et al. (1957) reported the hydrogenation of oleic acid to stearic acid by sheep rumen contents. It is assumed that the rumen microorganisms hydrogenated part of the $C_{18:1}$ acid present in the ingested oleic acid to the $C_{18}$ acid. The greater amount of $C_{18:1}$ acid of the crude fat entering the duodenum

TABLE IX

FATTY ACID COMPOSITION OF CRUDE FAT INGESTED AND CRUDE FAT WHICH ENTERED THE DUODENUM WHEN OLEIC AND LINOLEIC ACIDS WERE FED AND DURING THE CONTROL PERIOD

| | | Grams/Day | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Item | | $C_{14}$ | $C_{16}$ | $C_{16:1}$ | $C_{18}$ | $C_{18:1}$ | $C_{18:2}$ | $C_{18:3}$ | x* | Total |
| Control | Ingested | 0.09 | 1.83 | 0.10 | 0.54 | 1.03 | 2.14 | 0.47 | 0.17 | 6.37 |
| | Duodenum | 0.71 | 7.57 | 0.42 | 15.83 | 3.17 | 0.87 | - | 3.80 | 32.37 |
| Oleic Fed | Ingested | 1.17 | 3.14 | 4.83 | 0.61 | 26.52 | 2.84 | 0.47 | 1.79 | 41.37 |
| | Duodenum | 0.91 | 10.24 | 0.19 | 25.11 | 12.34 | 0.26 | - | 3.38 | 52.43 |
| Linoleic Fed | Ingested | 0.27 | 3.27 | 0.22 | 0.63 | 9.45 | 24.90 | 2.41 | 0.22 | 41.37 |
| | Duodenum | 0.36 | 4.62 | 0.06 | 22.48 | 21.40 | 1.25 | - | 1.26 | 51.42 |

*Represents unidentified fatty acids.

as compared to the control, 12.34 vs 3.17 grams respectively, suggests that not all of the $C_{18:1}$ acid was hydrogenated to the saturated form. Wright (1960) reported that the hydrogenation of the monoenoic acid does not proceed as rapidly as the hydrogenation of the tri- and dienoic forms.

When linoleic acid was fed a considerable shift towards saturation of the 18-carbon fatty acids was again noted. There was 27.31 grams of di- and trienoic acid ingested but only 1.25 grams appeared in the duodenal digesta. The duodenal crude fat contained 21.40 grams of $C_{18:1}$ acid compared with 3.17 grams in the control period. The saturated $C_{18}$ acid increased from 15.83 grams in the control period to 22.48 grams in the linoleic acid fed treatment. This latter increase was smaller than was found when oleic acid was fed.

These data seem to support the contention of Garton (1964) that there are different rates of hydrogenation of di- and trienoic acids as compared with monoenoic 18-carbon fatty acids.

The quantity and composition of the soaps entering the duodenum were virtually identical in the oleic and linoleic feeding treatment and the control treatment (Table X). Thus the quantity of soap entering the duodenum does not appear to be dependent on the quantity of lipid entering the duodenum.

TABLE X

FATTY ACID COMPOSITION OF THE SOAPS ENTERING THE DUODENUM WHEN OLEIC AND LINOLEIC ACIDS WERE FED AND DURING THE CONTROL PERIOD

| | Grams/Day | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | $C_{14}$ | $C_{16}$ | $C_{16:1}$ | $C_{18}$ | $C_{18:1}$ | $C_{18:2}$ | $C_{18:3}$ | x* | Total |
| Control | 0.14 | 1.37 | 0.11 | 0.75 | 0.48 | 0.17 | - | 0.64 | 3.66 |
| Oleic Fed | 0.15 | 1.20 | 0.19 | 0.45 | 1.08 | 0.09 | - | 0.54 | 3.70 |
| Linoleic Fed | 0.17 | 1.25 | 0.06 | 0.50 | 1.15 | 0.19 | - | 0.63 | 3.95 |

*Represents unidentified fatty acids.

## The Intestinal Effect on Lipids

A significant increase in the disappearance of crude fat occurred in the intestine when oleic and linoleic acids were infused or fed (Table XI) compared with the control, but less crude fat was entering the intestines during the control period. The infusion of oleic and linoleic acid resulted in greater disappearance of crude fat compared with the feeding of the same two acids. Although, less crude fat was calculated to be entering the duodenum when the fatty acids were fed, there was also greater fecal excretion of crude fat in this treatment.

Estimated intestinal digestibility of crude fat was 87.49% and 88.91, respectively, when oleic and linoleic acids were infused, both of which were significantly higher than the 83.04% crude fat digestibility which occurred in the control period. Decreased intestinal digestibility of crude fat occurred ($P < .05$) when oleic and linoleic acids were fed as compared to the infusion of the same two fatty acids. This suggests that the effect of the rumen on the ingested fat resulted in decreased efficiency of absorption of fatty acids in the intestine.

Apparent digestibility of crude fat in the control period (Table VI), was 14.61%. But, calculated on the basis of the crude fat entering the duodenum the intestinal digestibility of crude fat was 83.04%. It thus appears that the fat

TABLE XI

THE AMOUNT OF CRUDE FAT ENTERING THE DUODENUM, EXCRETED IN THE FECES, DIFFERENCE AND PARTITIONED APPARENT DIGESTIBILITY COEFFICIENTS

| | Treatments | | | | |
|---|---|---|---|---|---|
| | | Infused | | Fed | |
| Item | Control | Oleic | Linoleic | Oleic | Linoleic |
| Grams Entering Duodenum Daily | 32.37 | 67.37 | 67.37 | 52.43 | 51.42 |
| Grams Daily Fecal Excretion | 5.44 | 8.38 | 7.26 | 10.25 | 9.88 |
| Grams Daily Disappearing | 26.93 | 58.99 | 58.05 | 42.18 | 41.54 |
| Partitioned Intestinal Digestibility Coeffs % | 83.04 | 87.49 | 88.91 | 79.62 | 80.67 |

which is synthesized by the rumen microorganisms is highly digestible.

The fatty acid composition of the crude fat which entered the duodenum and which was excreted during each treatment is shown in Table XII.

The lower apparent digestibilities of crude fat when oleic and linoleic acid were fed were associated with higher levels of more saturated acids present in the duodenal crude fat. Furthermore, the fecal crude fat contained greater amounts of $C_{18}$ fatty acid when oleic and linoleic were fed compared with duodenal infusion. On the basis of individual fatty acid digestibility the data suggest that the $C_{18}$ acid was slightly more digestible than the $C_{16}$ acid with digestibility coefficients of 83% and 78% respectively. The apparent digestibility coefficients found for the $C_{16}$ and $C_{18}$ fatty acids are considerably higher than the true coefficients reported for the same acids in rats, by Carroll (1958). However, this worker fed pure fatty acids individually thus precluding the possibility of associative effects of mixtures of fatty acids (Young and Garret 1963). The digestibility of the $C_{18:1}$ acid determined in the present experiment was 92% compared with 84% reported by Carroll (1958). It appears on the basis of the present results that ruminants are well able to digest long chain fatty acids in the intestine.

TABLE XII

FATTY ACIDS ENTERING THE INTESTINE AND FATTY ACIDS EXCRETED IN FECES (GRAMS/DAY)

| Treatment | | $C_{14}$ | $C_{16}$ | $C_{16:1}$ | $C_{18}$ | $C_{18:1}$ | $C_{18:2}$ | $C_{18:3}$ | x* | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| Control | Enter | 0.71 | 7.57 | 0.42 | 15.83 | 3.17 | 0.87 | - | 3.80 | 32.37 |
| | Excreted | 0.28 | 1.78 | 0.17 | 1.75 | 0.28 | 0.03 | - | 1.15 | 5.44 |
| Infused Oleic | Enter | 1.79 | 8.88 | 5.15 | 15.90 | 28.66 | 1.57 | - | 5.42 | 67.37 |
| | Excreted | 0.23 | 1.80 | 0.15 | 3.17 | 1.59 | 0.06 | - | 1.38 | 8.38 |
| Infused Linoleic | Enter | 0.89 | 9.01 | 0.54 | 15.92 | 11.59 | 23.63 | 1.94 | 3.85 | 67.37 |
| | Excreted | 0.20 | 1.45 | 0.09 | 2.67 | 1.39 | 0.15 | - | 1.39 | 7.26 |
| Fed Oleic | Enter | 0.91 | 10.23 | 0.19 | 25.11 | 12.34 | 0.26 | - | 3.38 | 52.43 |
| | Excreted | 0.35 | 2.33 | 0.28 | 4.38 | 1.27 | 0.03 | - | 1.61 | 10.25 |
| Fed Linoleic | Enter | 0.36 | 4.62 | 0.06 | 22.48 | 21.40 | 1.25 | - | 1.26 | 51.42 |
| | Excreted | 0.34 | 1.58 | 0.20 | 4.06 | 1.90 | 0.36 | - | 1.44 | 9.88 |
| Weighted Mean | Enter | 0.93 | 8.06 | 1.27 | 19.05 | 15.43 | 5.52 | 0.38 | 3.54 | 54.19 |
| | Excreted | 0.28 | 1.79 | 0.18 | 3.21 | 1.29 | 0.13 | - | 1.39 | 8.24 |
| Apparent Digestibility % | | 70.0 | 77.8 | 90.3 | 83.1 | 91.6 | 97.6 | 100.0 | - | - |

*Represents unidentified fatty acids.

## Nature of Fecal Lipids

The fecal crude fat has previously been discussed. The fecal excretion of soaps, ether extract and free fatty acids when oleic and linoleic acid were infused and fed, and during the control period is shown in Table XIII.

In general, an increase in fecal excretion of soaps and free fatty acid occurred when the fatty acids were administered either in the ration or in the duodenum. On the basis of this experiment it is not possible to determine whether the increased amounts of soap excreted represent unabsorbable lipid or lipid which escaped absorption and was complexed in the large intestine. Devel (1955) reported that fecal lipids can arise from intestinal secretion into the lower gut, from synthesis by microorganism within the large intestine, from undigested dietary lipid and from other endogenous sources. The free fatty acids excreted may have originated from any one of these sources as also may the fatty acids in the fecal soaps.

The fatty acid composition of the fecal soaps is shown in Table XIV.

A pattern very similar to that which occurred for the fecal crude fat excretion is evident in fatty acid composition of the fecal soaps. In particular the $C_{16}$ and $C_{18}$ fatty acids accounted for most of the fecal soaps excreted. Thus it appears that the fecal soap excretion represents a

TABLE XIII

FECAL EXCRETION OF SOAPS, ETHER EXTRACT AND FREE FATTY ACIDS - GMS/DAY

| | Treatments | | | | |
|---|---|---|---|---|---|
| | | Infused | | Fed | |
| Analysis | Control | Oleic | Linoleic | Oleic | Linoleic |
| Soaps | $1.09^{a}$ | $3.26^{ab}$ | $2.50^{b}$ | $3.75^{b}$ | $4.44^{b}$ |
| Ether Extract | 4.35 | 5.12 | 4.76 | 6.50 | 5.44 |
| Free Fatty Acids | 1.65 | 1.95 | 1.59 | 2.75 | 2.37 |

Treatments with different subscripts indicate significance ($P < .05$).

TABLE XIV

FATTY ACID COMPOSITION OF FECAL SOAPS

| | Grams/Day | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Treatment | $C_{14}$ | $C_{16}$ | $C_{16:1}$ | $C_{18}$ | $C_{18:1}$ | $C_{18:2}$ | $C_{18:3}$ | x* | Total |
| Control | 0.05 | 0.36 | 0.03 | 0.37 | 0.09 | 0.02 | - | 0.18 | 1.09 |
| Infused Oleic | 0.09 | 0.72 | 0.04 | 1.57 | 0.38 | 0.02 | - | 0.44 | 3.26 |
| Infused Linoleic | 0.05 | 0.49 | 0.01 | 1.30 | 0.27 | 0.04 | - | 0.34 | 2.50 |
| Fed Oleic | 0.07 | 0.81 | 0.03 | 2.41 | 0.21 | - | - | 0.22 | 3.75 |
| Fed Linoleic | 0.08 | 0.58 | 0.04 | 2.67 | 0.78 | - | - | 0.29 | 4.44 |

*Represents unidentified fatty acids.

binding of the fatty acids in the greatest concentration with a divalent cation. In general the amount of the $C_{18}$ acid excreted as soap constitutes only half or less of the total $C_{18}$ acid excreted as fecal crude fat. As a result few conclusions can be drawn concerning the origin of the fatty acids associated with fecal soaps.

## Nature of Jugular Plasma Lipids

The mean percentage fatty acid composition of jugular plasma is shown in Table XV.

There was a marked tendency for the jugular plasma ether extract to reflect the fatty acid content of the duodenal crude fat. When oleic acid was infused, an increase in the $C_{18:1}$ acid content of the jugular plasma was evident. When linoleic acid was infused an increase in the $C_{18:2}$ acid content of jugular plasma was evident. The feeding of oleic acid resulted in the plasma ether extract to reflect the high levels of the $C_{18}$ and $C_{18:1}$ acids present in the duodenal fat. Similarly, when linoleic acid was fed the plasma ether extract reflected the high content of the $C_{18}$ and $C_{18:1}$ acids present in the duodenal crude fat.

TABLE XV

MEAN % FATTY ACID COMPOSITION OF JUGULAR PLASMA ETHER EXTRACT

| Treatment | $C_{14}$ | $C_{16}$ | $C_{16:1}$ | $C_{18}$ | $C_{18:1}$ | $C_{18:2}$ | $C_{18:3}$ | x* |
|---|---|---|---|---|---|---|---|---|
| Control | 3.11 | 26.19 | 5.24 | 17.90 | 27.97 | 9.93 | - | 9.66 |
| Infused Oleic | 2.94 | 16.63 | 10.73 | 9.53 | 44.89 | 5.88 | - | 9.40 |
| Infused Linoleic | 1.68 | 18.99 | 1.88 | 12.83 | 16.48 | 44.38 | - | 3.76 |
| Fed Oleic | 3.02 | 22.74 | 4.29 | 26.15 | 28.24 | 4.94 | - | 10.62 |
| Fed Linoleic | 1.88 | 22.22 | 2.50 | 33.14 | 20.83 | 11.05 | - | 8.38 |

*Represents unidentified fatty acids.

# SUMMARY AND CONCLUSIONS

A preliminary experiment was conducted to determine the effect of duodenal infusion of rapeseed oil and sunflower oil, at three different levels, on the digestibility of crude fat in sheep.

The main experiment was conducted to determine the ruminal and intestinal effects on crude fat when no fat was added to the ration and when oleic and linoleic acids were fed and infused into the duodenum of sheep. Estimates were calculated for the digestibility of individual fatty acids. The effect of method of administration of the two fatty acids on the fatty acid composition of the jugular plasma was determined as well as the effect on the digestibility of ration components.

Under the conditions of these investigations the following observations were made.

1. The infusion of sunflower oil resulted in increased fecal excretion of crude fat compared with infusion of the same quantity of rapeseed oil. This difference was associated with a greater excretion of fecal soaps for sunflower oil infusion. Little difference was apparent in the fecal excretion of the ether extract fraction between the two oils when infused.

2. In general the feeding of oleic and linoleic acids depressed ration digestibility as compared to the infusion of the same acids into the duodenum or the control period.

3. The digestibility of crude fat was markedly affected by the route of administration of oleic and linoleic acids. A significantly higher digestibility of crude fat occurred when the two fatty acids were infused as compared to when they were fed. The digestibility of crude fat for the control period was significantly lower than when oleic and linoleic acids were infused or fed.

4. During the control period considerable synthesis of fat occurred within the rumen which was assumed to result from microbial synthesis. The crude fat calculated to be entering the rumen each day was 6.37 grams and the crude fat entering the duodenum each day was calculated to be 32.37 grams. The soap content of the crude fat entering the duodenum was calculated to be 11.31% and the free fatty acid content represented 45.54% of the crude fat.

5. The crude fat entering the duodenum during the control period was found to be composed of approximately 50% of the $C_{18}$ acid, approximately 23% of the $C_{16}$ acid and approximately 10% of the $C_{18:1}$ acid. Hence, the main fatty acids which appear to have been synthesized are the $C_{16}$ and $C_{18}$ acids. The addition of 35 grams of oleic acid and 35 grams of linoleic acid to the daily ration did not result in a corresponding increase in the crude fat which entered the duodenum. It is suggested that this was due to a decrease in the synthesis of crude fat when the two fatty acids were fed.

6. The fatty acid composition of the soaps which entered

the duqdenum during the control period were composed of approximately 45% as the $C_{16}$ acid, 20% as the $C_{18}$ acid and 12% as the $C_{18:1}$ acid. The high proportion of the $C_{16}$ acid present in the duodenum soap could not be accounted for on the basis of the proportion of the same acid present in the crude fat which entered the duodenum. The addition of oleic and linoleic acid to the basal ration did not result in an increase in the amount of soaps entering the small intestine as compared to the control period. If soap formation was significant within the rumen when the fatty acids were fed it was suggested that these were hydrolysed in the abomasum.

7. The amounts of free fatty acids which were present in the duodenal crude fat when oleic and linoleic acids were fed appeared to reflect the amount of oleic and linoleic acid which were mixed with the ingested feed.

8. The fatty acid composition of the crude fat which entered the duodenum when oleic acid was fed suggests that considerable hydrogenation of the unsaturated ingested fatty acids occurred. When oleic acid was fed an increase in the level of the $C_{16}$, $C_{18}$ and $C_{18:1}$ acids occurred in the crude fat of the duodenal contents as compared to the control. It is suggested that the increase in the $C_{16}$ acid resulted from the hydrogenation of the ingested $C_{16:1}$ acid augmented by the small proportion of the $C_{16}$ acid present in the ingested oleic acid. It is suggested that the greater amount of the $C_{18}$ acid in the duodenal crude fat resulted from the hydrogenation

of the ingested oleic acid. The greater proportion of the $C_{18:1}$ acid in the duodenal crude fat was accounted for by the high level of oleic acid ingested which escaped hydrogenation in the rumen.

9. The fatty acid composition of the crude fat which entered the duodenum when linoleic acid was fed suggested that considerable hydrogenation of this fatty acid had occurred within the rumen as well. A considerable increase was again noted in the $C_{18}$ acid content of the duodenal crude fat as compared to the control. The high level of the $C_{18:1}$ acid present in the duodenal crude fat is suggested to arise from incomplete hydrogenation of the ingested linoleic acid.

10. The calculated intestinal digestibility coefficients for the saturated $C_{16}$ and $C_{18}$ acids were higher than those reported for the same fatty acids in monogastric animals. The intestinal digestibility coefficients for unsaturated fatty acids were considerably higher than for the saturated acids, being 90.3, 91.6, 97.6 and 100.0% for $C_{16:1}$, $C_{18:1}$, $C_{18:2}$ and $C_{18:3}$ respectively.

11. An increase in the fecal excretion of soaps and free fatty acids occurred when oleic and linoleic acids were infused and when fed as compared to the control. The $C_{16}$ and $C_{18}$ acids accounted for most of the fecal soaps excreted.

12. There was a marked tendency for the fatty acid composition of the jugular plasma to reflect the fatty acid composition of the duodenal crude fat.

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# A P P E N D I X

TABLE I

PRELIMINARY EXPERIMENT - APPARENT DIGESTIBILITY COEFFICIENTS

| | Rapeseed Oil | | | Sunflower Oil | | |
|---|---|---|---|---|---|---|
| Treatment | % Dry Matter | % Ether Extract | % Crude Fat | % Dry Matter | % Ether Extract | % Crude Fat |
| Control | 61.19 | 41.36 | 34.89 | 60.48 | 40.44 | 31.01 |
| | 61.77 | 39.66 | 35.10 | 60.24 | 36.39 | 25.57 |
| Mean | 61.48 | 40.51 | 35.00 | 60.36 | 38.42 | 28.29 |
| Infused Oil @ | 63.24 | 72.48 | 63.70 | 56.08 | 66.55 | 52.56 |
| 22 gms/day | 61.09 | 73.19 | 63.70 | 58.15 | 65.27 | 52.08 |
| Mean | 62.17 | 72.84 | 63.70 | 57.12 | 65.91 | 52.32 |
| Infused Oil @ | 60.92 | 77.98 | 67.42 | 57.86 | 72.26 | 58.71 |
| 39.60 gms/day | 62.00 | 79.73 | 71.43 | 60.65 | 75.47 | 54.27 |
| Mean | 61.46 | 78.86 | 69.43 | 59.26 | 75.37 | 56.48 |
| Infused Oil @ | 62.48 | 82.44 | 77.06 | 46.96 | 67.25 | 35.19 |
| 61.60 gms/day | 52.71 | 72.44 | 50.16 | 70.42 | 82.67 | 66.65 |
| Mean | 57.60 | 77.44 | 63.61 | 58.69 | 74.96 | 50.92 |

TABLE II

PRELIMINARY EXPERIMENT - FECAL EXCRETION OF FATS - GMS/DAY

| | Rapeseed Oil | | | Sunflower Oil | | |
|---|---|---|---|---|---|---|
| Treatments | Ether Extract | Crude Fat | Soap | Ether Extract | Crude Fat | Soap |
| Control | 12.73 | 15.58 | 2.85 | 12.93 | 16.51 | 3.58 |
| | 13.10 | 15.53 | 2.43 | 13.81 | 17.81 | 4.00 |
| Mean | 12.92 | 15.56 | 2.64 | 13.37 | 17.16 | 3.79 |
| Infused Oil @ | 12.03 | 16.67 | 4.64 | 14.62 | 21.79 | 7.17 |
| 22 gms/day | 11.72 | 16.67 | 4.95 | 15.18 | 22.01 | 6.83 |
| Mean | 11.88 | 16.67 | 4.79 | 14.90 | 21.90 | 7.00 |
| Infused Oil @ | 13.50 | 20.70 | 7.20 | 15.17 | 26.23 | 11.06 |
| 39.60 gms/day | 12.43 | 18.15 | 5.72 | 15.04 | 29.05 | 14.01 |
| Mean | 12.97 | 19.43 | 6.46 | 15.11 | 27.64 | 12.53 |
| Infused Oil @ | 14.63 | 19.62 | 4.99 | 27.28 | 55.43 | 28.15 |
| 61.60 gms/day | 22.96 | 42.63 | 19.67 | 14.44 | 28.52 | 14.08 |
| Mean | 18.80 | 31.13 | 12.33 | 20.86 | 41.98 | 21.12 |

TABLE III

PRELIMINARY EXPERIMENT - DAILY DRY FECES PRODUCTION

| Rapeseed Oil | | | | Sunflower Oil | | | |
|---|---|---|---|---|---|---|---|
| Control | Infused 22 gms/day | Infused 39.60 gms/day | Infused 61.60 gms/day | Control | Infused 22 gms/day | Infused 39.60 gms/day | Infused 61.60 gms/day |
| 374.48 | 354.77 | 377.04 | 362.05 | 381.40 | 423.83 | 406.62 | 511.80 |
| 368.95 | 575.49 | 366.70 | 456.37 | 383.72 | 403.81 | 379.75 | 285.45 |

TABLE IVa

CHEMICAL ANALYSIS OF FECES - % OF DRY MATTER

| Treatment | Control | Infused Oleic Acid | Infused Linoleic Acid | Fed Oleic Acid | Fed Linoleic Acid |
|---|---|---|---|---|---|
| Crude Fat % | 4.22 | 5.04 | * | 4.55 | 4.91 |
| | 4.95 | 5.66 | * | * | * |
| | 4.13 | 6.22 | 6.03 | 6.22 | 5.73 |
| | 4.26 | 7.31 | 5.46 | 5.73 | 5.39 |
| Soap % | 0.78 | 1.89 | * | 1.20 | 2.04 |
| | 1.03 | 1.92 | * | * | * |
| | 0.91 | 2.10 | 2.43 | 2.44 | 2.61 |
| | 0.76 | 3.48 | 1.48 | 2.27 | 2.56 |
| Ether % | 3.44 | 3.15 | * | 3.35 | 2.87 |
| | 3.92 | 3.74 | * | * | * |
| | 3.22 | 4.12 | 3.60 | 3.78 | 3.12 |
| | 3.50 | 3.83 | 3.98 | 3.46 | 2.83 |
| Free Fatty Acids % | 1.37 | 1.14 | * | 1.32 | 1.24 |
| | 1.52 | 1.39 | * | * | * |
| | 1.24 | 1.65 | 1.28 | 1.65 | 1.41 |
| | 1.20 | 1.48 | 1.24 | 1.48 | 1.19 |

TABLE IVb

CHEMICAL ANALYSIS OF FECES - % OF DRY MATTER

| Treatment | Control | Infused Oleic Acid | Infused Linoleic Acid | Fed Oleic Acid | Fed Linoleic Acid |
|---|---|---|---|---|---|
| | 2.26 | 2.48 | * | 2.23 | 1.95 |
| Nitrogen % | 2.40 | 2.36 | * | * | * |
| | 2.03 | 2.65 | 2.40 | 2.12 | 2.24 |
| | 2.10 | 2.68 | 2.50 | 2.01 | 2.32 |
| | 32.37 | 30.78 | * | 37.82 | 41.49 |
| Fibre % | 28.39 | 31.02 | * | * | * |
| | 34.79 | 27.28 | 25.40 | 40.81 | 41.43 |
| | 32.07 | 29.39 | 25.81 | 41.77 | 40.90 |
| | 87.18 | 86.46 | * | 89.58 | 89.12 |
| Organic | 86.53 | 86.03 | * | * | * |
| Matter % | 88.29 | 82.30 | 84.25 | 92.41 | 91.98 |
| | 85.97 | 83.29 | 83.09 | 96.16 | 91.94 |

TABLE V

CHEMICAL ANALYSIS OF DUODENAL CONTENTS

| Treatment | Control | Fed Oleic Acid | Fed Linoleic Acid |
|---|---|---|---|
| Crude Fat % | 6.42 | 12.85 | 10.13 |
| | 7.92 | * | * |
| | 6.63 | 10.06 | 11.90 |
| | 6.00 | 9.86 | 10.11 |
| Soap % | 0.73 | 0.76 | 0.82 |
| | 0.94 | * | * |
| | 0.69 | 0.76 | 0.87 |
| | 0.69 | 0.79 | 0.78 |
| Ether Extract % | 5.69 | 12.09 | 9.31 |
| | 6.98 | * | * |
| | 5.94 | 9.30 | 11.03 |
| | 5.31 | 9.07 | 9.33 |
| Free Fatty Acids % | 3.29 | 11.45 | 9.31 |
| | 3.33 | * | * |
| | 2.91 | 8.47 | 11.27 |
| | 2.73 | 8.80 | 9.15 |
| Nitrogen % | 3.60 | 3.83 | 3.95 |
| | 3.65 | * | * |
| | 3.83 | 3.51 | 3.74 |
| | 3.76 | 3.60 | 3.99 |
| Fibre % | 20.79 | 18.63 | 22.59 |
| | 19.97 | * | * |
| | 19.96 | 26.04 | 22.61 |
| | 16.31 | 22.88 | 20.36 |
| Organic Matter % | 82.45 | 84.23 | 83.61 |
| | 81.79 | * | * |
| | 80.11 | 85.49 | 87.36 |
| | 75.61 | 80.18 | 81.21 |

TABLE VIa

TOTAL APPARENT DIGESTIBILITY COEFFICIENTS

| Treatment | Control | Infused Oleic Acid | Infused Linoleic Acid | Fed Oleic Acid | Fed Linoleic Acid |
|---|---|---|---|---|---|
| Dry Matter % | 84.54 | 81.64 | * | 80.73 | 73.99 |
| | 85.42 | 82.08 | * | * | * |
| | 78.58 | 82.76 | 82.56 | 73.35 | 77.50 |
| | 83.27 | 81.45 | 84.58 | 74.27 | 75.89 |
| Ether Extract % | 9.84 | 88.71 | * | 87.40 | 85.44 |
| | 3.16 | 86.93 | * | * | * |
| | -16.93 | 86.14 | 87.75 | 80.35 | 86.31 |
| | 0.75 | 86.14 | 88.02 | 82.63 | 86.69 |
| Crude Fat % | 25.01 | 82.84 | * | 83.74 | 76.32 |
| | 17.06 | 81.20 | * | * | * |
| | -1.71 | 80.12 | 80.50 | 69.26 | 76.10 |
| | 18.08 | 74.85 | 84.38 | 72.66 | 75.91 |

TABLE VIb

TOTAL APPARENT DIGESTIBILITY COEFFICIENTS

| Treatment | Control | Infused Oleic Acid | Infused Linoleic Acid | Fed Oleic Acid | Fed Linoleic Acid |
|---|---|---|---|---|---|
| Nitrogen % | 77.31 | 69.01 | * | 70.76 | 65.49 |
| | 77.28 | 71.22 | * | * | * |
| | 71.76 | 68.91 | 71.51 | 61.56 | 65.71 |
| | 77.18 | 66.17 | 73.76 | 64.80 | 61.95 |
| Fibre % | 76.44 | 72.11 | * | 64.04 | 46.76 |
| | 80.52 | 72.58 | * | * | * |
| | 64.91 | 76.79 | 78.14 | 46.34 | 54.02 |
| | 74.69 | 73.10 | 80.36 | 46,97 | 51.36 |
| Organic Matter % | 85.61 | 83.10 | * | 81.62 | 75.33 |
| | 86.53 | 83.59 | * | * | * |
| | 79.80 | 84.89 | 84.36 | 73.78 | 77.97 |
| | 84.64 | 83.55 | 86.36 | 73.66 | 76.41 |

TABLE VII

PARTITIONED INTESTINAL DIGESTIBILITY COEFFICIENTS

(BASED ON ESTIMATED DUODENAL DRY MATTER FLOW

OF 20 GMS PER HOUR)

| Component | Control | Infused Oleic Acid | Infused Linoleic Acid | Fed Oleic Acid | Fed Linoleic Acid |
|---|---|---|---|---|---|
| | 85.74 | 92.88 | * | 91.47 | 87.19 |
| Ether Extract % | 87.52 | 92.50 | * | * | * |
| | 82.29 | 91.42 | 92.42 | 82.70 | 89.83 |
| | 83.18 | 90.99 | 92.22 | 84.32 | 88.32 |
| | 84.50 | 89.21 | * | 89.10 | 79.86 |
| Crude Fat % | 86.11 | 89.35 | * | * | * |
| | 79.65 | 87.69 | 87.93 | 73.67 | 82.69 |
| | 81.88 | 83.70 | 89.88 | 76.10 | 79.46 |
| | 85.20 | 79.78 | * | 82.07 | 79.48 |
| Nitrogen % | 85.38 | 81.49 | * | * | * |
| | 82.68 | 80.93 | 82.53 | 74.28 | 78.47 |
| | 85.75 | 78.87 | 83.61 | 77.04 | 77.60 |
| | 63.29 | 56.55 | * | 37.48 | 23.67 |
| Fibre % | 68.40 | 55.53 | * | * | * |
| | 43.05 | 62.34 | 64.53 | 33.25 | 34.12 |
| | 49.83 | 46.57 | 61.00 | 24.93 | 22.62 |

TABLE VIII

PERCENT FATTY ACID COMPOSITION OF FECAL ETHER EXTRACT

| | | $C_{14}$ | $C_{16}$ | $C_{16:1}$ | $C_{18}$ | $C_{18:1}$ | $C_{18:2}$ | $C_{18:3}$ | x* |
|---|---|---|---|---|---|---|---|---|---|
| Feces Control | 1 | 7.23 | 36.15 | 23.61 | 22.89 | 8.43 | - | - | 21.69 |
| | 2 | 6.36 | 34.10 | 4.62 | 24.28 | 3.47 | - | - | 27.17 |
| | 3 | 3.12 | 22.60 | 2.60 | 53.51 | 3.64 | 0.78 | - | 13.77 |
| | 4 | 4.31 | 39.66 | 2.80 | 21.34 | 3.88 | 0.65 | - | 27.36 |
| Feces Oleic Infused | 1 | 3.32 | 22.75 | 1.19 | 31.04 | 13.63 | 1.07 | - | 27.02 |
| | 2 | 3.19 | 25.32 | 1.92 | 33.83 | 17.02 | - | - | 18.72 |
| | 3 | 2.11 | 15.85 | 2.47 | 31.69 | 33.80 | 1.06 | - | 13.02 |
| | 4 | 2.95 | 20.48 | 2.58 | 28.41 | 28.41 | 1.11 | - | 16.06 |
| Feces Linoleic Infused | 3 | 2.43 | 17.54 | 1.08 | 32.39 | 23.21 | 1.75 | - | 21.00 |
| | 4 | 3.69 | 22.03 | 2.01 | 24.87 | 20.35 | 2.51 | - | 24.54 |
| Feces Oleic Fed | 1 | 5.05 | 28.06 | 3.99 | 24.60 | 16.89 | 0.67 | - | 20.74 |
| | 3 | 4.12 | 21.40 | 4.39 | 27.57 | 15.64 | 0.82 | - | 26.06 |
| | 4 | 3.93 | 22.14 | 3.39 | 37.32 | 16.25 | - | - | 16.97 |
| Feces Linoleic Fed | 1 | 6.23 | 21.31 | 1.64 | 33.12 | 13.11 | - | - | 24.59 |
| | 3 | 3.63 | 17.06 | 3.63 | 15.01 | 25.91 | 18.48 | - | 16.28 |
| | 4 | 4.41 | 16.63 | 3.61 | 27.66 | 23.45 | 1.60 | - | 22.64 |

*Represents unidentified fatty acids.

TABLE IX

PERCENT FATTY ACID COMPOSITION OF FECAL SOAP

| | | $C_{14}$ | $C_{16}$ | $C_{16:1}$ | $C_{18}$ | $C_{18:1}$ | $C_{18:2}$ | $C_{18:3}$ | x* |
|---|---|---|---|---|---|---|---|---|---|
| Control | 1 | 6.57 | 33.87 | 2.39 | 24.50 | 10.96 | 0.80 | - | 20.92 |
| | 2 | 4.44 | 35.65 | 2.07 | 29.44 | 6.36 | 1.33 | - | 20.71 |
| | 3 | 3.54 | 28.30 | 2.89 | 46.62 | 6.11 | 1.29 | - | 11.25 |
| | 4 | 5.98 | 38.65 | 2.39 | 30.68 | 5.58 | 2.39 | - | 14.33 |
| Oleic Infused | 1 | 3.78 | 24.76 | 1.46 | 36.59 | 11.71 | 1.95 | - | 19.76 |
| | 2 | 2.73 | 24.53 | 0.47 | 37.66 | 14.53 | 1.09 | - | 18.99 |
| | 3 | 2.93 | 24.10 | 1.86 | 48.74 | 9.99 | - | - | 12.38 |
| | 4 | 1.84 | 18.59 | 1.01 | 59.63 | 10.72 | - | - | 8.21 |
| Linoleic Infused | 3 | 1.62 | 16.33 | 0.34 | 56.72 | 11.23 | 1.79 | - | 11.99 |
| | 4 | 3.19 | 26.12 | 0.96 | 43.63 | 9.55 | 1.59 | - | 14.97 |
| Oleic Fed | 2 | 3.14 | 31.77 | 0.78 | 51.37 | 3.14 | - | - | 9.80 |
| | 3 | 1.67 | 21.71 | 1.30 | 62.52 | 7.05 | - | - | 5.75 |
| | 4 | 1.31 | 17.23 | - | 71.54 | 5.22 | - | - | 4.70 |
| Linoleic Fed | 1 | 1.18 | 9.65 | 0.51 | 75.47 | 8.46 | - | - | 4.73 |
| | 3 | 2.71 | 18.41 | 1.81 | 45.31 | 22.02 | - | - | 9.74 |
| | 4 | 1.24 | 10.81 | 0.56 | 61.37 | 20.95 | - | - | 5.07 |

*Represents unidentified fatty acids.

TABLE X

PERCENT FATTY ACID COMPOSITION OF DUODENAL ETHER EXTRACT

| Treatments | | $C_{14}$ | $C_{16}$ | $C_{16:1}$ | $C_{18}$ | $C_{18:1}$ | $C_{18:2}$ | $C_{18:3}$ | x* |
|---|---|---|---|---|---|---|---|---|---|
| Control | 1 | 1.89 | 19.37 | 0.95 | 51.97 | 11.66 | 2.84 | - | 11.32 |
| | 2 | 2.28 | 22.05 | 1.28 | 49.79 | 9.96 | 1.85 | - | 12.80 |
| | 3 | 1.88 | 19.25 | 0.94 | 56.96 | 7.98 | 3.13 | - | 9.86 |
| | 4 | 1.80 | 26.03 | 1.16 | 51.81 | 7.73 | 1.93 | - | 9.54 |
| Oleic Fed | 1 | 1.60 | 19.04 | - | 46.25 | 25.05 | 0.85 | - | 7.21 |
| | 3 | 1.84 | 20.18 | - | 49.31 | 22.25 | - | - | 6.42 |
| | 4 | 1.23 | 16.22 | - | 57.70 | 21.36 | - | - | 3.49 |
| Linoleic Fed | 1 | 0.53 | 6.55 | - | 61.06 | 27.43 | 2.30 | - | 2.13 |
| | 3 | 0.33 | 8.14 | - | 33.55 | 55.38 | 1.63 | - | 0.97 |
| | 4 | 0.32 | 6.37 | - | 46.66 | 42.82 | 2.87 | - | 0.96 |

*Represents unidentified fatty acids.

TABLE XI

PERCENT FATTY ACID COMPOSITION OF DUODENAL SOAP

| Treatments | | $C_{14}$ | $C_{16}$ | $C_{16:1}$ | $C_{18}$ | $C_{18:1}$ | $C_{18:2}$ | $C_{18:3}$ | x* |
|---|---|---|---|---|---|---|---|---|---|
| Control | 1 | 3.28 | 32.79 | 2.66 | 20.49 | 14.96 | 5.53 | - | 20.29 |
| | 2 | 4.58 | 40.85 | 3.52 | 19.72 | 11.27 | 4.58 | - | 15.49 |
| | 3 | 3.23 | 36.07 | 3.48 | 21.39 | 13.93 | 3.73 | - | 18.16 |
| | 4 | 3.98 | 38.56 | 1.99 | 20.40 | 12.94 | 4.73 | - | 17.41 |
| Oleic Fed | 1 | 4.27 | 29.92 | 6.84 | 12.39 | 34.19 | 0.86 | - | 11.53 |
| | 3 | 4.12 | 33.95 | 4.12 | 10.29 | 27.57 | 3.29 | - | 16.65 |
| | 4 | 3.76 | 33.42 | 4.38 | 14.02 | 26.16 | 3.13 | - | 15.13 |
| Linoleic Fed | 1 | 3.38 | 33.46 | 1.13 | 21.05 | 23.31 | 4.51 | - | 13.16 |
| | 3 | 5.33 | 30.18 | 0.59 | 7.10 | 35.50 | 3.55 | - | 17.75 |
| | 4 | 4.08 | 31.65 | 2.95 | 9.85 | 28.13 | 6.47 | - | 16.87 |

*Represents unidentified fatty acids.

TABLE XII

PERCENT FATTY ACID COMPOSITION OF PLASMA ETHER EXTRACT

| Treatment | | $C_{14}$ | $C_{16}$ | $C_{16:1}$ | $C_{18}$ | $C_{18:1}$ | $C_{18:2}$ | $C_{18:3}$ | x* |
|---|---|---|---|---|---|---|---|---|---|
| Control | 1 | 3.70 | 24.08 | 6.48 | 13.89 | 30.56 | 11.11 | - | 10.19 |
| | 2 | 2.61 | 26.25 | 7.01 | 16.03 | 29.26 | 12.42 | - | 6.41 |
| | 3 | 2.76 | 27.41 | 3.68 | 24.81 | 20.83 | 5.67 | - | 14.86 |
| | 4 | 3.38 | 27.00 | 3.80 | 16.88 | 31.22 | 10.55 | - | 7.17 |
| Mean | | 3.11 | 26.19 | 5.24 | 17.90 | 27.97 | 9.93 | - | 9.66 |
| Oleic Infused | 1 | 2.12 | 16.72 | 18.76 | 9.30 | 44.37 | 4.16 | - | 4.57 |
| | 2 | 1.94 | 20.16 | 10.86 | 11.24 | 46.32 | 6.40 | - | 3.10 |
| | 3 | 2.53 | 15.19 | 5.06 | 11.39 | 45.57 | 8.86 | - | 11.40 |
| | 4 | 5.15 | 14.43 | 8.25 | 6.19 | 43.30 | 4.12 | - | 18.56 |
| Mean | | 2.94 | 16.63 | 10.73 | 9.53 | 44.89 | 5.88 | - | 9.40 |
| Linoleic | 3 | 1.60 | 17.27 | 1.99 | 13.75 | 18.11 | 43.24 | - | 4.05 |
| Infused | 4 | 1.76 | 20.70 | 1.76 | 11.91 | 14.84 | 45.51 | - | 3.52 |
| Mean | | 1.68 | 18.99 | 1.88 | 12.83 | 16.48 | 44.38 | - | 3.76 |
| Oleic Fed | 1 | 3.33 | 24.82 | 4.45 | 22.22 | 30.74 | 4.07 | - | 10.37 |
| | 3 | 2.96 | 20.92 | 3.57 | 33.88 | 25.61 | 4.18 | - | 8.88 |
| | 4 | 2.76 | 22.47 | 4.86 | 22.34 | 28.38 | 6.57 | - | 12.62 |
| Mean | | 3.02 | 22.74 | 4.29 | 26.15 | 28.24 | 4.94 | - | 10.62 |
| Linoleic Fed | 1 | 2.27 | 18.75 | 2.84 | 31.53 | 22.59 | 11.22 | - | 10.80 |
| | 3 | 2.38 | 20.78 | 2.38 | 25.76 | 24.89 | 16.23 | - | 7.58 |
| | 4 | 1.00 | 27.14 | 2.29 | 42.14 | 15.00 | 5.71 | - | 6.72 |
| Mean | | 1.88 | 22.22 | 2.50 | 33.14 | 20.83 | 11.05 | - | 8.38 |

*Represents unidentified fatty acids.

TABLE XIII

DUPLICATE ANALYSES OF % FATTY ACID COMPOSITION OF RANDOM SAMPLES

| Treatment | Duplicate | $C_{14}$ | $C_{16}$ | $C_{16:1}$ | $C_{18}$ | $C_{18:1}$ | $C_{18:2}$ | $C_{18:3}$ | x* |
|---|---|---|---|---|---|---|---|---|---|
| Oleic Acid | 1 | 3.09 | 3.73 | 13.51 | 0.19 | 72.84 | 2.00 | - | 4.64 |
| | 2 | 3.09 | 3.85 | 11.83 | 0.22 | 73.79 | 2.82 | - | 4.40 |
| Linoleic Acid | 1 | 0.51 | 4.10 | 0.34 | 0.26 | 24.06 | 65.02 | 5.55 | 0.16 |
| | 2 | 0.64 | 3.97 | 0.21 | 0.42 | 24.15 | 64.41 | 5.78 | 0.42 |
| Basal Ether Extract | 1 | 1.53 | 26.87 | 1.96 | 9.78 | 18.45 | 31.21 | 7.65 | 2.55 |
| | 2 | 1.42 | 26.42 | 1.18 | 8.73 | 17.69 | 34.91 | 7.60 | 2.05 |
| Plasma Ether Extract Linoleic-Infused | 1 | 1.00 | 27.14 | 2.29 | 42.14 | 15.00 | 5.71 | - | 6.72 |
| | 2 | 1.36 | 27.26 | 2.49 | 41.95 | 14.71 | 6.11 | - | 6.12 |
| Fecal Ether Extract Oleic-Fed | 1 | 3.93 | 22.14 | 3.39 | 37.32 | 16.25 | - | - | 16.97 |
| | 2 | 4.15 | 22.94 | 3.25 | 36.46 | 16.97 | - | - | 16.23 |
| Duodenal Ether Extract Linoleic Fed | 1 | 0.53 | 6.55 | - | 61.06 | 27.43 | 2.30 | - | 2.13 |
| | 2 | 0.41 | 6.68 | - | 60.73 | 27.53 | 3.04 | - | 1.61 |
| Duodenal Soap Oleic-Fed | 1 | 3.76 | 33.42 | 4.38 | 14.02 | 26.16 | 3.13 | - | 15.13 |
| | 2 | 3.50 | 32.24 | 3.73 | 15.32 | 26.18 | 3.96 | - | 15.07 |

*Represents unidentified fatty acids.

TABLE XIV

DAILY DRY FECES PRODUCTION - DRY WEIGHT BASIS

GMS/DAY

| Control | Infused Oleic Acid | Infused Linoleic Acid | Fed Oleic Acid | Fed Linoleic Acid |
|---|---|---|---|---|
| 113.18 | 140.86 | * | 145.33 | 199.49 |
| 104.21 | 137.43 | * | * | * |
| 156.83 | 132.26 | 133.80 | 204.44 | 172.57 |
| 122.49 | 142.31 | 118.31 | 197.35 | 184.91 |