Indian J. Anim. Nutr. 2019. 36 (2): 113-121
doi: 10.5958/2231-6744.2019.00021.5

Indian Journal of Animal Nutrition

Growth Performance, Feed Efficiency and Ingestive Behavior of Sahiwal Calves Divergently Selected for Residual Feed Intake

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ABSTRACT

This study aimed to evaluate differences in performance, feed utilization efficiency, and ingestive behavior between low and high residual feed intake (RFI) growing cattle. Eighteen growing female Sahiwal calves (age 10±4 months,body weight 100±45 kg) were fed individually using *ad libitum* feeding of total mixed ration for a period of 90 days. RFI varied from -0.53 to 0.40 kg dry matter (DM)/day with a mean RFI of -0.27 to 0.17 kg DM/day in low and high RFI calves, respectively. Significant ($P<0.001$) differences between low and high RFI calves were observed for daily DM intake (DMI). Calves with low RFI consumed 26% less DM compared to high RFI group yet gaining at similar rate. Low RFI calves needed 35% less metabolizable energy for body maintenance (MEm) compared to high RFI calves while metabolizable energy for gain (MEg) was similar among both groups. Low RFI calves digested feed more efficiently than high RFI calves. Low RFI calves were also more efficient in feed conversion, feed efficiency, Kleiber ratio (KR), and relative growth rate (RGR) than high RFI calves. Low RFI calves consumed less feed than high RFI calves, therefore, spent less time in feeding, rumination, and chewing. RFI was positively correlated with DMI, MEm and MEg and gain while negatively correlated with traditional feed efficiency measures and ingestive behavior. This study suggests that low RFI calves are more efficient because they eat less and require less energy for physical activity and feeding pattern.

Keywords: Efficiency, Ingestive behavior, Performance, Residual feed intake, Sahiwal calves

INTRODUCTION

India harbors world's largest cattle population and ranked first in milk production in the world. In spite of achieving the highest milk production, the performance of Indian cattle has been extremely poor and the average milk productivity per milch cow falls far below that what has been achieved by the developed countries. Poor performance of indigenous cattle is due to older age at maturity, thus, they consume larger amount of feed before attaining sexual maturity. Feed cost for maintenance is estimated to represent at least 60 to 65% of the total feed requirements for the cow herd with considerable variation among individual animals independent of body size (NIANP, 2013). Improving feed utilization efficiency and selection of energetically efficient animals could help in reducing the burden of already scarce feed resources particularly in developing countries (Nkrumah *et al.,* 2006).

Earlier, genetic selection programs have focused on production traits with lesser attention given to production costs. Recently, this view begun to change and the efficiency of conversion of feed has been recognized as more important tool.Several measures of feed utilization efficiency calculated as a function of individual intake and body weight gain have been proposed over the years in an attempt to quantify the capacity of animals to convert the ingested feed into a product. Selection based on traditional measures like feed conversion ratio (FCR) and feed conversion efficiency (FCE) is most common, but these measured ratios are closely associated with feed intake and rate of gain (Koots *et al.,* 1994a) which may result in higher mature body weight that may not be desirable under many circumstances (Archer *et al.,* 1998).Therefore, residual feed intake (RFI) was introduced as an alternate measure of feed efficiency. The RFI referred

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to as net feed intake or net feed efficiency and it is defined as the difference between actual feed intake and predicted feed intake on the basis of requirements for maintenance and current level of production (Koch *et al.,* 1963). It has been found that more efficient cattle (low RFI) have multiple benefits such as decreased feed intake, less manure production, and less methane emission (Nkrumah *et al.,* 2006; Hegarty *et al.,* 2007; Kuldeep Dudi *et al.,* 2016; Negesse *et al.,* 2016).

The biological basis that contribute to the variation in RFI includes, ingestive behavior, feed intake, digestion of feed and associated energy use, metabolism, including anabolism and catabolism, activity and thermoregulation (Nguyen *et al.,* 2005). The RFI tended to be correlated with apparent digestibility of nutrients and animals with low RFI had higher nutrients digestibility compared to animals with high RFI. Low and high RFI animals differ in their feeding pattern, a fact that is mainly due to differences in amount of feed ingested and in rumination time.The identification of low RFI farm animals and ultimately using them for breed improvement programme can go a long way in attaining the objectives of breed improvement and efficient nutrient utilization. Considering these facts, the present study is designed to investigate the performance of dairy calves divergently selected for low and high RFI. The hypothesis of the present study is that RFI is related to feed efficiency and performance and difference exist between calves with divergent RFI.

MATERIALS AND METHODS

The use of the animals and the experimental procedure was approved by the Institutional Animal Ethics Committee (IAEC) constituted as per the article number 13 of the Committee for the Purpose of Control and Supervision on Experiments on Animals (CPCSEA) rules, laid down by the Government of India (approval no. 110/ IAEC/16).

Eighteen growing female Sahiwal calves (Av. age = 4 months, BW=100 kg) were selected from the herd maintained at Instructional Livestock Farm Complex (ILFC), DUVASU, Mathura, India. All the experimental calves were fed *ad lib* on total mixed ration (TMR) based diet consisted of concentrate mixture: green oat fodder: wheat straw in the proportion of 50: 20: 30 (on DM basis) for a period of 90 days based on the recommendations of Archer *et al.* (1997) for the optimum test duration for measuring RFI.The compounded concentrate consisted of 20 parts barley grain, 20 parts wheat grain, 8 parts gram chuni, 20 parts wheat bran, 30 parts mustard oil cake (expeller extracted) and 2 parts mineral mixture. The TMR was prepared daily by hand mixing separately for each calf. TMR contained 14.80% CP, 46.70% TDN and 2.33 Mcal ME/kg DM (Table 1). The calves were fed TMR in such an amount that at least 1 kg refusals were left daily per calf. All experimental calves were housed in a well ventilated shed having proper arrangements for individual animal feeding. One daily meal of TMR was offered at 09:00 h to each calf. Fresh drinking water was offered *ad lib* twice daily at 08:00 h and 17:00 h. Deworming of all the experimental animals was done before the start of the experiment by oral administration of Fentas bolus (Intas Pharmaceuticals Pvt. Ltd., India).

To compare the efficiency of nutrient utilisation in low and high RFI calves, a digestion trial with an adaptation period of 4 days followed by a collection period of 6 days was conducted at the end of the study. TMR offered and refusal left were sampled daily for chemical analysis. Faces excreted during 24 h were collected and measured daily for 6 days. 1/100 part of thoroughly mixed total faecal matter was taken for chemical analysis. Daily, 1% of total faecal sample was collected separately and stored in plastic containers having 30 ml of 25% sulphuric acid solution for nitrogen (N) estimation.

All experimental calves were monitored daily for DMI and fortnightly for growth performance, feed efficiency measures and ingestive behavior.Feed offered and refusal left were weighed daily, sampled twice per week, and pooled to represent each period of 90 days for DM determination. DMI was calculated as the difference between the amount offered and refusal left. To increase the accuracy of estimation of average daily gain (ADG), calves were weighed at fortnight intervals in early morning (06:00h) before offering feed and water. Along with RFI, calves were also monitored fortnightly for other feed efficiency measures like FCR (feed-to-gain-ratio), FCE (gain-to-feed-ratio), Kleiber ratio (KR), partial efficiency of growth (PEG), and relative growth rate (RGR). FCR was calculated as the ratio among DMI and ADG; FCE was calculated as the ratio between ADG and DMI. KR was calculated as the ratio between ADG and average metabolic body weight, and PEG was calculated as the ratio between ADG per unit of feed used for growth (NRC, 2001). RGR was calculated according to Fitzhugh and Taylor (1971):

$$\text{RGR} = 100 \times \frac{(\text{log Final BW} - \text{log Initial BW})}{\text{days of experiment}}$$

At mid of study, ingestive behavior was determined by monitoring calves for feeding, chewing, rumination, idleness, standing and lying. The behavioral events were recorded manually by four observers, each of them responsible for a daily period of 6 h. Feeding time (FT; min/d) was counted as total time spend by calf in consuming TMR during 24 h. Three rumen boluses per calf were observed during rumination and the number and time of chewing per bolus was counted as chewing rate (CT). Rumination time (RT) was total time during 24 h in which calf ruminated. Time spent on idleness (TI) was calculated by deducting duration of events (min/d) with total duration of day (1440 min). To determine the time of activity spent with the diet (min/kg DM) like feeding time per kg DM (FTDM), rumination time per kg DM (RTDM) and chewing time per kg DM (CTDM), total duration of the activities was divided by the total amount of feed consumed.

ADG was determined by using linear regression coefficient of weights as a function of days in trial

Table 1. Ingredient and chemical composition of TMR fed during experimental period (expressed as g/kg of DM)

Item	Concentrate	TMR
Oat fodder		200
Wheat straw		300
Concentrate		500
Barley grain	200	
Wheat grain	200	
Gram chuni	80	
Wheat bran	200	
Mustard oil cake	300	
Mineral mixture	20	
Chemical composition of TMR (g/kg DM)		
Dry matter	556	
Organic matter	918	
Crude protein	148	
Total ash	92	
Ether extract	32.7	
Crude fibre	325	
Nitrogen free extract	392.3	
Neutral detergent fibre	653.2	
Acid detergent fibre	391.1	
Acid detergent lignin	67.5	
Total digestible nutrient	467	
Metabolizable energy (Mcal/kg DM)	2.33	

TMR, total mixed ration; ME, metabolizable energy (calculated as per NRC, 2001) following Archer *et al.* (1997):

$$y_i = \alpha + \beta \times DIT_i + e_i$$

Where, y_i is the calves' bodyweight in the i^{th} observation, α is the intercept of the regression equation corresponding to the initial body weight, β is the linear regression coefficient corresponding to ADG, DITi is the days in trial in the i^{th} observation and e_i is the random error. Mid-test metabolic body weight (MBW) was calculated by using following equation:

$$MBW = [\alpha + \beta \times \text{study period}/2]^{0.75}$$

Where, α is the intercept of the regression equation corresponding to the initial body weight and β is the linear regression coefficient corresponding to ADG. Calves were classified into low and high RFI groups. RFI was calculated by using the following formula:

RFI (kg/d)=Actual DMI (kg/d)–Predicted DMI (kg/d)

The amounts of DM offered and refusal left were measured daily and the actual DMI was calculated by difference. Predicted DMI of individual calf was calculated by using multiple regression models:

$$Y_j = \beta_0 + \beta_1 MBWj + \beta_2 ADGj + e_j$$

Where, Y_j is the predicted DMI of the j^{th} animal, β_0 is the regression intercept, β_1 is the regression coefficient on MBW, β_2 is the regression coefficient on ADG, e_j is the uncontrolled error of the j^{th} animal. Observed and required MEm and MEg were calculated by following equations:

MEI observed (Mcal/d)=DMI ×ME of feed

Where, MEI is the metabolizable energy intake.

MEm observed (Mcal/d) = MEI observed – MEg observed

MEm required (Mcal/d) = 122 × $BW^{0.75}$/1000

MEg observed (Mcal/d) = (4.1 + 0.0332 × W-0.000009 × W^2)) / (1-0.1475 × WG)

Where, W is the live weight (kg) and WG is the live weight gain (kg/d).

MEg required (Mcal/d) = MEI required –MEm required

The representative samples of TMR offered, residues left and faeces (collected during digestion trial) were dried in a hot air oven at 60°C till a constant weight was attained and then ground in a Wiley mill to pass a 1 mm sieve. Dried and ground samples were pooled animal wise and stored at dry place for further analysis of DM, CP, ether extract and acid insoluble ash (AOAC, 2005). Neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) were determined according to the procedures described by Van Soest*et al.* (1991).

The data were analysed for significance (P<0.05) and correlation coefficient (r) by using Statistical Package for the Social Sciences (SPSS for Windows, V21.0; SPSS Inc., Chicago, IL, USA). Significance was analysed by using one way analysis of variance (ANOVA). An alpha level of 0.05 was used for the determination of statistical significance.Greater or lower than zero value of Pearson square correlation coefficient shows positive or negative correlation between RFI and attributes, whereas, zero value of Pearson square correlation coefficient shows no correlation between RFI and attributes.

RESULTS AND DISCUSSION

Significant differences (P<0.05) between low and high RFI calves were observed for feed intake, low RFI calves consumed 26% less DM than calves of high RFI group (Table 2).Out of eighteen calves, the observed DMI of eleven calves was lower than the expected DMI (low RFI), whereas, that of remaining seven calves was higher than the expected DMI (high RFI) (Fig. 1). The difference in observed and required DMI (RFI) averaged 0.17 kg/day and -0.27 kg/day in low and high RFI groups, respectively.

The minimum and maximum values for RFI were -0.53 and 0.40 kg DM/day. The least efficient calf consumed 0.930 kg DM/day more feed than the most efficient calf. ADG was statistically similar among low and high RFI groups.In this study, positive correlation were observed among RFI and DMI (r = 0.756) while correlation with ADG (*r* = 0.191) was weak. On an average, low RFI calves consumed 26% less feed than high RFI calves, a value that agrees very well with the 19% differences in the Murrah buffalo calves divergently selected for low (-0.14 kg/day) and high RFI (0.14 kg/day) with no difference in body weight gain (Sharma *et al.,* 2016).Nascimento *et al.* (2015) noted that low RFI (≤0.128 kg/day) Nellore cattle consumed 7.2 kg DM/day which was 14.0% less than animals with

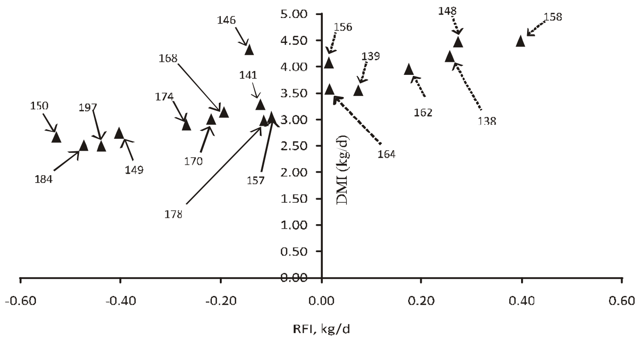

Fig. 1. Dry matter intake in low and high RFI Sahiwal calves

high RFI (>0.135 kg/day), although no significant differences in ADG were observed among RFI classes. The 10% reduction in DMI by the low RFI Murrah buffalo calves than high RFI (-0.20 *vs.* 0.23 kg DM/day) despite no differences in body weight gain was reported by Bose *et al.* (2014). Accordingly, no differences in ADG were detected between Sahiwal calves of low and high RFI despite the fact that high RFI calves consumed 19.6% more feed than low RFI calves (Sharma *et al.,* 2014). Results of low DMI in more efficient animals were also reported Bonilha *et al.* (2013), who found a difference of 0.656 kg/day between low and high RFI Nellore bulls with similar body size and growth rate. Fitzsimons *et al.* (2014) observed similar ADG among low and high RFI heifers (-0.43 *vs.* 0.44 kg/day) even though high RFI beef heifers consumed 16% more feed DM than low RFI heifers. Other studies also reported lower feed intake and similar growth rate in low RFI animals than high RFI animals (Sobrinho *et al.,* 2011; Steyn *et al.,* 2014). In this regard, Bonilha *et al.* (2013), Nascimento *et al.* (2015) and Sharma *et al.* (2016) reported a positive correlation between RFI and feed intake whereas the

Table 2. Intake and digestibility of nutrients in low and high RFI calves

Attribute	**RFI**		**SEM**	**P-value**$^{\beta}$	**r**$^{¥}$
	Low (-0.27)	**High (0.17)**			
Initial BW(kg)	85	114	5.64	0.003	0.652
Mid-test BW(kg)	108	137	5.89	0.028	0.659
Final BW(kg)	135	165	6.05	0.002	0.669
MBW(kg)	33.50	46.04	1.57	0.003	0.667
DMI (kg/d)	3.01^{a}	4.06^{b}	0.38	<0.001	0.756
DMI(kg/100 kg BW)	2.95	3.01	0.08	0.072	0.293
DCPI (kg/d)	0.348^{a}	0.456^{b}	0.03	0.002	0.673
ME intake observed (Mcal/d)	6.50^{a}	8.77^{b}	0.34	<0.001	0.756
MEm observed (Mcal/d)	4.09^{a}	6.28^{b}	0.30	<0.001	0.767
MEg observed (Mcal/d)	2.41	2.49	0.05	0.085	0.417
ADG (kg/d)	0.549	0.570	0.02	0.346	0.191
Apparent nutrient digestibility (g/kg DM)					
Dry matter	631	610	7.60	0.153	-0.351
Organic matter	678	664	4.62	0.398	-0.212
Crude protein	782	759	9.70	0.106	-0.393
Ether extract	918	896	6.30	0.319	-0.547
Neutral detergent fibre	587	580	13.2	0.721	-0.090
Acid detergent fibre	503	502	18.5	0.797	-0.007

$^{\beta}$Mean with different superscript in a row differs significantly (P< 0.05); $^{¥}$Pearson square correlation coefficient between RFI and attributes; RFI, residual feed intake; SEM, standard error of mean; BW, body weight; MBW, mid-test metabolic body weight; DMI, dry matter intake; DMIBW, dry matter intake in relation to body weight; DCPI, digestible crude protein intake (estimated during digestion trial); MEm, metabolizable energy for maintenance (as per NRC, 2001); MEg, metabolizable energy for gain; ADG, average daily gain correlation between RFI and body weight gain was 0. A lower feed intake in more efficient calves without alteration in growth rate imply that these animals were more efficient in utilizing feed nutrients for tissue growth as a result of higher metabolizability of consumed feed.

The total ME intake observed and ME used for body maintenance (MEm) was significantly higher (P<0.001) in less efficient (high RFI) calves than more efficient (low RFI) calves (Table 2). Low RFI calves required 35% less MEm compared to high RFI despite no difference observed for MEg between both groups. Medium positive correlation were noted among RFI and MEm observed (r = 0.767) and MEg observed (r = 0.417). RFI takes into account the energy requirements for maintenance and production and is more sensitive to variations in energy efficiency of the individual animals (Dittmar, 2007). Sharma *et al.* (2016) observed 12.5 *vs.* 16.7 MJ/dayMEm and 7.5 *vs.* 7.9 MJ/dayMEg, respectively in low and high RFI Murrah buffalo calves which is in accordance with the findings of our study. Bose *et al.* (2014) have also reported that more efficient calves needed lower ME for body maintenance than the less efficient calves, whereas, ME required for gain was similar among two groups. Lower energy requirement for body maintenance in more efficient animals were also reported by Pitchford (2004) and Richardson and Herd (2004). Lower feed intake, high metabolizability of feed, and lower energy expenditure for feeding and rumination are some of the reasons that contribute to lower maintenance energy requirements in more efficient calves when compared to less efficient calves (Oddy and Herd, 2001). The differences in feed intake between animals could affect RFI status because increased feed intake is associated with increased energy expenditure towards digestion processes, thereby, increasing the maintenance requirement (Oddy and Herd, 2001). This could be due to an increased mass of digestive tissues, as the mass of digestive tissues increases, the metabolism of these tissues may be altered, reducing digestive efficiency.

Although the digestibility coefficients for majority of the nutrients were higher for low RFI group as

Table 3. Measures of feed efficiency and ingestive behavior in low and high RFI calves

Attribute	RFI		SEM	P-value[β]	r[¥]
	Low	High			
Feed efficiency measures					
RFI, kg DM/d	-0.27	0.17			
Feed conversion ratio	5.51[a]	7.28[b]	0.4	0.002	0.670
Feed conversion efficiency	0.20[b]	0.15[a]	0.01	0.002	-0.668
Kleiber ratio	0.02[b]	0.01[a]	0.001	0.004	-0.645
Relative growth rate	0.225[b]	0.105[a]	0.01	0.013	-0.575
Body condition score	2.55	2.75	0.17	0.153	0.351
Partial efficiency of growth	2.90	2.95	0.36	<0.001	0.019
Ingestive behavior (min/d)					
Feeding time	271.91	281.71	4.30	0.595	0.134
FTDM (min/kg DM)	92.38[b]	69.56[a]	3.93	0.006	-0.619
RTDM (min/kg DM)	55.65	44.97	9.37	0.137	-0.364
Chewing time	227.64	236,29	11.20	0.365	0.227
CTDM (min/kg DM)	77	58.35	5.19	0.238	-0.293
Time spent on idleness (min/d)	1004	980	10.50	0.357	-0.231

[β]Mean with different superscript in a row differs significantly (P< 0.05); [¥]Pearson square correlation coefficient; RFI, residual feed intake; SEM, standard error of mean; FTDM, feeding time kg^{-1} dry matter; RTDM, rumination time kg^{-1} dry matter; CTDM, chewing time kg^{-1} dry matter.

compared to the high RFI group but mean value showed non-significant differences between the groups (Table 2). The correlation between RFI and nutrient digestibility were weak to medium negative, *viz*. -0.351 with DM digestibility, -0.393 with CP digestibility and -0.090 with NDF digestibility. Nkrumah *et al.* (2006) observed 6% higher apparent digestibility of DM in low RFI group than high RFI group, indicating that animals with a low RFI are more efficient in nutrient utilization than with a high RFI. Richardson *et al.* (2001) observed digestibility estimates in growing cattle divergently selected for low and high RFI after one generation. When fed the roughage-based diets, low RFI bulls and heifers tended to have higher digestibility compared to the high RFI bulls and heifers. However, similar nutrient digestibility between low and high RFI animals were observed by Bose *et al.* (2014) and Sharma *et al.* (2016) which might be due to a closer variation in RFI among groups with low and high RFI. Variations in intake and digestibility could be attributed to the shift in rumen microbial community between efficient and inefficient animals (Guan *et al.,* 2008). There were significant differences in FCR (P=0.002), FCE (P=0.002), KR (P=0.004), RGR (P=0.013), and PEG (P<0.001) (Table 3).

Low RFI calves were 24% more efficient than high RFI calves in feed conversion, 25% more efficient in feed efficiency, 29% more efficient in the KR, and 31% more efficient in RGR. RFI showed negative correlation with FCE (*r*=-0.668), KR (*r*=-0.645), and RGR (*r*=-0.575) and positive correlation with FCR (*r*=0.670), PEG (*r*=0.019), and BCS (*r*=0.351).Low RFI animals showed greater residual weight gain, residual intake-weight gain, feed efficiency, and PEG as well as lower FCR than animals with medium and high RFI, respectively (Nascimento *et al.,* 2015). Earlier reports (Bose *et al.,* 2014; Sharma *et al.,* 2014; Sharma *et al.* 2016) also noted better FCR in low RFI animals than high RFI animals. Nkrumah *et al.* (2006) and Kayser and Hill (2013) obtained a difference of 18% and 17%, respectively in FCR between animals classified as low RFI and high RFI group. In contrast, Nkrumah *et al.* (2004) found that the two measures (PEG and RFI) were similar among low and high RFI groups. Kelly *et al.* (2014) observed negative correlation between RFI and FCE but not with ADG, KR, or RGR. A weak positive correlation of 0.12 between KR and RFI was estimated, as well as a strong negative correlation of -0.64 between KR and FCR (Steyn *et al.,* 2014). The correlation between RFI and FCR was estimated to be 0.67 which is similar to previously published estimates ranging from 0.57 to 0.85 (Nkrumah *et al.,* 2004; Van der Westhuizen *et al.,* 2004). Our findings also agree with these indicating that applying selection pressure for FCR or FCE would likely lead to an increase in mature size and thus an increase in maintenance energy and feed requirements.

Less efficient (high RFI) calves consumed more feed than more efficient (low RFI) calves (3.01 *vs.* 4.06 kg/day), therefore, spent more time in feeding (P=0.595), rumination (P=0.479) and chewing (P=0.365) (Table 3).Less efficient calves consumed 26% more feed and took 7.72% more time in feeding, 23% more time in rumination and 18% more time in chewing than more efficient calves. The time of activity spent with the diet i.e. FTDM and CTDM (min/kg DM) were significantly (P<0.05) higher in more efficient calves as compared to less efficient calves. More efficient calves spent more (P=0.357) time in resting (idleness) than less efficient calves. RFI showed positive correlation with FT (*r*=0.134), RT (*r*=0.178), and CT (*r*=0.227) while negative correlation with TI (*r*=-0.231). The correlation between RFI and time of activity spent with the diet was medium to high, including -0.619 with FTDM, -0.364 with RTDM and -0.293 with CTDM. The feeding behavior of animal can alter physical activity and thus influence total energy expenditure and feed efficiency (Susenbeth *et al.,* 1998). Similar to the findings of present study, Kelly *et al.* (2010a) found that high efficient animals spent less time and energy in this activity and more time in sedentary activities possibly saving energy that is directed towards weight gain. A shorter bunk visit duration in more efficient animals than less efficient animals was also noted by Lancaster *et al.* (2009) and McGee *et al.* (2014). High-efficiency animals used less energy in the physiological processes involved in maintenance resulting in more net energy available for tissue accretion (Castro Bulle *et al.,* 2007). Kelly *et al.* (2014) observed positive relationships between feeding events and DMI (r = 0.31), ADG (r = 0.28), and RFI (r = 0.24), but not with gain: feed ratio in finishing heifers. In agreement, the present study observed a trend toward a positive relationship of RFI with both number of daily feeding events and eating rate. McGee *et al.* (2014), and Lancaster *et al.* (2009) reported a moderate correlation between RFI and bunk visit frequency (r = 0.29) and Kayser and Hill (2013) found a moderate correlation between RFI and DMI per visit in Angus (r = 0.52) and Hereford (r = 0.36) cattle.

CONCLUSION

Therefore, low RFI calves are more efficient because they consumed less feed, spent lesser time in feeding events and required less metabolizable energy for body maintenance.

ACKNOWLEDGEMENTS

Financial assistance for the research was provided under University Grant supported by Indian Council of Agricultural Research, New Delhi, India. We thanks to the Faculty and Staff of the Department of Animal Nutrition and Instructional Livestock Farm Complex, College of Veterinary Science and Animal Husbandry, DUVASU, Mathura, Uttar Pradesh, India.

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Received on 29-03-2019 and accepted on 30-05-2019