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Energy efficiency of grazing Hereford heifers classified by paternal residual feed intake

María F. Marín,[†,1] Hugo Naya,[†] Ana C. Espasandin,[†] Elly Navajas,[‡] Thais Devincenzi,[||] and Mariana Carriquiry[†]

[†]Departamento de Producción Animal y Pasturas, Facultad de Agronomía, Universidad de la República, Montevideo 12900, Uruguay
[‡]Instituto Nacional de Investigación Agropecuaria (INIA), Estación Experimental INIA Las Brujas, Canelones 90100, Uruguay
[||]Instituto Nacional de Investigación Agropecuaria (INIA), Estación Experimental INIA Tacuarembó, Tacuarembó 45000, Uruguay
[1]Corresponding author: mfedericamarin@gmail.com

Abstract

Residual feed intake (RFI) has become a widely spread index of feed efficiency. Although most of beef cattle systems in the world are pasture based, RFI evaluation and research is usually performed in confinement conditions. In this context, residual heat production (RHP) estimated as the difference between actual and expected heat production (HP), could allow to identify efficient animals. Thus, the aim of this work was to evaluate the relationship between paternal estimated breeding values (EBV) for RFI and beef heifer efficiency, measured as RHP, as well as its association with heifers' productive and reproductive performance on grazing conditions. Seventy-one 25 ± 0.8-mo-old and seventy-four 24 ± 0.7-mo-old Hereford heifers were managed as contemporary groups in spring 2019 and 2020, respectively. Heifers were sired by 10 RFI-evaluated bulls and classified into three groups according to the paternal EBV for RFI: five bulls of low RFI (high efficiency, pHE), two bulls of medium RFI (medium efficiency), and three bulls of high RFI (low efficiency, pLE). The experimental period lasted 70 d prior to their first insemination where HP was determined by the heart rate-O_2 pulse technique. In addition, reproductive performances during the first and second breeding and calving seasons were recorded. Heifers' RHPs expressed as MJ/d and kJ/kg of body weight $(BW)^{0.75}$/d were positively correlated with paternal RFI EBVs ($P < 0.05$; $r > 0.60$). Moreover, BW and average daily gain (ADG) were greater ($P < 0.01$) for pHE than pLE heifers while expressed as units of $BW^{0.75}$/d, neither total HP nor metabolizable energy (ME) intake differed between groups, but pHE heifers had greater retained energy (RE; $P < 0.01$) and lower RHP ($P < 0.05$) than pLE ones. Gross energy efficiency (RE/ME intake) was greater ($P < 0.001$) for pHE than pLE heifers while the HP/ADG and RHP/ADG were reduced ($P < 0.05$) and feed-to-gain ratio (ADG/DM intake) tended to be greater ($P = 0.07$) for pHE than pLE heifers. In addition, during the first breeding and calving seasons, small but significant ($P < 0.01$) differences in reproductive responses between groups suggested an earlier pregnancy in pHE heifers than the pLE group, differences that disappeared during the second breeding and calving seasons. Thus, heifers sired by high-efficiency bulls measured as RFI were more efficient measured as RHP in grazing conditions, without significant differences in reproductive performance.

Lay Summary

In the last decades, animal efficiency has increasingly gained worldwide attention and the development of automated feeding systems has allowed significant advances in feeding efficiency, being residual feed intake (RFI) a widely used index to quantify it. Nonetheless, although most of beef cattle systems in the world are pasture based, RFI evaluation and research is usually performed in confinement conditions with little published information related to RFI for grazing beef cattle. In this context, residual heat production (RHP) appears as an alternative index to identify efficient animals without the need of determining feed intake, thus, allowing to measure animals in grazing conditions. In this study, we found that there is an association between paternal expected breeding value for RFI and its progeny RHP, and we proved that the RFI measured in confinement could be useful for breeding efficient heifers in grazing conditions without permanent impacts on reproductive performance.

Key words: beef cattle, rangelands, reproduction, residual heat production

Introduction

Feed and energy efficiency have been topics of extensive research in recent years as feed costs can account for up to 75% of total production cost in beef cattle systems (Nielsen et al., 2013). Moreover, most of feed consumed in cow-calf systems is associated with the supply of energy required for animal maintenance which represents 70% to 75% of the total annual energy requirements of the breeding cow (Ferrell and Jenkins, 1985). Over the last decade, residual feed intake (RFI) defined as the difference between actual feed intake and expected feed requirements for maintenance and body weight (BW) gain, has become a widely spread index of feed efficiency (Berry, 2009; Moore et al., 2009). Genetic parameter estimates indicate that RFI is moderately heritable; a review by Berry and Crowley (2013) reported that RFI heritability varied between 0.07 and 0.62 with a mean of 0.33 ± 0.013, based on an extensive number of studies with growing animals. Moreover, a single generation of selection in favor of negative postweaning RFI values improved efficiency of young bulls and heifers (Herd et al., 1997) and feedlot steers (Richardson et al., 1998).

Although most of beef cattle production is pasture based, RFI is measured in confinement conditions with little published information related to RFI for grazing beef cattle,

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due to the difficulties of obtaining accurate individual records on feed intake. Wiley et al. (2016), working with bulls classified by RFI in confinement, reported that 47% ± 13% of animals maintained their ranking in grazing conditions and Trujillo et al. (2013) reported a moderate correlation (r = 0.50) between heifers' RFI measured consecutively in confinement and grazing conditions while Manafiazar et al. (2015) reported a lower correlation (r = 0.30) between RFI measured as growing heifers under dry-lot conditions and as pregnant cows in grazing conditions. In addition, although in confinement conditions RFI has been positively correlated with dry matter (DM) intake, with low-RFI (more efficient) animals consuming less DM (Cantalapiedra-Hijar et al., 2018), herbage DM intake of previously ranked low or high-RFI heifers or steers has not differed when evaluated under grazing conditions (Herd et al., 1998, 2002; Meyer et al., 2008; Lawrence et al., 2012; Oliveira et al., 2016). In contrast, other studies reported decreased herbage DM intake for low-ranked RFI heifers when evaluated consecutively (Trujillo et al., 2013) or as pregnant cows (Knight et al., 2015) at pasture. The scarce and contrasting results of RFI in grazing conditions are probably associated with the great difficulty of obtaining accurate measurements of DM intake in grazing animals (Lawrence et al., 2012)., as well as the characteristics of the grazing process (Lahart et al., 2020) which would also explain the variation detected between studies.

The heart rate-O_2 pulse method (Brosh, 2007) could be of use to measure energy expenditure of free-range animals, thus, it could be used as an alternative to identify efficient animals in grazing conditions without the need to determine DM intake, as most of the metabolizable energy (ME) consumed is lost as heat. Thus, residual heat production (RHP) estimated as the difference between actual heat production (HP) and the one expected based on the animals' BW and level of production, could allow identification of efficient individuals: animals with lower RHP would be energetically more efficient since they would produce less heat than expected. Few studies have measured or estimated total HP in RFI-ranked animals and reported decreased HP, when expressed as a unit of $BW^{0.75}$, for low-RFI animals (Richardson et al., 2001; Basarab et al., 2003; Nkrumah et al., 2006; Chaves et al., 2015; Asher et al., 2018; Menezes et al., 2020). However, of the latter studies only two studies investigated RHP and its association with RFI (Richardson et al., 2001; Asher et al., 2018); Richardson et al. (2001) reported that the progeny of high-RFI bulls had higher RHP per unit of gain in protein than the progeny of low-RFI bulls, whereas Asher et al. (2018) found a positive association between individual RFI and RHP on young bulls fed a high-quality diet, although this relationship was not evident when animals were calves.

In this context, we hypothesized that there is an association between paternal RFI measured in confinement conditions and RHP measured in its progeny in grazing conditions in the growing stages, with daughters of more efficient bulls retaining more energy in body tissue at similar energy intakes with minimal impact on reproductive performance. The objective of this work was to evaluate the relationship between paternal estimated breeding values (EBV) for RFI and beef heifer efficiency, measured as RHP, as well as the association with heifers' productive and reproductive performance on grazing conditions.

Materials and Methods

The experiment was conducted during the springs of 2019 and 2020 at the Experimental Station of the Instituto Nacional de Investigación Agropecuaria, "Glencoe" (INIA; Paysandú, Uruguay; latitude: S 32º 00m 21s, longitude: W 57º 08m 01s). All experimental procedures were previously approved by INIA's Commission on Ethics in the Use of Experimental Animals (CNEA; 0009/11) and by the Animal Experimentation Committee of Universidad de la República (CHEA; 020300-001143-19). Temperature and relative humidity were recorded daily by a meteorological station located on the experimental site. During the first year of the measurement protocol (2019) the average daily temperature and relative humidity were 16.1 °C and 77%, respectively. Whereas, in the second year (2020) the average daily temperature and relative humidity were 16.8 °C and 71%, respectively.

Animals, experimental design, and measurement protocol

Seventy-one 25 ± 0.8-month-old and seventy-four 24 ± 0.7-month-old Hereford heifers were managed as contemporary groups in spring 2019 and 2020, respectively. At the beginning of the experimental periods, heifers weighed on average 262 ± 27 kg in 2019 and 272 ± 23 kg in 2020, with a mode of body condition score (BCS; range 1 to 8) of four in both years. Heifers were sired by 10 RFI-evaluated bulls and classified into three groups according to the paternal EBV for RFI (Ravagnolo et al., 2018; https://www.geneticabovina.com.uy): five bulls classified as low RFI (high efficiency, pHE; RFI EBV percentile ≤ 20; 62 heifers evaluated, n = 13 ± 5 heifers/bull), two bulls classified as medium RFI (medium efficiency; 25 heifers evaluated, RFI EBV percentiles between 30 and 60; n = 13 ± 4 heifers/bull), and three bulls classified as high RFI (low efficiency, pLE; RFI EBV percentiles ≥ 80; 58 heifers evaluated, n = 19 ± 7 heifers/bull). The sires were randomly assigned to dams within age group (3.8 ± 2.0 yr of age on average) and dams were either artificially inseminated or naturally bred. This is based on a sire model where the only effect evaluated is the paternal one, where it is considered that by randomizing the dams, their effects cancel each other. Heifer paternity was checked using a DNA paternity test. Since they were born, heifers were managed as contemporary groups on grazing conditions (*Campos* grasslands; Allen et al., 2011) without supplementation and were weaned at 201 ± 33 d and 182 ± 40 kg without differences in BW corrected by age between groups. There were no differences in birth weight between groups.

In both years, the experimental period lasted 70 d prior to the first insemination when heifers grazed with an herbage mass of 2,746 ± 1,275 kg DM/ha; 10 ± 3 kg DM/kg BW of herbage allowance and 8 ± 3 cm of height, and a chemical composition of 86.5% ± 1.7% organic matter, 7.73% ± 0.15% crude protein, 70.72% ± 0.26% neutral detergent fiber, 43.79% ± 4.07% acid detergent fiber, and 7.93 ± 0.19 MJ/kg DM of ME. Herbage mass and height were recorded monthly by the comparative yield method (Haydock and Shaw, 1975) using 10 reference quadrants (0.25 m^2) corresponding to a 5-point calibration scale and 100 randomly selected quadrants for paddock sampling. Herbage samples of the 5-point scales were dried at 60 °C and 1-mm ground to be composited according to the frequency of the scale point. Herbage pooled samples were analyzed for DM, crude protein, neutral detergent fiber, and acid detergent fiber and ash (Van Soest et al., 1991; AOAC, 2005).

During the experimental period, individual HP was assessed three times: at the first third, during the mid-portion, and at the last third of the experimental period, and the three measures were averaged for statistical analysis. Heifers were weighed (scale ID3000; True Test, Auckland, New Zealand) weekly after 12 h-fasting and BCS (scale 1 to 8; 1 = excessively thin and 8 = excessively fat; Vizcarra et al., 1986) was determined every 14-d by the same trained operator. At the end of the experimental period (25.5 ± 0.9 mo of age), heifers had their estrous cycles synchronized with two doses of 2 mL of prostaglandin (Glandinex, Laboratorio Universal Lab Ltda., Montevideo, Uruguay) 10 d apart and were monitored for estrous by visual observation twice a day by two trained observers during 5 d after the last prostaglandin injection. All heifers showing estrus were artificially inseminated by two inseminators and thereafter, heifers were exposed to bulls 27 d after the first prostaglandin injection for a mating period that lasted 60 d. In addition, to determine if there were any lasting effects of feed efficiency on reproduction, we evaluated heifers' performance during the second mating period (37.5 ± 0.9 mo of age), as primiparous cows which were exposed to bulls at 73 ± 18 d of calving for 60 d.

HP measurements

HP was determined by HR-O_2P technique (Brosh, 2007), as described by Talmón et al. (2020). This technique has been validated to estimate HP and ME intake for different ruminant species, diets, and environmental conditions (Brosh, 2007), and has shown to have a great potential to estimate the HP on free-ranging animals (Oss et al., 2016); as when evaluated against respiration chamber HP estimations it has been demonstrated that it can accurately estimate HP by continuously measuring HR and using a single O_2P value per cow measured when cows are in a standing or idling position (Talmón et al., 2023). The technique is based on the measurement of O_2 consumption (VO_2) as a means to indirectly establish HP assuming 20.47 kJ/L O_2 consumed (Nicol and Young, 1990). The VO_2 of each animal is estimated through its HR and the O_2 consumed per heartbeat (O_2P) and it is calculated as VO_2 = HR × O_2P. The HR was recorded at 5 s intervals using Polar devices (Polar Electro Oy, Kempele, Finland), with a model H10 HR transmitter and a RCX3 data logger watch model for 4 to 5 continuous d. As O_2P is the ratio between HR and O_2, short-term (10 min) measures of both variables were conducted simultaneously. Oxygen consumption was measured using a face mask open-circuit respiratory system (Fedak et al., 1981), and a paramagnetic O_2 analyzer model Servopro 1,440 (Servomex, Crowborough, East Sussex, UK) to determine O_2 concentration. To determine VO_2 under standard conditions, relative humidity and temperature within the system were recorded by HygroClip S electronic sensor (Rotronic AG, Basserdorf, Switzerland), additionally, the air flux into the system was calculated by differential pressure measurement with a differential pressure transducer (Model 267; Setra; Boxborough; USA). The accuracy of the system was checked gravimetrically by N_2 injection (N_2 recovery) into the facemask (McLean and Tobin, 1990). The N_2 recovery was 97 ± 3 and 99 ± 5 for 2019 and 2020, respectively. HP was calculated as specific HP (kJ/BW $^{0.75}$/d) = HR (beats/min) × O_2P (mL O_2/kg BW $^{0.75}$/beat) × 20.47 (kJ/mL O_2) × 60 min/h × 24 h/d and daily HP (MJ/animal/d) = specific HP (kJ/BW $^{0.75}$/d) × BW $^{0.75}$/1000.

Reproductive traits

Ovarian activity or pregnancy were determined by transrectal ultrasonographic examinations, using a real-time, Agroscan ALR 575 scanner with a 5/7.5 MHz—60 mm transducer (ECM, Noveko International Inc., QC, Canada) before the AI synchronization protocol to record presence of corpus luteum (CL) and maximum follicle diameter, at day 30 after AI to record presence of CL or pregnancy (presence of an amniotic vesicle with an embryo with the heartbeat) and at 45 d after bull removal to determine total pregnancy and fetal age. Cows with follicles > 8 mm in without CL were considered in superficial anestrus and those with follicles ≤ 8 mm in diameter without CL were considered in deep anestrus according to Griffin and Ginther (1992) criteria (Clariget et al., 2016). The first service to conception interval was calculated as date of first conception minus date of service. Calving day was calculated using the date of calving of the first heifer of the season as reference (day 1). Calving to conception interval was determined using the fetal age determined by ultrasound at the end heifers' second breeding season minus date of first calving.

Calculations and statistical analysis

A linear regression of BW on the day of study was fitted to each heifers' records to estimate changes in BW throughout the experimental period, this resulting in each heifer having a model ($P < 0.05$, $r^2 > 0.9$) that represented the BW evolution during the measurements. Average daily gain (ADG) was estimated as the slope of each regression. Predicted HP was calculated as the slope and intercept of a multiple linear regression of daily HP dependency on heifers' mid-period $BW^{0.75}$ and ADG, using individual ADG as a proxy to individually retained energy (RE; Asher et al., 2018) and the residuals from this multiple linear regression were used to determine RHP (observed minus expected HP). RE was estimated using the empty BW (EBW) and EBW gain (EBG) as: RE (MJ/d) = 0.266 × EBW $^{0.75}$ × EBG $^{1.097}$ according to NASEM (2016) where EBW = 0.891 × 0.96BW and EBG = 0.956 × ADG. ME intake was calculated as the sum of HP + RE and DM intake was estimated based on ME intake and herbage ME concentration (MJ/kgDM). Herbage ME concentration was estimated based on DM in vitro digestibility (DMIVD) of the forage as: DMIVD = 88.9 − (%ADF × 0.779; NASEM, 2016).

Heart rate and O_2P data were processed using R software to assess the quality of data (R Core Team, 2021, Viena, Austria) and later analyzed using SAS software (SAS University Edition, SAS Institute Inc., Cary, NC, USA). Pearson correlation and regression coefficients were estimated between heifers' RHP and paternal RFI EBV, as well as between paternal RFI EBV and productive and energy efficiency traits. Initially, it was tested if EBV for weaning weight and weight at 18 months had any effect in ADG or RE, but no significant effect was found, thus it was not included in the models.

In addition, productive, reproductive, and efficiency variables by paternal efficiency group (pHE vs. pLE groups) were estimated; heifers in the medium RFI efficiency group were not considered in this analysis due to the smaller number of animals when compared with the other two groups. Productive and efficiency variables were analyzed with a mixed model using repeated measurements by the

Table 1. Body weight and average daily gain, and energy partitioning and efficiency of heifers sired by high and low residual feed intake EBV bulls (pHE vs. pLE)

	Paternal residual feed intake group			
	pHE	pLE	SEM	*P*-value
Paternal RFI, kg DMI/d	−0.23	0.29	0.02	<0.01
Number of heifers	62	58	—	—
Initial body weight, kg	279	259	4	<0.01
Final body weight, kg	329	305	4	<0.01
Average daily gain (ADG), g/d	738	673	21	<0.01
Heart rate, beat/min	82	85	1	0.01
O_2 pulse, mL O_2/BW$^{0.75}$/beat	0.282	0.274	0.008	0.06
Energy partitioning, MJ/d				
Metabolizable energy intake (MEI)	61.6	58.3	1.0	<0.01
Retained energy (RE)	13.4	11.6	0.5	<0.01
Heat production (HP)	48.4	46.8	0.8	0.04
Residual heat production (RHP)	−0.95	0.51	0.73	0.05
Energy partitioning, kJ/kg BW$^{0.75}$/d				
Metabolizable energy intake (MEI)	868	862	13	0.67
Retained energy (RE)	191	172	6	<0.01
Heat production (HP)	678	693	10	0.15
Residual heat production (RHP)	−14	7	11	0.04
DM intake (DMI), kg/d	7.16	6.78	0.12	<0.01
DM intake (DMI), g/BW$^{0.75}$/d	109.3	108.6	1.6	0.67
Energy and feed efficiency				
RE/MEI	220	199	6	<0.01
Gain to feed ratio (ADG/DMI)	95	92	2	0.07
HP/ADG	65	70	2	0.03
RHP/ADG	−26	8	15	0.03

MIXED procedure where the model included paternal RFI EBV group and year as fixed effects and heifer within sire as random effect.

Reproductive traits were analyzed using the GLIMMIX procedure using binomial or Poisson distributions depending on the distribution of the variable. Heifers that were not inseminated, sold, died, or remained non-pregnant were censored on the respective dates during the analyses. Results are presented as least square means ± pooled standard errors and least square means were considered to differ when $P \le 0.05$, and trends were identified when $0.05 < P < 0.10$.

Results

Associations between paternal EBV for RFI and heifer RHP

Heifers' RHP, both expressed as MJ/d and kJ/kg of BW$^{0.75}$/d, were positively correlated with paternal EBV for RFI ($P = 0.03$ and $r = 0.64$; $P = 0.04$ and $r = 0.63$, respectively). Neither heifer total HP (MJ/d; $P = 0.62$) or ADG (as g/d or g/kgBW$^{0.75}$/d; $P = 0.11$ and $P = 0.69$, respectively) nor estimated ME intake (as MJ/d or kJ/kgBW$^{0.75}$/d; $P = 0.11$ and $P = 0.30$, respectively) or DM intake (as kg/d or g/BW$^{0.75}$/d; $P = 0.11$ and $P = 0.29$, respectively) were correlated with paternal EBV for RFI. However, when expressed as unit of kg/BW$^{0.75}$, HP showed a positive correlation with paternal EBV for RFI ($r = 0.77$; $P = 0.02$).

Heifer BW and gain, energy partitioning, and efficiency for high- and low paternal RFI groups

BW and ADG were greater ($P < 0.01$) for pHE than pLE heifers, while BCS mode was similar between groups (Table 1). Average HR was lower ($P = 0.01$) while O_2P tended to be greater ($P = 0.06$) for pHE than pLE heifers (Table 1). Although HR varied along the day (data not shown), individual average HR did not vary across evaluated periods, with an average coefficient of variation of individual records of 2.6% in 2019 and 3.3% in 2020. Similarly, average coefficient of variation of the difference between the two measures of individual O_2P was 5.0% in 2019 and 5.2% in 2020, while Pearson correlation coefficients between the two individual O_2P measures were 0.61 and 0.59 in 2019 and 2020, respectively.

Total HP ($P = 0.04$), RE ($P < 0.01$), and ME intake (MJ/d; $P < 0.01$) were greater in pHE than pLE heifers while RHP was lower ($P = 0.05$) in pHE than pLE group (Table 1). However, when expressed as units of BW$^{0.75}$/d, total HP ($P = 0.16$) and ME intake ($P = 0.68$) did not differ between groups, but pHE heifers had higher RE ($P < 0.01$) and lower RHP ($P = 0.04$) than pLE ones. Estimated DM intake (kg/d) was greater ($P < 0.01$) for pHE than pLE heifers but no differences between groups were found in DM intake when expressed as percentage of BW$^{0.75}$ (Table 1).

Heifers in the pHE group had higher gross energy efficiency (RE/ME intake) than those in the pLE group ($P < 0.01$), while the ratios HP/ADG and RHP/ADG were lower ($P = 0.03$)

and the gain to feed ratio (G:F; ADG/DM intake) tended to be greater ($P = 0.07$) in the pHE group than pLE heifers (Table 1).

Heifer reproductive responses for high and low paternal RFI groups

There were more inseminated heifers from the pHE than pLE group ($P < 0.01$). There were no differences between groups either in the percentage of cycling heifers before the first service ($P = 0.16$) or in the percentage of cows in superficial or deep anestrous ($P = 0.72$), but maximum follicle diameter was larger ($P = 0.04$) for pHE than pLE heifers (Table 2). Percentage of anestrous cows at day 30 of the first breeding season was lower ($P < 0.04$) for pHE than pLE heifers but no differences were detected between groups for total pregnancy percentage ($P = 0.58$) or service to conception interval ($P = 0.51$). The pHE heifers calved earlier ($P = 0.05$) in the season than pLE heifers (Table 2). No differences ($P = 0.53$) were observed in the percentage of cows leaving the breeding herd after the first season (5 vs. 10%, 3/62 vs. 6/58 for pHE vs. pLE, respectively). During the second breeding and calving seasons, neither pregnancy ($P = 0.59$), cycling ($P = 0.36$), nor anestrous percentages ($P = 0.57$) at day 30 of breeding season nor total pregnancy percentage ($P = 0.58$) or first calving-conception interval differed ($P > 0.61$) between paternal RFI groups.

Discussion

Our results demonstrated that heifers´ RHP measured in grazing conditions was positively correlated to paternal EBV for RFI, being feed and energy efficiency greater for pHE than pLE heifers as they had greater BW, ADG, and RE without differences neither in total HP, nor in estimated DM or ME intake by unit of $BW^{0.75}$. In addition, we did not observe any major effect of paternal RFI EBV on reproductive performance during the two first breeding and calving seasons. Thus, selection by RFI measured in confinement conditions could be an effective selection criterion for improving animal efficiency in grazing conditions.

Indeed, it has been reported that feed efficiency measured as RFI is moderately heritable ($h^2 = 0.33 \pm 0.013$; Berry and Crowley 2013) and improved feed efficiency implies reductions of 3.8% to 5% of feedlot DM intake in the progeny of low vs. high-RFI bulls (Herd et al., 1997; Richardson et al., 1998). Although genotype-by-environment interactions for RFI in growing beef cattle have been reported (Kenny et al., 2018), we showed that a single-generation selection for RFI improves efficiency of grazing heifers, measured as RHP. Moreover, using the variance and covariance effects of the model estimated heritability of RHP was 0.33, in agreement with RFI heritability.

Although decreased DM intake has been associated with animals with lower RFI (high efficiency) in confined (Cantalapiedra-Hijar et al., 2018) and grazing (Trujillo et al., 2013) conditions, no correlation between paternal RFI EBV and estimated DM or ME intake was found in the present study. Moreover, when corrected by BW, neither DM nor ME intake per unit of $BW^{0.75}$ differed between pHE and pLE heifers. In agreement with our results, previous research indicated that in grazing conditions, a reduction of herbage DM intake in low-RFI-ranked animals has not always been

Table 2. Ovarian activity and reproductive performance in first and second breeding and calving seasons of heifers sired by high and low residual feed intake EBV bulls (pHE vs. pLE)

	Paternal residual feed intake group			
	pHE	pLE	SEM	*P*-value
Ovarian activity previous AI				
Cycling, % (*n*/*n*)	34 (21/62)	22 (13/58)	—	0.16
Anestrous, % (*n*/*n*)	66 (41/62)	78 (45/58)	—	0.16
Superficial anestrus, % (*n*/*n*)	44 (27/62)	52 (30/58)	—	0.55
Maximum follicle diameter, mm	8.6	7.8	0.4	0.04
Maximum follicle diameter anestrous cows, mm	8.0	7.9	0.5	0.79
First breeding and calving seasons				
Inseminated heifers, % (*n*/*n*)	79 (49/62)	41 (24/58)	—	<0.01
Pregnant day 30, % (*n*/*n*)	42 (26/62)	38 (22/58)	—	0.81
Cycling day 30, % (*n*/*n*)	55 (34/62)	48 (28/58)	—	0.48
Anestrus day 30, % (*n*/*n*)	3 (2/62)	14 (8/58)	—	0.04
Pregnancy, % (n/n)	97 (60/62)	95 (55/58)	—	0.67
Service to conception interval, d	16.7	16.9	2.1	0.51
Calving day, d	25	33	3	0.05
Second breeding and calving seasons				
Discarded after first breeding season, %	5 (3/62)	10 (6/58)	—	0.53
Pregnant day 30, % (*n*/*n*)	5 (3/59)	10 (5/52)	—	0.59
Cycling day 30, % (*n*/*n*)	44 (26/59)	48 (25/52)	—	0.36
Anestrus day 30, % (*n*/*n*)	51 (30/59)	42 (22/52)	—	0.57
Pregnancy, % (*n*/*n*)	88 (52/59)	83 (45/54)	—	0.58
Calving to conception interval, d	104.8	101.4	5.1	0.61

found (Meyer et al. 2008; Lawrence et al., 2012; Oliveira et al., 2016). Consistently, Bormann et al. (2010) reported no differences in DM intake of a high-roughage complete diet, offered ad libitum for heifers sired by high and low-RFI bulls. The difficulty of obtaining accurate individual measures of DM intake in grazing conditions has been noted as one of the main reasons for not finding differences in DM intake between RFI groups (Lawrence et al., 2012; Oliveira et al., 2016). In the present study, we avoided that difficulty as we determined animal efficiency based on HP and not on DM intake.

However, daily estimated DM and ME intakes (kg or MJ/d) were greater for pHE than pLE heifers as, pHE heifers had higher initial and final BW, ADG, and more RE than pLE heifers, although they did not differ in weaning BW and were managed as a contemporary group not only during the experiments but also since birth. Feed intake is regulated by a combination of physical and metabolic mechanisms and is a function of meal size and frequency (Fitzsimons et al., 2017). Therefore, feeding behavior could contribute to explain the underlying variation in feed efficiency of beef cattle (Kelly et al., 2010; Fitzsimons et al., 2017, Cantalapiedra-Hijar et al., 2018). Kenny et al. (2018) conducted a meta-analysis of studies with growing beef cattle offered energy-dense high-concentrate diets and found that high-RFI cattle spent 0.12 more time eating than their low-RFI contemporaries with a 0.17 times higher DM intake which implied that efficient animals had a faster eating rate. Moreover, the space and time variation in nutrient supply that occurs under grazing conditions, make ingestive-digestive behaviors significant sources of inter-animal variation, indicating that the differential energy expenditures associated with the harvesting and defoliation processes must also be considered (Gregorini et al., 2008). It has been reported that efficient beef cows explore ~0.5 km/d further on rangelands than inefficient ones (Knight et al., 2015; Sprinkle et al., 2020). Knight et al. (2015) also found differences in the areas where high- and low-RFI cows grazed and hypothesized that efficient cattle could search out for higher quality forage to meet their nutritional needs, which may be located in different areas depending on the pasture. Thus, differences in the spatial exploration would be possibly an adaptation mechanism to grazing conditions, that in more restrictive nutritional situations such as rangeland grazing, more efficient animals are able to make a better use of forage available and eventually, consume more forage or of better quality.

In agreement with our results, Herd et al. (1998) reported that low-RFI grazing cows were 7% heavier than high-RFI ones without differences in pasture DM intake. Also, Jones et al. (2011) found that low-RFI cows were heavier while grazing both high- and low-quality pastures without differences in DM intake. Additionally, Sprinkle et al. (2020) working with high- and low-RFI cows grazing a low-quality forage reported that both groups had lower BCS, but the reductions in BCS and BW were greater and more variable for high- than low-RFI cows. This suggests that the greater reductions of BCS of inefficient cattle were due to greater maintenance requirements, and in combination with the lower losses in BW of more efficient cows could indicate an ability for adapting to poorer forage quality (Sprinkle et al., 2020). Therefore, the ability to adapt their ingestive-digestive behaviors and decreased maintenance energy requirements may explain differences in production responses, as well as in feed and energy efficiency between paternal RFI heifers' groups in rangelands when forage diminished in quantity and quality.

Our results showed a greater partitioning of consumed ME towards body reserves, indicated by RE, with a reduction in HP. Even though total HP (kJ/BW$^{0.75}$) did not differ between pHE and pLE heifers, paternal RFI EBV was positively correlated with HP expressed by unit BW$^{0.75}$. Few studies evaluated HP in high and low-efficiency animals, and in agreement with our results, reported that HP (kJ/BW$^{0.75}$) showed a positive correlation with RFI (Basarab et al., 2003; Asher et al., 2018) or that it was increased between 8% and 21 % for high (low-efficient) than low-RFI animals (Nkurmah et al., 2006; Paddock, 2010; Menezes et al., 2020), suggesting decreased energy expenditure for maintenance in low than high-RFI cattle. Total HP is the sum of HP for maintenance (HPm) and HP for production (HPp; Miron et al., 2008) and in the present study, total HP did not differ between paternal RFI groups but RE was 11% greater for pHE than pLE heifers, when corrected per unit of BW$^{0.75}$, indicating that greater HPp and lower HPm in efficient heifers could be expected. Nkrumah et al. (2006) and Chaves et al (2015) reported greater ME intake and RE with lower or similar HP while Menezes et al. (2020) and Asher et al (2018) found decreased ME intake and HP with similar or lower RE for high vs. low-efficiency animals. Differences in techniques used to determine DM (ME) intake, RE, and total HP, as well as in diets, conditions, and type of animals among experiments could explain the discrepancies between studies. Nonetheless, relationships between ME intake, RE, and total HP would indicate decreased HPm in more efficient animals in the previous studies. In agreement with these results, Menezes et al. (2020) reported reduced energy requirements for basal metabolism and ME for maintenance in high vs. low-efficiency steers, without differences in the conversion efficiency of consumed ME (k).

The lower maintenance energy explains, at least partially, the increased efficiency observed. In the present study not only RE/ME intake but also G:F were, or tended to be, greater in pHE vs. pLE heifers. Other authors reported similar associations between RFI and RE/ME intake or G:F in steers or bulls in positive energy balance (Nkrumah et al., 2004; Asher et al., 2018). Moreover, our results show that HP/ADG and RHP/ADG were lower in pHE heifers compared to the pLE, suggesting that the partial efficiency for growth above maintenance could be also increased in pHE heifers (Cantalapiedra-Hijar et al., 2018). Asher et al. (2018) reported a negative correlation between HP/ME intake and RFI but similarly to our results, found that RHP was positively correlated ($r = 0.33$, $P = 10$) with RFI or was lower in efficiency than in inefficient calves (~300 to 570 kg) in positive energy balance. In addition, Richardson et al. (2001) reported a positive correlation ($r = 0.46$, $P < 0.05$) between RHP/kg of protein gain and paternal RFI EBV and 35% less RHP/kg of protein gain in low than high-RFI steers, while no differences in RHP per kg of fat gain between groups were observed. Similarly, in the present work, it could be expected that body gain tissue had a greater protein-to-fat ratio than later in life, given the age of heifers evaluated during the growth phase. Although not consistent, several studies have associated RFI with changes in body composition, with small but significant increases in carcass leanness and reductions in carcass fatness (Richardson et al., 2001; Lancaster et al., 2009; Basarab et al., 2011). Therefore, it could be suggested that low-RFI animals were more efficient in depositing body protein and/or in maintaining it when deposited, probably associated with decreased protein turnover, which is an energetically expensive process (Cantalapiedra-Hijar et al., 2018).

There are relatively few studies that have examined the association between RFI and fertility or maternal productivity. Previous research indicated that pregnancy, calving, or weaning rates were not associated with RFI, or decreased in low vs. high-RFI beef cows (Kenny et al., 2018). Later calving dates were reported in heifers with low-RFI (high efficiency), associated with a later puberty and lower levels of body fat (Arthur et al., 2005; Basarab et al., 2011; Shaffer et al., 2011). In agreement with these results, we did not find any major effect on the reproductive performance of pHE vs. pLE heifers. However, pHE (high efficiency) group had higher percentage of inseminated heifers and lower percentage of heifers in anestrus 30 d after the start of breeding season in the first breeding and calving season, in contrast with previous reports (Shaffer et al., 2011; Kenny et al., 2018). Efficient heifers (pHE) also had an earlier calving date, suggesting an earlier pregnancy during the first breeding season than pLE heifers. This agrees with Knight et al. (2015) who found that high-efficiency cows got pregnant earlier and, consequently, bred 16 d earlier than low-efficiency ones. The observed differences in the first breeding and calving seasons, in our study, could be attributed to BW differences between groups that could imply different development and a latter puberty in the pLE heifers. These differences between pHE and pLE heifers disappeared during the second breeding and calving seasons, which could indicate that as heifers finished their development, the impact on the reproductive performance was minimized.

Conclusions

Heifers sired by high-efficiency bulls, measured as RFI, were more efficient in grazing conditions measured as RHP. Greater RE without differences in HP, ME, or DM intake expressed as a unit of $BW^{0.75}$ as well as feed and energy efficiency (increased RE/ME and G:F and decreased HP/ADG and RHP/ADG) were observed for pHE than pLE heifers, suggesting a reduction in maintenance energy cost and/or an increase of the partial efficiency for growth. The slight differences observed in reproductive performance during the first breeding and calving seasons were in favor of pHE heifers but differences between paternal RFI groups were not maintained thereafter during the second breeding and calving seasons.

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Conflict of Interest Statement

The authors declare no conflicts of interest.

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