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Skeletal changes and some muscle-skeletal relationships during growth and undernutrition in sheep

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ABSTRACT

A serial slaughter experiment was conducted with sheep under continuous growth and during realimentation following body weight stasis at c. 20 kg for 56 days.

Undernutrition resulted in negative protein and energy balance. Skeletal remodelling facilitated growth in linear dimensions while protein, water and ash decreased or remained unchanged in bone. Bone weight increases were solely attributable to large increases in bone fat.

Protein appeared to be depleted in similar proportions from muscle, bone and the whole body.

Realimentation resulted in a trend for compensatory growth of muscle mass relative to bone length and protein content. Within bone there was a trend for restoration of bone protein content rather than growth in bone length. Bone weight was inadequate in describing these phenomena.

Keywords Bone; muscle; growth; realimentation; body composition; sheep; undernutrition; skeletal remodelling.

INTRODUCTION

Gravimetric relationships between muscle and bone have traditionally been used as an index of "degree of muscling" of a carcass (Palsson, 1955; Berg and Butterfield, 1976). Bone fulfills a structural function, muscle being associated with it to provide locomotion. Growth in length (endochondral ossification) and in diameter (intracartilaginous ossification) of bone occur by different means, but comprise accretion of protein, water, fat and mineral which gross weight crudely describes.

The impetus or "pacemaker" for growth of muscle is considered to be stretch induction caused by growth in length of bone (Holly *et al.*, 1980; Hooper, 1978). The latter author suggested that increase in bone diameter, muscle fibre length and fibre diameter result from changes in mechanical forces due to longitudinal bone growth.

Reductions in bone growth due to undernutrition, metabolic disorders or pathogenic disease can alter internal relationships of bone (Jubb and Kennedy, 1970). Poor growth in young animals may have long-term effects in production systems as body weight deficits induced early in life are not always rapidly restored (Coop and Clark, 1955), but the degree of involvement of bone is not understood.

This work was initiated to investigate the normal development of bone and bone-muscle relationships and to determine the impact of undernutrition on the tissue relationships and their capacity for realimentation.

MATERIALS AND METHODS

Seventy-two female sheep ((Border Leicester x Corriedale) x Dorset Down, c. 20 kg and 56 d of age)

were allocated at weaning to 2 nutritional treatments. A control group (CTRL, n=36) was offered pasture *ad libitum* to maintain uninterrupted growth. A restricted group (REST, n=36) maintained constancy of body weight until CTRL animals had increased in body weight by 75%. This period of weight stasis lasted for 56 d. After restriction REST animals were realimented by offering pasture *ad libitum*. Six animals were slaughtered at 5 kg weight increments from 20 kg to 45 kg body weight, inclusive.

Animal grazed high quality, white clover dominant pasture during *ad libitum* feeding. This was obtained by herbicide treatment of a 2-year old irrigated, ryegrass/white clover pasture to suppress growth of ryegrass. REST animals grazed permanent pasture of low quality and quantity during restriction. Both groups were drenched fortnightly and vaccinated against clostridial disease at 8 and 16 weeks.

Four bones and 3 muscles were dissected from the carcass but only the following data were used in this paper:— femur (F) — weight, volume, length and circumference; M. semitendinosus (ST) — weight, length and circumference. Subsequently dry matter, fat, protein and ash content of bones, muscles and of the empty body were determined by standard procedures.

Statistical analyses were performed using the MINITAB statistical package. Differences between CTRL animals at 56 d and REST animals at 113 d were examined by paired t-test. Estimated parameters in CTRL animals at 112 d are also presented. Recovery of "normal" relationships between and within muscle and bone were examined

by linear regression, after log transformation of data where appropriate and differences tested by standard procedures (Snedecor and Cochran, 1967).

RESULTS AND DISCUSSION

Body form and composition were markedly affected by undernutrition. Animals increased in size, in terms of linear dimensions of the skeleton, yet lost body weight while in negative protein and energy balance (Table 1). Of the body chemical components measured, all except ash were significantly depleted (–57% for fat and –13% for protein and water). Total body energy fell from 191 to 110 MJ.

Despite these large changes in body composition, bone growth in length and weight continued, although at only 46% and 17%,

respectively, of the rate in CTRL animals. There was a non-significant reduction in bone protein or osteoporosis, though the reduction was significant in 2 of the other 3 bones examined. In all bones, protein losses of 11 to 13% occurred implying extensive remodelling of the tissue. The impact of this change on bone strength is difficult to judge since strength is determined by protein mass/unit volume relative to bone length, protein distribution within bone and degree of mineralisation of protein matrix. Mineralisation (A:R ratio) in REST animals was very high and comparable at the end of restriction to that of CTRL animals at that time. This may simply reflect a predominance of old, highly mineralised bone consequent upon a reduced rate of bone protein turnover. The marked increase in fat deposition in the bone of undernourished animals (c. 300%) at a

TABLE 1 Body component, muscle and bone changes. Comparison of animals before and after feed restriction. Differences between CTRL at 56 days and REST at 113 days tested by t-test.

Variate	CTRL at 56 d	REST at 113 d	SED	Significance	CTRL at 112 d (not tested)
Whole body components (kg)					
Body weight	19.8	19.1	0.52	NS	35.1
Gut contents	1.35	4.96	0.331	***	4.65
Empty body weight	18.3	14.6	0.51	***	30.4
Body fat	3.30	1.42	0.348	***	6.68
Body protein	2.72	2.37	0.088	**	4.47
Body water	11.61	10.14	0.256	***	18.16
Body ash	0.71	0.66	0.028	NS	1.12
Body energy (MJ)	191	110	14.0	***	362
Bone and muscle parameters					
Femur					
Weight (g)	77.0	84.3	3.00	*	118.9
Fat (g)	3.4	14.0	1.53	***	19.14
Protein (g)	15.0	13.4	0.80	†	23.3
Water (g)	33.4	31.7	1.71	NS	33.1
Ash (g)	25.1	25.2	1.20	NS	43.0
Length (mm)	125	136	2.2	***	149
Circumference (mm)	48	53	1.3	**	61
Protein density (g/ml)	0.267	0.206	0.0090	***	0.274
Ash density (g/ml)	0.447	0.388	0.0160	***	0.506
A:R ratio	1.67	1.89	0.077	*	1.85
M. semitendinosus					
Weight (g)	46.6	39.6	2.37	*	84.6
Dry weight (g)	11.2	8.8	0.62	**	22.1
Length (mm)	138	145	1.78	**	169
Circumference (mm)	76.8	70.5	2.77	*	98.3
Muscle : bone ratios					
Muscle = M. semitendinosus — weight (g)					
Bone = femur (F)					
F weight (g)	0.606	0.471	0.0328	**	0.723
F length (mm)	0.372	0.291	0.0187	**	0.567
F protein weight (g)	3.11	2.98	0.221	NS	3.69
F ash weight (g)	1.86	1.59	0.323	*	1.99
F fat-free dry weight (g)	1.16	1.03	0.075	NS	1.29
F volume (ml)	0.829	0.610	0.0436	***	1.00

† $P < 0.10$

TABLE 2 Growth rates (regression coefficient (standard deviation of coefficient)) of body components during *ad libitum* feeding of CTRL for 70 d and REST for 85 d and tests for heterogeneity of variance (residual variance) and differences in regression coefficients.

Variate	CTRL	REST	Residual variance	Regression coefficients
Empty body components (g/d)				
Weight	246 (10.6)	198 (11.1)	*	—
Fat	66.0 (8.80)	51.0 (6.30)	NS	NS
Protein	34.5 (2.02)	24.8 (1.60)	NS	**
Water	137 (7.9)	114 (6.9)	NS	*
Ash	8.6 (0.49)	6.0 (0.50)	*	—
Bone and muscle				
Femur				
Length ($\mu\text{m/d}$)	487 (46.7)	169 (38.1)	NS	***
Circumference ($\mu\text{m/d}$)	248 (30.8)	68 (21.8)	NS	***
Weight (mg/d)	870 (73.2)	338 (58.6)	NS	***
Fat (mg/d)	279 (41.7)	78 (34.2)	NS	**
Protein (mg/d)	200 (15.1)	94 (13.1)	NS	***
Water (mg/d)	16 (37.7)	-24 (26.7)	NS	NS
Ash (mg/d)	376 (29.5)	191 (23.9)	NS	***
M. semitendinosus				
Dry weight (mg/d)	217 (16.9)	161 (11.5)	NS	**

time when body fat had been reduced by almost 60%, may reflect substitution during osteoporosis of high gravity constituents of bone by fat to reduce bone weight (A.S. Davies, pers. comm.). Such apparent substitution has been observed in the bones of dairy cows during lactation-induced osteoporosis (Priboth, 1984).

During the normal uninterrupted growth of CTRL animals bone length and weight accounted for 89.5% and 92.9%, respectively, of the variation in weight of the semitendinosus muscle. The close correlation between bone length and weight ($r=0.96$) precludes determination of which component is more important in influencing muscle growth. The primary determinant of muscle mass is considered to be the size and shape of the skeleton it has to move (Holly *et al.*, 1980) and Hooper (1978) considered growth in length of the bone to be the "pacemaker" of muscle growth. Our data suggest that bone weight is a complex entity, and that bone composition can vary considerably in relation to weight and length. Bone length would, therefore, appear to be a more reliable and appropriate benchmark in studies of muscle:bone relationships.

Muscle growth in length occurred in conjunction with reduction in muscle weight in REST animals during undernutrition. Since fibre number does not increase post-natally (McMeekan, 1940; Hooper, 1978), this must be due to increase in fibre length associated with a decrease in fibre diameter and hence decreased muscle cross-sectional area.

Several methods of describing muscle to bone (M:B) ratio have been employed to test functional

relationships of muscle with bone (Table 1). In all cases the ratio of muscle parameter to bone parameter fell although not all changes were significantly different. Of these changes, the ratio of muscle weight to bone protein weight was least affected by undernutrition. Protein appeared to be lost from bone and its associated muscle in similar proportions to changes in whole body protein.

We cannot determine whether bone protein and muscle protein responded independently to the energy and protein deficiency. Reduced bone strength, as induced by osteoporosis, has been considered to result in muscle atrophy (Jubb and Kennedy, 1970), and conversely, reductions in muscle size (atrophy) may evoke corresponding reductions in skeletal mass or osteoporosis.

Evidence for compensatory growth can be sought at several levels; empirically, as growth of the whole body mass, or specifically in terms of whole body chemical components or the functional tissue units which determine growth of the whole body.

Growth rates between 17.3 and 31.9 kg empty body weight (70 days) in CTRL and between 13.7 and 31.2 kg (85 days) in REST animals, during *ad libitum* feeding periods were compared (Table 2). Growth was linear during this phase, and subsequently displayed curvilinearity for some relationships. In the case of muscle/bone regressions, log transformations were performed (Table 3). In some relationships investigated (not all of which are reported here) the REST group exhibited a greater residual variance than did CTRL animals. Tests for line differences are therefore invalidated and where encountered note is

TABLE 3 Relative growth during *ad libitum* feeding of CTRL (70 d) and REST (85 d) (regression coefficient (standard deviation of coefficient)) of femur (F) and M. semitendinosus (ST) and tests for heterogeneity of variance (residual variance) and differences in regression slope and intercept).

log X	log Y	CTRL	REST	Residual variance	Slope	Intercept
F length	F circumference	1.18 (0.136)	0.88 (0.209)	NS	NS	NS
F length	F protein	2.42 (0.256)	3.13 (0.550)	NS	NS	**
F length	ST dry weight	3.42 (0.298)	5.23 (1.186)	**	—	—
F volume	ST dry weight	1.42 (0.120)	2.36 (0.472)	**	—	—
F weight	ST dry weight	1.44 (0.103)	2.33 (0.358)	**	—	—
F protein	ST dry weight	1.25 (0.133)	1.66 (0.193)	NS	NS	NS

made in the tables under "residual variance".

Assessment of compensatory growth was therefore restricted to the body weight range 20 kg to 31 kg for 2 reasons;

a. growth was linear during this period and
 b. to minimise the effect of onset of puberty which could be expected to occur near 230 d of age (Cleverdon and Hart, 1981) or body weight of 35 kg (Hight *et al.*, 1973). Both CTRL and REST animals during realimentation were offered uniformly high quality legume-dominated swards. Nutritional differences were unlikely to be important in interpretation.

Empty body weight showed no evidence of compensatory growth. The proportion of each of the 4 body chemical constituents in body weight gain was virtually identical for both groups (fat, 27% v 26%; protein, 14% v 13%; water, 56% v 58%; ash, 3% v 3%; for CTRL and REST respectively — Table 2). Muscle growth after restriction was only 74% of that of CTRL animals. Bone parameters, however, appeared to be more severely affected. During realimentation growth in length and protein content of the femur was only 35% and 47%, respectively of that in CTRL animals. Clearly in this situation muscle had priority over bone for available protein and energy and judging from its growth compared to that of bone length or bone protein content (Table 3), showed compensatory growth and restoration of normal proportions with bone. It may be argued that the slow growth of bone length post-restriction, restricted the rate of recovery of muscle mass to normal size for age. There was also a trend within bone for compensatory protein deposition relative to growth in length. Bone weight was ineffective in describing these phenomena.

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