Consistency of feed efficiency ranking and mechanisms associated with inter-animal variation among growing calves

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ABSTRACT: This study investigated the possible mechanisms for explaining interanimal variation in efficiency of feed utilization in intact male Holstein calves. Additionally, we examined whether the feed efficiency (FE) ranking of calves ($n = 26$) changed due to age and/or diet quality. Calves were evaluated during three periods (P1, P2, and P3) while fed a high-quality diet (calculated mobilizable energy [ME] of 11.8 MJ/kg DM) during P1 and P3, and a low-quality diet (calculated ME of 7.7 MJ/kg DM) during P2. The study periods were 84, 119, and 127 d, respectively. Initial ages of the calves in P1, P2, and P3 were 7, 11, and 15 mo, respectively, and initial body weight (BW) were 245, 367, and 458 kg, respectively. Individual dry matter intake (DMI), average daily gain (ADG), diet digestibility, and heat production (HP) were measured in all periods. The measured FE indexes were: residual feed intake (RFI), the gain-to-feed ratio (G:F), residual gain (RG), residual gain and intake (RIG), the ratio of HP-to-ME intake (HP/MEI), and residual heat production (RHP). For statistical analysis, animals' performance data in each period, were ranked by RFI, and categorized

into high-, medium-, and low-RFI groups (H-RFI, M-RFI, and L-RFI). RFI was not correlated with in vivo digestibility, age, BW, BCS, or ADG in all three periods. The L-RFI group had lowest DMI, MEI, HP, retained energy (RE), and RE/ADG. Chemical analysis of the longissimus dorsi muscle shows that the L-RFI group had a higher percentage of protein and a lower percentage of fat compared to the H-RFI group. We suggested that the main mechanism separating L- from H-RFI calves is the protein-to-fat ratio in the deposited tissues. When efficiency was related to kg/day (DMI and ADG) and not to daily retained energy, the selected efficient L-RFI calves deposited more protein and less fat per daily gain than less efficient H-RFI calves. However, when the significant greater heat increment and maintenance energy requirement of protein compared to fat deposition in tissue were considered, we could not exclude the hypothesis that variation in efficiency is partly explained by efficient energy utilization. The ranking classification of calves to groups according to their RFI efficiency was independent of diet quality and age.

Key words: cattle, feed efficiency, heat production, residual feed intake, residual gain

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INTRODUCTION

Residual feed intake (RFI) has been used to estimate feed efficiency (FE) in beef cattle (Moore

et al., 2009), as it is moderately heritable and genetically independent of average daily gain (ADG) and body weight (BW) (Crowley *et al.*, 2010). The RFI is defined as the difference between observed dry matter intake (DMI) and DMI predicted with ADG and metabolic BW of a given feeding period (Koch *et al.*, 1963). Others, however, included backfat thickness to calculate an RFI independent from the effect of body composition, i.e., the energy content of BW gain (Basarab *et al.*, 2003; Crews *et al.*, 2003; Tedeschi *et al.*, 2006). Other traits such as G:F and residual BW gain (RG), which is calculated by regressing ADG on DMI and BW (Crowley *et al.*, 2010), have also been used to estimate FE. Berry and Crowley (2012) proposed an amalgamation of both RFI and RG, to generate an alternative FE trait called residual intake and gain (RIG). The above FE indexes are, however, not directly related to energy utilization. We included two energetic efficiency indexes: residual heat production (RHP), defined as measured heat production (HP) minus expected HP, which is calculated from ADG (a proxy for retained energy, RE) and BW (Aharoni *et al.*, 2006), and the HP-to-mobilizable energy (ME) intake (MEI) ratio (HP/MEI). Only a limited number of studies have focused on the biological mechanisms underlying RFI.

Our hypotheses were: 1) individual animals' RFI ranking remains independent of physiological age and diet quality; 2) RFI is affected by inter- or among-animal variation due to differences in protein-to-fat deposition, energy partitioning between HP and RE, physical activity, and feed digestibility. Accordingly, the objectives were: 1) to determine the explained variance in RFI by measuring calves' performance- and energy-related parameters (e.g., MEI, HP, RE, and diet *in vivo* OM digestibility), 2) to examine the correlations between RFI and other FE traits, and 3) to examine the consistency of calves' RFI ranking and other FE traits across different diet qualities and ages.

MATERIAL AND METHODS

Animal Management and Facilities

All procedures involving animals in the present study were approved by the Israeli Committee for Animal Care and Experimentation (Bet-Dagan, Israel; Volcani file number 11807 IL). The study was carried out at Newe Ya'ar Research Center, Israel. Calves selected for the study were without any previous health and low ADG problems. The study started with 28 intact Israeli Holstein

male calves, however, due to medical problems two calves were excluded from data analysis. Twenty-six healthy calves were housed for 405 d in a shaded open feedlot with 5 m maximal roof height that provided 10 m²/calf under the roof and 8 m²/calf in the open yard. The feedlot contained six individual feed troughs controlled by electro-pneumatic yokes (Halachmi *et al.*, 1998) in a feeding area (15 × 3 m) that included two drinking troughs, which allowed free access to water. The feeding area was separated from the resting area by a fence. Calves passed in and out of the feeding area through one-direction doors. While moving out of the feeding area the calves walked over an automatic weighing scale (Shekel, Israel) to enable BW to be recorded an average six times/day. Calves were fitted with electronic ID tags to facilitate measurements of activity and rumination (SCR, Israel). A computerized monitoring system (SCR, Israel) was designed to record individual feed intake and BW.

Feedbunks' accuracy was calibrated against standard weights of 20 g. Each calf was allowed to eat from each of the six feedbunks. A tin metal corridor of 45 cm wide and 145 cm long led to each feeding bunk to prevent disturbance of a calf while eating by others calves. A horizontal metal rod controlled by hydraulic piston blocked the access of calf's head to eat from the feedbunk. A photoelectric sensor identified approaching of the calf to the feedbunk and activated infrared ID sensor. When calf had permission to eat from the feedbunk, the number of the calf eating from the feedbunk was recorded in the computerized system. When calf went out of the feedbunk to a distance of about 30 cm, where it was no longer identified by the photoelectric sensor, the access to the feedbunk was blocked by the rod (turn back to horizontal position) and feedbunk weight was recorded. Feedbunk weight was also recorded every 5 min where no calf attended the feedbunk. Feed consumption of each meal was calculated as the difference in feedbunk weight before and after the meal. The computerized system summarized every meal by its duration and consumed feed. It summarized also total daily feed intake per calf and feedbunk. To verify the computerized feed intake recordings, total feed consumption from each feedbunk was recorded also manually.

Weekly average difference of total daily intake, measured manually minus the automatic measurements, from each feedbunk, was $-0.87 \text{ g/kg} \pm \text{SE of } 2.29 \text{ g/kg}$ ($N = 6$ feedbunks) of the daily feed weight used in the feedbunk (weighed manually).

Study Diets and Measurements Protocol

Scheme of study diets and measurements time table are presented in the Appendix section (Figure 1).

The calves were adapted to the first study diet and to the individual-animal feeding system for 21 d prior to the start of the study. The study was carried out in three periods (P1, P2, and P3) and data were recorded for 84, 119, and 127 d, respectively. Calves were adapted to diets for 30 d between P1 and P2 and for 45 d between P2 and P3. The total duration of the study from the start of P1 to end of P3 was 405 d. Calves were fed the same high-quality TMR during P1 and P3 and a coarsely chopped wheat hay diet during P2 (Table 1). Diets were delivered once daily at 0700 for ad libitum intake (5% to 10% of the given diet in the feedbunk during 6 d of the week) and adjusted to have minimal ort of about 5% of daily intake for last day of the week. Consequently, for the total week intake, maximal feedbunk orts that were taken out from the feedbunk were 5% of average daily intake, which it was 0.71% of calves'

Table 1. Ingredients and chemical composition of the study diets

Diet ingredients, % in DM	Period 1	Period 2	Period 3
Wheat hay	25.1	100	25.1
Corn grain, ground	42.7	-	42.7
Soybean meal	7.6	-	7.6
Wheat bran	8.9	-	8.9
Corn gluten feed	13.2	-	13.2
NaCl	0.6	-	0.6
Limestone	1.0	-	1.0
Vitamins and minerals	0.2	-	0.2
Calcium bicarbonate	0.7	-	0.7
Calculated diet ME ¹ (MJ/kg DM)	11.8	7.7	11.8
Calculated crude protein concentration ¹ (%)	13.8	5.5	13.8
Chemical composition analysis (%) ³			
Dry matter ²	90.8	89.8	91.9
Organic matter ²	90.1	90.8	90.7
Crude protein ²	12.9	5.1	13.1
Ether extract ²	2.65	1.38	2.77
NDF ³	39.7	62.9	38.6
In vitro digestibility (%) ⁴			
DM	83.4 ^a	67.9 ^b	85.3 ^a
OM	83.7 ^a	69.3 ^b	86.2 ^a
Diets ME (MJ/kg DM)	11.9 ^a	7.7 ^b	12.9 ^c

¹Calculated diet ME based on NRC (1989)

²Based on AOAC (1990)

³Van Soest *et al.* (1991)

⁴Three analyses per period.

^{a-c}Least squares means within a row with different superscripts differ ($P < 0.05$).

total week intake, computed as 5% of daily intake divided by 7 d. Individual-animal HP and in vivo diet digestibility were measured twice during each study period, during the mid-portion of the first third and last third of each study period, and the two measurements were averaged for statistical analysis.

BW and DMI were monitored beginning at 0700 each day and summarized daily (from 0700 to 0700).

The performance variables and efficiency values were summarized, for each period.

Diets and Fecal Sampling, Chemical Analyses, Digestibility Measurements, and Diets Energy Calculations

Diets and orts were sampled once weekly, and chemical analysis and in vitro digestibility estimates measured 3× during each study period (approximately midway during the first, second, and later third of each study period). The DM of the given diet was used to calculate the actual consumed diet DM and its chemical and nutritional composition. As diets orts were less than 1% of the daily intake, only diets nutritional composition were used for calculating diets nutritional composition and in vitro and in vivo digestibility. During each study period, fecal grab samples were collected three times per day for three consecutive days from each calf. Sampling time was changed from day-to-day to represent an entire day. Diet, orts, and fecal samples were dried at 60 °C for 48 h in a forced-air oven, ground to pass through a 1-mm screen (Retsch S-M-100, Haan, Germany), and analyzed for DM, protein, NDF, ADF, and OM contents. To calculate ingredient concentrations per DM and OM, the ground dry samples were dried to 60 °C for 48 h and then to 100 °C for 24 h and ash content was measured by burning at 550 °C for 3 h (AOAC, 1990; method 984.13). The NDF and ADF concentrations were determined with an Ankom fiber analyzer (Ankom Technology, Fairport, NY) according to Van Soest *et al.* (1991).

In vivo digestibility was determined according to Lippke *et al.* (1986) and Voelker *et al.* (2002), using the indigestible neutral detergent fiber (INDF) concentration as an internal marker. The in vivo digestibility of DM, OM, and NDF were calculated for each calf, using the average individual DM intake and fecal INDF concentration. The two-stage in vitro digestibility technique (Tilley and Terry, 1963) was used to analyze the INDF concentration (after incubation with

rumen fluid for 72 h) of offered feeds, orts, and feces samples.

In vitro analysis of the diets samples were conducted using the [Tilley and Terry \(1963\)](#) procedure described above for the INDF analysis, with the exception that the incubation of rumen fluid was for 48 h. As expected, the in vitro DM and OM digestibilities did not differ between P1 and P3, as the diet ingredient composition was similar ([Table 1](#)). The ash content of the orts of stage two of the analysis was determined in order to calculate OM digestibility.

The digestibility of DM and the above-mentioned nutrient ingredients were determined as follows ([Bondy, 1987](#)):

$$\text{Digestibility of DM} = 1 - \left(\frac{\text{INDF in Diet}}{\text{INDF in Feces}} \right)$$

$$\text{Digestibility of nutrient} = 1 - \left[\left(\frac{\text{INDF in Diet}}{\text{INDF in Feces}} \right) \times \left(\frac{\text{Nutrient in Feces}}{\text{Nutrient in Diet}} \right) \right]$$

The digested amounts (kg/day) of each chemical component were calculated by using the average individual DMI of the 7 d. In vivo OM digestibility and its OM content were assumed to be respectively equivalent to TDN and its contents ([Moore and Kunkle, 1999](#)).

The conversion of OM into digestible energy (DE) was calculated by the following equation: DE (Mcal/kg DM) = 4.409 Mcal/kg DM × TDN (kg DM/kg DM) ([NRC, 2001](#), page 13). Diet ME was calculated as 1.01 × DE – 0.45 ([NRC, 2001](#), page 13). The Mcal energy unit was converted to MJ using 1 Mcal = 4.184 MJ.

MEI of individuals in each period was calculated by multiplying the calf's DMI by the ME of the individually measured diet. Retained energy (RE) was calculated as MEI minus HP. Procedure of HP measurements is described in the following paragraph. Body condition score (BCS) was estimated by the same trained person at the initial and final day of each period, using a 1 to 5 scale ([Edmonson et al., 1989](#)). The changes in BCS (BCS_{diff}) were calculated as the final BCS minus initial BCS of the period.

Measuring HP by the HR O₂P Method

Most of the oxygen consumed (VO₂) in mammals is transferred to the tissues through the blood,

pumped by the heart; therefore, in each period, individual VO₂ was measured by multiplying the individual average daily measured heart rate (HR) that was recorded at 1-min intervals for 5 d (HR_D) by a short measurement (10 to 20 min) of VO₂ per heart-beat, the O₂-Pulse (O₂P), of the same animal. Direct measurements of VO₂ and O₂P were obtained immediately after the HR_D measurement ([Brosh, 2007](#)). Each calf was measured in the morning and afternoon, and the average O₂P was used to calculate daily VO₂ and HP. During The VO₂ measurement, HR was simultaneously recorded at 5-s intervals. Heart rate was recorded by a Polar instrument (Polar Electro Oy, Kempele, Finland), a model T51H HR transmitter, and a watch model S610i. The device was attached to the thorax behind the forelegs by means of a specifically designed elastic belt (Pegasus, Eli-ad, Israel). This procedure of HR_D and O₂P measurements was conducted twice in each period, at the midst of the first and last thirds of the period, and the results were averaged for statistical analyses.

Oxygen consumed was measured by an open-circuit system with a facemask as described by [Fedak et al. \(1981\)](#). In each VO₂ measurement, the N₂ recovery of this system was measured gravimetrically three times according to [McLean and Tobin \(1990\)](#). The O₂P was calculated as described by [Aharoni et al. \(2003\)](#) and [Brosh et al. \(1998, 2002\)](#). Animal HP was calculated by multiplying O₂P by the HR_D recording throughout the daily measurements, assuming 20.47 kJ (4.892 kcal) per liter of O₂ consumed ([Nicol and Young, 1990; Brosh et al., 1998](#)). To determine daily HP, O₂P was multiplied by the total number of heartbeats per day ([Brosh, 2007](#)), calculation equations 1, 2, and 3.

- 1) Animal VO₂^a (mL/min) = O₂ diff %^b × 100⁻¹ × Facemask air flow rate (mL/min)
- 2) O₂ pulse (mL/heartbeat) per kg BW = VO₂/HR_s^c per kg BW
- 3) Daily HP (Mcal/d) = HR_D^d × O₂ pulse × 4.892 × 10⁻⁶ × kg BW × 60 × 24

^aAnimal' oxygen consumption measured at short time simultaneously with HR for measuring oxygen pulse (O₂P).

^bO₂ diff % = (O₂ % in fresh air flow into the animal's facemask) – (O₂ % in air flow sucked from the facemask)

^cHR_s frequency (beats/min) measured throughout the short time of the direct oxygen consumption measurement

$^d\text{HR}_p$ = Average daily of Heartbeat rate (beats/min) measured throughout the five days of the sub period study.

Efficiency Calculations

For each period, DMI was calculated as the average of daily DMI. ADG and initial BW were obtained from linear regression of BW on day of the study period. Period final BW was computed from the slope of the linear regression of BW (kg) on time (d) of the last week of the study period, the slope and intercept were used to calculate the expected BW of last day of the period final week. The period mid-BW was calculated as the average of initial BW and final BW.

FE traits evaluated in this study included RFI, G:F, RG, and RIG. Expected DMI was derived from multiple linear regression of DMI on mid-period $\text{BW}^{0.75}$ and ADG, whereas, expected ADG was derived from multiple linear regression of ADG on mid-period $\text{BW}^{0.75}$ and DMI. RFI was computed as the difference between actual DMI and expected DMI, and RG as the difference between actual ADG and expected ADG. RIG was computed as the sum of $-1 \times \text{RFI}$ and RG, both standardized to one variance (Berry and Crowley, 2012). Multiplying RFI by -1 was to account for a negative RFI being favorable compared with a positive RG being favorable. RIG is a linear function of both RFI and RG, which, in turn, are linear functions of feed intake, ADG, and BW (Berry and Crowley, 2012).

FE variables in energy units were computed for each calf as HP/MEI (MJ/MJ), with higher values indicating less efficient animals as RHP (MJ/d). The RHP, expressed as $\text{kJ}/(\text{kg BW}^{0.75} \text{ d})$, was defined as the difference between measured and predicted expected HP (Aharoni et al., 2006). Aharoni et al. (2006) calculated the RHP index for lactating dairy cows, where the expected HP was based on cows' $\text{BW}^{0.75}$ and energy retained in milk and body balance, using BCS difference. In the present study, the calculation of expected HP was based on the slope and intercept of a multiple linear regression of HP dependency on calves' mid-period $\text{BW}^{0.75}$ and ADG, assuming that an individual calf's ADG represented individual RE.

Physical Activity of Calves

The total daily activity of each calf was measured using commercial neck-mounted accelerometer

data tags (HR-Tag, SCR Engineers Ltd., Netanya, Israel), as reported by Van Hertem et al. (2014) and by Steensels et al. (2017) for activity measurements of dairy cows.

Slaughter Traits and Carcass Composition Analyses

Animals were shipped to a commercial abattoir at the average age of 611 d. After slaughter, hot carcass, kidney fat, heart fat, pelvic fat, and testicle fat weights were recorded. Samples of the longissimus dorsi (LD) muscle from the 12th to 13th rib section were separated from the subcutaneous fat and DM (AOAC, 1990; method 930.15) and OM (AOAC, 1990; method 923.03) measured. Lipids were extracted from subsamples of 5.0 g dry muscle samples using petroleum ether according to AOAC (1990), method 920.39. Total N was determined and crude protein was calculated according to AOAC, 1990 method 984.13.

Statistical Analysis

The data were analyzed using SPSS ver. 17 (SPSS Inc., Chicago, IL, USA). The performance variables used for the efficiency calculations were as follows: BW, ADG, DMI, and HP. An ANOVA with a repeated measurement procedure was used to test the differences of the above variables among the calves.

Pearson correlation coefficients (SPSS Inst. Inc.) between classified FE traits were determined for each study period.

To evaluate the effect of study period on change in individual-animal rank in RFI, calves were categorized into high-, medium-, and low-RFI (H-RFI, M-RFI, and L-RFI, respectively) groups based on ± 0.50 SD from mean RFI ($0 \pm$ actual SD value kg DM/d). Calves were assigned to efficiency groups according to Nkrumah et al. (2004). The H-RFI and L-RFI groups included calves with RFI that were 0.5 SD above and below the group averages, respectively, while the M-RFI group included all the other calves. Average RFI was zero by definition.

The effect of RFI on performance and energy balance components was determined using the REML Procedure for mixed models by GenStat, 7th Edition (VSN International Ltd, UK). The model included the period factor and RFI variable as fixed effects and animal as random effect, across the entire experiment.

Simple linear regressions were performed using GenStat to test the dependency of performance

and energy balance variables, as dependent variables, on RFI as the independent variable within each period.

In addition to RFI, calves were also ranked for G:F, RG, and RIG, and the rank according to each FE trait was tested by the frequency of identical grouping levels as high, medium and low (total agreement) for each study period. These rankings were statistically evaluated using the chance-corrected measure of agreement (Kappa index; Fleiss, 1981) as described by Asher *et al.* (2014).

RESULTS

Calves' RFI Range

The SD for RFI in P1, P2, and P3 were 0.75, 0.61, and 1.34, respectively. The corresponding coefficient of variation (CV) were 9.7%, 11.4%, and 10.9%, respectively. RFI ranged from -1.28 to 1.43 kg DM/d in P1, a difference of 2.71 kg DM/d, from -1.23 to $+1.17$ kg DM/d in P2, a difference of 2.4 kg DM/d, and from -2.83 to 3.04 kg DM/d in P3, a difference of 5.87 kg DM/d. These RFI variations among the individuals reflected differences of 35%, 46%, and 48% in average DMI for P1, P2, and P3, respectively, between the most and least efficient animals grouped according to RFI.

Performance, In Vivo Digestibility and Energy Variables of Calves' Classified to RFI Groups in the Study Periods

Calves' performance (Table 2) of mid-period age, initial, mid and final BW and mid-period BCS were not different among classified RFI groups in all study periods. Calves' BCS_{diff} differed among RFI groups in P2. Daily DMI differed between RFI groups in all periods, where the H-RFI group ate more than the L-RFI group. In vivo OMD differed among RFI groups in period 1 only. No changes in daily activity were revealed among RFI groups, however, in P2, activity tended to be different among RFI groups. Effects of periods and calves' RFI classification on calves' performance and energy balance variables, using a mix model regression analysis, are presented in Table 3. Periods significantly affected all tested variables. RFI significantly affected calves' DMI, MEI, RE, HP when presented as $\text{kJ/d per BW}^{0.75}$ (per MBW), and the calculated value of $\text{RE/BCS}_{\text{diff}}$. In vivo DMD tended to be affected by RFI.

The values presented in the RFI effect column, represent the effect of calves variation, per 1 RFI

unit (kg DM/d), on each tested variable. Positive value of RFI effect (slope) for each tested variable means that the variable was negatively related to efficiency and vice versa, for the negative RFI effect.

The effect of RFI on DMI and energy balance variables within study periods is presented in Table 4. In P1, RFI affected ($P < 0.05$) DMI, MEI, and HP per MBW, and tended ($P < 0.10$) to affect RE and RE/ADG. In P2, RFI only affected ($P < 0.05$) DMI, whereas during P3, RFI affected ($P < 0.05$) DMI, MEI, RE, RE/ADG, and RE/BCS.

Comparison Between Efficiency Indexes

During each study period, calves were classified into divergent groups according to their RFI, and rank agreement between RFI and other FE traits evaluated (Table 5). For most of the FE indexes in most of the periods, differences among efficiency groups were highly significant, i.e., classification of the calves to efficiency groups by other tested indexes were similar to those classified by RFI.

Differences among efficiency groups only tended to be significant for G:F during P2 and for RG during P1 and P2. Differences among efficiency groups were not significant for HP/MEI during P2 and for RHP during P1 and P2.

Correlations of RFI values with other FE and energy-balance traits are presented in Table 6. A significant negative correlation was observed between the G:F ratio and RFI in P1 and P3, i.e., the more efficient calves according to RFI had greater efficiency expressed as G:F. However, significant correlations were not detected between RG and RFI during either of the study periods. RIG and HP/MEI ratio were negatively correlated ($P < 0.05$) with RFI during all three study periods, i.e., the more efficient calves based on RFI were defined as more efficient by the RIG index. However, the negative correlations between RFI and HP/MEI imply that feed efficient calves, based on RFI, were less efficient in energy terms, as their HP per MEI was higher. RHP tended ($P = 0.12$) toward positive correlation with RFI only in P1, i.e., during P1 more efficient calves according to RFI were defined as more efficient by RHP.

Slaughter Data

Carcass yield, internal fat depot weights, and LD muscle composition data are presented in Table 7. Slaughter data did not differ among the RFI groups, except for the fat and protein concentrations in the LD muscle. The L-RFI group had

Table 2. Performance of calves classified to RFI groups in the three experiment periods

Calves measured		RFI groups ¹			SEM ²	P-Value ³
Trait	Period	Low	Medium	High		
No of calves	1	9	8	9		
	2	10	7	9		
	3	9	8	9		
Age, month	1	7.6	6.9	7.1	0.27	0.33
	2	11.9	9.4	11.6	0.64	0.13
	3	15.3	15.8	15.8	0.38	0.55
BW initial, kg	1	253	236	245	11.6	0.31
	2	369	363	370	12.4	0.92
	3	456	462	457	17.4	0.97
BW mid-period, kg	1	309	290	304	13.0	0.46
	2	392	383	386	14.3	0.89
	3	565	576	557	17.1	0.72
BW final, kg	1	366	344	362	15.0	0.43
	2	409	402	403	15.9	0.93
	3	674	695	657	17.3	0.28
ADG, kg/d	1	1.34	1.30	1.34	0.06	0.75
	2	0.34	0.31	0.30	0.05	0.77
	3	1.70	1.86	1.56	0.06	0.78
BCS, mid-period	1	2.86	2.82	2.83	0.10	0.67
	2	1.97	1.99	2.00	0.09	0.65
	3	3.28	3.27	3.28	0.23	0.97
BCS _{diff} ⁴	1	0.43	0.45	0.48	0.07	0.81
	2	-0.14	-0.17	-0.06	0.04	<0.05
	3	0.79	0.73	0.76	0.03	0.29
DMI, kg DM/d	1	7.01 ^a	7.62 ^b	8.61 ^c	0.40	<0.05
	2	4.94 ^a	4.68 ^a	6.17 ^b	0.34	<0.001
	3	10.3 ^a	12.8 ^b	13.8 ^c	0.44	<0.001
OM digestibility	1	66.7 ^a	69.3 ^b	66.1 ^a	0.01	<0.05
<i>In vivo</i> , (%)	2	48.6	48.9	49.1	1.65	0.98
	3	71.1	69.2	68.5	1.16	0.26
Activity, min/day	1	496	518	480	15.3	0.46
	2	505	462	417	44.2	0.07
	3	500	520	509	49.3	0.87

¹High RFI was > 0.5 SD above the mean; medium RFI was the range from 0.5 SD below the mean up to 0.5 SD above the mean; low RFI was below -0.5 SD of the mean.

²SEM = standard error of mean

³P = P value obtained by ANOVA F-test for differences between RFI groups.

⁴BCS_{diff} = BCS initial – BCS final

^{a-c}Least squares means within a row with different superscripts differ ($P < 0.05$).

more protein and less fat in the muscle compared to the H-RFI group ($P < 0.05$).

Ranking Consistency of FE and Energy Utilization Efficiency Indexes

The ranking consistency of the efficiency groups classified by the RFI, G:F, RG, RIG, HP/MEI, and RHP indexes, across the three study periods, is presented in Table 8. Group ranking across all three periods was consistent only when calves were ranked by RFI and RIG.

Based on the Kappa index, there were no significant reranking changes in the RFI groups between P1 and P2, P2 and P3, and P1 and P3 ($P < 0.001$, $P < 0.05$, $P < 0.001$, respectively) (Table 8). The same finding was also observed for RIG, however, the magnitude of significance for the 3 study comparisons was less for the RIG ($P < 0.05$, $P < 0.05$, $P < 0.001$, respectively).

A weaker consistency of efficiency group ranking was observed when calves were classified by RG (between P2 and P3; $P < 0.05$) and HP/MEI (between P1 and P3; $P < 0.05$). Similar FE rankings

Table 3. Effects of period and RFI on performance and energy balance components

Variable	Period means			Effect RFI	SEM ¹		P-value ²	
	1	2	3		Period	RFI	Period	RFI
Age, month	7.17	11.41	17.93	0.01	0.06	0.04	<0.001	0.73
BW initial, kg	244	368	460	-0.57	6.21	3.86	<0.001	0.88
BW mid-period, kg	301	388	569	-2.67	6.20	3.90	<0.001	0.50
BW final, kg	357	405	679	-2.35	7.42	4.59	<0.001	0.61
BCS initial	2.83	2.08	3.28	0.00	0.02	0.01	<0.001	0.82
BCS final	3.29	1.50	3.77	-0.01	0.04	0.02	<0.001	0.78
BCS _{diff} ³	0.46	-0.58	0.50	0.01	0.04	0.01	<0.001	0.42
ADG, kg/d	1.33	0.32	1.72	-0.01	0.05	0.02	<0.001	0.76
DMI, kg DM/d	7.81	5.52	12.46	1.04	0.17	0.10	<0.001	<0.001
DMD (%)	66.0	45.3	68.3	-0.64	0.80	0.39	<0.001	0.11
OMD (%)	67.1	49.8	69.5	-0.48	0.73	0.38	<0.001	0.22
Diets DE (MJ/kg DM)	9.11	6.82	10.43	-0.09	0.19	0.09	<0.001	0.32
Diets ME (MJ/kg DM)	8.75	6.44	10.08	-0.09	0.19	0.10	<0.001	0.32
MEI, MJ/d	67.9	41.7	126.0	7.71	2.27	1.24	<0.001	<0.001
HP, MJ/d	60.9	51.3	104.2	1.32	1.62	0.92	<0.001	0.16
RE, MJ/d	6.94	-9.01	21.77	6.47	2.27	1.12	<0.001	<0.001
MEI, kJ/(kg BW ^{0.75} ·d)	944	479	1,082	72.8	23.3	12.0	<0.001	<0.001
HP, kJ/(kg BW ^{0.75} ·d)	845	581	895	16.8	18.0	7.17	<0.001	0.02
RE, kJ/(kg BW ^{0.75} ·d)	98.4	-101.3	186.9	57.6	21.7	11.3	<0.001	<0.001
RE/ADG, MJ/kg	5.08	-24.6	12.9	3.13	7.08	3.11	<0.001	0.32
RE (MJ)/BCS _{diff}	16.79	15.72	46.01	14.5	5.76	2.26	<0.001	<0.001
RE (kJ)/BCS _{diff}	239	177	393	128	58.6	23.8	0.002	<0.001

¹SEM = standard error of mean.²P = P-value obtained by using a mixed procedure (period and RFI were used as fixed effects with random effect of animal, for the entire experiment).³BCS_{diff} = (BCS_{final} - BCS_{initial}).**Table 4.** Regression coefficients of performance and energy traits, as dependent variables, on RFI within periods

Depended variable	Slope ¹			Standard error ²			Probability ³		
	Period 1	Period 2	Period 3	Period 1	Period 2	Period 3	Period 1	Period 2	Period 3
DMI, kg/d	0.82	0.98	1.16	0.27	0.16	0.17	<0.01	<0.001	<0.001
MEI, MJ/d	5.41	2.58	9.71	2.39	2.32	1.92	0.03	0.28	<0.001
HP, MJ/d	2.45	1.47	1.16	1.81	2.35	1.42	0.19	0.54	0.42
RE, MJ/d	3.13	1.73	8.55	1.72	2.68	1.58	0.08	0.53	<0.001
MEI, kJ/(kg BW ^{0.75} ·d)	77.8	30.8	83.5	29.8	27.2	13.2	0.02	0.27	<0.001
HP, kJ/(kg BW ^{0.75} ·d)	35.9	14.2	11.0	16.1	20.0	9.46	0.04	0.49	0.26
RE, kJ/(kg BW ^{0.75} ·d)	41.9	16.5	72.6	25.0	28.4	13.4	0.11	0.57	<0.001
RE/ADG, MJ/kg	2.42	-7.30	5.31	1.23	14.9	0.93	0.06	0.63	<0.001
RE (MJ)/BCS _{diff}	6.24	-1.65	20.1	4.3	4.05	3.51	0.16	0.69	<0.001
RE (kJ)/BCS _{diff}	84.3	-13.4	169	63.4	43.2	28.9	0.20	0.76	<0.001

¹Linear regression slopes of each depended variable on RFI.²Standard error of the regression slope.³Probability represents significance of the effect of RFI on the dependent variable within each period.

were not maintained across the three study periods when calves were classified based on G:F or RHP.

Transition of calves between the H-RFI and L-RFI groups represented a switch in the assignment of the least efficient and most efficient individuals. Accordingly, the transition percentage between

L-RFI and H-RFI efficiency groups was 15.4% between P1 and P2, 11.5% between P2 and P3 when the calves' diets were dramatically changed, and only 3.8% between P1 and P3 when the difference between periods was mainly the calves' age. The highest percentage transitions between the H-RFI and L-RFI

Table 5. Feed efficiency indexes of growing calves ($N = 26$) in the three study periods. The same individuals were used in each classified efficiency group for all indexes. In each period calves were classified to groups according RFI.

Trait	Period	RFI group ¹				SEM ²	P-value
		Low	Medium	High	Average		
Residual Feed Intake, Kg DM/d	1	-0.94 ^a	0.14 ^b	0.80 ^c	0.00	0.09	<0.001
	2	-0.63 ^a	0.002 ^b	0.63 ^c	0.00	0.10	<0.001
	3	-1.50 ^a	0.23 ^b	1.27 ^c	0.00	0.29	<0.001
Gain: Feed, g/kg DM	1	191 ^a	171 ^b	156 ^c	172	8.91	0.01
	2	68.8	66.2	48.6	61.2	9.22	0.11
	3	165 ^a	145 ^a	113 ^b	141	5.72	<0.001
Residual Gain, g/d	1	69.7	37.7	-82.7	8.2	30.7	0.10
	2	0.06	0.01	-0.05	0.01	0.04	0.15
	3	-0.02 ^a	0.14 ^b	-0.16 ^c	-0.01	0.06	0.05
Residual Intake and Gain	1	1.04 ^a	0.06 ^b	0.88 ^c	0.66	0.11	<0.001
	2	0.69 ^a	0.06 ^b	-0.16 ^c	0.20	0.15	<0.001
	3	1.49 ^a	0.01 ^b	-0.68 ^c	0.27	0.13	<0.001
Heat Production/MEI, ratio	1	0.83	0.82	0.78	0.81	0.01	0.20
	2	1.22	1.24	1.13	1.19	0.04	0.33
	3	0.92 ^a	0.84 ^b	0.76 ^c	0.84	0.03	<0.001
Residual Heat Production kJ/(kg BW ^{0.75} ·d)	1	-12.21	-5.70	9.62	-2.76	0.42	0.93
	2	-39.75	-0.93	20.70	-6.66	0.34	0.37
	3	-10.37 ^a	-1.87 ^{a,b}	5.32 ^b	-2.31	0.37	<0.05

¹High RFI was 0.5 SD above the mean; medium RFI was the range from 0.5 SD below the mean up to 0.5 SD above the mean; low RFI was below -0.5 SD of the mean.

²SEM = standard error of mean.

^{a-c}Least square means within a row with different superscripts differ ($P < 0.05$).

Table 6. Pearson partial correlations (r_p) between calves' RFI indexes values to other feed efficiency indexes values, in each of the study period

Efficiency index	RFI-period 1		RFI-period 2		RFI-period 3	
	r_p	P-value	r_p	P-value	r_p	P-value
Gain:Feed ratio	-0.66	<0.001	-0.11	0.62	-0.38	<0.05
Residual Gain	-0.03	0.87	-0.33	0.10	0.18	0.37
Residual Intake and Gain	-0.99	<0.001	-0.98	<0.001	-0.82	<0.001
Heat Production/ME Intake	-0.34	0.09	-0.40	<0.05	-0.70	<0.001
Residual Heat Production	0.33	0.10	0.23	0.17	0.21	0.30

efficiency groups occurred when calves were ranked according to HP/MEI index (30.8%).

The transition percentage between all three RFI efficiency groups (H-RFI, M-RFI, and L-RFI), was 19.2% between P1 and P2, 23.1% between P2 and P3, and 15.4% between P1 and P3. The classification of an RFI efficiency group showed the lowest percentage of calves' transition between study periods compared to all other efficiency indexes.

DISCUSSION

In the discussion, we highlighted several physiological and energetic pathways that potentially

relate FE and energy utilization, for maintenance and growth.

Performance and RFI

Similar to previous reports, DMI was positively correlated with RFI during all three study periods (Castro Bulle *et al.*, 2007; Kelly *et al.*, 2010; Green *et al.*, 2013), and RFI was phenotypically independent of age, BW (initial, middle, and final), ADG, and BCS (Arthur *et al.*, 2001; Nkrumah *et al.*, 2004; Crowley *et al.*, 2010).

The positive relationships between RFI and MEI, RE and HP reported for the entire study analysis, indicated that H-RFI calves

Table 7. Slaughter data of the high, medium, and low RFI classified calves

Parameter	RFI groups				SEM	P-value
	Low	Medium	High	Average		
Final calves age, days	619	608	605	611	10.8	0.69
Final weight, kg	679	675	678	677	19.7	0.98
Carcass weight, kg	360	357	344	354	9.91	0.48
Carcass/final live weight, %	53.1	52.9	50.7	52.3	0.85	0.13
Pelvic fat, kg	3.01	2.68	2.28	2.66	0.25	0.13
Heart fat, kg	1.05	1.05	0.78	0.96	0.11	0.16
Testicle fat, kg	3.07	2.68	2.40	2.72	0.23	0.12
Kidney fat, kg	9.14	8.53	7.40	8.36	0.98	0.44
Total internal fat ¹ , kg	16.2	14.9	12.8	14.7	1.43	0.24
Total fat/Final weight, %	2.39	2.21	1.89	2.16	0.18	0.38
Total fat/carcass weight, %	4.50	4.17	3.72	4.13	0.36	0.52
Longissimus muscle composition ²						
Dry matter, %	27.2	26.6	26.5	26.8	0.35	0.30
Ash, %	1.34	1.36	1.41	1.37	0.03	0.44
Water, %	72.8	73.4	73.5	73.2	0.35	0.51
Protein, %	23.7 ^a	22.3 ^{a,b}	21.8 ^b	22.6	0.29	<0.05
Fat, %	2.12 ^a	2.90 ^b	3.26 ^c	2.76	0.18	<0.05

^{a-c}Least square means within a row with different superscripts differ ($P < 0.05$).

¹Total internal fat = pelvic fat + heart fat + testicles fat + kidneys fat.

²Longissimus muscle sample between 12th and 13th ribs.

Table 8. Consistency of efficiency indexes' groups ranked by: RFI, G:F, RG, HP/MEI, and by RHP indexes, across the three study periods

Efficiency traits	Periods	Total agreement	Kappa	Transit H&L ¹	Transit H&M&L ²	P-value ³
		(%)	(%)	(%)	(%)	
RFI	1&2	65.4	42.1	15.4	19.2	<0.001
	2&3	53.8	36.9	11.5	23.1	<0.05
	1&3	73.1	42.4	3.8	15.4	<0.001
G:F	1&2	19.2	15.8	26.9	80.8	0.72
	2&3	30.9	3.1	19.2	73.1	0.82
	1&3	30.7	2.9	15.4	69.3	0.83
RG	1&2	30.7	4.2	11.5	69.3	0.75
	2&3	57.7	33.1	3.8	42.3	<0.05
	1&3	30.8	4.2	26.9	69.2	0.75
RIG	1&2	50.0	24.6	11.5	50.0	<0.05
	2&3	53.7	31.1	11.5	46.2	<0.05
	1&3	65.4	48.2	3.8	34.6	<0.001
HP/MEI	1&2	34.6	3.2	26.9	65.4	0.82
	2&3	34.6	1.4	30.8	65.4	0.91
	1&3	57.7	34.4	7.7	42.3	<0.05
RHP	1&2	34.6	2.4	23.1	65.4	0.86
	2&3	26.9	13.3	7.7	73.1	0.34
	1&3	38.4	8.4	23.1	61.5	0.53

¹Transit H&L (%) represents the number of calves from the H and L groups that switched between efficiency classifications, in each period of experiment.

²Transit H&M&L (%) represents the number of calves from the H, M and L groups that switched from H to M, H to L and M to L, in each period of experiment.

³P - Significance of Kappa value.

had significantly higher MEI, retained more energy and produced more heat compared to L-RFI calves, which is in agreement with results

reported by [Basarab et al. \(2003\)](#). As diet digestibility and consequently diet ME in the study were not related to RFI, the individual-animal

variation in MEI mainly represented variation in DMI.

The Present Study Validates a Mechanism of Individual Variation in Calves' Efficiency

As RFI is defined by weight units and not by energy units, the selection for efficient calves by RFI is by definition not necessarily selection for energy efficiency.

In the Appendix section, we provided theoretical discussion about the possible mechanisms related to the variation in animals' production efficiency and we used published data for developing the equations related to the energy cost of protein and fat deposition and its maintenance cost. We also presented the values of transformation constants between efficiency presented in weight units to efficiency presented in energy units.

Diet Digestibility

In vitro DM and OM digestibility and consequently calculated ME of the diets in P1 and P3 were identical. However, in vivo DMD, OMD, and consequently actual diet DE and ME of the P3 TMR were higher ($P < 0.05$) compared to the P1 TMR. We propose that digestive gut fill was increased in P2. Brosh *et al.* (1995) showed that rumen fill increased significantly when intact growing Holstein bull calves were fed a low-energy diet. Greater digestive gut fill enables longer mean retention time of the feed in the digestive tract, resulting in improved feed digestibility. Although there was a long period of adaptation between P2 and P3, we suggest that gut fill was still significantly greater than normal in proportion to BW in calves at this age. Consequently, this high gut fill may have led, in the present study, to a smaller carcass weight to BW ratio (52.2%) than acceptable for this breed (55.6%, Brosh *et al.*, 1995). The negative relation between RFI and in vivo DMD could be interpreted as a tendency of the more efficient calves for improved digestibility. We suggest that this tendency could be resulted from the smaller DMI of the more efficient calves, which led to longer retention time of the feed in the digestive tract and thus to increased diet digestibility.

Individual Variation of Fat and of Protein in Tissue Gain

Carcass fat and protein proportions represent the accumulated effects of all study periods, plus

adaptation time between periods, including P2 with a long period of 149 d (30 d adaptation + 119 d test), where the calves were maintained on a negative energy balance. To prevent bloating, MEI and consequently ADG were also limited throughout part of the 45-d adaptation time between P2 and P3. Thus, conclusions regarding carcass traits are limited and surely do not represent specific period effects. Throughout all study periods, we measured individual calves' MEI, HP, ADG, and BCS_{diff} . As it is well known and discussed in the Appendix section, the energy content of fat tissue is significantly greater than that of protein tissue. Thus, the energy content of body gain is a reliable indicator of the proportion of protein-to-fat in body tissue gain. The weight of body bones and gut fill also affect the energy content of body gain. In the present study, the calves were purebred Holsteins and in each period all calves consumed the same diet. Thus, we can assume that the effects of changes in bones mass and gut fill on the individual variation in energy content of body gain and among classified calves to RFI groups are negligible. Therefore, the variation in RE/ADG (MJ/kg) was a highly reliable indicator of the proportion of fat-to-protein in body gain among calves' classified RFI groups. In growing calves, the amount of fat deposited in tissues (intermuscular, subcutaneous, visceral, and intramuscular) changes with age (Sainz and Hasting, 2000). Because intramuscular (marbling) fat is deposited last in growing calves (Sainz and Hasting, 2000), it mainly represents P3 in the current study. The periods' BCS_{diff} indicated only changes among subcutaneous fat and did not represent changes in the entire body fat. We assumed internal fat depot weights were significantly decreased to a very low level throughout P2 and the adaption period to P2 due to the negative energy balance in this time. This assumption was also confirmed by the significance negative BCS_{diff} in P2. As for the more mature growing calves, accretion of internal depot fat is relatively small, and intramuscular fat deposition was prominent (Sainz and Hasting, 2000). Therefore, we suggest that in the present study differences between proteins-to-fat ratio in gain were expressed in slaughter analysis, mainly by differences in intramuscular fat deposition.

We suggest that the positive ADG during P2 can be explained by the use of catabolized fat energy mainly for protein' tissue production (Schroeder and Titgemeyer, 2008). It is logical to assume that calves that had a strong drive for growth at this age would mobilize energy from fat tissue catabolism towards protein tissue anabolism. Another

possible explanation for the positive ADG in P2 is the growth of bones and expansion of digestive tract tissues and content. Growth in animals is defined as accretion of protein, fat, and bone (Owens *et al.*, 1995). Brosh *et al.* (1995) showed that rumen volume of growing calves fed a low-energy diet significantly increased. This enabled positive ADG when the energy balance was negative. To minimize the effects of gut fill in the present study, calves were adapted to the roughage diet for 30 d prior the start P2, but it is still possible that gut fill increased in proportion to BW throughout P2 and contributed to the positive ADG.

Findings of the present study led us to conclude that L-RFI calves deposit more protein and less fat compared to H-RFI calves, when they were in positive energy balance. This is supported by the following phenomena revealed herein: Calves' ADG, during the entire study and in each period, was not affected by RFI, unlike RE which was positively related ($P < 0.001$) to RFI (Table 3). Retained energy of 6.47 MJ/d per unit of RFI (Table 3) is equal to 1.237 kg/d protein tissue or to 0.199 kg/d fat tissue (see Appendix section 2). Therefore, we suggest that increased RE by increased RFI, should be invested in fat rather than protein, in the BW weight gain. In accordance with the above, energy retained in the tissue gain (RE/ADG ratio) of the H-RFI group was greater than the L-RFI group during P1 ($P = 0.06$) and P3 ($P > 0.001$) (Table 4). Although we can estimate the proportion of protein-to-fat in body gain from the RE/ADG ratio and analyze it statistically, we decided to forego this calculation because we could not determine how changes in gut fill affected ADG, which would influence the estimation of the protein-to-fat ratio in body gain. In addition, the proportion of bone growth in ADG may not be constant in all periods, especially in P2 when calves were in negative energy balance and positive ADG. In this state, the proportion of bone growth in relation to the total daily gain was probably higher than in P1 and P3.

The significance of higher protein concentration and lower fat concentration in the longissimus muscle of the L-RFI compared to the H-RFI group (Table 7) is in agreement with the variation between L and H RFI groups in the RE/ADG measured in P3, i.e., H-RFI calves are fatter than L-RFI calves.

The effect of RFI on the ratio RE/BCS_{diff} in P3 was large and highly significant (Table 4). Because ADG and BCS_{diff} were not affected by RFI and did not differ between RFI groups, we suggest that

most of the additional RE in H-RFI, compared with L-RFI calves, was probably retained as fat in body tissues other than the subcutaneous fat, which is represented by the BCS. This conclusion is supported by the higher fat and lower protein proportion that was found in the LD of H-RFI calves at slaughter (Table 7).

Our findings with purebred Holstein bull calves are supported by previous research demonstrating that RFI is positively associated with carcass fat deposition (Herd and Bishop, 2000; Arthur *et al.*, 2001; Santana *et al.*, 2012). Richardson *et al.* (2001) examined Angus steer progeny of parents divergently selected for RFI for one generation. They found that improvement in RFI was accompanied by small changes in body composition, with greater leanness and less fat in the progeny of low-RFI parents. Several studies have found that 5% to 10% of the variation in RFI was due to inter-animal differences in carcass or empty body fat (Richardson *et al.*, 2001; Lancaster *et al.*, 2009; Basarab *et al.*, 2011).

In young crossbreed steers, Basarab *et al.* (2003) found relationships between RFI and empty body fat and water contents that were similar to our findings. It includes our finding of greater HP of the H-RFI compared to the L-RFI. Basarab *et al.* (2003) calculated HP by difference (MEI-RE), and suggested that an estimate of body fat content (e.g., backfat thickness) be included when determining RFI. Their correction is a practical method for correcting the effect of variation in body composition on selected RFI groups. In real, this correction changes the RFI units from its' original pure weight unit to a unit that is affected by energy. One of the purposes of our study was to investigate and explain the mechanism underlying individual-animal variation in efficiency among growing calves. Thus, we strongly suggest that the nonsignificant effect of RFI on ADG and its significant positive effect on the RE and on the RE/ADG ratio, which represents the greater proportion of protein-to-fat in tissue gain of the L-RFI compared to the H-RFI, is the essence of the differences between calves classified as L-RFI vs. H-RFI.

As calculated and presented (see Appendix chapter), for equal energy retained in calves' BW, greater protein deposition compared to fat deposition, should increase the HI of production. For comparable energy deposit, HI of protein deposition is 17.5 times greater than that of fat deposition (Appendix section 3). However, as protein tissue has significantly lower energy content than fat, the HI per comparable tissue weight deposition are

5.70 (Mcal/kg tissue) for protein and 2.02 (Mcal/kg tissue) for fat, i.e., per weight of tissue deposition (Appendix section 3). Consequently, HI per kg of protein tissue is 2.82 times greater than that of fat. In addition, HP for maintenance of protein tissue is 9.3 times greater than for the maintenance of fat tissues (Appendix section 4). Assuming the available substrate that is transformed to energy on the cellular level (which is related to mitochondrial function and ATP production) is not related to efficiency, leaner calves will be expected to have greater HI of production and a greater maintenance requirement among calves with the same BW and the same ADG. Thus, leaner calves should have significantly greater HP than the fatter calves. Consequently, in the present study, calves classified as L-RFI are expected to have significantly greater HP than the calves classified as H-RFI.

However, during the entire study, daily HP was positively related to RFI ($P = 0.16$ and ($P = 0.02$), when calculated per animal and MBW, respectively (Table 3). Thus, a positive RFI slope indicates an HP increase as the efficiency measured by RFI decrease.

Thus, for the present study utilizing intact growing Holstein bull calves, we conclude that calves classified as efficient according to their RFI, beyond the significant mechanism of greater protein to fat deposition, are also characterized by lower than expected HP, compared to the H-RFI calves. Similar findings related to greater protein to fat deposition, and more interesting, to lower HP of the L-RFI compared to the H-RFI steers, were described by Richardson *et al.* (2001) and Basarab *et al.* (2003) that calculated HP by difference ($HP = MEI - RE$). We suggest that after implementing Basarab *et al.* (2003) modification to include off-test back-fat thickness, the variation among classified RFI calves in FE is probably mainly related to the variation among calves HP. The variation in calves HP can be expressed by greater efficiency of substrate used for ATP production and/or by lower rate of protein degradation of the L-RFI compared to the H-RFI groups. Validation, by genomic analysis, of the above possible mechanism was presented by Karisa *et al.* (2014) and Hendriks *et al.* (2013) (Appendix sections 5 and 6).

An additional reduction in the HP of the L-RFI compared to the H-RFI group could be also related to the weight of the visceral tissues and its HP. Visceral tissue consumes a significant amount of the energy used by animals, and increased intake is positively correlated with visceral tissue weight (Meyer *et al.*, 2012, Ortigues

and Doreau, 1995). As the DMI and the MEI of the H-RFI calves were significantly greater than those of the L-RFI calves, the H-RFI calves were expected to have greater visceral tissue, which will increase their HP. The trend of lighter carcass percentage of BW of the H-RFI calves compared to the L-RFI calves could be explained by a greater bulk of visceral tissue of the H-RFI calves. This probably contributed to the lower than expected difference of HP between the L-RFI and the H-RFI calves.

Physical Activity

The activity measurements obtained in the present study did not support the hypothesis that individual-animal variation in physical activity of growing calves contributes to variation in RFI. In the present study, neck-mounted accelerometer devices designed for detection of estrus in dairy cows were used to measure physical activity. For detection of estrus, these activity devices were not validated to measure eating activity, i.e., cow's head position was down. To verify the results obtained by the neck tags' accelerometer devices, physical activity of each calf was simultaneously recorded by IceRobotic pedometers and the accelerometer devices for 2 wk during P3 (Asher, unpublished data). Indeed, also in the case of pedometers recordings, no effect of RFI on calves' activity was revealed; whereas average daily steps, measured by pedometers, were 2,891, 3,386, and 3,753, for the L-, M-, and H-RFI calves, respectively (SEM = 361, $P = 0.25$), during the same periods, activity data obtained by the neck tags were 465, 469, and 478 min/d, for the L, M, and H-RFI calves, respectively (SEM = 31, $P = 0.97$).

Herd *et al.* (2004) estimated that 5% of the intervariation in RFI of beef cattle was due physical activity. Lancaster *et al.* (2009) reported that RFI was positively related to meal duration and meal frequency. Bulls with low RFI spent 13% less time consuming meals and consumed 11% fewer meals per day compared with bulls with high RFI phenotypes. However Brosh *et al.* (2006, 2010) found that the maximum cost of total daily activity (grazing plus standing) of grazed cows was about 11% of the total daily HP (see Appendix section 7). It was found when the cows grazed on low-quality forage, when grazing time, DMI, and total daily HP were low. When cows grazed on high-quality forage, cows' intake, grazing time, and activity cost were significantly higher, but as the cows' total daily HP

were significantly higher, cows' total daily activity cost, relative to their total daily HP, was smaller (5.8% to 7.6%) (Brosh *et al.*, 2006). Consequently, we suggest that in spite of the weak positive relation between intake and daily eating and activity duration, the interanimal variation in RFI was only slightly associated with differences in total daily energy cost of activity, which is a minor proportion of the entire daily HP.

Correlation Between RFI and Other FE Indexes

When calves were in positive energy balance during P1 and P3, their efficiency (defined by RFI) was positively correlated with G:F. Others have reported similar findings in growing bulls (Nkrumah *et al.*, 2004) and in steers, during a dry summer period of low pasture availability (Herd *et al.*, 2002). Although RFI was not correlated with RG in either of the three study periods, differences in RG between calves with divergent RFI were detected during P1 ($P = 0.10$) and P3 ($P = 0.05$).

The RIG index, which combines growth and FE, was positively correlated with RFI in all study periods. Berry and Crowley (2012) also reported a positive relationship between RFI and RIG in a study with more than 3,500 bulls in Ireland. The strong correlation between RFI and RIG reported herein supports the use of RIG in addition to RFI to identify animals that are both feed efficient and fast growing.

Correlations Between RFI and Energy Utilization Indexes

RFI, by definition, is negatively associated with efficiency, with lesser values indicating favorable FE. The HP/MEI ratio is also negatively corrected with energy efficiency of production. Therefore, it is logical to assume that if RFI represents energy efficiency, it should be positively correlated with HP/MEI. However, in the current study, HP/MEI was negatively correlated with RFI in all three periods, indicating that RFI is negatively related to energetic efficiency.

Residual heat production (actual measured HP minus expected HP) may be a method to identify feed-efficient animals without the need to measure individual feed intake. In the present study, ADG was used as a proxy of RE to calculate expected HP. In comparison, Aharoni *et al.* (2006) estimated RHP in cows by calculating expected HP using RE measured directly from energy of milk production and energy balance. By

definition, animals with lower RHP are energetically more efficient as they produce less HP than expected based on BW and level of production. In the present study, the correlation coefficients of RHP to RFI were positive in all periods with P -values ranging between 0.1 and 0.3 in the three periods (Table 7).

The RHP efficiency index was based on the hypothesis that there are variations among animals in their efficiency of energy use for maintenance and production. The fact that RHP was significantly different between the RFI groups in P3 (Table 5) and that the L-RFI group had the lowest RHP is an indication of variation in basic HP among RFI groups. As the BW of the calves in P3 were significantly high, i.e., their maintenance requirements were high, the variation in HP may be related to maintenance requirements more than to ADG. Richardson *et al.* (2001) calculated RHP of steers, progeny of parents selected against RFI. They used the amount of fat and protein in gain, its specific HI for production, feeding HI and expected maintenance requirements for calculate expected HP. The observed HP was calculated as MEI – RE. Similar to our finding in P3 they found that the H-RFI calves have greater RHP than of the L-RFI calves. So, we can conclude that RHP can be used to characterize growing calves, but the expected HP calculation should be based on the protein-to-fat ratio in gain and on its energy content, and its HI. This may significantly decrease the advantage of the method.

Repeatability of Efficiency Ranking Across Diets and Ages

In this study, we report that calves classified as having high or low FE phenotypes based on RFI or RIG maintained similar rankings independent of change in diet or change in physiological age.

Compared to RIG, classification by RFI revealed the highest degree of group ranking consistency across diets (i.e., production level) and ages. These results are similar to Crews *et al.* (2003), who reported a positive correlation ($r = 0.55$) between the RFI of Charolais-crossbred steers fed roughage- or barley grain-based diets during the growing phase or the subsequent finishing phase, respectively. Archer *et al.* (2002) also reported strong phenotypic correlations with RFI ranking repeatability ($r = 0.98$; this is the genetic correlation; suggest reporting the phenotypic correlation in this discussion) in heifers and ensuing mature cows fed roughage-based diets.

However, compared to the level of repeatability of RFI ranking in our study and the above-mentioned studies, other authors reported only a moderate repeatability of RFI ranking in steers fed a growing diet followed by a finishing diet ($r = 0.33$; Durunna et al., 2011) and in beef heifers fed high-forage and high-concentrate diets during the growing and finishing periods, respectively ($r = 0.62$; Kelly et al., 2010).

Dissimilarity in the degree of RFI repeatability in the present study vs. Durunna et al. (2011) and Kelly et al. (2010) might be due to differences between the animals used in the studies. The pure Holstein intact bull calves used in the present study keep their potential for protein deposition at least until the age of 17 mo (Brosh et al., 1995), whereas the potential for protein (muscle) deposition decreases at an early age in castrated calves, steers, and heifers.

Recently, Potts et al. (2015) reported significant RFI ranking repeatability in lactating cows fed a high-starch diet compared with the RFI of the same cows fed a low-starch diet, suggesting that dietary starch and fiber content had little effect on a cow's relative ranking for RFI efficiency. Moreover, RFI ranking also seems to be repeatable across lactations and stages within lactation (Connor et al., 2013; Tempelman et al., 2015). Recent studies have demonstrated that postweaning RFI in growing heifers was favorably associated with RFI in pregnant beef cows (Hafila et al., 2013) and lactating dairy cows (Macdonald et al., 2014).

The novel findings reported herein and by others demonstrate that RFI ranking is highly repeatable across diets and ages, highlighting its reliability as a FE trait. In practice, this means that RFI can be potentially used to select feed-efficient calves over a wide range of production levels and ages. The high correlation between RFI and RIG reported herein can assuage the concern that selection for L-RFI may affect calves' potential for high ADG.

Plausible contribution to the current observed differences between high vs. low-RFI calves, may be acquired from a recent genome-based analysis, performed on their DNA. In that analysis, single-nucleotide polymorphisms (SNP) associated with RFI, in at least one of the three nutritional stages described in the current study were identified (Cohen-Zinder et al., 2016). Some of the polymorphisms were detected in genes encoding for proteins involved in biological pathways

associated with fat and protein metabolism, and energy expenditure. For example, 11 SNP were detected in the *FABP4* gene, a lipid transporter involved in fatty acid uptake and metabolism in fat tissue. Of these, the promoter polymorphism *FABP4_5* differed significantly between H and L-RFI calves in all three periods. Other significant SNP were found in peroxisome proliferator-activated receptor-gamma (*PPARG*), a master regulator of adipocyte differentiation. Polymorphisms involved in protein metabolism were found in the myosin heavy chain 3 and 13 (*MYH3*; *MYH13*) genes that differed significantly between L- and H-RFI calves. The genomic analysis we performed uncovered SNPs in the promoter region of uncoupling proteins 1 (*UCP1*) and 2 (*UCP2*) genes, both involved in oxidative phosphorylation-dependent ATP synthesis from energy dissipated as heat (mitochondrial proton leak). Additional SNPs differing between the H-RFI and the L-RFI calves were found in the promoter region of the *ATP5A1* gene, which encodes a subunit of mitochondrial ATP synthase that catalyses ATP synthesis, using an electrochemical gradient of protons across the inner membrane during oxidative phosphorylation. These findings may support the assumption of involvement of mitochondrial ATP production in the mechanism of higher efficiency mediated by HP, as reflected in the current study. However, such assumptions need to be functionally validated at cellular level.

CONCLUSIONS

In the present study utilizing growing Holstein bull calves, classifying the calves according to their RFI and RIG efficiency indexes was consistent across a wide range of diets and ages. The greater protein-to-fat ratio in tissue gain was the major factor that characterized the more efficient calves as classified by RFI and RIG. RFI represented production efficiency in weight units, but it was negatively related to efficiency presented in energy units. RFI, as measured in confined pens for this study was not related to variation in physical activity. The present study indirectly supports the hypothesis that more efficient energy utilization contributes significantly to the more efficient maintenance and production, which characterizes the calves classified as L-RFI compared to the calves classified as H-RFI.

Conflict of interest statement. None declared.

Figure 1. Schematic diagram of experimental design. Twenty-six healthy Israeli Holstein intact male calves were housed for 405 d in a shaded open feedlot. The study was carried out in three periods (P1, P2, and P3). Energy balance presented by: Metabolizable energy, ME intake, MEI; Retained energy RE; Heat production, HP. Efficiency traits were calculated as: Residual feed intake, RFI; Gain-to-feed ratio, G:F; Residual BW gain, RG; Residual intake and gain, RIG; Residual heat production, RHP; HP to MEI ratio, HP/MEI.

APPENDIX

POSSIBLE MECHANISMS TO EXPLAIN INTERANIMAL VARIATION OF PRODUCTION EFFICIENCY, A THEORETICAL INTRODUCTION

Factors affecting energy efficiency of DMI and MEI partitioning for growth and maintenance throughout growth are mainly defined by the following factors:

1) Feed digestibility, which is calculated to diet ME (Oddy and Herd, 2001):

As diet digestibility increased, the available energy for production and maintenance per kg DM intake and per daily consumption increases the efficiency of using the energy for production and maintenance (NRC, 1984)

2) Energy accumulated in tissue gain that depends on the composition of the deposit tissues:

The heat of combustion (Mcal/kg DM) of protein is 5.68 (Lofgreen, 1965, Tedeschi

et al., 2004), and that of fat is 9.37 (Geay, 1984, Tedeschi *et al.*, 2004). The ash and water content of the deposited tissue are 5% and 73%, respectively, for protein tissue (Tedeschi *et al.*, 2004), and 3.89% and 13.14%, respectively, for fat tissue (Ferrell and Jenkins, 1998). Thus, the proportion of protein and fat tissues, free of water and ash, are 22% and 83%, respectively.

Based on the above, this accounts for:

Protein tissue energy content of $5.68 \times 0.22 = 1.25$ Mcal/kg tissue.

Fat tissue energy content of $9.37 \times 0.83 = 7.78$ Mcal/kg tissue.

Which are equivalent of 5.23 kJ/kg tissue and 32.54 kJ/kg tissue for protein and fat deposit tissues, respectively.

3) The energy cost required for tissue deposition, and the HI of protein and fat deposition: According to DiCostanzo *et al.* (1990), the ME needed for the production of protein and fat with a content of 1 kcal are 5.56 kcal and 1.26 kcal, respectively.

This constitutes energy efficiency of production for:

Protein deposition $(1 \text{ kcal})/(5.56 \text{ kcal}) = 18.0\%$, which is HI of 82%, i.e., the $1 - \text{efficiency}$ fraction.

Fat deposition $(1 \text{ kcal})/(1.26 \text{ kcal}) = 79.4\%$ which is HI of 19.6%.

Tedeschi et al. (2004, page 187) discuss the subject, citing Lofgreen (1965), CSIRO (1990), and Rattray et al. (1974). Rattray et al. (1974) reported energy cost of 8.14 (instead of 5.56) Mcal ME diet for Mcal protein tissue deposition and 1.1 (instead of 1.26) Mcal ME diet to Mcal fat deposition. This constitutes energy efficiency of production for:

Protein deposition $(1 \text{ kcal})/(8.14 \text{ kcal}) = 12.3\%$ which is HI of 87.7% (instead of 82%).

Fat deposition $1 \text{ (kcal)}/1.1 \text{ (kcal)} = 90.9\%$ which is HI of 9.1% (instead of 19.6%).

The difference between the above-cited efficiencies can be related to the variation in diet quality (ME) used for tissue deposition, i.e., efficiency of ME use for NE, which increases with diet quality (NRC, 1984, Page 3).

Considering the range of the above two references, the energy cost of using energy of diet ME, to energy of tissue gain, of protein deposition is 4.4 to 7.4 times greater than that of fat deposition.

Thus, according to DiCostanzo et al. (1990) the energy cost of using an ME diet (Mcal) for depositing 1 kg tissue are:

For protein tissue = $5.56 \text{ (Mcal/Mcal)} \times 1.25 \text{ (Mcal/kg protein tissue)} = 6.95 \text{ (Mcal ME/kg protein tissue gain)}$.

For fat tissue = $1.26 \text{ (Mcal/Mcal)} \times 7.77 \text{ (Mcal/kg fat tissue)} = 9.79 \text{ (Mcal ME/kg fat tissue gain)}$.

Consequently the HI (Mcal) of production of 1 kg tissues are:

For protein tissue = $6.95 \text{ (Mcal ME/kg protein tissue production)} - 1.25 \text{ (Mcal/kg protein tissue content)} = 5.70 \text{ (Mcal/kg protein tissue gain)}$.

For fat tissue = $9.79 \text{ (Mcal ME/kg fat tissue production)} - 7.77 \text{ Mcal/kg fat tissue content} = 2.02 \text{ (Mcal/kg fat tissue gain)}$.

When the HI of protein and fat are calculated per energy deposit in tissue:

HI of protein = $5.70 \text{ (Mcal/kg)}/1.25 \text{ (Mcal/kg protein tissue)} = 4.56 \text{ (Mcal/Mcal)}$

HI of fat = $2.02 \text{ (Mcal/kg)}/7.77 \text{ (Mcal/kg protein tissue)} = 0.26 \text{ (Mcal/Mcal)}$

Thus, according to energy-based calculation the HI of protein deposition is 17.5 times greater than that of fat deposition.

4) The effect of protein and fat accumulated in BW, i.e., the protein to fat ratio in BW and its effect on the maintenance requirement:

The energy required for the maintenance of protein or fat tissues are 192.9 and $20.7 \text{ kcal} \times \text{kg BW}^{-0.75} \times \text{d}^{-1}$ respectively (DiCostanzo et al., 1990), which is the equivalent of 807.1 and $86.6 \text{ kJ} \times \text{kg BW}^{-0.75} \times \text{d}^{-1}$, respectively. This means that the maintenance requirement of protein tissue is 9.3 times greater than that of fat tissue. As discussed above, the proportion of protein and fat, free of water and ash, in their respective live tissues are 22% and 83%, consequently per protein and fat, free of water and ash, the maintenance requirement of protein tissue is 35.2 times greater than that of fat tissue. This means that cattle with significantly higher protein than fat content will have greater maintenance requirements, which negatively affect the energy efficiency of production. The above effect on the maintenance requirement was combined with the effect of animals' increased BW with age, which increased maintenance requirements and consequently decreased the animals' production efficiency. Thus, the rate of decrease of calves' efficiency with age, as BW increased, is expected to be greater for leaner calves compared to fatter calves.

5) The effect of the variation in calves' HP and efficiency:

Animals' HP is defined as the metabolizable energy required for maintenance and HI of production (AFRC, 1993; NRC, 2001). In addition to the above discussed sources of variations of calves efficiency, there is individual variation in production efficiency that is related to the efficiency of using the available substrate for energy supplements, i.e., the processes that may account for interanimal HP variation include ion pumping ($\text{Na}^+/\text{K}^+ \text{ATPase}$), mitochondrial proton leak, uncoupling proteins (UCP), thyroid hormone, leptin and IGF-1 (Bottje et al., 2002; Chilliard et al., 2005; Kolath et al., 2006).

In the present study, we did not investigate the above subject directly, but we suggest that energy efficiency indexes such as the HP/

MEI ratio and RHP and also the other efficiency indexes can be affected by variation among individuals in processes related to energy utilization on a cellular basis. Genetics' markers for this possible mechanism among individuals classified to efficiency groups are presented by [Karisa *et al.* \(2014\)](#) and by [Hendriks *et al.* \(2013\)](#).

6) Protein tissue degradation rate:

Part of the maintenance energy cost of protein tissue is the energy cost of protein tissue turnover, i.e., the cost of depositing new protein tissue replacing degraded protein tissue. Any reduction in the protein tissue degradation rate will reduce the energy cost of maintenance, as presented by [Karisa *et al.* \(2014\)](#) and by [Hendriks *et al.* \(2013\)](#).

7) Calves' physical activity:

Physical activity increases the maintenance requirement, which is expressed by greater HP and less energy for production, i.e., for RE. [Brosh *et al.* \(2006, 2010\)](#) found that the cost of total daily activity (standing, grazing, walking, and locomotion cost) for grazing cows is not high, its maximum values are about 11% of the total daily HP. However, physical activity, especially of growing grazing animals, and its effect on the difference of MEI-HP, i.e., on the daily RE, may still affect the calves' efficiency significantly.

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