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Effects of Feeding Prepubertal Heifers a High-Energy Diet for Three, Six, or Twelve Weeks on Feed Intake, Body Growth, and Fat Deposition

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ABSTRACT

The objective was to determine the effects of feeding prepubertal dairy heifers a high-energy diet for a duration of 0, 3, 6, or 12 wk on feed intake, growth, and fat deposition. We also used feed composition, daily intake, and body growth data to evaluate the nutritional model of the 2001 National Research Council (NRC) Nutrient Requirements of Dairy Cattle. Holstein heifers (age = 11 wk; body weight = 107 ± 1 kg) were assigned to 1 of 4 treatments (n = 16/treatment) designated H0, H3, H6, and H12 and fed a low-energy diet for 12, 9, 6, or 0 wk, followed by a high-energy diet for 0, 3, 6, or 12 wk, respectively. Four heifers were killed initially (11 wk of age) and 64 heifers were killed at the end of the treatment period (23 wk of age). The low-energy diet was formulated to achieve 0.6 kg of average daily gain and contained 16% crude protein, and 45% neutral detergent fiber. The high-energy diet was formulated to achieve an average daily gain of 1.2 kg and contained 18% crude protein and 23% neutral detergent fiber. Actual daily gains averaged over the 12-wk treatment period were 0.64, 0.65, 0.83, and 1.09 kg for the H0, H3, H6, and H12 groups, respectively. Body weight, withers height, hip width, carcass weight, liver weight, and perirenal fat increased in heifers fed a high-energy diet for a longer duration. In addition, percentage of fat increased and percentage of protein decreased in rib sections with a longer duration on the high-energy diet. Uterine and ovarian weights adjusted for body weight decreased when heifers were fed the high-energy diet for a longer duration. The 2001 NRC underestimated dry matter intake of the high-energy diet and overestimated dry matter intake of the low-energy diet. On the basis of actual intakes of each diet, the NRC slightly underestimated gain for the low-energy diet and overestimated gain by 40% for the high-energy diet. The likely explanation for this is that the NRC underestimated the proportion of gain that was fat in the heifers fed the high-energy diet and therefore predicted more body gain per unit of energy intake. We concluded that feeding a high-energy diet for a short duration altered body growth and fat deposition in a time-dependent, linear manner consistent with feeding a high-energy diet for a long duration.

Key words: heifer, nutrition, growth, carcass

INTRODUCTION

Raising replacement dairy heifers accounts for approximately 20% of total dairy herd expenses, with actual costs until calving ranging from $1,000 to $1,300 per heifer (Cady and Smith, 1996). The optimal BW of heifers before calving ranges from 590 to 640 kg (Hoffman, 1997); typically, calving occurs at 24 to 26 mo of age. Feeding a high-energy diet to allow for rapid growth enables heifers to be bred and calve earlier, potentially reducing the costs associated with raising replacement heifers while still achieving the optimal BW. However, mammary growth relative to body growth and milk yield potential are reduced when heifers that are approximately 3 to 10 mo of age are fed high-energy diets that promote gains of >1 kg/d for periods of 12 wk or longer (Sejrsen et al., 1982; Petitclerc et al., 1999; Radcliff et al., 2000). Feeding heifers for gains of >1 kg/d also increases the amount of fat deposition (Radcliff et al., 1997). Thus, a major goal in raising replacement heifers is to manage them for rapid structural growth along with optimal development of the mammary gland. Although some fat deposition is necessary, fat gain contributes little to structural growth, decreases the efficiency of feed use, and may compromise mammary development.

If prepubertal heifers are fed high-energy diets to promote rapid BW gains for >3 mo, their body tissue gain has a greater proportion of fat (Radcliff et al., 1997; Waldo et al., 1997). However, steers fed a high-energy diet following a period of a low-energy diet deposited more protein and less fat than control steers during the first weeks of the new diet (Fox et al., 1972). Therefore, we hypothesized that feeding heifers high-energy diets for a short duration also might increase gains, with

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little increase in body fatness and no inhibition of mammary development. Such an effect would be consistent with our previous finding that high-energy intake before weaning increases structural growth without increased fatness and mammary impairment (Brown et al., 2005a,b). Such an effect also would be consistent with the reported benefits of a stairstep feeding program for dairy heifers (Park et al., 1987; Choi et al., 1997). Short periods of high-energy feeding in young heifers might be one cost-effective way to decrease age at first calving and improve the efficiency of growth without causing a detrimental effect on mammary development or an increase in body fatness.

The major objective of this study was to determine whether feeding prepubertal dairy heifers a high-energy diet for a short duration altered body growth, organ weights, and body fatness differently from what would be expected based on feeding a high-energy diet for a long duration. Prior studies with prepubertal heifers that involved treatment periods of 12 wk or longer indicated that high-energy intake caused excessive fat deposition and hampered mammary growth relative to body growth. Thus, 12 wk was selected as a long duration time point, 6 and 3 wk as shorter duration time points, and 0 wk of feeding a high-energy diet as a baseline control treatment. Treatment effects on mammary growth are reported in a companion paper (Davis Rincker et al., 2008).

The Nutrient Requirements of Dairy Cattle (NRC, 2001) is commonly used as a reference for nutrient analysis, nutrient utilization, and diet formulation. Few studies have been published that have evaluated the 2001 NRC (Gabler and Heinrichs, 2003). Van Amburgh (2005) suggested that actual gains of heifers are typically higher than those predicted by the model. However, despite data showing that increased daily gain increases the proportion of gain that is fat in 5- to 10-mo-old heifers (Radcliff et al., 1997; Waldo et al., 1997), the composition of gain in the 2001 NRC is relatively insensitive to changes in the rate of gain. Thus, a second objective of this study was to evaluate the nutritional model of the 2001 NRC for heifers between 3 and 6 mo.

MATERIALS AND METHODS

Animals and Dietary Treatments

Animals. For the study, we used Holstein heifers from 11 to 23 wk of age. This age was selected because we were confident that almost all the animals would not reach puberty before slaughter. Furthermore, recent evidence from our laboratory showed that feeding for rapid growth before 14 wk of age increases mammary parenchymal gain as much as or more than the increase in body growth (Brown et al., 2005a,b). Sixty-eight heifers (approximate age = 8 wk) were purchased from a supplier during 4 consecutive weeks in the fall (17 heifers/wk), with each week classified as a separate purchase group. Heifers were housed at the Michigan State University Beef Cattle Research Center and were exposed to ambient temperatures and lighting during the adaptation and treatment periods, which occurred during late fall and winter. Heifers were housed with 4 animals per pen in an open-sided barn with enough space per pen (50 m^2/pen) to allow for exercise. All procedures were approved by the Michigan State University Animal Care and Use Committee.

Each purchase group was allowed a 3-wk adaptation period for adjustment to facilities and diet. At the beginning of the adaptation period, heifers were fed a texturized complete feed (21% CP; ADM, Quincy, IL) and alfalfa hay; this was similar to how they were fed before arrival on campus. Alfalfa silage, corn silage, oatlage, and straw were slowly introduced into the diet during the first 2 wk of the adaptation period. For the last week of the adaptation period, heifers were consuming a TMR that was a 1:1 mixture of the high- and low-energy treatment diets. One heifer within each purchase group was randomly selected and slaughtered at 11 wk of age for baseline measurements used for calculation of accretion rate data (see Davis Rincker et al., 2008).

Body temperatures was measured daily during the first week of the adaptation period, and thereafter only if heifers appeared ill; heifers were treated if body temperatures were greater than 39.7°C, appeared ill, or were lame. During the second week of the adaptation period, heifers were vaccinated against bovine rhinotracheitis, bovine viral diarrhea, parainfluenza type 3, and leptospirosis (BoviShield4, Pfizer, New York, NY); pasteurella (Pfizer); and *Clostridium perfringens* (Ultrabac7/Somubac, Pfizer). No animals died during the adaptation or treatment periods. A total of 6 heifers appeared ill and were medicated during the treatment period. One heifer (treatment H3) had chronic bloat, and the other 5 heifers were treated once for respiratory-type symptoms (H0 = 1; H3 = 2; H6 = 2; H12 = 0). All heifers given medication were being fed the low-energy diet at the time of the apparent illness.

Treatments. At 11 wk of age, 16 heifers within each purchase group were blocked by BW and randomly assigned within block to 1 of 4 treatments (BW = 107 ± 1 kg). All heifers within a given treatment in the same purchase group were housed in the same pen. Thus, 4 pens of 4 heifers (1 pen per purchase group) were used in each of the 4 treatments. The timeline for the experiment is depicted in Figure 1. In our study, we used 2 basic diets (high energy or low energy), but the treatments were the number of weeks that heifers were fed

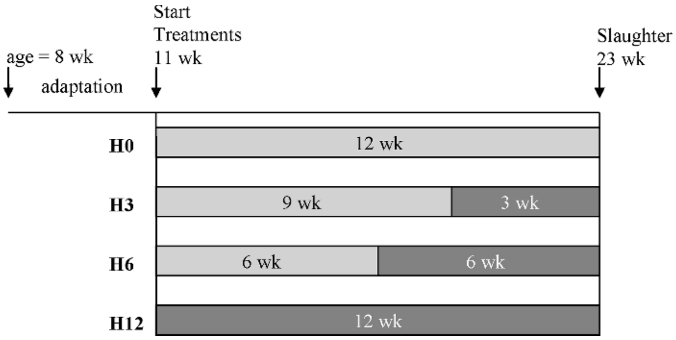

Figure 1. Timeline for the experiment. The low-energy diet is represented by the lighter shaded bar and the high-energy diet is represented by the darker shaded bar. The low- and high-energy diets were formulated for gains of 0.6 and 1.2 kg/d, respectively. Heifers (n = 15 or 16/treatment) in the H0, H3, H6, and H12 treatment groups were fed the low-energy diet for 12, 9, 6, or 0 wk, followed by the high-energy diet for 0, 3, 6, or 12 wk, respectively.

the high-energy diet. The treatment period lasted 12 wk and treatments were as follows: H0 (low-energy diet fed for 12 wk with no weeks on the high-energy diet); H3 (low-energy diet fed for 9 wk, followed by the high-energy diet for 3 wk); H6 (low-energy diet fed for 6 wk, followed by the high-energy diet for 6 wk); and H12 (high-energy diet for all 12 wk).

The low-energy diet was formulated for 0.6 kg of average daily gain based on the 2001 NRC guidelines, with adjustments to account for actual gains in our previous studies (Radcliff et al., 1997, 2000). This diet was adjusted on December 20 during the treatment period (average = wk 5 of the treatment period) to reflect changes in dietary requirements for cold stress according to the NRC. Both low-energy diets are presented in Table 1. Overall, the low-energy diet consisted of 10% straw, 33% mature alfalfa silage, 33% oatlage, and 24% concentrate on a DM basis. The low-energy diet averaged 16% CP and 45% NDF. The high-energy diet was formulated for 1.2 kg of average daily gain based on previous studies (Radcliff et al., 1997, 2000; Whitlock et al., 2002) and consisted of 20% immature alfalfa silage, 20% corn silage, and 60% concentrate on a DM basis. The high-energy diet had 18% CP and 23% NDF. Both diets and water were available ad libitum. Diet composition of the high-energy diet was not changed during the treatment period because the NRC model indicated the heifers could better handle cold stress and we did not want to feed less than 23% NDF. Composition of diets based on actual individual feedstuff analyses (Dairy One Forage Analysis Laboratory, Ithaca, NY) is given in Table 1. Sodium decoquinate (Deccox, Alpharma, Fort Lee, NJ) was included in both vitamin-mineral mixes as a coccidiostat to supply approximately 0.5 mg/kg of BW per day. Diets were fed as a TMR once daily between 0900 and 0930 h and refusals were measured daily at 0700 h. The amount of TMR fed was adjusted so that daily refusals were approximately 10%. Daily intakes for each pen were collected and measured by pen but were reported as an average per heifer.

During the treatment period, BW was measured weekly, before feeding. Withers height and hip width were measured on odd weeks and in the last week of the study for each heifer; hip width was measured by using a Hipometer (Dingwell et al., 2006). Heifers were slaughtered at the end of the treatment period when they were 23 wk of age. Heifers were allowed to consume the TMR from the prior day's feeding until they were transported at 0600 h via trailer to the abattoir at the Michigan State University Meats Laboratory.

Tissue Collection and Analysis

Heifers were weighed, stunned by captive bolt, and killed by exsanguination. Heifers were killed on 2 different days each week for 4 consecutive weeks, with 8 heifers (2/treatment) killed per day. The gallbladder was removed from the liver and the liver was weighed. After the hide was removed, the carcass was split into halves. Perirenal fat was removed and weighed by a person blinded to the treatment. The carcass was then weighed (carcass weight; **CW**).

Reproductive tracts were examined to confirm that heifers were not freemartins and had not reached puberty. The uterus and ovaries were removed and weighed. One heifer (treatment = H3) was a freemartin, and her data were eliminated from the results. Another heifer (treatment = H12) was postpubertal (a corpus luteum was detected), and her data also were removed from the study.

The day after slaughter, the left half of the carcass was cut between the 7th and 8th and the 12th and 13th ribs. The 8th through the 12th rib section was removed, vacuum sealed, and stored at –20°C until composition was analyzed. For analysis, the rib section was slightly thawed, and ribs 9, 10, and 11 were dissected according to Hankins and Howe (1946) and weighed. The soft tissue was dissected from the bone, weighed, and then ground, mixed, and subsampled. The tissue was stored at –20°C until further analysis. Fat was determined by Soxhlet ether extraction (AOAC, 1990). Crude protein was determined by using the method of Hach et al. (1987). Water was determined as the difference in weight after drying samples in a 106°C oven for 24 h.

Evaluation of 2001 NRC

Diet composition, DMI, slaughter weight, and rib composition of heifers from the H0 and H12 treatment

Table 1. Composition of diets

Item	Low-energy diet 1	Low-energy diet 2	High-energy diet
Ingredient, % of DM			
Alfalfa silage, early stage[1]	—	—	20.0
Alfalfa silage, late stage[2]	35.8	28.6	—
Corn silage[3]	—	—	20.0
Oatlage[4]	35.8	28.6	—
Straw	10.0	10.0	—
Ground corn	10.0	21.5	42.9
Solvent-extracted soybean meal	—	2.5	7.6
Expeller soybean meal[5]	7.2	7.5	7.5
Minerals and vitamins	1.2[6]	1.3[7]	2.0[8]
Nutrient composition, DM basis[9]			
NDF, %	49.3	42.7	22.9
ME 2001, Mcal/kg	2.24	2.39	2.82
NE_M 2001, Mcal/kg	1.35	1.49	1.87
NE_G 2001, Mcal/kg	0.77	0.90	1.23
CP, %	16.1	16.3	18.3
RUP, % of CP	42	43	39
CP:ME, g of CP/Mcal of ME	72	68	65

[1] Alfalfa silage, early stage: 24.7% CP, 37.2% NDF.

[2] Alfalfa silage, late stage: 15.0% CP, 54.8% NDF.

[3] Corn silage: 8.9% CP, 44.2% NDF.

[4] Oatlage: 16.6% CP, 55.8% NDF.

[5] The expeller soybean meal was SoyPlus (West Central Cooperative, Ralston, IA).

[6] Composition: 43.3% salt, 32.9% sodium decoquinate (5,007 mg/kg), 13.7% calcium:phosphorus (17 %:21%), 8.6% mineral mix, 1.4% vitamin mix. The mineral and vitamin mix was formulated so that the diet provided 100% of mineral and vitamin requirements.

[7] Composition: 34.6% salt, 25.3% sodium decoquinate (5,007 mg/kg), 22.1% limestone, 10.0% calcium:phosphorus (17%:21%), 6.9% mineral mix, 1.1% vitamin mix. The mineral and vitamin mix was formulated so that the diet provided 100% of mineral and vitamin requirements.

[8] Composition: 48.5% limestone, 24.2% salt, 16.2% sodium decoquinate (5,007 mg/kg), 5.5% calcium:phosphorus (17%:21%), 4.9% mineral mix, 0.8% vitamin mix. The mineral and vitamin mix was formulated so that the diet provided 100% of mineral and vitamin requirement.

[9] Energy values for the low and high diets were estimated by using NRC (2001) guidelines for the average BW of the heifers in the H0 and H12 groups for the low-energy and high-energy diets, respectively. The average ME, NE_M, and NE_G values for H0 heifers after accounting for time on both low-energy diets were 2.34, 1.44, and 0.85 Mcal/kg, respectively. Average ME intake per unit of metabolic BW was 0.22 and 0.32 Mcal/kg for the H0 and H12 groups, respectively.

groups and from heifers killed initially were used to evaluate predictions for intakes and gains of the NRC (2001) program. Treatment groups H3 and H6 were not included because these heifers were fed both the low- and high-energy diets. Assumptions used in the model included a mature BW of 680 kg (a standard value used in NRC example tables), a coat factor of 1 (clean and dry), a hair depth of 1.0 cm, a wind speed of 1 km/h (the heifers were housed in a barn with an open face to the south), and average BCS of 2.8 and 3.2 for the H0 and H12 treatments, respectively. Average temperature for the treatment period of each pen was also included in the analysis as the previous and current temperature. Predicted daily gain was calculated by using actual feed intakes. Estimated energy gain was calculated, assuming that the percentage of fat and protein in shrunk weight was similar to that in the 9th to 11th rib section. This assumption was based on data from several studies. Ainslie et al. (1993) showed that for Holstein steers ranging from 113 to 208 kg of BW, the percentage of lipid in the rib and carcass was very similar, from 7 to 12% lipid. In addition, Jesse et al. (1976) found that the percentages of fat of empty body gain and carcass gain were nearly identical. Empty body gain was 25.1% fat and 15.1% protein, whereas carcass gain was 27.1% fat and 25.2% protein in Hereford steers from 227 to 341 kg of shrunk BW. This difference in composition between carcass and empty body gain was greater in older steers in the study of Jesse et al. (1976), suggesting that the difference in young dairy heifers would be very small. Finally, Danner (1978) found that fat and protein composition of the carcass and body were similar in Hereford heifers, and, more important, that the slightly higher percentage of fat in carcass compared with empty body was true whether heifers were fed all grain or all corn silage.

The equations used to determine NRC energy and protein requirements for actual gains and the implied composition of gain were simplifications of those in the NRC (2001) guidelines:

$$RE = 5.668 \times SWG^{1.097} \times BW^{0.75} / \text{mature } BW^{0.75},$$

$$RP = SWG \times (268 - 29.4 \times RE / SWG), \text{ and}$$

$$RF = 1000 \times (RE - 5.6 \times RP/1000) / 9.4,$$

where SWG is shrunk weight gain in kilograms per day, BW is in kilograms, RE is retained energy in megacalories per day, RP is retained protein in grams per day, and RF is retained fat in grams per day.

Statistical Analysis

The PROC GLM procedure of SAS (SAS Institute, 1999) was used in statistical analysis. For all variables, pen (n = 4 heifers/treatment in each purchase group) was used as the experimental unit, with purchase group as a random variable and treatment × purchase group as the error term. Comparisons were tested by using a linear (**L**) contrast with coefficients –7, –3, 1, and 9; a quadratic (**Q**) contrast with coefficients 7, –4, –8, and 5; and a cubic (**C**) contrast with coefficients –3, 8, –6, and 1 for the H0, H3, H6, and H12 treatment groups, respectively. Although pen was the experimental unit, least squares means and standard errors of the mean are presented on a per heifer basis. Differences were declared to be statistically significant at $P < 0.05$ and tendencies at $P < 0.10$. All data from the 2 heifers that were eliminated from the trial were removed so that final animal numbers were 16, 15, 16, and 15 for treatment groups H0, H3, H6, and H12, respectively. Evaluation of the nutritional model of NRC included data from all heifers within the H0 and H12 treatment groups (n = 16/treatment).

Carcass accretion rates were calculated by using baseline values estimated from previous work (Brown et al., 2005b) as initial values. These accretion rates were then calculated on a fractional basis (fractional accretion rates) that was compounded over time.

Data that were collected every week or every other week were treated as a repeated measure and analyzed by using PROC MIXED, with either compound symmetry or first-order autoregressive as the covariance structure. The data for rib protein percentage, ovarian weight relative to BW, and ovarian weight relative to CW were log transformed to achieve homogeneous variance and normality, and the results presented were back transformed. The error term for the transformed data is the average of the back-transformed lower and upper 68% (±1 SE) confidence intervals.

RESULTS AND DISCUSSION

Growth and Feed Intake

Initial withers height and hip width measurements were not different among treatment groups (Table 2). Hip width and withers height increased as heifers aged (Figure 2B and 2C). A longer duration on the high-energy diet increased hip width and withers height at wk 12 of the study (Table 2; L: $P < 0.01$) so that the H12 heifers were 5 cm taller and 4 cm wider than the H0 heifers at 23 wk of age. This agrees with previous reports (Lammers et al., 1999; Brown et al., 2005b). Measurements of BW and withers height of heifers in the present study were within the range of previous reports for heifers of a similar age (Heinrichs and Hargrove, 1987; Hoffman, 1997), except that H12 heifers were heavier than the range reported for 5- to 6-mo-old heifers.

Initial BW was not different among treatments (Table 2). The effect of treatment on BW averaged for the treatment period was significant for both an L and Q response as heifers were fed the high-energy diet for a longer duration (Figure 2A; L: $P < 0.01$; Q: $P = 0.02$). The ending BW increased with a longer duration on the high-energy diet, with significant L, Q, and C contrasts (all $P < 0.01$). Over the treatment period, daily gain averaged 0.64, 0.65, 0.83, and 1.09 kg for the H0, H3, H6, and H12 groups, respectively, and all treatment contrasts were significant (Figure 3A and Table 3). If the growth response had been linear alone, we would have expected a slower gain for the H0 groups and a faster gain for the H3 groups. The actual gains for the low-energy diet (0.64 kg/d) and the high-energy diet (1.09 kg/d) were very close to the formulation targets of 0.6 and 1.2 kg/d, respectively.

A longer duration on the high-energy diet increased CW and CW as a percentage of BW in a linear fashion (Table 4; L: $P < 0.01$). The Q contrast for CW as a percentage of BW also was significant, and CW:BW for the H0 group was 2 units lower than expected based on a straight line through the H3, H6, and H12 data points. This lower dressing percentage was likely caused by greater gut fill in H0 heifers at the end of the study and would explain the apparent lack of difference in BW (i.e., mean difference was 2 kg) between the H0 and H3 treatment groups at slaughter. The effect of treatment on CW, which is a better measure of body growth than is BW, followed a straight line (Q and C contrasts were not significant) and more closely mirrored changes in withers height and hip width.

The effect of treatment on average daily gain during the last 2 wk was also significant for all 3 contrasts tested and averaged 0.72, 1.05, 1.34, and 1.19 kg for the H0, H3, H6, and H12 groups, respectively (Table 3; $P < 0.01$). During the first week after the switch from the low- to the high-energy diet, true changes in BW were likely masked by changes in gut contents. Thus, changes during the second and third weeks should better reflect empty body gains. Gains calculated during

Table 2. Least squares means for body growth

Item	H0	H3	H6	H12	SE[2]	L	Q	C
	Treatment group[1]					*P*-value for contrast[3]		
Heifers, n	16	15	16	15				
Initial BW, kg	106	108	108	108	0.74	0.25	0.19	0.72
Initial withers height, cm	89.9	90.0	90.4	90.1	0.32	0.52	0.41	0.61
Initial hip width, cm	29.8	30.0	29.7	30.0	0.28	0.80	0.69	0.44
BW at slaughter, kg	165	167	181	203	1.1	<0.01	<0.01	<0.01
Final withers height, cm	99.3	100	102	104	0.32	<0.01	0.21	0.04
Final hip width, cm	32.9	33.6	34.7	36.7	0.22	<0.01	0.50	0.43

[1] Treatment groups were as follows: heifers in the H0, H3, H6, and H12 treatment groups were fed the low-energy diet for 12, 9, 6, or 0 wk followed by the high-energy diet for 0, 3, 6, or 12 wk, respectively. The low-energy diet and high-energy diet were formulated for gains of 0.6 and 1.2 kg/d, respectively.

[2] Pooled SE using treatment × purchase group or pen as the error term, with 4 pens per treatment.

[3] L = linear; Q = quadratic; C = cubic.

the second and third week after the dietary switch for H6 (wk 8 and 9) and H3 (wk 11 and 12) were 1.22 and 1.05 g/d, respectively (Table 3). The H3 treatment group did not respond to the high-energy diet as rapidly as the H6 group. Perhaps this is related to the average temperature being –5°C during wk 6 to 9 and –9°C during wk 9 to 12, but this does not seem adequate to explain the slower response.

Daily DMI, averaged over the entire 12-wk period, was greater with a longer duration on the high-energy diet (Table 3 and Figure 3B; L: $P < 0.01$). Daily DMI of all groups increased gradually over the first 4 wk of the treatment period, and this increase was more pronounced with the low-energy diets (H0, H3, and H6 treatments). After wk 4, feed consumption was relatively constant for the H0 and H12 heifers but increased for the H3 and H6 heifers as they were switched to the high-energy diet (Table 3). The fact that DMI was initially greater for the H12 heifers than those fed the low-energy (high-fiber) diet, and that DMI increased in the 2 wk following the switch to the high-energy (low-fiber) diet in the H6 and H3 groups indicates that gut distension limited DMI with the low-energy diet. The pronounced increase in DMI at the start of the study in heifers fed the low-energy diet indicates that gut capacity was expanding in these heifers. An increase in gut capacity in heifers fed the high-fiber diet would be consistent with the idea that animals eat to minimize discomfort so that both gut distension and metabolic needs control appetite concurrently (Forbes, 2003). When adjusted for BW, daily DMI over the 12 wk was greater with a longer duration on the high-energy diet (L: $P < 0.01$), with DMI of the H0 and H12 treatments averaging 2.8 and 3.3% of BW.

Fat and Protein Deposition

A longer duration on the high-energy diet increased the percentage of fat and slightly decreased the percentage of protein in the 9th to 11th rib section (Table 4; L: $P < 0.01$). The Q contrast was also significant for rib fat percentage (Q: $P < 0.01$) because of a small difference in means for the H6 and H12 treatments. Assuming that rib fat percentage is similar to carcass fat percentage, as shown by Ainslie et al. (1993), the increase in rib fat suggests that H12 heifers had double the body fat of H0 heifers. This is consistent with our measures of perirenal fat and mammary fat pad (see Davis Rincker et al., 2008), which also doubled as a percentage of BW. These 3 separate measures of body fatness were all highly and positively correlated with each other at $r = 0.9$ for each correlation (data not shown). The amount of perirenal fat unadjusted and adjusted for BW increased in a linear fashion with time fed the high-energy diet (L: $P < 0.01$). Petitclerc et al. (1984) noted that at similar BW, heifers fed on a higher plane of nutrition had increased fat deposition, which was the case in this study when perirenal fat was adjusted to BW. The linear increase in rib fat percentage and perirenal fat observed in this study may be a concern for the future performance of dairy heifers fed for rapid gains. Recent evidence has indicated that the degree of body fatness is negatively correlated with mammary parenchymal DNA and milk production (Silva et al., 2002).

We observed little evidence of a beneficial compensatory growth response in the H6 and H3 heifers. We thought that the H3 and H6 heifers might have greater CW or feed efficiency than what was observed based on a straight-line response for the H0 and H12 heifers; however, only the L contrast was significant for final CW, and gain:feed was actually lower than expected, with both Q and C contrasts significant (Table 3). The H6 heifers grew faster and had greater gain:feed than all other groups during wk 8 and 9 (after adaptation to the high-energy diet), based on a significant C contrast (Table 3; $P < 0.01$). Although this supports a compensa-

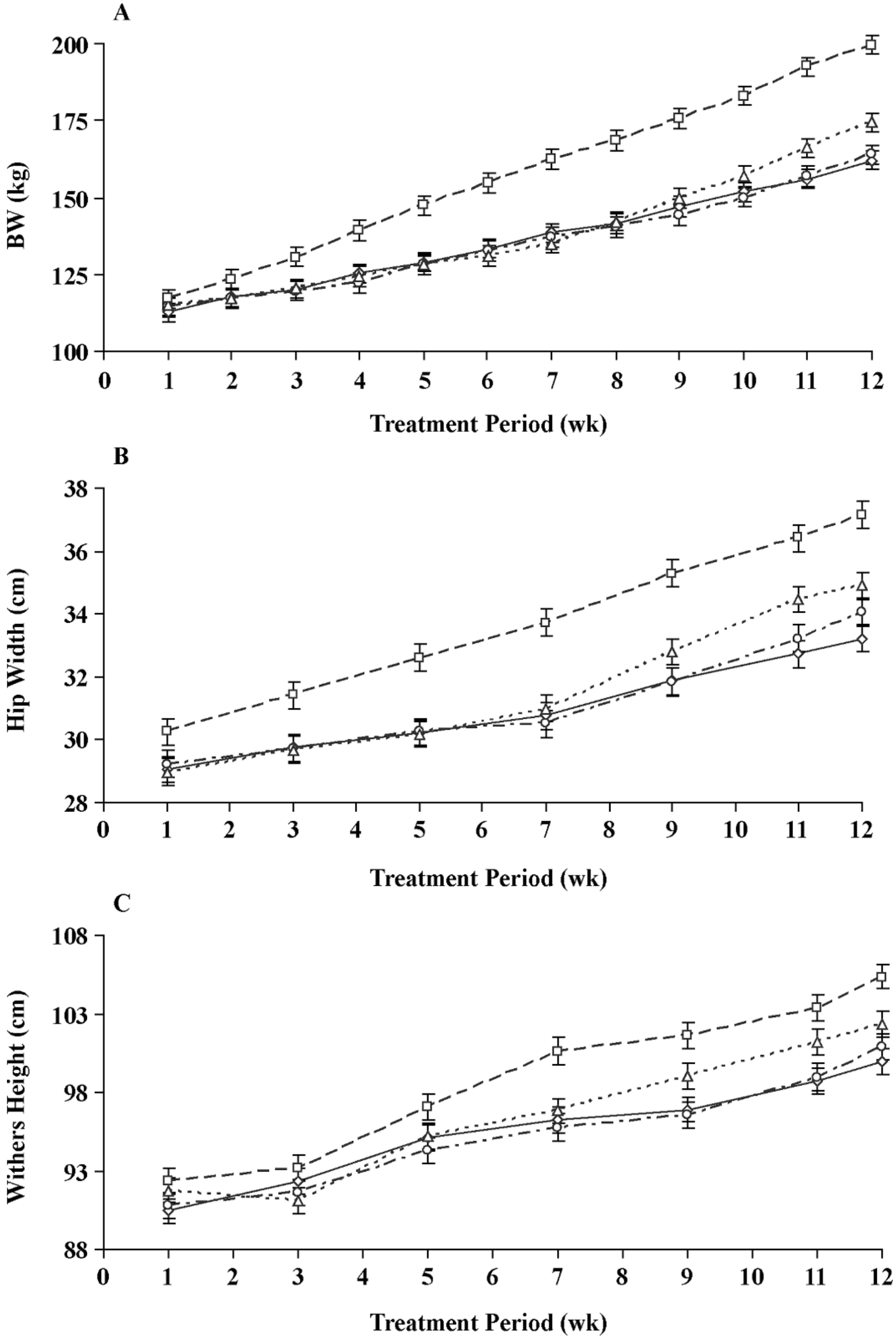

Figure 2. Body weight (A), hip width (B), and withers height (C) measurements of heifers in the H0 (—◇—), H3 (- – -○- – -), H6 (- - -△- - -), and H12 (– –□– –) treatment groups. Heifers (n = 15 or 16/treatment) in the H0, H3, H6, and H12 treatment groups were fed the low-energy diet for 12, 9, 6, or 0 wk, followed by the high-energy diet for 0, 3, 6, or 12 wk, respectively. All measurements: linear: $P < 0.01$. Body weight and hip width: quadratic: $P = 0.02$ and $P = 0.03$, respectively.

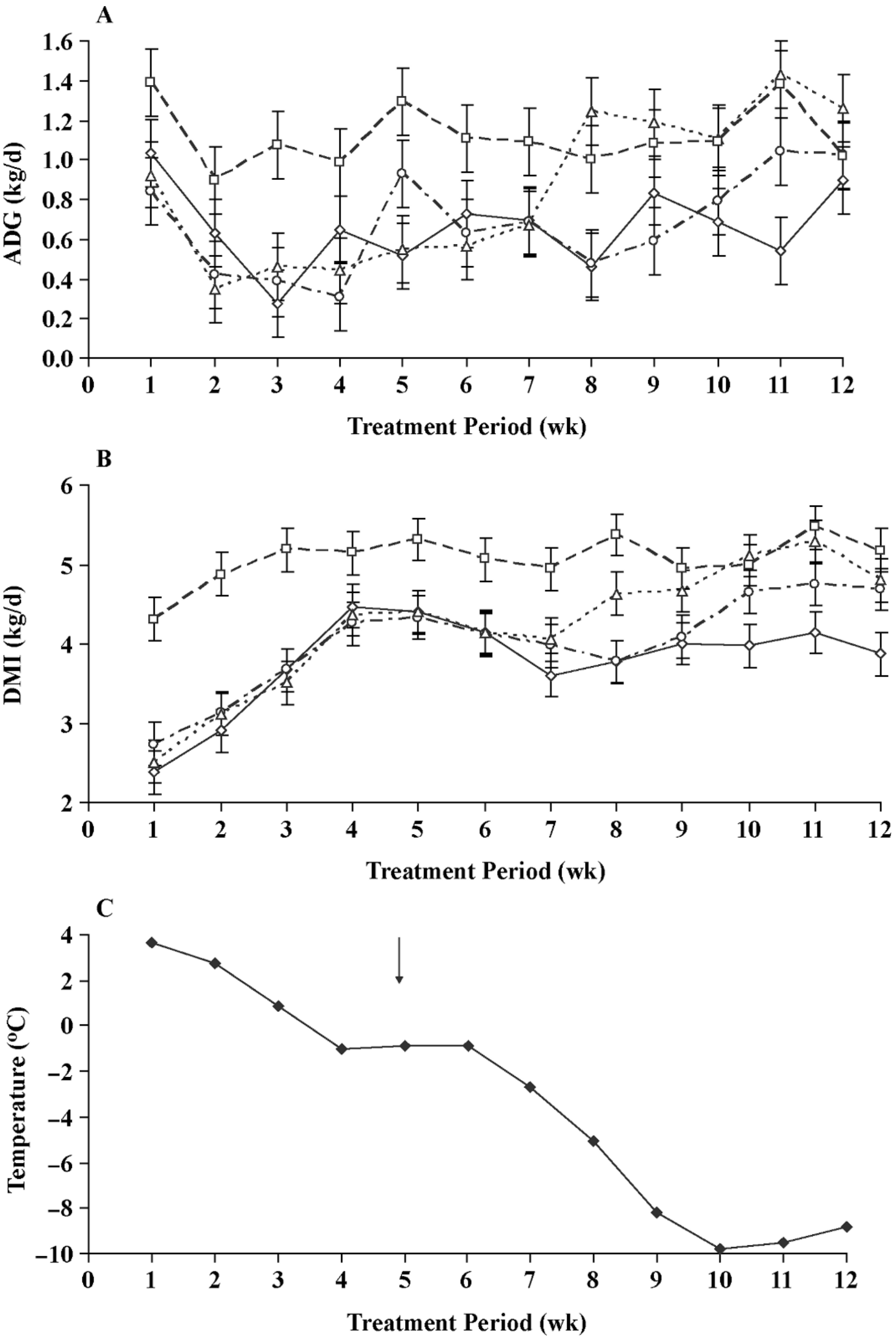

Figure 3. Weekly average daily gain (ADG; A) and daily DMI (B) averaged each week for heifers in the H0 (—◇—), H3 (- – -○- – -), H6 (- - -△- - -), and H12 (– –□– –) treatment groups. Heifers (n = 15 or 16/treatment) in the H0, H3, H6, and H12 treatment groups were fed the low-energy diet for 12, 9, 6, or 0 wk, followed by the high-energy diet for 0, 3, 6, or 12 wk, respectively. Data are presented as the average of the previous week. Average daily gain and DMI: linear: $P < 0.01$. Weekly average temperatures (°C) are averaged for all purchase groups. The arrow indicates the average week when the low-energy diet was adjusted to reflect changes in dietary requirements for cold stress.

Table 3. Least squares means for feed intake and efficiency during specific week of the treatment period

	Treatment group[1]					*P*-value for contrast[3]		
Item	H0	H3	H6	H12	SE[2]	L	Q	C
DMI, kg/d								
1 through 12 wk	3.78	4.01	4.22	5.07	0.09	<0.01	0.10	0.59
2 through 6 wk	3.92	3.90	3.91	5.12	0.34	<0.01	<0.01	0.51
8 and 9 wk	3.89	3.93	4.65	5.16	0.23	<0.01	0.97	0.17
11 and 12 wk	4.01	4.72	5.04	5.32	0.21	<0.01	0.04	0.64
Average daily gain, kg/d								
1 through 12 wk	0.64	0.65	0.83	1.09	0.01	<0.01	<0.01	<0.01
2 through 6 wk	0.57	0.54	0.48	1.07	0.19	<0.01	<0.01	0.06
8 and 9 wk	0.65	0.53	1.22	1.05	0.13	<0.01	0.09	<0.01
11 and 12 wk	0.72	1.05	1.34	1.19	0.18	<0.01	<0.01	0.54
Gain:feed, kg/kg								
1 through 12 wk	0.18	0.17	0.19	0.22	0.004	<0.01	0.02	<0.01
2 through 6 wk	0.15	0.15	0.12	0.21	0.01	<0.01	<0.01	0.17
8 and 9 wk	0.16	0.13	0.27	0.20	0.02	0.04	0.07	<0.01
11 and 12 wk	0.18	0.22	0.26	0.22	0.02	0.17	0.03	0.65
Carcass weight gain:feed, kg/kg	0.08	0.10	0.12	0.13	0.002	<0.01	0.04	0.07

[1] Treatment groups are as follows: heifers in the H0, H3, H6, and H12 treatment groups were fed the low-energy diet for 12, 9, 6, or 0 wk, followed by the high-energy diet for 0, 3, 6, or 12 wk, respectively. The low-energy diet and high-energy diet were formulated for gains of 0.6 and 1.2 kg/d, respectively.

[2] Pooled SE using treatment × purchase group or pen as the error term, with 4 pens per treatment.

[3] L = linear; Q = quadratic; C = cubic.

tory response, the same response was not observed for H3 heifers during wk 11 and 12. Furthermore, the deposition of fat in rib sections and in the perirenal cavity increased with a longer duration on the high-energy diet and was greater for the H3 and H6 groups than expected for a straight-line response (Table 4; Q: $P < 0.01$ for rib percentage fat, and $P = 0.06$ for perirenal fat adjusted for BW). Given that fat deposition was greater than expected for the H3 and H6 heifers but that CW followed a straight-line response, our data suggest that the H3 and H6 heifers likely had less fat-free carcass growth than expected, based on the H0 and H12 heifers. Carcasses from steers fed at maintenance and then fed ad libitum compared with control steers fed ad libitum continuously were higher in protein and lower in fat when harvested at similar BW (364 kg)

Table 4. Least squares means for body and estimated carcass composition[1]

		Treatment group[2]					*P*-value for contrast[4]		
Item	Baseline	H0	H3	H6	H12	SE[3]	L	Q	C
Heifers, n	4	16	15	16	15				
Carcass weight, kg	$50.0^{\#}$	76.6	82.5	91.5	107	0.65	<0.01	0.40	0.10
Carcass weight, % of BW	$48.5^{\#}$	46.4	49.4	50.6	52.6	0.36	<0.01	<0.01	0.24
Carcass fractional accretion rate,[5] %	—	0.40	0.48	0.60	0.78	0.009	<0.01	0.36	0.12
Rib protein, %	21.6	19.0	18.8	18.1	18.1	A*	<0.01	0.12	0.38
Rib fat, %	6.10	7.33	10.1	13.5	14.4	0.61	<0.01	<0.01	0.24
Rib water, %	71.2	71.9	69.4	66.5	65.3	0.52	<0.01	<0.01	0.31
Liver weight, kg	—	2.66	3.62	3.71	3.94	0.04	<0.01	<0.01	0.01
Liver weight, % of BW	—	1.62	2.17	2.05	1.97	0.02	<0.01	<0.01	<0.01
Perirenal fat, g	—	693	987	1,480	1,856	100	<0.01	0.20	0.27
Perirenal fat, g/100 kg of BW	—	418	588	814	914	54	<0.01	0.06	0.37

[1] A pound sign ($^{\#}$) indicates that baseline carcass weight measurements were estimated by using previous work (Brown et al., 2005b). An asterisk (*) indicates that data were log transformed to achieve homogeneous variance. Means presented are back transformed. The error term indicated below is the average of the lower and upper confidence intervals for each treatment group. An "A" indicates the average confidence intervals are 0.16, 0.17, 0.16, and 0.16 for the H0, H3, H6, and H12 treatment groups, respectively.

[2] Treatment groups are as follows: heifers in the H0, H3, H6, and H12 treatment groups were fed the low-energy diet for 12, 9, 6, or 0 wk followed by the high-energy diet for 0, 3, 6, or 12 wk, respectively. The low-energy diet and high-energy diet were formulated for gains of 0.6 and 1.2 kg/d, respectively.

[3] Pooled SE using treatment × purchase group or pen as the error term, with 4 pens per treatment.

[4] L = linear; Q = quadratic; C = cubic.

[5] Fractional accretion rate = $\exp\{[\ln(\text{carcass weight at end of study}) - \ln(\text{carcass weight for baseline})]/84\ \text{d}\} - 1$.

during the early refeeding period, but were similar in composition at final slaughter weights (454 kg; Fox et al., 1972). Fox et al. (1972) suggested that steers deposit lean gain during the early compensatory growth period. Kabbali et al. (1992) found that feeding sheep a high-energy diet after a low-energy diet increased the rate of gain and efficiency of feed use compared with continuously high-fed controls, whereas feeding a high-energy diet following a moderate diet had no compensatory effect. Perhaps our low-energy diet (which supported gains of 480 to 540 g/d at ad libitum intake before wk 6) was not low enough in energy or was not fed long enough to yield a compensatory response with the high-energy diet, or perhaps we did not observe a compensatory response because our animals were young dairy heifers.

Liver

Four heifers on the H12 treatment had liver abscesses that were likely due to acidosis caused by the high-grain diet. In addition, 2 heifers on the H6 treatment had telangiectasis or "sawdust liver." Liver weight as a proportion of BW increased in a curvilinear fashion with a longer duration on the high-energy diet (L, Q, and C contrasts were all $P < 0.01$; Table 4) and was highest for heifers on the H3 treatment. Thus, the liver grew rapidly and allometrically in response to a higher energy diet, and then its growth leveled off. This is consistent with a compensatory growth response and has been reported previously for beef steers and lambs (Carstens et al., 1991; Kabbali et al., 1992).

Reproductive Tissues

In general, treatment had little effect on the weights of the uterus and ovaries, except that the C contrast was significant for uterine weight (Table 5). However, once adjusted for CW, the weights of these organs were decreased linearly as heifers were fed the high-energy diet for a longer duration (L: $P \leq 0.04$). We hypothesized that the weights of uterine and ovarian tissue would have a linear increase with a longer duration on the high-energy diet and thus parallel overall body growth. This would seem likely if heifers were to have similar reproductive organ weights at the onset of puberty. There is limited evidence to support a role for nutrition in altering reproductive organ weights in prepubertal heifers. Pritchard et al. (1972) indicated that when heifers consumed ad libitum intake of corn silage and alfalfa hay and were fed grain to gain either 0.83 or 1.08 kg/d, treatments had similar uterine weights at the onset of puberty. Body weight and possibly the degree of body fatness are factors that affect the onset of puberty, and heifers fed for rapid growth attain puberty at an earlier age (Schillo et al., 1992; Radcliff et al., 1997; Lammers et al., 1999). Overall, our results suggest that heifers fed a high-energy diet will have smaller reproductive organs at puberty than heifers fed a low-energy diet. However, high-energy intake during the prepubertal period did not significantly alter pelvic area, conception rates, or calving rates of heifers (Radcliff et al., 1997, 2000), and therefore may not be a long-term concern.

Evaluation of the 2001 NRC Model

The 2001 NRC model overpredicted DMI by 8% ($P = 0.05$) for the low-energy diet and underpredicted DMI by 12% ($P = 0.02$) for the high-energy diet (Table 6). Dietary NE_M density is used in the prediction of DMI in the NRC, but our data suggest that the sensitivity of the DMI prediction to NE_M density (or percentage of NDF) is inadequate.

On the basis of actual intake of each diet, the 2001 NRC model performed reasonably well at predicting gains for H0 heifers but overpredicted gains for H12 heifers. The energy-allowable gain in NRC was 15% less (but not significantly less) than the actual live weight gain of H0 heifers, but it was 41% greater ($P < 0.01$) than the actual live weight gain of H12 heifers.

The most likely reason that NRC overpredicted gains in heifers fed the high-energy diet is that the composition of gain in the NRC model is relatively insensitive to changes in dietary energy intake. For example, retained energy per kilogram of shrunk body gain in NRC Table 11-1 is 2.23 Mcal for a 200-kg heifer gaining 600 g/d and increases to 2.34 Mcal for one gaining 1,000 g/d.

In our study, we estimated the energy density of gain, based on rib composition, to be considerably greater for H12 than H0 heifers (1.7 Mcal/kg for H0 and 3.2 Mcal/kg for H12). When NRC requirement equations were used for our average gains and BW, however, the energy density of shrunk weight gain was calculated to be 1.55 and 1.82 Mcal/kg for H0 and H12 heifers, respectively. The implicit assumptions in the NRC equations for retained energy and protein are that the gain of these animals would be 4% fat and 1% protein for H0 heifers and 7% fat and 20% protein for H12 heifers. However, if rib fat content is similar to that of the carcass for dairy animals of this age, as previously demonstrated (Ainslie et al., 1993), we estimate gain to be 10% fat for H0 heifers and 25% fat for H12 heifers. Interestingly, these values closely match those using the equations of Fox and Black (1984), which predict empty body gain to be 10 and 24% fat for the H0 and H12 treatments, respectively. Moreover, the estimated NE_G available for gain based on diet composition and intake

Table 5. Least squares means for uterine and ovarian weights[1]

	Treatment group[2]					P-value for contrast[4]		
Item	H0	H3	H6	H12	SE[3]	L	Q	C
Heifers, n	16	15	16	15				
Uterine weight, g	56.3	71.0	60.1	67.4	4.6	0.27	0.54	0.05
Uterine weight, g/100 kg of BW	34.5	42.4	33.3	33.2	2.6	0.25	0.37	0.03
Uterine weight, g/100 kg of carcass weight	74.2	85.9	66.0	63.1	5.4	0.04	0.57	0.04
Ovarian weight, g	8.30	7.75	6.91	7.75	0.62	0.52	0.18	0.61
Ovarian weight, g/100 kg of BW	4.94	4.37	3.63	3.71	A*	0.02	0.14	0.50
Ovarian weight, g/100 kg of carcass weight	10.5	8.85	7.17	7.06	B*	<0.01	0.12	0.56

[1] An asterisk (*) indicates the data were log transformed to achieve homogeneous variance. Means presented are back transformed. The error term indicated below is the average of the lower and upper confidence intervals for each treatment group. An "A" indicates that the average confidence intervals are 0.39, 0.35, 0.27, and 0.28 for the H0, H3, H6, and H12 treatment groups, respectively. A "B" indicates that the average confidence intervals are 0.84, 0.77, 0.58, and 0.57 for the H0, H3, H6, and H12 treatment groups, respectively.

[2] Treatment groups are as follows: heifers in the H0, H3, H6, and H12 treatment groups were fed the low-energy diet for 12, 9, 6, or 0 wk, followed by the high-energy diet for 0, 3, 6, or 12 wk, respectively. The low-energy diet and high-energy diet were formulated for gains of 0.6 and 1.2 kg/d, respectively.

[3] Pooled SE using treatment × purchase group or pen as the error term, with 4 pens per treatment.

[4] L = linear; Q = quadratic; C = cubic.

of the H12 heifers was 3.4 Mcal/d, which more closely matches our estimated retention of 3.3 Mcal/d based on actual gain and rib composition than it does NRC's estimated NE_G requirement of 2.0 Mcal/d needed to achieve the actual gain.

Unfortunately, we did not measure actual body composition; however, we suggest that rib sections give reasonable estimates of carcass composition, especially for fat, as shown by Ainslie et al. (1993). In addition, the percentages of fat and protein of rib sections in our study were similar to those expected based on actual composition of 3- to 6-mo-old Holstein heifers in previous studies (Moallem et al., 2004; Brown et al., 2005b; Rius et al., 2005). Finally, we found that the rib percentage of fat was highly correlated ($r = 0.9$) with perirenal fat (percentage of BW) and with mammary extra parenchymal fat (percentage of BW). Thus, we suggest that the NRC requirement equations do not adequately account for the increased fat deposition that occurs when heifers are fed energy intakes to support rapid gains. Although Waldo et al. (1997) and Radcliff et al. (1997) are cited by the 2001 NRC as evidence that the proportion of retained energy from fat increases with increased energy intake, the NRC equations incorporate

Table 6. Evaluation of NRC (2001) model

Item	H0	H12	P-value for diet[1]	P-value for H0[2]	P-value for H12[3]
Data based on actual measurements					
Average BW during study, kg	136	158	<0.01		
Average BW gain, g/d	653	1,080	<0.01		
Average shrunk BW gain, g/d	624	1,037	<0.01		
Average DMI, kg/d	3.79	5.06	<0.01		
Estimated NE_G,[4] Mcal/d	1.07	3.28	<0.01		
NRC predictions					
Predicted DMI from NRC, kg/d	4.11	4.46	<0.01		
Predicted DMI, % of actual	108	88	0.01	0.05	0.02
Energy-allowable gain,[5] g/d	558	1,773	<0.01		
Protein-allowable gain,[5] g/d	838	1,525	<0.01		
Most limiting gain, g/d	558	1,525	<0.01		
Predicted, % of actual	85	141	0.02	0.14	<0.01
NE_G required to achieve actual gain, Mcal/d	1.02	1.97	<0.01		
NE_G available from diet using NRC, Mcal/d	0.86	3.40	<0.01		

[1] P-value for H0 vs. H12.

[2] P-value for actual vs. predicted values for the H0 treatment.

[3] P-value for actual vs. predicted values for the H12 treatment.

[4] Calculated using actual gains and assuming that rib composition is similar to body composition.

[5] Allowable gain based on NRC predictions using actual intake and diet composition.

little of this concept. This underprediction of fat gain in the NRC with higher energy diets resulted in an overprediction of BW gain in young heifers.

We used the average temperature during the entire study as the "previous" and "current" temperatures in the NRC model. The "previous" temperature in the NRC model affects energy partitioning anytime it is below 20°C, which was the case throughout our study (Figure 3C). However, "current" temperature affects available NE_G only when it is below a lower critical temperature. Thus, average temperature would underestimate the energy needed for thermoregulation compared with an evaluation in which we evaluated each pen of heifers each day. Interestingly, however, the lower critical temperature in NRC was approximately −12°C for heifers fed the high-energy diet and −2°C for heifers fed the low-energy diet. Thus, our average temperature method made little difference for evaluation of the high-energy diet but would have decreased predicted gains on the low-energy diet by an additional 100 g/d, thus decreasing the accuracy of the prediction.

Because the NRC energy model grossly overpredicted gains of the H12 heifers, protein was predicted to be most limiting for these heifers. This seems unlikely. With both diets, we supplied more net protein for gain (176 and 301 g/d for H0 and H12 heifers, respectively) than that required by the NRC for the gains actually achieved (138 and 220 g/d for H0 and H12 heifers, respectively).

CONCLUSIONS

Body weight, skeletal growth, and CW of prepubertal dairy heifers increased in a linear fashion with a high-energy diet fed for a longer duration. Uterine and ovarian weights, adjusted for CW, decreased as heifers were fed a high-energy diet for a longer duration. An increase in body or carcass growth without a proportional increase in reproductive organ weight might result in smaller organs at puberty in heifers fed a high-energy diet. The 2001 NRC underestimated DMI of the high-energy diet and overestimated DMI of the low-energy diet. On the basis of actual intakes of each diet, the NRC slightly underestimated gain for the low-energy diet and overestimated gain for the high-energy diet, primarily because it underestimated fat gain in heifers fed the high-energy diet. A major shortfall of the current NRC growth model is that it does not adequately account for changes in the composition of gain in response to changes in energy intake.

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REFERENCES

Ainslie, S. J., D. G. Fox, T. C. Perry, D. J. Ketchen, and M. C. Barry. 1993. Predicting amino acid adequacy of diets fed to Holstein steers. J. Anim. Sci. 71:1312–1319.

AOAC. 1990. Official Methods of Analysis. 15th ed. Assoc. Off. Anal. Chem., Arlington, VA.

Brown, E. G., M. J. VandeHaar, K. M. Daniels, J. S. Liesman, L. T. Chapin, J. W. Forrest, R. M. Akers, R. E. Pearson, and M. S. Weber Nielsen. 2005a. Effect of increasing energy and protein intake on mammary development in heifer calves. J. Dairy Sci. 88:595–603.

Brown, E. G., M. J. VandeHaar, K. M. Daniels, J. S. Liesman, L. T. Chapin, D. H. Keisler, and M. S. Weber Nielsen. 2005b. Effect of increasing energy and protein intake on body growth and carcass composition of heifer calves. J. Dairy Sci. 88:585–594.

Cady, R. A., and T. R. Smith. 1996. Economics of heifer raising programs. Proc. Calves, Heifers and Dairy Profitability Natl. Conf., Harrisburg, PA. Nat. Resour., Agric., Eng. Serv. Publ. 74. Natural Resour., Agric., Eng. Serv., Ithaca, NY.

Carstens, G. E., D. E. Johnson, M. A. Ellenberger, and J. D. Tatum. 1991. Physical and chemical components of the empty body during compensatory growth in beef steers. J. Anim. Sci. 69:3251–3264.

Choi, Y. J., I. K. Han, J. H. Woo, H. J. Lee, K. Jang, K. H. Myung, and Y. S. Kim. 1997. Compensatory growth in dairy heifers: The effect of a compensatory growth pattern on growth rate and lactation performance. J. Dairy Sci. 80:519–524.

Danner, M. L. 1978. The effect of feeding system on the performance and carcass characteristics of yearling steers, steer calves and heifer calves. Michigan State Univ., East Lansing.

Davis Rincker, L. E., M. S. Weber Nielsen, L. T. Chapin, J. S. Liesman, K. M. Daniels, R. M. Akers, and M. J. VandeHaar. 2008. Effects of feeding prepubertal heifers a high energy diet for three, six, or twelve weeks on mammary growth and composition. J. Dairy Sci. 91:1926–1935.

Dingwell, R. T., M. M. Wallace, C. J. McLaren, C. F. Leslie, and K. E. Leslie. 2006. An evaluation of two indirect methods of estimating body weight in Holstein calves and heifers. J. Dairy Sci. 89:3992–3998.

Forbes, J. M. 2003. The multifactorial nature of food intake control. J. Anim. Sci. 81(Suppl. 2):E139–E144.

Fox, D. G., and J. R. Black. 1984. A system of predicting body composition and performance of growing cattle. J. Anim. Sci. 58:725–739.

Fox, D. G., R. R. Johnson, R. L. Preston, T. R. Dockerty, and E. W. Klosterman. 1972. Protein and energy utilization during compensatory growth in beef cattle. J. Anim. Sci. 34:310–318.

Gabler, M. T., and A. J. Heinrichs. 2003. Dietary protein to metabolizable energy ratios on feed efficiency and structural growth of prepubertal Holstein heifers. J. Dairy Sci. 86:268–274.

Hach, C. C., B. K. Bowden, A. B. Kopelove, and S. V. Brayton. 1987. More powerful Kjeldahl digestion method. J. AOAC 70:783–787.

Hankins, O. G., and P. E. Howe. 1946. Estimation of the composition of beef carcasses and cuts. USDA Tech. Bull. 926. USDA, Washington, DC.

Heinrichs, A. J., and G. L. Hargrove. 1987. Standards of weight and height for Holstein heifers. J. Dairy Sci. 70:653–660.

Hoffman, P. C. 1997. Optimum body size of Holstein replacement heifers. J. Anim. Sci. 75:836–845.

Jesse, G. W., G. B. Thomson, J. L. Clark, H. B. Hedrick, and K. G. Weimer. 1976. Effects of ration energy and slaughter weight on composition of empty body and carcass gain of beef cattle. J. Anim. Sci. 43:418–425.

Kabbali, A., W. L. Johnson, D. W. Johnson, R. D. Goodrich, and C. E. Allen. 1992. Effects of compensatory growth on some body component weights and on carcass and noncarcass composition of growing lambs. J. Anim. Sci. 70:2852–2858.

Lammers, B. P., A. J. Heinrichs, and R. S. Kensinger. 1999. The effects of accelerated growth rates and estrogen implants in prepubertal Holstein heifers on estimates of mammary development and subsequent reproduction and milk production. J. Dairy Sci. 82:1753–1764.

Moallem, U., G. E. Dahl, E. K. Duffey, A. V. Capuco, D. L. Wood, K. R. McLeod, R. L. Baldwin, and R. A. Erdman. 2004. Bovine somatotropin and rumen-undegradable protein effects in prepubertal dairy heifers: Effects on body composition and organ and tissue weights. J. Dairy Sci. 87:3869–3880.

NRC. 2001. Nutrient Requirements of Dairy Cattle. 7th rev. ed. Natl. Acad. Sci., Washington, DC.

Park, C. S., G. M. Erickson, Y. J. Choi, and G. D. Marx. 1987. Effect of compensatory growth on regulation of growth and lactation: Response of dairy heifers to a stair-step growth pattern. J. Anim. Sci. 64:1751–1758.

Petitclerc, D., L. T. Chapin, and H. A. Tucker. 1984. Carcass composition and mammary development responses to photoperiod and plane of nutrition in Holstein heifers. J. Anim. Sci. 58:913–919.

Petitclerc, D., P. Dumoulin, H. Ringuet, J. Matte, and C. Girard. 1999. Plane of nutrition and folic acid supplementation between birth and four months of age on mammary development of dairy heifers. Can. J. Anim. Sci. 79:227–234.

Pritchard, D. E., H. D. Hafs, H. A. Tucker, L. J. Boyd, R. W. Purchas, and J. T. Huber. 1972. Growth, mammary, reproductive, and pituitary hormone characteristics of Holstein heifers fed extra grain and melengesterol acetate. J. Dairy Sci. 55:995–1004.

Radcliff, R. P., M. J. VandeHaar, L. T. Chapin, T. E. Pilbeam, D. K. Beede, E. P. Stanisiewski, and H. A. Tucker. 2000. Effects of diet and injection of bovine somatotropin on prepubertal growth and first-lactation milk yields of Holstein cows. J. Dairy Sci. 83:23–29.

Radcliff, R. P., M. J. VandeHaar, A. L. Skidmore, L. T. Chapin, B. R. Radke, J. W. Lloyd, E. P. Stanisiewski, and H. A. Tucker. 1997. Effects of diet and bovine somatotropin on heifer growth and mammary development. J. Dairy Sci. 80:1996–2003.

Rius, A. G., E. E. Connor, A. V. Capuco, P. E. Kendall, T. L. Auchtung-Montgomery, and G. E. Dahl. 2005. Long-day photoperiod that enhances puberty does not limit body growth in Holstein heifers. J. Dairy Sci. 88:4356–4365.

SAS Institute. 1999. SAS/STAT User's Guide. Release 8.1 Edition. SAS Inst., Inc., Cary, NC.

Schillo, K. K., J. B. Hall, and S. M. Hileman. 1992. Effects of nutrition and season on the onset of puberty in the beef heifer. J. Anim. Sci. 70:3994–4005.

Sejrsen, K., J. T. Huber, H. A. Tucker, and R. M. Akers. 1982. Influence of nutrition of mammary development in pre- and postpubertal heifers. J. Dairy Sci. 65:793–800.

Silva, L. F. P., M. J. VandeHaar, B. K. Whitlock, R. P. Radcliff, and H. A. Tucker. 2002. Short communication: Relationship between body growth and mammary development in dairy heifers. J. Dairy Sci. 85:2600–2602.

Van Amburgh, M. E. 2005. An evaluation of the calf and heifer models within the 2001 dairy NRC publication. J. Dairy Sci. 88(Suppl. 1):439. (Abstr.)

Waldo, D. R., H. F. Tyrrell, A. V. Capuco, and C. E. Rexroad Jr. 1997. Components of growth in Holstein heifers fed either alfalfa or corn silage diets to produce two daily gains. J. Dairy Sci. 80:1674–1684.

Whitlock, B. K., M. J. VandeHaar, L. F. P. Silva, and H. A. Tucker. 2002. Effect of dietary protein on prepubertal mammary development in rapidly growing dairy heifers. J. Dairy Sci. 85:1516–1525.