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Growth performance, feed digestibility, body composition, and feeding behavior of high– and low–residual feed intake fat-tailed lambs under moderate feed restriction[1]

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ABSTRACT: Two experiments were conducted to evaluate the effect of moderate feed restriction on productivity of lambs classified on the basis of phenotypic expression of residual feed intake (RFI). In Exp. 1, 58 fat-tailed Kurdi ram lambs (32.1 ± 4.2 kg BW) were individually fed, ad libitum, a pelleted diet (35% alfalfa hay and 65% concentrate). Feed intake and ADG were determined for a 6-wk period and 3 feed efficiency measures including RFI, G:F, and partial efficiency of maintenance (PEM) were calculated. The lambs were sorted based on RFI and the 16 highest RFI (RFI ≥ mean + 0.5 SD) and 16 lowest RFI (RFI ≤ mean – 0.5 SD) lambs were subjected to body composition (BC) and DM digestibility (DMD) analysis. Feeding behavior traits (FB) were also evaluated for 24 h using a regular 5-min interval observation method. The high- and low-RFI lambs (14 lambs/RFI group) so classified in Exp. 1 were used in Exp. 2. Half of the lambs in each RFI group were randomly selected to be fed ad libitum or 85% of ad libitum (restricted feeding), which resulted in 4 experimental groups: 1) ad libitum high-RFI, 2) feed restricted high-RFI, 3) ad libitum low-RFI, and 4) feed restricted low-RFI. The lambs were fed the same diet as Exp. 1, and growth efficiency during a 6-wk test period as well as BC, DMD, and FB were also determined in Exp. 2. In Exp. 1, the low-RFI lambs consumed 14% ($P < 0.01$) less feed than high-RFI lambs. Differences were also observed between high- and low-RFI groups for G:F ($P = 0.01$), RFI ($P < 0.01$), and PEM ($P < 0.01$) in Exp. 1, but no differences were detected between high- and low-RFI lambs for ADG ($P = 0.79$), DMD ($P = 0.42$), BC ($P > 0.72$), and FB ($P > 0.24$). In Exp.2, the restriction feeding regime negatively affected ADG ($P < 0.01$) and G:F ($P = 0.02$) in low-RFI lambs, whereas G:F ($P = 0.02$) and PEM ($P < 0.01$) were improved in high-RFI lambs under the feed restriction condition. No effects of feed restriction on DMD ($P = 0.87$) and BC ($P > 0.05$) were observed. The lambs fed at the restricted level of intake presented a greater time ($P < 0.01$) and rate ($P = 0.01$) of eating than those fed ad libitum. Although bunk visits and feeding events were decreased ($P < 0.01$) with feed restriction, no interaction ($P > 0.05$) was detected between RFI phenotype and feeding regime for FB. In summary, feeding high-RFI lambs at 85% of ad libitum level improved G:F with no effect on ADG, whereas growth performance was reduced by feeding low-RFI lambs at 85% of ad libitum. However, these changes in feed efficiency were not related to DMD, BC, or FB.

Key words: body composition, feed efficiency, feed restriction, feeding behavior, lamb, residual feed intake

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INTRODUCTION

The concept of residual feed intake (**RFI**) was first proposed by Koch et al. (1963) as an alternative measure of feed efficiency that is independent of both production and maintenance levels (Herd and Arthur, 2009). Research efforts for years indicate that RFI is a powerful selection tool for improving feed efficiency and decreasing feed costs, especially in beef cattle (Herd et al., 2003; Arthur and Herd, 2008; Hoque and Suzuki, 2009). Because RFI is defined as the difference between actual feed intake and expected feed intake, most of these studies have been conducted on free-access feeding of cattle (Meyer et al., 2008; Welch et al., 2012) or sheep (Snowder and Van Vleck, 2003) using medium- to high-energy diets. However, it is important to know whether the animals that were efficient or inefficient on a feeding regime are also efficient or inefficient on other feeding conditions such as programmed or restricted feeding regimes. A few reports indicated that phenotypic expression of RFI in cattle (Herd et al., 2006; Durunna et al., 2011) and sheep (Redden et al., 2011) may vary under different feeding strategies. Restriction feeding, in which animals are fed at some level that is less than ad libitum, has been suggested to improve feed efficiency (Sainz, 1995). This improvement in efficiency is thought to be due, in part, to improvements in digestive efficiency and more efficient utilization of energy for maintenance and growth (Galyean, 1999). Therefore, moderate feed restriction may improve feed efficiency in inefficient animals. To our knowledge, however, little is known about the performance of animals classified on the basis of RFI under different concurrent feeding regimes. The objectives of this study were to evaluate growth performance, feed digestibility, body composition, and feeding behavior in low- versus high-RFI lambs fed 2 different levels of feed intake (ad libitum or moderate feed restriction).

MATERIALS AND METHODS

Fifty-eight Kurdi ram lambs (6 mo of age and 32.1 ± 4.2 kg BW) were randomly selected from the Jovain Industrial and Agricultural Company's (Razavi Khorasan, Iran) 2013 spring-born flock. Lambs were housed in 1 by 1.2 m individual cages, and all procedures involving animals were approved by the Ferdowsi University of Mashhad, Mashhad, Iran.. Two experiments were conducted over 12 consecutive weeks. All lambs had free access to water and were fed a high-concentrate pelleted diet (Table 1) throughout both experiments.

Table 1. Ingredient and chemical composition of the diet used in Exp. 1 and Exp. 2

Dietary component	Pelleted diet
Ingredient, % DM basis	
Alfalfa hay	35
Barley grain	29.25
Corn grain	6.5
Wheat bran	16.25
Cottonseed meal	6.5
Sugar beet pulp	3.25
Urea	0.33
$CaCO_3$	0.78
$NaHCO_3$	0.26
Salt	0.33
MgO	0.26
Mineral premix[1]	0.65
Bentonite	0.65
Chemical composition	
DM, %, as-fed basis	91.70
ME, Mcal/kg DM[2]	2.46
CP, % of DM	14.85

[1]Vitamin and mineral premix (per kg DM): 200,000 IU of protected vitamin A, 30,000 IU of vitamin D, 1,500 IU of vitamin E, 70 g Ca, 30 g P, 40 g Na, 25 g Mg, 2.5 g Zn, 2.5 mg Mn, 2 g Fe, 1 g S, 100 mg Cu, 80 mg I, 25 mg Co, and 10 mg Se.

[2]An in vitro gas production method was used to measure of gas production and ME was calculated using equation of Menke and Steingass (1988).

Experiment 1

After a 10-d acclimation period, feed efficiency was measured for 6 wk (Redden et al., 2011). All 58 lambs had ad libitum access to feed in individual bunks. The pelleted feed was added to the bunks twice daily to make sure that at least 10% of the feed offered daily remained for next day. To avoid the accumulation of feed in the bunks, feed remaining in the bunks in excess of 20% of the feed offered daily was replaced by fresh feed. The orts were weighed at the end of each week and ort samples were analyzed for DM. Average daily DMI was then calculated using the total DMI for 42 d. The lambs were weighed weekly and 2 consecutive day BW records were determined at the beginning (d 0 and 1) and end of Exp. 1. To measure feeding behavior traits (**FB**), animals were visually observed at 5-min intervals for 24 h (Galvani et al., 2010) on d 41 of Exp. 1. The 5 behavior traits calculated included bunk visit events (the number of times that an animal visited a feed bunk), feeding events (the number of times that an animal visited feed bunk for >300 s), nonfeeding events (the number of times that an animal visited feed bunk for <300 s), eating time (daily time taken to consume the recorded intake), and eating rate (DMI divided by eating time).

Average daily gain and midtest metabolic BW (**MMBW**; $BW^{0.73}$) of individual lambs were modeled by linear regression, as described by Lancaster et al. (2009). To measure the RFI, expected DMI was calculated by regressing actual DMI against ADG and MMBW. The model used to estimate expected DMI was

$$\mathrm{DMI}_i = \alpha + \beta_1(\mathrm{ADG}_i) + \beta_2(\mathrm{MMBW}_i),$$

in which α = regression intercept, β_1 = partial regression coefficient of DMI on ADG, and β_2 = partial regression coefficient of DMI on MMBW. The RFI was calculated as the difference between actual DMI and expected DMI (Rajaei Sharifabadi et al., 2012). Gain:feed ratio and partial efficiency of maintenance (**PEM**; (DMI − ADG)/MMBW) were also calculated.

At the end of Exp. 1, the lambs were sorted on the basis of RFI. The 16 highest RFI (RFI ≥ mean + 0.5 SD) and 16 lowest RFI (RFI ≤ mean − 0.5 SD) lambs were subjected to body composition measurements (**BC**). For BC, longissimus dorsi muscle area (**LDA**) and back fat thickness at the 12th rib (**BF**) were measured by a Honda Electronics HS-101V ultrasonic instrument with a HLV-155 probe (Honda Electronics Co., LTD., Toyohashi, Japan). To measure of DM digestibility (**DMD**), diet and feces samples were collected for 5 consecutive days during d 35 through 39 of Exp. 1 and stored at −20°C until later analysis. The fecal samples were collected twice daily (0800 and 1600 h) via rectal palpation. The feed and feces grab samples (composited over 5 d) were oven-dried at 60°C for 48 h and then milled to pass through a 1-mm screen. Acid insoluble ash was used as an internal marker to determine the DMD as described by Block et al. (1981). The AIA content of feed and fecal samples was determined using the procedure of Van Keulen and Young (1977). Dry matter digestibility was calculated as [1 − (AIA percentage in the feed/AIA percentage in the feces)] × 100. The analyses were performed in triplicate and DMD values were expressed as a percentage of diet DM.

Experiment 2

Two high- and 2 low-RFI lambs so classified in Exp. 1 were excluded due to tissue sampling, and 28 remaining lambs (14 lambs per RFI group) were used in Exp. 2. Half of the lambs in each RFI group were randomly selected to be fed ad libitum or a restricted feeding regime (85% of ad libitum), which resulted in 4 experimental groups: 1) ad libitum high-RFI, 2) feed restricted high-RFI, 3) ad libitum low-RFI, and 4) feed restricted low-RFI. The first week of Exp. 2 (d 0–7 of Exp. 2), the restricted lambs received 85% of the mean average feed weight that each animal consumed during the last week of Exp. 1. From then until the end of experiment period (d 8–42 of Exp. 2), the individual offered feed for restricted lambs in each RFI group was calculated weekly as 85% of average weight of feed per BW that lambs in the same RFI group consumed ad libitum during the previous week. Body weight of lambs as well as DMI of ad libitum individuals was measured during the next 6 wk, similar to Exp. 1. Feed samples and feces grab samples from each lamb were collected for 5 consecutive days during d 35 through 39 of Exp. 2. Average daily gain and MMBW as well as FB, BC, and DMD were determined as described in Exp. 1. Dry matter intake, ADG, and MMBW data were used to calculate of G:F and PEM.

Statistical Analysis

For Exp. 1, all data were analyzed as a completely randomized design with individual lamb as the experimental unit and RFI group as the fixed effect in the PROC GLM procedures of SAS (SAS 9.1; SAS Inst. Inc., Cary, NC). Pearson correlation analysis (PROC CORR of SAS) was also conducted to determine associations among feed efficiency measures (RFI, G:F, and PEM), DMI, ADG, and MMBW.

The Exp. 2 data were analyzed in a completely randomized design with a 2 × 2 factorial arrangement consisted of 2 RFI phenotypes (high-RFI and low-RFI) and 2 feeding regimes (ad libitum and restricted feeding). The statistical model was $Y = \mu + \text{Phen} + \text{Reg} + (\text{Phen} \times \text{Reg}) + \varepsilon$, in which Y is the dependent variable, μ is the overall mean, Phen is the main effect of RFI phenotype, Reg is the main effect of feeding regime, Phen × Reg is interaction of RFI phenotype and feeding regime, and ε is the associated error. Means were determined using the least squares means statement of SAS and were separated by Fisher's LSD and were considered different if $P \leq 0.05$.

RESULTS AND DISCUSSION

Experiment 1

Experiment 1 was conducted to determine individual RFI on a group of lambs and evaluate groups of lambs with divergent RFI for Exp. 2. As expected, a significant difference ($P < 0.01$) in RFI was observed between low- (−0.16) and high- (0.16) RFI lambs. Two other feed efficiency measures (G:F [$P = 0.01$] and PEM [$P < 0.01$]) differed between RFI groups (Table 2). The Pearson correlation analysis showed that G:F had a weak negative correlation ($r = -0.29$, $P = 0.03$) with RFI and a high positive correlation with ADG ($r = 0.86$, $P < 0.01$), similar to what Redden et al.

Table 2. Growth performance of fat-tailed Kurdi lambs grouped according to phenotypes of high- or low-residual feed intake (RFI) in Exp. 1

Growth performance traits[1]	RFI groups[2] Low-RFI	High-RFI	SEM	*P*-value
No.	16	16		
Initial BW, kg	32.60	32.51	1.05	0.95
Final BW, kg	43.87	43.34	1.11	0.74
MMBW, kg	14.28	14.20	0.28	0.84
ADG, kg	0.26	0.26	0.014	0.79
DMI, kg	1.82	2.11	0.055	<0.01
G:F	0.14	0.12	0.005	0.01
RFI	−0.16	0.16	0.019	<0.01
PEM	0.11	0.13	0.002	<0.01

[1]MMBW = midtest metabolic BW; PEM = partial efficiency of maintenance [(DMI − ADG)/MMBW].

[2]Low-RFI = RFI ≤ mean – 0.5 SD; high-RFI = RFI ≥ mean + 0.5 SD.

Table 3. Pearson correlation coefficients (*P*-value) among performance traits[1] of fat-tailed Kurdi lambs in Exp. 1

	G:F	PEM	ADG	DMI	MMBW
RFI	−0.29 (0.03)	0.92 (<0.01)	0.01 (0.95)	0.58 (<0.01)	0.00 (0.98)
G:F	–	−0.15 (0.26)	0.86 (<0.01)	−0.08 (0.552)	−0.36 (<0.01)
PEM		–	0.18 (0.17)	0.66 (<0.01)	0.08 (0.56)
ADG			–	0.42 (<0.01)	0.03 (0.83)
DMI				–	0.71 (<0.01)

[1]PEM = partial efficiency of maintenance [(DMI − ADG)/MMBW]; MMBW = midtest metabolic BW; RFI = residual feed intake.

(2011) and Rajaei Sharifabadi et al. (2012) reported in ewe and ram lambs, respectively. Although G:F may explain feed efficiency of low- and high-RFI lambs under restricted feeding condition, there is, however, general agreement that unlike RFI, G:F may be influenced by the difference in growth rate (Archer et al., 1999; Nkrumah et al., 2004). Therefore, changes in G:F of low- or high-RFI lambs due to restricted feeding may also be a reflection of expected changes in ADG and not necessarily feed efficiency.

To measure PEM, it was assumed that if the efficiency of consumed DMI for gain is 100% in an ideal situation in which PEM = 0, then DMI above ADG per unit of MMBW is the amount of feed energy devoted to maintenance requirements. Similar to RFI, therefore, the animals with greater PEM need more feed for maintenance requirements and are less efficient. The high correlation ($r = 0.92$, $P < 0.01$) between RFI and PEM observed in this study (Table 3) was expected, as both measurements incorporate components of feed intake due to maintenance and growth (Nkrumah et al., 2004). Moreover, the lack of association between PEM and ADG ($r = 0.03$, $P = 0.83$) indicates that PEM may be a convenient alternative for RFI to assess feed efficiency of lambs in Exp. 2 in which the calculation of RFI was impossible because of the experiment design.

Despite the similar initial BW ($P = 0.95$), final BW ($P = 0.74$), and MMBW ($P = 0.84$) as well as ADG ($P = 0.79$) between low- and high-RFI groups in Exp. 1, the lambs in the low-RFI group consumed about 14% ($P < 0.01$) less feed than lambs in the high-RFI group. The correlation analysis showed that the DMI was related to both RFI ($r = 0.58$, $P < 0.01$) and PEM ($r = 0.66$, $P < 0.01$). The relationship between feed consumption and RFI has been widely reported by previous studies (Snowder and Van Vleck, 2003; Arthur and Herd, 2008). Therefore, to induce a more accurate feed restriction, the feed offered to restricted lambs was calculated based on the ad libitum feed consumed by same RFI group.

The lack of difference ($P > 0.24$) in FB detected between low- and high-RFI lambs in Exp. 1 (Table 4) contrasts what has been reported in beef cattle (Lancaster et al., 2009; McGee et al., 2014). There

Table 4. Feeding behavior traits of fat-tailed Kurdi lambs grouped according to phenotypes of high- or low-residual feed intake (RFI) in Exp. 1

Feeding behavior traits[1]	RFI groups[2] Low-RFI	High-RFI	SEM	*P*-value
No.	16	16		
Bunk visits, events/d	17	17	1	0.99
Feeding events, events/d	7	8	1	0.24
Nonfeeding events, events/d	10	9	1	0.46
Eating time, min/d	79.37	87.33	8.00	0.49
Eating rate, g/min	25.23	27.81	3.44	0.25

[1]Bunk visit = the number of times that an animal visited the feed bunk; feeding events = the number of times that an animal visited the feed bunk for >300 s; nonfeeding events = the number of times that an animal visited the feed bunk for <300 s; eating time = daily time taken to consume the recorded intake; eating rate = DMI divided by eating time.

[2]Low-RFI = RFI ≤ mean – 0.5 SD; high-RFI = RFI ≥ mean + 0.5 SD.

Table 5. Dry matter digestibility (DMD), longissimus dorsi muscle area (LDA), and back fat thickness at the 12th rib (BF) at the 12th rib of fat-tailed Kurdi lambs grouped according to phenotypes of high- or low-residual feed intake (RFI) in Exp. 1

Items	RFI groups[1] Low-RFI	High-RFI	SEM	*P*-value
No.	8	8		
DMD, %	68.70	66.68	1.70	0.42
LDA, cm^2	13.77	13.55	0.75	0.72
BF, mm	1.94	1.86	0.14	0.84

[1]Low-RFI = RFI ≤ mean – 0.5 SD; high-RFI = RFI ≥ mean + 0.5 SD.

Table 6. Growth performance of low– and high–residual feed intake (RFI) fat-tailed Kurdi lambs fed ad libitum or at 85% of ad libitum (restricted) level in Exp. 2

Growth performance traits[1]	Feed efficiency groups[2]				SEM	*P*-value[3]		
	Low-RFI		High-RFI					
	Ad libitum	Restricted	Ad libitum	Restricted		Phen	Reg	Phen × Reg
No.	7	7	7	7				
Initial BW, kg	41.53	43.04	43.66	41.94	1.46	0.75	0.95	0.30
Final BW, kg	52.48	51.07	54.23	52.56	1.59	0.33	0.34	0.94
MMBW, kg	16.60	16.62	17.11	16.68	0.39	0.49	0.61	0.58
ADG, kg	0.26[a]	0.19[b]	0.25[a]	0.25[a]	0.012	0.04	<0.01	<0.01
DMI, kg	1.97	1.70	2.26	1.84	0.09	0.04	<0.01	0.47
G:F	0.14[b]	0.11[a]	0.11[a]	0.15[b]	0.008	0.44	0.62	<0.01
PEM	0.10[b]	0.09[b]	0.12[a]	0.09[b]	0.006	0.19	<0.01	0.05

[a,b]Within each column, means with different superscript letters differ ($P \le 0.05$).

[1]MMBW = midtest metabolic BW; PEM = partial efficiency of maintenance [(DMI − ADG)/MMBW].

[2]Low-RFI = RFI ≤ mean – 0.5 SD; high-RFI = RFI ≥ mean + 0.5 SD.

[3]Phen = main effect of RFI phenotype (low-RFI vs. high-RFI); Reg = main effect of feeding regime (ad libitum vs. restricted); Phen × Reg = RFI phenotype × feeding regime interaction.

were also no differences in DMD ($P = 0.42$) and BC (LDA; $P = 0.72$; BF, $P = 0.84$) between high- and low-RFI lambs in Exp. 1 (Table 5). Previously, Rajaei Sharifabadi et al. (2012) failed to find a correlation between carcass traits and RFI in fat-tailed lambs grouped according to phenotypic RFI. However, only 15% of variation in RFI is associated with digestibility and BC (Herd and Arthur, 2009), so it is not surprising that DMD and BC (LDA and BF) are not different among high- and low-RFI groups in our study.

Experiment 2

In Exp. 2, the growth rates of ad libitum high- and low-RFI lambs were similar to those observed in Exp. 1. Although the feeding regime had no effect on ADG ($P = 0.89$) of high-RFI lambs, the rate of BW gain was depressed approximately 27% ($P < 0.01$) for the restricted-fed low-RFI lambs compared with ad libitum low-RFI lambs (Table 6). At a common feeding level, low-RFI beef cattle may have a greater growth rate than high-RFI beef cattle because of less maintenance requirements (Herd et al., 2003). Redden et al. (2013) reported a slightly greater ADG in low-RFI ewes compared with high-RFI ewes fed at maintenance level. Similarly, low-RFI pigs fed at 55% ad libitum levels showed numerically greater growth rate than a randomly selected line (Boddicker et al., 2011). In the Boddicker et al. (2011) study, voluntary feed intake and RFI were determined in randomly selected pig lines (control) and low-RFI pigs that were fed at 75% of feed intake of the ad libitum control group. In agreement with our results, Boddicker et al. (2011) found that ADG was decreased in low-RFI pigs fed a moderately feed restricted diet. In a group of individuals classified on the basis of RFI phenotype, low-RFI animals have less feed intake at a similar production and maintenance level as their higher-RFI counterparts. Therefore, moderate feed restriction may negatively impact growth rates in low-RFI animals due to reduced intake of nutrients required for body development. However, moderate feed restriction appears to have no effect on ADG of the high-RFI lambs that consume

Table 7. Dry matter digestibility (DMD), longissimus dorsi muscle area (LDA), and back fat thickness at the 12th rib (BF) at the 12th rib of low– and high–residual feed intake (RFI) fat-tailed Kurdi lambs fed ad libitum or at 85% of ad libitum (restricted) level in Exp. 2

Items	Feed efficiency groups[1]				SEM	*P*-value[2]		
	Low-RFI		High-RFI					
	Ad libitum	Restricted	Ad libitum	Restricted		Phen	Reg	Phen × Reg
No.	7	7	7	7				
DMD, %	66.06	67.87	67.59	66.39	1.13	0.69	0.87	0.70
LDA, cm^2	18.30	17.82	18.45	18.13	0.70	0.88	0.93	0.89
BF, mm	2.10	2.15	2.19	2.16	0.15	0.73	0.95	0.30

[1]Low-RFI = RFI ≤ mean – 0.5 SD; high-RFI = RFI ≥ mean + 0.5 SD.

[2]Phen = main effect of RFI phenotype (low-RFI vs. high-RFI); Reg = main effect of feeding regime (ad libitum vs. restricted); Phen × Reg = RFI phenotype × feeding regime interaction.

Table 8. Feeding behavior traits of low– and high–residual feed intake (RFI) fat-tailed Kurdi lambs fed ad libitum or at 85% of ad libitum (restricted) level in Exp. 2

	Feed efficiency groups[2]							
	Low-RFI		High-RFI			*P*-value[3]		
Feeding behavior traits[1]	Ad libitum	Restricted	Ad libitum	Restricted	SEM	Phen	Reg	Phen × Reg
No.	7	7	7	7				
Bunk visits, events/d	15	9	13	8	1	0.20	<0.01	0.90
Feeding events, events/d	8	4	9	4	1	0.61	<0.01	0.63
Nonfeeding events, events/d	5	5	5	4	1	0.09	0.15	0.73
Eating time, min/d	96.00	45.00	98.57	54.29	7.33	0.74	<0.01	0.24
Eating rate, g/min	21.75	40.67	24.87	35.31	4.05	0.63	<0.01	0.25

[1]Bunk visit = the number of times that an animal visited feed bunk; feeding events = the number of times that an animal visited feed bunk for >300 s; nonfeeding events = the number of times that an animal visited feed bunk for <300 s; eating time = daily time taken to consume the recorded intake; eating rate = DMI divided by eating time.

[2]Low-RFI = RFI ≤ mean – 0.5 SD; high-RFI = RFI ≥ mean + 0.5 SD.

[3]Phen = main effect of RFI phenotype (low-RFI vs. high-RFI); Reg = main effect of feeding regime (ad libitum vs. restricted); Phen × Reg = RFI phenotype × feeding regime interaction.

greater amounts of feed, as was observed in the present study. Although inputs for prediction of DMI by the model used in this study may be inadequate to properly describe ME utilization in growing animals (Old et al., 2015), it has been suggested that RFI represents inherent variation in basic metabolic processes such as tissue metabolism (Herd and Arthur, 2009) or physiological maturity (Randel and Welsh, 2013). There is evidence that a restricted feeding regime improves the function of some metabolic pathways in mice (Hatori et al., 2012). Although the exact mechanism for the improvement in feed efficiency in high-RFI lambs fed at 85% of ad libitum is unknown, it is our hypothesis that this improvement may be a result of the animal consuming sufficient amounts of nutrients that was not achieved in low-RFI lambs fed at 85% of ad libitum.

As shown in Table 6, G:F was found to be least ($P < 0.01$) in the feed restricted low-RFI lambs compared with the ad libitum low-RFI lambs, whereas feeding high-RFI lambs at 85% ad libitum level improved G:F by about 27% ($P = 0.02$) compared with ad libitum high-RFI. Feed efficiency of high-RFI lambs, expressed as PEM, was also improved by a restricted feeding regime. At a maintenance restricted feeding level for a predicted gain rate of 0.05 kg/d, Redden et al. (2013) reported that the feed efficiency of low-RFI yearling ewes was still greater than that of a high-RFI group. Boddicker et al. (2011) found no difference in feed efficiency between low-RFI pigs fed ad libitum or at 75 or 55% of ad libitum levels. However, level and method of feed restriction as well as sex and species differences may be reasons for the contrast in results.

Feed digestibility and BC have been described as sources of individual variation in RFI among animals (Herd and Arthur, 2009). The beneficial effects of moderate feed restriction on animal performance are partly associated with improvement of feed digestibility and change in BC (Galyean, 1999). Therefore, our hypothesis was that changes in DMD and BC may explain the changes in feed efficiency of high- and low-RFI lambs as a result of moderate feed restriction. There were no detectable differences in DMD ($P = 0.70$) as well as LDA ($P = 0.89$) and BF ($P = 0.30$) among experimental groups in Exp. 2 (Table 7). Redden et al. (2011) reported no difference in DMD between high- and low-RFI yearling ewes on a chopped hay maintenance diet. Residual feed intake was independent of BC in yearling ewes fed ad libitum or at a maintenance restricted feeding level (Redden et al., 2013). Clark et al. (2007) fed steers at 3 levels of feed consumption (ad libitum or 90 or 80% of ad libitum) with a given ME intake. They concluded that improvements in feed efficiency by this manner of restriction do not appear to be related to changes in diet digestion or ME intake, similar to what was observed in the present study.

The time and rate of feeding as well as bunk visits and feeding events were significantly ($P < 0.01$) affected by restricted feeding levels in Exp. 2 (Table 8). Similar to our results, Galvani et al. (2010) reported a less eating time and greater eating rate in lambs fed at restricted levels (70 or 55% of ad libitum) of intake than those fed ad libitum. However, no interaction was observed between RFI and feeding regime for FB.

Moderate feed restriction (85% of ad libitum) negatively affected growth performance of low-RFI lambs, whereas feed efficiency was improved in high-RFI lambs when their diet was restricted. However, these changes in feed efficiency were not related to DMD, BC, or FB. Further research is warranted to determine if changes in intermediary metabolites or alteration in gene and protein expression (e.g., muscle, liver) mediate the changes in feed efficiency due to feed restriction.

LITERATURE CITED

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