Effects of genotype on the performance and intake characteristics of sheep grazing contrasting hill vegetation communities

K. Osoro, M. Oliván, R. Celaya and A. Martínez

Centro de Investigación Aplicada y Tecnología Agroalimentaria, Apartado 13, 333000 — Villaviciosa, Asturias, Spain

Abstract

The live-weight responses, voluntary herbage intakes and diet compositions of two breeds of sheep of different mature live weights, grazing two contrasting hill vegetation communities, were studied over three consecutive grazing seasons. A total of 228 Latxa and 255 Gallega non-lactating ewes, with mature live weights of 42.4 and 33.1 kg respectively, grazed two replicates, each of two 5-ha plots comprising by area either 0.3 *Calluna vulgaris* and 0.7 grass species (*Agrostis capillaris*, *Festuca rubra* and *Nardus stricta*) (treatment C₃) or 0.7 *C. vulgaris* and 0.3 of the above grass species (treatment C₇).

The Latxa ewes achieved higher rates of live-weight gain than the Gallega ewes under conditions of high availability (sward surface height >3.0 cm) of the preferred grass species (*A. capillaris* and *F. rubra*) but had lower rates of live-weight gain in the later part of the grazing season when the availability of the preferred grass species was low. In general, the Latxa ewes had higher voluntary herbage intakes per unit live weight and selected a diet of higher digestibility than the Gallega ewes ($P < 0.001$). The composition of the diet was significantly affected by treatment ($P < 0.001$) and was of a higher digestibility in the earlier part of the grazing season ($P < 0.001$).

The results indicate the existence of a significant ($P < 0.001$) genotype $\times$ environment interaction affecting diet selection and animal performance. Between-breed differences in diet selection are likely to be important in determining grazing behaviour and thus the suitability of different genotypes for particular environments. Breeds with a small body size are likely to be better suited to the poorer land resources where the availability of preferred species is low.

Keywords: breeds, ewes, food intake, hill land, performance

Introduction

Differences between animal species in grazing behaviour and diet selection are well documented (Lechner-Doll *et al.*, 1995) and it is known that the nutritive value of plant communities will vary according to the interactions between the animal species, the available biomass, the vegetation components, and the system of grazing management (Osoro *et al.*, 1999). There is, however, little information available on differences between breeds within animal species in grazing behaviour and diet selection, or on the effects of such differences on animal performance.

In sheep, differences between breeds have been observed in herbage intake (Vulich *et al.*, 1990), diet selection (Revesado *et al.*, 1994) and ruminal degradation rate (Cairo *et al.*, 1993). There is also evidence in beef cattle of differences in efficiency between breeds (Wright *et al.*, 1994) and between animals of the same breed but differing in body size

(Ferrer Cazcarra *et al.*, 1995). In a review of the effects of cow size Morris and Wilton (1976) concluded that, although energy requirements and output were influenced by body size, there was no effect of size on overall biological efficiency. Fitzhugh (1978), however, concluded that important genotype $\times$ environment interactions could affect production efficiency as a consequence of differences in energy requirements and output.

Theoretical studies (Illius and Gordon, 1987) indicate that body size could influence an animal's ability to harvest herbage in conditions of low pasture availability, with larger animals being at a disadvantage in such situations. This assumption is supported by results of work by Allden and Whitaker (1970) with sheep and of Zoby and Holmes (1983) with cattle.

Illius (1989) concluded that changes in bite weight reflect both the limitations of sward structure and the

allometric differences in mouth dimensions. Bite size is determined by the interaction between sward height and sward density, regardless of other sward or animal factors (Laca *et al.*, 1993). If these results are to be generalized and of practical value, measurements of bite dimension and mass must be related to animal size and morphology (Demment *et al.*, 1995). In sheep, Penning *et al.* (1991) found that bite weight was linearly related to live weight, increasing by 0.7 mg/kg live weight and that larger ewes appeared to meet their higher energy requirements by having a greater bite weight rather than a higher bite rate or longer grazing time.

Current knowledge of the determinants of bite weight suggest an interaction between sward structure and animal size. Bite weight differences between animals of different size would be expected to be greatest in swards of high forage availability and high quality; as swards become shorter and sparser the absolute difference between animals with small and large bite sizes would be expected to decrease (Demment *et al.*, 1995).

Iason *et al.* (1994) observed that, in sheep, voluntary food intake was affected by a significant breed $\times$ month interaction. These factors, and the way in which different breeds respond in terms of their behaviour and grazing ecology to variation in the physical and nutritional environments, are important in determining the suitability of genotypes to particular situations and for particular functions.

The objective of the present work was to examine the differences in performance in terms of live weight and body condition and grazing behaviour (voluntary intake and diet selection) of two sheep breeds of markedly different mature body size, grazing two contrasting hill vegetation communities: one of predominantly *Agrostis*, *Festuca* and *Nardus* species with small areas of *Calluna vulgaris* and the

other dominated by *C. vulgaris* with some mosaics of the three grass species.

Material and methods

Experimental site

The experiment was conducted at Cueva Palacios Research Station in Quirós, Asturias, Spain, on a 20-ha site at an altitude of 1600 to 1800 m above sea level. The principal species in the vegetation community were *Agrostis capillaris*, *Festuca rubra*, *Nardus stricta* and *Calluna vulgaris*. One half of the site was dominated by the herbaceous species and the other by *C. vulgaris*. Four 5-ha plots were established, two on an area comprising 0.3 *Calluna* and 0.7 grass species (treatment C₃) and two on an area with 0.7 *Calluna* and 0.3 grass species (treatment C₇), providing two replicates of each pasture type.

Animals

The experimental animals comprised a total of 228 Latxa and 255 Gallega mature non-lactating ewes, with respective mean live weights (LW) of 42.4 and 33.1 (s.e.d. 1.10) kg. The two breeds are local, Gallega from Galicia (north-west Spain) and Latxa from the Basque Country (northern Spain) used for milk and cheese production. The ewes had all lambed during January and February and grazed low ground pasture (75 m above sea level) with their lambs from March to June. After weaning in June the ewes were transferred to the experimental site.

Experimental design

The experiment was conducted over three consecutive grazing seasons (June to September) in 1992 to 1994. The ewes were allocated to the experimental treatments (C₃ and C₇) and replicates on the basis of breed, LW and body condition score at the beginning of each of the three grazing seasons. Details of the number of ewes allocated to each plot in each year are given in Table 1.

Table 1 Numbers of ewes of two breeds grazing two replicated treatments with different vegetational compositions in each of 3 years

Replicate	Calluna vulgaris cover							
	0.3				0.7			
	1		2		1		2	
	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa
Year								
1992	29	21	30	23	31	18	29	24
1993	19	21	19	21	17	14	19	22
1994	16	17	16	17	15	15	15	15
Total	64	59	65	61	63	47	63	61

Measurements

Vegetation The mean sward surface heights of the preferred herbaceous species *A. capillaris* and *F. rubra*, (Grant *et al.*, 1985) were calculated weekly from 80 measurements per plot, made using the HFRO sward stick (Barthram, 1986). Mean sward surface heights of these species in each plot, in two periods (period 1: 20 June to 9 August, and period 2: 9 August to 29 September) in each of the 3 years, are presented in Table 2.

Animal live weight and body condition. Ewe LWs were recorded at the beginning, middle (except in 1994) and end of each grazing season. Body condition score was assessed to the nearest 0.25 score on the 0 to 5 scale of Russel *et al.* (1969) by the same operator at the time of the LW recordings.

Voluntary herbage intake. Daily herbage dry-matter intake (DMI) and digestible DMI (DDMI) were estimated on two occasions (July and September) in 1992, using Oliván and Osoro's (1997) modification of the n-alkane technique (Mayes *et al.*, 1986). On each occasion, the ewes were dosed once daily between 08:00 and 11:00 h for 11 days with a paper pellet containing 45 mg n-tetracontane (C_{24}), 50 mg n-dotriacontane (C_{32}) and 50 mg n-hexatriacontane (C_{36}). Faecal grab samples were collected once daily for the last 5 days of each period. Intake was estimated using the C_{32}/C_{33} alkane pair, based on the whole diet (from the estimated diet composition) and faecal concentrations of these alkanes and the C_{32} dosing rate.

Diet apparent digestibility Diet apparent digestibility was estimated from the calculated intake (based on the C_{32}/C_{33} alkane pair) and the calculated faecal output, estimated using the C_{36} alkane as an external marker assuming a faecal recovery of 0.94.

Diet composition Samples of the three principal vegetation components (*C. vulgaris*, *A. capillaris* + *F. rubra*, and *N. stricta*) were collected by hand plucking, to simulate grazing, on four occasions during each dosing period. The proportions of the three vegetation components in the diet were calculated by a least-squares method which determines the combination of dietary components which best matches the observed pattern of faecal alkane concentrations, after an adjustment for incomplete faecal alkane recovery (Oliván and Osoro, 1997).

Statistical analysis

Multifactorial analysis of variance ($2 \times 2 \times 3 \times 2$) were carried out, using GENSTAT V (Lawes Agricultural Trust, 1984) to test the effects of treatment, breed, year and replicate and their

Table 2 Mean sward surface height (cm) of the available preferred species in each replicated treatment

Replicate	<i>Calluna vulgaris</i> cover					
	0.3			0.7		
	1	2	s.e.	1	2	s.e.
1992						
Period 1	3.77	3.76	0.608	2.66	2.72	0.577
Period 2	2.13	2.22	0.355	1.76	1.69	0.171
Mean	2.97	3.01	0.968	2.22	2.22	0.702
1993						
Period 1	4.51	5.12	1.293	4.02	3.93	1.447
Period 2	2.40	2.51	0.534	2.09	1.88	0.330
Mean	3.44	3.80	1.600	3.04	2.89	1.526
1994						
Mean	3.28	3.79	1.395	2.87	2.49	1.031

interactions on ewe LW and body condition score. The effects of treatment, breed and period on dietary composition, voluntary herbage intake and diet apparent digestibility were similarly analysed by the multifactorial analysis using a $2 \times 2 \times 2$ design.

Results

Availability of preferred species

The surface heights of the preferred species in periods 1 and 2 and the mean heights for the grazing season are presented in Table 2. The availability of the preferred species decreased more quickly in the plots with the higher *Calluna* cover (C_7) as consequence of the higher grazing pressure on grass areas. In period 1 the grass heights ranged between 3.76 and 5.12 cm (mean 4.3) in the plots dominated by the grass species (C_3) and between 2.66 and 4.02 cm (mean 3.3) in those with the greater *Calluna* cover (C_7). In period 2 grass heights ranged between 2.13 and 2.51 cm (mean 2.3) and between 1.69 and 2.09 cm (mean 1.9) in treatments C_3 and C_7 respectively. Mean sward heights for the grazing season were 3.3 and 2.6 cm (s.e.d. 0.17; $P < 0.001$) respectively.

Live-weight changes

The live-weight change data in Table 3 show that the rate of live-weight gain increased significantly ($P < 0.001$) from 1992 (24 g/day) to 1994 (48 g/day) and that there were significant differences ($P < 0.001$) between treatments C_3 and C_7 (54 and 15 g/day respectively) and between the Gallega and Latxa breeds (40 and 29 g/day respectively). The results also show that live-weight change was significantly affected ($P < 0.001$) by the interaction between treatment and breed over the grazing season as a whole and by the interactions between treatment and

Table 3 Effects of vegetation treatment on live weight and body condition of two breeds of ewes

Year (Y)	1992						1993						1994						Significance		
	C. vulgaris cover (C)						0.3			0.7			0.3			0.7					
	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa					
Ewe breed (B)	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa	s.e.d.	Y	C	B	Y X C Y X B X C
No. of ewes	61	45	60	42	37	41	36	35	31	34	30	31									
Initial live weight (kg)	33.0	44.0	30.3	43.4	33.1	41.0	33.0	40.9	35.9	41.6	37.0	43.2	1.53					**	***	***	***
Initial condition score	2.76	2.65	2.78	2.65	2.54	2.38	2.56	2.42	2.89	2.57	2.89	2.56	0.073					***	***	*	*
Live-weight change (g/day)																					
Period 1	66	80	53	3	95	134	63	90									10.9	***	***	***	***
Period 2	10	-2	2	-38	23	-2	-20	-85									9.4	**	***	***	***
Total	39	40	27	-18	58	66	23	5	65	71	34	18	6.7				***	***	***	*	***
Condition score change	0.21	0.08	0.01	-0.26	0.32	0.30	0.03	-0.01	0.45	0.49	0.19	0.22	0.058				***	***	***	***	***

year ($P < 0.05$) and between year and breed ($P < 0.05$). Mean data for the 3 years show that the Gallega and Latxa ewes gained 52 and 56 g/day respectively on treatment C_3 . On treatment C_7 the Gallega ewes gained 28 g/day, while the Latxa ewes only maintained LW (s.e.d. 4.8). There was no significant difference between replicates, and the three-way treatment $\times$ ewe breed $\times$ year interaction was not significant.

In 1992 and 1993, when the grazing season was divided into two periods, the mean LW changes in period 1 in the Latxa and Gallega ewes were 103 and 78 g/day respectively on treatment C_3 , and 41 and 59 g/day respectively on treatment C_7 . The significant breed $\times$ year interaction, with Latxa ewes having a lower weight change in period 1 in 1992 than in 1993, may have been due to the Latxa ewes, unlike the Gallega ewes, having no previous experience of the grazing conditions at the experimental site. In period 2, when the grass heights were lower, the mean live-weight changes of the Latxa ewes on treatment C_3 (-2 g/day) were lower than those of the Gallega ewes (15 g/day); this breed difference was even more pronounced on treatment C_7 where the LW changes were -58 and -8 g/day respectively.

The relationships between the sward heights of the preferred grass species and the LW changes of the two breeds of ewes in treatments C_3 and C_7 , considering the data from both replicates (10 points) per breed and treatment, are shown in Figure 1. The

Figure 1 Relationship between sward height of preferred grass species and live-weight change in Gallega (circle) and Latxa (square) ewes grazing hill pastures with 0.3 (● and ■) or 0.7 (○ and □) *Calluna* cover

Table 4 Correlations between and regressions of live-weight change (g/day), in Gallega and Latxa ewes grazing treatments C₃ and C₇, on sward height (cm) of preferred grass species

	Regression coefficient	s.e.	Regression constant	s.e.	r ²
Treatment C ₃					
Gallega	30.5	3.53	-53.6	13.36	0.89***
Latxa	52.4	5.46	-122.7	19.12	0.91***
Treatment C ₇					
Gallega	35.2	6.98	-68.2	19.13	0.73***
Latxa	73.9	9.11	-199.2	24.97	0.88***

linear regression equations (Table 4) between sward height and ewe LW changes differ significantly ($P < 0.001$) in slope and intercept between genotypes on both treatments C₃ and C₇. In Latxa ewes however, the slope of the regression of weight change on sward height differed significantly ($P < 0.001$) between treatments C₃ and C₇, whereas there was no difference in slope between the treatments in Gallega ewes.

Body condition score changes

Changes in body condition score (Table 3) mirrored those in ewe LW. There were significant effects of treatment (C₃: +0.29, C₇: +0.01; s.e.d. 0.024; $P < 0.001$), breed (Gallega: +0.19, Latxa: +0.11; s.e.d. 0.024; $P < 0.001$) and year (1992: +0.03, 1993: +0.17, 1994: +0.35; s.e.d. 0.030; $P < 0.001$) on body condition score over the grazing season. The only significant interaction was that between breed and year ($P < 0.001$).

Diet composition

Estimates of dietary composition were made on the basis of three principal components, viz. the preferred grass species (*Agrostis capillaris* and *Festuca rubra*), *Nardus stricta* and *Calluna vulgaris*. The effects of treatment and period on the proportions of the preferred grass species and *Calluna* selected were highly significant ($P < 0.001$) but there were no significant effects of these factors on the proportion of *N. stricta* in the diet (Table 5). The proportions of the preferred grass species selected were substantially lower in treatment C₇ (Gallega: 0.63 and

Table 5 Effects of vegetation treatment on voluntary food intake and diet apparent digestibility in two breeds of ewes

		<i>C. vulgaris</i> cover (C)												
		0.3				0.7								
Period (P)	1		2		1		2		Significance					
	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa	s.e.d.	C	B	P	C × P	B × P
Ewe breed (B)	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa	Gallega	Latxa	s.e.d.	C	B	P	C × P	B × P
No. of ewes	13	15	13	14	14	15	14	15						
Initial live weight (LW) (kg)	30.6	44.4	33.2	48.9	27.6	42.7	29.9	42.9	1.30	***	***	**		
Final live weight (kg)	33.2	48.9	34.4	49.0	29.9	42.9	29.8	40.2	1.32	***	***			
Proportions of dietary components														
<i>C. vulgaris</i>	0.09	0.03	0.23	0.25	0.23	0.16	0.52	0.51	0.019	***	*	***	***	*
<i>A. capillaris</i> + <i>F. rubra</i>	0.91	0.97	0.63	0.57	0.63	0.70	0.48	0.49	0.021	***		***	***	**
<i>N. stricta</i>	0	0	0.14	0.18	0.14	0.13	0	0	0.012				***	
Herbage intake (g/day)														
Dry matter (DM)	521	788	533	882	507	809	541	685	41.3		***			
Digestible DM (DDM)	340	552	302	533	323	548	280	373	28.2	**	***	***	*	
DDM/kg LW	11.2	12.6	9.1	10.9	12.2	12.8	9.4	8.7	0.68			***		
DDM/kg LW ^{0.75}	28.1	34.9	23.5	31.2	29.3	35.2	23.4	23.9	1.77		***	***		
Apparent digestibility of DM	0.65	0.70	0.57	0.60	0.64	0.68	0.52	0.54	0.012	***	***	***		

Latxa: 0.70 in period 1; Gallega: 0.48 and Latxa: 0.49 in period 2) than in treatment C₃ (Gallega: 0.91 and Latxa: 0.97 in period 1; Gallega: 0.63 and Latxa: 0.57 in period 2). Although the Latxa ewes tended to select higher proportions of the preferred species, the difference between breeds was not significant. The diets selected by the Gallega ewes contained significantly higher ($P < 0.05$) proportions of *Calluna* than in those selected by the Latxa ewes in period 1 but not in period 2.

The treatment $\times$ breed and the three-way treatment $\times$ breed $\times$ period interactions were not significant. The proportions of all three dietary components were significantly affected by the treatment $\times$ period interaction ($P < 0.001$), while there were significant effects of the breed $\times$ period interaction on the proportions of *Calluna* ($P < 0.05$) and preferred grass species ($P < 0.01$) selected.

Voluntary herbage intake and diet apparent digestibility

The Latxa ewes had significantly higher ($P < 0.001$) voluntary intakes, expressed in terms of both actual DMI (789 v. 526 g/day) and DDMI per unit metabolic live weight (31 v. 26 g/kg LW^{0.75}), than the Gallega ewes (Table 5). The differences in mean DMI between treatments C₃ (688 g/day) and C₇ (639 g/day) and between periods 1 (662 g/day) and 2 (664 g/day) were not significant.

In the measurements made in July (period 1) the Latxa ewes on both grazing treatments had significantly higher ($P < 0.001$) total DMI and intakes per kg metabolic weight than the Gallega ewes. In the measurements made in September (period 2) this breed difference was apparent in the measurements of total DMI and DDMI ($P < 0.01$), although the breed differences expressed in terms of LW or LW^{0.75} were not statistically significant on either vegetation type. The effects of period on DDMI, expressed in absolute terms and as both per unit LW and LW^{0.75} and on diet apparent digestibility, were all highly significant ($P < 0.001$). Treatment $\times$ breed and breed $\times$ period interactions were not significant. However treatment $\times$ period and the three-way treatment $\times$ breed $\times$ period interactions were significant ($P < 0.05$) for DDMI and DMI respectively.

The apparent digestibility of the diet selected by ewes on treatment C₃ was significantly higher ($P < 0.001$) than that selected by the ewes on treatment C₇ (0.63 and 0.59 respectively, s.e.d. 0.008). There were also significant differences between the Gallega and Latxa ewes (0.59 and 0.63 respectively, s.e.d. 0.008, $P < 0.001$) and between periods 1 and 2 (0.67 and 0.56 respectively, s.e.d. 0.008, $P < 0.001$) for this trait.

The DM apparent digestibilities of the diets selected by the Latxa ewes in July (period 1) were significantly higher ($P < 0.01$) than those of the Gallega ewes on both treatments (C₃: 0.70 and 0.65 and C₇: 0.68 and 0.64 for Latxa and Gallega ewes respectively). There were no significant interactions or breed differences in the diet apparent digestibility measurements made in September (period 2).

Discussion

The results show clear evidence of a difference between sheep breeds in voluntary herbage intake, expressed both in absolute terms and per unit metabolic weight. This supports the observation of Vulich *et al.* (1990) of breed differences in voluntary intake at pasture. The higher intakes of the larger and heavier Latxa ewes, particularly on the treatment with greater availability of preferred species, are consistent with the observation that bite size and bite weight are related to animal size (Demment *et al.*, 1995) and to the higher intake potential of larger animals (Illius, 1989).

The relationships between live-weight change and sward surface height of the preferred grass species (Table 4) indicate that animal performance was more affected by herbage availability in the larger Latxa ewes than in those of the smaller Gallega breed. The corollary of this observation, supported by the animal performance data, particularly in period 2 (Table 3), is that the smaller breed was better able to maintain live weight under conditions of low availability of the preferred grass species. This advantage of the smaller breed is considered to be attributable in part to differences in bite size between large and small animals, as noted by Demment *et al.* (1995), resulting in greater intake limitations in large genotypes grazing short swards (Clutton-Brock and Harvey, 1983) and in part to higher proportions of *Calluna* in the diet of the smaller Gallega ewes.

The results also support the hypotheses of Illius and Gordon (1987) that body size influences an animal's ability to harvest herbage and of Illius (1989) that changes in bite weight reflect both the limitations of sward structure and allometric differences in mouth size. Penning *et al.* (1991) suggested that larger sheep meet their higher energy requirements by having greater bite weights, rather than higher bite rates or longer grazing times. This is the probable explanation for the greater reduction in intake and LW gain in the Latxa ewes compared with the Gallega ewes in the latter part of the grazing season, when the height of the preferred grass species was lower.

DMI and diet apparent digestibility were substantially higher in both periods on the grass-

dominant (C_3) treatment than on that dominated by *Calluna* (C_7). The decreases in both DMI and diet apparent digestibility, which occurred with advancing season and plant maturity, were greater in the *Calluna*-dominant treatment (C_7) than on that dominated by the grass species (C_3), as would be expected from the work of Hodgson *et al.* (1991). The seasonal decline in diet apparent digestibility from period 1 to period 2 was probably due to an increase in the proportion of dead plant material consumed, as observed by Grant *et al.* (1985), and to increases in the proportion of less digestible species, such as *Calluna*, in the diet.

The daily intakes of herbage of 9.1 to 12.8 g DDM per kg LW were considerably lower than the intakes of 22.6 g/kg LW of digestible organic matter (DOM) observed by Hodgson *et al.* (1991) in Scottish Blackface ewes weighing 56 kg LW grazing *Agrostis* communities. On the *Calluna*-dominant (C_7) treatment, however, the daily intakes of 8.7 to 9.4 g DDM per kg in period 2 were higher than those of 4.7 g of DOM per kg LW found by Hodgson *et al.* (1991) on monospecies *Calluna* moor. These values illustrate the poor nutritive value of *Calluna* noted by Milne *et al.* (1979).

Overall, the LW changes of the Gallega ewes were higher than those of the Latxa ewes on both treatments (C_3 : 1.47 and 1.35; C_7 : 0.78 and -0.16 g/kg initial LW respectively). There was no difference in performance between the two breeds when the height of preferred species was high, i.e. in period 1 of treatment C_3 (2.43 and 2.49 g/kg for the Gallega and Latxa ewes respectively) but in conditions of low height of preferred species, i.e. in treatment C_7 in both periods (period 1: 1.85 and 1.10 g/kg; period 2: -0.59 and -1.44 g/kg for the Gallega and Latxa ewes respectively) and in treatment C_3 in period 2 (0.49 and -0.04 g/kg for the Gallega and Latxa ewes respectively) the between-breed differences were substantial. These performance data demonstrate the lesser ability of large genotypes to exploit conditions of low herbage height as a consequence of their grazing behaviour and their higher absolute nutrient requirements. Working with cattle, Morris and Wilton (1976) concluded that the higher maintenance requirements associated with a greater body mass result in a reduced energetic efficiency, while Wright *et al.* (1994) suggested that attributes of the dam, such as body size and nutrient partitioning, influence the energetic efficiency of different genotypes and their suitability to different environments.

In work with the same two sheep breeds, Martínez and Osoro (1995) found that, in lactating ewes grazing perennial ryegrass-white clover pastures with sward heights varying between 3.0 and 8.0 cm,

the sward height at which the Latxa ewes and their lambs achieved the highest LW gains (6.5 cm) was significantly greater than that for the Gallega ewes and lambs (5.5 cm). Greeff *et al.* (1995) also concluded that body size was an important factor in determining the biological efficiency of lamb production and suggested that there was an optimum body size for each particular environment.

The differences noted in the dietary components of the Gallega and Latxa ewes in the present experiment are similar to the results of Revesado *et al.* (1994) working on a hill shrub community with two sheep breeds, the Churra and Merino, with mature body weights similar to those of the Gallega and Latxa respectively. They noted a greater degree of dietary adaptability in the smaller Churra breed, with a higher intensity of food selection and adaptation response when the quantity of available food is low.

The results of the present experiment point to the existence of a significant genotype $\times$ environment interaction affecting diet selection, voluntary intake and animal performance. Between-breed differences in diet selection and voluntary food intake are likely to be important in determining grazing behaviour and thus the suitability of different genotypes for particular environments. Breeds with a small body size are likely to be better suited to the poorer land resources where the availability of the preferred grass species is low. This advantage is expected to decrease as the quality of land resources increases.

Acknowledgements

The authors are indebted to the staff of the Meat Production and Grazing Ecology Research Programme for their work, often undertaken in difficult conditions, in the conduct of the experiment. We wish to thank Dr Angus Russel for his helpful comments on this manuscript. The financial support of projects GAN 88 - 0294 and GAN 91 - 0623 by CICYT is also gratefully acknowledged.

References

- Allden, W. G. and Whitaker, I. A. M. 1970. The determinants of herbage intake by grazing sheep: the interrelationship of factors influencing herbage intake and availability. *Australian Journal of Agricultural Research* **21**: 755-766.
- Barthram, G. I. 1986. Experimental techniques: the HFRO swardstick. *Biennial report, Hill Farming Research Organisation, 1984-85*, pp. 29-30.
- Carro, M. D., Giráldez, F. J., Ranilla, M. J., González, J. S. and Mantecón, A. R. 1993. Comparative study of rumen activity in Churra and Merino sheep. *Animal Production* **56**: 463 (abstr.).

- Clutton-Brock, I. H. and Harvey, P. H. 1983 The functional significance of variation in body size among mammals *American Society of Mammologists special publication* no 7, pp. 632-663
- Demment, M. W., Peyraud, J. I. and Laca, E. A. 1995. Herbage intake at grazing: a modelling approach. In *Recent developments in the nutrition of herbivores. Proceedings of the IVth international symposium on the nutrition of herbivores* (ed. M. Journet, E. Grenet, M.-H. Farce, M. Theriez and C. Demarquilly), pp. 121-141 INRA, Paris.
- Ferrer Cazcarra, R., Petit, M. and D'hour, P. 1995 The effect of sward height on grazing behaviour and herbage intake of three sizes of Charolais cattle grazing cocksfoot (*Dactylis glomerata*) swards *Animal Production* 61: 511-518
- Fitzhugh, H. A. 1978 Animal size and efficiency with special reference to the breeding female *Animal Production* 27: 393-401.
- Grant, S. A., Suckling, D. E., Smith, H. K., Torvell, I., Forbes, T. D. A. and Hodgson, J. 1985 Comparative studies of diet selection by sheep and cattle: the hill grasslands *Journal of Ecology* 73: 987-1004
- Greeff, J. C., Bouwer, L. and Hofmeyr, J. H. 1995 Biological efficiency of meat and wool production of seven sheep genotypes *Animal Science* 61: 259-264
- Hodgson, J., Forbes, I. D. A., Armstrong, R. H., Beattie, M. M. and Hunter, E. A. 1991 Comparative studies of the ingestive behaviour and herbage intake of sheep and cattle grazing indigenous hill plant communities. *Journal of Applied Ecology* 28: 205-227
- Iason, G. R., Sim, D. A., Foreman, E., Fenn, P. and Elston, D. A. 1994 Seasonal variation of voluntary food intake and metabolic rate in three contrasting breeds of sheep *Animal Production* 58: 381-387
- Illius, A. W. 1989 Allometry of food intake and grazing behaviour with body size in cattle. *Journal of Agricultural Science, Cambridge* 113: 259-266.
- Illius, A. W. and Gordon, I. J. 1987 The allometry of food intake in grazing ruminants *Journal of Animal Ecology* 56: 989-999.
- Laca, E. A., Demment, M. W., Distel, R. A. and Griggs, T. C. 1993 A conceptual model to explain variation in ingestive behaviour within a feeding patch. *Proceedings of the XVII international grassland congress*, pp. 710-712
- Lawes Agricultural Trust. 1984 *Genstat V*, mark 4.04B *Genstat 5 Committee*, Rothamsted, Hertfordshire
- Lechner-Doll, M., Hume, I. D. and Hofmann, R. R. 1995. Comparison of herbivore forage selection and digestion in *Recent developments in the nutrition of herbivores. Proceedings of the IVth international symposium on the nutrition of herbivores* (ed. M. Journet, E. Grenet, M.-H. Farce, M. Theriez and C. Demarquilly), pp. 231-248
- Martínez, A. and Osoro, K. 1995 Respuesta del ganado ovino a la altura de hierba disponible en pastos de raigrás y trébol. *VI Jornadas sobre Producción Animal*, ITEA vol extra 16, pp. 171-173
- Mayes, R. W., Lamb, C. S. and Colgrove, P. M. 1986 The use of dosed and herbage n-alkanes as markers for the determination of herbage intake. *Journal of Agricultural Science, Cambridge* 107: 161-170
- Milne, J. A., Bagley, I. and Grant, S. A. 1979. Effects of season and level of grazing on the utilization of heather by sheep 2. Diet selection and intake. *Grass and Forage Science* 34: 45-53
- Morris, C. A. and Wilton, W. 1976 Influence of body size on the ecological efficiency of cows: a review *Canadian Journal of Animal Science* 56: 613-647
- Oliván, M. and Osoro, K. 1997 Utilización de la técnica de los n-alcenos en estudios de ingestión y selección de dieta de los rumiantes en pastoreo: revisión. *ITEA* 93A: 193-208
- Osoro, K., Martínez, A. and Celaya, R. 1999 Conocimientos básicos para la gestión de los recursos pastables en la Cordillera Cantábrica. *V Jornadas prateses* Lugo. In press.
- Penning, P. D., Rook, A. J. and Orr, R. J. 1991 Patterns of ingestive behaviour of sheep continuously stocked on monocultures of ryegrass or white clover. *Applied Animal Behaviour Science* 31: 237-250
- Revesado, P. R., Mantecón, A. R., Frutos, P. and González, J. S. 1994 Comparative studies of diet selection by Churra and Merino genotypes grazing on a hill shrub community (ed. In *Livestock production and land use in hills and uplands*) British Society of Animal Production occasional publication no. 18, pp. 111-112
- Russel, A. J. F., Doney, J. M. and Gunn, R. G. 1969. Subjective assessment of body fat in live sheep. *Journal of Agricultural Science, Cambridge* 72: 451-454
- Vulich, S. A., Hanrahan, J. P. and O'Riordan, E. G. 1990. Variation of intake at pasture: differences among breeds of sheep of different mature size. *Proceedings of the fourth world congress on genetics applied to livestock production*, Edinburgh, vol. 15, pp. 57-60
- Wright, I. A., Jones, J. R., Maxwell, I. J., Russel, A. J. F. and Hunter, E. A. 1994. The effect of genotype X environment interactions on biological efficiency in beef cows. *Animal Production* 58: 197-207
- Zoby, J. I. F. and Holmes, W. 1983. The influence of size of animal and stocking rate on the herbage intake and grazing behaviour of cattle. *Journal of Agricultural Science, Cambridge* 100: 139-148

(Received 29 June 1998—Accepted 18 March 1999)