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Effects of feeding or abomasal infusion of canola oil in Holstein cows 1. Nutrient digestion and milk composition

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We determined the effects of feeding canola oil or infusing it into the abomasum on rumen fermentation, nutrient digestibility, duodenal flows of fatty acids, and milk composition in Holstein cows. Five ruminally and duodenally cannulated Holstein cows in late lactation were used in a 3×5 incomplete Latin square design. Treatments were 1) Control: basal diet (CON), 2) Control+supplementation of canola oil at 1 kg/d in the feed (FED), and 3) Control+abomasal infusion of canola oil at 1 kg/d (INF). Compared with CON, feed intake, ruminal fermentation characteristics, ruminal and total tract digestibilities of nutrients were not significantly affected by FED treatment but duodenal flows and milk concentrations of fatty acids (FA) such as *trans*-11 18:1 and *cis*-9 *trans*-11 18:2 (conjugated linoleic acid, CLA) were increased. In contrast to the effects of FED, INF reduced feed intake, total VFA production, intestinal flows of nutrients, FA digestibility and yields of milk and milk fat. Both FED and INF significantly reduced the proportions of saturated and medium-chain FA, and increased *cis* 18:1 in milk. Concentrations of 18:2*n*-6 and 18:3*n*-3 in milk were increased nearly 2-fold with INF relative to CON. Dietary or postruminal supplementation of canola oil to late-lactation cows reduced saturated FA and increased unsaturated C18 in milk but nutrient digestion was adversely affected with abomasal infusion of canola oil.

Keywords: Canola oil, digestibility, conjugated linoleic acid, milk fat.

Dietary fat profoundly affects feed intake, nutrient digestibility and milk composition in dairy cattle. When ruminants are fed large amounts of unsaturated fat, feed intake is reduced. These hypophagic effects are proposed to be due to impaired rumen fermentation, inhibition of fibre digestion leading to increased rumen fill, palatability, profile of fatty acids (FA) reaching the intestine, release of hormonal signals from the gut and oxidation of fat in the liver (Allen, 2000). In addition, unsaturated fats undergo considerable biohydrogenation in the rumen thereby altering the profile of FA reaching the intestine and their subsequent transfer into milk. Thus, FA composition of milk is influenced by the composition and digestibility of FA reaching the intestine.

Reduced intakes of animal fat are recommended on the basis of potential negative effects on human health associated with its saturated fat content. Thus, there has been considerable interest in increasing unsaturated FA in milk. The anti-cancer, anti-obesity, and anti-diabetic effects of conjugated linoleic acid (CLA) isomers (McGuire & McGuire, 2000), and improvements in glucose tolerance, plasma lipid profile and insulin sensitivity with oleic acid (18:1*n*-9)-enriched diets (Franz et al. 2002) have added momentum to research aimed at modifying the FA composition of milk. Among the dietary factors that can increase milk concentrations of CLA (Bauman et al. 2000) and other unsaturated FA (Ashes et al. 1997), plant-derived lipid supplements have the greatest impact. CLA in milk is derived either from incomplete ruminal biohydrogenation of 18:2*n*-6 (linoleic acid) or from Δ^9-desaturation of *trans*-11 18:1 (vaccenic acid) in the mammary gland; the latter is quantitatively the more important pathway (Bauman et al. 2000). There is also evidence that 18:1*n*-9 can be converted to *trans*-11 18:1 by the rumen microbes (Mosley et al. 2002) so that oleic and linoleic acids in canola oil are precursors for CLA synthesis in the rumen.

Canola oil is rich in unsaturated C18 (18:1*n*-9 52%; 18:2*n*-6 25%; 18:3*n*-3 12%; Kennelly, 1996) and it is readily available in Canada, both as the whole seed and the extracted oil. To date there have been no comprehensive studies of the effects of feeding relatively large amounts

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of canola oil on hormonal and metabolic regulators of feed intake, intestinal flow of FA and nutrient digestibility, and on the extent of CLA synthesis in lactating cows. Additionally, we simulated the feeding of a 'protected' lipid supplement by infusing canola oil postruminally to allow us to compare the effects of feeding and postruminal delivery of the lipid on nutrient digestibility and milk composition, as well as on hormonal and metabolic signals mediating its effects on intake. We describe here the effects on feed intake, nutrient digestibility, duodenal flows of fatty acids, milk yield and fatty acid composition. Hormonal and metabolic signals mediating the effects of fat on feed intake are the subject of the companion paper (Chelikani et al. 2004).

Materials and Methods

Cows, experimental design and treatments

Five ruminally and duodenally cannulated multiparous Holstein cows were used in an incomplete Latin square design with three treatments and three, 16-d periods. Cows were in late lactation and averaged 249 d in milk (SE 14 d) at the beginning of the experiment. They were housed in tie stalls with access to feed and water at all times, and were fed once daily at 09.00 to ensure 5% refusals; they were exercised and milked twice daily between 04.00 and 06.00, and between 16.00 and 18.00. All procedures were approved by the University of Alberta Animal Policy and Welfare Committee.

The three treatments were 1) Control (CON): basal total mixed ration (TMR), 2) Control+abomasal infusion (INF) of canola oil at 1 kg/d (Champion Feed Services Ltd, Edmonton, Canada), and 3) Control+canola oil mixed with feed at ~1 kg/d (FED). The basal TMR was formulated to meet or exceed NRC (1989) requirements for late lactation cows (Table 1). For the FED treatment, we anticipated losses of canola oil during mixing with other feed ingredients in the data rangers, at the time of delivery of feed to each animal, and also in the refusals. As a precaution against such losses, and to minimize potential effects of the oil on palatability, an excess 10% (~100 g) of oil per animal was added to the concentrate before mixing with forage in the data rangers. All cows had infusion lines in the abomasum, but the control and oil-fed cows did not receive any infusate. The oil was continuously pumped for 18 h (at ~60 g/h) by means of a Masterflex® peristaltic pump (Labcor Inc., QC, Canada) with a standard drive and four EasyloadII® pump heads. Tygon®tubing (L/S®16) that conveyed the infusate was anchored in the abomasum with a plastisol flange attached to a perforated polypropylene bottle. Placement and patency of the infusion lines in the abomasum were confirmed every 2 d. In each period the animals were adapted to the oil, which was either supplemented in the feed or continuously infused into the abomasum, by gradually increasing the amount by 250 g/d over a 4-d period.

Table 1. Ingredient and chemical composition of the basal diet

Ingredient composition, g/kg DM:	
Alfalfa silage	199
Barley silage	199
Grass hay	99
Rolled barley	302
Canola meal	86
Soybean meal	33
Dried distillers	65
Mineral-Vitamin mix†	15
Chemical composition:	Mean ± SE
DM, g/kg fresh weight	499·3 ± 51·1
Organic matter, g/kg DM	882·8 ± 24·4
Crude protein, g/kg DM	184·2 ± 26·3
Crude fat, g/kg DM	25·9 ± 5·7
Neutral detergent fibre, g/kg DM	367·2 ± 37·5
Acid detergent fibre, g/kg DM	233·2 ± 17·2
Ash, g/kg DM	14·9 ± 05·8
Gross energy, Mcal/kg DM	4·83 ± 1·03

† Contained (/kg DM) 125 g Na, 97 g Cl, 103 g Ca, 80 g P, 86 g Mg, 80 mg Co, 400 mg Cu, 200 mg I, 6000 mg Mn, 400 mg Se, 800 mg Zn, 3846 KIU Vitamin A, 2292 KIU Vitamin D, and 6539 IU Vitamin E (Champion Feed Services Ltd., Edmonton, Canada)

Sampling

Dry matter intake (DMI) was based on feed consumption during the last 7 d of each period. Samples of TMR, ingredients, and refusals were collected during the last 4 d of each period and composited by cow within period. Body weight and body condition score (BCS) were recorded once at the end of each period. Body weights were recorded between 07.00 and 08.00, which was after milking and before feeding. Beginning on day 15, ruminal fluid samples were collected at 08.50, 09.30, 10.00, 10.30, 11.00, 12.00, 13.00, 15.00, 17.00, 19.00, 21.00, 23.00, 01.00, 03.00, 05.00 and 07.00. Samples were filtered through a strainer and the pH of each sample was determined immediately using a glass electrode. An aliquot (~4 ml) of sample was acidified with 1 ml of H_3PO_4 (250 ml/l) and frozen for determination of volatile fatty acids (VFA) and ammonia nitrogen. For measuring nutrient flows and digestibilities, 10 g of Cr_2O_3 marker was administered into the rumen twice daily, at 06.00 and 18.00, during the last 10 d of each period (Elliott et al. 1997). Faecal grab samples were collected at 12-h intervals from days 12 to 16 of each period and composited on an equal wet weight basis by animal within period. Samples of duodenal digesta (~250 ml) were collected at 4-h intervals over a 48-h period on days 15 to 16, the pH was determined, and samples were composited for each animal within a period on an equal wet weight basis. Daily milk yield was recorded, and milk samples were collected on days 14 to 16. Individual samples were analysed for milk fat, protein and lactose by infrared analysis at the Alberta Central Milk Testing Laboratory (Edmonton, AB, Canada). On each sampling day, the samples collected in the morning and evening were

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composited as a percentage of yield and stored at −20 °C for subsequent fatty acid analysis.

Chemical analysis

Samples of feed, refusals, and digesta were dried at 60 °C for 72 h, and ground through a 1-mm screen (Thomas-Wiley laboratory mill model 4, PA, USA). Dry matter (DM) was determined by drying samples at 110 °C overnight, and organic matter (OM) was calculated as weight loss upon ashing for at least 6 h at 500 °C. Samples were analysed for crude protein (CP) (6·25 × N; Leco FP-428 nitrogen determinator, Leco® Corporation, MI, USA), neutral detergent fibre (NDF), acid detergent fibre (ADF), lignin (Ankom filter bag technique®, Ankom Company, NY, USA) and gross energy (Leco® Automatic Calorimeter, AC300, Leco Corporation, MI, USA). Ruminal fluid concentrations of VFA and NH_3-N were determined according to Khorasani et al. (1996). Faecal and duodenal samples were analysed for Cr by the procedure of Fenton & Fenton (1979). Milk fat extraction and transmethylation were performed by the procedure of Chouinard et al. (1999). Milk fatty acid methyl esters (FAME) were analysed on a Varian 3600 GC equipped with a septum programmable injector and flame ionization detector. FAME were separated on a BPX70 fused silica capillary column (50 m × 0·32 mm, SGE column, Melbourne, Australia). The injector temperature was increased from 70 °C to 230 °C at 150 deg C/min and held for 17 min. The detector temperature was held constant at 230 °C. Column conditions were: initial column temperature held at 50 °C for 0·1 min, increased at 25 deg C/min to 170 °C and held for 1 min, increased from 170 °C to 180 °C at 2 deg C/min, then raised to 230 °C at 10 deg C/min and held for 3 min. Flow rates of gases were: helium carrier gas at 1 ml/min, helium make-up gas at 30 ml/min, hydrogen at 30 ml/min, and air at 300 ml/min. Identification of peaks was by comparison with retention times of standard FAME (GLC 85, GLC 411, Methyl *trans*-11 18 : 1, and *cis*-9 *trans*-11 CLA, Nuchek Prep Inc., MN, USA). Peak areas of each fatty acid were expressed as a proportion of total FAME detected. Feed, duodenal, and faecal FAME were prepared by a modification of the procedures of Sukhija & Palmquist (1988) and Chin et al. (1992). To 0·5 g of sample in screw capped 16 × 125 mm test tubes, 1 ml of hexane, 1 ml of heptadecanoic acid internal standard (C17 : 0: 4 mg/ml in hexane), and 3 ml of fresh 4% methanolic HCl were added. The tubes were tightly capped, vortexed, and heated for 1 h at 60 °C. Methylation with 4% methanolic HCl at 60 °C is reported to convert only 5% of the *cis*-9 *trans*-11 CLA isomer to *trans*-9 *trans*-11/*trans*-10 *trans*-12 CLA isomers (Chin et al. 1992). After cooling, 5 ml of 6% K_2CO_3 and 2 ml of hexane were added, the tubes were vortexed and centrifuged. To the hexane extract 1 g of Na_2SO_4 and 1 g of activated charcoal were added, the tubes vortexed and centrifuged, and the clear hexane layer was transferred into GC vials. GC analysis was carried out as described for milk FAME.

Calculations

Fatty acid intake for cows on treatment INF was calculated by adding the intake of fatty acids from basal diet to the amount of fatty acids infused. Duodenal and total tract flows of DM were calculated by dividing the amount of Cr dosed per day (10 g) by the Cr concentration in duodenal and faecal samples, respectively. Dry matter (DM) flows were multiplied by nutrient concentration in duodenal or faecal samples to obtain duodenal or total flows of nutrients. Digestibilities were calculated as: (nutrient intake−nutrient flow)/nutrient intake. Energy balance was calculated according to NRC (1989) as the difference between net energy (NE) intake and NE required. NE required was calculated as NE for maintenance+NE for milk production. Net energy intake was calculated as the daily DM intake (DMI) multiplied by the NE_L concentration of the diet. Diet NE_L was determined from tables, and the assigned table value for fat was 38·9 kJ/g. NE for maintenance was calculated as $0{\cdot}08 \times \text{kg BW}^{0{\cdot}75}$.

Statistical analysis

Results were analysed by ANOVA for a 3 × 5 incomplete Latin square design using the general linear models procedure of SAS (1999). Intake and production variables were reduced to means for each cow in each period. The model for analysing these variables and digestibility was (Hicks, 1999):

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + e_{ijk}$$

where μ is the population mean, α_i is a population parameter corresponding to treatment i (i=1, 2, 3), β_j is a random variable corresponding to animal j (j=1, 2, 3, 4, 5), γ_k is a parameter corresponding to period k (k=1, 2, 3) and e_{ijk} is the residual error. Main effects of cow, period and treatment were tested using the residual error. Hourly values of ruminal variables (pH, VFA and ammonia) were analysed as a split-plot in time using the following model:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_k + (\alpha\gamma)_{ik} + (\alpha\beta\gamma)_{ijk} + \delta_l + (\alpha\delta)_{il} + (\beta\delta)_{jl} + (\gamma\delta)_{jk} + e_{ijkl}$$

where $(\alpha\gamma)_{ik}$ is the effect of treatment by period interaction, $(\alpha\beta\gamma)_{ijk}$ is the treatment by cow by period interaction, δ_l is the effect of time (l=1 to 16), $(\alpha\delta)_{il}$ is the effect of treatment by time interaction, $(\beta\delta)_{jl}$ is the effect of cow by time interaction, $(\gamma\delta)_{jk}$ is the effect of period by time interaction, and e_{ijkl} is the residual error. Main effects of cow, period and diet were tested using the whole-plot error term $(\alpha\beta\gamma)_{ijk}$ and the treatment by time interaction $(\alpha\delta)_{il}$ was tested using the residual error term (e_{ijkl}). Mean separation was performed using the LSMEANS statement with the PDIFF option after Tukey-Kramer's adjustment. Stepwise regression analysis was used for determining the relative contribution of individual FA flows at duodenum to variation in DMI.

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Table 2. Fatty acid composition of canola oil

Values are means ± SE for $n=15$

Fatty acid	Fatty acid methyl esters, g/100 g
14 : 0	0·04 ± 0·01
15 : 0	0·04 ± 0·01
16 : 0	4·21 ± 0·03
16 : 1	0·27 ± 0·02
18 : 0	2·08 ± 0·03
cis-18 : 1*n*-9	62·35 ± 0·14
18 : 2*n*-6	18·51 ± 0·06
18 : 3*n*-3	8·97 ± 0·36
Others	2·79 ± 0·06

Results

Intake, energy balance, duodenal flows, and total tract digestibility of nutrients

The ingredient and chemical composition of the basal diet and the FA composition of canola oil are given in Tables 1 and 2, respectively. Nutrient intake, duodenal flows, and total tract digestibility are in Table 3. Relative to CON treatment, INF caused a significant ($P<0·05$) reduction in DMI. Further, when expressed as a percentage of body weight, intake was also reduced ($P<0·05$) with INF compared with CON or FED (CON 2·57%, FED 2·58%, INF 2·07%, SE 0·10). Body weight (CON 544, FED 563, INF 548, SE 9·0, kg) and body conditions score (CON 2·48, FED 2·66, INF 2·29, SE 0·19) did not differ ($P>0·10$) among treatments. Energy balance did not differ ($P>0·10$) among treatments (CON 7·38, FED 11·64, INF 7·77, SE 1·46). With INF, intakes of OM, NDF, ADF, and cellulose were lower ($P<0·05$) than for CON or FED, and intakes of CP were lower ($P<0·05$) than for FED. Intakes of DM, OM, CP, NDF and ADF did not differ ($P>0·10$) between CON and FED treatments. Duodenal flows of DM and OM were lower for INF than for CON or FED ($P=0·05$). Except for greater ruminal digestion and lower duodenal flows of CP for FED than for CON ($P<0·05$), there were no differences among treatments ($P>0·10$) for either ruminal or total tract digestion of DM, OM, NDF, ADF and cellulose.

Ruminal fermentation

Since treatment × time interaction was not significant ($P>0·10$) for ruminal parameters, means across sampling times are presented in Table 4. Overall mean concentrations of ammonia and pH did not differ ($P>0·10$) among treatments. Total molar concentrations of VFA were reduced ($P<0·05$) with INF compared with CON or FED. Molar proportion of propionate decreased ($P<0·05$) for cows on INF relative to CON. Molar proportions of other VFA, and acetate : propionate ratio, did not differ ($P>0·10$) among treatments.

Table 3. Effect of feeding or abomasal infusion of canola oil on ruminal and total tract digestibilities of dry matter (DM), organic matter (OM), crude protein (CP), neutral detergent (NDF) and acid detergent fibre (ADF) and cellulose. Nutrient intake and duodenal flows are in kg/d; ruminal and total tract digestibilities are expressed as g/100 g

Values are means ± SEM for $n=5$

	Control	Feeding	Infusion	SEM
DM				
Intake	14·02^{a}	14·54^{a}	11·33^{b}	0·66
Duodenal flow	9·43^{a}	9·60^{a}	6·34^{b}	1·23
Ruminal digestibility	42·25	45·08	36·45	4·62
Total tract digestibility	62·26	61·11	57·45	2·54
OM				
Intake	12·19^{a}	12·38^{a}	10·10^{b}	0·53
Duodenal flow	7·83^{a}	8·08^{a}	5·22^{b}	1·09
Ruminal digestibility	45·37	48·47	41·77	5·43
Total tract digestibility	66·86	62·76	60·41	2·83
CP				
Intake	2·66^{ab}	3·23^{a}	2·13^{b}	0·27
Duodenal flow	2·16^{a}	1·95^{ab}	1·27^{b}	0·31
Ruminal digestibility	24·17^{a}	37·19^{b}	26·41^{ab}	1·98
Total tract digestibility	66·78	69·13	64·55	3·98
NDF				
Intake	7·40^{a}	8·39^{a}	6·08^{b}	0·39
Duodenal flow	5·57	5·54	3·64	0·70
Ruminal digestibility	43·29	50·66	41·78	6·59
Total tract digestibility	49·39	44·77	45·13	3·22
ADF				
Intake	4·29^{a}	4·56^{a}	3·36^{b}	0·18
Duodenal flow	3·68	3·53	2·39	0·47
Ruminal digestibility	34·69	44·29	31·26	6·09
Total tract digestibility	42·61	36·61	37·31	4·27
Cellulose				
Intake	3·16^{a}	3·38^{a}	2·48^{b}	0·16
Duodenal flow	1·95	1·90	1·19	0·25
Ruminal digestibility	53·13	60·35	54·18	5·76
Total tract digestibility	57·76	54·18	55·49	2·84

^{a,b} Means within the same row without a common superscript differ ($P<0·05$)

Intake, duodenal flows, and total tract digestibility of fatty acids

Intake and duodenal flows of FA are in Table 5. Compared with CON, both INF and FED increased ($P<0·001$) total FA intake. Intakes of total FA and individual FA did not differ ($P>0·10$) between FED and INF. Compared with CON, both FED and INF almost doubled ($P<0·01$) total FA flow at duodenum. The increase in duodenal flow of unsaturated FA ($P<0·05$) with FED over CON was due primarily to a 4-fold increase of both *cis* and *trans* isomers of 18 : 1; and the increased flow of saturated FA was due to greater flows of 18 : 0 (+150%) and 16 : 0 (+77%). Duodenal flow of *trans*-11 18 : 1 was greater (+367%) for FED than for INF ($P<0·05$), and flows of *cis*-9 *trans*-11 18 : 2 (CLA) were measurable only for FED but undetectable for CON or INF.

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Table 4. Effect of feeding or abomasal infusion of canola oil on ruminal pH and concentration of ammonia nitrogen (NH_3N) and volatile fatty acids (VFA) in dairy cows

Values are means ± SEM for $n=5$

	Control	Feeding	Infusion	SEM
pH	6·29	6·23	6·43	0·06
NH_3-N, mg/l	152·3	161·4	162·2	18·3
Total VFA, mM	107·26[a]	105·33[a]	93·94[b]	2·19
Individual VFA, mmol/mol				
Acetate, (A)	657·1	656·0	596·7	33·6
Propionate (P)	237·7[a]	206·3[ab]	180·6[b]	22·5
Butyrate	124·1[ab]	140·4[a]	112·4[b]	6·5
Isobutyrate	11·8	11·1	11·8	0·5
Valerate	21·5	16·9	15·0	1·4
Isovalerate	16·7	18·0	18·8	0·9
A : P ratio	3·11	3·23	3·35	0·11

[a,b] Means within the same row without a common superscript differ ($P<0·05$)

As expected, greater flows of 18 : 1*n*-9, 18 : 2*n*-6, and 18 : 3*n*-3 with INF ($P<0·01$) contributed to the increase in unsaturated FA flow and in the unsaturated : saturated FA ratio when compared with CON or FED ($P<0·05$). Although duodenal flows of unsaturated and saturated FA were greater with FED than with CON ($P<0·05$), the unsaturated : saturated FA ratio did not differ ($P>0·10$).

Total tract digestibility and postruminal absorption of FA are in Table 6. Total tract digestibility of FA did not differ ($P>0·10$) between CON and FED except for reduced ($P<0·05$) digestibility of 18 : 0 (−16%) and 15 : 0 (−22%) with FED. However, absorption (g/d) of all FA was greater ($P<0·05$) for FED than for CON. Relative to CON, with INF, digestibilities of 15 : 0, 16 : 0, 18 : 0, and 18 : 1*n*-9 were reduced ($P<0·05$) by nearly 20% leading to a reduction in total FA digestibility of 10%. Postruminal absorption (g/d) of 18 : 1*n*-9, 18 : 2*n*-6, and 18 : 3*n*-3 was greater ($P<0·05$) with INF than with CON or FED. Compared with CON, FED increased ($P<0·05$) postruminal absorption of 16 : 0, 18 : 0 and 18 : 1*n*-9. Total FA absorbed postruminally was nearly 2-fold greater ($P<0·001$) with FED or INF relative to CON. Relative to FED, digestibilities of 16 : 0, 18 : 1*n*-9 and total FA, and postruminal absorption of 18 : 0 were reduced ($P<0·05$) with INF.

Milk yield and fatty acid composition

Yields of milk and milk constituents did not differ ($P>0·10$) between CON and FED, but milk fat percentage was reduced ($P<0·05$) with FED (Table 7). Relative to CON, INF reduced milk fat percentage by 39% ($P=0·007$) and milk fat yield by 35% ($P=0·01$). Composition of milk FAME is in Table 8. Compared with CON, FED or INF caused ($P<0·001$) reductions in saturated and medium-chain FA (11 : 0 to 17 : 0), and increases in monounsaturated long-chain FA. Relative to CON, saturated FA were reduced by 16% with FED, and 30% with INF. There were no treatment differences ($P>0·10$) in the proportions of individual short chain (4 : 0 to 10 : 0) FA (results not shown). Proportions of medium-chain FA were reduced by 26% with FED and by 36% with INF compared with CON. This decrease was due primarily to a reduction of 14 : 0 by 18% with FED ($P<0·01$) and by 32% with INF ($P<0·001$); and a reduction ($P<0·001$) of 16 : 0 by 29% with FED and 39% with INF. Relative to CON, 18 : 0 increased by 29% with FED ($P<0·01$) but was reduced by 17% with INF ($P<0·05$). Proportions of 18 : 2*n*-6 and 18 : 3*n*-3 were similar for CON and FED ($P>0·10$), but were increased by 267% and 270% respectively with INF ($P<0·001$). Total 18 : 1 increased ($P<0·001$) by more than 40% with FED and INF relative to CON. Compared with CON, among the 18 : 1 isomers, 18 : 1*n*-9 was increased ($P<0·001$) by 26% with FED and 43% with INF, whereas *trans*-11 18 : 1 increased 194% with FED ($P<0·001$) but was not affected by INF ($P>0·10$). Proportions of the CLA isomer *cis*-9 *trans*-11 18 : 2 was increased by 166% with FED relative to CON or INF ($P<0·001$).

Discussion

Rumen fermentation was relatively stable with FED as evidenced by the lack of effect on rumen pH, ammonia nitrogen, VFA and fibre digestibility. Although duodenal flows of total unsaturated and saturated FA were greater with FED than with CON, their ratios were similar. Therefore, the relative stability of the rumen and postruminal environment with FED might explain the lack of any adverse effects on DMI and concurs with results from a recent study with canola oil supplementation (DePeters et al. 2001) but not with others (Jenkins, 1999; Jenkins et al. 2000).

Reduced feed intake with postruminal oil infusion in our study agrees with a majority of reports for fat infused postruminally or protected from rumen metabolism. The amount of oil infused in our study, and the associated 2·6 kg reduction in feed intake, is comparable to other reports. For example, duodenal infusion of canola oil at 1·1 kg/d (Gagliostro & Chilliard, 1991) or 0·7 kg/d (Ottou et al. 1995) resulted in drops in DMI of 2·6 kg and 1·8 kg respectively, while no change in DMI was reported with ruminal or abomasal infusion of 0·33 kg/d of canola oil (DePeters et al. 2001). Protection of canola from rumen digestion also reduced DMI in some studies (Jenkins, 1999; Jenkins et al. 2000) but not in others (Enjalbert et al. 1997; Khorasani & Kennelly, 1998). As expected, flows of unsaturated and total FA, and the ratio of unsaturated to saturated FA at the duodenum were much greater for INF than for CON or FED. In a stepwise regression approach to explain the variation in DMI caused by the flows of individual FA at the duodenum, we found that duodenal flows of 18 : 1*n*-9 and 18 : 2*n*-6 together explained 89% of the variation in DMI, with 18 : 2*n*-6 contributing 81% and 18 : 1*n*-9 contributing 8% of the total variation in DMI

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Table 5. Effect of feeding or abomasal infusion of canola oil on intake and duodenal flow of fatty acids in dairy cows

Values are means ± SEM for $n=5$

	Control	Feeding	Infusion†	SEM
Intake, g/d				
14 : 0	0·14[a]	2·65[b]	2·40[b]	0·10
15 : 0	3·12	4·39	4·77	0·92
16 : 0	43·96[a]	97·60[b]	89·48[b]	3·28
16 : 1	0·28[a]	3·82[b]	2·82[b]	0·69
18 : 0	75·06[a]	122·44[b]	112·07[b]	7·63
cis-18 : 1*n*-9	76·45[a]	620·59[b]	630·79[b]	41·33
18 : 2*n*-6	38·47[a]	195·38[b]	201·55[b]	15·89
18 : 3*n*-3	6·75[a]	100·80[b]	89·99[b]	5·99
Others	0·65[a]	3·36[a]	7·64[b]	1·37
Total	244·19[a]	1154·29[b]	1138·52[b]	62·52
Duodenal flow, g/d				
14 : 0	3·19	3·38	3·87	0·39
14 : 1	3·44	3·62	4·87	1·22
15 : 0	2·39	2·70	3·15	0·74
16 : 0	58·71[a]	104·19[b]	99·76[b]	7·73
16 : 1	6·54	6·74	6·96	1·46
18 : 0	175·05[a]	440·68[b]	278·01[c]	37·60
trans-11 18 : 1	11·51[a]	53·77[b]	13·02[a]	5·71
cis-18 : 1*n*-9	45·61[a]	241·63[b]	569·83[c]	92·88
18 : 2*n*-6	13·54[a]	16·94[a]	83·49[b]	8·21
cis-9 *trans*-11 18 : 2 (CLA)	not detected	3·09	not detected	0·51
18 : 3*n*-3	3·86[a]	2·32[a]	36·01[b]	3·53
Others	11·38	13·11	21·68	5·81
Total fatty acids	328·74[a]	880·41[b]	973·48[b]	88·92
Total saturated‡	238·53[a]	529·71[b]	329·90[a]	46·24
Total unsaturated§	88·87[a]	299·32[b]	599·03[c]	55·89
Unsaturated : Saturated	0·66[a]	0·65[a]	2·71[b]	0·45

† Intake and duodenal flows include values for the infused oil
‡ 14 : 0, 15 : 0, 16 : 0, 18 : 0
§ 14 : 1, 16 : 1, 18 : 1, 18 : 2, 18 : 3
[a,b,c] Means within the same row without a common superscript differ ($P<0·05$)

($P<0·01$). According to Bremmer et al. (1998) the amount of 18 : 1*n*-9, 18 : 2*n*-6 and 18 : 3*n*-3 infused into the abomasum together explained 64% of the variation in DMI. Therefore, in addition to the total amount of unsaturated FA reaching the intestine, the ratio of unsaturated : saturated FA, and increased flows of 18 : 1*n*-9 and 18 : 2*n*-6, might have contributed to the hypophagic effects of abomasal canola oil in our study. Potential hormonal and/or metabolic mediators involved in these effects are discussed in the companion paper (Chelikani et al. 2004).

Lower molar concentrations of propionate and total VFA with INF than with CON or FED might be due to lower substrate availability for fermentation. These changes in VFA patterns with postruminal oil infusion were similar to those in one report (Gagliostro & Chilliard, 1991), but not in another (Bremmer et al. 1998). These changes in VFA are probably due to the 20% drop in feed intake with INF.

As expected, both FED and INF substantially increased total FA flows at the duodenum. However, when the total FA flows at the duodenum are expressed as a percentage of total FA intake, there was a 35% increase in total FA flow at the duodenum for cows on CON, a 24% decrease for cows on FED, and a 14% decrease for cows on INF. This agrees generally with other reports (Ferlay et al. 1993; Pantoja et al. 1996; Loor et al. 2002). For example, feeding canola oil at 3·3% (Loor et al. 2002), or 7·7% (Ferlay et al. 1993), or a blend of canola oil and tallow at 5% (Pantoja et al. 1996) reduced total FA flows at the duodenum, as a percentage of intake, by 1%, 22%, and 11%, respectively, whereas the duodenal FA flows for the control diets in these studies were increased by 11%, 15%, and 3%, respectively. Similarly, feeding a rumen-protected source of canola fat such as canolamide at 3·3% (Loor et al. 2002), or calcium salts of canola oil at 8·4% of diet DM (Ferlay et al. 1993), reduced total FA flows at the duodenum by 32% and 37%, respectively. Therefore, across studies, the net loss of total FA at duodenum depends on the level of inclusion of canola fat. Although the causes are not completely understood, the reduced duodenal FA flows, relative to intake, for cows fed supplemental fat, could be due to ruminal absorption or degradation of FA, conversion of FA to ketone bodies by

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Table 6. Effect of feeding or abomasal infusion of canola oil on total tract digestibility and postruminal absorption of fatty acids (FA) in dairy cows

Values are means ± SEM for $n = 5$

	Control	Feeding	Infusion	SEM
Digestibility, g/kg				
14 : 0	739·9	938·6	650·2	148·9
15 : 0	941·3[a]	733·4[b]	726·1[b]	64·9
16 : 0	928·5[a]	879·3[a]	714·4[b]	60·3
18 : 0	851·9[a]	709·3[b]	697·1[b]	29·9
cis-18 : 1*n*-9	975·9[a]	958·7[a]	787·2[b]	17·3
18 : 2*n*-6	989·1	988·6	980·6	6·0
18 : 3*n*-3	988·8	981·5	965·1	12·1
Total FA	848·4[a]	910·9[a]	766·9[b]	60·6
Absorption, g/d				
14 : 0	2·83	3·16	2·24	0·66
15 : 0	2·29	2·25	2·12	0·90
16 : 0	53·59[a]	89·45[b]	81·05[b]	7·18
18 : 0	145·12[a]	314·20[b]	173·87[c]	17·79
cis-18 : 1*n*-9	39·20[a]	231·01[b]	438·32[c]	29·58
18 : 2*n*-6	12·87[a]	10·14[a]	82·23[b]	4·06
18 : 3*n*-3	3·10[a]	1·73[a]	35·45[b]	1·27
Total FA	265·98[a]	764·37[b]	867·45[b]	90·03

[a,b,c] Means within the same row without a common superscript differ ($P < 0·05$)

Table 7. Effect of feeding or abomasal infusion of canola oil on milk composition and yield in dairy cows

Values are means ± SEM for $n = 5$

	Control	Feeding	Infusion	SE
Milk yield, kg/d	11·35	14·05	12·37	0·89
Composition, g/kg				
Fat	33·9[a]	25·8[b]	20·3[b]	2·3
Protein	29·9	31·9	32·1	0·9
Lactose	40·8	42·8	40·2	1·4
Production, kg/d				
Fat	0·39[a]	0·37[a]	0·25[b]	0·02
Protein	0·33	0·45	0·39	0·03
Lactose	0·46	0·60	0·49	0·04

[a,b] Means within the same row without a common superscript differ ($P < 0·05$)

the ruminal epithelium and/or direct inhibition by excess FA available in the rumen of FA synthesis *de novo* by the rumen microbes (Doreau & Chilliard, 1997). In contrast, the contribution of microbial FA to total duodenal FA flows might be greater for cows on CON leading to a net increase in FA flow at the duodenum.

The degree of biohydrogenation of unsaturated FA in the rumen, their intestinal digestibility and subsequent absorption all influence the FA composition of milk. When large amounts of unsaturated C18 are fed, there is increased production of intermediate products of rumen biohydrogenation such as *trans*-11 18 : 1 and *cis*-9 *trans*-11 18 : 2 (Bauman et al. 2000) as seen for FED in this study. Conversion of 18 : 1*n*-9 to *trans*-11 18 : 1 by the ruminal microbes (Mosley et al. 2002) might also have contributed to the increased duodenal flows of *trans*-11 18 : 1. Biohydrogenation of 18 : 1*n*-9 and CLA to 18 : 0, in addition to dietary 18 : 0, undoubtedly contributed to the nearly 2-fold increase in 18 : 0 flow at the duodenum with FED.

Intestinal digestibility of FA varies with the degree of unsaturation. From an extensive review of literature, Doreau & Chilliard (1997) concluded that the digestibilities of 18 : 1*n*-9 and 18 : 2*n*-6 are higher than those of 18 : 0 and 18 : 3*n*-3, and that the capacity for FA absorption is much greater than 1 kg/d. Overall, total tract digestibilities of FA were similar between CON and FED except for a depression in digestibility of 18 : 0 and 15 : 0. Reduction in total tract digestibility of 18 : 0 with FED and INF might be due to greater duodenal flows, and hence lower postruminal digestibility of this FA. Postruminal infusion of relatively large amounts of 18 : 1*n*-9 may have overwhelmed the absorptive capacity of the intestine leading to a depression in digestibility. On the contrary, with FED, the biohydrogenation of 18 : 1*n*-9 and lower duodenal flows might have improved total tract digestibility. Absorption of C18 unsaturated FA was generally increased by both FED and INF, as evidenced by significantly increased plasma fatty acid concentrations for both FED and INF relative to CON (Chelikani et al. 2004). The CLA isomer, *cis*-9 *trans*-11 18 : 2, was detectable only in the duodenal contents and not in the faeces of FED cows. Both CLA and *trans*-11 18 : 1 are probably completely digested and absorbed, rather than transformed postruminally, because the proportions of these fatty acids were increased nearly 4-fold in plasma of FED compared with CON or INF (see Chelikani et al. 2004).

In this study, canola oil reduced milk fat percentage through potentially different mechanisms. Reduced milk fat percentage with FED may be attributable to a dilution of milk fat by the marginal increase in milk yield and to ruminally derived *trans*-11 18 : 1 (Romo et al. 2000). However, it is unlikely that *trans*-11 18 : 1 was responsible for the reduction in percentage and yield of milk fat with INF because neither duodenal flows (Table 5) nor milk concentrations of *trans*-11 18 : 1 (Table 8) differed from CON. A similar response was observed by Chouinard et al. (1998) when feeding calcium salts of canola oil. It is more likely that the depressed milk fat with INF resulted from inhibition of mammary lipogenesis *de novo* by long-chain FA (18 : 1*n*-9, 18 : 2*n*-6, and/or 18 : 3*n*-3). In contrast to our study on cows in late lactation, duodenal infusion of a similar amount of canola oil to mid-lactation Holsteins did not affect milk fat content or yield (Gagliostro & Chilliard, 1991), suggesting that late-lactation cows might be more susceptible than those in mid-lactation to milk fat depression caused by postruminal infusion of canola oil.

Canola oil supplementation affected milk FA composition profoundly. The reduction in 14 : 0 and 16 : 0 with INF was much greater than that reported by others for

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Table 8. Effect of feeding or abomasal infusion of canola oil on milk fatty acid composition (g/100 g FAME) in dairy cows

Values are means ± SEM for $n=5$

	Control	Feeding	Infusion	SEM
4:0–10:0	6·26	5·11	5·59	0·43
11:0	0·29^{a}	0·19^{ab}	0·12^{b}	0·03
12:0	3·63	2·82	3·68	0·57
12:1	0·19^{a}	0·08^{b}	0·02^{b}	0·03
14:0	11·94^{a}	9·77^{b}	8·07^{c}	0·45
14:1	0·88^{a}	0·84^{a}	0·41^{b}	0·07
15:0	1·87^{a}	1·11^{b}	0·79^{b}	0·18
15:1	0·22	0·29	0·15	0·09
16:0	30·12^{a}	21·19^{b}	18·33^{c}	0·55
16:1	1·62^{a}	1·29^{a}	0·86^{b}	0·11
17:0	0·86^{a}	0·56^{b}	0·47^{c}	0·03
17:1	0·29	0·13	0·15	0·05
18:0	10·65^{a}	13·76^{b}	8·75^{c}	0·59
trans-11 18:1	1·95^{a}	5·74^{b}	2·15^{a}	0·36
cis-18:1*n*-6	0·68^{a}	1·54^{b}	0·48^{c}	0·05
cis-18:1*n*-9	24·2^{a}	30·53^{b}	34·62^{c}	0·92
cis-18:1*n*-11	0·71^{a}	0·86^{a}	2·20^{b}	0·16
18:2*n*-6	2·37^{a}	1·87^{a}	8·69^{b}	0·29
cis-9 *trans*-11 18:2 (CLA)	0·51^{a}	1·36^{b}	0·51^{a}	0·03
18:3*n*-3	0·42^{a}	0·38^{a}	3·36^{b}	0·16
20:0	0·13^{a}	0·22^{b}	0·06^{a}	0·03
20:1	0·15^{a}	0·33^{b}	0·53^{c}	0·05
18:1*n*-9: 18:0	2·64^{a}	2·85^{a}	4·61^{b}	0·13
Saturated†	62·42^{a}	52·61^{b}	43·36^{c}	0·95
Monounsaturated‡	30·76^{a}	41·65^{b}	41·56^{b}	0·93
Polyunsaturated§	3·89^{a}	3·56^{a}	12·64^{b}	0·40
Medium-chain‖	51·95^{a}	38·29^{b}	33·05^{c}	1·31
Long-chain¶	41·79^{a}	56·59^{b}	61·35^{b}	1·55

^{a,b,c} Means within the same row without a common superscript differ ($P<0·05$)

† 4:0, 6:0, 8:0, 10:0, 11:0, 12:0, 14:0, 15:0, 16:0, 17:0, 18:0, 20:0

‡ 12:1, 14:1, 15:1, 16:1, 17:1, 18:1, 20:1

§ 18:2, 18:3

‖ 11:0, 12:0, 12:1, 14:0, 14:1, 15:0, 15:1, 16:0, 16:1, 17:0, 17:1

¶ 18:0, 18:1, 18:2, 18:3, 20:0, 20:1

abomasal infusion of canola oil (DePeters et al. 2001), but similar to the changes observed for duodenal infusion of canola oil to mid-lactation Holstein cows (Chilliard et al. 1991; Ottou et al. 1995). The greater reduction in medium-chain FA with postruminal oil infusion observed in our study, compared with most other studies, may be due to additive effects of a decrease in VFA production (Table 4), a direct inhibitory effect of long-chain FA on synthesis *de novo* of medium-chain FA in the mammary gland, or due to stage of lactation. However, confounding effects of reduction in VFA production on lipogenesis *de novo* could not be separated from direct effects of long-chain FA in this study. Despite this limitation, comparisons of the magnitude of reduction of these FA between studies reveals that the reduction is not linearly related to the amount of oil infused postruminally, which might be due to desensitization of mammary lipogenic activity to the inhibitory effects of large amounts of long chain FA and/or effects of stage of lactation. The increase in 18:1*n*-9: 18:0 ratio with INF relative to CON was probably due to increased supply of 18:1*n*-9 to the mammary gland. The magnitude of the drop in 14:0 and 16:0 with FED in this study is greater than that reported by DePeters et al. (2001) but similar to the decrease of 14:0 and 16:0 reported by Jenkins (1999). The lack of differences between CON and FED in their impact on 18:2*n*-6 and 18:3*n*-3 concentrations was due to their extensive biohydrogenation, which led to lower availability and intestinal absorption of these FA. Increased duodenal flows and absorption of the biohydrogenation intermediate *trans*-11 18:1 might have contributed to the increased levels of this isomer in milk of cows fed canola oil.

Dietary manipulation of milk CLA levels in late-lactation cows has received little attention. In this study, the proportion of CLA was increased by 166% by feeding canola oil. The relative increase of CLA in our study is greater than the 65% increase with feeding rapeseed to mid-lactation cows (Stanton et al. 1997), but lower than the 277% increase with feeding calcium salts of canola oil fatty acids in early-lactation (Chouinard et al. 2001). According to Bauman et al. (2000) the majority of this CLA isomer is probably synthesized by desaturation of *trans*-11 18:1 by mammary Δ^9-desaturase activity. In this study, the linearity between *trans*-11 18:1 and CLA in milk appeared to be much stronger ($y=0·221x+0·067$, $r^2=0·91$, $P<0·001$) than the relationship between these two FA in duodenal contents ($y=0·048x-0·007$, $r^2=0·76$, $P<0·01$) suggesting that mammary Δ^9-desaturase activity might be important in CLA synthesis. Current dietary guidelines for humans are to limit the intakes of saturated FA and polyunsaturated FA to 10% and 15% of total energy intake, with the combined intakes of oleic acid and carbohydrates at 60–70% of energy intake (Franz et al. 2002). In this study, feeding canola oil increased the proportion of oleic acid and CLA at the expense of saturated FA in milk, which may have favourable health implications.

In summary, feeding canola oil at 1 kg/d did not adversely affect ruminal fermentation, or ruminal and total tract digestibilities of DM, CP and fibre. Incomplete biohydrogenation of C18 unsaturated FA from canola oil might have resulted in increased duodenal flow of intermediates such as *trans*-11 18:1 and CLA, and their subsequent transfer to milk. In contrast to the effects of dietary canola oil, abomasal infusion of oil reduced feed intake, total VFA production, nutrient flows to the intestine, total FA digestibility and the percentage and yield of milk fat. Abomasal infusion of canola oil increased concentrations of 18:1*n*-9, 18:2*n*-6 and 18:3*n*-3 and, similar to feeding oil, reduced the proportions of saturated and medium-chain FA in milk.

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