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Effect of Refeeding on Lipid Metabolism in Kamphaengsaen Beef Heifers

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ABSTRACT

Five Kamphaengsaen (Charolais Crossbred) beef heifers were used to study lipid utilization during a 30-day controlled-feed realimentation period. Dry matter intake was adjusted according to individual metabolic body weight to provide the same energy intake as in the full feeding period. At the end of refeeding period the heifers showed better feed conversion ratio. Back fat thickness increased and returned to the same level as before restriction (0.284 vs. 0.262 cm.). The loin eye area exhibited slight accretion (less than 1% of the loin eye area at the onset of realimentation). Adipose tissue lipolytic rate remained elevated and the heifers also exhibited high rate of lipoprotein export as in the previous restriction period. Plasma albumin concentration was higher than the base-line concentration. NEFA concentration declined and tended to be less than the base line concentration level (86vs.127μ mol/l). Because the high lipolytic rate occurred at this period, less circulating NEFA concentration was suggested for the high NEFA uptake by the peripheral tissue. BHBA and glucose concentrations were rebounded toward the base-line concentrations. PUN concentration markedly declined with the level lower $P<0.05$ than the base-line concentration (9.2 vs.10.8 mg/dl).This might result from the decreasing rate of catabolism of labile protein reserved. In conclusion, it was found that during repletion, the heifers utilized fat as the essential source of fuel and decreased proteolysis in the body.

Key words: beef cattle, refeeding, lipid metabolism

INTRODUCTION

Enhanced levels of bodyweight gain after refeeding the animals following a period of food deprivation has been demonstrated and termed as compensatory growth. The cause of this phenomenon in cattle has been subject to reduce maintenance requirements and increase efficiency of energy utilization (Meyer *et al*.,1965;Ledger and Sayers, 1977), increase food intake (O· Donovan, 1984), changes in the composition of body gain (Fox *et al*., 1972), alteration in endocrine status (Fox *et al*., 1974; Blum *et al*., 1985) and increase in muscle protein retention (Hornick *et al*., 1999). All of these having been implicated in the complex of changes resulting in compensatory growth. However, the physiological reason for the compensatory growth has not been satisfactorily explained. Hood and Thornton (1980) noted that lipogenesis in adipose tissue, virtually ceased with

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restriction, returned to the level of continuously grown sheep during recovery. Wright and Russel (1991) postulated that compensatory growth in steers was due to the deposition of more protein and less fat in the carcass. This raised the question of whether the compensating cattle altered their lipid metabolism during the repletion period.

A major problem in studying the compensatory growth during feed-realimentation is the level of feeding differences, which prevents the separation of the refeeding effects associated with compensatory growth from any changes in the efficiency of energy utilization (Thomson *et al*., 1982). Therefore, a similar level of intake would be designed to overcome these difficulties i.e. when there was no increase in food intake as a result of previous restriction. The present experiment was designed to study the effects of refeeding on lipid utilization in heifers under the condition that they were consuming the same amount of food similar to the feeding level before restriction.

MATERIALS AND METHODS

Animals

Five healthy growing Kamphangsaen (KPS) heifers (Charolais crossbred) with weighing 263± 13 kg in weight were used.All animals were about 24 months old at the start of the experiment. The heifers were treated against gut parasites (Zodalben, Laboratorios Calier, S.A. Barcelona, Espana) and kept indoors in individual pen for half a month before the initiation of the experiments.

Experimental diets

Diets were commercially concentrated and ruzi hay (*Brachiaria ruziziensis*) containing 2,627 and 1,329 Kcal ME[1]/kg (Menke *et al.*, 1979) and 12.85 and 2.90 percent proteins on dry matter basis, respectively.

Experimental treatments

Experiments were partitioned into 3 phases of feeding period. **1 Full feeding period**. At the start of this period, heifers were weighed and fed the diet according to their metabolic weight ($W^{0.75}$) at the rate of 180% ME for maintenance (metabolizable energy for maintenance = 130 kcal/ $w^{0.75}$; NRC, 1976). In this period, heifers were fed for 32 days and weighed at the end of this period. **2 Restricted feeding period.** According to the final weights of full feeding period, heifers were fed with the same feeds at the rate of 85% ME for maintenance to induce negative energy balance status. All heifers were restricted for 20 days and weighed at the end of this period. **3 Refeeding period.** Following the restriction period, the heifers were fed the diet to the final weights of restriction period at the same rate of metabolizable energy intake as they were in the full feeding period (180% ME for maintenance). The heifers were refed for 30 days and weighed at the end of this period.

Concentrated diet and hay were fed at a constant ratio of 50:50 throughout the experiment. Water and mineral blocked salt were available *ad libitum*.

Back fat and loin eye determination

Apart from live weight determination, all heifers were recorded for their back fat thickness and loin eye area at the end of each period. Ultrasound determination of back fat and loin eye area was conducted using 100 Falco Vet Scanner (Pie Medical Equipment B.V., Maastricht, The Netherlands), a real-time ultrasound instrument equipped with a 3.5 MHz transducer. The imaging of the back fat and the *longissimus dorsi* muscle (loin eye) was performed approximately 5 cm. lateral from the spinous process of the spine and centered over the 12th rib. The images were recorded and automatic calculation for back fat thickness (cm) and loin area (cm^2).

Blood sampling

Heifers were blood sampled 4 times. The first and the second collections were on the days

at the beginning and at the end of full feeding periods. The average means of these two collections served as control to obtain baseline measurements. The third and fourth collections were at the end of the restricted feeding and the refeeding periods, respectively.

Blood samples (30 ml) were obtained by jugular venous puncture before the heifers received their morning diet. The blood samples were then divided as follows: 5 ml to glass tubes containing sodium fluoride (NaF) for the determination of glucose; 20 ml to glass tubes containing EDTA for the determination of non-esterified fatty acid (NEFA), albumin, β- hydroxybutyrate (BHBA) and plasma urea-nitrogen (PUN); 5 ml to glass tubes with no additives and used for the separation of lipoprotein fractions.

Blood were centrifuged at 1400 g for the separation of plasma or serum. Serum samples used for separating lipoprotein fraction were left refrigerated overnight and were separated for lipoprotein fractions on the following day. Aliquots of plasma and serum were stored at -20°C until analyze for the blood metabolites.

Metabolite analyses

NEFA concentrations in plasma were analyzed by colorimetric process according to the procedure described by Smith (1975). Other metabolites were determined with commercially available kits; BHBA (Radox Laboratories Ltd, Co.Antrim, UK.), Albumin (Human Gasellschaft f¸r Biochemica und Diagnostica mbH, Wiesbaden, Germany); Glucose and PUN (Life Science Dynamics of Arnaparn Co. Ltd, Bangkok, Thailand).

Separation of serum lipoproteins

The method was based on cellulose-acetate electrophoresis as described by Helena lipoprotein electrophoresis procedure (Helena Laboratories, Beaumont, Texas). Lipoprotein bands were stained with Oil Red O and scanned in the densitometer (BIORAD, Model GS-670; Richmond, Calif.) using 525 nm filter and the relative percent value of each lipoprotein band was calculated.

Adipose tissue samplings

At the end of each period, adipose tissue biopsies were surgically obtained on perianal region following the procedure of Rukkwamsuk *et al*. (1998). Upon excision, adipose tissue was rinsed in ice-cold 0.15 M KCl, blotted on cheese cloth and frozen at -20°C for later lipolysis analyses.

Lipolysis assay

Incubation procedures for measuring the rate of free fatty acid release were essentially as described by McNamara and Hillers (1986). Free fatty acid concentrations in media were analyzed in duplicate according to the method described by Smith (1975). Release of free fatty acid into the incubation media was used to measure the extent of lipolysis in incubated adipose tissue. All data were expressed as μ mol free fatty acid release per gm. of adipose tissue per 2 hrs.

Statistical analyses The model used for statistical analysis of the data was;

$$Y_{ij} = \mu + A_i + P_j + (AP)_{ij} + e_{ij}$$

Where Y_{ij} = the dependent variable,
μ = the overall mean of the population,
A_i = the average effect of heifers i^{th},
P_j = the average effect of period j^{th},
$(AP)_{ij}$ = the average effect of the interaction between heifers i^{th} and period j^{th}, and
e_{ij} = the unexplained residual element assumed to be independently and identically distributed ~ N (0, σ^2).

Data were analyzed using the GLM procedure of SAS (1997). The comparison of period effects were made using linear contrasts. Selected variables, expressed in percentage change

were performed using the pair t-test. A 0.05 probability level was used as the criterion to describe statistically significant differences.

RESULTS AND DISCUSSION

Effects of the previous restriction feeding

Prior to the implementation of feed-realimentation, the heifers in negative energy balance consumed 57.6 g of diet per kg of metabolic weight per day and loss 7.2 kg of body weight (Table 1 and Table 2, respectively). The heifers showed back fat thickness depletion but maintained their loin eye area. They exhibited decreased plasma glucose with elevated plasma albumin, NEFA, BHBA and PUN concentrations. The percentage of HDL-class lipoprotein in serum also elevated during this period.

Dry matter intake and change in the weight during refeeding period.

Dry matter and metabolizable energy intake during feed-realimentation are shown in Table 1. The heifers consumed significantly lower than the full feeding period ($P<0.05$). This was due to the gradual increase in feed offering to the heifers during the first week of refeeding period to prevent accidental metabolic disorder due to the abrupt increase in feed intake. After 7 days of adjustment, the heifers were provided with 180% metabolizable energy for maintenance level throughout the remaining period.

During the refeeding period, the heifers gained an average of 720 g/d (table 2) which were not significantly difference from those during the full feeding period ($P>0.05$). Thomson *et al*. (1982) reported the realimented steers gained

Table 1 Least square means of dry matter and energy intake of Kamphaengsaen heifers during the experimental periods.

Item	Treatment period			SE[1]
	Full feeding	Restricted feeding	Refeeding	
	(d 32)	(d 20)	(d 30)	
Dry matter intake, ($g/W^{0.75}$ day)	123.0[a]	57.6[b]	110.0[c]	0.88
Metabolizable energy intake, (kcal/ $W^{0.75}$ day)	241.2[a]	112.9[b]	215.8[c]	1.7

[1] Standard error.

[a,b,c] Least square mean in the same row bearing different superscripts are significantly different ($P<0.05$).

Table 2 Least square means of initial weight, body weight changes, average daily gain and feed per gain of Kamphaengsaen heifers during the experimental periods.

Item	Treatment period			SE[1]
	Full feeding	Restricted feeding	Refeeding	
	(d 32)	(d 20)	(d 30)	
Initial weight[2], (kg)	263	285	278	5
Final weight[2], (kg)	285	278	300	5
Body weight changes, (kg)	21.4[a]	-7.2[b]	21.6[a]	1.9
Body weight changes, (%)	8.1[a]	-2.5[b]	7.8[a]	0.5
Average daily gain, (gm/day)	668	-	720	74
Feed / gain	12.15	-	10.87	0.82

[1] Standard error.

[a,b] Least square mean in the same row bearing different superscripts are significantly different ($P<0.05$).

significantly more than steers on a continuous growth path from a similar ME intake. In this study, the difference in dry matter intake between these two periods was likely accounted for the contrast result. When the data were calculated for feeding efficiency, the feed/gain of the heifers during refeeding period showed better than the full feeding period (Table 2) but the difference was not statistically detectable. Previous research has shown the high feed efficiency in compensatory steers (Fox *et al.*, 1972).

Back fat and loin eye area response

The average means for back fat thickness and loin eye area in the entire periods are presented in Table 3. At day-30 of refeeding period, the heifers showed 22.7% in back fat thickness accretion where as the loin eye area exhibited slight accretion (less than 1%) and the mean values did not differ from those at day-20 of the restriction period. Because scanning of back fat thickness and loin eye area were not done at the onset of the experiment, the rate of these accretions between the full feeding and the refeeding periods could not be compared. However, it should be noted that the accretion in back fat thickness in this study was consistent with the results of Hood and Thornton (1980) who reported the lipogenesis in adipose tissues rebounded toward the normal levels following the period of restriction.

Rate of lipolytic response

During the restriction period, the rate of lipolysis in adipose tissue increased to supply free fatty acids as the energy source for feed deprived heifers. Surprisingly, adipose tissue lipolytic rate at day-30 of refeeding period remained elevated as in the restriction period (Table 4). This showed the high level of lipid mobilization to occurr despite the fact that the heifers were in positive-energy balance. The reason or reasons for this high rate of lipolysis were unknown but presumably were related to the endocrine actions. There are evidences of the hormonal responses associated with the compensatory growth. For instance, the increase of thyroid hormone concentration in

Table 3 Least square means and percentage changes for back fat thickness and loin eye area in Kamphaengsaen heifers during the experimental period.

Item	Treatment period			SE[1]	% Change[2]
	Full feeding	Restricted feeding	Refeeding		
	(d 32)	(d 20)	(d 30)		
Back fat thickness, (cm)	0.262[a]	0.200[b]	0.284[a]	0.009	46±15
Loin area, (cm^2)	47.67	47.22	48.00	0.41	1.8±3.5

[1] Standard error.

[a,b] Least square mean in the same row bearing different superscripts are significantly different ($P<0.05$).

Table 4 Least square means for rate of lipolysis in Kamphaengsaen heifers during the experimental periods.

Item	Treatment period			SE[1]
	Full feeding	Restricted feeding	Refeeding	
	(d 32)	(d 20)	(d 30)	
Rate of lipolysis, (*m* mol FFA/gm tissue/2 hrs)	1.049[a]	2.704[b]	2.262[b]	0.305

[1] Standard error.

[a,b] Least square mean in the same row bearing different superscripts are significantly different ($P<0.05$).

cattle and sheep during compensatory growth have been well documented (Fox *et al*., 1974; Blum *et al.*, 1980; 1985). Thyroid hormone has been confirmed to have a role in fat mobilization and in increasing energy utilization in many animals (Greco and Stabenfeldt, 2002). Hayden *et al*. (1993) also reported the strong association of plasma concentrations of growth hormone, insulin, thyroid hormones and IGF-I with body gain in compensating steers. However, the present study did not provide this data and needed warrants further investigation.

Regarding to the accretion of back fat thickness at this time, the result from the high lipolytic rate in adipose tissue indicated the accretive rate of lipid turnover. The observation in the accretion rate of lipid turnover indicated the high extent of lipid utilization imposed at the repletion period. Several studies reported the result in significantly more protein and less fat being deposited in steers followed the period of restriction (Fox *et al*., 1972; Carstens *et al.*, 1991; Wright and Russel, 1991). This evidence might be partly explained by the accretive rate of lipid turnover found in this experiment.

Serum lipoprotein response

The pattern of heifers· serum lipoprotein on cellulose-acetate electrophoresis demonstrated two bands of lipoprotein fractions mobility, the HDL-class with beta movement and LDL-class with alpha movement throughout the entire periods. The subsequent densitometer scanning on lipoprotein patterns for relative percentage of HDL and LDL fraction in the heifers are shown in Table 5. It was found that the restricted feeding elevated the HDL-class by 9% compared to the base-line percentage ($P<0.05$). It was also found that at day-30 of refeeding the percentage of HDL-class in serum remained elevated (Table 5). The increase in serum HDL concentration reflected the increase in VLDL turnover as described by Puppione (1978). This led to suggestion that the heifers under restricted and refeeding condition secreted their hepatic VLDL more than the previous full feeding condition. More of hepatic VLDL secretion indicated the high extent of lipid utilization in the heifers during these periods. This evidence was consistent with the high lipolytic rate seen in adipose tissue at this time.

Because the rate of hepatic fatty acid synthesis in ruminants is extremely low (Bell, 1981), the hepatic triacylglycerol is formed from free-fatty acids taken up from the blood and exported as VLDL to extrahepatic tissue (Pethick *et al*., 1984). Thus, the increase in hepatic VLDL secretion would be the mirror of the high free fatty acids uptake by the liver. Therefore, it was suggested the free fatty acid was highly taken up by the liver of heifers during the refeeding period.

Blood metabolites response

At day-30 of refeeding period, the albumin that functions as carrier for free fatty acids

Table 5 Least square means for lipoprotein fractions in Kamphaengsaen heifers during the experimental periods.

Item	Treatment period			SE[1]
	Full feeding (base line)	Restricted feeding (d 20)	Refeeding (d 30)	
% HDL[2]	83.50[a]	90.94[b]	93.33[b]	0.72
% LDL[3]	16.49[a]	9.06[b]	6.56[b]	0.72

[1] Standard error.

[2] High density lipoprotein.

[3] Low density lipoprotein.

[a,b] Least square mean in the same row bearing different superscripts are significantly different ($P<0.05$).

in the circulation, showed slight decrease from the concentration observed at day-20 of the restriction period (Table 6). However this concentration was higher than that found in the base-line concentration. The high level of albumin concentrations probably reflected the physiological response for the high lipolytic rate occurring during this time. However, contrary to the lipolysis rate, it was found that NEFA concentration declined from the restriction period concentration to the value of 32% less than the NEFA concentration at base-line (Table 6). Hayden *et al*. (1993) also reported the rapid decline of the circulating NEFA concentrating in compensating steers to a concentration comparable to that in the non-restricted steers by day-31 of energy repletion. In this study, the mean NEFA concentration at day-30 of refeeding period was seen to be paradoxical with the high lipolytic rate. In such a case, it was suggested that the high uptake of NEFA by the peripheral tissue of heifers. Although the mechanism of free fatty acid uptake by whole body was not clearly understood, Pethick and Dunshea (1993) described that the body tissue NEFA uptake appeared to depend on the physiological status of the animal. For instance, the NEFA uptake of skeletal muscle was limited as the blood concentration of NEFA increases with fasting. However, there were less information available for the fate of NEFA particularly the quantitative contribution of tissue to NEFA uptake and utilization as energy source during feed-realimentation.

During the restriction period, the mean concentration of plasma BHBA increased by 100% compared with the base-line BHBA concentration (Table 6). On a 30-day refeeding period, the level of plasma BHBA declined markedly and was comparable to the base-line concentration. The decrease in BHBA concentration in repletion cows has been previously demonstrated by Reist *et al*. (2003). However, data from the lipoprotein assay demonstrated the high hepatic free fatty acid uptake during this time and this condition favored the hepatic ketogenesis as described by Grummer (1993). The less BHBA concentration found in this study indicated the limitation of hepatic ketone production. Research result of Jarrett *et al*. (1976) indicated that hepatic ketogenesis was controlled by factor in addition to the availability of free fatty acids in hepatocyte. It was shown by Brindle *et al*. (1985) that methyl malonyl-CoA, an intermediate of propionate metabolism, inhibited CPT I, because methyl malonyl-CoA concentration was responded to the rate of propionate uptake by the liver (Zammit, 1990). In

Table 6 Least square means for plasma metabolite concentration in Kamphaengsaen heifers during the experimental periods

Item	Treatment period			SE[1]
	Full feeding	Restricted feeding	Refeeding	
	(d 32)	(d 20)	(d 30)	
Albumin, (g/dl)	4.0[a]	5.1[b]	4.5[c]	0.1
NEFA[2], (*m*mol/l)	127[a]	350[b]	86[a]	23
BHBA[3], (*m*mol/l)	162[a]	326[b]	210[a]	12
Glucose, (mg/dl)	75.3[a]	48.1[b]	71.1[a]	3.9
PUN[4] , (mg/dl)	10.8[a]	12.7[b]	9.2[c]	0.12

1 Standard error.

2 Non-esterified free fatty acid.

3 *b*-hydroxybutyrate.

4 Plasma urea-nitrogen.

[a,b,c] Least square mean in the same row bearing different superscripts are significantly different ($P<0.05$).

the fed state, propionate provides a major proportion of gluconeogenic precursors in ruminants (Young, 1977). In this study, it was found that at day-30 of refeeding period the glucose concentration elevated from the restriction period comparable to that in the base-line concentration (Table 6). One may infer that the hepatic uptake of propionate for glucose synthesis during this time results in elevated methyl malonyl-CoA, thus, diminishes the hepatic ketogenesis through its effect on inhibition to CPT I.

The response of PUN concentration to energy alteration is shown in Table 6. At day-20 of restriction, PUN concentration was higher than the base-line concentration ($P<0.05$). After the heifers were refed for 30 days, the PUN concentration declined and the level was lower than the base-line concentration ($P<0.05$). Similarity, Hayden *et al*. (1993) reported a rapid decrease in PUN level in low energy forage-fed steers refed high energy diet. The observed lower PUN concentration found in this study may have resulted in the decreased rate of catabolism of labile protein reserves. This may partly be due to the increase in NEFA utilization as a fuel by the repletion heifers. Pethick and Dunshea (1993) stated the increasing in utilization of NEFA by the extrahepatic tissues results in the sparing of glucose. Thereby, the oxidation of glucose declines. The diminishing in glucose oxidation reduce the glucose carbon transfer to alanine, thus allow less tissue protein degradation to provide glucose via the glucose-alanine cycle. This data supports such theory. The high NEFA uptake to the whole body, as suggested, indicated the high extent of free fatty acids that could be used for energy expenditure. If so, the increasing in free fatty acids oxidation due to the high NEFA uptake probably reduced tissue protein degradation, hence the PUN concentration declined.

With the lower of tissue protein degradation, one might speculate the accretion of protein in muscle. However, the data on loin eye area did not show consistent with this relationship. Observation on the heifer loin eye area at day-30 of refeeding period failed to show any accretion. This might be due to the fact that this type of muscle (*longissimus dorsi*) did not response to the deprivation effect during feed-restriction as described by Phongchai *et al*. (in press). Wilson and Osbourn (1960) stated that the degree to which growth patterns were modified because of growth restriction would affect the growth response during compensatory growth. Thus, the compensation of the organ or muscle during compensatory growth reflected the extent to which it was depleted during body-weight loss. Therefore, the lack in loin eye area reduction during feed-restriction might be responded for the absence of loin eye area accretion during feed-realimentation. Besides, those previous studies reported the major increase in protein gain during feed-realimentation occurring in the visceral organs (Bulter-Hogg, 1984; Carstens *et al*., 1991). It was possible that the recovery heifers might deposit protein in organs or muscles other than the loin.

CONCLUSION

In conclusion, following a period of feed restriction, the recovery heifers demonstrated the high lipid turnover with elevation of lipolytic rate concomitant with the accretion of back fat thickness. The serum lipoprotein assay indicated the high hepatic VLDL excretion and it was suggested for the high hepatic free fatty acid uptake by this time. NEFA concentration declined and tended to be less than the base line concentration. This might be due to the highly uptake of free fatty acids by the peripheral tissue. The high free fatty acid uptake to the whole body, coincided with the less tissue protein degradation, indicated that free fatty acids appeared to be a significant energy sources for the heifers during feed-realimentation. Although the decrease in tissue protein degradation and the accretion of loin eye area reported herein did not establish a direct cause-effect relationship,

this data suggested the alteration of lipid metabolism occurring during recovery beneficially supported the compensatory growth.

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