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Effect of postweaning diet on ovarian development and fertility in replacement beef heifers[1]

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ABSTRACT: Programs for developing replacement heifers are designed for heifers to calve at 2 yr of age and to extend their stayability in the herd and minimize feed cost. The experimental objective was to determine whether developing prepubertal heifers on less dietary energy and to a BW of 55% rather than 65% of mature BW at 14 mo of age would compromise ovarian development and reduce fertility. In a 3-yr study, 8-mo-old Angus (n = 60/yr) and composite MARC II (n = 60/yr) heifers were assigned equally by age, BW, and breed to receive either a low (LG) or high (HG) BW gain diet fed to achieve an ADG of either 0.45 or 0.8 kg/d from 8 to 15 mo of age, including the first 21 d of breeding, and then transferred to pasture. At 14 mo, heifers were housed with fertile bulls for 47 d. Estrus was monitored for 21 d. Within 12 h after detection of estrus, ovarian length and height, preovulatory follicle diam., and antral follicle count (AFC) were measured by transrectal ultrasonography. Corpus luteum (CL) volume and plasma progesterone concentration were measured 5 to 15 d after estrus. Data were analyzed by ANOVA with treatment, breed, and year and their 2-way interactions as independent variables. At breeding, HG heifers were heavier than LG heifers (419.9 vs. 361.8 ± 7.5 kg; $P < 0.01$); ADG for the treatment period was 0.79 vs. 0.47 ± 0.04 kg/d ($P < 0.01$), respectively. In 2010 and 2011, 97.2% of heifers were cyclic by 21 d of breeding. Size of the ovary, preovulatory follicle, CL, and AFC did not differ between HG and LG, but preovulatory follicle diam. and ovarian length were greater ($P \leq 0.05$) for MARC II vs. Angus heifers. Progesterone concentrations were less for LG vs. HG heifers ($P \leq 0.02$), whereas CL volume was not affected by treatment or breed but was correlated positively with preovulatory follicle size ($P < 0.01$). Total AFC ranged from 5 to 49 and was correlated positively with ovarian volume but was not associated with fertility. A greater proportion of HG vs. LG heifers conceived within the first 21 d of the breeding period (64.4% vs. 49.2% ± 3.8%, respectively; $P < 0.01$), but overall pregnancy rate was not affected by treatment (83.0% vs. 77.7% ± 3.1%, respectively; $P > 0.10$). Pregnancy rate was 10% less ($P < 0.01$) for Angus vs. MARC II heifers. Developing beef heifers at a lesser ADG to a lighter BW (55% vs. 64% of mature BW) at breeding did not influence postweaning ovarian development or AFC or compromise pregnancy rate during the 47-d breeding period.

Key words: body weight gain, fertility, ovarian development, replacement beef heifers

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INTRODUCTION

Beef producers replace 12% to 15% of the cow herd annually, but a lower pregnancy rate for heifers necessitates retention of additional heifers (Maurer and Chenault, 1983). Management of replacement heifers from weaning to breeding is critical to their lifetime productivity. The goals in development of replacement beef heifers are for them to conceive early in the breeding period and to maximize pregnancy rate within a 45-d breeding period. Commensurate with puberty is recruitment of ovarian follicles, induction of ovulation, and initiation of estrous cycles, events that can be affected by nutrition and postweaning growth (Ferrell, 1982). The size of the ovulatory follicle (Perry et al., 2007; Echternkamp et al., 2009) and corpus luteum (**CL**) function (Inskeep, 2004) affect embryonic survival in cattle; both are reduced in nutrient-restricted heifers (Bergfeld et al., 1994; Bossis et al., 1999). The number of antral follicles (**AFC**) within the ovaries of mammalian females may be predictive of reproductive longevity (Broekmans et al., 2007; Cushman et al., 2009), but limited information is available regarding postweaning dietary effects on AFC and ovarian reserve in heifers and their association with reproductive lifespan. Historically, replacement heifers are fed a diet to achieve 65% of mature BW by 14 mo of age (Patterson et al., 1992), whereas purebred beef heifers fed to 55% of mature BW had increased dystocia and calf mortality and decreased fertility after first calving. Conversely, recent studies found that feeding crossbred beef heifers to 50% to 55% of mature BW reduced body size and development costs without compromising pregnancy rate (Funston and Deutscher, 2004; Martin et al., 2008; Roberts et al., 2009). Thus, it is hypothesized that developing beef heifers to achieve 55% vs. 65% of mature BW at breeding on less dietary energy and ADG (0.45 vs. 0.80 kg/d) will not affect ovarian development or compromise fertility.

MATERIALS AND METHODS

The experimental design and procedures used in this study were approved by the U.S. Meat Animal Research Center (**USMARC**) Animal Care and Use Committee. Experimental procedures were conducted in accordance with the Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching.

Animals and Experimental Design

In a 2 × 2 factorial treatment arrangement, 8-mo-old Angus (*n* = 60/yr) and MARC II (stable composite of 1/4 Angus, 1/4 Hereford, 1/4 Simmental, and 1/4 Gelbvieh; *n* = 60/yr) heifers were assigned equally by breed group and stratified by age and BW to 1 of 2 dietary treatments to be fed from 8 to 15 mo of age, which included the first 21 d of the breeding period, as illustrated in Fig. 1. The study was replicated for 3 yr (2009, 2010, and 2011). Heifers were fed a low-gain diet of 30% corn silage and 70% alfalfa haylage (2.16 Mcal ME/kg DM, 61.6% TDN, and 12.97% CP) or a high-gain diet of 69% corn silage and 31% high-moisture corn (2.73 Mcal ME/kg DM, 74.4% TDN, and 11.81% CP), plus a vitamin and mineral supplement, at rates to attain an ADG of either 0.45 kg or 0.80 kg/d, respectively. These calculated rates of ADG were expected to allow for the heifers to attain either 55% or 65% of their mature BW at 14 mo of age; BW for mature USMARC Angus and MARC II cows (BCS = 6) at the end of the breeding season are approximately 650 and 660 kg, respectively. Body weight, hip height, and BCS were measured at the initiation and end of dietary treatments and at the end of the 47-d breeding period. Measurements were conducted about 18 h after feeding, and BCS was scored on a schedule of 1 to 9 (NRC, 2000) by the same experienced technician; a calculated BW:hip height ratio was also used to estimate animal differences in body condition. Additional measurements of BW were conducted at 28-d intervals during the treatment period and were used to adjust feed intake by pen to achieve targeted treatment ADG and prebreeding BW of 55% or 65% of mature BW. Birth weight and BW at weaning were recorded also. Dry matter consumption per heifer ranged between 5.1 and 6.2 kg/d for the low and 6.2 and 7.0 kg/d for the high BW gain with feed intake nearing ad libitum consumption. Diets provided approximately 100% of NRC recommended energy requirement and 98.8% to 107.3% of the protein requirement for growing heifers gaining 0.45 or 0.80 kg/d (NRC, 2000). Angus and MARC II heifers were housed separately by dietary treatment in feedlot pens providing pen and bunk space/head in excess of the recommended allowance. At the onset of the breeding period, each pen of heifers (*n* = 30 heifers) was housed with 2 fertile bulls of the same breed; bulls were rotated within a breed between pens every 3 d. After the first 21 d, heifers and bulls of the same breed were combined and transferred to separate improved pastures (i.e., 2 pastures) for an additional 26 d with the same bulls.

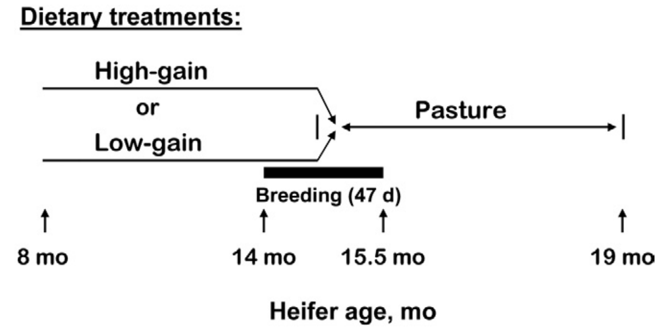

Figure 1. Timeline for experimental treatments and procedures.

Ovarian Measurements and Pregnancy Diagnosis

To fully assess dietary effects on ovarian development and cyclicity, heifers remained on assigned diets in the feedlot for the first 21 d of the breeding period. Commensurate with the onset of the breeding period, heifers were monitored for 1 h twice daily for estrus and breeding activity for 21 d, aided by the use of Estrotect Heat Detectors (Rockway Inc., Spring Valley, WI). Ovarian follicular and CL development were measured transrectally by real-time ultrasonography using a 7.5-MHz linear-array probe (Aloka 500, Corometrics Medical Systems, Wallingford, CT; Cushman et al., 2009; Echternkamp et al., 2009). Ovarian measurements (Cushman et al., 2009) were performed within 12 h after first detection of estrous behavior and included a 2-dimensional measurement of the large (≥10 mm) antral follicles, the length and height for both ovaries, and the number of small (2 to 5 mm), medium (6 to 10 mm), and large (>10 mm) antral follicles for the left and right ovaries of the 62, 67, and 83 heifers detected in estrus in 2009, 2010, and 2011, respectively. Heifers were returned to the pen of origin within a few minutes after the measurements. A second ultrasonography was performed within the same heifers 5 to 15 d after estrus to obtain a 2-dimensional measurement of the CL. In 2010 and 2011, ovaries of heifers not detected in estrus during the first 21 d of breeding were scanned by ultrasonography to measure ovarian size and AFC; the scan was performed just before heifers were transferred from pens to breeding pastures. Heifers diagnosed with a CL present at ultrasonography were classified as cyclic. Thus, ovarian size and cyclicity and AFC measurements were recorded for 62, 120, and 118 heifers in 2009, 2010, and 2011, respectively. Two MARC II heifers with an abnormal reproductive tract were excluded from the study in 2011. In 2010 and 2011, a reproductive tract score (**RTS**), using criteria described by Anderson et al. (1991), the diameter of 1 uterine horn per heifer, and ovarian cyclicity were measured for 238 heifers by transrectal ultrasonography in conjunction with measurement of the ovarian traits either 5 to 15 d after estrus or at transfer to pasture for heifers not detected in estrus.

A blood sample (10 mL) for quantification of plasma progesterone concentration was collected from the tail by venipuncture into a heparinized syringe (15 IU of lithium heparin, Sarstedt Inc., Newton, NC) at the time of measurement of the preovulatory follicle (estrous sample) and, subsequently, at measurement of the CL (luteal phase). Samples were stored on ice up to 1 h until processed. Plasma was recovered from blood by centrifugation (1,250 × *g* for 20 min at 4°C) and stored at –20°C until assayed by RIA. Progesterone was measured directly in plasma using a commercial solid-phase RIA (Coat-A-Count kit, Siemens Medical Diagnostic Solutions, Los Angeles, CA) procedure published previously (Echternkamp and Thallman, 2011). The intra-assay CV was 2.3%, and the interassay CV was 2.8%. The minimal detectable amount of progesterone in plasma was 0.05 ng/mL.

Pregnancy status and fetal age were determined by ultrasonography 35 d after the last day of the breeding period using a 3.5-MHz convex-array probe (Aloka 500, Corometrics Medical Systems; Echternkamp and Gregory, 1999). Heifers were assigned a numerical diagnostic value of 1 for pregnant or 0 for nonpregnant, and the age of the fetus was estimated by crown-rump length and anatomical development, which was subsequently confirmed by calving date; nonpregnant heifers were removed from the study at pregnancy diagnosis.

Data Analyses

Dietary treatment, breed, year, and all 2-way interactions were tested as independent variables by ANOVA using the PROC GLM procedure (SAS Inst. Inc., Cary, NC) to determine their effects on BW, hip height, BW:height ratio, and BCS prebreeding and postbreeding, on ADG during dietary treatment, and on Julian calving date; pen was the experimental unit. Effects of treatment, breed, year, and their 2-way interactions on length and height of left and right ovaries; average ovarian length and height; total AFC; small, medium, and large AFC for left and right ovaries; preovulatory follicle diameter; CL volume; estrous and luteal phase plasma progesterone concentration; uterine horn diameter; and RTS were evaluated using the same statistical procedures and model described above. Luteal phase progesterone concentration and CL volume data were analyzed with day of the estrous cycle (estrus = d 0) in the model, or data were adjusted to d 10 by least squares analysis (Harvey, 1985); uterine diameter and RTS were not measured in 2009. Binomial data for ovarian cyclicity by 21 d (i.e., 2010 and 2011) and conception at 21 and 47 d of the breeding period were analyzed by the PROC GLIMMIX procedure of SAS with dietary treatment, breed, year, and their 2-way interactions as independent variables. In addition, heifers were classified as described by Ireland et al. (2008) as having a low AFC (≤15 antral follicles), intermediate AFC (16 to 24 antral follicles), or high AFC (≥25 antral follicles). The relationship between AFC and birth weight, prebreeding BW, hip height, BW:height ratio, ADG, ovarian length and height, preovulatory follicle diameter, CL volume, ovarian cyclicity, and pregnancy rate was analyzed by ANOVA with AFC classification, dietary treatment, breed, and year as independent variables; ovarian cyclicity at ovarian measurements and pregnancy rate were evaluated by PROC GLIMMIX. The association between pregnancy status and AFC, preovulatory follicle diameter, CL volume, estrous and luteal phase plasma progesterone concentration, uterine diameter, or RTS was analyzed by PROC

Table 1. Comparisons of pretreatment BW, pre- and postbreeding BW, BW:hip height ratio, BCS, and ADG by dietary treatment and breed

	Diet		Breed	
Trait	Low gain[1]	High gain[2]	Angus	MARC II
Pretreatment BW, kg	285.9 ± 2.2	288.0 ± 2.2	287.4 ± 2.2	286.4 ± 2.2
Prebreeding BW (14 mo of age), kg	361.8 ± 2.4[a]	414.9 ± 2.4[b]	389.3 ± 2.4	387.4 ± 2.4
Prebreeding BW:hip height ratio	2.88 ± 0.02[a]	3.30 ± 0.02[b]	3.14 ± 0.02[e]	3.05 ± 0.02[f]
Prebreeding BCS	5.1 ± 0.02[a]	6.3 ± 0.02[b]	5.9 ± 0.02[a]	5.4 ± 0.02[b]
Treatment ADG, kg/d	0.47 ± 0.01[a]	0.79 ± 0.01[b]	0.63 ± 0.01	0.63 ± 0.01
Postbreeding BW, kg	373.8 ± 2.8[a]	417.7 ± 2.8[b]	394.4 ± 2.8	397.2 ± 2.8
Postbreeding BW:hip height ratio	2.97 ± 0.02[a]	3.30 ± 0.02[b]	3.17 ± 0.02[e]	3.11 ± 0.02[f]
Postbreeding BCS	5.6 ± 0.06[a]	6.4 ± 0.06[b]	6.1 ± 0.06	6.0 ± 0.06

[a,b]Means (least squares mean ± SEM) within a class without a common superscript differ; $P \leq 0.01$.

[c,d]Means within a class without a common superscript differ; $P \leq 0.05$.

[e,f]Means within a class without a common superscript differ; $P = 0.07$.

[1]Heifers were fed to achieve an ADG of 0.45 kg/d.

[2]Heifers were fed to achieve an ADG of 0.80 kg/d.

GLM ANOVA, with pregnancy status, breed, year, and their 2-way interactions as independent variables. Associations among production traits, ovarian measurements, and hormone concentrations were assessed by Pearson (SAS PROC CORR) and partial (Manova) correlation procedures.

RESULTS

Body Measurements

By design, BW (Table 1) did not differ between treatment groups at the initiation of the dietary treatments. Average daily gain during the treatment period was 0.79 ± 0.04 kg/d for the high-gain heifers compared with 0.47 ± 0.04 for the low-gain heifers ($P \leq 0.01$). Body weight diverged ($P \leq 0.05$) between the low- and high-gain treatments within 56 d after initiation of dietary treatments (Fig. 2), and the divergence continued into the breeding period; thus, the high-gain heifers were 16% heavier ($P \leq 0.01$) and had a greater ($P \leq 0.01$) BCS and BW:height ratio than the low-gain heifers (Table 1) at onset of the breeding period (i.e., 14 mo of age) as well as at the end of the 47-d breeding period ($P \leq 0.01$). Also, prebreeding BW differed within treatments among years (treatment × year, $P \leq 0.05$; Fig. 3) because of the high-gain heifers being lighter in 2011 and the low-gain heifers being heavier in 2010 relative to their counterparts in the other 2 yr. Hip height was less for Angus than MARC II heifers at breeding (124.2 vs. 127.5 ± 1.0 cm, respectively; $P \leq 0.01$), but BW and ADG (Table 1) did not differ ($P > 0.10$) between breeds; thus, BCS ($P \leq 0.01$) and BW:height ratio ($P = 0.07$) were greater at breeding

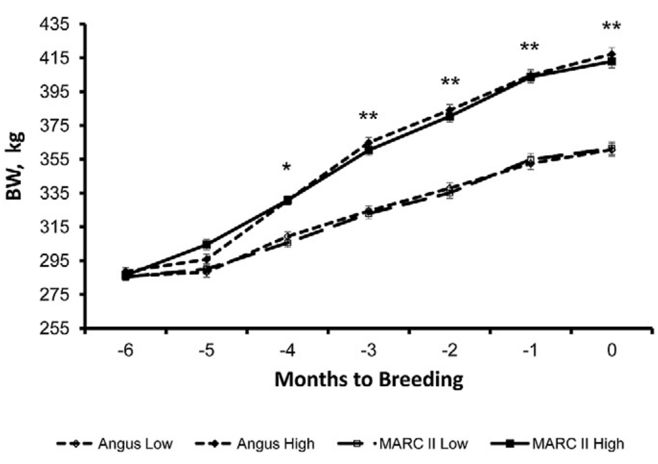

Figure 2. Comparison of prebreeding BW (kg) gains between low- and high-gain Angus and MARC II heifers from beginning of dietary treatment to breeding (8 to 14 mo of age). Means (least squares mean) differ between low- and high-gain heifers (SEM = 4.5); $^{**}P \leq 0.01$, $^{*}P \leq 0.05$. Treatment × breed means of 30 heifers per year.

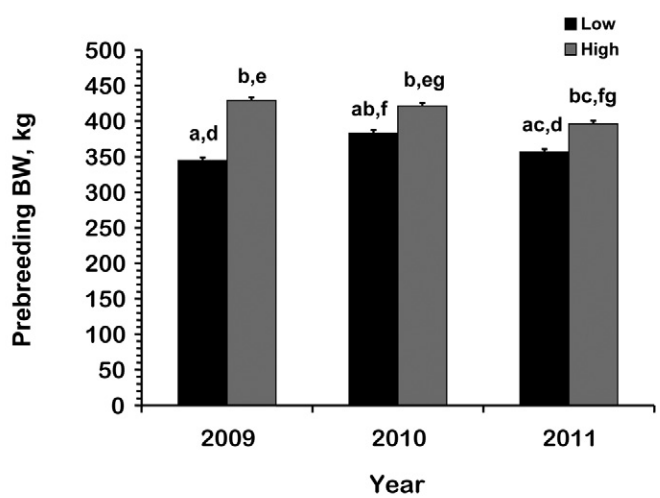

Figure 3. Comparison of prebreeding BW (kg) between low- and high-gain heifers among the 3 yr (treatment × year, $P < 0.05$). Means (least squares mean ± SEM) without a common superscript differ; $^{a–g}P \leq 0.05$.

Table 2. Comparisons of ovarian size and antral follicle count (AFC) among low- and high-gain Angus and MARC II heifers

	Diet		Breed	
Trait	Low gain[1]	High gain[2]	Angus	MARC II
Left ovarian length, mm	26.2 ± 0.2	26.0 ± 0.2	25.6 ± 0.2[a]	26.6 ± 0.2[b]
Left ovarian height, mm	14.2 ± 0.1	14.2 ± 0.1	14.0 ± 0.1[c]	14.4 ± 0.1[d]
Right ovarian length, mm	27.1 ± 0.2[a]	28.1 ± 0.2[b]	27.1 ± 0.2[a]	28.1 ± 0.2[b]
Right ovarian height, mm	15.1 ± 0.4	15.9 ± 0.4	15.0 ± 0.4[c]	16.0 ± 0.4[d]
Average ovarian length, mm	26.7 ± 0.2	27.1 ± 0.2	26.4 ± 0.2[a]	27.3 ± 0.2[b]
Average ovarian height, mm	14.6 ± 0.1	15.1 ± 0.1	14.5 ± 0.1[a]	15.2 ± 0.1[b]
Left ovarian AFC	11.0 ± 0.5	11.1 ± 0.5	10.9 ± 0.5	11.2 ± 0.5
Right ovarian AFC	11.1 ± 0.6	11.6 ± 0.6	11.4 ± 0.6	11.4 ± 0.6
Total ovarian AFC	21.9 ± 1.2	22.6 ± 1.2	22.2 ± 1.2	22.3 ± 1.2

[a,b]Means (least squares mean ± SEM) within a class without a common superscript differ; $P < 0.05$.

[c,d]Means within a class without a common superscript tend to differ; $P = 0.08$.

[1]Heifers were fed to achieve an ADG of 0.45 kg/d.

[2]Heifers were fed to achieve an ADG of 0.80 kg/d.

for Angus than MARC II heifers. Trends in BW change during the treatment period were similar for the Angus and MARC II heifers (Fig. 2) within either the high- or low-gain treatment; the treatment × breed interaction was not significant ($P > 0.10$) for prebreeding BW, BCS, BW:height ratio, or ADG.

Ovarian Measurements

Length ($P \leq 0.05$) of the right ovary (Table 2) was greater for the high-gain heifers than the low-gain heifers, whereas measurements for length and height of the left ovary and average length and height of the 2 ovaries were not affected ($P > 0.10$) by treatment. In addition, length ($P \leq 0.05$) and height ($P = 0.08$) of the left and right ovary were greater for MARC II vs. Angus heifers; thus, average ovarian length and height were also greater ($P \leq 0.05$) for MARC II vs. Angus heifers (Table 2). The trend for the larger MARC II heifers to have larger ovaries was reflected in positive correlations (Table 3 and 4; $P \leq 0.01$) between average ovarian length and prebreeding hip height ($r = 0.14$) and between average ovarian height and prebreeding BW ($r = 0.19$), hip height ($r = 0.20$), BW:height ratio ($r = 0.14$), and ADG ($r = 0.21$). Ovarian length and height did not differ ($P > 0.10$) between the left and right ovaries.

Antral Follicle Numbers

The total number of antral follicles visible by ultrasonography within the left and right ovaries combined ranged from 5 to 49. Numbers of medium and large antral follicles present within the ovaries during the estrous cycle constitute only a small portion of the total AFC; thus, AFC was primarily predictive of trends among heifers in the number of small (≤5 mm) antral follicles (total AFC vs. left small AFC or right small AFC, $r = 0.92$, $P \leq 0.01$; Table 5).

Antral follicle count for the left or right ovary or both ovaries combined (Table 2) did not differ between dietary

Table 3. Relationships among ovarian size, antral follicle count (AFC), and body measurements (Pearson correlation coefficients)[1]

		Prebreeding				
Trait	Birth weight	BW	Height	BW:height	BCS	ADG
Left length	0.06	0.04	0.10	0.01	0.08	0.04
Left height	0.02	0.09	0.08	0.08	0.04	0.10
Left small AFC	0.01	0.07	0.01	0.09	0.12*	0.07
Left total AFC	0.01	0.08	0.01	0.10	0.12*	0.06
Right length	0.09	0.05	0.11*	0.02	0.15**	0.11*
Right height	0.12*	0.18**	0.22**	0.13*	0.14**	0.21**
Right small AFC	0.05	0.12*	0.02	0.11*	0.14**	0.11*
Right total AFC	0.04	0.13*	0.02	0.13*	0.14**	0.12*
Total AFC	0.02	0.11*	0.01	0.12*	0.14**	0.10
Avg. ovarian length	0.10	0.05	0.14**	0.02	0.15**	0.09
Avg. ovarian height	0.09	0.19**	0.20**	0.14**	0.13*	0.21**

[1]In 2010 and 2011, ovarian measurements were performed on all heifers ($n = 238$), whereas only those detected in estrus ($n = 62$) were evaluated in 2009.

** $P \leq 0.01$; *$P \leq 0.05$.

Table 4. Relationships among ovarian size, antral follicle count (AFC), and body measurements (partial correlation coefficients)[1]

Trait	Birth weight	Prebreeding				
		BW	Height	BW:height	BCS	ADG
Left ovarian length	0.00	0.10	0.00	0.12*	0.08	0.11*
Left ovarian height	0.00	0.12*	0.03	0.13*	0.04	0.11*
Left small AFC	0.01	0.09	0.01	0.12*	0.12*	0.12*
Left total AFC	0.01	0.11*	0.01	0.14**	0.12*	0.14**
Right ovarian length	0.00	0.03	0.00	0.05	0.15**	0.06
Right ovarian height	0.05	0.12*	0.10	0.10	0.14**	0.12*
Right small AFC	0.03	0.13*	0.01	0.14**	0.14**	0.16**
Right total AFC	0.02	0.12*	0.01	0.13*	0.14**	0.16**
Avg. ovarian length	0.00	0.09	0.00	0.12*	0.15**	0.11*
Avg. ovarian height	0.04	0.17**	0.09	0.16**	0.13*	0.16**
Total AFC	0.00	0.12*	0.00	0.14**	0.14**	0.15**

[1]In 2010 and 2011, ovarian measurements were performed on all heifers (n = 238), whereas only those detected in estrus (n = 62) were evaluated in 2009.
** $P \leq 0.01$; *$P \leq 0.05$.

treatments or breeds or among years. The number of antral follicles was associated positively ($P \leq 0.01$) with the length and height of the left and right ovaries as evaluated by Pearson correlation (Table 5). Positive coefficients for the partial correlations between AFC and ovarian size were also significant ($P \leq 0.01$): left ovary AFC vs. left ovarian length or height, $r = 0.50$ or 0.41; right ovary AFC vs. right ovarian length or height, r = 0.38 or 0.25; and total AFC vs. average ovarian length or height, $r = 0.59$ or 0.46. Total AFC was similar ($P > 0.10$; Table 2) between the left and right ovaries, and thus, AFC was correlated positively ($r = 0.78$, $P \leq 0.01$; Table 5) between the 2 ovaries. In addition, categorization of heifers as having a low, intermediate, or high AFC (Table 6) revealed a positive association ($P \leq 0.01$) between ovarian size and AFC.

Although AFC did not differ between low- and high-gain heifers (Table 2), heifers with a low AFC vs. high AFC were lighter ($P \leq 0.05$) and gained less ($P \leq 0.05$) BW prebreeding (Table 7), whereas birth weight was not associated with AFC (Table 7). In addition, coefficients for Pearson (Table 3) and partial (Table 4) correlations between AFC or ovarian size and physical status revealed a positive association of AFC and ovarian size with prebreeding BW, BW:height, and ADG, inferring a positive relationship or association between AFC and BW gain or condition at the end of the development period.

Follicle Development and CL Size and Function

Because trends were similar for preovulatory follicle diameter and volume, numerical data are only reported for diameter. The diameter of the preovulatory follicle ranged between 10.4 to 18.9 mm and was greater ($P \leq 0.01$) for MARC II heifers compared with Angus heifers (Table 8). In contrast, the size of the preovulatory follicle was not influenced by dietary treatment (Table 8) or by AFC category (Table 9). In addition, comparison of the preovulatory follicle diameter between heif-

Table 5. Relationships between size of left and right ovaries and antral follicle count (AFC)[1]

Trait	Total AFC	Left ovary					Right ovary			
		Length	Height	Area	Small AFC	Total AFC	Length	Height	Area	Small AFC
Left length	0.47									
Left height	0.37	0.62								
Left area	0.44	0.86	0.92							
Left small AFC	0.92	0.44	0.35	0.41						
Left total AFC	0.93	0.47	0.36	0.43	0.98					
Right length	0.33	0.25	0.13	0.19	0.32	0.30				
Right height	0.22	0.10	0.09	0.09	0.22	0.19	0.61			
Right area	0.29	0.16	0.10	0.13	0.28	0.26	0.85	0.92		
Right small AFC	0.92	0.45	0.35	0.42	0.77	0.78	0.31	0.20	0.26	
Right total AFC	0.93	0.42	0.32	0.39	0.77	0.78	0.34	0.24	0.30	0.98
Average length	0.51									
Average height	0.40									

[1]In 2010 and 2011, ovarian measurements were performed on all heifers (n = 238), whereas only those detected in estrus (n = 62) were evaluated in 2009. Pearson correlation coefficients (r) ≥ 0.15 are significant at $P \leq 0.01$, and $r \geq 0.11$ are significant at $P \leq 0.05$.

Table 6. Relationship between antral follicle count and ovarian size[1]

Trait	Antral follicle count[2] Low	Intermediate	High
No. of heifers	57	124	119
Left ovarian length, mm	22.6 ± 0.4[a]	25.7 ± 0.4[b]	28.5 ± 0.4[c]
Left ovarian height, mm	12.1 ± 0.3[a]	13.9 ± 0.3[b]	15.6 ± 0.3[c]
Right ovarian length, mm	25.0 ± 0.4[a]	27.2 ± 0.4[b]	29.5 ± 0.4[c]
Right ovarian height, mm	14.5 ± 0.3[a]	15.2 ± 0.3[b]	16.4 ± 0.3[c]
Avg. ovarian length, mm	23.8 ± 0.3[a]	26.4 ± 0.3[b]	29.0 ± 0.3[c]
Avg. ovarian height, mm	13.4 ± 0.2[a]	14.6 ± 0.2[b]	16.0 ± 0.2[c]

[a–c]Means (least squares mean ± SEM) within a row without a common superscript differ; $P \leq 0.01$.

[1]In 2010 and 2011, ovarian measurements were performed on all heifers (n = 238), whereas only those detected in estrus (n = 62) were evaluated in 2009.

[2]Total number of antral follicles (AFC) and ovarian size measured for the left and right ovaries combined. Heifers were categorized as having a low (≤15), intermediate (16 to 24), or high (≥25) AFC.

Table 7. Relationship between antral follicle count and body size and condition at breeding

Trait	Antral follicle count[1] Low	Intermediate	High
No. of heifers	57	124	119
Birth weight, kg	36.0 ± 0.6	36.7 ± 0.4	36.9 ± 0.4
Prebreeding			
BW, kg	380.5 ± 4.4[a]	393.0 ± 3.0[b]	393.8 ± 3.1[b]
Hip height, cm	125.4 ± 0.4	126.0 ± 0.3	125.6 ± 0.3
BW:hip height ratio	3.04 ± 0.04[a]	3.12 ± 0.02[b]	3.13 ± 0.02[b]
Treatment ADG, kg/d	0.60 ± 0.03[a]	0.63 ± 0.01[ab]	0.65 ± 0.01[b]

[a,b]Means (least squares mean ± SEM) within a row without a common superscript differ; $P \leq 0.05$.

[1]Total number of antral follicles (AFC) for the left and right ovaries combined was measured for all heifers in 2010 and 2011 but only for heifers detected in estrus in 2009. Heifers were categorized as having a low (≤15), intermediate (16 to 24), or high (≥25) AFC.

ers becoming or not becoming pregnant at the evaluated estrus did not reveal an influence of follicle diameter on whether heifers became pregnant (13.7 vs. 13.9 ± 0.2 mm, respectively).

Both plasma progesterone concentration and CL volume increased ($P \leq 0.01$) between d 5 and 15 of the estrous cycle. Thus, progesterone concentrations were correlated positively with volume of CL ($r = 0.27$; $P \leq 0.01$) present at the time of blood collection; the partial correlation coefficient adjusted for day of estrous cycle was r = 0.16 ($P \leq 0.05$). In addition, luteal phase (adjusted to d 10) plasma progesterone concentrations (Fig. 4) were greater ($P \leq 0.01$) during the estrous cycle for the high- vs. low-gain heifers and differed ($P \leq 0.01$) among the 3 yr (least in 2009 and greatest in 2010), whereas CL volume did not differ between low- and high-gain heifers (Table 8) or among years. The volume of the CL was influenced positively by the diameter of the preovulatory follicle of origin ($r = 0.36$; $P \leq 0.01$). In addition, luteal plasma progesterone concentrations tended to be greater for heifers that became pregnant compared with heifers that did not become pregnant at the evaluated mating (6.9 ± 0.2 ng/mL vs. 6.2 ± 0.4 ng/mL, respectively; $P = 0.10$). Also, there was a trend ($P = 0.08$) for luteal phase plasma progesterone concentrations to be less for heifers with a low vs. high AFC (Table 9), whereas the size of the preovulatory follicle or CL did not differ among the AFC categories. In

Table 8. Comparisons of reproductive traits by BW gain and breed[1]

Trait	Diet Low gain[2]	Diet High gain[3]	Breed Angus	Breed MARC II
Preovulatory follicle diameter, mm	13.7 ± 0.2	14.0 ± 0.2	13.2 ± 0.2[c]	14.4 ± 0.2[d]
Estrual plasma progesterone, ng/mL	0.73 ± 0.03	0.82 ± 0.03	0.68 ± 0.03[c]	0.89 ± 0.03[d]
Corpus luteum volume, cm^3	4.7 ± 0.3	4.8 ± 0.3	4.5 ± 0.3	4.9 ± 0.3
Luteal plasma progesterone, ng/mL	5.9 ± 0.2[a]	7.5 ± 0.2[b]	6.7 ± 0.2	6.9 ± 0.2
Uterine horn diameter,[4] mm	11.3 ± 0.2	11.1 ± 0.2	11.2 ± 0.2	11.4 ± 0.2
RTS[4]	4.89 ± 0.03	4.95 ± 0.03	4.96 ± 0.03	4.88 ± 0.03

[a,b]Means [least squares mean (LSM) ± SEM] within a class without a common superscript differ; $P \leq 0.01$.

[c,d]Means (LSM ± SEM) within a class without a common superscript differ; $P \leq 0.05$.

[1]Preovulatory follicle diameter was measured at estrus, and corpus luteum volume and uterine horn diam. were measured 5 to 15 d after estrus (n = 212); heifers not detected in estrus were excluded. A blood sample was collected at both measurements for progesterone analysis; luteal samples were adjusted to d 10 of cycle.

[2]Heifers were fed to achieve an ADG of 0.45 kg/d.

[3]Heifers were fed to achieve an ADG of 0.80 kg/d.

[4]Uterine horn diameter and reproductive tract score (RTS) were not measured in 2009

Table 9. Relationship between antral follicle count and ovarian function[1]

Trait	Antral follicle count[2] Low	Intermediate	High
No. of heifers	49	84	79
Preovulatory follicle diameter, mm	14.2 ± 0.5	13.8 ± 0.4	13.7 ± 0.4
Corpus luteum volume, cm^3	4.5 ± 0.5	5.4 ± 0.4	4.4 ± 0.4
Luteal plasma progesterone, ng/mL	5.8 ± 0.4[a]	6.6 ± 0.3[a,b]	6.9 ± 0.3[b]
Cyclicity,[3] %	98.0 ± 0.4	97.5 ± 0.3	97.7 ± 0.3
21-d Pregnancy rate, %	58.8 ± 7.7	54.1 ± 4.9	62.9 ± 4.7
Overall pregnancy rate, %	83.2 ± 5.3	82.9 ± 3.8	83.3 ± 3.7

[a,b]Means (least squares mean ± SEM) within a row without a common superscript differ; $P = 0.08$.

[1]Preovulatory follicle diam. and antral follicle count (AFC) were measured by ultrasonography at estrus, and corpus luteum volume and uterine horn diam. were measured at 5 to 15 d after estrus. A blood sample was collected for progesterone analysis at both measurements; luteal samples were adjusted to d 10 of cycle.

[2]Total AFC for the left and right ovaries combined. Heifers were categorized as having a low (≤15), intermediate (16 to 24), or high (≥25) AFC.

[3]Proportion of evaluated heifers having a CL 5 to 15 d after estrus determined by ultrasonography.

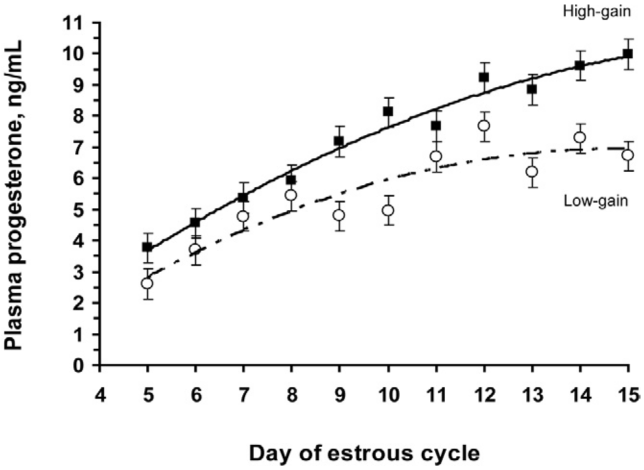

Figure 4. Comparison of plasma progesterone concentrations between low- and high-gain heifers. Concentrations differed ($P \le 0.01$) among days of the estrous cycle and between treatments. Number of heifers contributing progesterone data to the day × treatment means ranged from 3 to 5 per year.

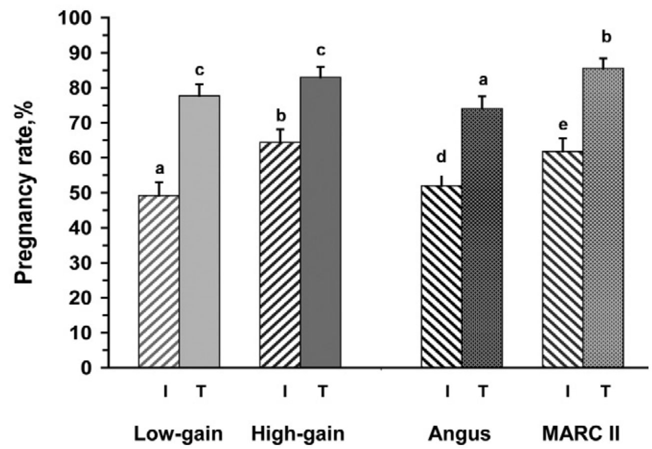

Figure 5. Comparison of proportion of heifers becoming pregnant within the first 21 d of the breeding period (initial, I) or 47-d breeding period (total, T) between low- and high-gain heifers and between Angus and MARC II heifers. Means (least squares mean ± SEM) within a class without a common superscript differ; [a–c]$P \le 0.01$, [d,e]$P = 0.07$.

contrast, progesterone concentrations at estrus (Table 8) were low and did not differ between dietary treatments but were greater ($P \le 0.05$) for MARC II vs. Angus heifers (0.89 vs. 0.68 ± 0.07 ng/mL).

Pregnancy Rate

A greater proportion ($P \le 0.01$) of the high-gain compared with the low-gain heifers conceived within the first 21 d of the breeding period (Fig. 5), whereas after 47 d of breeding, pregnancy rate was greater for high-gain heifers only in 2010 (71.6% vs. 89.5% ± 5.0%, respectively; treatment × year, $P = 0.07$). The earlier conception for the high-gain heifers was also confirmed by an earlier average Julian calving date for the high- vs. low-gain group (82.3 vs. 86.4 ± 1.1 d; $P \le 0.05$). In addition, a greater proportion of MARC II vs. Angus heifers became pregnant during the first 21 d of the breeding period ($P = 0.07$) and during the total breeding period ($P \le 0.01$). Comparison of pregnancy rate among heifers with low, intermediate, and high AFC (Table 9) did not indicate ($P > 0.10$) an association between AFC and fertility. Likewise, AFC did not differ ($P > 0.10$) between heifers becoming pregnant or not pregnant (22.5 vs. 23.2 ± 1.1, respectively) in the 47-d breeding period.

Reproductive Tract Scores and Uterine Horn Diameter

The proportion of heifers determined by ultrasonography to be cyclic (97.2% ± 1.2%) by 21 d of the breeding period in 2010 and 2011 did not differ ($P > 0.10$) between treatments (96.8% vs. 97.6% ± 2.4%, low vs. high gain), breeds (97.6% vs. 96.8% ± 2.4%, Angus vs. MARC II), or years. Similarly, RTS by 21 d of breeding in 2010 and 2011 did not differ ($P > 0.10$) between treatments (4.89 vs. 4.95 ± 0.02, low vs. high gain) or breeds (4.96 vs. 4.88 ± 0.02, Angus vs. MARC II), but RTS was greater for heifers diagnosed pregnant vs. nonpregnant (4.98 vs. 4.91 ± 0.02, respectively; $P < 0.05$). Uterine horn diameter (11.4 ± 0.4 mm) did not differ ($P > 0.10$) between treatments, breeds, or pregnancy status or among AFC categories, but the diameter was greater ($P \le 0.05$) in 2010 than 2011 (11.7 vs. 11.0 ± 0.2 mm).

DISCUSSION

Development of replacement beef heifers to achieve puberty and conceive early in the breeding period is critical to improving their likelihood of remaining in the herd, maximizing their lifetime productivity (Burris and Priode, 1958; Lesmeister et al., 1973), and minimizing feed, management, and overhead costs associated with their development. In the present study, development of prepubertal beef heifers on a lower level of energy and a smaller ADG from 8 mo of age through the first 21 d of breeding period to achieve 55% rather than the traditional 65% of mature BW at breeding did not compromise the proportion of heifers becoming pregnant during a 47-d breeding period. Conversely, the proportion of heifers becoming pregnant during the first 21 d of the breeding period was less for low- vs. high-gain heifers; thus, reducing heifer growth and body condition during the prepubertal and pubertal periods may potentially delay fertility. These observed effects of decreased dietary energy and development to 55% of mature BW on pregnancy rate concur with results from previous studies in which restricting feed during development reduced pregnancy rate to synchronized AI at initiation of the breeding period (Roberts et al., 2009), but final pregnancy rates did not differ between BW gain groups (Funston and Deutscher, 2004; Martin et al., 2008; Roberts et al., 2009). Reduced fertility in the present study was not due to delayed initiation of ovarian cyclicity, for 97% of the heifers had ovulated by 21 d of breeding in 2010 and 2011. Furthermore, decreasing dietary energy and prebreeding BW did not compromise ovarian size or folliculogenesis; however, circulating progesterone concentrations, but not CL volume, were decreased during the luteal phase of the estrous cycle in low-gain heifers detected in estrus in the first 21 d. Thus, the lower fertility for low-gain heifers may be due to lower fertilization rates or greater early embryonic mortality (Inskeep, 2004).

In earlier studies, heifers were provided with a higher-energy diet or improved pasture 4 to 6 wk before onset of breeding (Funston and Deutscher, 2004; Roberts et al., 2009) or were treated with progesterone (Martin et al., 2008; Roberts et al., 2009) to facilitate ovarian cyclicity and ovulation, especially in the low-gain heifers. In the present study, housing the heifers with fertile bulls for the entire breeding period may have facilitated cyclicity and contributed to the high proportion (97.2%) of heifers being cyclic by 21 d of the breeding period (Roberson et al., 1991). The smaller proportion of pregnant Angus compared with MARC II heifers in both BW gain groups is consistent with pregnancy rate being about 10% less for Angus heifers compared with other cattle populations at USMARC (Thallman et al., 1999). This breed difference in pregnancy rate was not linked to breed differences in the proportion of heifers cyclic during the first 21 d of breeding or ovarian follicular development.

Development of the female reproductive system, as measured by ovarian size, AFC, follicular development, and RTS, was not compromised by the lower dietary energy intake and the smaller BW gain, BCS, and BW:height ratio. As observed previously (Ireland et al., 2008; Cushman et al., 2009), the number of antral follicles identifiable by transrectal ultrasonography was highly variable (5 to 49 follicles/heifer) among heifers. Several investigators have proposed that the repeatable variation in AFC within the ovarian cortex among beef and dairy cattle during ovarian follicular waves is predictive of the size of the ovarian reserve and a biomarker of phenotypic differences among bovine females in recruitment and atresia of secondary ovarian follicles and oocyte quality (Cushman et al., 1999; Ireland et al., 2008). Changes in AFC include a decrease in follicle numbers with aging in cattle (Cushman et al., 2009) analogous with the depletion of the ovarian reserve associated with menopause in women (Broekmans et al., 2007). Maurer and Echternkamp (1985) reported that repeat-breeder cows had fewer 1- to 3-mm antral follicles in the ovarian cortex than high-fertility beef cows, indicating that repeat-breeder cows either had fewer vesicular follicles or insufficient paracrine or endocrine status to support folliculogenesis. Ovarian gametogenesis and folliculogenesis occur early in fetal development, with the peak number of follicles and oocytes present in bovine fetal ovaries during the first trimester of gestation (Erickson, 1966), and mammalian ovaries reportedly contain a finite number of gametes at birth. Consequently, potential effects of nutrient restriction on the size of the ovarian reserve postnatally would likely be manifested through an increase in rate of follicular atresia or a decrease in oocyte quality; however, the effects of BW gain and BCS on ovarian size and follicular activity were small between the low- and high-gain heifers regardless of breed.

Although AFC did not differ between low- and high-gain heifers, low (≤15) AFC heifers had a decreased ADG, lighter BW, and smaller BW:height ratio at breeding compared with the high (≥25) AFC heifers, which likely accounted for the significant small positive partial correlation coefficients between AFC and prebreeding BW, BW:height ratio, and ADG. This positive association between AFC and animal growth may indicate that an increase in BW gain and condition during the treatment period did provide a small positive influence on ovarian follicular development. Alternatively, the positive associations between AFC and animal growth may indicate that ovarian follicular development was impaired or delayed in the low-AFC heifers as a consequence of their fetal development being compromised. Evans et al. (2010) reported a 60% reduction in AFC for female progeny born to dams fed 60% vs. 100% of maintenance requirement during the first third of gestation without birth weight being affected. In contrast, Cushman et al. (2009) reported a lighter birth weight for low- vs. high-AFC females; birth weight did not differ statistically between low- and high-AFC heifers in the present study. Positive partial correlations were also found between ovarian size and prebreeding BW, weight:height ratio, or ADG; thus, the association between AFC and body size and growth performance may be the consequence of a treatment or genetic effect on body size, with AFC being increased because of positive relationships between ovarian size and body size and between ovarian size and AFC. In contrast with recently reported decreased fertility in beef (Cushman et al., 2009) and dairy (Mossa et al., 2012) cows and heifers with low (≤15 follicles) vs. high (≥25 follicles) AFC, pregnancy rate did not differ between low- and high-AFC beef heifers in the present study or in a study reported by Starbuck-Clemmer et al. (2007). Cushman et al. (2009) reported that AFC increases with age, reaching a maximum at about 5 yr and declining thereafter. The present study only evaluated the relationship between AFC and fertility in yearling heifers; therefore, a lack of association between AFC and pregnancy rate in the present study may be because fertility of yearling heifers is less affected by AFC and its underlying mechanisms that become more pronounced with age. Studies evaluating long-term relationships among AFC, follicle turnover and depletion of the ovarian reserve, and reproductive stayability are still limited for domestic animals.

Plasma progesterone concentrations during the luteal phase subsequent to breeding were greater for the cyclic high- vs. low-gain heifers, whereas CL volume or diameter did not differ between the cyclic high- and low-gain heifers, suggesting that progesterone secretion by the CL was compromised in the low-gain heifers. The lower systemic progesterone concentrations in the low-gain heifers may be due to the dietary restriction reducing LH secretion and its stimulation of progesterone secretion by the CL observed previously in both pubertal heifers and cyclic cows (Bossis et al., 1999, 2000; Diskin et al., 2003). Alternatively, differences in plasma progesterone concentrations may reflect dietary differences in hepatic blood flow and progesterone metabolism (Sangsritavong et al., 2002); however, a comparison of splanchnic clearance of progesterone between ovariectomized ewes receiving a low- vs. high-ME intake indicated no difference in delivery of circulating progesterone to the liver or in hepatic progesterone metabolism (Freetly and Ferrell, 1994). Plasma progesterone concentrations also tended to be less in heifers with a low AFC compared with a high AFC. Unlike with feed restriction, Jimenez-Krassel et al. (2009) reported that the reduction in progesterone in low-AFC heifers was not associated with a reduction in LH secretion, but luteal cells from low- compared with high-AFC heifers were found to be less responsive to LH in culture.

A minimal concentration of progesterone is required for the maintenance of pregnancy and embryo survival (Inskeep, 2004), but reported associations between systemic progesterone concentrations and the establishment of pregnancy in ruminants have been variable (Henricks et al., 1971). In the present study, plasma progesterone concentrations tended to be greater for heifers that became pregnant compared with heifers that did not become pregnant. Thus, the greater progesterone in the greater-gain heifers may have accounted for the greater proportion of high- vs. low-gain heifers becoming pregnant within the first 21 d of the breeding period. Conversely, a similar proportion of the Angus vs. MARC II heifers had a CL within the first 21 d of the breeding period, and plasma progesterone concentrations did not differ between the Angus and MARC II heifers. Therefore, it is unlikely that the lesser pregnancy rate for Angus vs. MARC II heifers was associated with a reduction in progesterone support or failure to be cyclic.

Measurement of the preovulatory follicle within 12 h after detection of estrus revealed no difference between low- vs. high-gain heifers for diameter or volume of the preovulatory follicle, whereas some previous investigators have reported a reduction in the size of the dominant follicle in nutritionally restricted heifers and cows (Diskin et al., 2003). Previous assessment of dietary effects on follicular development in prepubertal heifers revealed that chronological development of dominant follicles and induction of the pubertal ovulation were delayed several weeks in heifers fed a lower-energy diet, whereas the diameter of the ovulatory follicle at first ovulation (i.e., same physiological age) did not differ between dietary groups (Bergfeld et al., 1994). Similarly, the diameter of dominant follicles diminished immediately preceding nutritionally induced anestrus in cyclic heifers, increased during realimentation, and was of similar size to control dominant follicles after resumption of cyclicity (Bossis et al., 1999, 2000). In the present study, the size of the dominant follicles was evaluated only in heifers observed in estrus; thus, assessment of the effect of prepubertal ADG on development of dominant follicles may have been biased by the exclusion of possibly smaller dominant follicles of heifers not detected in estrus. Likewise, preovulatory follicle diameter did not differ among heifers with low, intermediate, or high AFC. Similarly, Ireland et al. (2009) did not observe a difference in the size of the 3 largest follicles between low- and high-AFC crossbred beef cows, but follicular fluid estradiol concentrations were decreased in the follicles of the low-AFC cows.

The diameter of the preovulatory follicle differed between the Angus and MARC II heifers. An association between the size of the ovulatory follicle and fertility has been detected in both single- (Vasconcelos et al., 2001; Perry et al., 2007) and twin-ovulating (Echternkamp et al., 2009) cattle populations, with pregnancy rate and early embryonic survival being reduced in cattle with either small (<11 mm) or large (>16 mm) ovulatory follicles relative to an intermediate diameter. Because the preovulatory follicles for both Angus and MARC II heifers ranged between 11 and 16 mm, it is unlikely that differences in follicle diameter accounted for breed difference in fertility or for earlier pregnancy in the high-gain heifers. Likewise, the diameter of the ovulatory follicle did not differ between heifers pregnant or not pregnant to the monitored estrus in the present study. Although the size of the ovulatory follicle reportedly has a positive effect on CL development and function (Vasconcelos et al., 2001; Echternkamp et al., 2009; Fields et al., 2012) and CL volume and progesterone were correlated positively in the present study, CL volume and luteal progesterone concentrations did not differ between Angus and MARC II heifers.

Measurement of uterine horn diameter in 2010 and 2011 revealed no significant differences in diameter between the 2 weight gain groups, between Angus and MARC II heifers, or among AFC size groups. Conversely, it was reported previously that endometrial thickness from d 0 to 4 of the estrous cycle was reduced in low-AFC compared with high-AFC cows (Jimenez-Krassel et al., 2009).

Ninety-seven percent of the 2010 and 2011 heifers had a CL identifiable by transrectal ultrasonography during the first 21 d of the breeding period with no significant difference between low- and high-gain heifers; thus, the majority of the heifers had a RTS of 4 or 5 at examination. Early initiation of puberty is characteristic of the Angus breed (Thallman et al., 1999), and a CL was identified on the ovaries during the first 21 d of breeding in a greater proportion of Angus heifers compared with MARC II heifers (99.0% vs. 96.1%). Thus, the reduced pregnancy rate for the Angus compared with MARC II heifers was not associated with a reduction in systemic progesterone concentrations, a lower RTS, or fewer antral follicles, traits reported to be associated with reduced fertility.

In summary, results from the present study agree with previous studies indicating that development of replacement beef heifers on less energy and at a smaller ADG from 8 mo of age to achieve 55% of their mature BW at breeding may enable producers to reduce associated feed costs without compromising ovarian development and the proportion of heifers becoming pregnant during a 45-d breeding period. Furthermore, final pregnancy rates were comparable between low- and high-gain heifers even when the energy restriction was continued during the first 21 d of the breeding period as opposed to studies in which the low-gain heifers received compensatory BW gain or progesterone therapy prebreeding to enhance fertility. However, a smaller proportion of low-gain heifers becoming pregnant within the first 21 d of the breeding period may compromise their stayability in the herd as a result of calving and breeding later in subsequent years, especially if a greater restriction in BW gain was imposed during the postweaning period. Plasma progesterone concentrations were reduced during the luteal phase in the low-gain heifers expressing estrus, whereas the size of the preovulatory follicle and CL were not affected by dietary treatment, suggesting a reduction in luteal function. Associations reported previously between AFC and fertility were not observed among the yearling heifers in the present study.

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