

CAN COMPENSATORY GROWTH MITIGATE A FEEDING RESTRICTION IN GROWING LAMBS?

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ABSTRACT

The aim of the study was to evaluate compensatory growth in lambs under semi-extensive growing conditions utilizing pasture haylage from *Lotus uliginosus* cv. E-Tanin as the main feed resource. Single (n = 36) and twin-born (n = 35) crossed Polwarth x Finnish Landrace lambs were assigned to three feeding treatments (restriction period) to achieve: low weight gain (LWG) less than 30 g a⁻¹ d⁻¹, medium weight gain (MWG) ~ 60 g a⁻¹ d⁻¹; and high weight gain (HWG) (~90 g a⁻¹ d⁻¹ for 82 days. Lambs were offered pasture haylage at LWG, haylage plus corn at MWG, and haylage plus corn and soybean meal at HWG, restricted at 2.5 to 3% of BW. Afterwards, lambs were individually penned and fed *ad libitum* for 82 days (refeeding phase). Live weight and feed intake (FI) were recorded during the experimental period, and average daily gain (ADG) and feed conversion ratio (FCR) were estimated. Ribeye area (REA) and fat depth (FAT) were measured in the refeeding phase. Both ADG and FI were significantly different ($P < 0.05$) among treatments (HWG > MWG > LWG) in the feeding restriction period. FCR did not differ ($P > 0.05$) between MWG and HWG but were lower ($P < 0.05$) than LWG. No differences ($P > 0.05$) were found in ADG between single and twin-born lambs during the refeeding period. Initial and final REA was greater ($P < 0.05$) in MWG and HWG than LWG. Even though haylage is a cheap feed alternative in semi-extensive production systems, it does not enable a full compensatory growth of LWG and MWG lambs.

Key words: lamb performance, compensatory growth, feed intake, feed conversion ratio.

INTRODUCTION

Livestock extensive production systems in Uruguay are subject to some extent, to nutritional restriction as a consequence of low quality in summer (Berretta et al., 2000) or availability in winter (Bermúdez and Ayala, 2005) of native grassland. Under extensive conditions, wool type lambs are usually weaned in summer with 4 to 5-month-old facing important nutrition-related challenges during early post-weaning. First, they are offered a poor-quality diet; and secondly, they must cope with parasites, mainly *Haemonchus*

contortus (Castells et al., 2011). Therefore, these lambs usually have little daily weight gain during summer and early fall. A well-known mechanism used to minimize this negative effect is the use of compensatory growth rate, with pastures as main nutrition resource. Haylage is an inexpensive alternative to conserve high quality forage from spring and use it throughout the year when feed resources are scarce in semi-extensive livestock conditions. In our conditions, it could have an additional benefit that haylage can transfer clean-parasites-pastures from spring to summer.

Compensatory growth or catch-up growth are

terms used as synonyms to describe the faster than optimal growth that occurs following a period of dietary restriction in the development of many animals (Hector and Nakagawa, 2012). Compensatory growth enables either complete or partial compensation depending on the persistence of the increased growth rate, although there may be no increase in growth rate and hence no compensation. Age at restriction, the severity and duration of the restriction are three major factors contributing to the variation in compensatory growth response of animals (Ryan, 1990; Mitchell, 2009). Several studies have reported some mechanisms that would be associated with compensatory growth, such as feed intake (Graham and Searle, 1979; Hornick et al., 1998; Mc Gregor et al., 2012), growth efficiency (Ryan, 1990; Connor et al., 2010; Keogh et al., 2015a), maintenance energy requirements (Fox et al., 1972; Butler-Hogg and Tulloh, 1982; Sainz et al., 1995) and tissue deposition patterns (Levy et al., 1971; Keogh et al., 2015b).

The objective of the present study was to evaluate animal performance, feed intake and feed conversion ratio during a nutritional restriction period (summer) and *ad libitum* refeeding phase (fall) in lambs under semi-extensive conditions.

MATERIALS AND METHODS

Experimental treatments and lamb management

The experiment was carried out at the Experimental Unit "La Estanzuela" of INIA, Uruguay (34°20' S, 57°41' W) in summer-fall of 2018. The experimental procedures were approved by the Committee for Animal Ethics of INIA, Uruguay, number 2016.48. After weaning at an average age of 132 days, single (n = 36) and twin-born (n = 35), crossbred lambs (Polwarth x Finnish Landrace) were assigned to three feeding treatments (restriction period) in order to achieve: low weight gain (less than 30 g/lamb/day; LWG), medium weight gain (~ 60 g/lamb/day; MWG), and high weight gain (~ 90 g/lamb/day; HWG) for 82 days. The Australian Graz Feed software (Graz Feed™, 2010) was used. Lambs at LWG were offered haylage from *Lotus uliginosus* cv. E-Tanin (596 g DM kg⁻¹, 194 g CP kg⁻¹ DM, and 2.31 Mcal ME kg⁻¹ DM), haylage plus corn (623 g DM kg⁻¹, 182 g CP kg⁻¹ DM, and 2.41 Mcal ME kg⁻¹ DM) at MWG, and haylage plus corn and soybean meal (644 g DM kg⁻¹, 185 g CP kg⁻¹ DM, and 2.46 Mcal ME kg⁻¹ DM) at HWG. The feed was restricted between 2.5 to 3 kg of DM per 100 kg of live weight (LW) to maintain the average daily gain in each treatment. During the feeding restriction period, lambs of each treatment were

collectively fed in uncovered collective pens, with an area of 30 m²/lamb.

Subsequently, lambs were individually penned during the refeeding phase and fed *ad libitum* for 82 days with haylage (492 g DM kg⁻¹, 165 g CP kg⁻¹ DM, and 2.24 Mcal ME kg⁻¹ DM). The pens had an area of 5 m² each. Lambs in both experimental phases had fresh water and shade available *ad libitum*.

Lamb measurements

Lambs were weighed (LW) in a crate with a scale (Allflex, FX 11, Dallas, Texas, USA) on a biweekly basis at 08:00 am without fasting; average daily gain (ADG) was estimated for the restricted and not restricted phases. Feed intake (FI) was recorded daily during both experimental periods (restriction and *ad libitum* refeeding). Feed conversion ratio (FCR) was calculated as kg of feed per kg of weight gain for both periods.

Ribeye area (REA) and fat depth (FAT) were measured by ultrasound at the beginning and end of the refeeding phase. Measurements were taken using an Aloka SSD-500V real-time scanner (Aloka Co. Ltd., Tokyo, Japan) equipped with 12 cm, 3.5 MHz linear probe set over the *Longissimus dorsi* muscle between the 12th and 13th ribs. Before each measurement, lamb's wool was brushed, and vegetable oil was used as a coupling medium between the skin and the probe.

Statistical analysis

Response variables during the feeding restriction period were analyzed as a 3 x 2 factorial design with treatment (LWR, MWR, or HWR) and litter size (single or twin) as fixed effects and the random effect of replicate using the PROC MIXED procedure of the Statistical Analysis System software (SAS Institute, 2013). Lamb LW was analyzed as repeated measures and the autoregressive (AR [1]) covariance structure was used based on the Akaike Information Criterion (Akaike, 1973). Birth weight was used as a covariate for LW, REA and FAT analysis. The refeeding phase was analyzed in the same way as the feeding restriction period (considered as previous treatments). Studentized residual plots were evaluated to test homogeneity of variance and normality for all data. Kenward-Roger approximation was used to calculate denominator degrees of freedom for different covariance structures for adjustment of the F-statistic. After the Analysis of Variance was performed, least square means were calculated for treatment comparisons with a significance level of $\alpha = 0.05$, using the PDIFF option of LSMEANS, when F-tests were significant ($P < 0.05$).

RESULTS

As expected, feeding restriction treatments had an effect ($P < 0.05$) on ADG (HWG > MWG > LWG) and lambs achieved different ($P < 0.05$) weights at the end of the restriction period (Table 1). Feed intake was different ($P < 0.05$) among nutritional restriction treatments, showing the same pattern than ADG (Table 1). However,

when FI was calculated as a percentage of BW or as percentage of metabolic BW, no differences ($P > 0.05$) were found. Feed conversion ratio did not differ ($P > 0.05$) between MWG and HWG, but it was lower ($P < 0.05$) than LWG.

In the *ad libitum* refeeding phase with haylage, ADG did not differ ($P > 0.05$) among previous feeding treatments. No differences ($P > 0.05$) were found in ADG between single and twin-

Table 1. Least square means \pm standard error of initial (LWi) and final live weight (LWf), average daily gain (ADG), average feed intake per day (FI), and feed conversion ratio (FCR) according to the feeding restriction treatment (LWG, MWG and HWG), litter size (LS), and its interactions.

	Treatment (Trt)				LS ⁴			P-values	
	LWG ¹	MWG ²	HWG ³	Trt	Single	Twins	Trt	LS	Trt x LS
LWi (kg)	21.9 \pm 0.71	21.7 \pm 0.70	21.9 \pm 0.70	0.9793	23.7 ^a \pm 0.64	19.9 ^b \pm 0.65	0.9793	0.0003	0.9904
LWf (kg)	23.3 ^a \pm 0.71	26.8 ^{ab} \pm 0.69	29.1 ^b \pm 0.69	0.0022	28.2 ^a \pm 0.61	24.6 ^b \pm 0.62	0.0022	<0.0001	0.7993
ADG (g d ⁻¹)	17.0 ^c \pm 5.6	62.1 ^b \pm 5.5	87.5 ^a \pm 5.5	<0.0001	54.5 \pm 4.5	56.6 \pm 4.5	<0.0001	0.7449	0.2665
FI (kg d ⁻¹)	0.515 ^c \pm 0.012	0.711 ^b \pm 0.012	0.962 ^a \pm 0.012	<0.0001	-	-	<0.0001	-	-
FI (% BW)	3.98 \pm 0.15	3.88 \pm 0.13	3.55 \pm 0.15	0.0958	-	-	0.0958	-	-
FI (% BW ^{0.75})	9.26 \pm 0.33	9.21 \pm 0.30	8.54 \pm 0.33	0.2286	-	-	0.2286	-	-
FCR ⁵ (kg kg ⁻¹)	35.7 ^b \pm 5.3	11.8 ^a \pm 5.1	13.9 ^a \pm 5.2	0.0031	-	-	0.0031	-	-

¹ LWG: low average daily weight gain during the restriction period.
² MWG: medium average daily weight gain during the restriction period.
³ HWG: high average daily weight gain during the restriction period.
⁴ LS: litter size.
⁵ FCR: Feed conversion ratio expressed as kg of feed intake per kilogram of weight gain.
^{a, b, c}: LS Means with different superscripts in the same row differ significantly ($P < 0.05$).

born lambs during the refeeding period (Table 2). Initial REA in the refeeding phase was greater ($P < 0.05$) in MWG and HWG lambs compared to the LWG treatment as a consequence of the dietary restriction period. These differences ($P < 0.05$) were still present at the end of the refeeding phase, indicating that there was a carryover

effect that was not overcome when lambs were fed *ad libitum* with haylage (Table 2). Lambs feed intake as a percentage of the metabolic weight was not different ($P > 0.05$) during the refeeding period with haylage among previous nutritional treatments. However, twin-born lambs showed a greater FI ($P < 0.05$) than single lambs, which

Table 2. Least square means \pm standard error of initial (LWi) and final live weight (LWf), average daily gain (ADG), initial and final ribeye area (REa) and fat depth (FAT), average feed intake per day (FI), and feed conversion ratio (FCR) during the refeeding period with haylage according to the previous dietary restriction treatment (LWG, MWG and HWG), litter size (LS), and its interactions.

	LWG ¹	MWG ²	HWG ³	LS ⁴			P-values	
				Single	Twins	Trt	LS	Trt x LS
LWi (kg)	23.2 ^b \pm 1.05	26.8 ^{ab} \pm 1.00	29.9 ^a \pm 1.09	28.6 ^a \pm 0.94	24.6 ^b \pm 0.87	0.0137	0.0037	0.0094
REaI (cm ²)	2.8 ^b \pm 0.3	3.9 ^b \pm 0.3	4.8 ^a \pm 0.3	4.2 \pm 0.3	3.5 \pm 0.3	0.0005	0.1308	0.6926
FATi (mm)	1.2 \pm 0.1	1.4 \pm 0.1	1.2 \pm 0.1	1.1 ^b \pm 0.1	1.4 ^a \pm 0.1	0.3584	0.0301	0.6497
LWf (kg)	31.8 ^b \pm 1.05	33.8 ^b \pm 1.00	37.1 ^a \pm 1.09	36.3 ^a \pm 0.95	32.1 ^b \pm 0.87	0.0159	0.0066	0.0165
REAf (cm ²)	5.8 ^b \pm 0.3	6.9 ^a \pm 0.3	7.0 ^a \pm 0.3	6.9 \pm 0.3	6.2 \pm 0.3	0.0080	0.0722	0.9108
FATf (mm)	1.8 \pm 0.1	1.6 \pm 0.1	1.7 \pm 0.1	1.7 \pm 0.1	1.7 \pm 0.1	0.1103	0.5942	0.0008
ADG (g d ⁻¹)	104.8 \pm 7.3	85.7 \pm 7.0	87.0 \pm 7.6	93.1 \pm 6.4	91.9 \pm 7.0	0.0895	0.4602	0.5836
FI (kg d ⁻¹)	1.03 ^c \pm 0.010	1.07 ^b \pm 0.009	1.12 ^a \pm 0.010	1.11 ^a \pm 0.008	1.03 ^b \pm 0.008	< 0.0001	< 0.0001	0.0006
FI (% BW)	3.64 ^b \pm 0.10	3.44 ^{ab} \pm 0.10	3.25 ^b \pm 0.11	3.26 ^b \pm 0.10	3.63 ^b \pm 0.08	0.0501	0.0042	0.8773
FI (% BW ^{0.75})	8.38 \pm 0.20	8.10 \pm 0.19	7.85 \pm 0.21	7.86 ^b \pm 0.17	8.36 ^a \pm 0.21	0.1985	0.0379	0.7662
FCR ⁵ (kg kg ⁻¹)	10.2 ^b \pm 0.9	13.2 ^a \pm 0.8	13.1 ^a \pm 0.9	12.4 \pm 0.7	12.0 \pm 0.7	0.0292	0.7005	0.9613

¹LWG: low average daily weight gain during the restriction period and refeeding with haylage.

²MWG: medium average daily weight gain during the restriction period and refeeding with haylage. ³HWG: high average daily weight gain during the restriction period and refeeding with haylage. ⁴LS: litter size. ⁵FCR: Feed conversion ratio expressed as kg of feed intake per kilogram of weight gain.

^{a, b, c}: LS Means with different superscripts in the same row differ significantly ($P < 0.05$).

is associated to their metabolic weight (Table 2). Lambs from the previous LWG treatment presented a lower ($P < 0.05$) FCR (more efficient) than values from MWG and HWG during the refeeding period.

DISCUSSION

When animals undergo compensatory growth is indicative that growth rate is usually below the potential maximum. Compensatory growth is based on the existence of feedback mechanisms that lead to the induction of appropriate responses for the animal to meet certain growth-related targets (Jobling, 2010). Even though dietary treatments determined significant differences in ADG during the restriction period, the magnitude of these differences, particularly between MWG and HWG, does not seem to be too big from a productive perspective. In this sense, and considering that the goal of this study was to evaluate compensatory growth, more contrasting nutritional treatments would have been necessary during the restriction phase. Sivanagendra Babu et al. (2017) indicated that the requirements for maintaining body weight are not a constant function of body weight but may be altered by plane of nutrition. In this study, ADG during the refeeding period did not differ among treatments. Similarly, a study conducted by Mahouachi and Atti (2005) did not find differences in ADG among the treatments during the refeeding phase when lambs presented an ADG of 61, 76 and 108 g d⁻¹ in the previous restricted treatments. However, Li et al. (2015) reported that restricted lambs reduced markedly the weight of the rumen and abomasum; therefore, energy expenditure of these tissues could also decrease, which enabled more metabolic energy ingested by restricted lambs to be used for weight gain during the refeeding stage. In addition, Kamalzadeh et al. (1998) indicated that restriction affected carcass earlier than non-carcass components, while under nutrient restriction, the weight of highly metabolically active organs (gastrointestinal tract, liver and heart) as proportions of body weight are affected to a lesser extent than body weight.

No differences were found in terms of FI as a percentage of metabolic weight, indicating that animals consumed the same proportion of feed during the restriction period. However, LWG lambs presented a greater FCR, which indicates less efficiency converting feed to weight gain. This agrees with the findings of Greeff et al. (1986), who reported a dramatic decrease in feed utilization in lambs with an ADG of 30 g d⁻¹. Reduction of growth rate in restricted animals may be due to the influence of the plane of nutrition on feed

utilization efficiency and the amount of feed required for maintenance (Sivanagendra Babu et al., 2017). During the feed restriction phase, Abouheif et al. (2013) also reported that feed efficiency decreased as the level of restriction increased.

Thomson et al. (1982) found that although underfed animals took longer to reach slaughter weight, their total intake of gross energy and overall energy conversion ratio (considering restricted feeding and refeeding phases) were similar to those under non-restricted feeding conditions. However, the overall feed conversion ratio in our study was greater (less efficient) in LWG lambs.

The increase of feed intake during the compensatory growth seems to be driven by meeting protein requirements. Sheep have the capacity to select their diets to maximize growth (Kyriazakis and Oldham, 1993), but probably protein intake during the refeeding phase was not enough to promote compensatory growth. Addah et al. (2017) reported that refeeding of protein was more effective at inducing compensatory growth compared to energy intake. However, even if the magnitude of compensation is proportional to the intensity of the previous growth restriction, the response varies largely (Hornick et al., 2000). In this study, LW differences between LWG and HWG were 6.7 kg at the beginning and 5.3 kg at the end of the refeeding phase, which indicates a partial compensation (Jobling, 2010).

CONCLUSIONS

Even though haylage is a cheap feed alternative in semi-extensive lamb production systems, it does not enable a full compensatory growth of LWG and MWG lambs. It seems that a minimum ADG of 90 g a⁻¹ d⁻¹ in the summer is necessary to achieve (in the fall) the minimum weight (34 kg) required to qualify for the Uruguayan heavy lamb program, particularly when refeeding conditions may limit compensatory growth.

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