

Energy efficiency in grazing lambs differing in sire body size, determined by the *in vitro* respiration rate and weight of liver and rumen

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ABSTRACT: The energy efficiency of four groups of lambs sired by rams of different body size was inferred from observation of liver and rumen weights and *in vitro* respiration rates (both total and the part attributable to sodium, potassium ATPase activity). The animals were raised in a common grazing-dependent environment from birth (September 1996) until reaching a market weight of 42.5 ± 0.9 kg (December 1997). The four groups (four ewes and four wether lambs per group) were progeny of Corriedale and Romney Marsh dams with sires of the Hampshire Down (H), Texel (T), and Ile France (I) breed, or of the same breed as the dam, as the control (C). At slaughter, livers and rumens were weighed, and in samples (5-10 g) of the caudal lobule and ventral sac, respectively, oxygen consumption was measured polarographically. The Na^+ , K^+ -ATPase dependent respiration was measured as the difference in O_2 intake before and after the addition of 1 mM of ouabain. The genotypes did not affect mean daily gain (86.2 ± 2.0 g). Neither were relative weights of liver and rumen (16.2 ± 0.2 and 21.3 ± 0.9 g/kg of body weight, respectively) nor *in vitro* O_2 consumption in fresh liver tissue ($63.0 \pm 2.4 \mu\text{mol h}^{-1} \text{g}^{-1}$) affected by sire breed. For fresh ruminal papillae tissue there were differences ($P < 0.05$), but of small magnitude, among groups in O_2 consumption (T, 8.0, C, 8.7; I, 9.5; and H, 10.3 $\mu\text{mol h}^{-1} \text{g}^{-1}$). In all breed groups Na^+ , K^+ -ATPase dependent respiration accounted for 30 to 34% of the total O_2 intake in liver and rumen tissues. It is concluded that all four groups of lambs gained weight with essentially the same energy efficiency in this study under conditions of nonintensive nutrition.

Key words: Energy efficiency, grazing lambs, sodium-potassium ATPase activity, tissue *in vitro* respiration, visceral organ weight

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Eficiencia energética en corderos en pastoreo hijos de padres de diferente tamaño corporal determinada por el peso de hígado y rumen y sus correspondientes tasas de respiración tisular *in vitro*

RESUMEN: Se evaluó la eficiencia energética en cuatro grupos de corderos hijos de padres de diferente tamaño corporal, a través del peso del hígado y rumen y de la tasa de respiración *in vitro* (total y atribuible a la actividad de ATPasa sodio-potasio). Los animales se criaron en condiciones comunes de pastoreo desde el nacimiento (septiembre de 1996) hasta el peso de faena de 42.5 ± 0.9 kg (diciembre de 1997). Los cuatro grupos de corderos (4 machos y 4 hembras en cada uno) fueron hijos de madres Corriedale y Romney Marsh con padres de las razas Hampshire Down (H), Texel (T), Ile France (I) o de la misma raza que las madres, como el control (C). Al sacrificio se pesó el hígado y rumen y en muestras (5-10 g) del lóbulo caudal y saco ventral, respectivamente, se midió polarográficamente el consumo de oxígeno. La actividad de la ATPasa Na^+ - K^+ fue medida por diferencia en el consumo de O_2 antes y después de la adición de 1 mM de ouabaina. La ganancia diaria de peso promedio (86.2 ± 2.0 g/día) no se diferenció entre genotipos. El peso relativo del hígado y rumen (16.2 ± 0.2 y 21.3 ± 0.9 g/kg peso corporal, respectivamente) y el consumo *in vitro* de oxígeno del tejido hepático fresco ($63.0 \pm 2.4 \mu\text{mol h}^{-1} \text{g}^{-1}$) no fue afectado por la raza paterna. Para tejido fresco de papilas ruminales hubo diferencias ($P < 0.05$), si bien de pequeña magnitud, entre grupos en consumo de O_2 (T, 8.0; C, 8.7; I, 9.5; H, 10.3 $\mu\text{mol h}^{-1} \text{g}^{-1}$). En todos los grupos raciales la respiración dependiente de la ATPasa Na^+ - K^+ representó el 30-34% del consumo total de O_2 en tejido de hígado y rumen. Se concluye que los cuatro grupos de corderos ganaron peso con similar eficiencia energética en este estudio bajo condiciones de nutrición no intensiva.

Palabras clave: Actividad ATPasa sodio-potasio, corderos en pastoreo, eficiencia energética, peso órganos viscerales, respiración tisular *in vitro*

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Introduction

Lamb carcasses which meet market weight and fat depth specifications have been successfully produced in the southeast of Buenos Aires Province (Argentina) with progenies of Corriedale and Romney Marsh ewes mated to meat producing rams of larger body size, such as Texel and Ile de France (Solanet *et al.*, 1997), however, no local information is available on the energy efficiency of such crosses. The introduction of sires of larger body size may have the advantage of improving rate of body gain, but also the drawback of increasing the energy cost of maintenance of lambs (Taylor *et al.*, 1986; Webster, 1989).

Energy efficiency is not impaired in animals of high growth potential fed high energy diets in corrals (Webster, 1989), but their increased maintenance cost may impose a penalty on energy efficiency at pasture (Solis *et al.*, 1988; DiConstanzo *et al.*, 1990), since then they are subjected to restrictions to expressing their full genetic potential for growth (Molinuevo, 1997).

The main obstacle to evaluating the energy cost of maintenance is that it can not be assessed directly in producing animals, especially not in grazing systems. Therefore it is necessary to measure other variables that can be associated with the cost of maintenance. For example, variations in energy expenditures of cattle and sheep have been investigated using weight of the liver by Koong *et al.* (1985) and Ferrell and Jenkins, (1998); weight of the rumen by Rompala *et al.* (1991) and the *in vitro* cost of ion pumping in visceral tissues by Milligan and McBride (1985). These measurements have been useful to explain variations in energy expenditure for maintenance associated with level of nutrition, genotype and diet composition (Gregg and Milligan, 1982a,b; Ferrell and Koong, 1985; Johnson *et al.*, 1985; Jenkins *et al.*, 1986; Kelly and McBride, 1989; Webster, 1989; McBride and Kelly, 1990).

The present study was carried out to determine the effect of genotype on the weight and the *in vitro* oxygen consumption (ion pumping) of liver and ruminal papillae tissues of lambs sired by rams of different breeds and raised for meat production in the same environment.

Materials and Methods

This trial was conducted in Balcarce, Argentina (37° 45' South, 58° 18' West). Four breed groups were produced by mating Corriedale and Romney Marsh dams to rams of three other breeds: Hampshire Down (H), Texel (T), and Ile France (I) and rams of the same Corriedale and Romney Marsh breeds. The latter were used as controls (C). Eight animals of each breed group (four ewes and four wethers) were raised, from September 1996 to December 1997, in a rotational grazing system on a fertilized pasture of ryegrass plus white and red clover. Lambs were slaughtered at 42.5 ± 0.9 kg (fleece-free body weight), the reticulo-rumens were

removed, emptied, washed with tap water, and weighed. The livers were also removed and weighed.

Samples (5-10 g) of rumen wall ventral sac and liver caudal lobule tissues were taken and placed in glass containers at 0-4°C in medium M199 with Earle's salts (0.6 mM L-glutamine, 25 mM HEPES, 20 g BSA/l, 4 mM NaHCO₃; pH 7.4 (Sigma Chemical Company). Finally glycerol was added (0.125 v/v) and samples stored frozen (-30° C) until analyzed, as described by Milligan and McBride (1985).

The rate of O₂ consumption in each tissue was measured polarographically (Gregg and Milligan, 1982; Milligan and McBride, 1985) with an oxymeter (Oxi 320 WTW, Germany). Duplicate samples of each tissue (liver slices and ruminal papillae) of 10-15 mm length and 0.1-0.5 mm thickness) were incubated for 10 minutes at 37°C in a solution of 138 mM NaCl; 2.7 mM KCl; 8.1 mM Na₂HPO₄; 1.47 mM KH₂PO₄; 0.9 mM CaCl₂; 0.5 mM MgCl₂; 7.5 mM glucose (pH 7.4) and five determinations of oxygen disappearance were made. Then, 1 mM of ouabain (Jorgensen, 1974) was added and the insensitive-to-ouabain respiration was measured for another 10 minutes. The Na⁺,K⁺-ATPase-dependent respiration was determined by the difference in O₂ consumption rates between the initial and the ouabain-treated samples.

The rate of O₂ consumption was calculated by linear regression analysis. Liver and rumen weights and rate of oxygen consumption (total and Na⁺,K⁺-ATPase dependent respiration) were compared by one way analyses of variance. Since no differences were found between groups, animals were pooled and the following relationships were analyzed by linear regression: 1) O₂ consumption and weights of liver and rumen, 2) Na⁺,K⁺-ATPase dependent respiration and total O₂ consumption in rumen and liver.

Results

The mean growth rate for the four groups of lambs over the total period of grazing was 86.2 ± 2.0 g/day. However, in spring, two months before slaughter, the rate of gain increased to 208.4 ± 8.5 g/day. There were no differences between groups in both cases. The lambs grazed on the same pastures from September 1996 to December 1997 and were slaughtered at a target market weight of 42.5 ± 0.9 kg.

Weights of liver and rumen, expressed per unit of fleece-free shrunk body weight, were not affected by sire breed as shown in Table 1. Mean relative weights were 16.2 ± 0.2 g/kg for liver and 21.2 ± 0.9 g/kg for rumen. Mean oxygen consumption rate in liver was 63.0 μmol/h per g of fresh tissue. There were no differences (P > 0.05) between sire groups. Oxygen consumption rate in rumen papillae was 9.2 μmol/h per g of fresh tissue. The rate in lambs sired by Texel rams was lower (8.0) than that in lambs sired by Hampshire Down rams (10.3) (P < 0.05). *In vitro* oxygen consumption in the liver was 7 times higher than in the rumen, but the proportion of the Na⁺,K⁺-ATPase respiration

Table 1. Liver and rumen weight, *in vitro* total oxygen consumption and Na⁺,K⁺-ATPase dependent respiration ($\mu\text{mol/h}$ per g of fresh tissue) in lambs differing in sire breed.

Variable	Sire breed							
	H. Down		Texel		Ile France		Control group	
	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.
Slaughter weight (kg)	41.3	(1.7)	43.4	(1.2)	44.5	(1.8)	42.8	(1.2)
Liver								
Relative weight (g/kg)	16.0	(0.6)	16.4	(0.5)	16.3	(0.4)	16.1	(0.7)
Total O ₂ consumption	64.5	(4.8)	58.5	(4.7)	64.5	(4.8)	66.5	(4.7)
Na ⁺ ,K ⁺ -ATPase-dependent O ₂ consumption	20.7	(2.8)	16.3	(2.4)	19.7	(3.1)	18.0	(1.5)
Rumen								
Relative weight (g/kg)	20.0	(1.0)	21.5	(0.7)	22.4	(0.8)	20.9	(0.5)
Total O ₂ consumption	10.3 ^a	(0.6)	8.0 ^b	(0.5)	9.5 ^{ab}	(0.6)	8.7 ^{ab}	(0.5)
Na ⁺ ,K ⁺ -ATPase-dependent O ₂ consumption	2.6	(0.3)	2.4	(0.2)	2.4	(0.2)	2.7	(0.4)

Means in the same row with different superscripts are significantly different ($P < 0.05$).

was similar in both tissues (30 to 34%) and did not differ among the four breed groups.

The rates of total oxygen consumption and the proportion of respiration attributable to Na⁺,K⁺-ATPase activity in liver and rumen, were unchanged with the respective increase in weight of liver and rumen, as shown in Figure 1.

Variations in oxygen consumption in liver and rumen were paralleled by the respective respiration attributable to Na⁺,K⁺-ATPase activity in each tissue. A unit change in total oxygen consumption in liver and in rumen papillae caused 0.34 ($R^2 = 0.40$) and 0.30 ($R^2 = 0.49$) unit increases in the ATPase dependent respiration, respectively (Figure 2).

Discussion

Lambs used in this experiment were part of a larger meat production project which studied the advantages of producing meat on high quality pastures from lambs sired by rams of different breeds (Solonet *et al.*, 1997). Lambs of large breeds fed well balanced diets have been shown to express a rate of body gain of 300 to 350 g/day (Fluharty and McClure, 1997). In the present production system the rate of gain was 86.2 ± 2.0 g/day over the whole grazing period, with a maximum in spring of 208.4 ± 8.5 g/day. The higher rate of growth in spring can be ascribed to very favorable conditions of pasture availability and quality. There were no differences in growth rate between the four sire groups. This may have been because the limited intake of energy in this production system mitigated expression of differences in genetic potential for growth. Webster (1989) pointed out that the metabolizable energy (ME) even in high quality pastures (10 to 11 MJ/kg dry matter) may not be enough for cattle with sires of different breeds to express their differences in growth potential.

A similar rate of gain among the four lines of lambs is not necessarily an indicator of similar efficiency of growth. Webster (1989) pointed out that to understand the energetic

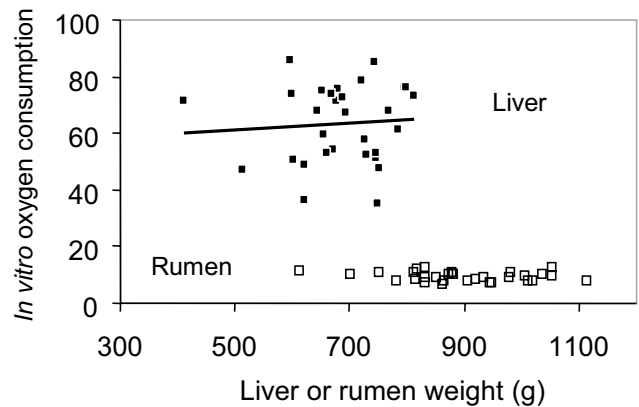


Figure 1. Relationship between hepatic tissue and ruminal papillae *in vitro* oxygen consumption ($\mu\text{mol/h}$ per g of fresh tissue) and the respective weights of liver or rumen of lambs.

basis of growth it is necessary to consider the fraction of feed energy that is converted into products and into body heat (energy expenditure). Since heat represents the amount of nutrients that is undergoing oxidation to provide ATPs for metabolic processes, the increase in heat production implies lower energy efficiency (e.g. lower retained energy per unit of metabolizable energy). For this reason the weight of tissues of high metabolic activity (i.e., high demand for ATP) such as liver and rumen (Milligan and McBride, 1985; Solis *et al.*, 1988; Webster, 1989; Di-Costanzo *et al.*, 1990) are useful indexes to understand the interplay between heat production and growth (Johnson *et al.*, 1985; Koong *et al.*, 1985; Rompala and Hoagland, 1987; Kelly *et al.*, 1993). In other words, if breeding with larger size rams produces offspring with larger liver and rumen weights, and/or higher tissue metabolic activities, their maintenance requirement will also increase (Webster, 1989; Rompala *et al.*, 1991). These lambs require feed of

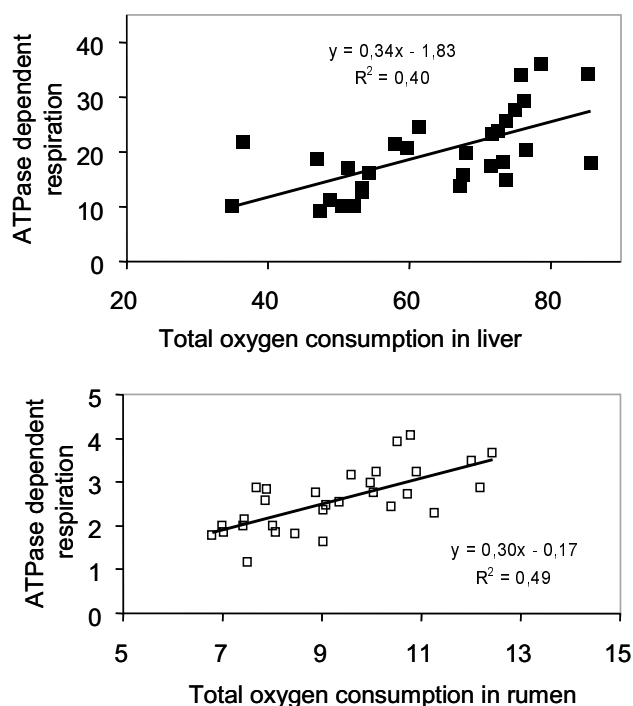


Figure 2. Relationship between the Na^+K^+ -ATPase dependent respiration and the total *in vitro* oxygen consumption in liver and rumen of lambs ($\mu\text{mol/h}$ per g of fresh tissue).

high energy concentration and a high level of feed intake to perform efficiently (Webster, 1989). On the other hand, such lambs could be inefficient under conditions in which growth is limited (Solis *et al.*, 1988; DiCostanzo *et al.*, 1990), since heat production per unit of body gain will increase proportionally to the increase in the cost of maintenance.

Two of the four groups of lambs (Texel and Ile France) differed in ram body size. However, there were no differences in relative liver (16.2 g/kg) and rumen (21.2 g/kg) weights. This is in contrast with the results of Rompala *et al.* (1991) who found an increase of 100 g in rumen weight, in a line of lambs selected for growth. These authors also reported a lack of difference in visceral organ mass between the selected and non-selected lines, which agrees with our results.

Rate of total liver oxygen consumption and the oxygen consumption attributable to Na transport (63.0 and 18.7 $\mu\text{mol/h}$ per g of fresh tissue, respectively) was not different between groups. There was a slightly lower total O_2 consumption ($P < 0.05$) in ruminal papillae in the group sired by the Texel than by Hampshire Down rams (8.0 vs. 10.3 $\mu\text{mol/h}$ per g of fresh tissue, Table 1), however these differences seem too small to be relevant in terms of differences in whole body energy expenditure. Determinations of O_2 consumption were made in frozen tissue samples since no

differences were previously found in measurements of *in vitro* O_2 consumption between fresh samples and samples stored 24 hours or 30 days at -30° or in liquid nitrogen (Massa, 1999).

The lack of differences in liver and rumen weights, or in tissue metabolic activities, suggest that lambs gaining weight at similar rates, may have similar efficiency of growth regardless of sire size. Rompala *et al.* (1991) reported that a line of lambs selected for growth rate presented similar heat production when they were fed at low and high level of intake, although they differed in fasting heat production. Differences between breeding lines may be expressed at different levels of nutrition, because liver weight may respond differently to variations in nutrients status or hormone levels (Webster, 1989; Rompala *et al.*, 1991; Ferrell and Jenkins, 1998).

Liver tissue showed seven times more oxygen consumption than that of rumen (Table 1), in accordance with its higher metabolic rate (McBride and Kelly, 1990). Oxygen consumption did not change with the increase in weight of the respective tissues (Figure 1). This agrees with Johnson *et al.* (1990) who pointed out that metabolic activity per unit of tissue does not vary. However, Rompala *et al.* (1991) reported that tissue metabolic activity could be variable in animals fed at different levels of energy consumption.

The increase in liver and rumen total O_2 consumption was paralleled by an increase of approximately 32% in the respiration attributable to the Na^+K^+ -ATPase activity. These data are in reasonable agreement with results of Milligan and McBride (1985) who reported that Na-transport contributed 40% of the *in vitro* liver respiration, and with Kelly *et al.* (1993) who found that Na^+K^+ -ATPase dependent respiration accounted for 20 to 25% of the ruminal papillae oxygen consumption.

Conclusions

Lambs of the four breed groups with sires differing in body size, had a similar efficiency of growth (gain/heat production) when all animals were gaining weight at a similar rate on high quality pasture. Conditions of either move intensive nutrition or undernutrition might enable expression of differences in energy efficiency among the groups.

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