Body Composition and Metabolic Profiles Associated with Puberty in Beef Heifers[1]

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ABSTRACT: Rapid growth large frame (RL, n = 61) or average growth medium frame (AM, n = 71) biotype heifers fed to achieve either moderate (MOD, .6 kg/d) or high ADG (HI, 1.0 kg/d) were used to determine whether puberty occurs at similar body composition or metabolic status. A heifer was considered pubertal after being detected in estrus and then forming a functional corpus luteum. Live animal estimates of body composition and blood samples for assessment of metabolic status were taken at 13 ± .2 d after estrus for all heifers. Body composition and metabolic status were assessed every 56 d from 7 mo of age until puberty in a subset of 80 heifers representing all biotype-diet combinations. At puberty, 32 of these 80 heifers were slaughtered and physical and chemical composition of the empty body were determined. High-gain diet heifers were younger, heavier, taller, and more muscular (all $P < .01$) at puberty than MOD heifers. Slaughter measurements paralleled live animal estimates; bodies of HI and RL heifers contained more ($P < .01$) carcass and noncarcass components than those of MOD and AM heifers, respectively. Carcasses of RL and HI heifers were more ($P < .05$) muscular and fatter than AM and MOD heifers. At puberty, HI heifers had a greater ($P < .01$) mass of moisture, fat, and fat-free organic matter (FFOM) than MOD, whereas RL heifers had more moisture, ash, and FFOM than AM. Percentage of fat was greater (22.1 ± 1.0 vs 19.1 ± 1.0; $P < .05$) and percentage of moisture was less (55.4 ± .6 vs 58.1 ± .6; $P < .01$) in bodies of HI than in those of MOD heifers. Concentrations of blood urea nitrogen and insulin were greater ($P < .05$) in HI than in MOD heifers. Diet did not influence concentration of IGF-I or glucose, and metabolic markers were unaffected by biotype. No dramatic changes in body composition or metabolic signals were detected before puberty. Puberty did not occur at similar body composition or metabolic status in all heifers.

Key Words: Heifers, Puberty, Nutrition, Body Composition, Metabolism

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Introduction

Lifetime productivity of beef cows is affected by age at first calving. Management of heifers to conceive early in their first breeding season improves productivity (Lesmeister et al., 1973). Conception rates are greater when heifers are bred at third rather than at pubertal estrus (Byerley et al., 1987). Therefore, age at puberty is an important factor influencing production efficiency.

Nutrition and breed influence age at puberty in beef heifers (Wiltbank et al., 1966; Short and Bellows, 1971). The effects of nutrition or breed may be mediated by changes in body composition (Frisch, 1984) or metabolic signals (Steiner et al., 1983). Several researchers used indirect methods or extrapolated carcass composition to estimate body composition at puberty in heifers with variable results (Brooks et al., 1985; Hopper et al., 1993). In addition, metabolic indicators (e.g., insulin, glucose, growth hormone, IGF-I) that may signal puberty have been identified in beef heifers (Jones et al., 1991). Early attainment of a specific body composition or metabolic status may be the mechanism by which nutrition or breed influence age at puberty.

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Therefore, we tested the hypotheses that puberty in heifers 1) occurs at a similar body composition; 2) occurs at similar concentrations in metabolites and metabolic hormones; or 3) is preceded by a significant sustained change in body composition or metabolic status.

Materials and Methods

Rapid growth large frame (**RL**, n = 61) or average growth medium frame (**AM**, n = 71) heifers were fed different diets (Table 1) to obtain either moderate (**MOD**, ADG = .6 kg/d) or high (**HI**, ADG = 1.0 kg/d) growth rates. The RL and AM biotypes were developed by mating crossbred dams (British × British and British × continental) to selected Charolais and Hereford sires, respectively. Dietary treatment began when heifers averaged 8 mo of age and weighed 220.4 ± 4.0 kg, and continued until experiment termination when heifers averaged 16 mo of age. Heifers were fed the complete mixed rations, which were adjusted daily to ensure ad libitum access. Diet composition was evaluated every 56 d and adjusted if necessary to maintain specified ADG and meet NRC (NRC, 1984) requirements for protein and minerals. Heifers were stratified by biotype and weaning weight to six pens at Fort Keogh Livestock and Range Research Laboratory in Miles City, MT.

Repeated measurements of indicators of growth, body composition, and metabolic status were taken every 56 d to examine changes in metabolism and body composition associated with sexual development. These measures were taken in 20 RL and 20 AM heifers randomly selected from each of the dietary treatments (n = 80). Thirty-two of these heifers (eight from each biotype-diet combination) were slaughtered for carcass and whole-body composition analysis between 18 and 20 d after pubertal estrus.

Puberty. All heifers were checked twice daily for estrus with the aid of an androgenized steer. Between d 7 and 10 after estrus, ovaries of heifers were examined per rectum for presence of a corpus luteum (**CL**) using ultrasound echography (Tokyo Keiki, LS-1000 with 5 MHz Transducer, Products Group, Boulder, CO), and a blood sample was drawn from the coccygeal vein for determination of progesterone. Puberty was defined as occurrence of estrus, subsequent formation of a CL, and serum progesterone exceeding 1 ng/mL.

Growth and Body Composition. Heifers were weighed every 14 d. Repeated measurements of body composition and metabolic status were quantified every 56 d during the dietary treatment period in the 80 selected heifers, and 13 ± .2 d after puberty in all heifers. Body weight, hip height, heart girth circumference, body condition score, longissimus muscle area, and backfat thickness were measured as indicators of growth and body composition. Longissimus muscle area and backfat thickness between the 12th and 13th ribs were measured using real-time, B-mode ultrasound with a 3.5-MHz transducer (Tokyo Keiki LS-1000). Backfat thickness was quantified with the on-screen caliper system. Longissimus muscle area was recorded on videotape, traced, and measured using a grid system. Twenty-five ribeyes were randomly selected for remeasurement to determine the CV for the tracing-grid procedure. The CV for ribeye measurements was 4.5%.

Table 1. Composition and analysis of diets fed to developing heifers

Ingredient	Treatment: High gain diet	Treatment: Moderate gain diet	
	% in Diet, DM basis		
		Day 1 to 110	Day 111 to end
Corn silage	55.5	69.8	62.4
Barley	35.6	0	0
Alfalfa hay	0	20.4	28.2
Concentrate[a]	8.9	9.8	9.4
Analysis	Actual	Actual	Estimated
CP	11.3	9.9	10.2
TDN	76.1	69.5	68.0
Ca	.30	.36	.41
P	.32	.29	.30

[a]Concentrate consisted of 63% barley, 20% soybean meal, 5.5% urea, 3.5% limestone, .5% trace mineral, .5% vitamin A, 2% dicalcium phosphate, and 5% salt.

Heifers used for carcass and whole-body composition measurements were processed at a local abattoir. Weight of the hot carcass and noncarcass constituents were obtained at slaughter. These weights were used to calculate empty-body weight. Noncarcass components consisted of blood, head, hide, rumen (empty), intestine (empty), liver, omental fat, and remaining offal (shanks, hooves, spleen, etc.). On the day of slaughter, all noncarcass constituents were combined, ground, and subsampled for proximate analysis. Measurements of longissimus muscle area and fat thickness over the ribeye as well as weights of edible and inedible trim were obtained 72 h after slaughter from the right side of the carcass. The edible trim consisted of all carcass skeletal muscle and associated subcutaneous and intra- and intermuscular fat. The inedible trim included all carcass bone, kidney, pelvic, and heart fat (**KPH**), and udder fat. Weights of edible and inedible trim were doubled for calculation of total weight, and each trim type was combined, ground, and subsampled for analysis.

Subsamples of the noncarcass, edible, and inedible carcass pools were analyzed directly for moisture, fat, and ash using AOAC (1984) methods to determine empty-body composition. The remainder was considered fat-free organic matter (**FFOM**), which was determined by subtraction.

Blood Sampling and Assays. Blood samples to quantify serum progesterone concentrations were allowed to clot at 4°C for 4 h, and serum was harvested and stored at −20°C until it was analyzed. Serum progesterone was quantified with a coated-tube RIA (Diagnostic Products, Los Angeles, CA) using procedures of Bellows et al. (1991). Intra- and interassay CV were 9 and 10%, respectively.

Blood samples analyzed for metabolic hormones and metabolites were drawn at 0800 before the daily feeding every 56 d during the prepubertal period from the 80 heifers selected for repeat measurements and between 10 and 16 d after estrus from all heifers. Samples were kept on ice, and serum was harvested within 2 h after sampling. Due to the sampling procedure, three to five samples per heifer were analyzed for metabolic hormones. Serum was analyzed for IGF-I, insulin, blood urea nitrogen (**BUN**), and glucose concentrations as indicators of metabolic status. The IGF-I analysis was only available for pubertal blood samples. Concentrations of glucose and BUN were determined with enzymatic assays (Marsch et al., 1965; Trinder, 1969). Intra- and interassay CV for glucose and BUN assays were 5.4, 7.2, 1.9, and 11.5%, respectively. The IGF-I and insulin concentrations were quantified with RIA (Dahl et al., 1994; McShane et al., 1989b). Intra- and interassay CV for the insulin assay were 5.8 and 8.5%, respectively, and the intraassay CV for the IGF-I assay was 6.6%.

Statistical Analyses. Growth, body composition, metabolic characteristics, and age at puberty were analyzed with two-way ANOVA; weaning weight was a covariate, and the GLM procedures of SAS (1988) were used. The data were analyzed for main effects of diet and biotype and the two-way interaction. The main effects of diet and biotype and their interaction were analyzed using heifer within diet × biotype as the error term. To control for the variation in days before puberty, repeated measures of growth, body composition, and metabolic characteristics were analyzed by subplot regression (GLM procedure of SAS) using day relative to puberty as a covariate. Parameters developed from the sub-plot analysis were used to estimate the changes in BW, hip height, heart girth, BW:height ratio, body condition score, backfat thickness, longissimus muscle area, and concentrations of insulin, glucose, and BUN between d -75 and 13 relative to puberty.

Results

Pubertal Measurements. Of the 132 heifers, 115 attained puberty by the termination of the experiment. The experiment was terminated in August when heifers averaged 16 mo of age. Pubertal measurements taken 13 ± .2 d after detection of first estrus are shown in Table 2. Heifers that consumed the HI diet were 42.7 d younger ($P < .01$) at puberty than heifers that consumed the MOD diet (Table 2). High growth diet heifers had greater ($P < .01$) BW, heart girth, body condition score, BW:height ratio, and longissimus muscle area than MOD heifers. Rapid growth large frame heifers were heavier and taller ($P < .01$) than AM heifers. The AM heifers consuming the MOD diet had the least backfat and HI AM heifers had the most backfat of all the biotype-diet combinations (diet × biotype, $P < .05$). Backfat thicknesses were 6.1, 8.1, 5.8, and 4.7 mm (SEM = .6 mm) for HI RL, HI AM, MOD RL, and MOD AM, respectively.

At puberty, serum concentrations of BUN were greater ($P < .01$) in HI than in MOD heifers (8.6 ± .4 vs 3.6 ± .4 mg/dL, respectively), but diet did not influence ($P > .25$) glucose concentrations, which averaged 96.6 ± 3.2 mg/dL. Concentrations of IGF-I were similar (mean = 118.7 ± 4.0 ng/mL), whereas insulin concentrations were increased ($P < .05$) in HI compared with MOD heifers (25.8 ± 4.0 vs 14.4 ± 4.0 IU/mL, respectively). Biotype did not affect ($P > .15$) concentrations of BUN, glucose, insulin, or IGF-I.

Table 2. Age and indirect estimates of body composition at puberty for all heifers[a]

	Treatment						
Variable	High diet	Moderate diet	Rapid growth sired	Average growth sired	SEM	Diet ($P <$)	Biotype ($P <$)
Age, d	378.8	421.5	401.9	398.5	7.3	.01	NS[b]
Weight, kg	397.0	354.7	390.1	361.7	6.4	.01	.01
Body condition score	7.0	5.9	6.5	6.3	.1	.01	NS
Hip height, cm	121.0	120.7	124.5	117.2	.8	NS	.01
Heart girth, cm	173.7	164.6	170.7	167.7	1.3	.01	NS
Weight:height	3.3	2.9	3.1	3.1	.1	.01	NS
Longissimus muscle area, cm^2	63.5	52.1	59.2	56.4	1.6	.01	NS

[a]Least squares means.
[b]Not significant (NS).

Table 3. Age and indirect estimates of body composition at puberty for heifers used for empty body composition[a]

Variable	Treatment: High diet	Moderate diet	Rapid growth	Average growth	SEM	Diet ($P <$)	Biotype ($P <$)
Age, d	386.3	415.3	407.6	394.1	12.2	.1	NS[b]
Preslaughter measurements							
Weight, kg	394.5	341.3	391.6	344.3	9.2	.01	.01
Backfat, mm	6.8	5.1	6.2	5.7	.6	.1	NS
Body condition score	6.7	5.7	6.3	6.0	.2	.01	NS
Hip height, cm	122.3	119.2	125.3	116.1	1.3	NS	.01
Heart girth, cm	174.1	163.3	171.7	165.7	2.5	.01	.05
Weight:height	3.2	2.8	3.1	2.9	.1	.01	NS
Longissimus muscle area, cm^2	59.6	51.7	58.1	53.2	1.5	.01	NS
Slaughter measurements							
Carcass weight, kg	230.6	187.4	232.1	185.9	7.3	.01	.01
Noncarcass, kg	119.2	104.9	120.3	103.8	3.6	.01	.01
Longissimus muscle area, cm^2	66.5	56.8	66.7	56.7	1.8	.01	.01
Backfat thickness, mm	6.8	4.4	6.3	5.0	.4	.01	.05
Marbling score[c]	4.2	2.6	3.1	3.6	.2	.01	NS
Edible trim, kg	166.4	134.2	165.4	135.2	4.8	.01	.01
Inedible trim, kg	62.6	51.5	64.2	49.8	2.6	.01	.01

[a]Least squares means.
[b]Not significant (NS).
[c]Marbling score: 2 = trace, 3 = slight, 4 = small.

Slaughter Measurements. Analysis of progesterone concentrations revealed that one HI RL heifer selected for slaughter had not attained puberty and was eliminated from analysis. Means and relationships among means for whole-body composition traits obtained on the remaining 31 heifers at puberty (Table 3) were similar to and representative of all the heifers that attained puberty (Table 2). Weights of carcass and noncarcass components were greater ($P < .01$) in HI than in MOD heifers (Table 3). Carcasses of HI heifers had larger ($P < .01$) longissimus muscle areas, more backfat, greater marbling scores, and greater amounts of edible and inedible trim than carcasses of MOD heifers. The inedible trim of HI heifers consisted of more ($P < .01$) udder fat (6.0 ± .6 vs 4.0 ± .6 kg) and tended ($P < .06$) to have more bone (48.6 ± 2.3 vs 43.2 ± 2.3 kg) than that of MOD heifers. Within the noncarcass component, HI heifers had greater ($P < .05$) weights of blood, liver, heart and lungs, rumen and intestinal fat, hide, and remaining offal than MOD heifers (Table 4).

The weight of carcass and noncarcass components was greater ($P < .01$) for RL heifers than for AM heifers (Table 3). Carcasses of RL heifers had larger longissimus muscle areas, more fat over the ribeye, and greater amounts of edible trim, inedible trim, and

Table 4. Weights of various noncarcass components of beef heifers at puberty[a]

Item	Treatment: High gain diet	Moderate gain diet	Rapid growth	Average growth	SEM	Diet ($P <$)	Biotype ($P <$)
No. of heifers	15	16	15	16			
Blood, kg	12.1	10.4	12.0	10.5	.4	.01	.01
Head, kg	11.4	11.0	12.0	10.5	.9	NS[b]	.01
Liver, kg	5.0	4.2	5.0	4.2	.1	.01	.01
Heart and lungs, kg	6.0	5.1	6.0	5.0	.2	.01	.01
Rumen and intestinal fat, kg	7.1	4.1	6.0	5.1	.4	.01	NS
Rumen (empty), kg	17.9	18.1	19.1	17.0	.8	NS	NS
Intestines (empty), kg	6.7	6.8	7.1	6.4	.2	NS	.05
Hide, kg	34.1	30.2	34.1	30.2	1.2	.05	.05
Remainder, kg	20.2	15.1	19.0	16.3	.9	.01	.05

[a]Least squares means.
[b]Not significant (NS).

Table 5. Empty body composition of beef heifers at puberty[a]

Item	Treatments: High gain diet	Moderate gain diet	Rapid growth	Average growth	SEM	Diet ($P <$)	Biotype ($P <$)
Moisture, kg	191.7	168.0	197.0	162.7	4.8	.01	.01
Fat, kg	78.4	55.7	73.4	60.7	5.1	.01	NS[b]
Ash, kg	13.6	11.9	14.1	11.5	.6	NS	.01
FFOM, kg	64.1	54.2	65.4	52.9	1.6	.01	.01
Moisture, %	55.4	58.1	56.6	56.8	.6	.01	NS
Fat, %	22.1	19.1	20.5	20.7	1.0	.05	NS
Ash, %	3.9	4.1	4.0	4.0	.1	NS	NS
FFOM, %	18.6	18.7	18.8	18.5	.4	NS	NS

[a]Least squares means.
[b]Not significant (NS).

bone (51.1 ± 2.3 vs 40.7 ± 2.3 kg, respectively) than AM heifers. There were greater ($P < .01$) weights of blood, liver, head, and heart and lung, as well as more ($P < .05$) hide, intestine, and remaining offal in the noncarcass component of RL heifers than that of AM heifers (Table 4). The RL heifers fed the HI diet had more KPH than the other treatment groups (biotype × diet; $P < .01$). Weights of KPH were 4.4, 3.6, 3.0, and 3.0 kg (SEM = .37 kg) for HI RL, HI AM, MOD RL, and MOD AM, respectively.

Empty Body Composition. The chemical analysis of empty body (Table 5) indicated that HI heifers contained greater ($P < .01$) weights of moisture, fat, and FFOM than MOD heifers. Bodies of RL heifers contained more ($P < .01$) moisture, ash, and FFOM than bodies of AM heifers. As a percentage of empty body weight, HI heifers contained less ($P < .01$) moisture and more ($P < .05$) fat than MOD heifers. Ranges of percentage of body fat at puberty were 12.2 to 27.3% for RL and 13.1 to 28.3% for AM heifers.

Repeated Measures. Between –75 and 13 d relative to puberty, BW, heart girth, BW:height, and backfat thickness increased linearly ($P < .05$) as puberty approached in all heifers; however, the rate of increase was greatest in AM heifers consuming the HI diet and least in AM heifers fed the MOD diet (day × diet × biotype, $P < .05$; Figure 1a,b,c,d; Table 6). Hip height increased linearly in all treatments ($P < .01$; Figure 1e; Table 6). Throughout the treatment period, RL heifers were taller ($P < .01$) than AM heifers, and HI diet heifers tended ($P < .07$) to be taller than MOD heifers. Longissimus muscle area and body condition score increased curvilinearly as puberty approached (Figure 1f,g; Table 6). The components of this increase were a positive linear interaction of day and diet (day × diet, $P < .01$) and a differential quadratic effect of day and biotype (day^2 × biotype, $P < .05$). Briefly, there was a greater increase in longissimus muscle area and change in body condition score in HI than in MOD fed heifers, and this change was further modified by biotype, positively for RL and negatively for AM.

Regression lines describing changes in BUN, insulin, and glucose are shown in Figure 2a,b,c and Table 6. As puberty approached, concentrations of BUN changed, and concentrations were dependent on diet, biotype, and a quadratic effect of day resulting in a day^2 × diet × biotype interaction ($P < .05$). In general, concentrations of BUN decreased in HI RL and MOD AM heifers, whereas BUN increased in HI AM and MOD RL heifers as puberty approached. The changes in BUN concentrations were most dramatic in AM heifers. Concentrations of insulin increased linearly ($P < .01$) in all heifers as puberty approached, and insulin was greater ($P < .01$) in HI than in MOD heifers throughout the prepubertal period. Concentrations of glucose were greater ($P < .05$) in HI than in MOD heifers, but concentrations of this metabolite were not altered as puberty approached.

Discussion

Heifers fed the high-gain diet in this study reached puberty 43 d sooner than those on the moderate gain diet. These observations are in agreement with a multitude of studies on the effects of nutrition and rate of gain on age at puberty in heifers (Arije and Wiltbank, 1971; Short and Bellows, 1971; McShane et al., 1989a). Breed or biotype can affect age at puberty of heifers (Gregory et al., 1979; Ferrell, 1982); however, biotype did not influence age at puberty in the present experiment. Our results are in agreement with Ferrell (1982) and Laster and coworkers (1972), who reported no difference in age at puberty between Charolais- and Hereford-sired heifers. The mechanisms that mediate the effects of nutrition and biotype on age at puberty are unknown. Frisch (1976) proposed that attainment of a critical percentage of body fat triggers puberty in rodents and women. Steiner (1987) suggested that changes in metabolism result in metabolic signals that are the cues for onset of puberty. In the present experiment, we used nutrition and biotype to examine these two possible mechanisms.

Table 6. Regression parameters relative to puberty for growth, body composition, and metabolic traits for heifers from day −75 to 13

Biotype[a]	Diet[b]	Intercept	Linear, d	Quadratic, d^2	Corresponding graph
		Body weight, kg[c]			
RL	HI	435.5 ± 2.8	1.079 ± .059	—	Figure 1a
RL	MOD	369.1 ± 3.1	.78 ± .065	—	
AM	HI	363.9 ± 2.8	1.168 ± .060	—	
AM	MOD	312.4 ± 2.7	.618 ± .058	—	
		Heart girth, cm[c]			
RL	HI	178.0 ± .61	.16 ± .01	—	Figure 1b
RL	MOD	166.3 ± .7	.14 ± .01	—	
AM	HI	169.1 ± .6	.21 ± .01	—	
AM	MOD	157.7 ± .6	.10 ± .01	—	
		Weight:height[c]			
RL	HI	3.4 ± .02	.007 ± .0005	—	Figure 1c
RL	MOD	2.9 ± .03	.006 ± .0006	—	
AM	HI	3.1 ± .02	.009 ± .0005	—	
AM	MOD	2.7 ± .02	.005 ± .0005	—	
		Backfat thickness, mm[c]			
RL	HI	6.91 ± .21	.023 ± .004	—	Figure 1d
RL	MOD	5.19 ± .23	.020 ± .005	—	
AM	HI	6.83 ± .21	.035 ± .004	—	
AM	MOD	4.4 ± .20	.010 ± .004	—	
		Hip height, cm[de]			
RL	HI	127.30 ± .52	.063 ± .011	—	Figure 1e
RL	MOD	123.59 ± .59	.044 ± .012	—	
AM	HI	116.97 ± .53	.028 ± .011	—	
AM	MOD	115.59 ± .52	.042 ± .011	—	
		Longissimus muscle area, cm^2 [fg]			
RL	HI	64.86 ± 1.27	.29 ± .05	.0017 ± .0006	Figure 1f
RL	MOD	55.49 ± 1.73	.23 ± .05	.0017 ± .0006	
AM	HI	59.04 ± 1.24	.20 ± .05	−.00015 ± .0006	
AM	MOD	45.94 ± 1.29	.05 ± .05	−.00015 ± .0006	
		Body condition score[fg]			
RL	HI	6.89 ± .07	.011 ± .003	.00007 ± .00003	Figure 1g
RL	MOD	5.9 ± .08	.005 ± .003	.00007 ± .00003	
AM	HI	6.83 ± .07	.006 ± .003	−.00004 ± .00003	
AM	MOD	5.71 ± .07	−.00025 ± .003	−.00004 ± .00003	
		Blood urea nitrogen, mg/dL[h]			
RL	HI	8.5 ± .37	−.02 ± .018	0	Figure 2a
RL	MOD	3.9 ± .41	.003 ± .029	.0002 ± .0003	
AM	HI	8.0 ± .38	.03 ± .02	.0003 ± .0003	
AM	MOD	4.0 ± .37	−.05 ± .02	−.0005 ± .0003	
		Insulin, IU/mL[ei]			
RL	HI	24.0 ± 2.5	.15 ± .05	—	Figure 2b
RL	MOD	10.4 ± 2.8	.03 ± .06	—	
AM	HI	22.5 ± 2.6	.11 ± .05	—	
AM	MOD	13.4 ± 2.5	.07 ± .05	—	
		Glucose, mg/dL[i]			
RL	HI	94.85 ± 2.48	—	—	Figure 2c
RL	MOD	92.20 ± 2.78	—	—	
AM	HI	105.26 ± 2.54	—	—	
AM	MOD	93.21 ± 2.44	—	—	

[a]RL = rapid growth large frame; AM = average growth medium frame.
[b]HI = high gain diet; MOD = moderate gain diet.
[c]Day × diet × biotype interaction ($P < .05$).
[d]Effect of biotype ($P < .01$).
[e]Effect of day ($P < .01$).
[f]Day × diet interaction ($P < .01$).
[g]Day^2 × biotype interaction ($P < .05$).
[h]Day^2 × diet × biotype interaction ($P < .05$).
[i]Effect of diet ($P < .05$).

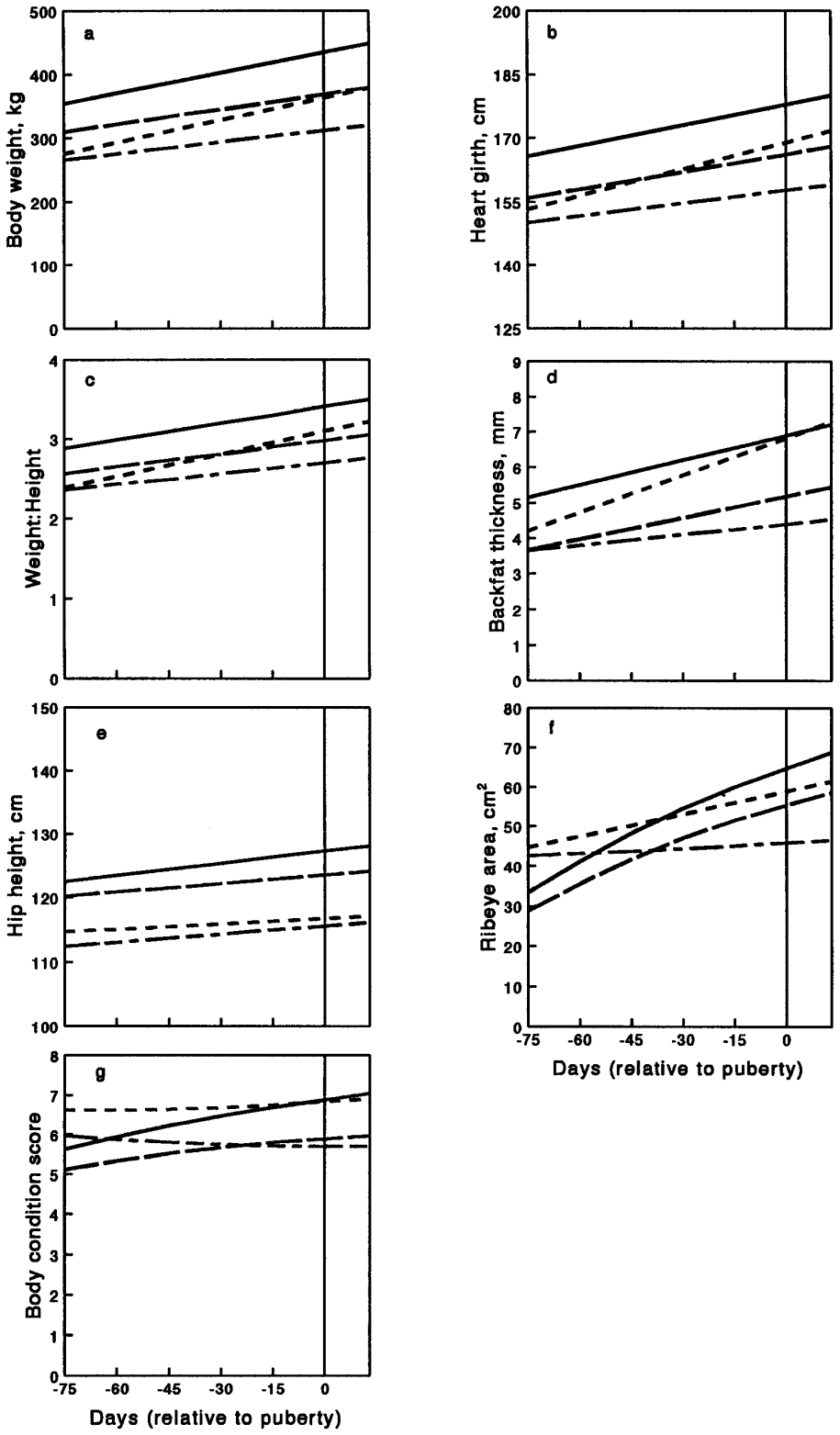

Figure 1. Regression lines illustrating changes in indirect indicators of body composition in rapid growth large frame (RL) or average growth medium frame (AM) heifers fed to gain 1 kg/d (HI) or .6 kg/d (MOD) between d −75 and 13 relative to puberty. (— HI RL, n = 18; – – – HI AM, n = 17; — — MOD RL, n = 15; — – - — MOD AM, n = 18). Body weight (a), heart girth (b), weight:height (c), and backfat thickness (d) increased linearly as puberty approached for all treatments. However, the rate of increase was greatest for HI AM and least for MOD AM heifers (day × diet × biotype, $P < .05$). Hip height (e) increased linearly ($P < .01$) in all heifers. The RL heifers were taller ($P < .01$) than AM heifers throughout the period. Longissimus muscle (ribeye) area (f) and body condition score (g) increased in a curvilinear fashion (day × diet, $P < .01$; day^2 × biotype, $P < .05$) as puberty approached.

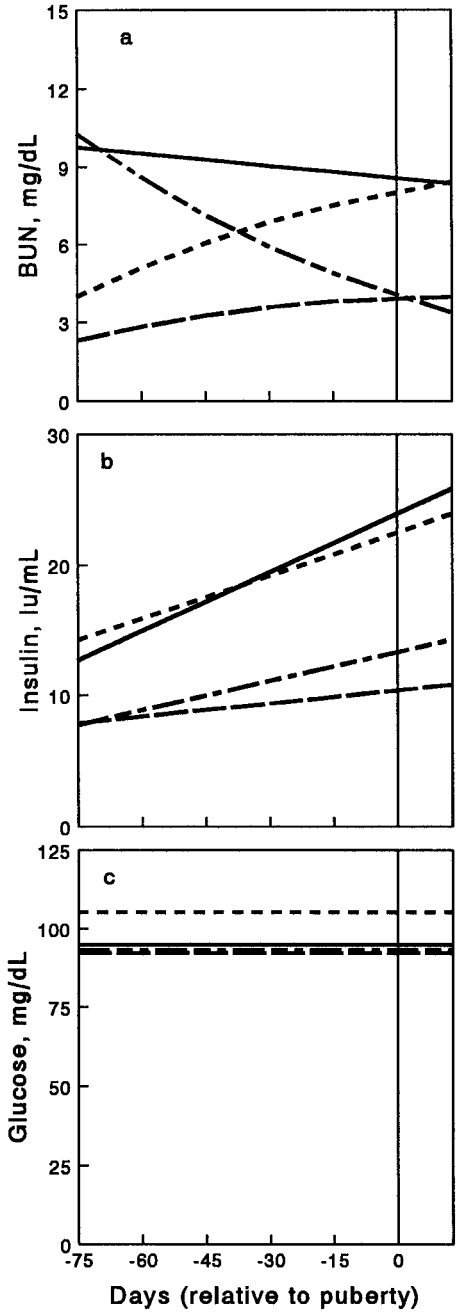

Figure 2. Regression lines illustrating changes in blood urea nitrogen (BUN; a), insulin (b), and glucose (c) in rapid growth large frame (RL) or average growth medium frame (AM) heifers fed to gain 1 kg/d (HI) or .6 kg/d (MOD) between d −75 and 13 relative to puberty. (— HI RL, n = 18; – – – – HI AM, n = 17; — — MOD RL, n = 15; — – - — MOD AM, n = 18). As puberty approached, concentrations of BUN changed ($P < .05$) and concentrations were dependent on diet, biotype, and day^2, resulting in a day^2 × diet × biotype interaction ($P < .05$). Concentrations of insulin increased linearly ($P < .01$) in all heifers as puberty approached, and insulin was greater ($P < .01$) in HI than in MOD heifers. Concentrations of glucose were greater ($P < .05$) in HI than in MOD heifers, but concentrations of this metabolite were not affected by day.

Diet and biotype altered indirect indicators of body composition at puberty. Dietary effects are in agreement with previous reports that indicated that enhanced nutrient intake, particularly energy, increased body size and fatness at puberty (Arije and Wiltbank, 1971; Short and Bellows, 1971; McShane et al., 1989a; Hall et al., 1994). However, other investigators reported decreased BW (Dufour, 1975; Grass et al., 1982), similar BW (Crichton et al., 1972), or similar BW:height (Crichton et al., 1972; Nelsen et al., 1982) at puberty in heifers with enhanced nutrient intake. Rapid growth large frame heifers were heavier and taller at puberty, and this agrees with previous reports (Laster et al., 1972; Ferrell, 1982). In this study, we also used ultrasound measurements of ribeye and backfat thickness as indirect estimates of body composition. At puberty, longissimus muscle area was increased by high nutrient intake in the present study, but diet interacted with biotype to influence backfat thickness at puberty; HI AM had the greatest and MOD AM had the least amount of backfat. Other studies indicated that heifers (Hedrick et al., 1970) and steers (Guenther et al., 1965) consuming high-nutrient diets had larger longissimus muscle areas and greater amounts of fat over the ribeye than animals consuming lower-nutrient diets, and the nutritional effects were apparent regardless of whether measurements were taken at a common chronological or physiological end point.

All heifers used for carcass and empty body composition measurements were slaughtered within 20 d after first estrus. The effects of nutrition on carcass traits at puberty in our study are similar to other evaluations of carcass characteristics at a common physiological end point in steers (Prior et al., 1977; Tatum et al., 1988) and heifers (Hopper et al., 1993). Increases in carcass weight due to diet were a result of increased muscle mass and larger fat depots, as indicated by greater longissimus muscle area, combined weights of edible trim, backfat thickness, and marbling score. Tatum et al. (1988) reported increased amounts of separable fat and greater muscle to bone ratio in steers fed high-grain diets compared with steers fed high-roughage diets slaughtered at the same physiological age. Hopper et al. (1993) did not detect an effect of diet on a majority of carcass components in heifers slaughtered at puberty; however, as in the present study, increased dietary energy increased the amount of subcutaneous fat over the 12th rib. The difference in gain between the two dietary treatments in our study was twice as great as that noted by Hopper et al. (1993), which may explain some of the discrepancies between the two studies. Age of heifers during treatment may also account for the difference in results between the two experiments. Heifers in their study were older than ours at the initiation of treatments. In general, carcass measurements agreed with live animal measurements and indicated that nutrition altered indirect

measures of body composition as well as age at puberty.

Rapid growth large frame heifers produced larger carcasses containing greater longissimus muscle areas, more edible trim, and more backfat than AM heifers. Increased carcass weight is not surprising due to the large differences in live weight between RL and AM heifers and the high correlation between BW and carcass weight (Gilbert et al., 1993). In addition, breed differences have been reported in a variety of carcass traits whether animals are slaughtered at a constant chronological or physiological age (Guenther et al., 1965; Tatum et al., 1988). However, in our study, differences between the two biotypes in carcass longissimus muscle area and backfat thickness were not detected in the live animal. Large longissimus muscle areas may be underestimated and low backfat thicknesses may be overestimated by ultrasonic measurements (Brethour, 1992).

A majority of the investigations into body composition of heifers at puberty have focused on indirect estimates of carcass composition (Short and Bellows, 1971; Brooks et al., 1985; Hopper et al., 1993). These studies did not directly address the contribution of internal fat depots to body composition at puberty. In addition to this aspect, we were interested in weights and composition of visceral organs and fat stores, because differences in weights of visceral organs are related to differences in energy expenditures for maintenance (Ferrell, 1988). Nutrition, breed, and physiological status alter weights of the gastrointestinal tract and visceral organs in livestock (Ferrell, 1988). Also, Buckley et al. (1990) reported a dramatic increase in internal fat stores in beef heifers between 8 and 14 mo of age, a time that normally corresponds to puberty onset. In the present study, diet and biotype independently altered weights of visceral organs and associated internal fat depots at puberty. Therefore, heifers attained puberty when mass of the gastrointestinal tract and visceral organs, and presumably energy expenditure by these tissues, differed among heifers.

Heifers attained puberty at different masses and percentages of moisture, fat, ash, and fat-free organic matter as determined with proximate analysis. Rapid growth large frame heifers attained puberty at a greater fat-free tissue mass than AM heifers. However, this difference was probably due to increased amounts of edible trim and bone in the carcass, because there was no difference between biotypes when composition was expressed as a percentage of empty body weight. Buckley et al. (1990) found that Hereford heifers were fatter than Charolais heifers when slaughtered at a common chronological age, but when large- and medium-framed cattle were slaughtered at similar physiological maturity, there was no difference in percentage of fat in the carcass (Tatum et al., 1988). Although RL and AM reached puberty at a similar body composition, the wide range of percentage of body fat does not support the critical body fat hypothesis.

In contrast to biotype, dietary treatment altered the mass of fat and fat-free tissue and the percentage of moisture and fat in the empty body. Similar effects of diet on body composition have been reported for steers slaughtered at 60% of mature weight (Tatum et al., 1988) and heifers subjected to live body composition estimates or carcass composition determinations at puberty (Brooks et al., 1985; Yelich et al., 1992). Percentage of water in the carcass at puberty was decreased by increased energy intake (Hopper et al., 1993). Percentage of FFOM was similar at puberty regardless of treatment. The relationship between lean content and puberty has not been extensively examined. Diet did not influence the amount of lean in carcasses of heifers at puberty (Hopper et al., 1993). Whether percentage of lean in the body is related to puberty onset, to physiological maturity, or to partitioning of nutrients may warrant further study.

In our study, live animal measurements, carcass composition, internal organs and fat depots, and proximate analysis of the empty body indicate that nutrition and biotype alter body composition at puberty. Frisch (1976) suggested the “critical body composition hypothesis” for puberty onset in rodents and humans was applicable to livestock. Results from our study and several others (Short and Bellows, 1971; Brooks et al., 1985; Yelich et al., 1992; Hopper et al., 1993) do not support the critical body composition hypothesis in beef heifers. In addition, increasing the rate of fat deposition through nutrition (Rhodes et al., 1978; Hopper et al., 1993) or breeding (Bergfeld et al., 1993) has not necessarily reduced age at puberty. These experiments reinforce the assertions of Bronson and Manning (1991) that body composition has little direct physiological or biological relationship to the onset of estrous cycles. Body fat stores are related to maintenance of estrous cycles in cattle (Imakawa et al., 1986; Richards et al., 1989), but body fat is probably a marker for the relative availability of energy for reproductive activity.

Attainment of a specific metabolic status may be necessary for onset of puberty (Steiner et al., 1983). Several metabolites and metabolic hormones, including glucose, insulin, and IGF-I, have been implicated as potential metabolic signals for puberty (Steiner, 1987; Schillo, 1992). Concentrations of BUN and insulin at puberty were affected by dietary treatment, but other metabolites and metabolic hormones studied were not affected. Differences in BUN and insulin indicate that heifers were probably at a different metabolic status (McShane et al., 1989b) at puberty. Although several metabolites and hormones change with nutritional and production status, no definitive causal relationship between metabolites and metabolic hormones and onset of estrous cycles has been

established (Schillo et al., 1992). None of the metabolites or hormones investigated was affected by breed. In comparing several breeds, Jones et al. (1991) found that concentrations of metabolic signals at puberty were only different in Angus heifers.

Changes in body composition and(or) metabolic status during the prepuberal period may be as important as measurements at puberty. The significant changes in the hypothalamic-pituitary-ovarian axis that result in the first ovulation occur approximately 40 d before puberty in heifers (Kinder et al., 1987). Therefore, we investigated the changes in a variety of indirect measures of body composition, metabolites, and hormones from 75 d before until 13 d after puberty. If a distinct change in body composition or metabolism is necessary for induction of the events leading to puberty, we hypothesized that these changes would be apparent during this time period. The pattern of change in body composition, as measured by empty body weight and percentage of fat in the empty body, can be influenced by nutrition and breed (Brown et al., 1972; Carstens et al., 1991; Keele et al., 1992). In addition, several reports indicate an increase in adipose tissue deposition in beef heifers around the time of puberty (McShane et al., 1989a; Buckley et al., 1990). In our study, dietary energy and breed interacted to modify the rate of change in body composition before puberty, but no abrupt change in body composition was detected during the 75 d before puberty.

Identification of specific metabolic signals related to puberty may be difficult. Individual variation in age at puberty in heifers requires sampling over several months to characterize metabolic markers during the prepuberal period. Previous attempts to identify prepuberal changes in metabolism in growing heifers (McShane et al., 1989b; Jones et al., 1991) used limited numbers (5 to 10 heifers) and relatively infrequent sampling periods (14 to 56 d). We chose to use larger numbers of heifers (n = 20 per treatment) and an infrequent sampling regimen of 56 d, then subjected the data to regression analysis. This procedure would identify sustained changes in metabolism. Concentrations of insulin and BUN changed, but only insulin increased in all treatments throughout the prepuberal period. Changes in BUN were not consistent in their magnitude, direction, or timing relative to puberty. Although changes in BUN are related to differences in diet (Kennedy, 1980) or rate of protein accretion and degradation, they seem to be unrelated to puberty. McShane et al. (1989b) reported an increase in insulin concentrations before puberty in heifers. However, they attributed this increase to a change in feed intake. Insulin concentrations are influenced by feed intake and energy density of the diet (Bassett et al., 1971; Richards et al., 1989), and dry matter intake is proportional to body weight (NRC, 1984). Heifers in our study were allowed ad libitum access to feed; therefore, dry matter intake increased as heifers grew heavier. Increased insulin concentrations, as puberty approached, may be a result of increased dry matter intake. In addition, increased insulin concentrations may be a marker for increased energy availability. The function of insulin in the regulation of reproductive activity is uncertain. Decreased insulin concentrations are associated with decreased LH release in ruminants deprived of feed (McCann and Hansel, 1986). However, regardless of nutritional status, short-term infusions of insulin systematically or directly into the central nervous system do not enhance LH release (Harrison and Randel, 1986; Hileman et al., 1993). Whether chronic exposure to increased insulin concentrations hastens puberty remains to be determined.

Glucose concentrations remained constant as puberty approached, although concentrations were affected by treatment. In ruminants, glucose is principally a product of gluconeogenesis and circulating concentrations tend to be stable (Bassett, 1975). Hypoglycemia decreased pulsatile LH release in ovariectomized ewes (Clarke et al., 1990), but it only decreased LH pulse amplitude in intact cows (Rutter and Manns, 1987). Pharmacological blockage of the utilization of energy substrates decreased reproductive activity and LH secretion in rodents and ewes (Schneider and Wade, 1989; Hileman et al., 1991). In addition, the reproductive axis seems to be more sensitive than the growth axis to reductions in nutrient availability (Hileman et al., 1991). In heifers in our study, glucose concentrations were probably adequate for reproductive activity during the 75 d before puberty; however, whether glucose was available to the reproductive axis or partitioned to other tissues is unknown. Schillo (1992) reviewed numerous experiments investigating nutritional control of LH secretion in ruminants, and he concluded that the existence of specific metabolic signals remained to be demonstrated. Our data also do not support the metabolic signal hypothesis proposed by Steiner et al. (1983). Perhaps, the availability of metabolic fuels is the most important factor influencing reproduction.

In summary, body composition at puberty was a function of diet and biotype, and heifers did not attain puberty at similar body compositions. Also, differences in metabolites and hormones indicate that heifers did not attain puberty at the same metabolic status. Finally, there were neither consistent changes nor apparent thresholds in body composition or metabolic signals before puberty.

Therefore, we reject the hypotheses that puberty in beef heifers occurs at similar body composition or similar concentrations of metabolic hormones and metabolites. In addition, we reject the hypothesis that puberty in heifers is preceded by a significant sustained change in body composition or metabolic status. However, we do not preclude the possibility

that subtle or acute changes in metabolic status initiate the physiological events leading to puberty. Based on the results of the present study and discussion of data from related studies, we suggest that 1) body composition at puberty is a result of the differential manner by which nutrition affects genetic propensity for somatic growth and maturation of the reproductive axis and 2) metabolites and hormones reflect nutritional status, but metabolic signals for the onset of puberty remain to be identified.

Implications

Neither a sudden change in body composition, metabolites, metabolic hormones, nor attainment of a critical body composition or metabolic status seem to trigger onset of puberty in beef heifers. Selecting or managing heifers for rapid attainment of a specific body composition or metabolic status would not be an efficient method for reducing age at puberty. The manner in which the growth and reproductive axes are differentially regulated by nutrition and biotype warrants further investigation.

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