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Relationships between feed efficiency and puberty in *Bos taurus* and *Bos indicus*-influenced replacement beef heifers

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Abstract

The objective of this experiment was to investigate the relationship between residual feed intake (RFI) and parameters associated with reproductive efficiency in growing beef heifers. One hundred and seventy-nine replacement beef heifers (*Bos taurus* and *Bos indicus*-influenced) were enrolled in a retrospective cohort design. Heifers were assigned to a 70-d feed efficiency test, and results were utilized to retrospectively classify heifers into low ($n = 51$), medium ($n = 66$), or high ($n = 62$) RFI groups based on their individual RFI values. Blood samples were collected weekly throughout the feed efficiency test and breeding season, which were analyzed for plasma concentration of progesterone to determine age at puberty (PUB). By design, residual feed intake differed among RFI groups where high (1.21 ± 0.08 kg/d) had greater ($P < 0.01$) RFI than medium (0.00 ± 0.08 kg/d) and low RFI groups (-1.49 ± 0.09 kg/d), and medium had greater ($P < 0.01$) RFI than low RFI heifers. Yet, no differences were observed between breed types for RFI ($P = 0.53$). Average daily gain (ADG) differed between breed types where *Bos taurus* heifers had greater ADG ($P = 0.02$) than *B. indicus*-influenced heifers. Furthermore, ADG tended ($P = 0.08$) to differ among RFI groups, where medium RFI heifers tended to have reduced ADG compared with low and high RFI heifers. No differences were determined between breed types for gain-to-feed ratio (G:F; $P = 0.20$); however, G:F differed among RFI groups and was greater ($P < 0.01$) in low vs. high, and low vs. medium RFI heifers. The percentage of cycling heifers by the start of the breeding season differed ($P = 0.03$) by RFI group, where a greater percentage of low RFI heifers were cycling compared with high RFI heifers. A difference was determined on PUB between breed types ($P = 0.03$), where *Bos taurus* (393.40 ± 4.64 d) heifers had a reduced PUB compared with *B. indicus*-influenced (406.90 ± 5.07 d) heifers. In addition, PUB differed by RFI group where low (385.96 ± 6.20 d; $P < 0.01$) and medium (398.47 ± 5.47 d; $P = 0.02$) RFI heifers had a reduced PUB compared with High RFI heifers (416.03 ± 5.58 d). In conclusion, more feed efficient heifers attained PUB earlier than less feed efficient heifers. Therefore, selection of heifers for feed efficiency may positively impact reproductive performance of replacement beef heifers.

Key words: Beef heifer, *Bos indicus*-influenced, *Bos taurus*, Feed efficiency, Puberty

Abbreviations

ADG	average daily gain
BCS	body condition score
BW	body weight
DMI	dry matter intake
G:F	gain to feed ratio
PUB	age at puberty
RFI	residual feed intake

Introduction

Beef cattle productivity is largely influenced by age at first calving, where beef heifers that calve as 2 yr olds have greater overall productivity compared with heifers that calve at 3 yr of age (Lesmeister et al., 1973; Patterson et al., 1992; López-Paredes et al., 2018). In addition, heifers that become pregnant early in their first breeding season have the potential to calve early in the subsequent calving season and, as a result, wean heavier calves and have increased longevity in the herd compared with heifers that become pregnant later in the breeding season (Funston et al., 2012; Cushman et al., 2013). Therefore, emphasis should be placed on increasing the proportion of heifers that become pregnant at the beginning of the breeding season. However, puberty (PUB) achievement represents a major challenge in accomplishing the abovementioned goals, as prepubertal heifers may not become pregnant early in the breeding season. As a result, heifer development strategies aimed at increasing the number of pubertal heifers at the initiation of the breeding season may benefit overall productivity of cow–calf operations.

The age at PUB is primarily controlled by genetics and nutrient availability (Amstalden et al., 2011); therefore, adequate nutritional management of replacement heifers is critical for them to achieve PUB earlier (Gasser et al., 2006). However, feed expenses account for two-thirds of the annual production costs in the beef industry, serving as an incentive for producers to search for methods to reduce inputs without compromising overall production (Arthur et al., 2001a). Residual feed intake (RFI) has been proposed as a measure of feed efficiency and is calculated as the actual feed intake minus the expected feed intake of each animal, where lower values indicate that less feed was consumed than expected (Koch et al., 1963). Selection of animals with superior feed efficiency may result in a reduction of feed costs, yet studies indicate that selecting cattle for lower RFI has the potential to negatively impact carcass composition and quality (McDonagh et al., 2001; Richardson et al., 2001; Basarab et al., 2003). Previous research has also investigated the relationship between feed efficiency and fertility in beef heifers (Basarab et al., 2011; Shaffer et al., 2011; Callum et al., 2019), where studies have reported a negative relationship between RFI and age of PUB, even when adjusted for end-of-test backfat thickness (Basarab et al., 2011; Shaffer et al., 2011). Conversely, numerous studies have reported no differences in other reproductive traits, such as estrus detection rate, conception and pregnancy rates, calving rate, and age at first calving (Basarab et al., 2011; Shaffer et al., 2011; Callum et al., 2019). However, most of the studies examining the relationship between feed efficiency and fertility have been conducted in *Bos taurus* beef heifers.

Further research on the relationship between feed efficiency and the onset of PUB in beef heifers is required, particularly in *Bos indicus* and *B. indicus*-influenced females. Therefore, the objective of this experiment was to investigate the relationship between RFI and age at PUB in *Bos taurus* and *B. indicus*-influenced

replacement beef heifers. We hypothesized that both *B. taurus* and *B. indicus*-influenced heifers with lower RFI would reach PUB later than those with greater RFI.

Materials and Methods

All heifers were handled in accordance with procedures approved by the University of Florida's Animal Care and Use Committee.

Animals and management

One hundred and seventy-nine *B. taurus* (Angus; $n = 98$) and *B. indicus*-influenced (Brangus and Braford; $n = 81$) replacement beef heifers housed at the North Florida Research and Education Center were enrolled in a retrospective cohort design over the course of 2 yr (2017: $n = 89$; 2018: $n = 90$). Heifers were weaned at 7 to 8 mo of age and backgrounded for 3 mo on a bahiagrass pasture (*Paspalum notatum*) with ad libitum access to bermudagrass hay (*Cynodon dactylon*). Following the backgrounding phase, heifers were placed in the University of Florida's Feed Efficiency Facility (FEF) in Marianna, FL. Each year, upon arrival to the FEF, heifers were fitted with electronic identification tags (Allflex USA Inc., Dallas-Fort Worth, TX), weighed over 2 consecutive days, and were randomly assigned to 1 of 8 pens (108 m²/pen; 10 to 13 heifers/pen), each equipped with 2 GrowSafe feed bunks (GrowSafe Systems Ltd., Alberta, Canada, 2011). A 14-d acclimation period to the diet and facilities preceded a 70-d feeding trial, where the daily feed intake was recorded for each heifer. Data were collected during the feeding trial to determine average daily gain (ADG), gain-to-feed ratio (G:F), and RFI. Retrospectively, heifers were sorted into low (< -0.5 SD from the mean; $n = 51$), medium (≥ -0.5 and $\leq +0.5$ SD from the mean; $n = 66$), and high ($> +0.5$ SD from the mean; $n = 62$) feed efficiency groups based on their RFI values. This approach resulted in 31 *B. taurus* heifers in the low group, 37 in the medium group, and 30 in the high group, and 20 *B. indicus*-influenced heifers in the low group, 29 in the medium group, and 32 in the high group. Weekly throughout the 70-d feeding trial, heifers were assigned a body condition score (BCS) from 1 to 9 (1 emaciated; 9 extremely obese; Wagner et al., 1988). In addition, unshrunk BW was collected weekly before daily feeding. Heifers had ad libitum access to water and a diet consisting of 22% corn gluten feed pellets, 22% soyhull pellets, 5% mineral supplement pellets (Furst-McNess Company, Freeport, IL), and 51% Fiber Pellets (commercial feed made from cotton burrs and peanut hulls, AFG Feed LLC, Donalsonville, GA), on a dry matter basis. Diet samples were collected every 2 wk from each feed bunk. All feed samples that were analyzed for nutritive values were dried at 55 °C for 72 h in a forced air oven. At the end of the drying period, all samples were ground in a Wiley mill (Arthur H. Thomas Company, Philadelphia, PA) using a 2.0 mm screen. After grinding, individual samples were composited within year for analysis on an equal weight basis. All nutritive value samples were analyzed by a commercial laboratory using a wet chemistry package (Dairy One Forage Laboratory, Ithaca, NY), and results are presented in Table 1. The observed NE for each diet was calculated from the performance data using the equation proposed by Zinn and Shen (1998) based on individual animal intake and ADG. Energy gain (EG) was calculated as $EG = (0.0557 \times BW^{0.75}) \times ADG^{1.097}$ (NRC, 1984), in which EG is daily energy deposited (Mcal/d) and BW is mean shrunk BW. The equation used to calculate maintenance energy expended (EM; Mcal/d) was $EM = 0.077 \times BW^{0.75}$ (Lofgreen and Garrett, 1968). From the calculated amounts of energy required

Table 1. Composition of diet fed to replacement heifers by year¹

Nutrient composition (dry matter basis)	2017	2018
Dry matter, %	94.9	92.1
Total digestible nutrients, %	65.0	69.0
Crude protein, %	13.7	14.3
Acid detergent fiber, %	40.9	36.6
Neutral detergent fiber, %	63.4	54.4
NE _m (Mcal/kg of DM) ²	1.35	1.23
NE _g (Mcal/kg of DM) ²	0.77	0.68

¹Analyzed by a commercial laboratory using a wet chemistry package (Dairy One, Ithaca, NY).

²NE_m = net energy for maintenance; NE_g = net energy for gain. Values calculated from performance and individual feed intake from days 0 to 70, based on the study Zinn and Shen (1998).

for maintenance and gain, the NE_m of each diet was obtained by the quadratic equation $NE_m = [-b \pm (b^2 - 4ac)^{1/2}] / 2a$, in which $a = -0.41 \times EM$, $b = 0.877 \times EM + 0.41 \times DMI + EG$, and $c = -0.877 \times DMI$ (Zinn and Shen, 1998). The NE_g of each diet was obtained by the equation $NE_g = 0.877 \times NE_m - 0.41$ (Zinn and Shen, 1998).

Heifers were estrus synchronized with 2 injections of prostaglandin F_{2α} (PGF_{2α}; Lutalyse; 25 mg dinoprost tromethamine; Zoetis Animal Health, Parsippany, NJ) administered 12 d apart, beginning 35 d into the feeding trial. Following the second injection of PGF_{2α}, estrus detection patches (Estroject, Rockway, Inc., Spring Valley, WI) were placed on the tail head of each heifer to assist with detection of estrus. Estrus detection was conducted twice daily for 45 min at 0600 and 1800 hours over a period of 23 d. Heifers were considered to be in estrus when at least 50% of the rub-off coating was removed from the estrus detection patch or when a heifer was determined to be in standing estrus. Heifers were artificially inseminated (AI) by an experienced technician 12 h after estrus was detected. After completion of the feeding trial period, heifers were weighed over 2 consecutive days and were removed from the FEF and placed on a bahiagrass pasture. Seven days after the final AI, natural service sires were introduced into the herd for 60 d.

Conception rates were determined 33 d after the last day of AI via transrectal ultrasonography utilizing an Ibex portable ultrasound equipped with a 5.0-MHz linear multi-frequency transducer (Ibex Pro, E.I. Medical Imaging, Loveland, CO). Final pregnancy rates were determined by transrectal ultrasonography 37 d after bulls were removed from the herd.

Blood sampling and PUB assessment

Blood samples were collected weekly for analysis of plasma concentration of progesterone starting from the first day that the heifers entered the FEF until 40 d after they had left. The collections were made via jugular venipuncture using 10 mL glass vials containing 143 IU units of sodium heparin (Vacutainer; Becton Dickinson, Franklin Lakes, NJ). All blood samples were immediately placed on ice after collection and were then centrifuged for 18 min at 4,000 × g and 4 °C. Following centrifugation, plasma was transferred into polypropylene vials and stored at -20 °C for further analyses. Concentrations of plasma progesterone were determined by a chemoluminescent assay (Immulite 2000 XPi Immunoassay System; Siemens Healthcare Diagnostics, Malvern, PA) as previously validated for bovine samples (Bedford et al., 2018).

The first increase in plasma progesterone concentration above or equal to 1 ng/mL was used to determine attainment of PUB. Age of PUB was defined as the age of the heifer at the

first rise in progesterone followed by a cyclic pattern of rises in progesterone concentrations suggestive of the establishment of normal estrous cycle (Reis et al., 2015). Heifers that had not attained PUB by the conclusion of the blood collection period were assigned a PUB coinciding with the final blood collection date.

Statistical analysis

All data were analyzed using the SAS statistical package (version 9.4; SAS/STAT, SAS Inst., Inc., Cary, NC). Heifer was considered the experimental unit in all analyses.

Residual feed intake was computed as the residual of the regression of dry matter intake (DMI), ADG, and metabolic BW (MBW), using the GLM procedure of SAS. The model was as follows:

$$Y_i = \beta_0 + \beta_1 MBW_i + \beta_2 ADG_i + e_i$$

where Y_i is the expected daily DMI of the i th animal, β_0 is the regression intercept, β_1 is the partial regression coefficient of DMI on MBW, β_2 is the partial regression coefficient of DMI on ADG, and e_i is the random error term for RFI. Since RFI is calculated as the observed DMI minus the predicted DMI, the more negative the RFI value (feed consumption was less than predicted), the more feed efficient the heifer is (Koch et al., 1963; Archer et al., 1997; Arthur et al., 2001a, 2001b).

The MIXED procedure of SAS was used to analyze the continuous response variables (ADG, BCS, BW, DMI, G:F, PUB, and RFI), whereas the GLIMMIX procedure of SAS was used to analyze binary response variables (estrus expression, conception rate, and final pregnancy rate). The models included the fixed effect of RFI group, breed, and the interaction; as well as the random effect of year. The PROC CORR procedure of SAS was used to detect correlations between ADG, DMI, G:F, PUB, and RFI among heifers. Survival analyses were performed using the LIFETEST procedure of SAS to establish the effect of breed and RFI group on attainment of PUB and on calving distribution. Survival analysis regressed the proportion of pubertal heifers on the day of PUB occurrence as well as the proportion of heifers that had calved on the day of the calving season. Survival curves were compared using the Wilcoxon test. Throughout the statistical analyses, significance was declared at $P \leq 0.05$, with $0.05 < P \leq 0.10$ considered a tendency. Least square means $\pm$ SEM are reported.

Results

Effects of heifer breed on recorded variables are presented in Table 2, whereas effects of RFI Group are described in Table 3. Heifer age at the beginning of the trial differed ($P = 0.05$) between breed types, where *B. indicus*-influenced heifers were older (365.13 ± 6.49 d) than *B. taurus* (359.50 ± 6.42 d) heifers (data not shown in Table 2). However, no differences ($P = 0.24$) in age were determined among low (360.20 ± 6.71 d), medium (361.04 ± 6.57 d), or high (365.71 ± 6.59 d) RFI heifers at the initiation of the experiment (data not shown in Table 3). No interaction ($P = 0.46$) was determined for initial age between breed and RFI group. Cyclicity at the start of the trial did not differ ($P = 0.56$) between *B. taurus* and *B. indicus*-influenced heifers (28.37 ± 8.98 vs. $24.55 \pm 9.24\%$, respectively). However, there was a tendency ($P = 0.09$) for cyclicity to differ by RFI group, where a greater percentage of low RFI heifers ($37.26 \pm 9.97\%$) tended to be cycling at the initiation of the trial than medium and high heifers (21.30 ± 9.49 and $20.83 \pm 9.56\%$, respectively).

Table 2. Fertility and performance data based on heifer breed (LSM $\pm$ SEM)

Item	Breed type ¹		P-value
	<i>B. taurus</i>	<i>B. indicus</i> -influenced	
Number of heifers	98	81	—
Fertility			
Age of PUB ² , d	393.40 $\pm$ 4.64	406.90 $\pm$ 5.07	0.03
Cyclicity ³ , %	75.85 $\pm$ 4.48	67.67 $\pm$ 5.00	0.23
Estrus expression ⁴ , %	69.77 $\pm$ 23.59	68.00 $\pm$ 23.67	0.77
Conception rate ⁵ , %	30.20 $\pm$ 5.89	38.25 $\pm$ 6.68	0.37
Final pregnancy rate ⁶ , %	81.26 $\pm$ 4.28	71.10 $\pm$ 4.75	0.11
Animal performance			
Initial BW, kg	354.41 $\pm$ 3.34	349.34 $\pm$ 3.73	0.31
Final BW, kg	438.98 $\pm$ 4.27	428.70 $\pm$ 4.67	0.07
Initial BCS	6.29 $\pm$ 0.40	6.27 $\pm$ 0.40	0.77
Final BCS	6.95 $\pm$ 0.55	6.95 $\pm$ 0.55	0.99
DMI, kg/d	13.57 $\pm$ 0.29	13.22 $\pm$ 0.30	0.02
ADG, kg	1.51 $\pm$ 0.07	1.42 $\pm$ 0.07	0.02
G:F	0.112 $\pm$ 0.008	0.109 $\pm$ 0.008	0.20
RFI, kg/d	-0.06 $\pm$ 0.06	-0.12 $\pm$ 0.07	0.53

¹*B. taurus*, Angus; *B. indicus*-influenced, Brangus and Braford heifers.²The age of the heifer when the first increase in plasma progesterone concentration above or equal to 1 ng/mL was determined.³Percentage of heifers cycling by the start of the breeding season.⁴Percentage of heifers that showed estrus after being estrus synchronized with 2 injections of prostaglandin $F_{2\alpha}$ administered 12 d apart.⁵Percentage of heifers pregnant 33 d following the last insemination, as determined by transrectal ultrasonography.⁶Total heifers pregnant 37 d following bull removal.**Table 3.** Fertility and performance data based on RFI heifer group (LSM $\pm$ SEM)

Item	RFI classification ¹			P-value
	Low	Medium	High	
No. of heifers	51	66	62	—
<i>B. taurus</i>	31	37	30	—
<i>B. indicus</i> -influenced	20	29	32	—
Fertility				
Age of PUB ² , d	385.96 $\pm$ 6.20 ^b	398.47 $\pm$ 5.47 ^a	416.03 $\pm$ 5.58 ^a	<0.01
Cyclicity ³ , %	81.05 $\pm$ 6.33 ^a	74.65 $\pm$ 5.47 ^{ab}	59.58 $\pm$ 5.61 ^b	0.03
Estrus expression ⁴ , %	65.73 $\pm$ 23.93	74.02 $\pm$ 23.76	66.93 $\pm$ 23.78	0.47
Conception rate ⁵ , %	29.29 $\pm$ 8.38	38.05 $\pm$ 7.25	35.35 $\pm$ 7.45	0.73
Final pregnancy rate ⁶ , %	83.33 $\pm$ 6.05	69.48 $\pm$ 5.20	75.73 $\pm$ 5.33	0.22
Animal performance				
Initial BW, kg	351.01 $\pm$ 4.72	351.78 $\pm$ 4.08	352.84 $\pm$ 4.18	0.96
Final BW, kg	434.52 $\pm$ 5.72	430.08 $\pm$ 5.04	436.94 $\pm$ 4.15	0.58
Initial BCS	6.29 $\pm$ 0.40	6.27 $\pm$ 0.40	6.28 $\pm$ 0.40	0.94
Final BCS	6.97 $\pm$ 0.55	6.95 $\pm$ 0.55	6.94 $\pm$ 0.55	0.91
DMI, kg/d	12.03 $\pm$ 0.31 ^c	13.39 $\pm$ 0.30 ^b	14.77 $\pm$ 0.30 ^a	<0.01
ADG, kg	1.49 $\pm$ 0.08	1.40 $\pm$ 0.08	1.49 $\pm$ 0.08	0.08
G:F	0.124 $\pm$ 0.008 ^a	0.105 $\pm$ 0.008 ^b	0.101 $\pm$ 0.008 ^b	<0.01
RFI, kg/d	-1.49 $\pm$ 0.09 ^c	0.00 $\pm$ 0.08 ^b	1.21 $\pm$ 0.08 ^a	<0.01

¹Heifers were sorted and placed into low (< -0.5 SD from the mean; $n = 51$), medium (≥ -0.5 and $\leq +0.5$ SD from the mean; $n = 66$), and high ($> +0.5$ SD from the mean; $n = 62$) feed efficiency groups based on their RFI values. ^{a-c}Rows with different superscripts differ ($P \leq 0.05$).²Age of the heifer when the first rise in progesterone was detected.³Percentage of heifers cycling by the start of the breeding season.⁴Percentage of heifers that showed estrus after being estrus synchronized with 2 injections of prostaglandin $F_{2\alpha}$ administered 12 d apart.⁵Percentage of heifers pregnant 33 d after final insemination, as determined by transrectal ultrasonography.⁶Total heifers pregnant 37 d following bull removal.

No differences in BW at the initiation of the feeding trial were observed between breed types ($P \geq 0.31$) or among RFI groups ($P \geq 0.96$). Furthermore, there was no interaction ($P = 0.34$) between breed and RFI group. Body weight at the end of the feeding trial tended ($P = 0.07$) to differ by breed, where *B. taurus* heifers tended

to have greater BW than *B. indicus*-influenced heifers. However, no differences in RFI group ($P = 0.58$) were determined and there was no interaction ($P = 0.63$) between breed and RFI group. No differences ($P \geq 0.77$) were determined for BCS between breed types or among RFI groups at either the beginning or end of the

feeding trial. In addition, no interaction ($P = 0.39$) was determined between breed and RFI group at either time point for heifer BCS.

DMI differed ($P = 0.02$) by breed where *B. taurus* heifers had greater DMI than *B. indicus*-influenced heifers. Furthermore, DMI differed by RFI group where high RFI heifers had greater ($P < 0.01$) DMI than both medium and low RFI heifers, and medium RFI heifers had greater ($P < 0.01$) DMI than low RFI heifers. There was no interaction ($P = 0.61$) between breed and RFI group on DMI.

ADG was greater ($P = 0.02$) in *B. taurus* heifers when compared with *B. indicus*-influenced heifers. Moreover, RFI groups tended ($P = 0.08$) to have different ADG where medium RFI heifers had reduced ADG compared with low and high RFI heifers. No interaction ($P = 0.61$) between breed and RFI group was determined.

G:F did not differ ($P = 0.20$) between breed types and no interaction ($P = 0.32$) between breed and RFI group was determined. However, G:F differed ($P < 0.01$) by RFI group where high RFI heifers had reduced ($P < 0.01$) G:F than low RFI heifers, and medium RFI heifers had reduced ($P < 0.01$) G:F than low RFI heifers. No difference ($P = 0.20$) in G:F was determined between high and medium RFI heifers. Furthermore, no interaction ($P = 0.32$) between breed and RFI group was determined for G:F.

No difference ($P = 0.53$) in RFI between breed types was determined; however, RFI was greater ($P < 0.01$) in high vs. medium and low RFI heifers, and was greater ($P < 0.01$) in medium vs. low RFI heifers. No interaction ($P = 0.69$) between breed and RFI group was determined.

Age of PUB differed ($P = 0.03$) by breed where *B. taurus* heifers had a reduced PUB compared with *B. indicus*-influenced heifers. In addition, a survival analysis indicated a tendency ($P = 0.08$) for a difference in PUB attainment between breed types, where *B. taurus* heifers tended to attain PUB earlier than *B. indicus*-influenced heifers (Figure 1). Among RFI groups, PUB differed ($P < 0.01$), where low and medium RFI heifers had a reduced ($P \leq 0.02$) PUB compared with high RFI heifers. No difference ($P = 0.11$) was determined between medium and low RFI heifers. Similarly, a survival analysis indicated a difference ($P < 0.01$) in attainment of PUB among RFI groups, where low RFI heifers had reduced ($P < 0.01$) PUB than high RFI heifers and low RFI heifers tended ($P = 0.07$) to have lower PUB than medium RFI heifers (Figure 2). However, no difference ($P = 0.73$) in PUB was determined between medium and high RFI heifers according to

Figure 1. Survival analysis representing the percentage of pubertal heifers during the 125 d blood collection period for *B. taurus* (Angus; $n = 98$) and *B. indicus*-influenced (Brangus and Braford; $n = 81$) heifers. A 14-d acclimation period to the diet and facilities preceded a 70-d feeding trial, where the daily feed intake was recorded for each heifer. Final blood samples were collected 40 d after the completion of the feeding trial. Survival analysis indicated a tendency ($P = 0.08$) for a difference in attainment of PUB between breed types, where *B. taurus* heifers tended to reach PUB earlier than *B. indicus*-influenced heifers.

the survival analysis. No interaction ($P = 0.43$) was determined between breed and RFI group on PUB.

The percentage of heifers cycling by the beginning of the breeding season did not differ ($P = 0.23$) between *B. taurus* and *B. indicus*-influenced heifers. However, cyclicity differed ($P = 0.03$) by group where a greater percentage of low RFI heifers were cycling by the start of the breeding season than high RFI heifers. In addition, there was a tendency ($P = 0.06$) for a greater cycling percentage in medium RFI heifers compared with high RFI heifers, yet no difference ($P = 0.45$) in cyclicity between low and medium RFI heifers was determined. There was no breed by RFI group interaction ($P = 0.29$).

No differences in estrus expression were determined between breed types ($P = 0.77$) or among RFI groups ($P = 0.47$). Furthermore, there was no interaction ($P = 0.39$) between breed type and RFI group on estrus expression. Conception rates to AI were also similar between breed types ($P = 0.37$) and among RFI groups ($P = 0.73$). No interaction ($P = 0.68$) was determined between breed and RFI group on conception rates. Final pregnancy rate did not differ between breed types ($P = 0.11$) or among RFI groups ($P = 0.22$). There was a tendency ($P = 0.08$) for an interaction between breed and RFI group; however, the least square mean differences were not significant. Calving distribution according to survival analyses did not differ between breed types ($P = 0.58$) or among RFI groups ($P = 0.62$).

Pearson correlation coefficients for feed efficiency traits and PUB are presented in Table 4.

Discussion

The goal of this experiment was to investigate the relationship between RFI, breed, and PUB in replacement beef heifers. We hypothesized that heifers with lower RFI would reach PUB later than those with greater RFI. After retrospective classification into low, medium, and high RFI groups, our results indicate that *B. taurus* and *B. indicus*-influenced low and medium RFI heifers reached PUB at a younger age than high RFI heifers and, therefore, contradict our hypothesis.

Figure 2. Survival analysis representing the percentage of pubertal heifers during the 125 d blood collection period for different RFI groups. A 14-d acclimation period to the diet and facilities preceded a 70-d feeding trial, where the daily feed intake was recorded for each heifer. Final blood samples were collected 40 d after the completion of the feeding trial. Retrospectively, heifers were classified as low (< -0.5 SD from the mean; $n = 51$), medium (≥ -0.5 and $\leq +0.5$ SD from the mean; $n = 66$), or high ($> +0.5$ SD from the mean; $n = 62$) feed efficiency groups based on their RFI values. Survival analysis indicated a difference ($P < 0.01$) in attainment of PUB among RFI groups, where low RFI heifers had reduced ($P < 0.01$) PUB than high RFI heifers and low RFI heifers tended ($P = 0.07$) to have lower PUB than medium RFI heifers.

Table 4. Pearson correlation coefficients (top value) and P-value (bottom value) among feed efficiency traits and age of PUB in replacement beef heifers (n = 179)

Item	PUB, d	RFI, kg	ADG, kg	G:F	DMI, kg/d
PUB, d	1	0.216 0.004	0.038 0.612	-0.086 0.251	0.182 0.015
RFI, kg		1	-0.005 0.943	-0.531 <0.001	0.833 <0.001
ADG, kg			1	0.794 <0.001	0.257 <0.001
G:F				1	-0.365 <0.001
DMI, kg/d					1

In the past, utilizing feed conversion ratio, evaluated as feed to gain ratio, was the preferred method of determining feed efficient cattle; however, this measure of feed efficiency does not take into account differences in maintenance requirements and can be influenced by differences in growth and mature size (Archer et al., 1999). As a result, it is possible that larger cattle with greater rates of growth may be selected for, resulting in an increase in mature cow size, which may negatively influence cow productivity (Hill and Ahola, 2012). Residual feed intake as a measure of feed efficiency is able to account for maintenance requirements and is phenotypically independent of BW, growth, and mature size. Therefore, it is unsurprising that no differences in initial or final BW or BCS were determined among RFI groups in the present experiment. Phenotypic independence between RFI and BW has been reported in beef heifers (Kelly et al., 2010; Black et al., 2013), and others have observed a similar range in RFI values as observed in the present experiment (Kelly et al., 2010; Shaffer et al., 2011). Research has indicated that genetic variation for RFI exists in *B. taurus* and *B. indicus* cattle, where feed efficiency tends to improve with increasing percentage of *B. indicus* influence (Elzo et al., 2009). Nevertheless, no differences were determined for RFI between *B. taurus*- and *B. indicus*-influenced heifers in the current experiment. In addition, no breed by RFI group interactions was determined, indicating that the effects of feed efficiency were independent of breed.

Positive phenotypic correlations between RFI and DMI have been reported, indicating that selection for a more favorable RFI phenotype could result in a reduction in feed intake (Arthur et al., 2001b; Hoque et al., 2005; Hafla et al., 2013). Systematic reductions in DMI in more feed efficient RFI groups have previously been described and indicate that feed intake in more feed efficient animals is reduced without hampering animal performance (Elzo et al., 2009; Shaffer et al., 2011; Black et al., 2013). In the present experiment, similar reductions in DMI were determined among RFI groups as well as a strong positive correlation between RFI and DMI, confirming that feed intake was reduced in more feed efficient heifers. Maintenance requirements for energy have been reported to differ between breed types (Frisch and Vercoe, 1977; Sainz et al., 2013), where crossbred cattle consisting of both *B. indicus* and *B. taurus* genetics had ~5% lesser energy requirements when compared with *B. taurus* (Frisch and Vercoe, 1977). In addition, daily feed intake has been reported to decrease as the fraction of *B. indicus* genetics increases (Elzo et al., 2009). In the current experiment, DMI was greater in *B. taurus* heifers. However, because those heifers tended to have greater final BW, it is unsurprising that RFI did not differ by breed.

As previously mentioned, RFI is genetically independent of growth and body size in heifers (Arthur et al., 2001b); therefore, it was foreseeable that no differences in ADG among RFI groups and no correlation between RFI and ADG would be determined in the present experiment. Nevertheless, *B. taurus* heifers had greater ADG during the feed efficiency test than *B. indicus*-influenced heifers, as previously reported by others (Brown et al., 1993; Cundiff, 2005).

Feed conversion ratio has been reported to differ by breed composition, where calves with greater *B. indicus* influence had a greater feed conversion ratio than *B. taurus* calves (Elzo et al., 2009). However, an experiment using mainly crossbred animals obtained by crossing bulls of different breeds to *B. indicus* females, indicated that breed differences in feed conversion ratio were not significant (Schutt et al., 2009). Similarly, in the present experiment, no differences in G:F were determined between breed types; yet, heifers with lower RFI had a greater G:F, and a moderately negative correlation between RFI and G:F was determined. Strong positive correlations between G:F and ADG have been reported, which are consistent with the results of the present experiment (Arthur et al., 2001b; Schenkel et al., 2004; Kelly et al., 2010).

PUB attainment in heifers involves both physical and behavioral changes and requires activation of the hypothalamic-pituitary-ovarian axis, which leads to an increase in the frequency of gonadotropin-releasing hormone pulsatility, thereby stimulating sexual maturation and reproductive behavior (Cardoso et al., 2018). Accelerated rates of BW gain during early heifer development can mediate the nutritional programming of PUB, and reports indicate that there is a degree of fatness, or a certain body composition that must be achieved before PUB can be attained in replacement heifers (Nelsen et al., 1982; Gasser et al., 2006; Amstalden et al., 2014). Beef heifers that attained PUB by the start of breeding had greater feed intake and G:F during postweaning development and had greater loin muscle area and fat thickness than nonpubertal heifers (Roberts et al., 2017). However, body composition has also been reported to differ between more feed efficient and less feed efficient animals, where low RFI heifers possessed less loin muscle area per 100 kg of BW than high RFI heifers (Shaffer et al., 2011), and backfat tended to be greater in heifers with positive RFI values than negative RFI values (Basarab et al., 2011). Previous research has also reported a trend for low RFI steers to have less dissectible carcass fat and intermuscular fat, and significantly less body cavity fat in the rump and loin than medium and high RFI steers (Basarab et al., 2003). This leanness associated with low RFI values is thought to negatively affect

PUB, where negative correlations for BCS (-0.34) and backfat thickness (-0.58) compared with PUB have been reported in crossbred beef heifers (Pereira et al., 2017). Nevertheless, in the current experiment, low and medium RFI heifers reached PUB sooner than high RFI heifers. These results are in contrast with those previously reported in beef heifers in which a tendency for a negative linear relationship between PUB and RFI was reported (Shaffer et al., 2011), and where PUB was delayed in heifers with negative RFI values when adjusted for backfat thickness (Basarab et al., 2011). Heifer age at the beginning of the present experiment did not differ among RFI groups, providing support that the difference observed in PUB was not related to age, but instead was associated with heifer RFI classification. In addition, although ~26% of heifers were already cycling by the initiation of the trial, and a greater percentage of low RFI heifers tended to be cycling than medium and high RFI heifers, it is clear that differences existed in PUB among RFI groups. These differences are supported by the survival analysis, which demonstrates a change in the percentage of animals reaching PUB over time where low RFI heifers achieved PUB sooner than high RFI heifers. *B. taurus* heifers in the current experiment had reduced PUB, even though they were younger at the beginning of the trial, which is unsurprising as *B. indicus*-influenced breeds are known to reach PUB later than *B. taurus* breeds (Randel, 2005).

The mechanism responsible for the reduced PUB in Low RFI heifers is unclear; however, heifers in this experiment were on average ≥ 6 BCS and had greater ADG (1.46 ± 0.26 kg) when compared with those in studies reporting a negative relationship between RFI and PUB (Basarab et al., 2011; Shaffer et al., 2011; mean ADG 0.90 and 1.14 kg, respectively). Measurements of bodyfat were not collected in this experiment; however, utilizing BCS as an indirect, subjective estimation of bodyfat deposition, bodyfat did not appear to differ among RFI groups and was relatively high overall (mean initial BCS: 6.28 ± 0.55 ; mean final BCS: 6.94 ± 0.65). Therefore, it is likely that leanness or lack of adiposity was not a limitation to attainment of PUB and heifers from all RFI groups had an equal opportunity to become pubertal. Nevertheless, further research is required to determine the mechanism of reduced PUB in Low RFI heifers under dietary conditions supporting high ADG.

Although PUB differed among RFI groups, no differences in conception rates were determined, which corroborates other reports that RFI group has no effect on pregnancy rates in beef females (Basarab et al., 2007; Shaffer et al., 2011; Callum et al., 2019). Genetic correlations between growth and fertility have been reported, where better fertility was correlated with greater feed intake and faster growing cattle; however, no genetic correlation was determined between RFI and pregnancy rate (Mu et al., 2016). It is important to emphasize that this experiment was not designed to conclusively determine differences in fertility between breed types or RFI groups, as heifer numbers were low for an analysis of binary response variables. Therefore, it is necessary to increase the number of animals in future research in order to reduce the potential for a type II statistical error.

In conclusion, results from this experiment indicate that more feed efficient heifers attained PUB at a younger age compared with less feed efficient heifers, regardless of breed. These results indicate the potential for an increase in lifetime productivity through selection of feed efficient heifers, as lifetime productivity is heavily dependent on a heifer's ability to reach reproductive competence, to conceive earlier during the breeding season, and to calve earlier in their first calving season (Lesmeister et al., 1973; Cushman et al., 2013). However, these

results should be interpreted with caution as they conflict with previous research indicating a negative relationship between RFI and PUB and where lower rates of gain were reported (Basarab et al., 2011; Shaffer et al., 2011). Therefore, additional research is required for corroboration of the results presented herein. If more feed efficient heifers are proven to reach PUB at a younger age under certain dietary conditions, then there may be potential to select females for feed efficiency while maintaining overall fertility.

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Conflict of interest statement

The authors declare no real or perceived conflicts of interest.

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