The effect of pattern of food supply on performance, compensatory growth and carcass composition of Beulah and Welsh Mountain lambs

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Abstract

Seventy-eight Beulah (BH) and 78 Welsh Mountain (WM) wether lambs (mature live weights (MLW) 60 and 70 kg respectively), were used to investigate genotypic differences in performance and compensatory growth during the post-weaning period. After an initial slaughter of 12 of each breed, a complete straw-based pelleted diet (122 g crude protein and 10.4 MJ metabolizable energy per kg dry matter (DM)) was offered *ad libitum* to a further 29 of each which were slaughtered at a range of live weights between proportionately 0.35 and 1.00 of MLW. As well as these groups undergoing normal growth (NG), the remaining lambs were given the same diet at a level sufficient to maintain constant live weight (LW) for 3 months. Eight of each breed were then slaughtered and the remaining 29 of each offered the diet *ad libitum* for a period of post-restricted growth (PRG); these 29 were also slaughtered between 0.35 and 1.00 of MLW. During the periods of *ad libitum* food supply, voluntary food intake was greater in BH than WM lambs (BH: 38.3, WM: 35.3 g DM per kg LW, $P < 0.01$) and during PRG as compared with NG although this result was due to a response only in WM lambs (NG – BH: 38.0, PRG-BH: 38.5, NG – WM: 33.3, PRG – WM: 37.2 g DM per kg LW, breed $\times$ pattern of food supply interaction, $P < 0.05$). Daily live-weight gain (LWG) was greater during PRG than NG in both breeds (NG: 3.15, PRG: 4.80 g/kg LW per day, $P < 0.05$). This effect was greatest in the first 8 weeks of growth but persisted into the period 16 weeks to maturity. WM lambs had overall slightly leaner carcasses and a lower proportion of protein in the fleece-free empty body than BH when compared at the same proportion of MLW; particularly during PRG. The protein in the carcass-weight gain (CWG) was greater in WM lambs during PRG than during NG (NG: 98, PRG: 123 g/kg, $P < 0.05$), but did not differ significantly in BH (NG: 106, PRG: 118 g/kg). The proportion of fat in CWG was concomitantly smaller during PRG. There are thus breed differences in the performance and carcass composition of lambs during compensatory growth. Genotypes to be finished by continuous feeding or a regimen incorporating food restriction should be carefully chosen for date of finishing in relation to desired carcass composition.

Keywords: carcass composition, food supply, growth, lambs.

Introduction

Periodic restriction of food supply is an important natural component of animal production systems in seasonal environments. This natural restriction can be overcome with supplementary feeding or alternatively it can be incorporated as a normal part of the annual cycle of production. This is especially feasible when considering impairment of growth of young animals which can be made good by compensatory growth when adequate food supply is restored (O'Donovan, 1984). The experiment here was designed to examine the effect of food restriction

and realimentation on performance, growth and carcass composition of Beulah and Welsh Mountain lambs, two breeds commonly produced on Welsh upland and hill farms.

Larger genotypes of sheep reach their mature live weight (MLW) at older ages than smaller genotypes (Taylor, 1980). This leads to differences in carcass composition when compared at the same live weight (LW) but most of these differences disappear when genotypes are compared at the same proportion of MLW (McClelland and Russel, 1972; McClelland, Bonaiti and Taylor, 1976; Butler-Hogg, 1984a). As well as being a function of stage of maturity, the chemical composition of the growth of the empty

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Table 1 Composition of diet

Ingredients	g/kg
Barley straw (chopped)	150
Dried sugar beet pulp	350
Dried grass (milled)	450
Vitamin/mineral/molasses	50
Analysis	
Estimated metabolizable energy (MJ/kg DM)	10.4
Dry matter (g/kg)	897
Organic matter (g/kg DM)	926
Crude protein (g/kg DM)	122
Neutral-detergent fibre (g/kg DM)	454

body and/or the carcass has been shown to differ between animals given food *ad libitum* following normal uninterrupted growth (normal growth; NG) and those on an *ad libitum* food supply following a period of intake restriction (post-restricted growth; PRG). Growth usually consists of more protein and less fat during PRG than during NG (Burton, Anderson and Reid, 1974; Butler-Hogg, 1984b; Hodge and Star, 1984) although other studies have shown that the fat content of the empty body may be greater at slaughter following realimentation to the same body weight as continuously fed controls (Meyer and Clawson, 1964; see also O'Donovan, 1984). The lack of agreement between studies may be due to differences in the precise treatments applied and/or the compensatory growth response may differ between breeds of sheep. This study aimed to compare two genotypes of lamb of contrasting MLW (Beulah (BH): 60 kg; Welsh Mountain (WM): 50 kg) given the same dietary restriction.

Material and methods

Animals

In August 1986, 78 Beulah and 78 Welsh mountain wether lambs were selected, each from a single flock in Dyfed, mid Wales. Both flocks lambed in April 1986 and after weaning in August, lambs were transported to Bush Estate, Midlothian, Scotland, where they were individually penned in indoor accommodation under natural lighting and temperature regimes. The mean initial live weights of the lambs were 21.7 kg for BH and 21.8 kg for WM.

Experimental design

For each of the two genotypes an initial group of 12 lambs was slaughtered in September (group I) and 29 others were offered the complete chopped-straw-based diet (Table 1) *ad libitum*. During this period of continuous *ad libitum* feeding and NG the 29 lambs of each breed were slaughtered at weights distributed evenly between proportionately 0.35 and 1.0 of MLW for that genotype. A further 37 of each breed were restricted to constant LW for 3 months after which time eight of each were slaughtered (group C). Restriction to constant LW was achieved by offering lambs 17.3 g dry matter (DM) per kg LW of the diet (Agricultural Research Council, 1980). The remaining 29 of each breed were realimented and received *ad libitum* feeding. These remaining lambs were slaughtered throughout the interval of 0.35 to 1.0 of MLW during this period of PRG. MLW was taken to be the breed average of 50 kg for WM (Meat and Livestock Commission, 1989) and was estimated at the outset of the experiment to be 60 kg for BH although no known published figure was available.

Table 2 Live-weight gains and food intakes of Beulah and Welsh Mountain lambs fed continuously *ad libitum* (NG) or during *ad libitum* feeding following restriction (PRG) in three periods during the time of growth

Dietary treatment	Period						s.e.d.
	0 to 8 weeks		9 to 16 weeks		16 weeks to maturity		
	NG	PRG	NG	PRG	NG	PRG	
Beulah							
Proportion of MLW+ (60 kg)	0.43	0.44	0.52	0.60	0.70	0.78	—
LWG (g/day)	82.4	177.5	115.4	157.0	143.1	181.8	20.28
LWG (g/kg LW per day)	3.80	6.77	3.69	4.38	3.00	3.89	0.610
Intake (g DM per day)	962	1028	1174	1308	1316	1431	72.8
Intake (g DM per kg LW per day)	39.8	39.8	38.6	37.3	28.6	31.4	2.05
Welsh Mountain							
Proportion of MLW+ (50 kg)	0.47	0.53	0.59	0.72	0.84	0.94	—
LWG (g/day)	48.6	144.4	113.7	178.3	106.9	157.0	18.59
LWG (g/kg LW per day)	2.07	5.43	3.87	4.98	2.48	3.33	0.60
Intake (g DM per day)	725	999	1027	1295	1180	1467	57.8
Intake (g DM per kg LW per day)	31.5	37.5	34.9	36.2	27.9	31.1	1.60

† Proportion of mature live weight (MLW) was calculated at the chronological median of each period.

Table 3 Probability values of main effects and interactions between factors from three-way analyses of variance, factorial design of the mass-specific live-weight gain (LWG) and food intake (see Table 2)

	LWG (g/kg LW per day)	Intake (g DM per kg LW per day)
Breed (BH, WM)†	*	***
Period (0 to 8, 9 to 16, 16+ weeks)	***	***
Pattern of food supply (NG, PRG)†	***	**
Breed × period	**	*
Breed × pattern of food supply		*
Period × pattern of food supply	***	
Breed × period × pattern of food supply		

† BH = Beulah; WM = Welsh Mountain; NG = continuous *ad libitum* feeding; PRG = *ad libitum* feeding after restriction.

In this experiment, five BH and four WM lambs fed *ad libitum* reached 'maturity' as defined by their mean LW remaining stable over a 4-week period, and these means were 58 kg and 52 kg respectively.

Measurements

Following a 2-week period of adjustment to the diet, the amounts of food offered and refused and thus the

voluntary food intake (VFI) by each lamb were recorded daily; LWs were recorded weekly. During periods of *ad libitum* feeding, food offered was adjusted to exceed intake by 100 g/kg. Lambs were shorn prior to slaughter. At slaughter the gastrointestinal tract was weighed full and empty. The pelt, feet, head and internal organs were weighed separately and combined with the empty gastrointestinal tract to form the non-carcass component. The complete carcass was weighed 'hot', chilled and split medially. One-half was retained and frozen at -20°C for subsequent mincing. The minced carcass and non-carcass components were chemically analysed for fat, ash and water; protein was determined by difference.

Results and discussion

Intake, LWG and food conversion ratio

As expected absolute VFI (g DM per day) was higher in the larger BH lambs but intake relative to LW was also greater in this breed (BH: 38.3, WM: 35.3 g DM per kg per day). Although some studies have shown no significant increase in VFI on realimentation over and above those on continuous *ad libitum* feeding (e.g. Meyer and Clawson, 1964; Murray and

Table 4 (a) The proportion of carcass and fleece-free empty body (FFEB) in the live weight (LW) and the composition of (b) carcass and (c) FFEB of lambs in the initial slaughter group (I), the slaughter group following restriction (C) and during growth periods on normal *ad libitum*-fed growth (NG) and post-restricted growth (PRG), categorized into three stages of maturity

		NG					PRG			
	Breed†	I	C	0.4-0.6	0.6-0.8	0.8-1.0	0.4-0.6	0.6-0.8	0.8-1.0	s.e.d.
(a) Proportion of carcass and										
FFEB in the LW										
Carcass in LW	BH	0.504	0.445	0.482	0.489	0.531	0.475	0.504	0.504	0.0114
	WM	0.518	0.448	0.474	0.487	0.485	0.444	0.458	0.464	0.0114
FFEB in LW	BH	0.863	0.806	0.838	0.845	0.836	0.829	0.828	0.840	0.0120
	WM	0.874	0.826	0.842	0.845	0.845	0.822	0.813	0.833	0.0199
(b) Composition of carcass										
Water	BH	0.487	0.495	0.458	0.467	0.381	0.462	0.458	0.420	0.0179
	WM	0.464	0.488	0.452	0.420	0.401	0.481	0.433	0.464	0.0198
Fat	BH	0.225	0.256	0.321	0.327	0.438	0.292	0.318	0.390	0.0226
	WM	0.260	0.250	0.319	0.379	0.403	0.265	0.291	0.358	0.0276
Ash	BH	0.059	0.059	0.038	0.036	0.034	0.050	0.047	0.038	0.0047
	WM	0.052	0.065	0.046	0.039	0.041	0.052	0.041	0.042	0.0045
Protein	BH	0.225	0.190	0.184	0.170	0.147	0.196	0.177	0.152	0.0095
	WM	0.218	0.197	0.182	0.163	0.149	0.202	0.188	0.168	0.0130
(c) Composition of FFEB										
Water	BH	0.547	0.536	0.510	0.499	0.422	0.510	0.508	0.460	0.0138
	WM	0.516	0.536	0.508	0.474	0.445	0.525	0.523	0.477	0.0141
Fat	BH	0.192	0.222	0.272	0.286	0.379	0.258	0.280	0.344	0.0197
	WM	0.230	0.217	0.267	0.309	0.366	0.237	0.252	0.323	0.0199
Ash	BH	0.049	0.049	0.039	0.034	0.032	0.044	0.042	0.037	0.0032
	WM	0.043	0.052	0.039	0.034	0.035	0.044	0.037	0.034	0.0028
Protein	BH	0.212	0.194	0.180	0.182	0.166	0.188	0.171	0.159	0.0096
	WM	0.206	0.195	0.186	0.183	0.154	0.193	0.189	0.166	0.0091

BH = Beulah; WM = Welsh Mountain.

Slezacek, 1980), this study concurs with others that have found that VFI during PRG is greater than that during NG (NG: 35.7, PRG: 37.9 g DM per kg LW per day, $P < 0.01$) (Allden, 1970; Graham and Searle, 1979). However, this overall greater VFI in PRG than NG groups is due solely to an effect within WM lambs (breed $\times$ pattern of food supply interaction, $P < 0.05$, Tables 2, 3).

Both absolute LWG and LWG relative to body weight were greater for BH than for WM lambs (BH, 4.25; WM, 3.69 g/kg LW per day, $P < 0.05$) and overall LWG during PRG was greater than during NG (NG, 3.15; PRG, 4.80 g/kg LW per day, $P < 0.001$), an effect present in both breeds (breed $\times$ pattern of food supply interaction, $P > 0.05$, Table 3). A short-term increase in VFI on realimentation is almost inevitable as animals are released from food restriction. This leads to immediate increases in LWG due to gutfill (Thornton, Hood, Jones and Re, 1979). Intake and LWG were hence calculated on a chronological basis in order to investigate the time course and persistence of any effects of PRG *v.* NG on these variables (Tables 2, 3). In WM lambs, the LWG remained higher in the PRG group than the NG group into the period 9 to 16 weeks following return to *ad libitum* feeding. This elevation in LWG was not accompanied by a correspondingly elevated VFI by WM lambs in this same period. The elevation in LWG also resulted in the WM lambs reaching a greater proportion of their MLW (0.72) in this period, relative to all BH lambs and to WM lambs undergoing normal growth (Table 2). When analysed on a chronological basis (Table 2), the proportions of

MLW at slaughter are more divergent with increasing age during PRG than during NG.

Carcass and empty body weights and their composition

In agreement with established allometric relationships (Thonney, Taylor, Murray and McClelland, 1987b), the BH lambs have a larger carcass relative to LW than the WM lambs, when compared at the same proportion of MLW (Table 4a). This breed difference is present within lambs on both NG and PRG, although the proportion of carcass in the LW is generally greater during normal growth as compared with compensatory growth. In contrast the fleece-free empty body weight (FFEBW) formed a relatively constant proportion of LW, varying little either with dietary treatment or genotype (Table 4a). Thus compensatory growth, especially that occurring soon after realimentation was due mainly to an increase in non-carcass components; a similar result has been found in steers and sheep (Winter, Tulloh and Murray, 1976; Carstens, Johnson and Ellenberger, 1989). Clearly, since carcass components are a greater proportion of LW in BH than in WM lambs, then so the relative size of the non-carcass components are smaller in the BH breed. Whilst it may be hypothesized that variation in the proportions of non-carcass components are due to changes in the digestive tract (e.g. Carstens *et al.* 1989), there are no *a priori* grounds for expecting that either breed should have a relatively larger digestive tract. This body characteristic does not vary systematically with LW either between genotypes of sheep (Thonney *et al.*, 1987b) or between species (Demment and Van Soest, 1985).

Table 5 Relationships between (a) carcass and fleece-free empty body components and live weight (LW) and (b) carcass components and carcass weight during normal continuous *ad libitum*-fed growth (NG) and *ad libitum*-fed growth post restriction (PRG) (S_a and S_b are standard errors of estimated parameters)

Standard errors of estimated parameters											
Y	Breed†	NG					PRG				
		a	S _a	b	S _b	r ²	a	S _a	b	S _b	r ²
(a) Equation: Components Y (kg) = a + bLW (kg)											
Carcass	BH	-1.09	0.515	0.534	0.0134	0.975	-2.160	0.386	0.545	0.0104	0.988
	WM	0.773	0.340	0.464	0.0102	0.982	-0.86	0.631	0.482	0.0176	0.957
EBW	BH	0.58	0.368	0.828	0.0096	0.995	-1.070	0.488	0.861	0.0132	0.992
	WM	0.67	0.243	0.828	0.0073	0.997	-0.700	0.443	0.845	0.0123	0.993
(b) Equation: Components Y (kg) = a + b carcass weight (kg)											
Water	BH	1.80	0.366	0.336	0.0192	0.894	1.22	0.308	0.376	0.0168	0.943
	WM	1.27	0.297	0.348	0.0188	0.917	1.39	0.375	0.371	0.0226	0.891
Fat	BH	-3.27	0.435	0.535	0.0228	0.938	-2.43	0.422	0.479	0.0231	0.935
	WM	-2.66	0.412	0.524	0.0261	0.929	-2.53	0.524	0.473	0.0316	0.872
Ash	BH	0.269	0.0791	0.024	0.0041	0.497	0.311	0.0722	0.027	0.0039	0.617
	WM	0.234	0.0889	0.030	0.0056	0.483	0.256	0.0749	0.030	0.0045	0.576
Protein	BH	1.17	0.162	0.106	0.0084	0.819	0.90	0.170	0.118	0.0093	0.843
	WM	1.15	0.179	0.098	0.0113	0.709	0.88	0.221	0.123	0.0133	0.728

† BH = Beulah; WM = Welsh Mountain.

The experiment confirms the general conclusions that the effect of food restriction and realimentation on carcass composition results in an overall lower proportion of fat in the carcass, a greater water content and a slightly greater proportion of protein (O'Donovan, 1984). This is especially true in WM lambs in which the proportion of carcass protein in the PRG group is greater than that in the NG group by 20 g/kg in the early stages of growth, a difference which persisted until 0.8 to 1.0 of maturity (proportion of protein: PRG: 168 g/kg; NG: 149 g/kg). In BH lambs the proportion of protein was only 12 g/kg greater in the PRG than the NG lambs at the early stages of growth, but this difference had largely disappeared by the time the lambs were at 0.8 to 1.0 of maturity (proportion of protein: PRG: 152 g/kg; NG: 147 g/kg; Table 4).

Composition of carcass gain

The relationship between weight of fat and empty body weight has been shown by some studies to be biphasic with an increase in rate of fattening above a transition point (Searle and Griffiths, 1976). It has been proposed that the transition point is at heavier body weights for animals of greater MLW (Black, 1983). Like many of the comparisons between breeds, this difference may also disappear if the transition points are considered to be a proportion of MLW (McClelland *et al.*, 1976). In this experiment the gain in components of the carcass was found to be a linear function of carcass weight (Table 5) and there was no evidence of biphasic relationships or curvilinearity. There was no difference between breeds in the proportion of fat or protein in the carcass gain within the different patterns of food supply. There was significantly more protein and water and less fat in the carcass gain of both genotypes during PRG than during NG (Table 5). Several other studies have also found a similar result, which is consistent with the hypothesis that compensatory growth is due to this change in chemical composition of the LWG (Black, 1983). The increase in carcass protein gain during PRG as compared with NG was greater in WM lambs (PRG: 125 g/kg; NG: 98 g/kg, $P < 0.05$) than in BH lambs (PRG: 118 g/kg; NG: 106 g/kg, $P > 0.05$).

Mechanisms of compensatory growth

The results have shown a greater compensatory growth response in WM than in BH lambs both in terms of LWG and protein composition of the carcass and EBW. It has been suggested that age and/or LW at the time of food restriction influence compensatory growth (see O'Donovan, 1984). When the experiment was begun, these lambs were of both similar age and LW, hence neither factor can explain the difference between these breeds. An alternative hypothesis is that the potential for compensatory

growth depends on the body composition at the time of restriction. Wright, Russel and Hunter (1987) proposed that cattle may exhibit compensatory growth if restriction is applied at a stage when nutrition can influence the quantity of fat deposited. The fat composition of both the carcass and the FFEBW of the WM lambs was slightly but not significantly greater than that of the BH lambs at the start of the experiment (Table 4). In this regard the results here would tend to support the hypothesis of Wright *et al.* (1987) in that food restriction had a greater effect on fatness of WM lambs which subsequently showed greater compensatory growth; this may have been a consequence of the WM lambs being at a greater proportion of their MLW than the BH lambs at the onset of the experiment. Surprisingly, the WM lambs actually decreased in proportion of fat in both the carcass and the FFEBW during restriction as compared with the BH, which increased their proportion of fat (Table 4), although the changes were small. Changes in fatness during restriction and utilization of fat after restriction may both be a result of a generally greater propensity of some genotypes to reallocate body reserves.

We cannot at this stage discern whether the difference in compensatory growth between the breeds is a consequence of fat dynamics, stage at which restriction is imposed relative to maturity or an inherently faster maximum growth rate in the WM breed. The results for both breeds however do support the general principle that compensatory growth is due primarily to protein gain early in the period of realimentation (Black, 1983). A comparative study of lambs has shown that genotypes of small mature LW reach maturity at younger ages (Thonney, Taylor and McClelland, 1987a). It was also shown that WM lambs mature more rapidly than predicted on the basis of their small mature size (Thonney *et al.*, 1987a). This rapid growth characteristic seems to be exaggerated further when considering compensatory growth. This may be a genotypic characteristic which is related to differences in metabolic rate (Derting, 1989).

Compensatory growth: the trade-off between food inputs, carcass composition and finishing date

The overall results of this experiment are summarized in Table 6. When reared on an *ad libitum* feeding regimen, at the same proportion of mature LW, the BH lambs provide larger carcasses with a slightly greater proportion of fat, but they take a longer time and hence more food to reach this stage than WM lambs (Table 6a). When lambs are reared to the same carcass weight of 16 kg, BH lambs are at a correspondingly earlier stage of maturity, but reach the target carcass weight sooner and consume

Table 6 Parameters relevant to animal production of Beulah (BH) and Welsh Mountain (WM) lambs when reared to slaughter at (a) 0.7 of mature live weight (MLW), (b) a carcass weight of 16 kg, (c) slaughter at 200 days from weaning and (d) to a carcass containing 3.50 kg fat

Genotype Pattern of food supply	LM/MLW				Carcass weight (kg)				Total intake (kg)				Time weaning to slaughter (days)				Carcass fat (kg)			
	BH		WM		BH		WM		BH		WM		BH		WM		BH		WM	
	NG	PRG	NG	PRG	NG	PRG	NG	PRG	NG	PRG	NG	PRG	NG	PRG	NG	PRG	NG	PRG	NG	PRG
(a)	0.70	0.70	0.70	0.70	21	20	17	16	230	196	142	131	173	204	128	161	7.96	7.63	6.25	5.04
(b)	0.53	0.55	0.66	0.70	16	16	16	16	116	126	121	132	87	152	109	162	5.29	5.23	5.72	5.04
(c)	0.75	0.68	0.84	0.82	23	20	20	19	266	191	222	181	200	200	200	200	9.03	7.15	7.82	6.46
(d)	0.43	0.43	0.48	0.58	13	12	12	13	46	67	22	87	35	109	20	126	3.50	3.50	3.50	3.50

slightly less food in doing so (Table 6b). When given food *ad libitum* to this carcass weight, because they are at an earlier stage of growth relative to maturity, the BH lambs have slightly less fat in the carcass than do the WM lambs. These relative merits of the BH and the WM genotypes of lamb may also pertain to other genotypic comparisons of large *v.* small mature weight.

When a period of food restriction to maintain body weight was incorporated into the feeding regime, the total time taken to reach a target stage of maturity or carcass weight was inevitably increased. When reared to slaughter at lighter carcass weights or lower proportions of maturity within both BH and WM genotypes, the total food intake was higher in the restricted and realimented groups than in the continuously fed lambs (Tables 6b, d). When growth following restriction was continued to heavier carcass weights or larger proportions of maturity, then the total food supplied to achieve the equivalent carcass production was lower for the restricted and realimented lambs than for the continuously fed lambs (Tables 6a, c). Thus, it is possible to derive a net benefit in terms of reduced food input by food restriction and subsequently re-feeding *ad libitum*, but this can be achieved only if the lambs are grown to a later stage of maturity and/or heavier weight. Since one of the chief goals of a period of food restriction of lambs may well be to produce later finished carcasses, the requirement for a longer growth period is probably no disadvantage. There was a clear difference between the breeds in terms of the effect of restriction and realimentation on carcass composition. Although carcass and empty body compositions of the two breeds were very similar during NG, under conditions of PRG the WM lambs became relatively leaner and less fat than the BH lambs.

Many hill farms produce lambs on rough grazings and sell them to lower-lying farms after weaning where they may be finished before slaughter. In

regions where this stratified system does not operate, as in Wales, and lambs are retained on their natal farm until slaughter, the merits of compensatory growth would be more important to the producer. On such hill farms, the strong seasonality of the environment means that low availability of overwinter grazing is a prominent characteristic providing natural circumstances of food restriction. The results here demonstrate the need to make careful choices of genotype suitable for using compensatory growth to maximum effect. The specific aims of the production system, but notably the desired timing of finishing and the carcass quality, should be considered.

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