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MYOFIBRILLAR PROTEIN TURNOVER IN FEED-RESTRICTED AND REALIMENTED BEEF CATTLE^{1,2}

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ABSTRACT

The objective of this study was to determine the effect of feed restriction and repletion on myofibrillar protein turnover in cattle. Crossbred steer calves ($n = 12$) about 310 d of age were assigned randomly to a diet of corn and silage that was 1) provided ad libitum for 146 d (ALC) or 2) restricted so steers gained .2 kg/d for 80 d but received ad libitum access to feed thereafter for 66 d (RFC). At 27, 55, 97, 118 and 146 d a 24-h urine sample and a blood sample were obtained. Urine was analyzed for N^t-methylhistidine (N^t-MH), creatinine (C), urea nitrogen (UN) and total nitrogen (TN). Serum samples were analyzed for hydroxyproline (HYP), C and albumin (A). Body weights were lower ($P < .05$) in RFC at 55, 97, 118 and 146 d. Excretion of N^t-MH was lower ($P < .05$) in the RFC at 27 and 55 d but higher at 118 d. Urinary C excretion was higher in ALC at the last four sample times. Urinary UN and TN excretion were lower ($P < .05$) in RFC at 55, 97 and 118 d; urinary UN also was lower ($P < .05$) at d 146. Serum A was higher ($P < .05$) in ALC at 55 and 118 d, respectively. Serum HYP was higher ($P < .05$) in RFC at 27 and 55 d. Calculated myofibrillar protein breakdown rates (FBR) and fractional synthesis rates (FSR) were higher ($P < .05$) in RFC at the last two sampling periods; FSR was lower for the RFC at the first sampling period. Realimentation after a period of feed restriction increased both synthesis and degradation of myofibrillar protein in beef cattle.

(Key Words: Protein Turnover, Protein Degradation, Methylhistidine, Restricted Feeding.)

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Introduction

Skeletal muscle is the major protein depot in beef cattle and functions as a protein reserve for whole-body metabolism (Daniel et al., 1977). Muscle protein accretion, defined as the net difference between protein synthesis and degradation, is the major reason for raising and producing meat animals. The primary mecha-

nism of postnatal muscle growth in beef cattle is the accretion of protein.

Nutritional status has a major impact on the rate of muscle protein turnover. Millward et al. (1975) observed that muscle protein turnover rates decreased when rats were fed a low-protein diet. However, upon realimentation to an adequate diet, rapid growth occurred concomitant with high rates of both muscle protein synthesis and breakdown. Haverberg et al. (1975) demonstrated that nutritional restrictions that retarded the normal rate of growth were associated with decreased rates of synthesis and degradation.

Measurement of urinary N^t-methylhistidine (N^t-MH) excretion is a nondestructive technique to quantify myofibrillar protein degradation under various physiological conditions. This technique has been validated in cattle

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(Harris and Milne, 1981; McCarthy et al., 1983). Gopinath and Kitts (1984) utilized N^{α} -MH excretion to measure myofibrillar protein degradation in growing steers. They concluded that rapid growth in steers is accompanied by a high rate of myofibrillar protein degradation. Alterations in the diet that cattle receive due to the availability of feedstuffs can affect the efficiency of production (Byers, 1980) and quality of the product (Aberle et al., 1981). Both alterations may be due to changes in the rate of muscle protein turnover. The objective of this study was to determine changes in the rate of myofibrillar protein degradation and estimated synthesis in cattle during periods of restricted feeding and subsequent realimentation.

Materials and Methods

Animals and Treatments. Twelve small to medium-framed, MARC III crossbred (1/4 Angus, 1/4 Hereford, 1/4 Pinzgauer and 1/4 Red Poll) steer calves with an average weight of 179 kg were weaned at approximately 230 d of age and given ad libitum access to a diet for 90 d. Throughout the study, the diet was composed on an "as-fed" basis of 36% corn silage, 60% wet corn and 4% supplement (supplement composition: 54% soybean meal, 17.9% corn, 21.7% limestone, 2% dicalcium phosphate, 3% urea, .6% vitamin A, .2% trace minerals, .5% Rumensin containing 132 g monensin/kg and .1% sulfur) with a TDN of 84.16% and 10.93% crude protein.

After the preconditioning period, the study was initiated by randomly assigning the cattle to two treatments: 1) a group fed to gain approximately .23 kg/d for the first 80 d, then given ad libitum access to feed for 66 d (RFC; $n = 6$) or 2) given ad libitum access to the corn and corn silage diet for 146 d (ALC; $n = 6$). The cattle weighed approximately 285 kg at the initiation of the study. For the first 80 d, the cattle fed the restricted diet were weighed twice each week to adjust feed intake to obtain the desired rate of gain. After the first 80 d, all cattle were weighed every 2 wk and placed in metabolism crates. Daily gain of the cattle was calculated for the restriction and repletion

phases.

Urine and Serum Collection. At 27, 55, 97, 118 and 146 d from the beginning of the study, cattle were weighed, placed in metabolism crates and allowed to adjust to the crates for 24 h. Urine was collected during the subsequent 24 h and weighed. Ten milliliters of 12 N HCl were added to the urine as a preservative. A 150-ml sample was obtained for each collection period and frozen at -20°C until it was analyzed. A 10-ml blood sample was obtained via venipuncture, allowed to clot and centrifuged at $1,500 \times g$ for 15 min; the serum was frozen at -20°C until it was analyzed.

Urine Analysis. Urine samples were thawed and their specific gravities were determined. Specific gravity was used to convert the weight of the 24-h urine collection to volume in order to determine the urine output for 24 h. Urinary creatinine (C) concentration was determined using kits⁴ following a method (Sigma Chemical Company, 1983) that was a modification of the procedures of Slot (1965) and Heinegard and Tiderstrom (1973). Urinary urea nitrogen (UN) was measured using the procedure of Frankel et al. (1970). Total urinary nitrogen (TN) was quantitated using the Kjeldahl procedure (AOAC, 1985).

N^{α} -methylhistidine concentration in the urine was determined using HPLC. Samples were prepared by diluting 100 μl of urine with 10 μl 30% sulfosalicylic acid. The sample was mixed for 5 min and centrifuged at $2,500 \times g$ for 15 min. After centrifugation, 75 μl of supernatant fractions were pipetted into a microfuge tube and 5 μl of 4% NaOH were added to adjust the pH to approximately 2.1. An equal volume of Pickering Diluent⁵ containing norleucine (.25 $\mu\text{mol/ml}$) was added, gently mixed, and filtered (.2- μm screen) prior to filling HPLC loading vials. Separation and quantitation of N^{α} -MH by HPLC was performed using a 3-mm \times 250-mm column containing 10- μm cation exchange column⁵ with a 2-mm \times 20-mm guard column⁵. Temperature of the column was maintained at 42°C and injection volume of each sample was set at 5 μl . A three-step gradient was used to elute the amino acids as follows: 100% .24 N lithium citrate buffer, pH 2.75, 70 min; 65% .24 N lithium citrate buffer and 35% .64 N lithium citrate buffer, 65 min; 100% .64 N lithium citrate buffer, pH 7.50, 50 min. The column was regenerated between each sample by elution with the first buffer for 30 min.

⁴Sigma Chemical Co., St. Louis, MO.

⁵Pickering Labs, Mountain View, CA.

Flow rate of the eluent was .3 ml/min. Post-column derivatization of N^T -MH with orthophthaldehyde (1, 2-benzene dicarbonyl) was performed and the fluorescence was quantified using a spectrofluorometer⁶ with emission set at 338 nm and excitation set at 425 nm.

Serum Analysis. Serum hydroxyproline (HYP) concentration was determined in thawed serum samples using the sample preparation procedures of Bannister and Burns (1970). Quantitation of HYP was performed using the procedure of Bergman and Loxley (1963). Albumin (A) concentration was measured by a method (Sigma Chemical Company, 1986) using the procedures of Doumas et al. (1971), Savory et al. (1976) and Corcoran and Duran (1977).

Calculations and Statistical Analysis. The calculations of the characteristics of muscle protein metabolism were performed according to Gopinath and Kitts (1984) and McCarthy et al. (1983). The N^T -MH pool in skeletal muscle was calculated by multiplying the estimated skeletal muscle mass (33% of body weight; Allen et al., 1968; Brannang, 1971) by the protein content of skeletal muscle mass (157 mg/g fresh weight; Gopinath and Kitts, 1984) and the N^T -MH content of skeletal muscle protein (3.5106 μ mol N^T -MH/g muscle protein; Nishizawa et al., 1979). The fractional breakdown rate (FBR) of muscle proteins was calculated by dividing the daily excretion of N^T -MH in urine by the amount of N^T -MH in the skeletal muscle pool and multiplying by 100.

Fractional accretion rate (FAR) was calculated as the rate of skeletal muscle protein gain divided by total skeletal muscle protein pool at the time urine samples were obtained. The calculation was: $FAR = ([MP_1 - MP_0]/T)/(MP_3)$, where MP_1 is the measure of total muscle protein 14 d after sampling, MP_0 is the measure of muscle protein 14 d before sampling, T is 28 d and MP_3 is the total muscle protein at sampling time. The numerator of the FAR equation is equal to the absolute rate of muscle protein accretion (MPA).

The fractional synthesis rate (FSR) of the mixed muscle protein pool was calculated as the sum of FBR and FAR. Measurement of N^T -MH excretion can be used to determine degradation of myofibrillar proteins, primarily

actin (Young and Munro 1978). However, the differences in turnover rate between myofibrillar, sarcoplasmic and stromal proteins are not major enough to negate the use of N^T -MH excretion to mark skeletal muscle protein breakdown (Bates and Millward, 1983). Thus, N^T -MH excretion is useful as an estimate of muscle protein turnover. This calculation is a modification of the calculation used by Millward et al. (1975), who used the FSR and FAR to calculate FBR. Myofibrillar protein degradation (MPD) was calculated by dividing the daily N^T -MH excretion by the concentration of N^T -MH in muscle. The rate of muscle protein synthesis (MPS) was calculated as the sum of MPD and MPA.

Data were analyzed using an analysis of variance with a sequential, split-plot treatment design (Steel and Torrie, 1980). The Least Significant Difference (LSD) method was used to compare treatment means at $P < .05$. A modified *t*-statistic was calculated to allow whole and subplot comparisons. Age-related differences were determined by analyzing the data of the ALC by analysis of variance. Linear, quadratic and cubic contrasts were determined at $P < .05$. Treatment means, standard deviations and analysis of variance were calculated and performed using SAS (1985).

Results and Discussion

The ALC cattle had higher ($P < .05$) ADG than RFC during the restricted phase (1.25 vs .61 kg/d), but ADG were not different ($P > .05$) after realimentation (1.35 vs 1.51 kg/d). Cattle with ad libitum access to feed had a higher ($P < .05$) urinary N^T -MH excretion during the first two collection periods; however, it was lower ($P < .05$) for ALC than for RFC at 118 d and not different at 146 d (Table 1). The quantities of N^T -MH excreted by our steers (Table 1) were in a range similar to that reported by McCarthy et al. (1983) and Gopinath and Kitts (1984) but slightly higher than reported by Nishizawa et al. (1979) and Harris and Milne (1981). The ALC showed a linear decrease ($P < .05$) in N^T -MH excretion in response to age or weight. This decrease may reflect the decline in degradation rates as the animals grow. Several researchers have observed age-related declines in FBR (Waterlow and Stephens, 1968; Millward et al.,

⁶Waters, Milford, MA.

TABLE 1. DAILY URINARY N¹⁵-METHYLHISTIDINE, CREATININE, UREA NITROGEN AND TOTAL URINARY NITROGEN EXCRETION IN CATTLE GIVEN AD LIBITUM OR RESTRICTED ACCESS TO FEED^a

Item and sample time ^b	Ad libitum ^c	Restricted ^d	Sig. ^e	SE
N¹⁵-methylhistidine, mmol/d				
27 d	2.19	1.56	*	.09
55 d	2.00	1.32	*	
97 d	2.43	2.37		
118 d	2.43	3.07	*	
146 d	1.78	2.38		
Creatinine, g/d				
27 d	7.88	7.36		.31
55 d	9.14	7.16	*	
97 d	10.36	8.78	*	
118 d	12.00	9.98	*	
146 d	11.53	9.41	*	
Urea nitrogen, g/d				
27 d	.95	.76		.198
55 d	2.14	1.01	*	
97 d	2.68	1.00	*	
118 d	3.46	2.11	*	
146 d	4.71	3.39	*	
Total urinary nitrogen, g/d				
27 d	25.83	20.63		2.40
55 d	40.24	19.79	*	
97 d	45.68	26.72	*	
118 d	55.50	41.35	*	
146 d	64.84	58.43		

^aEach treatment contained six cattle.

^bDays from initiation of the study.

^cCattle were offered ad libitum access to corn and corn silage diet (1.36 kg/d, daily gain).

^dRestricted cattle were held at .23 kg/d (daily gain) for the first 80 d of the study then offered ad libitum access to a corn and corn silage diet for the remainder of the study.

^eValues in a row marked with an asterisk differ ($P < .05$).

1975). Urinary C excretion was higher ($P < .05$) in ALC than in RFC during the last four sampling periods and increased linearly ($P < .05$) as the ALC aged (Table 1). Higher creatinine excretion in the ALC indicates that muscle mass was greater for ALC animals. Urinary UN and TN excretions were higher ($P < .05$) by ALC than by RFC at d 55, 97 and 118; UN also was higher ($P < .05$) at 146 d (Table 1). Urinary TN and urinary UN differences indicate differences in the rate of catabolism of endogenous and exogenous proteins. One additional reason for lower values of urinary UN and TN for the RFC is that lower amounts of protein were consumed by the cattle during feed restriction (d 0 to 80). Protein content of the diet has a dramatic effect on urinary N excretion. However, increased protein accretion may have caused the continued lower excretions seen in the RFC after d 80 during feed repletion.

Body weights of ALC were higher ($P < .05$) than those of restricted-fed cattle at the last four sampling periods (Table 2). A linear ($P < .05$) increase in body weight of ALC with age was observed. There was no difference ($P > 0.5$) between ALC and RFC in body weight to creatinine ratio (Table 2). This observation suggests that muscle mass per unit of body weight was not different, regardless of dietary treatment. However, this ratio declined numerically at 146 d in both treatments, possibly reflecting an increase in fat content of the cattle. When expressed as a ratio to body weight or to creatinine, N¹⁵-MH excretion was higher ($P < .05$) for RFC than for AFC during the last two collection periods (Table 2). When expressed in this manner, N¹⁵-MH should be an indicator of the amount of myofibrillar protein degradation per muscle mass.

Myofibrillar Protein Turnover. Quantification of an animal's muscle mass is necessary

TABLE 2. RELATIONSHIP BETWEEN BODY WEIGHT, N^c-METHYLHISTIDINE AND CREATININE EXCRETION IN CATTLE GIVEN AD LIBITUM OR RESTRICTED ACCESS TO FEED^a

Item and sample time ^b	Ad libitum ^c	Restricted ^d	Sig. ^e	SE
Body wt, kg				
27 d	319.	293.		8.58
55 d	360.	298.	*	
97 d	406.	344.	*	
118 d	435.	381.	*	
146 d	475.	418.	*	
Creatinine excretion/body wt, mg/kg				
27 d	24.83	24.96		.62
55 d	25.45	24.35		
97 d	25.47	25.58		
118 d	27.47	26.41		
146 d	23.95	23.01		
N ^c -methylhistidine excretion/body wt, μmol/kg				
27 d	6.89	5.24		.25
55 d	5.56	4.56		
97 d	5.95	7.04		
118 d	5.59	8.13	*	
146 d	3.73	5.78	*	
N ^c -methylhistidine to creatinine ratio				
27 d	.278	.203		.018
55 d	.221	.180		
97 d	.234	.273		
118 d	.205	.306	*	
146 d	.166	.272	*	

^aEach treatment contained six cattle.

^bDays from initiation of the study.

^cCattle were offered ad libitum access to a corn and corn silage diet (1.36 kg/d, daily gain).

^dRestricted cattle were held at .23 kg/d (daily gain) for the first 80 d of the study then offered ad libitum access to a corn and corn silage diet for the remainder of the study.

^eValues in a row marked with an asterisk are significantly different ($P < .05$).

to estimate FBR, FSR and FAR. Several attempts to accurately determine muscle mass have had limited success. Munro (1969) reported that most mammals have between 40 and 50% muscle in their bodies, regardless of species or sex of the animals. However, in ruminants, particularly cattle, most reports estimate muscle mass to be between 31 and 35% of body weight (Henricksen et al., 1965; Allen et al., 1968; Brannang, 1971; Nishizawa et al., 1979). In the present study, muscle mass was assumed to be 33% of body weight (Allen et al., 1968). Based on this value, the FBR we observed was similar to data reported by McCarthy et al. (1983), 2.46 to 3.42%/d, but slightly higher than data reported by Gopinath and Kitts (1984), 2.07 to 2.84%/d. Results indicate that FBR was higher ($P < .05$) for RFC than for ALC after realimentation (Table 3). These results are similar to those of Haverberg et al. (1975), who observed that rats

previously deprived of protein or energy exhibited a marked increase in FBR upon repletion. The RFC had lower ($P < .05$) FSR at 27 d but higher FSR ($P < .05$) at 118 and 146 d. These data indicate that feed restriction suppresses FSR whereas repletion increases FSR. Millward et al. (1975) observed that rates of protein synthesis in rats fed a marginally deficient diet were reduced. However, upon realimentation, muscle protein synthesis increased rapidly. Data from our study follow a similar trend.

The RFC had lower ($P < .05$) MPD and muscle protein synthesis (MPS) at periods of nutrient restriction but higher ($P < .05$) MPD and MPS at 118 d, during the period (> 80 d) of repletion (Table 4). Millward (1980) suggested that the rate of MPD may be elevated during periods of rapid growth or during conditions that cause muscle wasting.

Remodeling of myofibrils, which occurs at various stages of growth, probably is the cause

TABLE 3. SKELETAL MUSCLE N^c-METHYLHISTIDINE POOL, FRACTIONAL BREAKDOWN, ACCRETION AND SYNTHESIS RATES IN CATTLE GIVEN AD LIBITUM OR RESTRICTED ACCESS TO FEED^a

Item and sample time ^b	Ad libitum ^c	Restricted ^d	Sig. ^e	SE
Skeletal muscle N ^c -methylhistidine pool, mmol ^f				
27 d	58.05	53.45		1.56
55 d	65.49	54.29	*	
97 d	73.86	62.70	*	
118 d	79.24	69.34	*	
146 d	86.45	76.20	*	
Fractional breakdown rate, %/d ^f				
27 d	3.79	2.87		.14
55 d	3.05	2.50		
97 d	3.26	3.87		
118 d	3.07	4.46	*	
146 d	2.04	3.17	*	
Fractional accretion rate, %/d ^f				
27 d	.53	.26	*	.028
55 d	.16	.14		
97 d	.18	.43	*	
118 d	.32	.40		
146 d	.34	.38		
Fractional synthesis rate, %/d ^g				
27 d	4.32	3.14	*	.294
55 d	3.21	2.65		
97 d	3.45	4.30		
118 d	3.40	4.86	*	
146 d	2.39	3.55	*	

^aEach treatment contained six cattle.

^bDays from initiation of the study.

^cCattle were offered ad libitum access to a corn and corn silage diet (1.36 kg/d, daily gain).

^dRestricted cattle were held at .23 kg/d (daily gain) for the first 80 d of the study then offered ad libitum access to a corn and corn silage diet for the remainder of the study.

^eValues in a row marked with an asterisk are significantly different ($P < .05$).

^fMuscle mass assumed to be 33% of live weight.

^gThe summation of fractional breakdown rate and fractional accretion rate.

of increased rates of MPD (Goldspink, 1970; Millward et al., 1975). Increased MPS and MPD during repletion of the RFC, indicates that protein turnover rates were high in conjunction with increased growth rate. The increased rate of muscle protein turnover during repletion phase suggests that dietary requirements of energy also may be higher.

Serum Analysis. The synthesis of serum albumin accounts for about 10% of total liver protein synthesis (Morgan and Peters, 1971). Changes in albumin concentration can be useful as an index of amino acid flux and protein metabolism in the liver. The decrease ($P < .05$) in serum albumin levels observed in RFC at 55 d could be attributed to a decrease in synthesis of albumin due to a dietary protein deficiency (Table 5). Several researchers have

observed decreased synthesis of albumin and albumin messenger-RNA in response to a deficiency of dietary protein (Jeejeebhoy et al., 1975; Pain et al., 1978). When RFC were realimented, serum albumin levels were not different ($P < .05$) from ALC from 97 d through 146 d. Free-HYP in serum was higher ($P < .05$) in the RFC cattle during the first two collection periods. There also was a linear decline ($P < .05$) of AFC in serum free-HYP as animals aged. Higher concentrations of HYP in the serum of the RFC during restriction or at times of slow growth is contradictory to the data of Kivirikko (1970), who reported that during rapid rates of growth, serum HYP increased. One possible explanation for these differences is that the animal at maintenance is synthesizing collagen, which is

TABLE 4. ABSOLUTE RATE OF MUSCLE PROTEIN DEGRADATION, ACCRETION AND SYNTHESIS IN CATTLE GIVEN AD LIBITUM OR RESTRICTED ACCESS TO FEED^a

Item and sample time ^b	Ad libitum ^c	Restricted ^d	Sig. ^e	SE
Muscle protein degradation, g/d				
27 d	622.97	443.94	*	50.30
55 d	570.37	374.62	*	
97 d	693.56	679.75		
118 d	693.56	874.83	*	
146 d	507.65	677.52		
Muscle protein accretion, g/d				
27 d	93.53	41.86	*	5.268
55 d	30.66	24.08		
97 d	38.50	79.38	*	
118 d	73.21	78.49		
146 d	86.11	82.68		
Muscle protein synthesis, g/d^f				
27 d	716.50	485.80	*	49.03
55 d	601.03	398.71	*	
97 d	732.07	759.14		
118 d	766.77	953.31	*	
146 d	593.76	760.20		

^aEach treatment contained six cattle.

^bDays from initiation of the study.

^cCattle were offered ad libitum access to a corn and corn silage diet (1.36 kg/d, daily gain).

^dRestricted cattle were held at .23 kg/d (daily gain) for the first 80 d of the study then offered ad libitum access to a corn and corn silage diet for the remainder of the study.

^eValues in a row marked with an asterisk are significantly different ($P < .05$).

^fThe summation of muscle protein degradation and muscle protein accretion.

TABLE 5. SERUM ALBUMIN AND FREE HYDROXYPROLINE IN CATTLE GIVEN AD LIBITUM OR RESTRICTED ACCESS TO FEED^a

Item and period ^b	Ad libitum ^c	Restricted ^d	Sig. ^e	SE
Albumin, g/dl				
27 d	3.94	4.15		.057
55 d	4.06	3.52	*	
97 d	4.11	4.02		
118 d	4.32	4.11		
146 d	4.49	4.55		
Free hydroxyproline, g/ml				
27 d	5.43	8.12	*	.31
55 d	4.31	6.75	*	
97 d	4.43	3.89		
118 d	4.28	2.87		
146 d	2.82	2.74		

^aEach treatment contained six cattle.

^bDays from initiation of the study.

^cCattle were offered ad libitum access to a corn and corn silage diet (1.36 kg/d, daily gain).

^dRestricted cattle were held at .23 kg/d (daily gain) for the first 80 d of the study then offered ad libitum access to a corn and corn silage diet for the remainder of the study.

^eValues in a row marked with an asterisk are significantly different ($P < .05$).

readily degraded intracellularly to provide a protein source to sustain other, more important, maintenance functions of the body.

Implications

Restricting and repleting cattle changed the rate of muscle protein turnover; these changes may influence the efficiency of cattle growth. Myofibrillar protein degradation and synthesis decreased during the restriction period and increased following subsequent repletion. Muscle protein synthesis and accretion increased early during repletion, indicating that repleted cattle may have greater efficiency in reaching finishing weights. This information is valuable in understanding the changes in muscle protein metabolism that occur in cattle whose nutritional plane is varied.

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