J. Dairy Sci. 84:1182–1191

Effects of Abomasal Infusion of Long-Chain Fatty Acids on Intake, Feeding Behavior and Milk Production in Dairy Cows

J. A. Benson,* C. K. Reynolds,* D. J. Humphries,*
S. M. Rutter,† and D. E. Beever*
*Centre for Dairy Research, Department of Agriculture,
The University of Reading, Earley Gate, Reading RG6 6AT England
†Institute for Grassland and Environmental Research,
North Wyke, Devon EX20 2SB England

ABSTRACT

Fat is often fed to dairy cows to increase the energy concentration of their diet; however, feeding fat often reduces dry matter intake (DMI), which limits its impact on metabolizable energy (ME) intake. To investigate the effects of postruminal fat infusion on intake, feeding behavior, and milk production of dairy cows at two stages of lactation (55 and 111 d postpartum), six Holstein × British Friesian cows were infused into the abomasum, with a mixture of rapeseed and sunflower oils supplying predominantly unsaturated long-chain fatty acids (LCFA). Dry matter intake was significantly depressed by oil infusion, but estimated ME intake was unchanged, and thus there was no effect of oil infusion on milk yield. There was no effect of stage of lactation on the DM or ME intake response to oil infusion. Milk fat concentration was increased by oil infusion in midlactation but not in early lactation, suggesting that the infused LCFA were utilized differently in early compared with midlactation. Cows spent an average of 654 min idling, 462 min ruminating, and 248 min eating during the last 22.8 h of each infusion. There were no significant effects of oil infusion or stage of lactation on the total time spent engaged in these activities. An assessment of the circadian pattern of feeding behavior suggested that the depression in DMI in response to oil infusion occurred after the 1630 and 2230 h feeding times. This may reflect differences in mechanisms regulating feed intake behavior and appetite during the day. Comparison of the results of the present study with the results of other trials involving postruminal fat infusion suggests that polyunsaturated nonesterified fatty acids have the most potent effect on DMI intake.
(**Key words:** fat, dairy cows, intake, rumination)

Received July 7, 2000.
Accepted November 17, 2000.
Corresponding author: C. K. Reynolds; e-mail: c.k.reynolds@reading.ac.uk.

Abbreviation key: CCK = cholecystokinin, **ELAC** = early lactation, **LCFA** = long-chain fatty acids, **ME** = metabolizable energy, **MLAC** = midlactation, **MUFA** = monounsaturated fatty acids, **PUFA** = polyunsaturated fatty acids.

INTRODUCTION

Fat is fed to dairy cows chiefly because it is an energy-dense compound, thus it is often used to increase the metabolizable energy (**ME**) concentration of lactation rations. Fat is often fed in early lactation in attempting to increase ME intake and reduce mobilization of adipose tissue in early lactation cows (Chilliard, 1993), but in higher yielding cows supplemental fat energy is often used preferentially for additional milk synthesis. Rumen-protected long chain fatty acids (**LCFA**) have been fed to increase the incorporation of polyunsaturated fatty acids (**PUFA**) or monounsaturated fatty acids (**MUFA**) into milk fat, a potential health benefit for consumers (Grummer, 1991). Evidence also suggests that supplemental fatty acids may improve the fertility of dairy cows by influencing energy balance in early lactation or as precursors for the synthesis of progesterone and prostaglandins (Staples et al., 1998). However, supplementation of diets with ruminally protected LCFA or postruminal infusion of LCFA often decreases DMI (Palmquist, 1994).

Little work has been carried out investigating the physiological mechanisms for this postruminal effect in lactating dairy cows. In previous studies, PUFA have been shown to be a potent depressor of rumen motility in sheep (Nicholson and Omer, 1983), which can also cause digestive disturbances at relatively low levels of abomasal infusion (Drackley et al., 1992). It is also known that increased concentrations of certain fatty acids in the small intestine increase circulating levels of cholecystokinin (**CCK**), a gut peptide implicated in appetite regulation in nonruminants that may also affect gut motility (Grider, 1994; Reidelberger, 1994). Thus, the effects of postruminal fat supply on DMI in

Table 1. Composition of the total mixed ration (g/kg) on a DM basis.

Composition	g/kg of DM
Ingredient	
Grass silage	200
Dehydrated alfalfa	300
Wheat feed (middlings)	192
Barley	143
Corn	48
Molassed sugar beet shreds	48
Soyabean meal, solvent extracted, 48% CP	52
Sodium bicarbonate	5
High phosphorus mineral mix[1]	12
Chemical analysis	
DM	594
Oil	26
Nitrogen	29
NDF	293
ADF	185
Ash	80
Starch	196

[1]Containing 120 g of phosphorus, 50 g of magnesium, 180 g of calcium, 15 mg of selenium, 1500 mg of copper, 550 IU of vitamin E, 80 IU of vitamin D3, and 380 IU of vitamin A per kilogram.

lactating dairy cows also may be a consequence of increased release of CCK or other peptides that affect gut motility (Spiller et al., 1988) and rumination. The objective of the present study was to determine the effect of abomasal LCFA infusion on feed intake, rumination, patterns of feeding, and milk yield and composition.

MATERIALS AND METHODS

Cows, Diet, and Experimental Design

Six Holstein × British Friesian cows (684 ± 9 kg of BW) in their third (one cow), fourth (three cows), or fifth (two cows) lactation were used. Cows were surgically fitted with rumen cannulas before their previous lactation and permanent catheters for measurement of net nutrient absorption across the splanchnic tissues (Huntington et al., 1989) at the beginning of their previous lactation. All procedures used were licensed and regulated by the UK Home Office under the Animals (Scientific Procedures) Act of 1986. The animals were housed individually in tie stalls in a barn with translucent roofing to allow access to natural light, with artificially lighting used from 0600 to 1800 h. Beginning at calving, cows were fed a TMR (Table 1) ad libitum (10% refusals) with daily rations offered as three equal portions at 0830, 1630 and 2230 h. Cows had constant access to water and trace-mineralized salt blocks and were milked at 0630 and 1630 h.

Treatments

Treatments consisted of 7-d abomasal infusions of 400 g/d of water (control) followed immediately by a 7-d abomasal infusion of 400 g/d of vegetable oil. Postruminal infusion was used to ensure that direct effects of supplemental LCFA on ruminal microbes, or microbial hydrogenation of PUFA and MUFA, were eliminated. The experiment was carried at an average of 55 (range 46 to 66 d) (early lactation [**ELAC**]) and 111 (range 100 to 123 d) (midlactation [**MLAC**]) d postpartum to investigate whether differences in body energy balance affected the response to supplemental LCFA. Infusions were delivered to the abomasum with a peristaltic pump (Gilson Minipuls, Anachem Ltd, Luton, UK) and an infusion line (Tygon tubing, R3603), with a plastisol flange placed in the abomasum through the rumen. Plastisol flanges were cut from retired rumen cannula plugs (Bar Diamond, Parma, ID) and attached using tygon cuffs and cyclohexanone. Placement of tubing within the abomasum was confirmed daily by palpation. Infusions were started at 1630 h, and the pump rate was adjusted to deliver 400 g in 23 h. The vegetable oil infused was composed of 50% (by weight) sunflower oil (ASDA Pure Sunflower Oil, Leeds, UK) and 50% rapeseed oil (Goldenfields Rapeseed Oil, Merseyside, UK). A mixture of sunflower and rapeseed oils was infused to maximize PUFA and minimize saturated fatty acid concentration of the LCFA infused, as well as minimize the risk of diarrhea. The average fatty acid composition (Table 2) of a composite sample of the infused oil mixture was determined by a commercial laboratory (Central Laboratories, Banbury, UK). To allow digestive adaptation, 200 g/d of oil was infused on d 1, while 400 g/d was infused from d 2 onwards.

Measurements

Feed refusals were removed daily at 0810 h, and samples of refusals and diet were obtained to determine

Table 2. Fatty acid profile (g/100 g of total fatty acids) of the mixture of rapeseed and sunflower oils infused into abomasum.

Fatty acid	g/100 g of Fatty acids
$C_{14:0}$	0.04
$C_{16:0}$	5.93
$C_{16:1}$	0.14
$C_{18:0}$	2.86
$C_{18:1}$	41.59
$C_{18:2}$	44.13
$C_{18:3}$	4.41
$C_{20:0}$	0.18
$C_{20:1}$	0.63
$C_{22:0}$	0.05
$C_{22:6}$	0.06
Total saturated	9.06
Total MUFA[1]	42.36
Total PUFA[2]	48.60

[1]Monounsaturated fatty acids.

[2]Polyunsaturated fatty acids.

100°C DMI. Frozen composite ration samples were obtained for each experimental period and later anaylzed for volatile components or dried at 60°C, ground, and analyzed for chemical composition using accredited and Parliamentary approved procedures for feeding stuffs analysis (Statutory Instruments, 1982 and 1985) by a commercial laboratory (Natural Resources Management, Bracknell, UK). Samples from each milking were taken throughout each infusion period. Individual samples were treated with potassium dichromate preservative (1 mg/ml; Lactabs, Thompson and Capper, Runcorn, UK) and stored at 4°C until analyzed for lactose, fat, and protein concentrations using infrared spectrophotometric analysis (Foss Electric Ltd, York, UK). Blood samples for measurement of nutrient and hormone metabolism by splanchnic tissues were obtained from 0630 to 1430 h (Benson et al., 1997).

Detailed measurements of the feeding behavior of the cows were obtained during the last 24 h of each infusion, beginning at 1630 h on d 6 of infusion. The pattern of feed intake was monitored by means of a load cell underneath the feed manger. The load cell was connected to a computer that recorded weight of feed in the manger at 2-min intervals (Visual Data Link Software, Applied Weighing, Reading, UK). The load cells were cleaned, tared, and tested after refusals were removed each morning. Rumination patterns were measured with a jaw movement recorder (Rutter et al., 1997) consisting of a halter with a silicon graphite noseband. The noseband was connected to a mini-computer that recorded jaw movement and pattern as changes in the resistance of a current passed through the noseband. The original halter was designed for use by grazing cows and was modified for use in a tie stall by extending the computer and power supply cabling for laboratory-based use. The recording computer contained a PCMA card that stored up to 25 h of data. Data from the card were transferred to a computer and the changes in resistance were analyzed to identify periods of eating, ruminating, and idling using software developed for that purpose (Rutter, 2000). Due to scheduling problems, the limited availability of equipment and a mechanical failure, a complete record of daily feeding behavior was only available for 18 of the 24 measurement periods. However, feeding and rumination behavior during the 8-h period of blood sampling were obtained for 23 measurement periods.

Statistical Analyses

To allow for adaptation to abomasal infusions, mean daily DMI and milk yield and composition were calculated as the average for the last 4 d of each infusion. Effects of animal, infusion (water vs. oil), stage of lactation (ELAC vs. MLAC), and the interaction between infusion and stage of lactation were tested using residual error variance and the general linear models procedure of SAS (1999). Least squares means are presented. Due to the small number of cows used, differences were considered significant at $P < 0.10$.

RESULTS

Infusion of 400 g of a 50:50 mixture of sunflower and rapeseed oils containing 91% unsaturated fatty acids decreased daily DMI (Table 3) by 1.29 kg/d ($P < 0.01$); however, estimated ME intake (NRC, 1989; Hodgman et al., 1960; assuming 80% absorption of infused fat) was not changed. Daily DM and ME intake were not affected by stage of lactation, and there was no difference in the DM and ME response to oil infusion at the different stages of lactation (Table 3).

To compare DMI after each of the three feeding periods (morning, afternoon, and evening) DMI/h was calculated to account for slight variations in the evening feeding time over the course of the study. Circadian variation in DMI was evident, as the rate of eating was slowest during the evening period in both ELAC and MLAC (Figure 1). The depression in daily intake due to oil infusion occurred after the afternoon and evening feedings rather than after the morning feeding. While oil infusion had no effect on average DMI/h following the morning feeding, there were numerical decreases in DMI/h of 0.25 and 0.11 kg/h for the afternoon and evening periods, respectively.

Daily time spent engaged in eating, ruminating, and idling activities was not affected ($P > 0.28$) by either oil infusion or stage or lactation (Table 3). Cows spent an average of 654 min idling, 462 min ruminating, and 248 min eating. The 24-h pattern of eating behavior (Figures 2 and 3) was influenced strongly by feeding times. Periods of most intensive feeding activity (eating time and DMI) largely occurred after feed was offered, but a period of eating activity was also evident between 0530 and 0730 h, which coincided with a resumption of activity associated with the morning milking. The periods of most intense feeding activity coincided with periods of least ruminating activity. Overall, the pattern of ruminating, eating, and idling behavior was not altered markedly by either oil infusion or stage of lactation. However, from 0630 to 1430 h time spent eating was lower ($P < 0.02$) and conversely time spent idling was greater ($P < 0.06$) during MLAC compared with ELAC (Table 3). As DMI during this period was not affected by stage of lactation, rate of eating (DMI/min) was greater in MLAC.

During the night (1030 to 0530 h), the percentage of time spent ruminating was numerically lower during

Table 3. Effect of abomasal infusion of water or vegetable oil at 55 (early lactation; ELAC) and 111 (midlactation; MLAC) d postpartum on DM and estimated metabolizable energy intakes and feeding behavior.

	Lactation stage							
	ELAC		MLAC			$P <$		
Item	Water	Oil	Water	Oil	SEM	Stage	Oil	Stage × Oil
Daily intake								
DM, kg/d	23.1	21.4	22.4	21.5	0.5	0.58	0.01	0.41
ME, MJ/d[1]	275.8	268.3	268.1	269.8	5.4	0.58	0.60	0.42
n	6	6	6	6				
Daily feeding behavior, min[2]								
Eating	250	252	232	233	13	0.28	0.91	0.96
Ruminating	477	440	467	447	23	0.96	0.29	0.75
Idling	638	673	665	685	35	0.65	0.50	0.85
n	3	4	5	6				
Morning feeding behavior, min[3]								
Eating	122	123	99	106	7	0.02	0.58	0.73
Ruminating	156	144	137	139	12	0.32	0.69	0.58
Idling	200	211	243	234	15	0.06	0.96	0.55
n	6	6	5	6				

[1]Estimated metabolizable energy intake including gross energy supplied by the infused fat.

[2]Mean value over period 1700 to 1545 h.

[3]Mean value over period 0630 to 1430 h.

oil infusion, while the time spent eating during this period was numerically lower in MLAC than in ELAC. Even though there were no overall effects of oil infusion on the patterns of eating, ruminating, and idling activities, some cows showed strong responses. For example, when cow 323 was infused with oil in ELAC, there was a reduction in the time spent eating, but no change in eating pattern, as well as a striking reduction in the time spent ruminating (Figure 4).

Milk yield (Table 4) was greater in ELAC than in MLAC ($P < 0.01$) but was not affected by the infusion of oil. There was a numerical reduction in milk yield during oil infusion in ELAC, but oil infusion had little effect in MLAC ($P < 0.13$). Fat concentration of milk was lower in ELAC than MLAC ($P < 0.004$) and increased by oil infusion in MLAC but not in ELAC (lactation period × infusion interaction, $P < 0.06$). Milk fat yield was higher in ELAC than MLAC ($P < 0.10$) and increased when oil was infused in MLAC, but decreased when oil was infused in ELAC (lactation period × infusion interaction, $P < 0.02$). There was no effect of oil infusion on milk protein concentration ($P > 0.20$), but milk protein concentration was greater in MLAC than ELAC ($P < 0.001$). Protein yield was unaffected by either stage of lactation or oil infusion. Lactose concentration was increased in response to oil infusion ($P < 0.06$) but was not affected by stage of lactation, while lactose yield was significantly less ($P < 0.001$) in MLAC than in ELAC.

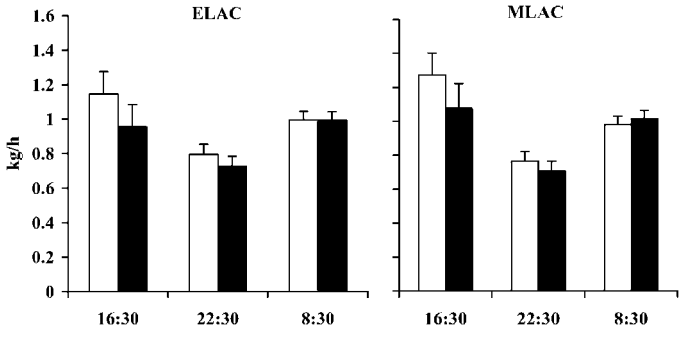

Figure 1. Dry matter intake (kg/h) during each of the 3 postfeeding periods in response to water (open bars) or long chain fatty acid (solid bars) infusion at 55 (early lactation; ELAC) and 111 (midlactation; MLAC) d postpartum.

DISCUSSION

It was unexpected that DMI and ME did not differ between stages of lactation, as initial analysis of the results for the first four cows to undergo the trial showed a significant decrease in DM and ME intake in MLAC compared with ELAC (Benson et al., 1997). However, an increased intake in MLAC occurred in the final two cows to complete the trial. These last two cows calved later in the year than the first four cows to complete the trial, thus their ELAC and MLAC periods included a gradual increase in photoperiod that may have contributed to the variation in the response of intake to the progression of lactation. Other factors, such as variations in silage quality and lactation performance, may also have contributed to this variation in DMI patterns among cows. Both cows had higher milk yields than the other cows that calved earlier in the year. In addition, one of the last two cows used in the

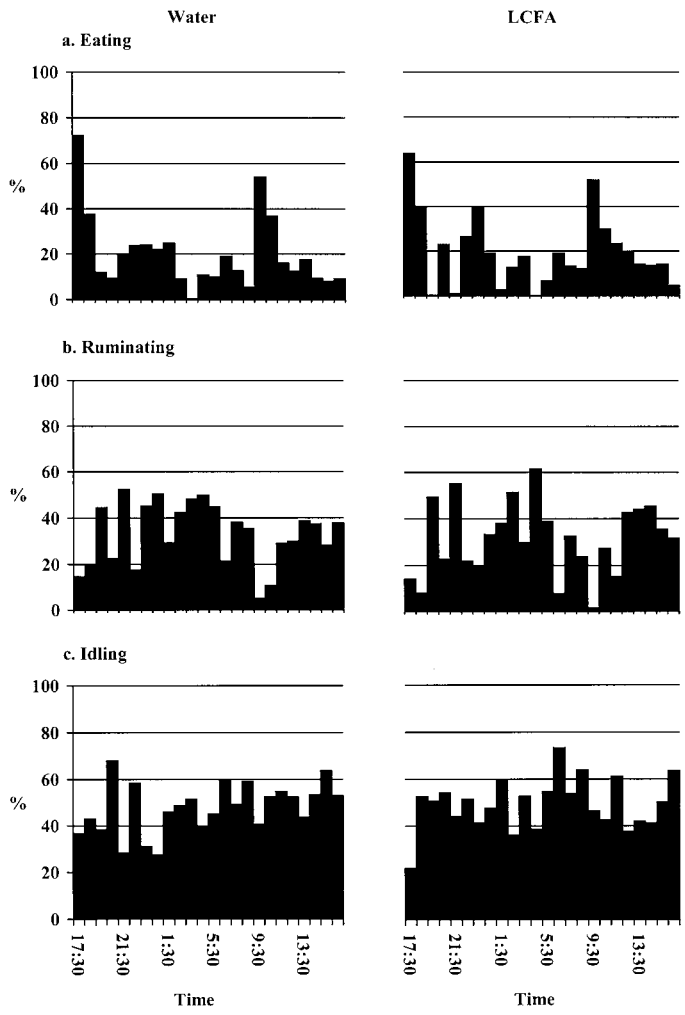

Figure 2. Diurnal pattern of eating, ruminating, and idling activity for dairy cattle abomasally infused with water and long-chain fatty acids (LCFA) in early lactation. Data shown are percentage of sequential 60-min periods engaged in each activity.

study had 'downer cow syndrome' for 2 d after calving, which delayed peak milk yield.

The decrease in total time spent eating during the period from 0630 to 1430 h (which corresponded to the period of blood sampling) in MLAC compared with ELAC perhaps reflects a greater physical capacity for feed consumption. Cows in MLAC would be expected to have a greater rumen mass and total rumen volume compared with ELAC (Gibb et al., 1994), which would perhaps enable more efficient feeding in terms of DMI/min. Cows in MLAC also appeared to have less variation across sequential hourly periods in the time spent eating following the morning meal (Figures 2 and 3), which also suggests some adaptation of intake behavior relative to appetite and other signals affecting intake during the morning period.

In the present study, abomasal infusion of a mixture of sunflower and rapeseed oils containing 91% unsaturated fatty acids (42% MUFA, 49% PUFA) decreased daily DMI. A partial summary of published studies reporting effects of postruminal LCFA infusion in lactating dairy cows is given in Table 5. In almost all studies reported to date, infusion of LCFA had a negative effect on DMI that was in most cases statistically significant. However, as observed previously (Bremmer et al., 1998), unsaturated fatty acids appear to have a more negative effect on DMI than saturated fats. The study of Gagliostro and Chilliard (1991) stands out, as they were able to infuse an exceptionally large amount of oil, which accounted for 7% of DMI, whereas for the other studies listed in Table 5, this varied between 1.7 and 3.6%. Drackley et al. (1992) and Grummer et al.

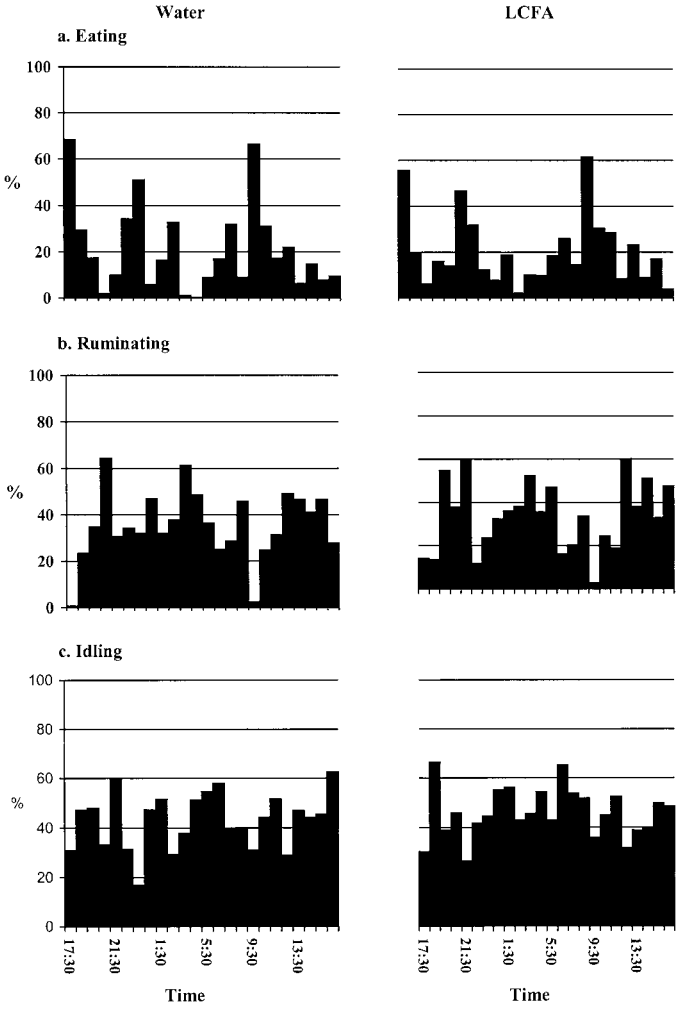

Figure 3. Diurnal pattern of eating, ruminating, and idling activity for dairy cattle abomasally infused with water and long-chain fatty acids (LCFA) in midlactation. Data shown are percentage of sequential 60-min periods engaged in each activity.

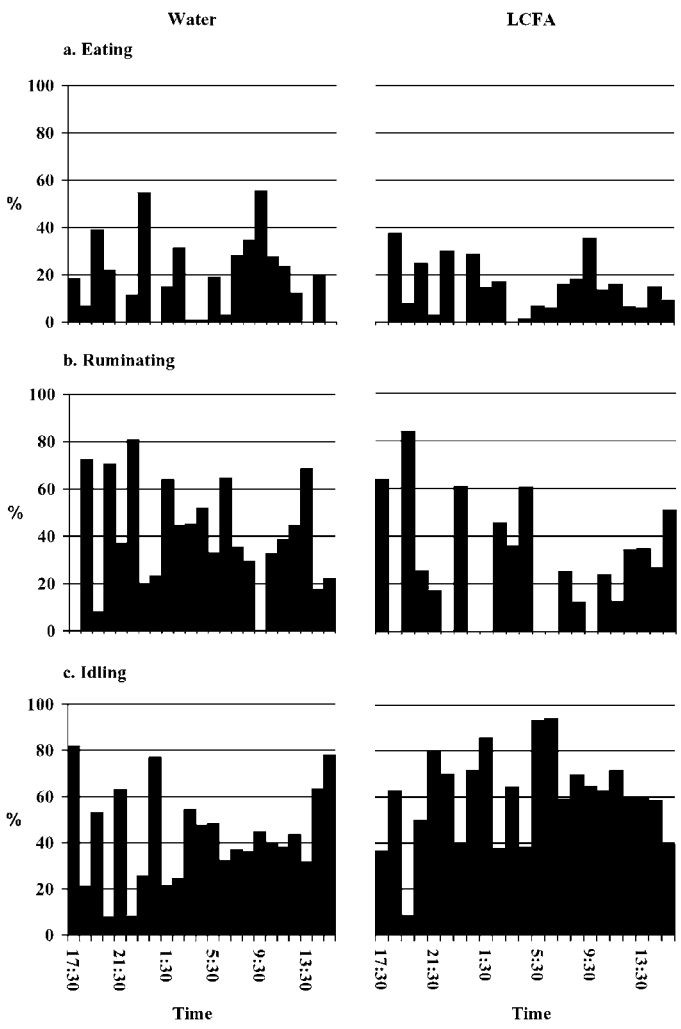

Figure 4. Diurnal pattern of eating, ruminating, and idling activity for cow 323 abomasally infused with water and long-chain fatty acids (LCFA) in early lactation. Data shown are percentage of sequential 60-min periods engaged in each activity.

(1987) were limited in the amount of unsaturated fatty acids and soy oil they could infuse because diarrhea developed at higher levels of infusion. A number of factors must be considered when comparing the results listed in Table 5. Site of infusion of the fats may be important in their effects on DMI as Gagliostro and Chilliard (1991) infused fat into the duodenum, while the other authors infused it into the abomasum. In addition, the form in which the LCFA are infused must be considered. In nonruminants, it has been shown that NEFA have a more potent effect on DMI than triacylglycerides (Woltman et al., 1995), and in some studies listed in Table 5 NEFA were infused. The length of the trials must also be considered. The infusion periods used by Gagliostro and Chilliard (1991) lasted for 42 d, during which time they gradually increased the amount of oil infused to achieve the maximum rate of 1.1 kg/d. The infusion period used in the present study is relatively short, yet the DMI response is comparable to other studies in which similar amounts of fat were infused for longer periods (Table 5).

Another important consideration when comparing the studies listed in Table 5 is the fatty acid profile of the LCFA infused. There is evidence that the polyunsaturated fatty acids ($C_{18:2}$ and $C_{18:3}$) are a more potent suppresser of intake than saturated fatty acids or MUFA (Bremmer et al., 1998). Large decreases in intake occurred with infusion of safflower, sunflower, and soy oils, all high in $C_{18:2}$ compared with rapeseed, canola, or high oleic sunflower oils containing high levels of $C_{18:1}$ (Table 5). A further assessment of published studies summarized in Table 5 is presented in Figure 5, which shows the relationship between amounts of $C_{18:1}$ or $C_{18:2}$ infused postruminally as triacylglycerides or NEFA and resulting changes in DMI relative to a control infusion. Averaged across a number of studies conducted at separate sites, a negative relationship is evident between DMI and the amount of $C_{18:2}$ infused, but the effects of much larger amounts of infused $C_{18:1}$

Table 4. Milk yield and concentration and yield of milk constituents during abomasal infusion of water or vegetable oil at 55 (early lactation; ELAC) and 111 (midlactation; MLAC) d postpartum

	Lactation stage							
	ELAC		MLAC			$P <$		
Item	Water	Oil	Water	Oil	SEM	Stage	Oil	Stage × oil
Milk yield, kg/d	41.3	38.6	35.2	35.0	0.9	0.01	0.13	0.17
Milk components								
Fat, g/kg	36.1	36.0	37.2	40.8	0.9	0.01	0.06	0.06
Fat, kg/d	1.48	1.39	1.31	1.42	0.04	0.10	0.78	0.02
Protein, g/kg	29.3	29.3	33.2	34.2	0.4	0.01	0.20	0.23
Protein, kg/d	1.20	1.13	1.17	1.20	0.03	0.67	0.54	0.15
Lactose, g/kg	48.0	48.6	47.9	48.1	0.2	0.24	0.06	0.40
Lactose, kg/d	1.98	1.87	1.68	1.68	0.05	0.01	0.29	0.28

Table 5. Summary of the results of studies investigating the effect of abomasal fat infusion on DMI (kg/d) in lactating dairy cows.

Reference	Source of LCFA[1] infused	Form	Length of infusion, d	Amount infused/d	Change in DMI, kg/d
Rindsig and Schultz, 1974	Safflower oil	TAG[2]	21	250 ml	–0.7[3]
	Safflower oil	TAG	7	500 ml	–1.5[3]
Grummer et al., 1987	Soy lecithin	TAG	11	900 ml	–3.1
	Soy oil	TAG	11	900 ml	–1.7
Gagliostro and Chilliard, 1991	Rapeseed oil[3]	TAG	42	1100 g	–2.6
Drackley et al., 1992	Mostly saturated fatty acids	NEFA	14	450 g	+0.6
	Mix of saturated and unsaturated fatty acids	NEFA	14	450 g	–0.9
	Mostly unsaturated fatty acids (soy oil)	NEFA	14	450 g	–1.8
Christensen et al., 1994	Prilled (mostly saturated) fat	NEFA	21	450 g	–1.6
	Canola oil	NEFA	21	450 g	–2.0
	Soybean oil	NEFA	21	450 g	–2.5
	Sunflower oil	NEFA	21	450 g	–3.6
Gaynor et al., 1994	65% high oleic sunflower oil + 35% cocoa butter	TAG	21	750 g	–1.4
	93% shortenings + 7% corn oil	TAG	21	750 g	–0.7
Ottou et al., 1995	Rapeseed oil[4]	TAG	21	700 ml	–0.5
Romo et al., 1996	68% High oleic sunflower oil + 32% cocoa butter	TAG	21	630 g	–1.5
	90% Partially hydrogenated soybean oil + 10% high linoleic safflower oil	TAG	21	630 g	–2.5
Oldick et al., 1997	Tallow	TAG	35	450 g	+0.2
	Yellow grease	TAG	35	450 g	–1.0
Bremmer et al., 1998	Prilled (mostly saturated) fat	NEFA	21	450 g	–1.2
	Palm oil low in lineoleic acid	NEFA	21	450 g	–2.0
	Palm oil	NEFA	21	450 g	–2.5
	Soybean oil	NEFA	21	450 g	–3.7
	Soybean oil high in palmitic acid	NEFA	21	450 g	–3.1
Present study	50% rapeseed oil + 50% sunflower oil	TAG	7	400 g	–1.3

[1]Long chain-fatty acid.
[2]Triacylglyceride.
[3]Change in fresh weight, kg.
[4]Infused into the duodenum.

LCFA on DMI were less pronounced, especially when infused as triacylglyceride. For both, LCFA infusion of NEFA was associated with a greater overall reduction in DMI. However, the relationships depicted in Figure 5 are not independent, as we are not aware of studies in which pure NEFA were infused individually. The considerable variability in the DMI reduction associated with lower levels of $C_{18:1}$ NEFA infusion in Figure 5 is partially because in many cases even greater amounts of $C_{18:2}$ NEFA were being infused simultaneously. Other LCFA were also being infused in the studies summarized, including *trans*-$C_{18:1}$ isomers. The extent of DMI reduction is in part determined by the total amount of fat infused, which in part explains why the regressions do not have an intercept of zero. Although the responses varied across the studies reported and are also related to a number of factors not considered, these comparisons suggest that it is possible to infuse more $C_{18:1}$ without causing large decreases in DMI compared with $C_{18:2}$. This is in part supported by the present study in which the mixture of sunflower and rapeseed oil infused had less impact on DMI compared with sunflower oil infusion in previous studies (Table 5). Bremmer et al. (1998) reported significant negative relationships between $C_{18:1}$ or $C_{18:2}$ NEFA infused abomasally and DMI in a series of studies conducted by their group (NEFA infusion studies listed in Table 5). However, they also concluded that confounding of $C_{18:1}$ and PUFA ($C_{18:2}$ and $C_{18:3}$) effects precluded any independent assessment of MUFA and PUFA effects on DMI. In an assessment of practical feeding trials, Firkins and Eastridge (1994) also concluded that DMI is reduced to a greater extent as the iodine value of supplemental dietary fat increases, but in their studies, the response may also be determined by digestive responses in the rumen.

Clearly then, it is important to understand why DMI is depressed by supplemental PUFA if high PUFA fat sources are to be used to increase ME intake in ruminants, or to alter the concentration of specific unsaturated fatty acids in milk. The results of the present trial indicate several mechanisms by which these fatty acids may depress DMI. Several of the cows had a marked decrease in rumination during the evening period, and, on average, there was a 6% numerical decrease in daily time spent ruminating in response to oil infusion. These are the first results to measure rumination time in response to supplemental LCFA in dairy cattle, although a larger number of animals and sampling periods would be required to establish the effect

as significant. Earlier work in sheep has shown that duodenal infusions of vegetable oils (e.g., peanut, soy, and olive; Titchen et al., 1966), intralipid (a soy oil emulsion designed for intravenous infusion in humans; Grovum, 1984) and long-chain C_{18} NEFA (Nicholson and Omer, 1983) cause a decrease in both rumination and rumen motility. In the current experiment, it is impossible to determine whether the decrease in rumination activity exhibited by some cows was a cause or a consequence of decreased DMI, but the time spent ruminating per kilogram of DMI was virtually the same across the four treatments. However, in the experiments by Grovum (1984) and Nicholson and Omer (1983) ruminal motility and rumination were inhibited directly by LCFA infusion, independent of DMI. The results of Titchen et al. (1966) must be interpreted with care, as the doses used caused diarrhea, and therefore may have been pharmacological. In nonruminants, it has been frequently observed that fats have a negative effect on gastric motility and that an enhanced release of gut peptides is involved in the response (Dreznek et al., 1994; Spiller et al. 1988). Therefore, the decreases in rumination due to LCFA infusion reported previously may be a consequence of increased gut peptide release.

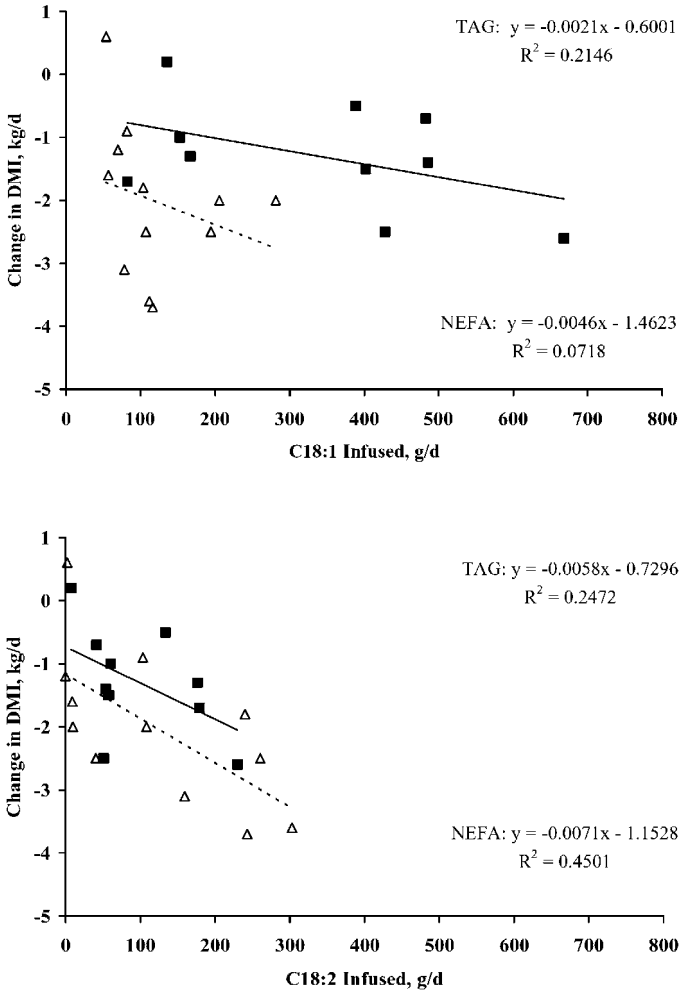

Figure 5. Relationship between $C_{18:1}$ or $C_{18:2}$ fatty acids infused postruminally (g/d) as triacylglyceride (TAG; —) or nonesterified fatty acids (NEFA; ····) and change in DMI (kg/d) for studies quoted in Table 5.

There was also evidence that oil infusion affected the circadian pattern of eating behavior. On average, times spent eating and ruminating (242 and 458 min, respectively) during the measurement period (22.8 h) were comparable to those reported for cows fed a TMR composed of 60% concentrate and 40% forage (Vasilatos and Wangsness, 1980) or 60% forage and 40% concentrate (Dado and Allen, 1994). Cows ate when provided with new feed, even though they were fed ad libitum and there was always feed in the manger. This is a conditioned response, which has been observed in cattle (Dürst et al., 1993; Vasilatos and Wangsness 1980) and sheep (Dulphy et al., 1980). There was also a period of eating activity observed around milking time, particularly in the morning (0530 to 0630 h), which has also been reported as a stimulus for feeding (Dürst et al., 1993). Afternoon milking occurred at about 1630 h and therefore was confounded with afternoon feeding time. Cows in the present experiment consumed less DM/h during the night than during the rest of the day and were observed to spend more time idling and ruminating during this time. Abomasal infusion of oil decreased daily DMI, but the present trial would suggest that this decrease occurred during the afternoon and evening periods (1630 to 0830 h) rather than during the morning period.

In other work examining effects of dietary fat on intake behavior of dairy cows, De Visser et al. (1982) noted that concentrates containing supplemental fat were eaten in several small quantities and at a slower rate than unsupplemented concentrates. Heinrichs et al. (1982) observed a decrease in the size of the initial meal after feeding a diet supplemented with tallow; however, the number of subsequent meals was increased, so there was no difference in daily intake. In both of these studies the differences in intake patterns may be the result of a change in the palatibilty of the diet or ruminal digestion, rather than a postruminal effect.

One concern with the present data is that blood sampling may have influenced feeding behavior after the morning feeding. Cows were blood sampled intermittently from 0630 to 1430 h and were made to stand up during sampling, which may have been a stimulus for eating. However, analysis of data available for the same period on nonsampling days showed no obvious effect of blood sampling on patterns of eating or ruminating.

Dürst et al. (1993) proposed that there was a diurnal pattern in the mechanisms of intake regulation, and this theory could explain the present results. During the daytime, they suggested that feeding occurred in response to external stimuli such as feeding time, milking, and the activity of other cows, while at night feeding was in response to the requirement for energy and its influence on appetite. In the current experiment, it could be hypothesized that the reduction in intake occurred during the evening and night periods due to the supply of energy by the continuous oil infusion.

The observation that estimated daily ME intake was unchanged by oil infusion in the present study suggests that DMI was being metabolically regulated to achieve energy homeostasis. Examples of DMI being adjusted for differing energy contents of the diet are frequent for dairy cattle (Conrad et al., 1964; Palmquist, 1994). The results from this trial suggest there may be a signal related to the energy supplied by the infused fat. A feedback signal relating to the oxidation of LCFA in the liver was proposed by Scharrer and Langhans (1986) for rats fed a high fat diet, and an increase in fatty acid oxidation in early lactation by cows in negative energy balance has been suggested to be a cause of low feed intake at this time (Emery et al., 1992). It may be hypothesized that in early lactation infused fat interacts with mobilized adipose tissue to cause a greater depression in intake than would be expected in midlactation when cows are in more positive energy balance. The present study provided no evidence to support this theory as there was no interaction between stage of lactation and the DMI response to oil infusion. However, this may have been because the cows were not in the very early weeks of lactation.

The failure of infused oil to increase ME intake in the present study is a plausible explanation for the lack of an effect of oil infusion on milk yield. While the infusion period in the present study was relatively short, Gagliostro and Chilliard (1991) also found no significant change in ME intake and milk production for cows in midlactation infused with 1100 g/d of rapeseed oil for 42 d. In contrast, in studies in which DMI was maintained during infusion of saturated LCFA, milk yield was increased (Drackley et al., 1992; Oldick et al., 1997). Milk fat concentration was increased significantly in response to oil infusion in MLAC, but not ELAC, suggesting a difference in the use of infused fatty acids between the two lactation stages. In ELAC, the LCFA infused may have been preferentially oxidized, whereas in MLAC, when cows were in more positive energy balance, the supplemental LCFA were secreted in milk or used for body adipose tissue. Protein concentration was not affected by oil infusion in the present study despite numerous studies showing that both postruminal infusion of fat and feeding rumen-protected fat has a negative effect on protein concentration (Chilliard, 1993; Coppock and Wilks, 1992). This may have been due to an adequate protein supply by the diet fed in the present study, the relatively short duration of the trial or because milk yield was not affected by fat infusions.

Stage of lactation did not influence the response of DM and ME intake to oil infusion. In contrast, Gagliostro and Chilliard (1991) compared the effects of duodenal rapeseed oil infusion in early lactation (3 wk postpartum) and midlactation and observed a more negative effect of fat infusion on DMI in midlactation. A similar conclusion was reached by Bines et al. (1978) who proposed that the negative effect of lipid supplementation increased as lactation progressed. The present study was conducted at 55 and 111 d postpartum and as cows in ELAC were near peak milk yield, there may have been less of an interaction between stage of lactation and effects of LCFA supplementation on DMI.

CONCLUSIONS

Abomasal infusion of a mixture of predominantly $C_{18:1}$ and $C_{18:2}$ fatty acids reduced DMI, but reductions in estimated feed ME intake were nearly equal the energy in infused fat. In these cows fed three times a day, the reductions in daily DMI caused by continuous fat infusion occurred during the afternoon and evening, while intake following the morning feeding was not affected. This may reflect differences in the mechanisms regulating feeding behavior and appetite during the course of the day. Abomasal fat infusion had no effect on milk yield in dairy cows at 55 or 111 d lactation, reflecting the constancy of estimated ME intake. Milk fat concentration was increased by fat infusion in midlactation, but not early lactation, suggesting the supplemental fat was partitioned differently as lactation progressed.

ACKNOWLEDGMENTS

The dedicated support of technical staff of the CEDAR Metabolism Unit in the daily management and care of cows and conduct of this study is gratefully acknowledged. The analysis of milk samples by staff of the Faculty Analytical Laboratory is also greatly appreciated. J. A. Benson was funded by a UK Ministry of Agriculture, Fisheries and Food Postgraduate Studentship.

REFERENCES

Benson, J. A., C. K. Reynolds, D. J. Humphries, D. E. Beever, and S. M. Rutter. 1997. Effects of abomasal fat infusion on dry matter

intake, milk production and splanchnic metabolism in dairy cows at two stages of lactation. Page 21 *in* Proc. Br. Soc. Anim. Sci., Br. Soc. Anim. Sci, UK.

Bines, J. A., P. E. Brumby, J. E. Storry, R. J. Fulford, and G. D. Braithwaite. 1978. The effect of protected lipids on nutrient intakes, blood and rumen metabolites and milk secretion in dairy cows during early lactation. J. Agric. Sci. (Camb.) 91:135–150.

Bremmer, D. R., L. D. Rupert, J. H. Clark, and J. K. Drackley. 1998. Effects of chain length and unsaturation of fatty acid mixtures infused into the abomasum of lactating dairy cows. J. Dairy Sci. 81:176–188.

Chilliard, Y. 1993. Dietary fat and adipose tissue metabolism in ruminants, pigs, and rodents: a review. J. Dairy Sci. 76:3897–3931.

Christensen, R. A., J. K. Drackley, D. W. LaCount, and J. H. Clark. 1994. Infusion of four long-chain fatty acid mixtures into the abomasum of lactating dairy cows. J. Dairy Sci. 77:1052–1069.

Conrad, H. R., A. D. Pratt, and J. W. Hibbs. 1964. Regulation of feed intake in dairy cows. 1. Change in importance of physical and physiological factors with increasing digestibility. J. Dairy Sci. 47:54–62.

Coppock, C. E., and D. L. Wilks. 1992. Supplemental fat in high-energy rations for lactating cows: effects on intake, digestion, milk yield and composition. J. Anim. Sci. 69:3826–3837.

Dado, R. G., and M. S. Allen. 1994. Variation in and relationships among feeding, chewing, and drinking variables for lactating dairy cows. J. Dairy Sci. 77:132–144.

De Visser, H., S. Tamminga, and L.G.M. van Gils. 1982. Further studies on the effect of fat supplementation of concentrates fed to lactating dairy cows. 1. Effect on feed intake, feed intake pattern and milk production and composition. Neth. J. Agric. Sci. 30:3347–3352.

Drackley, J. K., T. H. Klusmeyer, A. M. Trusk, and J. H. Clark. 1992. Infusion of long-chain fatty acids varying in saturation and chain length into the abomasum of lactating dairy cows. J. Dairy Sci. 75:1517–1526.

Dreznek, Z., T. A. Meiniger, J. A. Barteau, D. Brocksmith, and N. J. Soper. 1994. Effect of ileal oleate on interdigestive intestinal motility of the dog. Dig. Dis. Sci. 39:1511–1518.

Dulphy, J. P., B. Remond, and M. Theriez. 1980. Ingestive behaviour and related activities in ruminants. Pages 103–122 *in* Digestive Physiology and Metabolism in Ruminants: Proc. 5th Symposium on Ruminant Physiology, Clement-Ferrard. Y. Ruckebusch and P. Thivend, eds. MTP Press, Ltd, Lancaster, England.

Dürst, B., M. Senn, and W. Langhans. 1993. Eating patterns of lactating dairy cows of three different breeds fed grass ad lib. Physiol. Behav. 54:625–631.

Emery, R. S., J. S. Liesman, and T. H. Herdt. 1992. Metabolism of long chain fatty acids by ruminant liver. J. Nutr. 122:832–837.

Firkins, J. L., and M. L. Eastridge. 1994. Assessment of the effects of iodine value on fatty acid digestibility, feed intake, and milk production. J. Dairy Sci. 77:2357–2366.

Gagliostro, G., and Y. Chilliard. 1991. Duodenal rapeseed oil infusion in early and midlactation cows. 2. Voluntary intake, milk production, and composition. J. Dairy Sci. 74:499–509.

Gaynor, P. J., R. A. Erdman, B. B. Teter, J. Sampugna, A. V. Capuco, D. R. Waldo, and M. Hamosh. 1994. Milk fat yield and composition during abomasal infusion of cis and trans octodecenoates in Holstein cows. J. Dairy Sci. 77:157–165.

Gibb, M. J., W. E. Ivings, M. S. Dhanoa, and J. D. Sutton. 1992. Changes in body components of autumn-calving Holstein-Friesian cows over the first 29 weeks of lactation. Anim. Prod. 55:339.

Grider, J. R. 1994. Role of cholecystokinin in the regulation of gastrointestinal motility. J. Nutr. 124:1334–1339.

Grovum, W. L. 1984. The control of motility of the ruminoreticulum. Pages 18–40 *in* Control of Digestion and Metabolism in Ruminants. L. P. Milligan, W. L. Grovum and A. Dobson, ed. Prentice Hall, Englewood Cliffs, NJ.

Grummer, R. R. 1991. Effect of feed on composition of milk fat. J. Dairy Sci. 74:3244–3257.

Grummer, R. R., L. E. Armentano, and M. S. Marcus. 1987. Lactation response to short-term abomasal infusion of choline, inositol, and soy lecithin. J. Dairy Sci. 70:2518–2524.

Heinrichs, J. H., D. L. Palmquist, and H. R. Conrad. 1982. Feed intake patterns of cows fed high fat grain mixtures. J. Dairy Sci. 65:1325–1328.

Hodgman, C. D., R. C. Weast, and S. M. Selby. 1960. Handbook of Chemistry and Physics. 42nd ed. Chemical Rubber Publishing Company, Cleveland, OH.

Huntington, G. B., C. K. Reynolds, and B. H. Stroud. 1989. Techniques for measuring blood flow in splanchnic tissues of cattle. J. Dairy Sci. 72:1583–1595.

Nicholson, T., and S. A. Omer. 1983. The inhibitory effect of intestinal infusions of unsaturated long-chain fatty acids on forestomach motility of sheep. Br. J. Nutr. 50:141–149.

NRC. 1989. Nutrient Requirements of Dairy Cattle. 6th rev. ed. National Academy Press, Washington, DC.

Oldick, B. S., C. R. Staples, W. W. Thatcher, and P. Gyawu. 1997. Abomasal infusion of glucose and fat—effect on digestion, production, and ovarian and uterine function of cows. J. Dairy Sci. 80:1315–1328.

Ottou, J. F., M. Doreau, and Y. Chilliard. 1995. Duodenal infusion of rapeseed oil in midlactation cows. 6. Interaction with niacin on dairy performance and nutritional balance. J. Dairy Sci. 78:1345–1352.

Palmquist, D. L. 1994. The role of dietary fats in efficiency of ruminants. J. Nutr. 124:1377S–1382S.

Reidelberger, R. 1994. Cholecystokinin and control of food intake. J. Nutr. 124:1327S–1333S.

Rindsig, R. B., and L. H. Schultz. 1974. Effects of abomasal infusions of safflower oil or elaidic acid on blood lipids and milk fat in dairy cows. J. Dairy Sci. 57:1459–1466.

Romo, G. A., D. P. Caspar, R. A. Erdman, and B. B. Teter. 1996. Abomasal infusion of cis or trans fatty acid isomers and energy metabolism of lactating dairy cows. J. Dairy Sci. 79:2005–2015.

Rutter, S. M., R. A. Champion, and P. D. Penning, 1997. An automatic system to record foraging behaviour in free-ranging ruminants. Appl. Anim. Behav. Sci. 54:185–195.

Rutter, S. M., 2000. Graze: A program to analyze recordings of the jaw movements of ruminants. Behav. Res. Methods Instruments Computers 32:86–92.

SAS. 1999. SAS/STAT Users Guide. Version 6.12. SAS Institute Inc., Cary, NC.

Scharrer, E., and W. Langhans. 1986. Control of food intake by fatty acid oxidation. Am. J. Physiol. 250:R1003–R1006.

Spiller, R. C., I. F. Trotman, T. E. Adrian, S. R. Bloom, J. J. Misiewicz, and D.B.A. Silk. 1988. Futher characterisation of the 'ileal brake' reflex in man—effect of ileal infusion of partial digest of fat, protein, and starch on jejunal motility and release of neurotensin, enteroglucagon, and peptide YY. Gut 29:1042–1051.

Staples, C. R., J. M. Burke, and W. W. Thatcher. 1998. Influence of supplemental fats on reproductive tissues and performance of lactating cows. J. Dairy Sci. 81:856–871.

Statutory Instruments. 1982. Number 1144. Agriculture. The Feeding Stuffs (Sampling and Analysis) Regulations. Her Majesty's Stationary Office, London.

Statutory Instruments. 1985. Number 1119. Agriculture. The Feeding Stuffs (Sampling and Analysis Amendment) Regulations. Her Majesty's Stationary Office, London.

Titchen. D. A., C.S.W. Reid, and P. Vlieg. 1966. Effects of intraduodenal infusions of fat on the food intake of sheep. Proc. N.Z. Soc. Anim. Prod. 26:36–51.

Vasilatos, R., and P. J. Wangsness. 1980. Feeding behaviour of lactating dairy cows as measured by time-lapse photography. J. Dairy Sci. 63:412–416.

Woltman, T. D., D. Castellanos, and R. Reidelberger. 1995. Role of cholecystokinin in the anorexia produced by duodenal delivery of oleic acid in rats. Am. J. Physiol. 38:R1420–R1433.