Responses of Primiparous and Multiparous Holstein Cows to Additional Energy from Fat or Concentrate During Summer¹

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ABSTRACT

Supplemental fat has been advocated for use during hot weather and often increases milk yield of cows past peak production when energy intake should not be limiting. Relative responses of primiparous and multiparous cows to supplemental fat or isocaloric addition of concentrates under hot weather conditions have not been determined. Nine multiparous and nine primiparous Holstein cows (154 and 167 d in milk, respectively) were used in a replicated 3×3 Latin square design with 28-d periods. Diets were 1) control (35% alfalfa silage, 25% corn silage, and 40% concentrate, dry matter [DM] basis); 2) control plus 3% fat (HF); and 3) high concentrate ([HC] 15% alfalfa silage, 25% corn silage, and 60% concentrate). Diets were isonitrogenous; diets HF and HC were isocaloric (1.60 Mcal of net energy for lactation [NE_L] per kilogram DM) and higher energy than the control (1.52 Mcal/kg). No parity $\times$ diet interactions approached significance. DM intake (DMI) was greater when cows were fed HC than when they were fed HF (21.0, 20.1, and 21.3 kg/d for control, HF, and HC, respectively); intake of NE_L tended to be increased only for HC. Milk yield was increased by higher-energy diets, but milk fat content was decreased. Milk total protein content was decreased by HF and increased by HC. Yield of solids-corrected milk (SCM) was not different among diets. Efficiency of milk production, expressed either as total milk solids yield per kilogram of DMI or as kilograms of SCM per megacalorie of NE_L intake, was greater for HF than for HC. Plasma glucose was higher after feeding for cows fed HC; plasma nonesterified fatty acids were greater for HF. Respiration rate and rectal temperature were greater for HC than for HF. Regardless of parity, increased energy density from either fat or concentrate increased milk yield in

midlactation cows, but diets caused energy to be partitioned differently among milk components and body storage. Supplemental rumen-active fat had modest advantages over additional starch-based concentrate during summer heat conditions.

(Key words: dietary fat, heat stress, primiparous cow)

Abbreviation key: HC = high-concentrate diet, HF = high-fat diet, LCFA = long-chain fatty acids, THI = temperature-humidity index.

INTRODUCTION

Supplemental fat has become a common feed ingredient to increase dietary energy density for dairy cows. Although responses of milk production to supplemental fat have been variable, energy balance of cows has been improved consistently (Chilliard, 1993). Supplemental fat has increased milk production in cows during midlactation even when intake of energy from unsupplemented diets exceeded requirements (Steele et al., 1971; DePeters et al., 1989; Knapp et al., 1991; Drackley et al., 1994; Schingoethe et al., 1996). Anecdotal evidence from the field has suggested that primiparous cows may have greater production responses to supplemental fat, perhaps because of their additional energy requirements for growth as well as for milk production. Available research data, however, indicate that production responses generally were similar between primiparous and multiparous cows (Schneider et al., 1988; DePeters et al., 1989; Canale et al., 1990; Knapp et al., 1991). Grummer et al. (1995) found that supplemental tallow increased milk yield by primiparous cows by about 1.5 kg/d after 7 wk of lactation.

A satisfactory mechanistic explanation for the stimulatory effect of supplemental fat on milk production in midlactation cows already consuming adequate energy has been elusive. At least part of the effect seems to result from increased energy density and increased energy intake. Feeding higher-energy diets made isocaloric through addition of fat or concentrate increased yields of milk over lower-energy control diets in some (Canale et al., 1990; Vasquez-Añon et al., 1997) but not all studies (Palmquist and Conrad, 1980; Grum et al., 1996). Yield of FCM often has been greater with high-

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fat diets than with isocaloric high-grain diets because of diversion of energy from milk fat to body fat deposition by the latter (Palmquist and Conrad, 1978; DePeters et al., 1989; Chow et al., 1990; Grum et al. 1996). Supplemental fat also might increase milk yield during midlactation by increasing energetic efficiency. The addition of fat decreases methane production (Chilliard, 1993), thereby increasing the proportion of metabolizable energy in the diet. Furthermore, incorporation of preformed long-chain fatty acids (**LCFA**) into milk fat or body fat is energetically more efficient than de novo synthesis of LCFA from acetate (Baldwin et al., 1980). Suppression of de novo synthesis of fatty acids in the mammary gland by LCFA (Storry et al., 1973) decreases oxidative use of glucose to furnish NADPH in support of milk fat synthesis, thereby sparing glucose for lactose production (Palmquist and Jenkins, 1980). Fat may also alter the endocrine profile in a manner that favors milk synthesis rather than body reserve replenishment (Grummer and Carroll, 1991). Determination of effects of supplemental fat on milk production is complex, therefore, because of the need to consider differences in energy intake, efficiency of energy use, and partitioning of energy into milk solids vs. body tissue storage.

Environmental conditions may be another factor in responses of midlactation cows to additional energy. Because of the greater efficiency of LCFA use, less heat must be dissipated per unit of NE_L intake from dietary fat than from concentrate or forage. Consequently, supplemental fat has been advocated for cows under heat-stress conditions (Moody et al., 1967), although benefits have not been demonstrated under controlled experimental conditions (Moody et al., 1967; Knapp and Grummer, 1991; Nianogo et al., 1991; Chan et al., 1997).

Our hypothesis was that cows in midlactation during summer heat conditions would respond to increased energy density from either supplemental unprotected fat or additional starch-based concentrate, but that fat supplementation should result in greater responses than additional concentrate. Furthermore, we postulated that effects of supplemental fat should be greater in primiparous cows than in multiparous cows because of their greater energy requirements for growth. Our objectives in this experiment were 1) to compare responses of midlactation cows during summer heat to increased dietary energy density either from supplemental fat or from additional concentrate, and 2) to compare responses of primiparous and multiparous cows to increased energy density.

MATERIALS AND METHODS

All procedures involving animals were approved by the University of Illinois Laboratory Animal Care Advi-

Table 1. Ingredient and chemical composition of diets.

Component	Diet ¹		
	Control	HF	HC
Ingredient	(% of DM)		
Alfalfa silage	35.00	35.00	15.00
Corn silage	25.00	25.00	25.00
Corn, ground shelled	24.75	22.08	35.00
Soybean meal, 48% CP	10.00	10.65	14.10
Soybean hulls, pelleted	3.00	2.00	8.04
Fat ²	—	3.00	—
Sodium bicarbonate	0.75	0.75	0.75
Dicalcium phosphate	0.70	0.72	0.68
Calcium carbonate	0.25	0.25	0.83
Magnesium oxide	0.20	0.20	0.20
Sodium chloride	0.20	0.20	0.20
Mineral and vitamin premix ³	0.15	0.15	0.15
Chemical			
OM	92.40	92.37	93.21
CP	16.00	16.04	15.93
NDF	32.99	32.20	28.30
Forage NDF	28.04	28.01	18.68
ADF	23.04	22.58	18.77
Lignin ⁴	4.66	4.56	3.03
Ash	7.61	7.63	6.80
Ether extract	2.63	6.04	2.70
Nonfiber carbohydrates ⁵	40.76	38.10	46.26
Cellulose	18.27	17.98	15.56
NE_L , ⁶ Mcal/kg DM	1.525	1.615	1.585

¹HF = high fat; HC = high carbohydrate.

²Qual-Fat Dairy Blend (National By-Products, Inc., Mason City, IL).

³Contained 10.0% S, 7.5% K, 5.0% Mg, 3.0% Zn, 3.0% Mn, 2.0% Fe, 0.5% Cu, 0.025% I, 0.015% Se, 0.004% Co, 2200 IU vitamin A/g, 662 IU vitamin D/g, and 8 IU vitamin E/g.

⁴Acid-detergent lignin.

⁵100 - (CP% + NDF% + ash% + ether extract%).

⁶Calculated according to NRC (2001).

sory Committee. Nine primiparous Holstein cows ($\bar{x}$ = 167 DIM, SD = 33, range 108 to 224) and nine multiparous Holstein cows ($\bar{x}$ = 154 DIM, SD = 23, range 132 to 201) were used in a replicated 3 × 3 Latin square design with 28-d periods. The first 23 d of each period were for adjustment to diets, and data were collected during the last 5 d of each period. Cows were housed in tie stalls in a mechanically ventilated barn and were allowed to exercise in an outside lot from approximately 0800 to 1000 h daily. Ventilation consisted of a series of overhead fans placed along the length of the barn, and a large fan directing outside air down the alley between the two rows of outward-facing cows. No sprinklers or misters were used. Cows were milked twice daily in a milking parlor.

Experimental diets (Table 1) were 1) a control diet containing 60% forage and no supplemental fat, 2) the control diet supplemented with 3% (DM basis) fat (**HF**) replacing a portion of the ground shelled corn and soybean hulls, and 3) a diet containing 40% forage and thus more concentrate (**HC**), achieved by decreasing

the amount of alfalfa silage. The control diet was formulated to meet or exceed recommendations for all nutrients as specified by NRC (1989). Diets HF and HC were formulated to be isonitrogenous and isocaloric on an NE_L basis, as determined by the summative equation derived by Weiss et al. (1992) after chemical analysis of ingredients. Dietary NE_L calculated by this method was 1.572, 1.665, and 1.665 for control, HF, and HC diets, respectively. Diets HF and HC were formulated to be near practical limits for the amount of rumen-active fat addition and the forage-to-concentrate ratio, respectively.

The fat source (Qual-Fat Dairy Blend; National By-Products, Inc., Mason City, IL) consisted mainly of choice white grease. The fat was assigned an NE_L content of 4.95 Mcal/kg, based on a predicted LCFA digestibility of 66%. Derivation of the LCFA digestibility was based on previous measurement for this fat source (54% at an inclusion rate of 5% of dietary DM [Drackley et al., 1994]), which was adjusted for LCFA intake effects as described elsewhere (Drackley, 1999b). The fatty acid composition as determined by GLC analysis of methyl esters (Sukhija and Palmquist, 1988) was 1.8% C_{14:0}, 23.8% C_{16:0}, 3.0% C_{16:1}, 0.7% C_{17:0}, 16.1% C_{18:0}, 1.9% *trans*-C_{18:1}, 43.7% *cis*-C_{18:1}, 8.5% C_{18:2}, and 0.4% C_{18:3}. The fat had a calculated iodine value of 56 and an analyzed (Griffin Industries, Inc., Cold Spring, KY) content of 6.2% FFA. Fat was stored in a heated tank and was added as the last ingredient into the TMR (Drackley et al., 1994).

All cows were fed the control diet for a 1-wk standardization period before the start of the experimental periods. Diets were fed as TMR twice daily in amounts to ensure 10%orts. Amounts of feed offered and refused were recorded daily. Corn silage and alfalfa silage were sampled weekly for DM determination, and rations were adjusted to maintain desired proportions of ingredients on a DM basis. Individual ingredients (alfalfa silage, corn silage, and concentrate mixtures) and final TMR were sampled daily during the last 5 d of each period and composited by period. Samples were stored frozen (−20°C) until they were dried in a forced-air oven (55°C) and ground through a 1-mm screen in a Wiley mill (Arthur H. Thomas, Philadelphia, PA). Ground samples were analyzed for DM (110°C for 24 h), ash (550°C for 8 h), CP (Kjeldahl analysis; AOAC, 1984), and NDF, ADF, acid detergent lignin, and cellulose (Van Soest et al., 1991). The TMR samples were analyzed for content of ether extract (AOAC, 1984).

Orts were sampled daily during the last 5 d of each period. The DM content was determined for calculation of daily DMI, and then daily samples for each cow in each period were pooled in proportion to daily DMI. Composited samples were ground through a 1-mm

screen in a Wiley mill and analyzed for contents of CP, NDF, and ADF as described for feed samples.

Milk was sampled from four consecutive milkings on d 26 and 27 of each period. Samples were composited according to milk weight at each milking and then split into three aliquots. One portion was analyzed for contents of fat and total (crude) protein using midinfrared methods (Dairy Lab Services, Dubuque, IA). A second portion was used to determine total solids content in our laboratory by a gravimetric procedure in which aliquots of whole milk were weighed before and after drying at 100°C. The third portion was frozen (−20°C) for later analysis of fatty acid profile (data not reported here). Yields of SCM (using contents of protein and fat in milk) were calculated according to equations given by Tyrrell and Reid (1965).

Cows were weighed at the beginning of the experiment and then daily on d 25 to 27 of each period. Body weights were averaged for each cow in each period for statistical analysis. BCS were assigned at the start of the experiment and on d 26 of each period by three experienced individuals, using a five-point scale (1 = thin to 5 = obese [Wildman et al., 1982]). Rectal temperatures and respiration rates were measured at 0700 and 1400 h on d 25 to 27 of each period. Respiration rates were determined for three separate 1-min intervals for each cow at each time and averaged before statistical analysis. Barn temperatures and humidity measurements were not available. Environmental temperature and humidity data were obtained from Illinois State Water Survey records for the Water Survey Research Center, Champaign. The experiment was conducted between June 25 and September 17, 1994.

Blood was sampled from a tail vein at 0800 h (before the a.m. feeding) and 1400 h (approximately 4 h after feeding) on d 26 of each period. Plasma obtained by centrifugation of heparinized blood was stored at −20°C until analysis for concentrations of NEFA (Drackley et al., 1991) and glucose (kit 315; Sigma Chemical Co., St. Louis, MO).

Repeated measurements (e.g., milk yield, DMI) were reduced to period means for each cow before statistical analysis. Data were subjected to ANOVA for a replicated Latin square design using the GLM procedure of SAS (1985). Square nested within parity was used as the error term to test the effect of parity. Effects of period, cow within square, diet, and the interaction of parity and diet were tested using the residual error. Interactions of parity and diet did not approach statistical significance for any measured variable (all $P > 0.15$), but all terms were retained in the model. Means were compared by use of orthogonal contrasts of 1) control vs. both high-energy diets—i.e., HF and HC—and 2) HF vs. HC. Significance was declared when $P \leq 0.05$.

RESULTS AND DISCUSSION

Mean daily ambient temperatures during the week of experimental measurements in each period (d 21 to 28) were 24.4, 22.0, and 23.4°C for periods 1, 2, and 3, respectively. Mean daily maximum temperatures were 30.1 (range 27.8 to 34.4), 27.9 (range 23.3 to 33.3), and 30.1°C (range 25.6 to 32.8) for periods 1, 2, and 3, respectively. Mean daily minimum temperatures were 18.3 (range 15.6 to 21.1), 15.8 (range 12.8 to 22.2), and 16.3°C (range 14.4 to 18.9), respectively. Mean minimum relative humidity was 53.0 (range 38 to 72), 48.4 (range 44 to 56), and 45.5% (range 40 to 60), respectively. Temperatures were within $\pm 0.5^\circ\text{C}$ of 30-yr averages for periods 1 and 2, but were about 4.6°C higher than historic averages for period 3. Consequently, environmental conditions were typical of summer at this location and are representative of summer heat conditions in much of the Midwest United States.

Estimates of the ambient (outside) temperature-humidity index (THI) were generated using the following formula (National Oceanic and Atmospheric Administration, 1976):

$$\text{THI} = \text{td} - (0.55 - 0.55\text{RH})(\text{td} - 58),$$

where td is dry-bulb temperature (in degrees Fahrenheit) and RH is relative humidity. When mean daily THI exceeds 72, cows are subject to some loss of DMI and milk yield from heat stress (Johnson et al., 1963). Estimates of mean THI (71, 68, and 70 for periods 1, 2, and 3, respectively) were conservative because we used mean daily temperature but mean minimum relative humidity for each sampling period. Cows were housed in a tie-stall barn with the exception of time in the milking parlor or holding pen twice daily and the 2-h morning exercise period; temperatures and relative humidity in the barn were not recorded, so the actual degree of heat stress cannot be calculated.

Analyzed composition of the total diets was similar to formulated values (Table 1). The exception was dietary NE_L density. Subsequent to publication of the seventh revised edition of *Nutrient Requirements of Dairy Cattle* (NRC, 2001), dietary NE_L values were recalculated using the assumptions and model therein. Values for dietary NE_L density were lower than values used for formulation (1.525, 1.615, and 1.585 according to NRC [2001] vs. 1.572, 1.665, and 1.665 as formulated for control, HF, and HC diets, respectively). Although procedures for calculating digestible energy were similar between methodology used for formulation (Weiss et al., 1992) and that used by NRC (2001), the lower estimates of dietary NE_L density overall and differences in dietary NE_L density between HF and HC diets ac-

cording to NRC (2001) resulted from the greater discounts applied for effects of increasing DMI and the fact that energy from supplemental fat is discounted less.

The DMI was lower for cows fed HF than for those fed HC (Table 2). Differences among diets for DMI and dietary NE_L density resulted in a weak tendency ($P < 0.12$) for NE_L intakes to be greater for cows fed high-energy diets, although this effect was attributable only to cows fed HC (Table 2). Intakes of NDF, CP, and ADF (Table 2) followed those expected according to DMI and nutrient densities and indicated that sorting of ingredients in the TMR was minimal. Intakes of DM, NE_L , and other nutrient fractions were significantly lower for primiparous cows than for multiparous cows, as expected. However, DMI and NDF intake expressed as percentages of BW did not differ between primiparous and multiparous cows.

Decreases in DMI as a result of fat supplementation are common in the literature (Chilliard, 1993). From a review of 22 experimental treatments, Chilliard (1993) concluded that animal and blended fats decreased DMI by an average of 0.7 kg/d, compared with the difference of 0.97 kg/d in our study. That cows fed HF had lower DMI than cows fed the control diet indicates that dietary NDF did not constrain DMI for cows fed HF. Furthermore, cows had significantly greater DMI and tended to have greater NE_L intake when fed HC, which demonstrates that cows had the potential to consume greater amounts of DM and NE_L than they did when fed HF. Canale et al. (1990) and Vazquez-Añon et al. (1997) also noted similar relative changes in DMI when cows were fed diets higher in concentrate or supplemented with fat.

At least two explanations can be offered for the decreased DMI when cows were fed HF. First, the amount of unprotected fat used may have been excessive, resulting in decreased ruminal fiber digestion and thereby decreased DMI (Palmquist and Jenkins, 1980; Allen, 2000). Lower milk fat content (Table 3; discussed later) for cows fed HF indirectly supports an interference with ruminal fermentation. Cows fed the same fat source at 5% of dietary DM in a previous study had no alterations in ruminal fermentation characteristics, but DMI decreased by about 1 kg/d (Drackley et al., 1994). When Holstein steers were fed diets of similar composition and supplemented with 5% of the same fat source, the ruminal acetate-to-propionate ratio was decreased, but ruminal NDF digestion was unaffected (Elizalde et al., 1999). In contrast, Pantoja et al. (1994) reported that ruminal fermentation characteristics were not altered by supplementation of 5% animal-vegetable fat, yet ruminal NDF digestion was decreased by 15%; DMI was also decreased by about the same amount. Second, DMI may have been decreased by some factor or factors

Table 2. Intakes by cows fed control, high-fat (HF), or high-concentrate (HC) diets.

Intake	Diet			SE	<i>P</i> ¹	
	Control	HF	HC		Energy	Source
DM, ² kg/d	21.04	20.07	21.31	0.32	0.37	0.01
DMI, % BW	3.64	3.42	3.66	0.046	0.11	0.0007
NE _L , ² Mcal/d	32.1	32.4	33.7	0.5	0.12	0.07
NDF, ² kg/d	6.94	6.46	6.03	0.10	0.0001	0.004
NDF, % BW	1.20	1.10	1.04	0.014	0.0001	0.003
CP, ² kg/d	3.34	3.17	3.38	0.05	0.32	0.009
ADF, ² kg/d	4.79	4.43	3.94	0.07	0.0001	0.0001

¹Probability for contrasts: energy = control vs. HF + HC; source = HF vs. HC.

²Parity effect, *P* < 0.05. Parity × diet interactions were nonsignificant (*P* > 0.15) for all variables.

sensitive to intake of LCFA, as suggested by Drackley et al. (1992) and Palmquist (1994) and reviewed recently by Allen (2000). Unsaturated LCFA reaching the intestine decrease DMI (Drackley et al., 1992; Bremmer et al., 1998). Evidence has been presented for a role of increased concentrations of the gut hormones cholecystokinin (Choi and Palmquist, 1996) and glucagon-like peptide-1 (Benson and Reynolds, 2001) in response to LCFA reaching the intestine as mediators of decreased DMI.

The DMI for cows fed HC was greater than for those fed HF but was not increased appreciably when compared with cows fed the control diet. Although milk yield and DMI in our midlactation cows were moderate, removal of 20% forage from the diet might have been expected to increase DMI because of reduction in fill from slowly digested NDF (Canale et al., 1990). However, although content of NDF in diet HC exceeded the recommended minimum (NRC, 1989), forage NDF was lower than recommended and nonfiber carbohydrate content was high (46.3% of DM). Consequently, DMI

in cows fed HC may have been limited by increased propionate absorption, increased hypertonicity of ruminal fluid, and lower ruminal pH that decreased fiber digestibility, as reviewed by Allen (2000).

Milk yield (Table 3) was increased (*P* < 0.002) by higher energy diets, with no difference between HF and HC. Similar responses were observed by Vazquez-Añon et al. (1997) when multiparous cows in midlactation were fed diets containing 1.70 Mcal of NE_L/kg compared with controls fed a diet containing 1.61 Mcal NE_L/kg. In that study, tallow was supplemented at 2.3% of dietary DM for the HF diet, and the high-grain diet contained 50% concentrate. Canale et al. (1990) noted a greater milk yield response when dietary energy density was increased by decreasing the dietary forage to concentrate ratio than by an isocaloric addition of dietary fat. Supplemental fat increased yield of 3.5% FCM compared with cows fed the isocaloric HC (Table 3), but yields of SCM did not differ significantly among diets. Milk fat content was lower for cows fed either high-energy diet, and was lower for cows fed HC than for

Table 3. Milk yield, milk composition, and efficiency of cows fed control, high-fat (HF), or high-concentrate (HC) diets.

Variable	Diet			SE	<i>P</i> ¹	
	Control	HF	HC		Energy	Source
Milk, kg/d	28.5	30.4	30.1	0.4	0.002	0.60
3.5% FCM, kg/d	28.5	29.3	28.1	0.4	0.75	0.04
SCM, kg/d	26.7	27.6	26.8	0.4	0.29	0.18
Fat, %	3.50	3.31	3.10	0.07	0.002	0.04
Fat, kg/d	1.00	1.00	0.93	0.03	0.15	0.02
Protein, %	3.21	3.11	3.26	0.02	0.42	0.0001
Protein, kg/d	0.92	0.94	0.98	0.01	0.01	0.11
Total solids, %	12.39	12.16	12.09	0.08	0.008	0.53
Total solids, kg/d	3.53	3.68	3.63	0.05	0.04	0.45
SNF, %	8.89	8.85	9.00	0.03	0.39	0.002
SNF, kg/d	2.53	2.69	2.70	0.04	0.002	0.77
Efficiency						
Total solids/DMI, kg/kg	0.168	0.183	0.171	0.002	0.0009	0.0002
SCM/NE _L intake, kg/Mcal	0.830	0.846	0.794	0.010	0.43	0.0012

¹Probability for contrasts: energy = control vs. HF + HC; source = HF vs. HC. Effects of parity and parity × diet were nonsignificant (*P* > 0.15) for all variables.

Table 4. BW and BCS for cows fed control, high-fat (HF), or high-concentrate (HC) diets.

Variable	Diet			SE	<i>P</i> ¹	
	Control	HF	HC		Energy	Source
Final BW, ² kg						
Multiparous	626	628	623	5.9	0.61	0.41
Primiparous	535	542	538	5.9		
BW change, kg/d	0.08	0.35	0.30	0.20	0.31	0.84
Final BCS ³	2.71	2.73	2.79	0.03	0.26	0.18

¹Probability for contrasts: energy = control vs. HF + HC; source = HF vs. HC.

²Parity effect, $P < 0.02$; the parity $\times$ diet interaction was nonsignificant ($P > 0.15$) for all variables.

³Five-point scale (1 = thin to 5 = obese).

cows fed HF. Lower milk fat content for cows fed HC was indicative of milk fat depression because yield of milk fat was also decreased by 0.07 kg/d (Table 3). In contrast, milk protein content was significantly higher for cows fed HC than for cows fed HF. The milk protein content was 0.10 percentage units lower for cows fed HF than for controls, which is commonly observed when supplemental fats are fed (Wu and Huber, 1994). Total solids content of milk was lower, but total solids yield was greater, when cows were fed high-energy diets (Table 3). Similar to milk protein, the content of SNF in milk was greater when cows were fed HC than when they were fed HF, but SNF yield was increased by either high-energy diet. In a previous experiment from our laboratory (Drackley et al., 1994), the same fat source was fed at 5% of dietary DM to Holstein and Jersey cows past peak milk yield; supplemental fat increased milk yield, but yields of FCM and SCM were unchanged because of corresponding decreases in concentrations of fat and protein in milk.

Efficiency of milk production was examined in two ways. First, on a mass input-output basis (kilograms of milk total solids per kilogram of DMI), efficiency was increased by high-energy diets, with cows fed HF being most efficient. Second, from an energetic standpoint, cows fed HF were more efficient in producing milk energy (kilograms of SCM) per megacalorie of NE_L intake than were cows fed HC. Lower apparent efficiency of milk energy secretion for cows fed HC likely arose from the depression of milk fat synthesis and consequent diversion of feed energy to fat deposition in adipose tissue (Tyrrell, 1980). However, differences in BW or BCS (Table 4) did not achieve statistical significance. Although Tomlinson et al. (1994) demonstrated that Latin square designs with 28-d periods are adequate for detection of milk production responses to supplemental fat, without carryover effects, such designs may not be sufficiently sensitive to detect diet-induced changes in BW or BCS (Drackley et al., 1994).

Although means for energetic efficiency for control cows and cows fed HF were not compared statistically,

efficiency was 0.016 greater for cows fed HF (SE = 0.010). This difference is in the range of the potential improvement in efficiency of energy use when fat replaces dietary carbohydrates. The improvements in apparent efficiency for cows fed supplemental fat may arise from the greater efficiency of use of preformed LCFA rather than synthesis of LCFA from acetate (Baldwin et al., 1980) or to an optimization of the mixture of substrates for milk synthesis, as demonstrated by Brumby et al. (1978). If the efficiency of metabolizable energy use from fat is approximately 30% greater than that from corn grain (NRC, 2001) and fat is added at 3% of dietary DM, the potential improvement in efficiency is 0.009. Because methane is not produced from fat, energetic efficiency might be improved by an additional 0.003 (i.e., 10% greater efficiency times 3% fat addition). Thus, the theoretical improvement in efficiency (0.012) was similar to the observed improvement (0.016), although differences of this magnitude are unlikely to be detected statistically in experimental designs such as ours.

We used the NRC (2001) model to analyze nutrient intakes relative to predicted requirements. Primiparous and multiparous cows consumed 2.1 and 3.3 Mcal/d more NE_L , respectively, than required when the control diet was fed. Consequently, increased milk yield from feeding diets of higher energy density was not expected merely on the basis of increasing energy intake. The NRC (2001) model predicted slightly lower NE_L balance for primiparous and multiparous cows fed HF (1.7 and 2.8 Mcal/d, respectively), probably as a result of the lower DMI when fed HF. On the other hand, the NRC (2001) model predicted higher NE_L balance when primiparous (3.7 Mcal/d) and multiparous (5.2 Mcal/d) cows were fed HC. The model predicted metabolizable protein balances (supplied minus required) of 137, 19, and 338 g/d for multiparous cows fed control, HF, and HC diets, respectively, and 268, -87, and 175 g/d for primiparous cows fed control, HF, and HC diets, respectively. The Cornell Net Carbohydrate and Protein System (version 4.0.31; Cornell University, Ithaca, NY)

Table 5. Concentrations of glucose and NEFA in plasma from cows fed control, high-fat (HF), or high-concentrate (HC) diets.

Variable	Diet			SE	<i>P</i> ¹	
	Control	HF	HC		Energy	Source
Glucose, mg/dl						
Pre-feeding	68.4	67.6	68.4	0.7	0.69	0.47
4 h post-feeding	66.4	65.3	69.1	0.7	0.34	0.0008
NEFA, ² μequiv/L						
Pre-feeding	150.4	200.5	151.7	6.0	0.001	0.0001
4 h post-feeding	134.5	185.5	142.4	8.0	0.005	0.0006

¹Probability for contrasts: energy = control vs. HF + HC; source = HF vs. HC. The parity × diet interaction was nonsignificant (*P* > 0.15) for all variables.

²Parity effect (pre-feeding: primiparous $\bar{x}$ = 184.6, multiparous $\bar{x}$ = 150.5; post-feeding: primiparous $\bar{x}$ = 174.1, multiparous $\bar{x}$ = 134.2).

predicted similar differences in metabolizable protein balance between control and HF diets. No parity × diet interactions were detected for any milk component or yield, which makes it unlikely that metabolizable protein supply actually limited responses of primiparous cows to any greater extent than multiparous cows.

Concentrations of glucose and NEFA in plasma are shown in Table 5. Glucose concentrations did not differ between primiparous and multiparous cows and were similar among diets in plasma sampled before the a.m. feeding. However, cows fed HC had greater glucose concentrations 4 h postfeeding, suggesting that propionate supply and energy balance were greater than for cows fed the control or HF diets. The concentration of NEFA was increased by HF, which also resulted in significant differences between high-energy diets and the control diet for both pre- and postfeeding samples. Supplemental fat increases the concentration of NEFA in blood (Grummer and Carroll, 1991). From an analysis of results from seven experiments in which multiple dietary fat concentrations were fed, Drackley (1999a) derived a regression equation that predicted an increase in plasma NEFA concentration of about 40 μM as dietary LCFA intake increased by 500 g/d, which approximates the increase in LCFA intake by cows fed HF. Primipa-

rous cows had greater NEFA concentrations than multiparous cows, perhaps reflecting their slightly lower energy balance.

Respiration rates measured at 0700 h were elevated for cows fed HC; no differences were significant for measurements made at 1400 h (Table 6). Similarly, rectal temperatures were higher for cows fed HC than for those fed HF at 0700 h, but not at 1400 h (Table 6). Milk yield and DMI decrease when body temperature exceeds 38.9°C (Johnson et al., 1963). Measurements at 0700 h were before cows were allowed outside for exercise and may be better indicators of the effects of heat load than measurements at 1400 h. The inability of cows to dissipate heat over the night contributes to the severity of heat stress (West, 1999); elevated respiration and rectal temperature in the early morning may be more indicative of heat stress than measurements made at 1400 h before the maximum heating of the day occurred. Increased respiration and rectal temperatures for cows fed HC relative to those fed HF suggest that cows fed HC had a greater heat load to dissipate, perhaps because of the lower heat increment associated with metabolism of LCFA, but also likely as a result of lower DMI when cows were fed HF (Table 2). Primiparous cows had greater respiration rates than

Table 6. Respiration rate and rectal temperature for cows fed control, high-fat (HF), or high-concentrate (HC) diets.

Variable	Diet			SE	<i>P</i> ¹	
	Control	HF	HC		Energy	Source
Respiration, ² breaths/min						
0700 h	51.9	50.4	55.9	1.2	0.41	0.004
1400 h	67.4	69.3	70.3	1.6	0.20	0.66
Temperature, °C						
0700 h	38.73	38.67	38.80	0.05	0.96	0.08
1400 h	39.20	39.21	39.23	0.06	0.77	0.80

¹Probability for contrasts: energy = control vs. HF + HC; source = HF vs. HC. The parity × diet interaction was nonsignificant (*P* > 0.15) for all variables.

²Parity effect (*P* < 0.09) for 0700 h values (primiparous $\bar{x}$ = 57.0, multiparous $\bar{x}$ = 48.5).

did multiparous cows, but the lack of diet $\times$ parity interaction indicates that responses to diets did not differ between parity groups.

Previous experiments designed to determine whether supplemental fat is beneficial to cows during heat stress conditions generally have demonstrated little benefit to fat supplementation (Moody et al., 1967; Knapp and Grummer, 1991; Nianogo et al., 1991; Chan et al., 1997). Similarly, responses were modest in our experiment; the only clear advantage for cows fed HF over those fed HC was increased apparent efficiency of milk synthesis. The greater respiration rates in response to higher rectal temperatures for cows fed HC would increase maintenance energy expenditures relative to cows fed HF, which could contribute to the greater apparent efficiency of milk energy secretion for cows fed HF.

CONCLUSIONS

For midlactation Holstein cows under conditions of moderate heat stress, increasing dietary energy density either by supplementation of unprotected fat (HF) or by increasing starch-based concentrate and decreasing forage (HC) resulted in greater milk yields; however, only cows fed HC had small increases in NE_L intakes. Production of SCM did not differ among the three diets because of contrasting changes of fat and protein production in milk between HF and HC relative to the control. Consequently, dietary energy was partitioned differently among diets. Measures of apparent efficiency of milk production (kg of milk solids/kg of DMI and kg of SCM/Mcal of NE_L intake) were greater for HF than for HC. Improved efficiency resulted primarily from similar increases in milk production between HF and HC but decreased DMI when cows were fed HF. Greater morning respiration rates and rectal temperatures when cows were fed HC indicate that increased maintenance energy requirements resulting from greater expenditure of energy to dissipate heat load also may have been a factor in greater apparent efficiency for cows fed HF. No parity $\times$ diet interactions approached statistical significance in this study; consequently, first-lactation cows in midlactation responded to increased energy from either supplemental fat or increased concentrate in the same way as did multiparous cows. It must be noted, however, that evidence for a suboptimal ruminal environment was noted for cows fed either HF or HC. Consequently, future research should determine the effects of increasing dietary energy density by use of ruminally inert fat sources or by using nonforage fiber sources, such as soybean hulls, instead of cereal grains to replace forage during summer heat conditions.

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REFERENCES

- Allen, M. S. 2000. Effects of diet on short-term regulation of feed intake by lactating dairy cattle. *J. Dairy Sci.* 83:1598–1624.
- Association of Official Analytical Chemists. 1984. *Official Methods of Analysis*. 14th ed. AOAC, Arlington, VA.
- Baldwin, R. L., N. E. Smith, J. Taylor, and M. Sharp. 1980. Manipulating metabolic parameters to improve growth rate and milk secretion. *J. Anim. Sci.* 51:1416–1428.
- Benson, J. A., and C. K. Reynolds. 2001. Effects of abomasal infusion of long-chain fatty acids on splanchnic metabolism of pancreatic and gut hormones in lactating dairy cows. *J. Dairy Sci.* 84:1488–1500.
- Bremmer, D. R., L. D. Ruppert, 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.
- Brumby, P. E., J. E. Storry, J. A. Bines, and R. J. Fulford. 1978. Utilization of energy for maintenance and production in dairy cows given protected tallow during early lactation. *J. Agric. Sci. (Camb.)* 91:151–159.
- Canale, C. J., P. L. Burgess, L. D. Muller, and G. A. Varga. 1990. Calcium salts of fatty acids in diets that differ in neutral detergent fiber: Effect on lactation performance and nutrient digestibility. *J. Dairy Sci.* 73:1031–1038.
- Chan, S. C., J. T. Huber, K. H. Chen, J. M. Simas, and Z. Wu. 1997. Effects of ruminally inert fat and evaporative cooling on dairy cows in hot environmental temperatures. *J. Dairy Sci.* 80:1172–1178.
- Chilliard, Y. 1993. Dietary fat and adipose tissue metabolism in ruminants, pigs, and rodents: A review. *J. Dairy Sci.* 76:3897–3931.
- Choi, B. R., and D. L. Palmquist. 1996. High fat diets increase plasma cholecystokinin and pancreatic polypeptide, and decrease plasma insulin and feed intake in lactating cows. *J. Nutr.* 126:2913–2919.
- Chow, J. M., E. J. DePeters, and R. L. Baldwin. 1990. Effect of rumen-protected methionine and lysine on casein in milk when diets high in fat or concentrate are fed. *J. Dairy Sci.* 73:1051–1061.
- DePeters, E. J., S. J. Taylor, and R. L. Baldwin. 1989. Effect of dietary fat in isocaloric rations on the nitrogen content of milk from Holstein cows. *J. Dairy Sci.* 72:2949–2957.
- Drackley, J. K. 1999a. Biology of dairy cows during the transition period: The final frontier? *J. Dairy Sci.* 82:2259–2273.
- Drackley, J. K. 1999b. New perspectives on energy values and supplementation levels of supplemental fats. Pages 171–184 in *Advances in Dairy Technology*. Vol. 11. J. Kennelly, ed. Proc. Western Canadian Dairy Sem., Univ. Alberta, Edmonton, AB, Canada.
- Drackley, J. K., D. E. Grum, G. C. McCoy, and T. H. Klusmeyer. 1994. Comparison of three methods for incorporation of liquid fat into diets for lactating dairy cows. *J. Dairy Sci.* 77:1386–1398.
- 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.
- Drackley, J. K., J. J. Veenhuizen, M. J. Richard, and J. W. Young. 1991. Metabolic changes in blood and liver of dairy cows during either feed restriction or administration of 1,3-butanediol. *J. Dairy Sci.* 74:4254–4264.
- Elizalde, J. C., C. G. Aldrich, D. W. LaCount, J. K. Drackley, and N. R. Merchen. 1999. Ruminant and total tract digestibilities in steers fed diets containing liquified or prilled saturated fatty acids. *J. Anim. Sci.* 77:1930–1939.
- Grum, D. E., J. K. Drackley, L. R. Hansen, and J. D. Cremin, Jr. 1996. Production, digestion, and hepatic lipid metabolism of dairy cows fed increased energy from fat or concentrate. *J. Dairy Sci.* 79:1836–1849.

- Grummer, R. R., and D. J. Carroll. 1991. Effects of dietary fat on metabolic disorders and reproductive performance of dairy cattle. *J. Anim. Sci.* 69:3838–3852.
- Grummer, R. R., P. C. Hoffman, M. L. Luck, and S. J. Bertics. 1995. Effect of prepartum and postpartum dietary energy on growth and lactation of primiparous cows. *J. Dairy Sci.* 78:172–180.
- Johnson, H. D., A. C. Ragsdale, I. L. Berry, and M. D. Shanklin. 1963. Temperature-humidity effects including influence of acclimation in feed and water consumption of Holstein cattle. *Univ. Missouri Res. Bull.* No. 846. Columbia, MO.
- Knapp, D. M., and R. R. Grummer. 1991. Response of lactating dairy cows to fat supplementation during heat stress. *J. Dairy Sci.* 74:2573–2579.
- Knapp, D. M., R. R. Grummer, and M. R. Dentine. 1991. The response of lactating dairy cows to increasing levels of whole roasted soybeans. *J. Dairy Sci.* 74:2563–2572.
- Moody, E. G., P. J. Van Soest, R. E. McDowell, and G. L. Ford. 1967. Effect of high temperature and dietary fat on performance of lactating cows. *J. Dairy Sci.* 50:1909–1916.
- National Oceanic and Atmospheric Administration. 1976. *Livestock Hot Weather Stress. Reg. Operations Lett. C-31-76.* US Dep. Commerce, Natl. Weather Serv. Central Region, Kansas City, MO.
- National Research Council. 1989. *Nutrient Requirements of Dairy Cattle.* 6th rev. ed. Natl. Acad. Sci., Washington, DC.
- National Research Council. 2001. *Nutrient Requirements of Dairy Cattle.* 7th rev. ed. Natl. Acad. Sci., Washington, DC.
- Nianogo, A. J., H. E. Amos, M. A. Froetschel, and C. M. Keery. 1991. Dietary fat, protein degradability, and calving season: Effects on nutrient use and performance of early lactation cows. *J. Dairy Sci.* 74:2243–2255.
- Palmquist, D. L. 1994. The role of dietary fats in efficiency of ruminants. *J. Nutr.* 124:1377S–1382S.
- Palmquist, D. L., and H. R. Conrad. 1978. High fat rations for dairy cows. Effects on feed intake, milk and fat production, and plasma metabolites. *J. Dairy Sci.* 61:890–901.
- Palmquist, D. L., and H. R. Conrad. 1980. High fat rations for dairy cows. Tallow and hydrolyzed blended fat at two intakes. *J. Dairy Sci.* 63:391–395.
- Palmquist, D. L., and T. C. Jenkins. 1980. Fat in lactation rations: Review. *J. Dairy Sci.* 63:1–14.
- Pantoja, J., J. L. Firkins, M. L. Eastridge, and B. L. Hull. 1994. Effects of fat saturation and source of fiber on site of nutrient digestion and milk production by lactating dairy cows. *J. Dairy Sci.* 77:2341–2356.
- SAS User's Guide: Statistics, Version 5 Edition. 1985. SAS Inst., Inc., Cary, NC.
- Schingoethe, D. J., M. J. Brouk, K. D. Lightfield, and R. J. Baer. 1996. Lactational responses of dairy cows fed unsaturated fat from extruded soybeans or sunflower seeds. *J. Dairy Sci.* 79:1244–1249.
- Schneider, P., D. Sklan, W. Chalupa, and D. S. Kronfeld. 1988. Feeding calcium salts of fatty acids to lactating cows. *J. Dairy Sci.* 71:2143–2150.
- Steele, W., R. C. Noble, and J. H. Moore. 1971. The effects of 2 methods of incorporating soybean oil into the diet on milk yield and composition in the cow. *J. Dairy Res.* 38:43–48.
- Storry, J. E., A. J. Hall, and V. W. Johnson. 1973. The effects of increasing amounts of dietary tallow on milk-fat secretion in the cow. *J. Dairy Res.* 40:293–299.
- Sukhija, P. S., and D. L. Palmquist. 1988. Rapid method for determination of total fatty acid content and composition of feedstuffs and feces. *J. Agric. Food Chem.* 36:1202–1206.
- Tomlinson, A. P., H. H. Van Horn, C. J. Wilcox, and B. Harris, Jr. 1994. Effects of undegradable protein and supplemental fat on milk yield and composition and physiological responses of cows. *J. Dairy Sci.* 77:145–156.
- Tyrrell, H. F. 1980. Limits to milk production efficiency by the dairy cow. *J. Anim. Sci.* 51:1441–1447.
- Tyrrell, H. F., and J. T. Reid. 1965. Prediction of the energy value of cow's milk. *J. Dairy Sci.* 48:1215–1223.
- Van Soest, P. J., J. B. Robertson, and B. A. Lewis. 1991. Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *J. Dairy Sci.* 74:3583–3597.
- Vasquez-Añon, M., S. J. Bertics, and R. R. Grummer. 1997. The effect of dietary energy source during mid to late lactation on liver triglyceride and lactation performance of dairy cows. *J. Dairy Sci.* 80:2504–2512.
- Weiss, W. P., H. R. Conrad, and N. R. St-Pierre. 1992. A theoretically-based model for predicting total digestible nutrient values of forages and concentrates. *Anim. Feed Sci. Technol.* 39:95–110.
- West, J. W. 1999. Nutritional strategies for managing the heat-stressed dairy cow. *J. Anim. Sci.* 77(Suppl. 2):21–35.
- Wildman, E. E., G. M. Jones, P. E. Wagner, R. L. Boman, H. F. Troutt, Jr., and T. N. Lesch. 1982. A dairy cow body condition scoring system and its relationship to selected production characteristics. *J. Dairy Sci.* 65:495–501.
- Wu, Z., and J. T. Huber. 1994. Relationship between dietary fat supplementation and milk protein concentration in lactating cows: A review. *Livest. Prod. Sci.* 39:141–155.