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UNIVERSITY OF ALBERTA

CATCH-UP GROWTH IN BEEF HEIFERS

BY

E. K. YAMBAYAMBA ©

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND
RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF MASTER OF SCIENCE

IN

ANIMAL GROWTH AND DEVELOPMENT

DEPARTMENT OF ANIMAL SCIENCE

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ENTITLED "CATCH-UP GROWTH IN BEEF HEIFERS" SUBMITTED BY E.K. YAMBAYAMBA IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE IN ANIMAL GROWTH AND DEVELOPMENT

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DEDICATED TO MY WIFE MONICA,

AND SON KAUZYA-NZILA

ABSTRACT

Fifty-three Hereford crossbred heifers [211±28 (mean±sd) kg; 197±13 (mean±sd) days of age at day 1] were utilized to study the effects of catch-up growth on growth performance, carcass composition and some longissimus muscle fiber characteristics. Five animals were slaughtered on d 1 for initial carcass composition and muscle fiber characteristics. The remaining 48 animals were randomly penned in groups of six and assigned to treatments as follows: three pens to ad libitum feeding; three pens to 2 months feed restriction (target gain, 0.50 kg d^{-1}) followed by refeeding, and two pens to 4 months feed restriction (target gain, 0.50 kg d^{-1} for 2 months, followed by zero gain for 2 months) followed by refeeding. One pen was slaughtered from each treatment at the end of 2 months (except 4-month restricted animals), 4 months, and at the final slaughter weight of approximately 400 kg. Selected internal organs were weighed, and a standard 10-11-12th rib joint was collected from the left side of each carcass 24 hours postmortem and trimmed into muscle, bone and fat. The fat was further separated into subcutaneous fat (SCF) and intermuscular fat (IMF). Longissimus muscle samples were obtained from the mid-location of the rib joints, proportions of muscle fiber-types (βR, αW and αR) determined using an ATPase staining technique and fiber diameters measured. On refeeding, catch-up growth was exhibited more ($P<0.05$) in the 4-month restricted-refed animals (1.91 kg d^{-1}) than in the 2-month restricted-refed animals (1.32 kg d^{-1}). In terms of non-carcass and carcass composition, feed restriction for 2 months was associated with smaller livers but did not have a significant effect on any carcass tissue. Four months feed restriction significantly ($P<0.05$) lowered liver weight and the proportions of fat and individual fat depots in the 3-rib joint while percent bone increased. At final slaughter weight, 4-month restricted-refed animals had heavier ($P<0.05$) livers, but no differences were found in the proportions of the overall carcass tissues. At the cellular level, 2 months feed restriction did not cause any significant muscle fiber transformations while the mean fiber diameter was smaller ($P<0.05$) in the restricted than in the ad lib fed animals. Four months feed restriction was associated with a relatively higher ($P<0.05$) proportion of βR fibers and smaller ($P<0.05$) fiber diameters while refeeding reversed the trend to control levels. These results indicate that feed restriction did not have residual effects on the carcass tissues and muscle fiber characteristics.

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E. K. Sikazwe Yambayamba

September, 1990

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CHAPTER ONE

INTRODUCTION

Catch-up growth, sometimes referred to as "compensatory growth", may be defined as the acceleration in growth that occurs when a period of growth retardation ends and favourable conditions are restored (Ashworth and Millward, 1986). It is essentially a self-correcting response which restores the individual to the original growth channel. This physiological phenomenon is probably the most widely used (e.g. backgrounding cattle) and the least understood in the livestock industry (Coleman and Evans, 1982).

Catch-up growth has been studied virtually in all farm livestock including cattle (Coleman and Evans, 1982; Lofgreen and Kiesling, 1985; Park et al., 1987), sheep (Thomson et al., 1982; Ferrell et al., 1986), pigs (Mersmann et al., 1987; Pond and Mersmann, 1990), and poultry (Pokniak and Cornejo, 1982; Calvert et al., 1987). It has also been studied in rats (Ocken and Grunewald, 1988), rabbits (Asghar et al., 1981), and humans (Hermanussen et al., 1985; Georgieff et al., 1989).

The theory of catch-up growth predicts that chronically underfed growing animals will not necessarily be permanently stunted; in fact they will often grow more rapidly than normal to regain their growth curve. This is of practical use in the beef industry where, for example, certain feedlots commonly buy underfed steers, knowing they will compensate rapidly and efficiently. Similarly culled cows and heifers can be fed grain and make very rapid, efficient and often profitable gains (Graham and Price, 1982). More data are, however, needed in this respect, since many studies have been done mainly on castrated males.

Although different aspects of the phenomenon of catch-up growth have been investigated, the major concern, particularly in the last three to four decades, has been its effects on the carcass composition in castrated male animals destined for meat production. A wide spectrum of results on the ultimate carcass composition has been reported, ranging from leaner animals than controls (Levy et al., 1971; Fox et al., 1972) through unchanged (Drennan, 1979), to fatter animals (Meyer and Clawson, 1964; Thornton et al., 1979). Very little attention has been paid to female animals that are, for one reason or another, destined for meat production. Data are therefore needed to elucidate the regrowth patterns of the major carcass tissues in these animals.

The effect of catch-up growth on females destined for the breeding herd has also received little attention. Since the theory predicts that underfeeding the animals for a particular period will not necessarily result in stunting, it should also be applicable to the young females selected to join the breeding herd. Thus in the cattle industry, potential breeding heifers could be fed less during their first winter to reduce the maintenance costs. Unfortunately, the risk of permanent stunting is real if the feed restriction interferes with cell division by occuring "too early" in the animal's life, or by lasting "too long". Data are needed to quantify what is "too early" and what is "too long". This would allow producers to minimize maintenance costs without compromizing the heifer's potential.

At the muscle cellular level, studies on the influence of feed restriction on the proportions of different fiber-types (red, white and intermediate) in meat animals have been well documented (Moody et al., 1980; Johnston et al., 1981; Arnold and Meyer, 1988). Muscle fiber size as affected by feed restriction, and how this ultimately affects meat quantity, has also been studied extensively (Joubert, 1956; May et al., 1977; Reid et al., 1980).

Muscle fibers undergo a continual transformation throughout life as an adptation to changing functional demands (Guth and Yellin, 1971). Particularly the transformation of intermediate fibers to either white or red fibers is well established (Ashmore et al., 1972; Moody et al., 1980). It is postulated that environment can also influence the transformation of muscle fibers from one type to another (Moody et al., 1980; Rahelic and Puac, 1981). Different feeding systems have been found to cause such transformations; in particular intermediate fibers can be transformed to white fibers as found in lambs (Moody et al., 1980), cows (Reid et al., 1980) and steers (Johnston et al., 1981). The ultimate quantity and quality of meat is a function of the proportion of muscle fiber-types and fiber size (Tuma et al., 1962; May et al., 1977).

Despite a great deal of information on catch-up growth, many studies have been limited to the tissue (particularly carcass) level. Little attention has been paid to what is happening at the cellular level, particularly during the actual period of catch-up growth. It is necessary to elucidate how the muscle fiber proportions and sizes are affected by underfeeding and subsequent refeeding, especially for animals destined for meat production. In fact an understanding of the growth changes taking place at the cellular level is a pre-requisite to an understanding of the growth process at the whole animal level.

The main objective of this study was to investigate the effects of mild, chronic feed restriction and refeeding in early weaned Hereford crossbred heifers subjected to 2- and 4-months restricted rations on:

1. the growth performance traits (growth rate, feed intake and feed efficiency,
2. the pattern and degree of compensation of the major carcass tissues (muscle, bone and fat) and of selected internal organs,
3. some carcass characteristics other than the major carcass tissues, and on
4. the longissimus muscle fiber-type proportions and fiber diameters.

CHAPTER TWO

LIVE ANIMALS

2.1. LITERATURE REVIEW

The first agricultural reference to the subject of catch-up growth is by Waters (1908) who studied the effects of undernutrition and refeeding in steers. Following realimentation, he observed that the animals were able to recover and reached normal mature weights and heights. Since then, there have been numerous publications on the subject.

O'Donovan (1984) stated that an aspect which has, perhaps the greatest economic significance is compensatory gain achieved on pasture following previous restriction; a double saving ensues, in that the feed costs are minimized during restriction and there are rapid gains on low cost pasture. Several other workers (Bennet et al., 1970; Foot and Tulloh, 1977; Drennan, 1979) have reported that the resulting lower gains during feed restriction are appreciably offset by higher subsequent gains following realimentation.

Animals have been known to recover completely when realimented after a period of starvation, although some studies (Coleman and Evans, 1982) have indicated lack of complete recovery following realimentation. According to Drennan et al. (1982), weight recovery at pasture following winter restriction has been relatively clearly documented, but he cites studies involving realimentation indoors which gave rise to far more variable results (Meyer et al., 1965; Wilkinson and Prescott, 1970; Perry et al., 1972; Coleman et al., 1976). When compensation is recorded on high concentrate diets, recovery is usually low compared with recovery at pasture following winter restriction (Drennan et al., 1982). The validity of this statement, however, needs to be investigated further since several factors play a role in catch-up growth. Bohman (1955) in his study with weanling cattle observed that the ability of the animal to compensate for low winter gains appeared to be influenced by several factors including age of the animal, severity of winter growth retardation, and quantity of feed available during the summer. Generally, it has been found that cattle of at least five months of age can overcome periods of feed restriction varying in both severity and duration (Winchester and Howe, 1955; Heineman and Van Keuren, 1956). However, whether this is applicable to all genders, and to what extent recovery occurs needs to be established.

Despite the wide variation in reports on the growth performance of animals following realimentation, in general the animals undergoing catch-up growth have been observed to exhibit very high growth rates. Carstens et al. (1988) noted that a number of biological mechanisms have been investigated and found to account for catch-up growth and these include changes in feed intake, caloric value of tissue growth, maintenance energy requirement, efficiency of metabolizable energy use for growth, and gut fill weight. The extent to which each of these mechanisms contribute to catch-up growth remains unclear due to the divergence in experimental design, the interdependency of these mechanisms and the fact that few experiments have been undertaken to examine these mechanisms simultaneously.

It is clear from the preceding review that the phenomenon of catch-up growth involves some kind of feed restriction, followed by realimentation after a particular period. To appreciate the phenomenon, it is important to understand some biological responses within an animal during the periods of feed restriction and rehabilitation.

2.1.1. Feed restriction

Feed restriction may take different forms ranging from mild (animals allowed to gain some weight) through maintenance (keeping live weight constant) to severe (actual live weight loss). From a growth point of view, low plane nutrition can have different effects when imposed on animals varying in age and live weight. Maynard et al. (1979) noted that severe and prolonged undernutrition at an early age may result in permanent stunting (for example, if imposed at birth). The major reason for this is that at this early age, hyperplasia is still in progress and any interference with it can result in reduced total number of cells in the animal. This would certainly lead to stuntedness since cells have a maximum capacity to hypertrophy (Staun, 1972). Not only the severity but also the duration of restriction is considered to play an important role in catch-up growth (Wilson and Osbourn, 1960; Hight and Barton, 1965). On the other hand, Yeates (1964) showed that very severe loss of weight in adult cattle does not necessarily cause permanent damage to the muscles. The above two situations (feed restriction in younger and older animals) were demonstrated by Morgan (1972) who underfed cattle from 0 to 16 or 16 to 32 weeks of life. He found that catch-up growth was manifested only in the latter group.

Metabolically, sub-maintenance nutrition is a situation where protein catabolism exceeds anabolism (Lemon and Nagle, 1981). The metabolic events of starvation or low nutritional plane appear to have two phases: the initial response consists of attempting to maintain hepatic glucose output, largely increasing gluconeogenesis, and the secondary response (only in prolonged fasting) is concerned with minimizing protein catabolism. Koch (1982) in his analysis of nutritional models pointed out that a low plane of nutrition results in the decrease of growth energy and an increase in the catabolism of metabolically active tissue. As an example, in a study involving larger Charolais x Hereford steers and smaller Hereford x Hereford steers, Price (1976) found that during the sub-maintenance period, the heavier animals lost more weight than the light animals, presumably because of the former's greater maintenance requirement. However, the percentage loss was similar in all the steers. The author postulated that at any given time, all the cattle were mobilizing a similar ratio of fat to non-fat tissue to supply their energy requirements, despite the differences in the live weights. He noted that the basis for this was the large difference in the heat of combustion (and hence available energy on catabolism) between fat and other body tissues.

The other metabolic responses due to restricted feeding include a decrease in the basal metabolic rate (Ferrell et al., 1986); a decrease in methane production and urinary nitrogen losses (Thomson et al., 1982); a decrease in the blood concentrations of volatile fatty acids and an increase in those of glycerol and non-esterified fatty acids, and a decrease in some amino acids (Lomax and Baird, 1983). These responses (and many others) show how the animal's metabolic and physiological systems adapt to cope with feed restriction.

2.1.2. Realimentation

Realimentation of feed restricted animals normally results in a quick reverse of the metabolic and physiological responses in the animal's body. For example, Park et al. (1987) who restricted dairy heifers for five months, observed that after realimentation there was an immediate increase in the blood urea-nitrogen, glucose concentration, triglyceride concentration and enzymatic activity in the blood. The associated results with such responses included a very high feed efficiency (gain to feed ratio) (up to 570% increase), and increased energy (gain to metabolizable energy intake ratio) and protein (gain to protein intake ratio) utilization. Similar results have been observed by several other workers (McManus et al., 1972; Little and Sandland, 1975; Graham and Searle, 1979; Wright et al., 1986).

The improved efficiency is evident particularly in the early stages of realimentation (O'Donovan, 1984). In general, increased feed intake is accompanied with the above responses although conflicting results have been reported - again because of various factors prevailing under the experimental conditions.

Graham and Searle (1979) and Wright (1985) reported higher feed intakes in realimented sheep and beef cattle respectively. Others (Fox et al., 1972; Hironaka and Kozub, 1973) reported no changes in feed intake, while Foot and Tulloh (1977) and Murray (1980) reported reduced feed consumption in cattle.

Meyer and Clawson (1964) explained compensatory gain on the basis of an increased efficiency of feed utilization over and above that needed for maintenance. Similarly, Fox et al. (1972) and Folman et al. (1974) reported that feeding a maintenance ration for 90 days, although prolonging the fattening period, led to conversion rates equal to or better than those of continuously fed controls. Partly, such results may be explained by the increased apparent digestibility of the feed; for example, Thornton et al. (1979) found that following a period of restriction in sheep, the apparent digestibility increased from 53-68 percent to 80-90 percent.

In terms of nutrient utilization, Whittemore et al. (1978) demonstrated that compensatory protein retention (as measured by nitrogen balance) was possible in growing pigs following a 12-day period of nitrogen deprivation, and that enhanced nitrogen retention rates were associated with improved efficiency of utilization of dietary nitrogen. Similar findings were obtained by Fox et al. (1972) who found that the compensating steers at light weights were significantly more efficient in converting digestible protein into tissue than the full fed animals. The authors observed that the compensating animals were especially more efficient in the early recovery period. In terms of energy utilization, some studies have shown no difference between realimented and full fed animals. Baker et al. (1985) in comparing steers on low plane and high plane nutrition, found that the energy retention was fairly similar for both groups and there was no indication that the net efficiency of energy use differed between the groups.

The underlying factor for increased efficiencies is that the basal metabolism of an animal declines as energy intake is reduced (Wilson and Osbourn, 1960). Since the maintenance requirement is proportional to the live weight of an animal (NRC, 1984), it may be stated that animals subjected to undernutrition become more economical in their use of food. Such animals, when realimented, only slowly raise their basal metabolic rate to the normal rate for the new level of nutrition. This would result in a greater proportion of food being available for productive purposes, especially growth, and would result in an increased growth rate compared with that shown by control animals on similar diets. Such improved efficiency, however, would only be temporary, and would be gradually reduced throughout the period of realimentation.

2.1.3. Factors affecting the animal's ability to recover

Wilson and Osbourn (1960) summarized the following as factors that affect the animal's ability to recover from the effects of undernutrition:

1. The nature of undernutrition. An animal's growth can be retarded by restricting any one of the many components of its diet. The

ability to recover may, in certain instances, depend on whether the energy or the protein content of the diet has been limiting the weight gain. Maynard et al. (1979) reported that a deficiency of energy will immediately check the growth in mass, while a lack of calcium may not, since its primary effect is upon bone structure rather than its size. On the other hand, studies done by Winchester et al. (1957) showed that very severe protein restriction may have a more harmful effect than very severe energy restriction.

2. Severity of undernutrition. This may best be measured by the animal's rate of gain or loss of weight. The nature of severity may vary from little weight gain through maintaining the weight constant to an actual loss of weight.
3. Duration of the undernutrition period. The recovery of the animals on a catch-up growth scheme and their eventual achievement of the final weights depend to a large extent on the duration of the restriction period, particularly if the severity is harsh. Too long a duration coupled with severe restriction can result in failure of recovery.
4. Stage of development at which undernutrition is imposed. This is best measured by weight of the animal at the beginning of undernutrition, rather than its age. Undernutrition in the earlier stages of growth is more detrimental to an animal than restriction at a later stage, and the ability to recover and to reach normal mature size, is consequently impaired.
5. The relative rate at which an animal matures, and its effect upon

recovery. This is measured as time taken to reach puberty or full maturity. Joubert (1954), studying the effects of periodic undernutrition upon the growth of Shorthorn and Afrikander cattle in Africa, showed that whereas the differences between well fed and poorly fed Shorthorn cattle increased with age, differences between well fed and poorly fed Afrikander cattle tended to decrease. The author attributed this to the different maturation rates of the two breeds. The Shorthorns are much more early maturing than the Afrikander cattle, although the validity of this conclusion may be questioned on the grounds that the climatic conditions during the African summer period penalize the less heat-tolerant Shorthorns.

6. Pattern of realimentation. A high plane of nutrition will result in a more rapid recovery of animals than just an adequate plane. Bohman (1955) and Heinemann and Van Keuren (1956) showed that the higher the plane of nutrition upon realimentation, the more rapid and the greater the recovery.

2.2. MATERIALS AND METHODS

2.2.1. Animals and experimental design

Fifty-four Hereford crossbred heifers [211 ± 28 (mean±sd) kg, 197 ± 13 (mean±sd) days of age at day 1 (November 7, 1988)] born in April and May, 1988 were used in the experiment. They were born at the University of Alberta Ranch at Kinsella and weaned in October of the same year. They were immediately transported to Ellerslie Research Station (150 km) near Edmonton where the study was conducted.

The animals were housed in open front sheds. The floor was concrete, and wood shavings were used as bedding material. A 25-day adjustment period to the experimental diet (Table 2.1) was allowed before starting the experiment on November 7, 1988. During the adjustment period, one heifer died of bloat and was not replaced. The animals were weighed three consecutive days around d 1 of the experiment to give the initial weight.

A 3x2 factorial design was used. Five heifers, selected at random, were slaughtered at the onset of the experiment for initial body composition measurement. The remaining forty-eight animals were randomly penned in groups of six and assigned to treatments as follows: three pens to ad libitum feeding; three pens to 2 months feed restriction (target gain, 0.5 kg d^{-1}) followed by refeeding; two pens to 4 months feed restriction (target gain, 0.5 kg d^{-1} for 2 months, followed by a period of zero gain for 2 months) followed by refeeding (see Figure 2.1).

Serial slaughter of the animals was carried out. One pen of

TABLE 2.1. COMPOSITION OF THE EXPERIMENTAL DIET

Ingredient	% in diet (as-fed)
Barley	75.45
Alfalfa hay	20.00
Canola meal	3.00
Calcium carbonate	0.80
Salt, fortified	0.50
Vitamin ADE premix	0.25
	Analysis of dry matter
Barley	
Dry matter (DM), %	84.70
Crude protein, % of DM	12.70
Calcium, % of DM	0.45
Phosphorus, % of DM	0.39
DE, Mcal/kg DM	3.69
Alfalfa hay	
Dry matter (DM), %	83.00
Crude protein, % of DM	14.40
Calcium, % of DM	1.56
Phosphorus, % of DM	0.23
DE, Mcal/kg DM	2.60

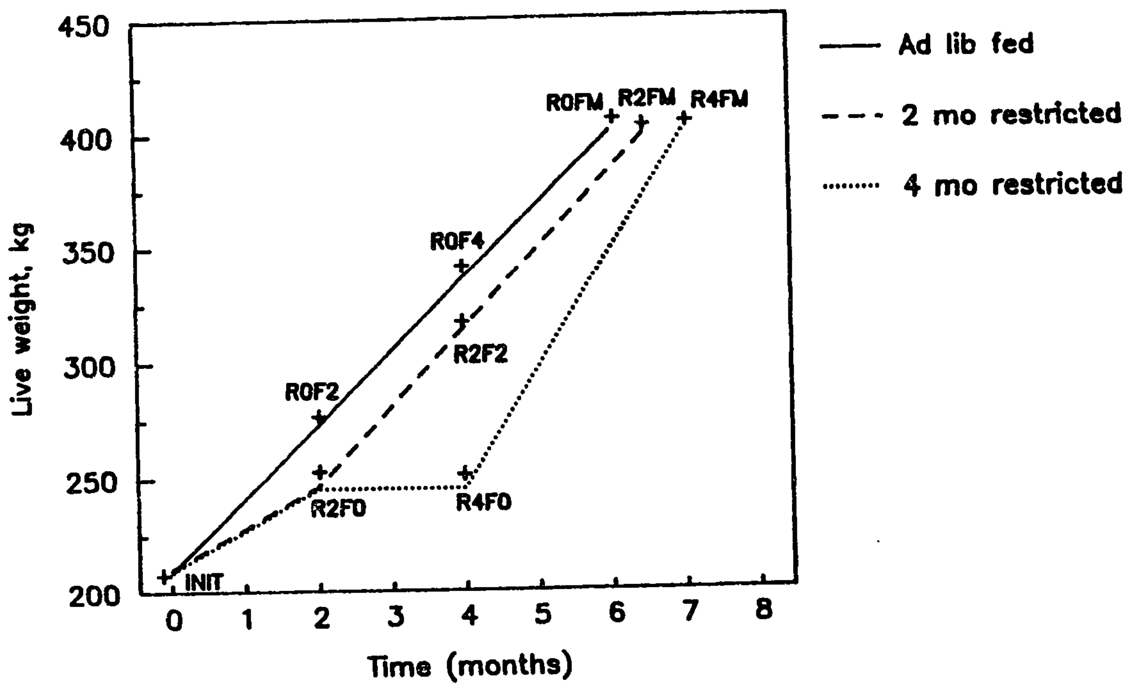

Figure 2.1. Diagramatic representation of experimental design.
+ = slaughter group of 6 heifers.

animals was slaughtered from the ad lib fed and 2-month restricted groups at day 62 (2 months) and the remaining two pens from the latter were switched to ad libitum feeding. The pattern of realimentation was such that it took two-and-half to three weeks before the restricted animals were put on a complete full feed regime, i.e. the ration was increased slowly rather than introduce a full regime at once. This was to allow animals to adapt slowly to increased feed. At day 119 (4 months), one pen from each of the three treatments was slaughtered and then the remaining pen from the 4-month restricted group was switched to ad libitum feeding in the same manner as described above. The remaining three pens (one from each treatment) were fed to a final target weight of approximately 400 kg and slaughtered. This made it possible to examine the specific effects of body weight stasis and regain on changes in body composition and muscle fiber characteristics. Thus the full design of the experiment was as follows:

INIT animals = restricted 0 months, full fed 0 months;
R0F2 animals = restricted 0 months, full fed 2 months;
R0F4 animals = restricted 0 months, full fed 4 months;
R0FM animals = restricted 0 months, full fed to market weight (about 400 kg);
R2F0 animals = restricted 2 months, full fed 0 months;
R2F2 animals = restricted 2 months, full fed 2 months;
R2FM animals = restricted 2 months, full fed to market weight (about 400 kg);
R4F0 animals = restricted 4 months, full fed 0 months;

R4FM animals - restricted 4 months, full fed to market weight (about 400 kg).

2.2.2. Feeding and routine measurements

The animals were fed once every day between 9.00 and 10.00 am. The ad lib fed animals had access to feed and water at all times while the 2- and 4-month restricted animals were fed only to achieve target gain, but had access to water at all times. Feed intake of pens was recorded in all treatments. Live weights of individual animals were taken weekly. Based on the pen average weight, the rations for the restricted animals were adjusted whenever necessary to keep them at the target rate of gain.

The restricted animals were allowed to gain an average of 30 kg during the first period (first two months) before realimenting the 2-month restricted animals. This was to keep the animals in a positive energy balance to ensure good health. The 4-month restricted animals were then maintained at that level for the next 2 months (second period) before being realimented (Figure 2.1).

As part of monitoring the growth of animals, hip heights at the first sacral bone were measured periodically. The measurements were taken on all animals on day 1 and thereafter, on days, 61, 118 and at final slaughter weight.

Back fat thickness was measured ultrasonically on the same days as the hip height measurements. The measurement was done with a scanogram (ultrasound instrument), Model 722 (Ithaco Inc., Ithaca, NY, USA). This instrument generated a two-dimensional image of the back fat on a polaroid picture, which could then be measured with a ruler. The instrument was calibrated such that 1 mm on the generated picture was equal to 2.54 mm on the animal.

The area to be scanned (left side of the animal) was soaked with mineral oil and then the guide rail (to which the transducer was attached) placed on the target area to take the picture. Each animal was scanned at right angles to the spine (mid-line) over the eye muscle between ribs 12 and 13. The animal was released only when a satisfactory picture had been taken. The back fat thickness on the generated picture was measured with a ruler two-thirds from the mid-line, to give the average thickness.

All health problems and veterinary treatment of individual animals were recorded.

2.2.3. Statistical analysis

Individual animal live weights were regressed on days within each period to estimate the rate of gain. The hip height and back fat data were analysed by a two-way analysis of variance (SPSSx, 1988) using a fixed model:

$$Y_{ijk} = \mu + F_i + T_j + FT_{ij} + E_{k(ij)}$$

where:

Y_{ijk} = Back fat thickness or hip height measured for each individual,

F_i = Feeding regime (ad lib, 2 mo restricted and 4 mo restricted),

T_j = Time or period (months) of slaughter,

FT_{ij} = Interaction between the feeding regime and period,

$E_{k(ij)}$ = The random error term.

Student-Newman-Keuls procedure was used ($P<0.05$) to separate the means when significant ($P<0.05$) main effects were found.

2.3. RESULTS AND DISCUSSION

2.3.1. Growth patterns

The growth patterns followed by animals on different nutritional regimes were more or less as designed (Figure 2.2) The target gain of 0.5 kg d^{-1} in the 2- and 4-month restricted groups was achieved during the first 2 months, although the latter slightly deviated (0.49 kg d^{-1}). The 4-month restricted group was then maintained at zero rate of gain during the second 2 months, as planned. At final slaughter weight, there was a slight deviation from the target of 400 kg in all the treatments. The final slaughter weights were 414, 419 and 408 kg for the ad lib, 2-month and 4-month restricted-refed animals respectively.

2.3.2. Feed intake and feed efficiency

The average daily feed intakes per animal during the first period were 7.4 and 3.5 kg for the ad lib fed and the two restricted groups respectively (Table 2.2). During the second period (refeeding of the 2-month restricted animals), the average daily feed intakes per animal were 8.0 and 7.0 kg for the ad lib fed and 2-month restricted animals respectively, while that for the 4-month restricted animals was reduced to 2.9 kg which resulted in zero gain for these animals.

The 2-month restricted animals slowly increased their feed intake during the refeeding period and it took three weeks before they were on a full feed regime. By the fourth week, they had increased their feed intake by more than 91% but they did not exceed

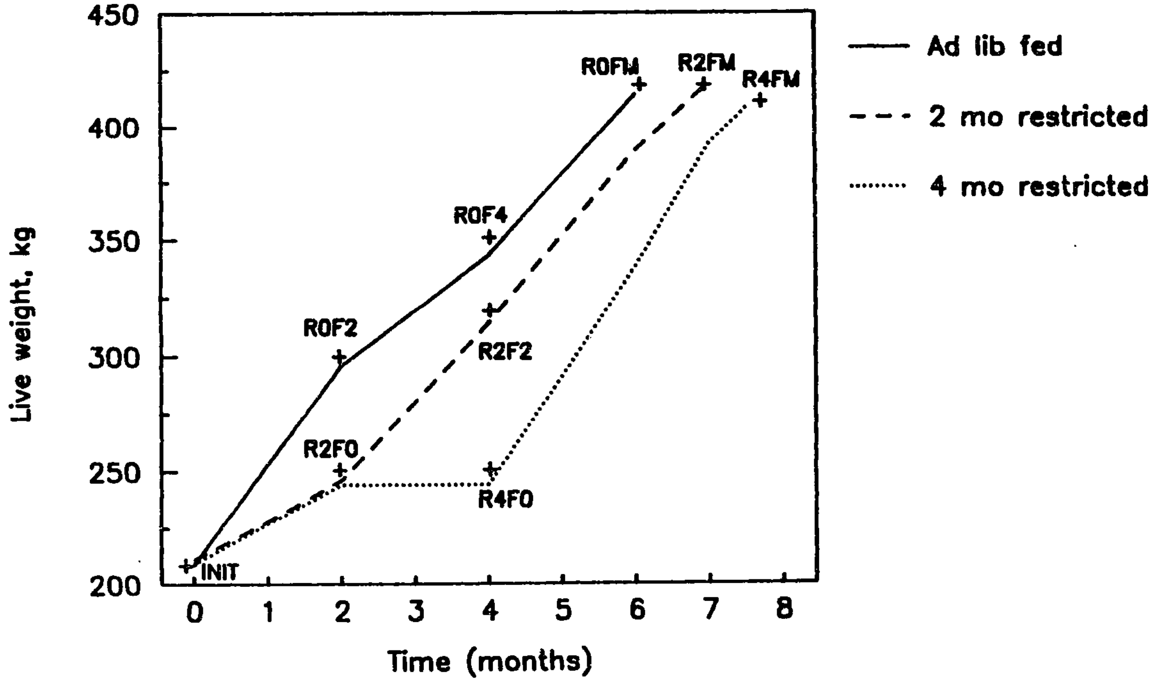

Figure 2.2. Growth patterns of heifers grown on different nutritional regimes from d 1 (25 d after weaning; see text) to about 400 kg. + = slaughter group of 6 heifers.

TABLE 2.2. DAILY FEED INTAKE, AVERAGE DAILY GAIN AND FEED EFFICIENCY OF HEIFERS BEFORE AND AFTER REFEEDING

	Ad libitum fed				2 months restricted				4 months restricted			
Period[a]	n	FI[b]	ADG[c]	FE[d]	n	FI	ADG	FE	n	FI	ADG	FE
1	18	7.4	1.23	0.17	18	3.5	0.50	-	12	3.5	0.49	-
2	12	8.0	1.14	0.14	12	7.0	1.32	0.19	12	2.9	0.00	-
3	6	8.0	1.02	0.12	6	8.9	1.18	0.13	6	9.5	1.91	0.20
TFI[e]	1358				1363				1383			

[a] Period 1 = First 2 months of the experiment.

2 = Second 2 months of the experiment (refeeding of 2-month restricted animals).

3 = Last phase of the experiment (refeeding of 4-month restricted animals).

[b] Average daily feed intake, kg animal^{-1}.

[c] Average daily gain, kg d^{-1}.

[d] Feed efficiency (gain:feed ratio).

[e] Total feed intake (kg) per animal for the whole experimental period.

that of the ad lib fed animals. These results differed from those observed in steers by Carstens et al. (1988) who reported that feed intake for compensatory growth animals had increased by 72% by day 19 after refeeding, with most of the increase occuring within the initial six days. Animals that are on restricted feed are known to have reduced basal metabolic rate (Wilson and Osbourn, 1960). Such animals, when realimented, only slowly raise their basal metabolic rate to the normal rate for the new level of nutrition. The implication here is that such animals with a reduced basal metabolism would have less feed intake and during realimentation, the intake increases slowly rather than abruptly until the normal rate is established.

Probably another explanation for the gradual increase in feed intake following realimentation would be in terms of the hypothalamic control centres in the brain (Harris, 1980). Since the appetite centre is in the brain, feed restriction would result in the appetite centre setting the appetite at a lower level than normal. During refeeding, the brain slowly adjusts and consequently the appetite is gradually raised to higher levels.

The results in the present study are, however, in agreement with those reported in sheep by Keenan et al. (1969) who found that feed intake was lower following refeeding, but this was limited to the first two weeks. They observed that the voluntary intake of the different diets only increased slowly when food was offered ad libitum after a period of restricted feeding; peak levels were not reached until after at least three weeks. In fact, in the present study, the average feed intake for the 2-month restricted-refed animals at the end of the second period was 13% less than that of the ad lib fed animals. This could have been due to increased feed efficiency (Table 2.2), a trend observed by other workers in steers (Fox et al., 1972).

Refeeding of the 4-month restricted animals (third period) was also associated with a gradual increase in feed intake until the peak was reached four weeks later. During this same period, the feed intake of the 2-month restricted-refed animals increased more and by the fourth week, their feed intake had slightly surpassed that of the ad lib fed animals. Apparently, the 4-month restricted-refed animals increased their feed intake at a faster rate than the 2-month restricted-refed animals, and by the sixth week in the third period, the former were consuming slightly more than both the ad lib fed and the 2-month restricted-refed animals. As the length of the feeding period progressed, the feed consumption increased even more. Similar results were reported by Hidiroglou et al. (1987) in Brahman beef cattle, although the authors did not offer an explanation. Saubidet and Verde (1976) working with steers found that the greater the severity of feed restriction, the higher was the feed intake at equal weight. What may be deduced from this is that the more severe the feed restriction is, the greater the tendency to compensate and the animal responds by consuming more feed.

The total feed intakes per animal for the whole experimental period were 1358, 1363 and 1383 kg for the ad lib fed, 2-month restricted-refed and 4-month restricted-refed animals respectively.

From these data, it can be seen that the realimented animals (particularly the 4-month restricted-refed animals) consumed on average more feed per day during refeeding than the ad lib fed animals. The overall total feed intakes per animal were, however, similar among treatments. These findings do not agree with those found with steers (Foot and Tulloh, 1977) where the mean total intake of the refed animals was 12% less than that of the control animals. The results, however, agree to some extent with those obtained by Hironaka and Kozub (1973) who found that the total feed intake was similar for both catch-up and control steers, and Turgeon et al. (1986) who reported similar dry matter intake in lambs fed ad libitum and those undergoing catch-up growth.

It can also be seen that the feed efficiency (gain:feed intake ratio) of the restricted animals during the refeeding periods was generally higher than the ad lib fed animals. Generally, high feed efficiencies result in higher growth rates than normal, a trend observed in this study.

2.3.3. Growth rates

The growth rate of the ad lib fed animals during the first period of the experiment was 1.23 kg d^{-1} while the 2-month and 4-month restricted animals were maintained at 0.50 kg d^{-1} and 0.49 kg d^{-1} respectively (Table 2.2 and Figure 2.2). Refeeding of the 2-month restricted animals in the second period resulted in a higher growth rate (1.32 kg d^{-1}). This was, however, not significantly higher than the ad lib fed animals whose growth rate was 1.14 kg

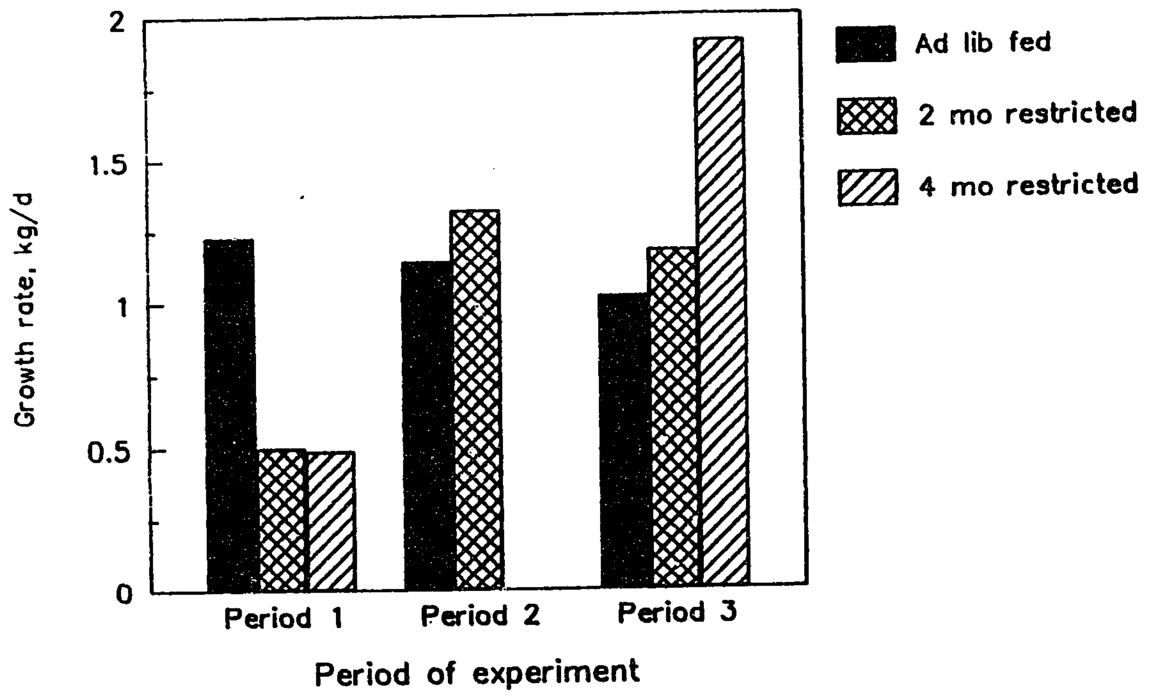

Figure 2.3. Growth rates of heifers before and after refeeding (see text) to about 400 kg.

d^{-1} during this period. The 4-month restricted animals, when realimented (third period), exhibited highly significant ($P<0.05$) growth rates (1.91 kg d^{-1}) from both the ad lib fed (1.02 kg d^{-1}) and 2-month restricted-refed animals (1.18 kg d^{-1}) (Figure 2.3). Some individual animals from the 4-month restricted-refed group were gaining more than 2 kg d^{-1}, particularly when feed consumption was high.

Thus the more severely restricted animals were able to make higher growth rates than the less restricted animals, contrary to the suggestion by Wilson and Osbourn (1960) that the more severe the restriction is, the less the capacity for animals to compensate fully. Ashworth and Millward (1986) stated that there is evidence that complete catch-up growth can occur even in situations where growth retardation has been extremely severe or prolonged. It is therefore not surprising that the animals that had been restricted for 4 months made such gains when they were realimented. The trend of these results is similar to the findings of Wright et al. (1989) who fed cattle on low, medium and high levels of winter feeding, and then turned out the animals on pasture in summer. The gains of such animals were 1.01, 0.79 and 0.65 kg d^{-1} for low, medium and high level animals, clearly demonstrating that the animals that had gained the least in winter gained the most in summer. Turgeon et al. (1986) found more or less similar results in lambs: the slower the lambs gained during the growing phase, the greater was the response in the rate of gain and feed efficiency during the periods of the finishing phase.

The magnitude of such gains in the present study has also been reported in other studies although such reports have been mainly in castrated male animals. For example Lawrence and Pearce (1964) reported gains of more than 2 kg d^{-1} in steers undergoing catch-up growth. The workers, however, mentioned that gut fill may have played an important part in as far as weight gain was concerned. Carstens et al. (1988) whose compensatory growth steers were gaining at 2.17 kg d^{-1}, also concluded that a substantial portion of the growth advantage exhibited by catch-up growth animals was due to a greater gut fill.

Physiologically, when an animal is underfed, there is a deviation from the normal physiological:chronological time relationship, the former proceeding at a relatively slower rate (Koch, 1982). Refeeding of such animals may accelerate the growth rate enormously in order to rebalance the physiological:chronological relationship. Since in the present study the rate of gain during catch-up was greater for the more severely restricted group, it is possible that the rebalancing of this deviation on realimentation is influenced by the severity of the feed restriction.

All the restricted animals that were refed to final slaughter weight (R2FM and R4FM) recovered and reached the target slaughter weight, although they needed more time. The R2FM and R4FM animals took an extra 28 and 49 days respectively to reach about 400 kg. From these results, it can be seen again that the 4-month restricted-refed animals exhibited a more vigorous catch-up growth than the 2-month restricted-refed animals. The former took a relatively shorter time than the latter to reach the target final weight. These results are similar to those obtained with steers by Hironaka and Kozub (1973) where the full fed animals required 230 days to reach 489 kg while those restricted for 168 days required only an extra 68 days to reach the same weight.

The statement by Coleman and Evans (1986) that "restricted animals rarely compensate totally" is not entirely true unless the feed restriction interferes with hyperplasia. Allden (1968) arrested growth in Merino lambs for 400 days, and found that none of the restrictions impaired the capacity of the sheep to resume normal growth. He found that the animals were able to undergo a period of arrested growth for several months without any long term adverse effects on either body weight or linear dimensions of the body. Likewise when an ad libitum feeding regime was restored, the efficiency of feed utilization for weight gain was unimpaired. He observed that the impetus to grow was more closely related to somatic development than to chronological age. The findings from the present study equally suggest that the capacity of the heifers to resume normal growth was not impaired in any way. In fact, the statement by Winchester and Howe (1955) and Heineman and Van Keuren (1956) that "cattle of at least five months of age can overcome periods of feed restriction varying in both severity and duration", can safely be applied.

2.3.4. Hip height and back fat measurements

The mean hip heights of the animals were relatively unaffected by the nutritional regimes over the entire experimental period (Figures 2.4 and 2.5), while back fat was significantly affected (Figures 2.6 and 2.7). As can be seen at the end of the first 2 month restriction period, there was no significant effect on the hip heights associated with either ad lib feeding or feed restriction (Table 2.3).

Hip height is a measure of skeletal size (Tatum et al., 1988), and it was therefore not surprising that nutrition did not have a significant effect. Hand et al. (1986) reported that the hip height of yearling steers measured just prior to the beginning of the grazing season was not related to steer gain; whether animals were gaining positively or negatively, they had similar hip heights. The results in the present study are consistent with those of Hand et al. (1986) but they do not agree with those of Coleman and Evans (1986) who found that the restricted nutritional regime (with a gain of 0.25 kg d^{-1}) during the growing phase of steers suppressed growth in both height and length.

Bone is almost entirely unaffected by any nutritional restrictions except in very extreme situations (Price, 1976, 1977). In fact it is not uncommon to find restricted animals growing even taller than the ad lib fed animals. For example, reports in rats (McCay, 1939; McAnulty, 1977) have revealed such findings. This can be observed to some extent in the present study when the hip height change associated with live weight change (Figure 2.5) is taken into

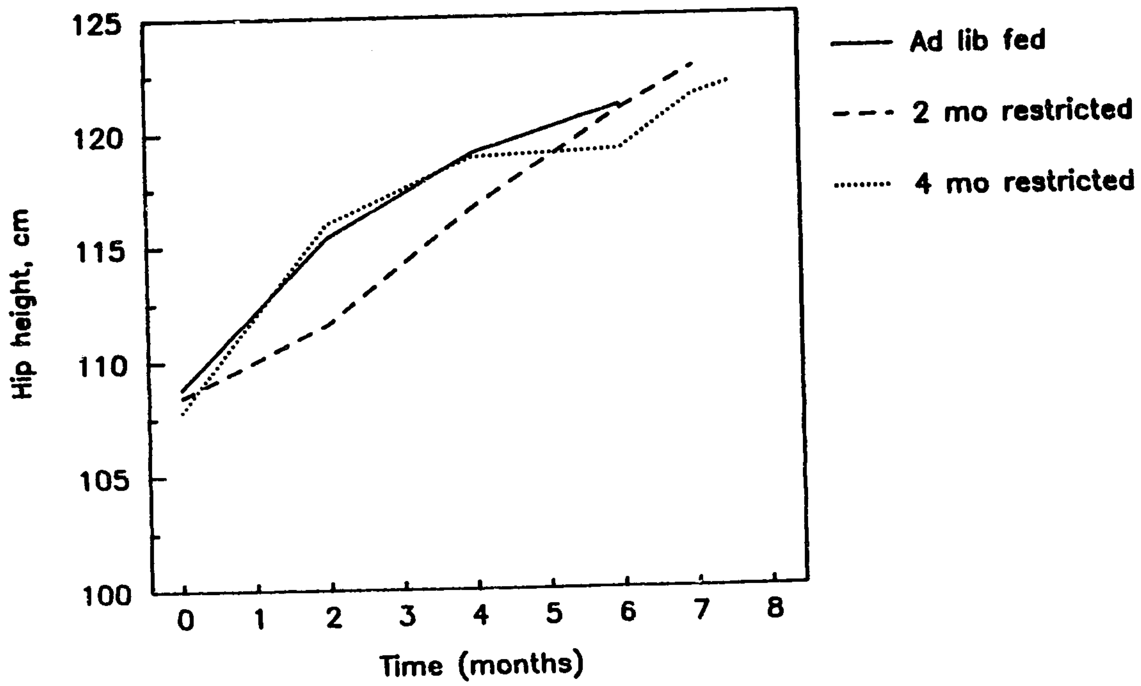

Figure 2.4. Change in the hip heights of heifers grown on different nutritional regimes from d 1 (25 d after weanirg; see text) to about 400 kg.

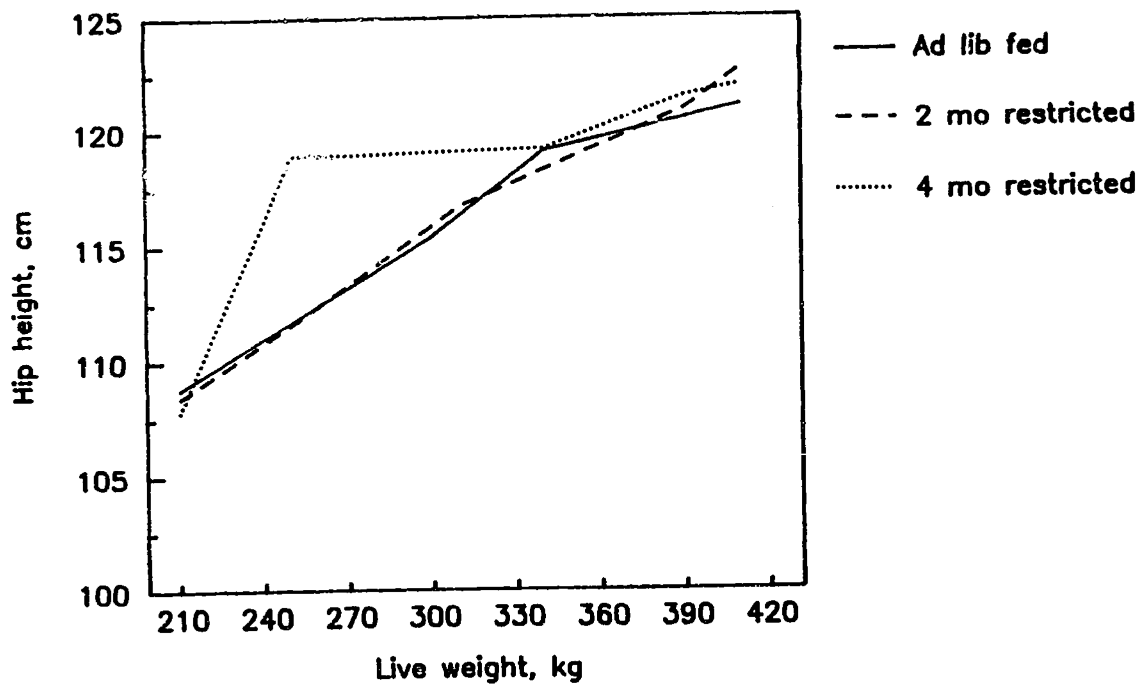

Figure 2.5. Change in the hip heights associated with change in live weight of heifers fed on different nutritional regimes from d 1 (25 d after weaning; see text) to about 400 kg.

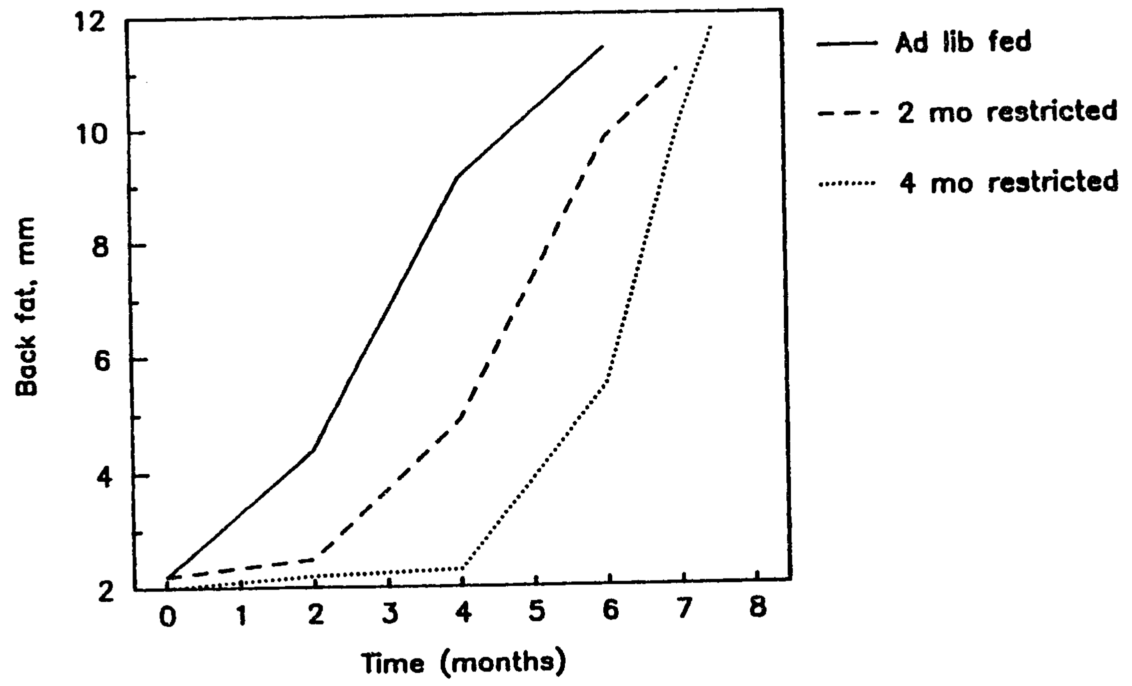

Figure 2.6. Change in the back fat thickness of heifers grown on different nutritional regimes from d 1 (25 d after weaning; see text) to about 400 kg.

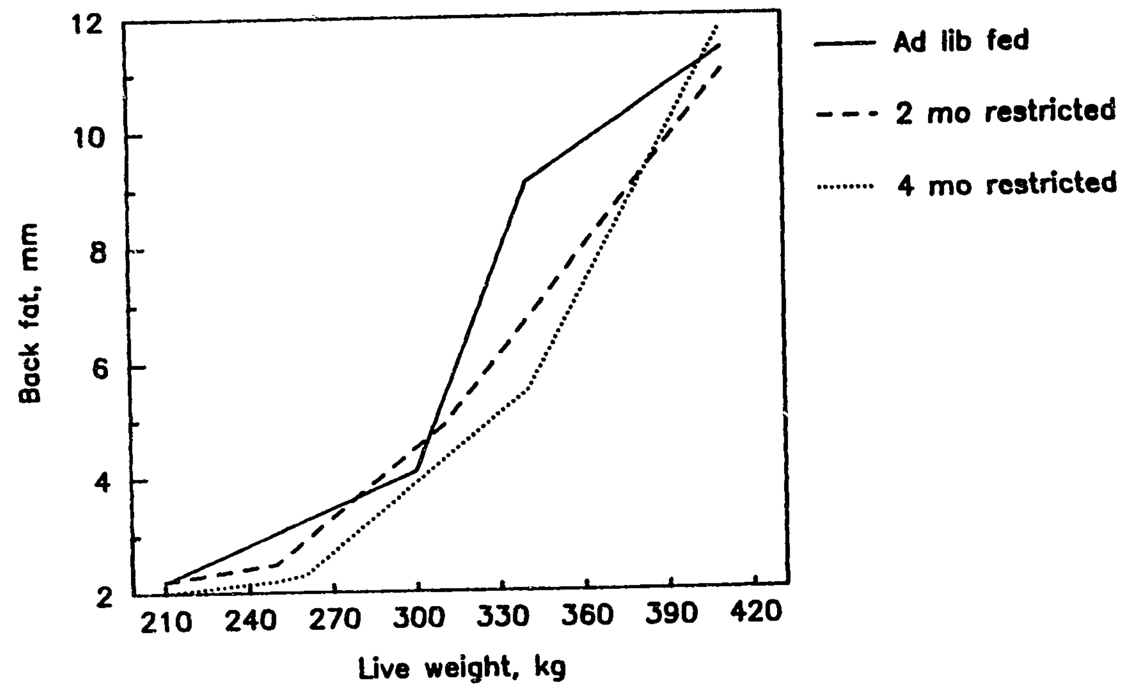

Figure 2.7. Change in the back fat thickness associated with change in live weight of heifers fed on different nutritional regimes from d 1 (25 d after weaning; see text) to about 400 kg.

TABLE 2.3. LEAST SQUARES MEANS ± STANDARD ERRORS OF HIP HEIGHTS AND BACK FAT THICKNESS OF HEIFERS FED FOR 2 MONTHS

Item	R0F2[a]	R2F0[b]	Probability
No. of animals	6	6	
Live weight, kg	296 ± 23	246 ± 12	0.08
Age, d	255 ± 5	254 ± 5	0.94
Hip height, cm	115.4 ± 2.5	111.6 ± 1.2	0.20
Back fat, mm	4.4 ± 0.6	2.5 ± 0.0	0.01

[a] Animals fed ad libitum for 2 mo.

[b] Animals restricted for 2 mo.

consideration. It can be seen that at 240 kg live weight, the 4-month restricted animals were relatively taller than the ad lib fed and 2-month restricted animals.

Back fat thickness in all the groups was equal and quite low at the onset of the experiment (2.0 to 2.2 mm). Within two months, the back fat of the ad lib fed animals had doubled in thickness while that of the restricted groups remained more or less at the "initial" stages, as can be seen from the comparison ($P=0.01$) between the R0F2 and R2F0 groups at the end of the first period (Table 2.3).

At the end of the second period, the hip heights were not different among the treatments while the back fat thickness of the R0F4 animals had more than doubled from the previous measurement at 2 months and was thicker ($P<0.05$) than that of the R2F2 animals which in turn was thicker ($P<0.05$) than that of the R4F0 animals (Table 2.4).

It can be seen from these data that feed restriction had a major effect on the accumulation of the back fat in both the 2-month and 4-month restricted animals. Since back fat is related to total body fat (Mersmann et al., 1987), it can be concluded that the body fat of the restricted animals did not accumulate significantly during the feed restriction period (see Figure 2.6). Thus despite some weight gain that occured in the restricted animals during the first period, the back fat thickness was almost unchanged from the d 1 measurements. The most probable reason for this could be that the mild feed restriction delayed the fattening phase resulting in no significant accumulation of fat. Also from Figure 2.6 it can be

TABLE 2.4. LEAST SQUARES MEANS ± STANDARD ERRORS OF HIP HEIGHTS AND BACK FAT THICKNESS OF HEIFERS FED FOR 4 MONTHS

Item	R0F4[a]	R2F2[b]	R4F0[c]	Probability
No. of animals	6	6	6	
Live weight, kg	343 ± 4^d	314 ± 7^d	244 ± 12^e	0.001
Age, d	315 ± 4	317 ± 5	311 ± 5	0.69
Hip height, cm	119.1 ± 1.0	116.7 ± 1.6	118.9 ± 1.6	0.31
Back fat, mm	9.1 ± 0.5^d	4.9 ± 0.9^e	2.3 ± 0.6^f	0.001

[a] Animals fed ad libitum for 4 mo.

[b] Animals restricted for 2 mo followed by refeeding for 2 mo.

[c] Animals restricted for 4 mo.

[d,e,f] Means within a row with different superscripts differ ($P<0.05$).

observed that the ad lib fed heifers accumulated fat slowly in the first period followed by a more rapid increase in the second period of the experiment.

The mean hip heights at final slaughter weight were not significantly different among treatments (Table 2.5). As for back fat, when the 2-month restricted animals were refed (from day 62), the back fat thickness doubled within 2 months, and increased by another 100% in the following 2 months, and at final slaughter weight, they were measuring 11.0±0.8 mm (Table 2.5). Similarly, when the 4-month restricted animals were refed (from day 119), the back fat thickness more than doubled within 2 months and again doubled in the following 1 month and at final slaughter weight, they were measuring 11.8±1.2 mm. Thus refeeding the animals allowed resumption and catch-up of fattening and at the final slaughter weight, there was no difference (P>0.05) among treatments. In particular, the R4FM animals accumulated the back fat at a much faster rate than the R0FM and R2FM animals.

The rapid rate of back fat accumulation was probably due to increased feed intake during the refeeding period. It is a well established concept (Marple, 1983) that there is a maximum rate at which feed can be converted into muscle; in other words muscle cannot be forced to grow faster than its genetically set pace. Thus any extra feed is laid down as fat, especially in the subcutaneous layer. Connected to this concept, Butterfield's (1966) suggestion that "since the gastrointestinal tract (GIT) is not affected to a high degree during feed restriction, this means there is an 'adult' GIT

TABLE 2.5. LEAST SQUARES MEANS ± STANDARD ERRORS OF HIP HEIGHTS AND BACK FAT THICKNESS OF HEIFERS AT ABOUT 400 kg

Item	R0FM[a]	R2FM[b]	R4FM[c]	Probability
No. of animals	6	6	6	
Live weight, kg	414 ± 19	419 ± 13	408 ± 13	0.88
Age, d	373 ± 8[d]	401 ± 5[e]	422 ± 7[f]	0.001
Hip height, cm	121.0 ± 1.5	122.7 ± 2.0	122.0 ± 0.7	0.72
Back fat, mm	11.4 ± 0.9	11.0 ± 0.8	11.8 ± 1.2	0.84

[a] Animals fed ad libitum throughout to final slaughter weight.

[b] Animals restricted for 2 mo followed by refeeding to final slaughter weight.

[c] Animals restricted for 4 mo followed by refeeding to final slaughter weight.

[d,e,f] Means within a row with different superscripts differ ($P<0.05$).

lying in a 'young' animal", may be applicable. This means that when the animals are rehabilitated, the GIT is able to handle a larger amount of feed than can the muscle. All the extra feed is therefore simply 'spilled over' into fat rather than muscle. The other reason for such a fast rate of back fat accumulation in the 4-month restricted-refed animals could be that chronologically, these animals were supposed to be in the fattening phase by the time the feed restriction ended, as it is evident from the ad lib animals (Figures 2.6 and 2.7). Therefore, when ad libitum feeding was offered, there was an acceleration in the accumulation of the back fat to 'catch-up'.

2.3.5. Interactions

There were significant treatment by period interactions for the live weight and back fat thickness. The ad lib fed and 2-month restricted-refed animals were heavier than the 4-month restricted-refed animals at the end of the second period. During the refeeding of the R4FM animals, these animals increased in live weight at a very high rate while the R0FM and refed R2FM animals increased at slower and more or less similar rates. The R4FM animals finally levelled off with the other groups.

For back fat thickness, its accumulation in the ad lib fed animals increased at a high rate during the first 2 periods of the experiment and then slowed down significantly in the third period. In the restricted-refed animals, the accumulation of back fat was not significant during the restriction periods but increased at a very high rate during the refeeding periods.

2.3.6. Health of the animals

Apart from the animal that died during the adjustment period, animals were generally in good health during the entire experimental period. About 70% of the problems occurred during the adjustment period. Health was therefore not a major factor during the actual experimental period.

The ad lib fed animals had the highest number (31) of treated cases, followed by 4-month restricted animals (15) and lastly 2-month restricted and INIT animals (7 each). Overall, there were nine cases of bloat, four cases of snotty nose, 13 cases of pink eye, one case of scours, three cases of respiratory problems and 15 cases each of high temperature and loss of appetite. The detailed records for individual animals are given in the appendix.

CHAPTER THREE

NON-CARCASS AND CARCASS CHARACTERISTICS

3.1. LITERATURE REVIEW

3.1.1. Growth and development of internal organs

An increase in live weight is associated with different growth patterns for the organs that make up the body. Most internal organs are early maturing relative to live weight and approach their mature weight long before final weight is reached (Black, 1988). In farm livestock such as cattle, sheep and pigs, the brain represents an extreme, having reached about 90% of its maximum size by the time the animal is 35% of mature weight (Black, 1983).

During the normal growth of the pig, McMeekan (1940) found that those parts of the body essential to life processes and body function are relatively well developed at birth, and make a relatively smaller increment in postnatal life than the body as a whole, whereas those organs primarily connected with movement or the storage of the reserves appear ill-developed at birth, but grow more during postnatal life.

Data reported from studies with cattle (Foot and Tulloh, 1977), sheep (Ledin, 1983) and swine (Koong and Nienaber, 1985) have shown that the weights of visceral organs, especially the liver and gut, vary in response to nutritional treatment. In similar lines, Ferrell et al. (1986) reported that when comparisons were made among groups of lambs of similar weight, lambs that had been fed to gain more rapidly had greater weights or proportions of liver, kidney, large intestine, small intestine and stomach than lambs fed to gain less rapidly. Thus nutrition plays quite an important role in the growth and development of some internal organs.

3.1.2. Effect of feed restriction and refeeding on internal organs

According to Palsson's (1955) hypothesis of differential growth, bones and internal organs are not affected by feed restriction to the same degree as muscle and fat. The internal organs such as the gastro-intestinal tract (GIT) and liver, however, can show a rapid and considerable variation in size due to actual functional demands (Goss, 1978).

Undernutrition affects some internal organs to a significant degree. Black (1988) observed that prolonged undernutrition dramatically reduced the size of many organs in adult sheep. Similar results were observed by Reid et al. (1980) who found that underfeeding resulted in a significant change in the size of the livers in dairy cattle. The authors noted that in particular there was a decrease in liver cell volume in all the underfed cows. Based on their previous findings (Reid et al., 1977), they speculated that the decreased liver cell size was associated with an increased concentration of lysosomes in the hepatic cytoplasm. The lysosomal enzymes are believed to play a role in the breakdown of cell constituents leading to a decreased cell size. Widdowson and McCance (1956) observed that if the animal is completely deprived of food, the loss in weight of the liver was relatively greater than that of the rest of the body; they suggested that if the undernutrition was less severe and more prolonged the findings could be similar.

In organ compensatory growth studies (Buhain and Brody, 1973; Alison et al., 1986; Schanbacher et al., 1987), organs have been found to have a tremendous capacity to compensate when they are surgically cut or one removed (for those that are in pairs). The capacity of such organs to recover in animals undergoing catch-up growth has received little attention; data in this respect are therefore needed to establish the degree of organ compensation in animals subjected to varying degrees of feed restriction and later brought to full feed.

3.1.3. The major carcass tissues: general growth and development

Wilson and Osbourn (1960) stated that the body composition, in terms of tissue proportions, is of agricultural significance and economic importance. Thus the occurence of compensatory growth is of greatest importance and significance to the agriculturalist in connection with the growth and development of farm animals, and the effects of periods of subnormal nutrition on their carcass composition.

In many of the catch-up growth studies, carcass composition has received more attention than any other trait although, unfortunately, the findings have been conflicting. Of course several factors ought to be taken into consideration to interpret the conflicting results that have been reported. Generally, all the factors affecting the animal's ability to recover (section 2.1.3.) also have an effect on the ultimate carcass composition of animals. However, to fully understand the role that each of these factors plays in the weight loss and recovery of animals, it is important to understand the basics of growth and development of the major carcass tissues in live animals; how they function, and how they might be affected by nutritrional manipulations.

The external appearance of any given animal is a function of muscle and bone quantity, distribution and dimensions and fat quantity and distribution (Shahin and Berg, 1985b). The patterns of development of these major carcass tissues and their distribution over the carcass have been elucidated in the past four decades or so. Berg and Walters (1983), in their review, noted that knowledge of the factors that influence growth and distribution patterns has provided opportunities to exert more control of these processes and ultimately of carcass composition. The authors, however, pointed out that the major changes in carcass composition are always produced at the risk of upsetting nature's homeostasis with respect to functional requirements which have developed in each species over its evolutionary history.

From a meat producer's point of view, a superior carcass is characterized by a high proportion of muscle, low proportion of bone and an optimal level of fatness (Berg and Butterfield, 1976). For several decades now, and particularly in the second half of the present century, man has been trying to "build" an animal with the above characteristics.

Bone, muscle and fat perform different, though integrated, functions in the animal's body. Their growth, development and distribution patterns as such differ from one another. The order of maturation of these tissues is bone, muscle and fat, with only fat approaching its maximum weight at a relatively faster rate than the whole body during the final stages of growth (Black, 1988).

Berg and Butterfield (1976) stated that in cattle the growth patterns of the tissues are such that bone grows at a steady but slow rate, and muscle grows relatively fast so that the ratio of muscle to bone increases. Fat comprises a relatively small amount of the carcass at birth, but eventually its growth rate increases so that it approaches, and occasionally in very fat animals, surpasses muscle in absolute amount (Berg and Butterfield, 1976; Marple, 1983). Thus muscle comprises a high percentage at birth, rises slightly, and begins to decrease in percentage as the fattening phase sets in. Therefore the proportion of muscle in a carcass varies indirectly with fat; a higher proportion of fat is associated with a lower proportion of muscle and vise versa. In fact Butterfield (1976) showed that fat being the most variable tissue has the greatest influence on the proportion of muscle. Similarly, he showed that fat also has the greatest influence on the proportion of bone.

The growth of the tissues relative to the body as a whole can be expressed mathematically with an equation $y = ax^b$, where y is the weight of the tissue (or any other part), a is a constant, x is the weight of the body, and the exponent b is the growth coefficient. This is the allometric equation developed by Huxley (1932), and in practice it is usually solved in the log form: $\log y = \log a + b.\log x$. If b has a value greater than 1.0, it means the part grows relatively faster than the whole body. Such parts are said to have a high impetus of growth and are late maturing. Those parts with the *b* value of less than 1.0 have a low impetus of growth and are early developing, while those with the *b* value of equal to 1.0 have an average impetus of growth; these grow at the same relative rate as the total body.

In this context, bone is classified as an early developing tissue; muscle is intermediate while fat is late developing. Berg and Butterfield (1976) noted that in cattle bone obviously must reach a level of development during ante-natal life which allows it to function at birth. On the other hand, muscle needs to function at birth, but at nowhere near the ultimate peak of efficiency of the young adult animal; it, therefore, has an intermediate degree of development at birth. The fat tissues are not as essential in early life and therefore are the least developed.

In general, Palsson (1955) and other workers have established the sequence in which the various body tissues grow relatively faster than the body as a whole. This order, considered over both pre- and post-natal life, is: Central Nervous System, Viscera, Bone, Muscle and Fat. Not only is there an order of development of different tissues, but similar changes can occur within various tissues (Butterfield, 1966; Pomeroy, 1978); for example each of the fat depots grows relatively faster at different stages of the fattening process.

3.1.3.1. Growth and development of bone

Bone makes up the skeletal system of the animal and its functions include the general support of the body, muscle attachment, locomotion, storage of macro-minerals such as calcium and phosphorus, and serve as site for the manufacture of red blood cells. It is therefore absolutely necessary that the skeletal system develops very early to support these vital functions.

The growth and development of bone is most often discussed in relation to the muscle since in meat production the desirable thing is maximum muscle and minimum bone. Berg and Butterfield (1976) and Berg and Walters (1983) stated that due to the early development of bone and later development of muscle, the ratio of muscle to bone at birth may be as low as 2:1. This ratio increases as the animal grows towards maturity; it can be as high as 5:1 at slaughter weight.

Studies of skeletal development in farm livestock have indicated that within species neither breed nor sex has a strong influence on the distribution of bones in the skeleton, and that the weights of individual bones retain a close allometric relationship with each other, and with the total weight of the skeleton (Berg and Butterfield, 1976).

3.1.3.2. Growth and development of muscle

Muscle is the most desirable carcass component from a meat producer's point of view. However, from an animal's point of view, muscle is there to perform certain functions that are vital to its survival. The muscle's major functions include contraction, locomotion, storage of protein, its metabolism and the metabolism of individual amino acids; energy metabolism from various substrates such as creatine phosphate, glucose and fats, and thermoregulation.

During the pre-natal stages of an animal, muscle grows mostly by the process of hyperplasia (Marple, 1983). This process is almost complete at birth, although it may continue for a few days in the immediate post-natal period (Berg and Butterfield, 1976). Therefore, the cells grow mostly by the process of hypertrophy in the post-natal period.

Being an intermediate developing tissue, muscle has a *b* value of 1.0. However, the growth patterns of muscles in different regions, and individual muscles within each regional grouping, differ. Some muscles are early developing, others are late developing while some are intermediate (Berg et al.,1978a; Bergstrom, 1978; Butterfield et al.,1983). For example, in sheep, study of individual muscles in Merino rams by Butterfield et al. (1983) revealed that most muscles in the distal parts of the hind limb were early developing. Muscles of the proximal limb were poorly developed at birth but grew relatively faster than total muscle in the immediate post-natal period.

3.1.3.3. The accumulation of fat

Fat is the most variable tissue in the animal's body (Marple, 1983). In fact, manipulation of the carcass composition by genetic or nutritional means depends largely on controlling the proportion of fat (Berg and Butterfield, 1976).

The major biological role of fat is the storage of energy in the form of triglycerides (Hood and Thornton, 1979). Fats provide the most concentrated source of energy of any foodstuff, supply essential fatty acids, contribute to the feeling of satiety after eating, are carriers of fat-soluble vitamins and serve to make other foods more palatable (Clandinin, 1984). Fat is also useful as an insulating layer against the cold. Although fat depots are primarily for energy storage or for mechanical and thermal insulation, they are far from passive (Marple, 1983; Swatland, 1984); they are dynamic and in a state of constant turnover. Anabolic processes are very active when an animal is depositing fat, while catabolic processes are very active when the animal is living off its reserves, either during prolonged feed restriction or between periods of feeding.

There is strong evidence that growing and even adult animals can recruit undifferentiated mesenchymal cells, which exist extensively throughout the connective tissue, to become adipocytes (Enser and Wood, 1978) although the ability to recruit in this way decreases markedly with age. The authors observed that as far as the fatty tissue is concerned, the growth of the fat depots up to slaughter is accompanied by an increase in size and number of fat cells. Somewhat similar findings were obtained by Kirtland and Harris (1980) who underfed a group of rats followed by rehabilitation. The authors found that rehabilitation of the animals from undernutrition stimulated the replication of fat cells which resulted in higher rates in all four depots examined. They suggested that one interpretation of the findings is that there is no finite period of hyperplasia of the adipose tissue; this would mean that replication could be initiated at any time in life, not only by a sudden excess of food, but by other circumstances such as "times of physiological deposition" of fat. Thus, the ability to store fat in adipocytes combined with the capacity to "recruit" cells, makes the animal's ability to store fat effectively limitless.

Berg et al. (1978b) studied the growth and distribution patterns of fat from eight different sire breeds of cattle. They found that the growth coefficients for fat in each joint studied were homogenous among breed groups, indicating similar fat development patterns over the weight range studied. The growth impetus for fat was lowest in the distal limbs and in the proximal hind limbs. Fat growth in the proximal fore limb was proportional to total fat. Along the dorsal line, low impetus was found in the neck and rump regions, increasing to a high impetus in the mid-back region. Ventrally the fat of the flank showed the highest growth impetus of all regions with fat in the brisket and flat ribs also showing an increasing proportion with increases in total fat. The authors also found that with increasing slaughter weight, the proportions of fat in the distal limbs, the round and the loin in the rib, flank and brisket rose; the proportions in the shoulder, fore rib and neck showed little change.

Such findings may be generalized to other breeds and species although there might be some specific differences. However, the important thing is that such results are a reflection of the differential development of fat distributed in various regions of an animal. This further reflects which parts are most and least affected during times of low nutrition.

3.1.3.4. The Fat Depots

The fat tissue may be partitioned into four major divisions called fat depots which grow at relatively different rates. These fat depots are defined as subcutaneous fat (SCF), intermuscular or seam fat (IMF), intramuscular or marbling fat (IaMF), and internal fat which includes all fat associated with the cavity and viscera of the body (e.g. kidney knob, channel, pelvic, heart fat, etc.). In cattle, the IMF and SCF depots comprise the major portions of carcass fat and typically account for approximately 80 percent of the total fat after the carcass contains 10kg or more of fat (Cianzio et al.,1982). Callow (1948) demonstrated that as cattle grow the carcass fat depots grow differentially with SCF having a higher impetus than IMF, a trend that has been observed in steers by Kempster et al. (1976) and Berg et al. (1978b).

That the different fat depots grow at relatively different rates has been demonstrated by several other workers (Davies and Pryor, 1977; Thompson and Barlow, 1981; Cianzio et al.,1982; Shahin and Berg, 1985a). Shahin and Berg (1985a) showed that in cattle IMF and carcass cavity fat (CCF) increased in weight at a slower rate and SCF at a faster rate relative to total fat. What could be deduced from these results is that SCF is a late developing depot while IMF and internal fat are early developing. On the contrary, however, Cianzio et al. (1982) reported that IMF is not an early developing depot and its contribution to total fat does not decrease as fattening progresses. Pothoven and Beitz (1973) found that in cattle, internal fat was deposited earlier than SCF and IMF. Cianzio et al. (1982) reported otherwise; they found that kidney and omental fats increased at the same rate as total fat in the body. The authors suggested that these internal fats should, therefore, not be considered as early developing tissues among fat depots. Kempster (1981) had earlier concluded that in cattle in the fattening phase, kidney knob and channel fat (KKCF) appears to grow more rapidly than IMF. He, however, pointed out that the growth of KKCF relative to other depots is more variable.

Such conflicting results are hard to explain since a lot of factors come into play. However, the growth coefficients for fat depots calculated by Trenkle (1983) from the data of Johnson et al. (1972) seem to be most reasonable. The following growth coefficients were found: IMF (Average); SCF (High-Average); Kidney fat (Low); Channel fat (Low). From these results, Trenkle (1983) concluded that SCF and IMF which include much of the fat trimmed from carcasses grow at faster rates relative to total carcass fat than does internal fat. Such an order of development of the fat depots may be evidenced from the experimental results involving fat depletion and recovery during periods of starvation followed by rehabilitation.

3.1.4. The major carcass tissues: general nutritional influence

Nutrition is perhaps the most important environmental factor which can affect growth (Malina, 1969). It is, no doubt, one of the most important factors influencing the growth and developmental patterns of the major carcass tissues. The fat tissue is the most affected by the plane of nutrition (Callow, 1961 for cattle; Fourie et al., 1970 for sheep; Richmond and Berg, 1971; Davies et al., 1980 for pigs). High plane of nutrition promotes earlier fattening while low plane delays the process. Callow (1961) slaughtered animals from four planes of nutrition and found a significant difference in the percentage of fat in the carcass; the animals on the high plane in the final feeding period had fatter carcasses than those on the moderate plane. McMeekan (1940) had similar findings in his classical experiment with pigs. From the different planes of nutrition, he found that low plane pigs had a higher percentage of bone, muscle, skin and tendon but a lower percentage of fat. Of the three major tissues, bone was affected least, muscle next and fat most.

Thus when feed restriction is imposed, the relative growth of bone, muscle and fat is altered under weight loss (Berg and Butterfield, 1976). The depletion of fat is the most rapid, and the degree of involvement of muscle and the bone depends on the severity and length of time of the undernutrition. Realimentation results in an increase in muscle towards a point of normal muscle to bone relationship, while the recovery of fat is given low priority.

3.1.4.1. Effect of feed restriction and refeeding on the skeletal system

Bone is in a state of active turnover throughout life, and as such the body is able to use it as a mineral store. Under conditions of negative mineral balance, the body can demineralize the bone to some extent, so that the body weight loss can, in extreme situations, be accompanied by some bone weight loss (Price, 1977). The actual bone weight loss rarely occurs unless the severity and duration of undernutrition is extreme. In normal situations of body weight loss, bone weight loss is insignificant (McCay et al., 1939; McAnulty, 1977). When feed restriction is imposed on an animal, it has been found that skeletal system in fact continues growing for some time while fat and muscle are being depleted (McAnulty, 1977).

McCay et al. (1939) showed that in undernourished rats, the body length had a better ability to recover than the body weight. The authors suggested that the superior capacity of the body length to recover compared with that of the body weight suggests that skeletal dimensions are either relatively spared during undernutrition or else they have greater recuperative powers than the other parameters of body size and mass. The authors measured the lengths of various limb bones and found that bone length continued to increase during undernutrition, and also increased in response to rehabilitation.

Comparison of body length of rehabilitating animals with that of normal animals of the same body weight revealed that the rehabilitating animals were consistently longer than the controls. The authors, however, noted that this probably does not represent a true increase in length over the controls, but reflects a failure of the rehabilitating animals to accumulate adipose tissue; this is important, for it suggests that the relationship between body length and body weight is not dependent upon either parameter, but stems from a central regulatory mechanism affecting each parameter.

In a study of compensatory growth in male rats, McAnulty (1977) underfed the experimental group for 85 weeks, keeping the body weight constant. He found that the skeleton continued to grow during the first seven weeks of undernutrition, but thereafter only the caudal half of the pelvic girdle continued to grow. On rehabilitation of the animals, all the skeletal dimensions increased, and all eventually reached the normal range of mature skeletal dimensions.

Similar findings have been shown in pigs (McMeekan, 1940) and sheep (Hight and Barton, 1965). McMeekan (1940) showed that the relative effect of plane of nutrition upon the total skeleton of pigs at the age of 16 weeks was less than on the other tissues. He observed that the effect of the differences in nutrition increased from head to tail, with the head bones the least affected and the pelvis the most affected. In their experiment with four- and five-year old ewes, Hight and Barton (1965) found that the total weight of bones did not appear to be sensitive to either undernutrition or realimentation. Information on the influence of nutrition on the skeletal length of beef heifers is lacking and therefore needs to be established.

3.1.4.2. Effect of feed restriction and refeeding on the muscular tissue

In a fasting animal protein degradation in muscle may exceed the process of synthesis, or the latter process may simply be slowed down (Muramatsu et al.,1987). If fasting is prolonged over a period of time, the ultimate result is more catabolism of the protein tissue leading to muscle depletion and consequently weight loss. During weight loss, the later developing muscles are affected most while the early developing muscles are affected least; this is in the reverse order of their development. Refeeding reverses the situation back to the order of development. In this context, Berg and Butterfield (1976) suggested that Hammond's (193[illegible] principle that "during starvation it would appear that the organs with an early period of maximum growth can draw on, or have prior claim, on the nutrition of those having a later period of growth" can be applied. Thus, muscles of the high growth impetus should be most affected by muscle weight loss; average impetus muscles should be affected to the same degree as total muscle, and low impetus muscles should be less affected than total muscle.

McMeekan (1940), for example found that by imposing feed restriction on pigs, the muscles of the head were relatively affected least and the loin most, with neck and thorax intermediate. The pelvis muscles were affected slightly less than those of the loin. Within the limb muscles, he found that the various units in both the fore- and hind-limbs showed a gradient in the effect between the lower and upper parts. The muscles around the cannon bone were least affected while those of the shoulder and thigh, in fore- and hind-limb respectively, showed the greatest effect. Muscles of the arm and leg were intermediate between these.

3.1.4.3. Effect of feed restriction and refeeding on the fat tissue

Like other carcass tissues, fat depots follow an order of depletion during starvation, opposite to the direction of their development. The high growth impetus tissues are depleted first while the low impetus tissues are the last to be utilized. The animal spares the most vital depots for its survival in emergencies, particularly during starvation.

Kirtland and Harris (1980) working with rats found that in undernourished animals, fat cell replication was slow in SCF depot compared with well nourished animals of the same age. Similarly, in his study with Poll Hereford steers, Butterfield (1966) found that during the fat depot loss, the SCF was the most affected, followed by the IMF and then kidney knob and channel fat (KKCF). It was in fact found that proportionately most fat was being taken away from the areas where most would normally have been added. Berg and Butterfield (1976) noted that the amount used from each depot must depend on the amounts available, and once a depot reaches a very low level, as did the SCF in Butterfield's (1966) study, then a much higher proportion of the needs must come from the other depots which are still not approaching depletion. The data from Butterfield's (1966) study support the idea that for the animal under recovery from undernutrition, the tendency is to replenish other fat stores before rebuilding the SCF depot.

Nutrition, therefore, has a big effect on the proportion of fat and its manipulation can result in either "fat" or "lean" carcasses. Of course several other factors cannot be ignored in interpreting the final results of the carcass composition.

With all this information on meat and non-meat animals undergoing catch-up growth, and general growth and development of the major carcass tissues, it should be interesting to look at the pattern and degree of compensation of these tissues in young heifers undergoing catch-up growth.

3.1.5. Factors affecting carcass composition in catch-up growth

Many factors influence carcass composition. These include genetic, nutritional, developmental and experimental design factors including feed restriction and realimentation times, slaughter weight and age. An understanding of the final outcome of the experiment must take into consideration the effects of all contributing factors.

Levy et al. (1971) working with Israeli-Friesian bull calves found that nutritionally restricted animals produced carcasses with 10-20 percent less kidney, pelvic and cod fat; 20 percent less trim; 3-6 percent more bone; and a slightly higher proportion of saleable meat. Fox et al. (1972) found that cattle undergoing catch-up growth slaughtered at 364 kg with the controls were leaner but there was no difference in carcass composition when both groups were slaughtered at 454 kg. In another study, Drennan (1979) put his weanling cattle (9 and 14 months of age) on three planes of nutrition (low, moderate, and high). At the end of 149 days, he observed that while it appeared that short periods of uninterrupted growth did not have any effect on the carcass composition, restriction causing major delays in reaching the fixed slaughter weight did not result in higher proportion of bone, a trend that Levy et al. (1971) had found.

Earlier, Butterfield (1966) had suggested that cattle which undergo semi-starvation at more mature ages have a larger proportion of muscle to fat in their weight gain during recovery than have calves submitted to similar treatments. In similar lines, Berg and Butterfield (1976) postulated that at the same live weight, the proportion of fat in carcasses of starved and then realimented cattle would usually be less than those on uninterrupted growth. The authors noted that if the weight loss occurs in the early stages of growth before rapid fattening normally takes place, compensation would be complete and normal proportions of fat, muscle and bone will result for given weights, even though the external appearance of the animals may suggest extreme changes in composition.

Meyer and Clawson (1964) found that their five-month old sheep that were starved for various periods and then refed were fatter than controls. The authors also observed that as the severity of undernutrition increased, the compensatory animals had difficulty in compensating. On the other hand, McManus et al. (1972) found that their five- to six-month old sheep laid down less body fat, more protein and retained more water in their bodies following a short period of undernutrition and then refeeding. Similar results were obtained by Drew and Reid (1975) who imposed a severe undernutrition on immature sheep. The workers found that during early regrowth, there was a marked stimulus of lean tissue growth and depressed fat synthesis, although this kind of response was reduced as the realimentation progressed.

In a catch-up growth study of both mature and immature sheep, Thornton et al. (1979) found that the amount of fat in meat of starved mature sheep was greater than controls at similar body weight. On the other hand, starved immature sheep were leaner than their control counterparts, following realimentation. The loss of fat from the meat of immature sheep was associated with both atrophy and hypoplasia of the SCF adipose cells, but in mature sheep there was atrophy without hypoplasia of these adipose cells. The authors observed that although the greatest loss of fat was from the meat, proportionately more fat was lost from the offal, particularly in immature sheep. They concluded that although the age of the animals may be a factor contributing to the disparity of findings in their experiment, it is clear from other studies that empty body weight at slaughter is the most critical base factor for the comparisons of body composition.

McMeekan (1940) found that refed pigs (after feed restriction from birth to 16 weeks of age) had less muscle and more fat in the carcass at 90kg than pigs continuously fed. Lately, Mersmann et al. (1987) found that following refeeding, the animals that were put on feed restriction at light weights (48kg) had fatter carcasses than controls at constant weight. Feed restriction at heavier weights (66kg) resulted in pigs that were leaner, more muscular and had larger skeletal mass than the fed pigs, at constant weight.

It is evident from these results that the composition of the animal's body is in a dynamic state which is constantly changing in response to alterations of internal and external environments.

Several factors are responsible for the differences among experiments in terms of carcass composition. O'Donovan (1984) suggested the most important factors at the root of such variable reponses as follows:

1. Animals differing in age, live weight and maturity, particularly with various breeds represented.
2. Stage of growth and condition (ratio of fat:lean:bone) of experimental animals.
3. Severity (i.e. above, at or how far below maintenance) and duration of restriction.
4. Rates of gain during, and length of, the recovery period.
5. Type of the feed offered, i.e. dry roughages or pasture and concentrate ingredients.
6. Level of energy, protein and possibly other nutrients in the concentrate.
7. Stage of maturity when slaughtered for carcass determination.

These factors together with those affecting recovery of the animals (Wilson and Osbourn 1960) are important in determining the carcass composition of the animal at slaughter. Although O'Donovan (1984) seemed skeptical about data interpretation due to either the additive or antagonistic nature of the above factors, a full consideration and a full understanding of the physiology of growth and development of the major carcass tissues can, lead to meaningful conclusions.

3.2. MATERIALS AND METHODS

3.2.1. Slaughter and determination of carcass composition

On the day before slaughter, the animals were fasted and trucked about 15 km to a commercial packing plant in Edmonton where they were slaughtered the following day in the normal commercial manner.

Fresh weights of the liver and kidneys from each carcass were measured soon after bleeding and removal of the viscera. The livers were also checked for abscesses. Internal fat (i.e. fat within the body cavity from the pelvis up to the heart region, excluding that from the internal surfaces of the ribs) was also removed and weighed fresh.

The carcasses were shrouded and chilled (1-3 C) overnight. The shrouds were removed the following morning, left sides of the carcasses quartered between the 12th and 13th ribs, and Agriculture Canada graders provided an appraisal for each carcass. The appraisal consisted of warm carcass weight, area of the longissimus (rib eye area) at the quartering position with the aid of a grid marked in 1.6 cm^2 units, marbling score (range 1-10, higher numbers mean less visible marbling), fat cover at three positions over the longissimus muscle at the quartering position (average fat), and the overall grade of the carcass. The carcass length was then measured on the unquartered right side from the anterior edge of the pubic bone to the junction of the seventh cervical and first thoracic vertebrae as described by Yeates (1952).

After carcass appraisal, a standard 10-11-12th rib joint was removed from the left side of all the carcasses. The rib sections, together with two left sides that had been pre-selected based on the pen average weight of the live animals (viz: those closest to the mean) were taken back to the University's Meat Laboratory for carcass composition determination. The rib joints were trimmed according to the method described by Hankins and Howe (1946), and separated into muscle, bone and fat. Fat was further separated into individual depots: subcutaneous fat (SCF) and intermuscular fat (IMF). Fat on the internal surfaces of the rib joints was included as IMF. The weight of each component was recorded.

The left sides were similarly physically separated into individual components (muscle, bone and fat) and fat was further separated into SCF and IMF. The raw data from the two corresponding rib joints for each treatment were added back to the data of their respective sides to determine physical composition of those sides.

3.2.2. Statistical analysis

The non-carcass components (livers, kidneys and internal fat) had their weights expressed as percentages of slaughter weights for each treatment. For carcass components, the weight of each 3-rib joint and left side was taken as the summation of the weights of its separated components, and similarly total fat weight was taken as the summation of individual fat depot weights. Individual weights of muscle, bone and total fat were computed as percentages of the weight of either the rib joint or the left side. Fat depot weights were computed as percentages of the weight of total fat in 3-rib joints and left sides.The correlations between 3-rib joints and sides transformed data were then computed to quantify the relationship between them. This was to give an indication of how good the estimates of carcass composition from the 3-rib joints were, compared to whole carcass tissue composition.

Analysis of variance for all the rib joint carcass components and non-carcass characteristics was done according to the model described under section 2.2.3. Logarithms of slaughter weight, liver weight, internal fat weight and 3-rib joint weight and all its component weights were computed to allow allometric regression. Then liver weight and internal fat weight were regressed on slaughter weight from the start of refeeding for each treatment, and slopes compared using either the *t-test* (ad lib fed vs 2-month restricted-refed animals, considered over three periods) or the SNK range test (comparing all the three treatments over the last two periods). The 3-rib joint components (muscle, bone and fat) were regressed on 3-rib joint weight while the individual fat depots were regressed on 3-rib joint total fat weight from the start of refeeding for each treatment and slopes compared as above.

3.3. RESULTS AND DISCUSSION

3.3.1. The non-carcass components: liver, kidney and internal fat

The weights of the liver and internal fat were significantly lowered ($P<0.05$) by 2 months feed restriction while kidney weight was not affected (Table 3.1). It can be seen that the mean liver weight of the R0F2 group was 32% heavier ($P<0.05$) than the INIT group while that of the R2F0 group was not different from the INIT group. This perhaps comforms with the statement made by Widdowson and McCance (1956) that "If the animal is deprived of food, the loss in weight of the liver is relatively greater than that of the rest of the body; similarly if the undernutrition is less severe and more prolonged the findings may be similar but the relative difference between the loss in the weight of the liver and that of the rest of the body tends to be less". This response of livers in the restricted animals is probably an indication of the high degree of metabolic activity of this organ. This is also in line with Goss's (1978) statement that internal organs such as the GIT and liver can show a rapid and considerable variation in size due to actual functional demand.

Kidney weight was not affected ($P>0.05$) to a significant degree by any nutritional treatment. In fact no significant change in the weight of this organ was found in either the R0F2 or R2F0 animals, taking the INIT group as the baseline. Reports in rats (Hegarty and Kim, 1980), rabbits (Asghar et al., 1981), pigs (Koong et al., 1985) and growing lambs (Ferrell et al., 1986) have shown significant decreases in the absolute weight of kidneys in animals subjected to nutritional restrictions. However, Widdowson et al. (1960) reported

TABLE 3.1. LEAST SQUARES MEANS ± STANDARD ERRORS OF THE NON-CARCASS COMPONENTS OF HEIFERS FED FOR 2 MONTHS

Item	INIT[a]	R0F2[b]	R2F0[c]	Probability
No. of animals	5	6	6	
Slaughter wt, kg	211 ± 17[d]	296 ± 23[e]	246 ± 12[e]	0.02
Liver wt, kg	3.4 ± 0.1[d]	4.5 ± 0.4[e]	2.9 ± 0.9[e]	0.002
Kidney wt, kg	0.6 ± 0.1	0.7 ± 0.1	0.5 ± 0.1	0.17
Internal fat, kg	2.1 ± 0.4[d]	2.7 ± 0.4[d]	1.5 ± 0.2[e]	0.04
Liver(%)[f]	1.7 ± 0.2[d]	1.5 ± 0.1[d]	1.2 ± 0.1[e]	0.08
Kidney(%)[f]	0.28 ± 0.05	0.23 ± 0.03	0.2 ± 0.03	0.33
Internal fat(%)[f]	1.0 ± 0.1[d]	0.9 ± 0.1[d]	0.6 ± 0.05[e]	0.03

[a] Animals slaughtered at d 1 (25 d after weaning).

[b] Animals fed ad libitum for 2 mo.

[c] Animals restricted for 2 mo.

[d,e] Means within a row with different superscripts differ ($P<0.05$).

[f] Component weight expressed as percentage of slaughter weight.

that in pigs the absolute weight of the kidneys in restricted animals was about the same as in their control groups, although in their study the weight of the organ increased with the weight of the body. In the present study the weight of the kidneys in all the animals remained similar despite the significant increase in body weight of both the R0F2 and R2F0 groups.

The mean weight of internal fat in the R2F0 animals was lower (P<0.05) than that in the R0F2 and INIT animals. Having been subjected to feed restriction, it was not surprising that the R2F0 animals had a lesser amount of internal fat. Generally, fat is the most affected component of all the tissues in the body when feed restriction is imposed (Berg and Butterfield, 1976). Although internal fat is an early developing depot (Pothoven and Beitz, 1973), and is affected to a lesser degree (Butterfield, 1966) than the other fat depots, results of the present study showed a significant depletion of this depot in feed restricted animals, possibly because the other fat depots were not yet fully developed.

Expressed as percentages of the slaughter weight, the livers of the R2F0 animals formed a smaller (P<0.05) proportion of their body weight than either the R0F2 or the INIT animals (Table 3.1). This is contrary to the results observed in pigs by Widdowson et al. (1960) who reported that the livers of the smallest undernourished animals formed a larger proportion of their body weight. However, the present findings confirm the earlier reports (Widdowson and McCance, 1956) that when animals are undernourished, the loss in weight of the liver is relatively larger than the rest of the body.

Kidney weight expressed as a percentage of slaughter weight behaved much the same as the absolute weight, and no difference ($P>0.05$) among treatments was found at the end of the first period.

Like percent liver, percent internal fat was found to be lower ($P<0.05$) in the R2F0 animals than in either the R0F2 or INIT animals, reflecting the effect of feed restriction.

The effect of 4 months feed restriction followed a similar trend to that of 2 months feed restriction for all three components (Table 3.2). Mean liver weight in the R4F0 group was not significantly different from the INIT animals, while that of the R0F4 and R2F2 groups was significantly heavier ($P<0.05$). Thus the mean liver weight of the R2F2 animals had already caught up with the R0F4 animals by the end of the second period, indicating the rapid response and recovery of this organ following increased feed intake.

Mean kidney weight again showed little effect of either feed restriction or realimentation, and there was no difference ($P>0.05$) among treatments after 4 months. This is contrary to the report in pigs (Widdowson et al., 1960) that the absolute weight of this organ increases with the weight of the body during normal growth and development. Perhaps, since the kidney is an early developing organ and seems resistant to nutritional stress, it is possible that the periods of 2 and 4 months of feed restriction were too short to test this hypothesis for cattle.

Internal fat weight was affected to a high degree at the end of the second period. There was a large depletion of this fat depot in the R4F0 animals resulting in a lesser ($P<0.05$) amount of the fat in

TABLE 3.2. LEAST SQUARES MEANS ± STANDARD ERRORS OF THE NON-CARCASS COMPONENTS OF HEIFERS FED FOR 4 MONTHS

Item	INIT[a]	R0F4[b]	R2F2[c]	R4F0[d]	Probability
No. of animals	5	6	6	6	
Slaughter wt, kg	211 ± 17^{e}	343 ± 4^{f}	314 ± 7^{f}	244 ± 12^{e}	0.001
Liver wt, kg	3.4 ± 0.1^{e}	4.9 ± 0.1^{f}	4.8 ± 0.2^{f}	3.0 ± 0.2^{e}	0.001
Kidney wt, kg	0.6 ± 0.1	0.7 ± 0.1	0.6 ± 0.0	0.6 ± 0.1	0.35
Internal fat, kg	2.1 ± 0.4^{e}	5.4 ± 0.3^{f}	2.9 ± 0.6^{g}	1.4 ± 0.3^{h}	0.001
Liver(%)[i]	1.7 ± 0.2^{e}	1.4 ± 0.0^{ef}	1.5 ± 0.1^{ef}	1.2 ± 0.1^{f}	0.05
Kidney(%)[i]	0.28 ± 0.05	0.2 ± 0.0	0.2 ± 0.0	0.21 ± 0.02	0.06
Internal fat(%)[i]	1.0 ± 0.1^{e}	1.6 ± 0.1^{f}	0.9 ± 0.2^{e}	0.6 ± 0.1^{e}	0.001

[a] Animals slaughtered at d 1 (25 d after weaning).

[b] Animals fed ad libitum for 4 mo.

[c] Animals restricted for 2 mo followed by refeeding for 2 mo.

[d] Animals restricted for 4 mo.

[e,f,g,h] Means within a row with different superscripts differ ($P<0.05$).

[i] Component weight expressed as percentage of slaughter weight.

these animals than in the INIT animals. Meanwhile, the R2F2 group had accumulated more fat and the amount was greater ($P<0.05$) than in the INIT group. The R0F4 animals had the greatest ($P<0.05$) amount of internal fat of all the treatments. According to Butterfield (1966), internal fat is supposed to be more 'essential' to the immediate survival of the animal than the subcutaneous and intermuscular fat depots. Therefore, during feed restriction, internal fat is supposed to be spared to a greater extent than the other depots. In the present study, however, both 2 and 4 months feed restriction resulted in a significant depletion of this fat depot. As pointed out earlier, it is possible that the other fat depots were not yet fully developed and this is evident from the initial estimate of the back fat thickness in live animals (refer to chapter 2). This could have resulted in the restricted animals resorting to utilizing the internal fat as an energy reserve, particularly in the second period when the animals were held at a zero rate of gain. This could have led to the observed significant depletion of this fat.

Expressing the weights of liver and kidney as percentages of slaughter weight gave similar results to those obtained at the end of the first period. For percent liver, the R4F0 animals had the lowest ($P<0.05$) proportion while INIT animals had the highest proportion. The R0F4 and R2F2 animals were intermediate and were not different from each other. As for internal fat, the R0F4 animals had a higher ($P<0.05$) proportion than the rest.

At the final slaughter weight, the mean liver weight of the refed R4FM group was greater ($P<0.05$) than that of the R0FM group while that of the R2FM group was not significantly different from either group (Table 3.3). This may not be surprising considering that the feed intake of the R4FM animals during refeeding was much higher than the R0FM animals. As suggested earlier, the liver responded by an increase in size and since the feed intake remained high up to the time of slaughter, the liver also remained in that 'expanded' position to cope with the work load. The mean kidney weight was similar ($P>0.05$) in all the treatments.

The amount of internal fat was less ($P<0.05$) in the R4FM animals than in the R0FM animals while the R2FM animals were intermediate and not significantly different from either group. It can be seen that internal fat did not recover completely, and it is not clear why. Most probably when the animals were refed, most of the extra energy was simply stored under the skin as subcutaneous fat rather than being deposited internally.

When the component weights were expressed as percentages of the slaughter weight, the liver weight of the refed R4FM animals made a larger ($P<0.05$) proportion of the body weight than the R0FM and the R2FM animals. No significant differences ($P>0.05$) were found among the treatments in percent kidney. On the other hand, percent internal fat was higher ($P<0.05$) in the R0FM animals than in the refed R2FM and R4FM animals, meaning that catch-up was not complete in this depot.

Figures 3.1, 3.2, and 3.3 illustrate the overall growth in weight of the liver, kidney and internal fat respectively. It can clearly be seen that the liver weight of the R4FM animals increased

TABLE 3.3. LEAST SQUARES MEANS ± STANDARD ERRORS OF THE NON-CARCASS COMPONENTS OF HEIFERS AT ABOUT 400 kg

Item	R0FM[a]	R2FM[b]	R4FM[c]	Probability
No. of animals	6	6	6	
Slaughter wt, kg	414 ± 19	419 ± 13	408 ± 13	0.88
Liver wt, kg	4.3 ± 0.3[d]	5.3 ± 0.3[de]	5.8 ± 0.2[e]	0.04
Kidney wt, kg	0.8 ± 0.05	0.7 ± 0.05	0.8 ± 0.03	0.40
Internal fat, kg	7.7 ± 0.7[d]	5.6 ± 0.7[de]	4.6 ± 0.7[e]	0.02
Liver(%)[f]	1.2 ± 0.03[d]	1.2 ± 0.1[d]	1.4 ± 0.1[e]	0.01
Kidney(%)[f]	0.2 ± 0.0	0.2 ± 0.02	0.2 ± 0.0	0.12
Internal fat(%)[f]	1.8 ± 0.1[d]	1.3 ± 0.1[e]	1.1 ± 0.1[e]	0.005

[a] Animals fed ad libitum throughout to final slaughter weight.

[b] Animals restricted for 2 mo followed by refeeding to final slaughter weight.

[c] Animals restricted for 4 mo followed by refeeding to final slaughter weight.

[d,e] Means within a row with different superscripts differ ($P<0.05$).

[f] Component weight expressed as percentage of slaughter weight.

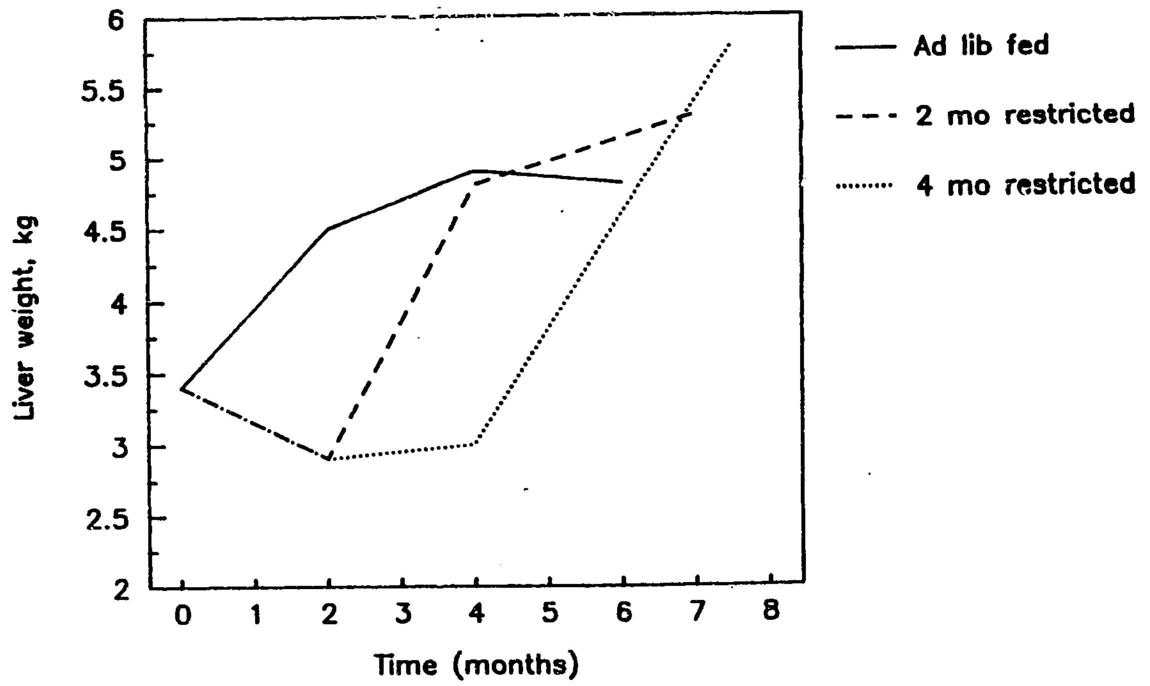

Figure 3.1. Change in the mean liver weight over time from ad lib, 2 mo and 4 mo feed restriction of heifers followed by refeeding to about 400 kg.

Maynard, L. A., Loosli, J. K., Hintz, H. F. and Warner, R. G. 1979. Retardation of growth. pp422-424. In: Animal Nutrition. Tata McGraw-Hill, New Delhi.

McAnulty, P. A. 1977. Growth and skeletal development of the rat during prolonged undernutrition and subsequent rehabilitation. Acta Anat. 98:39-51.

McCay, C. M., Maynard,G.A., Sperling,G. and Barnes,L.L. 1939. Retarded growth, life span, ultimate body size and age changes in the albino rat after feeding diets restricted in calories. J. Nutr. 18:1-13.

McManus, W R., Reid, J. T. and Donaldson, L. E. 1972. Studies of compensatory growth in sheep. J. Agric. Sci. (Camb.) 79:1-12.

McMeekan, C. P. 1940. Growth and development in the pig with special reference to carcass quality characters. I,II,III. J. Agric. Sci. (Camb.) 30:276-344, 387-436, 511-569.

Mersmann, H. J., MacNeil, M. D., Seideman, S. C. and Pond, W. G. 1987. Compensatory growth in finishing pigs after feed restriction. J. Anim. Sci. 64:752-764.

Meyer, J. H. and Clawson, W. J. 1964. Undernutrition and subsequent realimentation in rats and sheep. J. Anim. Sci. 23:214-224.

Meyer, J. H., Hull, J. L., Weitkamp, W. H. and Bonilla, S. 1965. Compensatory growth responses of fattening steers following various low energy intake regimes on hay or irrigated pasture. J. Anim. Sci. 24:29-37.

Miller, M. F., Cross, H. R. and Crouse, J. D. 1987. Effect of feeding regimen, breed and sex condition on carcass composition and feed efficiency. Meat Sci. 20:39-50.

Moody, W. G. and Cassens, R. G. 1968. Histochemical differentiation of red and white muscle fibers. J. Anim. Sci. 27: 961-968.

Moody, W. G., Kemp, J. D., Mahyuddin, M., Johnston, D. M. and Ely, D. G. 1980. Effect of feeding systems, slaughter weight and sex on histological properties of lamb carcasses. J. Anim. Sci. 50: 249-256.

Morgan, J. H. L. 1972. Effect of plane of nutrition in early life on subsequent liveweight gain, carcass and muscle characteristics and eating quality of meat in cattle. J. Agric. Sci. (Camb.) 78:417-423.

Mosier, H. D. 1986. The control of catch-up growth. Acta Endocr. 113(S279):1-7.

Muramatsu, T., Aoyagi, Y., Okumura, J. and Tasaki, I. 1987. Contribution of whole-body protein synthesis to basal metabolism in layer and broiler chikens. Br. J. Nutr. 57:269-277.

Murray, D. M. 1980. The effect of three different growth rates on feed utilization of cattle. Aust. J. Agric. Res. 31:1139-1145.

Murray, D. M., Tulloh, N. M. and Winter, W. H. 1974. The effect of three different growth rates on empty body weight, carcass weight and dissected carcass composition of cattle. J. Agric. Sci. 82:535-547.

National Research Council (NRC), 1984. Nutrient requirements of beef cattle. Sixth revised edition. National Academy Press, Washington D.C.

Ocken, D. A. and Grunewald, K. K. 1988. The Effects of exercise on catch-up growth of rats recovering from undernutrition. J. Nutr. 118:1410-1416.

O'Donovan, P. B. 1984. Compensatory gain in cattle and sheep. A review. Nutr. Abs. Rev. Series B. pp389-410.

Palsson, H. 1955. Conformation and body composition. In: J.Hammond (ed). Progress in the physiology of farm animals. Vol.2. pp430-542. Butterworths, London.

Park, C. S, Erickson, G. M. Choi, Y. J. and Marx, G. D. 1987. Effect of compensatory growth on regulation of growth and lactation: response of dairy heifers to a stair-step growth pattern. J. Anim. Sci. 64:1751-1758.

Perry, T. W., Huber, D. A., Mott, G. O., Rhykerd, C. L. and Taylor, R. W. 1972. Effect of level of pasture supplementation on pasture, drylot and total performance of beef cattle. Spring plus pasture. J. Anim. Sci. 34: 647-652.

Pokniak, J. A. and Cornejo, S. B. 1982. Effects of energy and protein undernutrtion on productive performance and carcass, liver and digestive tract composition of broiler males. Nutr. Rep. Int. 26:319-327.

Pomeroy, R. W. 1978. Historical and general review of growth and development. pp 3-11. In: H. De Boer and J. Martin (Eds.) Patterns of growth and development in cattle. Martinus Nijhoff. The Hague.

Pond, W. G. and Mersmann, H. J. 1990. Differential compensatory growth in swine following control of feed intake by a high-alfalfa diet fed ad libitum or by limited feed. J. Anim. Sci. 68:352-362.

Pothoven, M. A. and Beitz, D. C. 1973. Effect of adipose tissue site, animal weight and long-term fasting on lipogenesis in the bovine. J. Nutr. 103:468-475.

Price, M. A. 1976. Changes in body composition associated with weight loss in early- and later-maturing types of steers. Aust. J. Agric. Res. 27:729-738.

Price, M. A. 1977. The effects of severe feed restriction on bulls and steers. II. Carcass composition. Aus. J. Agric. Res. 28:529-541.

Rahelic, S. and Puac, S. 1981. Fiber types in longissimus dorsi from wild and highly selected pig breeds. Meat Sci. 5: 439-450.

Reid, I. M., Baird, G. D. and Heitzman, R. J. 1977. Effects of fasting in non-lactating cows. A correlated biochemical and stereological study of fasting-induced fatty liver. J. Agric. Sci. (Camb) 89:319-325.

Reid, I. M., Roberts, J. C. and Baird, G. D. 1980. The effects of underfeeding during pregnancy and lactation on structure and chemistry of bovine liver and muscle. J. Agric. Sci. 94: 239-245.

Richmond, R. J. and Berg, R. T. 1971. Tissue development in swine as influenced by liveweight, breed, sex and ration. Can. J. Anim. Sci. 51:31-39.

Saubidet, C. L. and Verde, L. S. 1976. Relationship between live weight, age and dry matter intake for beef cattle after different levels of food restriction. Anim. Prod. 22:61-69.

Schanbacher, B. D., Fletcher, P. W. and Reichert, L. E. Jr. 1987. Testicular compensatory hypertrophy in the hemicastrated calf: effects of exogenous estradiol. Biol. Reprod. 36:1142-1148.

Seebeck, R. M. 1983. The dependance of lean carcass composition on carcass fat, as assesed by multivariate shape/size methods. Anim. Prod. 37:321-327.

Seideman, S. C. and Theer, L. K. 1986. Relationships of instrumental textural properties and muscle fiber types to the sensory properties of beef. J. Food Quality 9: 251-261.

Shahin, K. A. and Berg, R. T. 1985a. Fat growth and partitioning among the depots in double muscled and normal cattle. Can. J. Anim. Sci. 65:295-306.

Shahin, K. A. and Berg, R. T. 1985b. Growth and distribution of muscle in double muscled and normal cattle. Can. J. Anim. Sci. 65:307-318.

Solomon, M. B., Campbell, R. G., Steele, N. C., Caperna, T. J. and McMurtry, J. P. 1988. Effect of feed intake and exogenous porcine somatotropin on longissimus muscle fiber characteristics of pigs weighing 55 kilograms live weight. J. Anim. Sci. 66:3279-3284.

SPSSx Guide. 1988. 3rd Ed. SPSSx Inc., New York.

Staun, H. 1963. Various factors affecting number and size of muscle fibers in the pig. Acta Agr. Scand. 13:293-322.

Staun, H. 1972. The nutritional and genetic influence on number and size of muscle fibers and their response to carcass quality in pigs. World Rev. Anim. Prod. 8:18-26.

Suzuki, A. and Cassens, R. G. 1983. A histochemical study of myofiber types in the serratus ventralis thoracis muscle of sheep during growth. J. Anim. Sci. 56: 1447-1458.

Swatland, H. J. 1984. Structure and development of meat animals. Prentice-Hall, Inc, Englewood Cliffs

Tatum, J. D., Klein, B. J., Williams, F. L. Jr., and Bowling, R. A. 1988. Influence of diet on growth rate and carcass composition of steers differing in frame size and muscle thickness. J. Anim. Sci. 66:1942-1954.

Thompson, J. M. and Barlow, R. 1981. The effect of sire breed on the partitioning of dissectible fat in steer carcasses. J. Agric. Sci. (Camb.) 96:699-701.

Thomson, E. F., Bichel, H. and Schurch, A. 1982. Growth performance and metabolic changes in lambs and steers after m[illegible] nutritional restriction. J. Agric. Sci. (Camb.) 98:183-194.

Thornton, F., Hood, R. L., Jones, P. N. and Re, V. M. 1979. Compensatory growth in sheep. Aust. J. Agric. Res. 30:135-151.

Trenkle, A. 1983. The influence of nutrition on growth of beef cattle. Proc. of the Growth Management Conference. pp18-25.

Tuma, H. J., Venable, J. H., Wuthier, P. R. and Henrickson, R. L. 1962. Relationship of fiber diameter to tenderness and meatiness as influenced by bovine age. J. Anim. Sci. 21:33-36.

Turgeon, O. A. Jr., Brink, D. R., Bartle, S. J., Klopfenstein, T. J. and Ferrell, C. L. 1986. Effects of growth rate and compensatory growth on body composition in lambs. J. Anim. Sci. 63:770-780.

West, R. L. 1974. Red to white muscle fiber ratios as an index of double muscling in beef cattle. J. Anim. sci. 38:1165-1175.

Waters, H. J. 1908. The capacity of animals to grow under adverse conditions. 29th Proc. Soc. Prom. Agric. Sci. 29: 71-96.

White, N. A., McGavin, M. D. and Smith, J. E. 1978. Age-Related changes in percentage of fiber types and mean fiber diameters of the ovine quadriceps muscles. Am. J. Vet. Res. 39: 1297-1302.

Whittemore, C. T., Tullis, J. B. and Hastie, S. W. 1978. Efficiency of use of nitrogen from dried microbial cells after a period of N deprivation in growing pigs. Br. J. Nutr. 39:193-200.

Widdowson, E. M., Dickerson, J. W. T. and McCance, R. A. 1960. Severe undernutrion in growing and adult animals. 4. The impact of severe undernutition on the chemical composition of the soft tissues of the pig. Br. J. Nutr. 14:457-471.

Widdowson, E. M. and McCance, R. A. 1956. The effects of chronic undernutrition and of total starvation on growing and adult rats. Br. J. Nutr. 10:363-373.

Wilkinson, J. M. and Precott, J. H. D. 1970. Beef production from grass and silage with autumn-born calves. 2. The effects on the performance of cattle fed on silage of barley supplementation and of previous grazing intensity. Anim. Prod. 12:443-450.

Wilson, P. N. and Osbourn, D. F. 1960. Compensatory growth after undernutrition in mammals and birds. Biol. Rev. 35:324-363.

Winchester, C. F., Hiner, R. L. and Scarborough,V.C. 1957. Some effects on beef cattle of protein and energy restriction. J. Anim. Sci. 16:426-436.

Winchester, C. F. and Howe, P. E. 1955. Relative effects of continous and interrupted growth on beef steers. Tech. Bull. US Dept. Agric. No. 1108. pp3-34.

Wright, I. A. 1985. Compensatory growth in beef cattle. pp195-201. In: F. H. Baker and M. E. Miller (Eds.) Emerging Technology and Management for ruminants. Livestock seminars, International Stockmen's school. Winrock International.

Wright, I. A., Russel, A. J. F. and Hunter, A. E. 1986. The effect of winter food level on compensatory growth of weaned, suckled calves grazed at two sward heights. Anim. Prod. 43:211-223.

Wright, I. A., Russel, A. J. F. and Hunter, A. E. 1989. Compensatory growth in cattle grazing different vegetation types. Anim. Prod. 48:43-50.

Yeates, N. T. M. 1952. The quantitative definition of cattle carcasses. Aust. J. Agric. Res. 3:68-94.

Yeates, N. T. M. 1964. Starvation changes and subsequent recovery of adult beef muscle. J. Agric. Sci. 64: 267-272.

APPENDIX

I. Heifers' Health Records

Date	Animal No	Treatment	Problem
Oct 15/88	191	INIT	Treated for pink eye.
Oct 16/88	191	INIT	Treated for pink eye.
Oct 17/88	108	R4FM	Treated for snotty nose, with oxytetracycline.
Oct 17/88	191	INIT	Treated for pink eye.
Oct 18/88	108	R4FM	Treated for snotty nose, with oxytetracycline.
Oct 18/88	191	INIT	Treated for pink eye.
Oct 19/88	108	R4FM	Treated for snotty nose, with oxytetracycline.
Oct 19/88	191	INIT	Treated for pink eye.
Oct 19/88	354	ROF2	Temperature high, no treatment.
Oct 20/88	191	INIT	Treated for pink eye.
Oct 20/88	99	ROF2	Treated for scours, with byko-digest plus water.
Oct 21/88	158	ROF2	Treated for bloat, with 1 gallon M.O.T.
Oct 22/88	292	R4FO	Treated for bloat, with 1 gallon M.O.T.
Oct 24/88	131	ROFM	Treated for bloat, with 1 gallon M.O.T.
Oct 24/88	151	ROFM	Treated for bloat, with 1 gallon M.O.T.

Date	Animal No	Treatment	Problem
Oct 24/88	163	INIT	Died of bloat.
Oct 25/88	44	R0F4	Heavy breathing; treated with oxytetracycline.
Oct 25/88	702	R0FM	Heavy breathing; treated with oxytetracycline.
Oct 26/88	702	R0FM	Heavy breathing; treated with oxytetracycline.
Oct 27/88	126	R4F0	Not eating; treated with bykodigest plus water.
Oct 27/88	168	R4F0	Not eating; treated with bykodigest plus water.
Oct 27/88	292	R4F0	Not eating; treated with bykodigest plus water.
Oct 27/88	16	R4F0	Not eating; treated with bykodigest plus water.
Oct 28/88	165	R2FM	Treated for snotty nose, with oxytetracycline.
Oct 29/88	60	R2FM	Treated for bloat, with 1 gallon M.O.T.
Oct 29/88	183	R2F0	Not eating; treated with bykodigest plus water.
Oct 29/88	88	R2F2	Not eating; treated with bykodigest plus water.
Oct 29/88	168	R0F0	Not eating; treated with bykodigest plus water.

Date	Animal No	Treatment	Problem
Oct 29/88	292	R4F0	Temperature high; treated with oxytetracycline.
Oct 29/88	165	R2FM	Temperature high; treated with oxytetracycline.
Oct 29/88	99	R0F2	Temperature high; treated with oxytetracycline.
Oct 30/88	289	R0FM	Treated for bloat, with 1 gallon M.O.T.
Oct 30/88	168	R4F0	Not eating; treated with Sulfa B, oxytetracycline and bykodigest.
Oct 30/88	99	R0F2	Not eating; treated with Sulfa B, oxytetracycline and bykodigest.
Nov 01/88	702	R0FM	Not eating; treated with bykodigest plus water.
Nov 02/88	39	R0F2	Treated for bloat, with 1 gallon M.O.T.
Nov 04/88	108	R4FM	Treated for bloat, with 1 gallon M.O.T.
Nov 05/88	158	R2F0	Not eating; treated with bykodigest plus water.
Nov 05/88	73	R2F0	Not eating; treated with Sulfa B, oxytetracycline and bykodigest.
Nov 05/88	172	R0F4	Treated for pink eye.
Nov 05/88	126	R4F0	Not eating; treated with bykodigest plus water.

Date	Animal No	Treatment	Problem
Nov 06/88	172	R0F2	Treated for pink eye.
Nov 08/88	172	R0F2	Treated for pink eye.
Nov 09/88	172	R0F2	Treated for pink eye.
Nov 10/88	172	R0F2	Treated for pink eye.
Nov 11/88	172	R0F2	Treated for pink eye.
Nov 13/88	172	R0F2	Treated for pink eye.
Nov 19/88	58	R4FM	Not eating; treated with bykodigest plus water.
Nov 30/88	289	R0FM	Temperature high; treated with oxytetracycline and Sulfa B.
Dec 01/88	289	R0FM	Temperature high; treated with oxytetracycline and Sulfa B.
Dec 01/88	69	R0F2	Temperature high; treated with oxytetracycline and Sulfa B.
Dec 01/88	354	R0F2	Temperature high; treated with oxytetracycline and Sulfa B.
Dec 01/88	702	R0FM	Temperature high; treated with oxytetracycline and Sulfa B.
Dec 02/88	289	R0FM	Temperature high; treated with oxytetracycline and Sulfa B.
Dec 02/88	69	R0F2	Temperature high; treated with oxytetracycline and Sulfa B.
Dec 02/88	702	R0FM	Temperature high; treated with oxytetracycline and Sulfa B.

Date	Animal No	Treatment	Problem
Dec 02/88	186	R4FM	Temperature high; treated with oxytetracycline and Sulfa B.
Dec 04/88	289	R0FM	Temperature high; treated with oxytetracycline and Sulfa B.
Dec 05/88	131	R0FM	Not eating; treated with bykodigest plus water.
Dec 06/88	131	R0FM	Not eating; treated with bykodigest plus water.
Jan 31/89			All animals treated for lice, with lysoff.
Mar 21/89			All animals treated for lice, with lysoff.

Definitions

INIT animals - restricted 0 months, full fed 0 months;

R0F2 animals - restricted 0 months, full fed 2 months;

R0F4 animals - restricted 0 months, full fed 4 months;

R0FM animals - restricted 0 months, full fed to market weight (400kg)

R2F0 animals - restricted 2 months, full fed 0 months;

R2F2 animals - restricted 2 months, full fed 2 months;

R2FM animals - restricted 2 months, full fed to market weight (400kg)

R4F0 animals - restricted 4 months, full fed 0 months;

R4FM animals - restricted 4 months, full fed to market weight (400kg)

M.O.T - Mineral Oil Treatment.

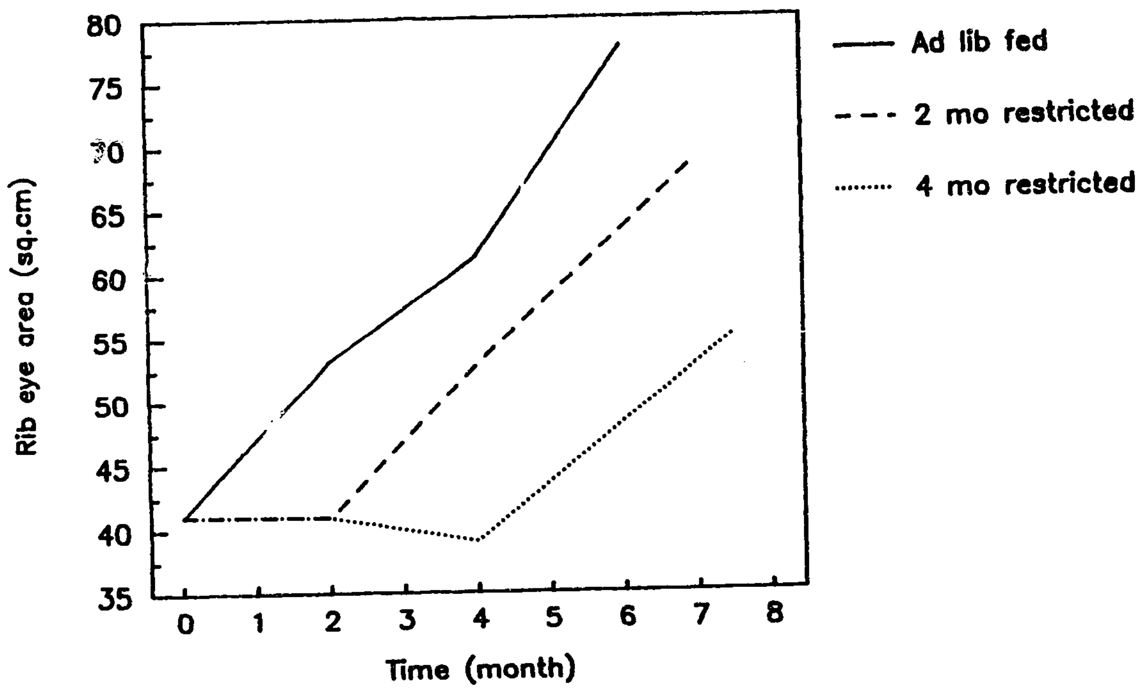

Figure 3.6. Change in the mean rib eye area over time from ad lib, 2 mo and 4 mo feed restriction of heifers followed by refeeding to about 400 kg.

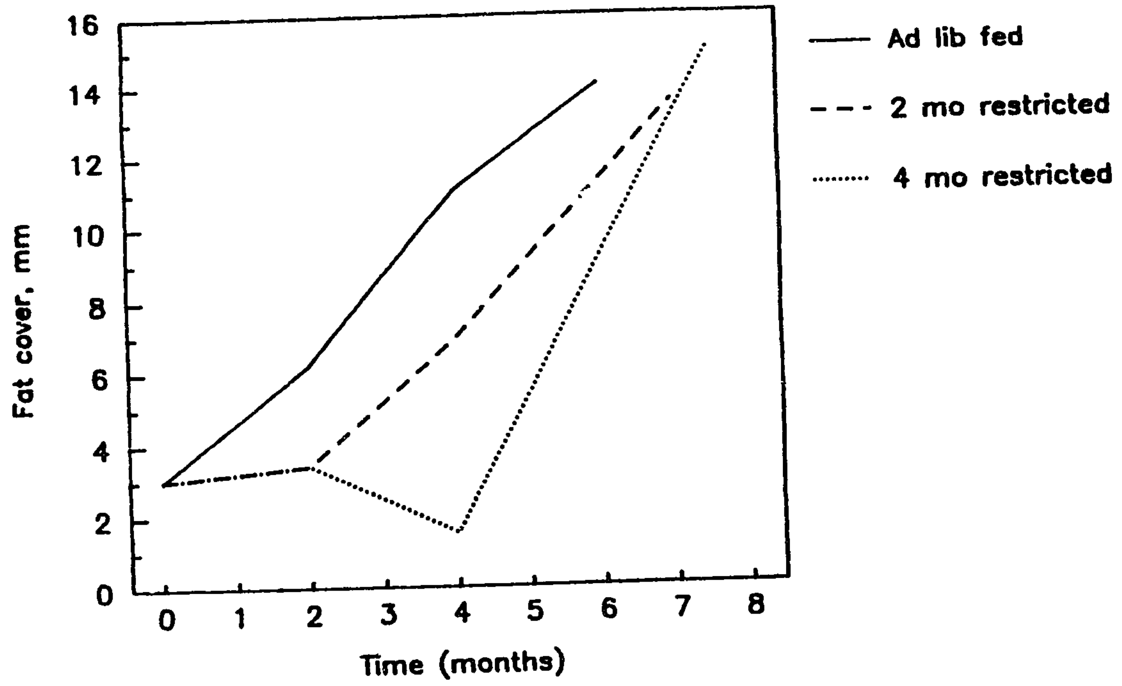

Figure 3.7. Change in the fat cover thickness over time from ad lib, 2 mo and 4 mo feed restriction of heifers followed by refeeding to about 400 kg.

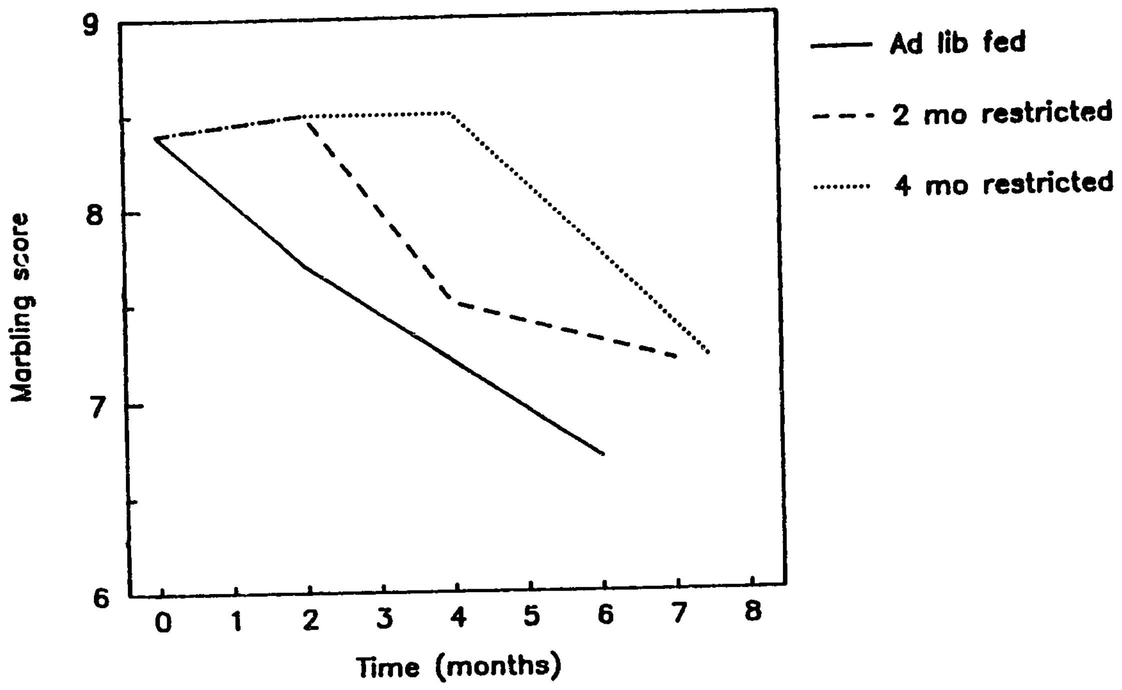

Figure 3.8. Change in the marbling score of carcasses over time from ad lib, 2 mo and 4 mo feed restriction of heifers followed by refeeding to about 400 kg.

(Figure 3.8). Generally, marbling (intramuscular fat) increases as carcasses get fatter; however, caution must be taken in such interpretations since Johnson et al. (1972) showed that this is not always so. In their study of bovine carcasses, as carcasses became fatter the intramuscular depot did not increase. Armbruster et al. (1983) also questioned whether marbling was highly correlated to total fat in the carcasses of beef cattle. They reported that marbling score was more highly correlated with carcass weight.

3.3.4. Interactions

There were treatment by period interactions for carcass weight. The carcass weight of the ad lib fed animals increased at a relatively faster rate during the first 2 periods and then slowed down significantly in the third period. On the other hand, that of the 2-month restricted-refed animals started at a slower rate in the first period, increased significantly during the second period and slowed down in the third period. The carcass weight of the 4-month restricted animals was significantly smaller than the other treatment groups at the end of the second period, but increased at a very high rate during the refeeding period.

Fat cover was affected by treatment by period interaction during the third period of the experiment. While there was a slight increase in the fat cover of the R0FM and R2FM animals, there was a significant increase in the refed R4FM animals, resulting in equal fat cover among the treatments at final slaughter weight.

3.3.5. The major carcass tissues: muscle, bone and fat

Dissection of the standard 3-rib joint revealed no significant differences among treatments in either the absolute weights or proportions of any of the major carcass tissues at the end of the first period (Table 3.9). The trends were, however, as expected with the restriction resulting in retarded fat and muscle development, but no apparent retardation of bone. Small numbers of carcasses may have contributed to the non-significance of the treatment effect. Tissue weights expressed as proportions of the 3-rib joints were also not significantly different among treatments. However, the muscle to bone ratio in the 3-rib joint was greater ($P<0.05$) in the R0F2 animals than in the INIT and R2F0 animals indicating a trend of increase in the amount of muscle in the 3-rib joint of the ad lib fed animals compared to the restricted animals. Muscle in the R0F2 animals was obviously growing at a relatively faster rate than in the R2F0 animals. On the other hand, the muscle to fat ratio in the 3-rib joint was not different ($P>0.05$) among treatments.

The effect of 4 months feed restriction was associated with a number of significant changes both in the absolute amounts and proportions of the major carcass tissues in the 3-rib joint (Table 3.10). Also the standard error was reduced due to increased number ofanimals. The amount of muscle in the 3-rib joint of the R0F4 and R2F2 groups had increased significantly over the second period while that of the R4F0 group had significantly decreased and was smaller ($P<0.05$) than that of the INIT group. The amount of fat in the 3-rib joint of the R0F4 and R2F2 groups had significantly increased

TABLE 3.9. LEAST SQUARES MEANS ± STANDARD ERRORS OF THE MAJOR CARCASS TISSUE WEIGHTS AND PROPORTIONS IN A 3-RIB JOINT OF HEIFERS FED FOR 2MONTHS

Item	INIT[a]	AD2[b]	R2F0[c]	Probability
No. of animals	5	4	4	
Slaughter wt, kg	211 ± 17[d]	296 ± 23[e]	246 ± 12[e]	0.02
3-Rib joint wt, g	1637 ± 219	1903 ± 198	1447 ± 147	0.25
Muscle wt, g	915 ± 130	1084 ± 93	826 ± 83	0.21
Bone wt, g	386 ± 22	352 ± 34	339 ± 25	0.55
Total fat wt, g	335 ± 100	464 ± 88	281 ± 44	0.27
Muscle(%)[f]	55.9 ± 2.1	57.4 ± 1.6	57.2 ± 0.1	0.75
Bone(%)[f]	24.9 ± 3.0	18.8 ± 1.3	23.7 ± 1.3	0.11
Total fat(%)[f]	19.7 ± 4.1	23.8 ± 2.8	19.1 ± 1.4	0.43
Muscle:Bone ratio	2.4 ± 0.3[d]	3.1 ± 0.2[e]	2.4 ± 0.1[d]	0.04
Muscle:Fat ratio	3.1 ± 0.6	2.6 ± 0.4	3.0 ± 0.2	0.59

[a] Animals slaughtered at d 1 (25 d after weaning).

[b] Animals fed ad libitum for 2 mo.

[c] Animals restricted for 2 mo.

[d,e] Means within a row with different superscripts differ ($P<0.05$).

[f] Tissue weight expressed as percentage of the 3-rib joint weight.

TABLE 3.10. LEAST SQUARES MEANS ± STANDARD ERRORS OF THE MAJOR CARCASS TISSUE WEIGHTS AND PROPORTIONS IN A 3-RIB JOINT OF HEIFERS FED FOR 4 MONTHS

Item	INIT[a]	R0F4[b]	R2F2[c]	R4F0[d]	Probability
No. of animals	5	6	6	6	
Slaughter wt, kg	211 ± 17^{e}	343 ± 4^{f}	314 ± 7^{f}	244 ± 12^{e}	0.001
3-Rib joint wt, g	1637 ± 219^{e}	2640 ± 153^{f}	2289 ± 143^{f}	1416 ± 122^{e}	0.001
Muscle wt, g	915 ± 130^{e}	1307 ± 78^{f}	1184 ± 77^{ef}	820 ± 63^{g}	0.001
Bone wt, g	386 ± 22	430 ± 18	426 ± 13	402 ± 32	0.58
Total fat wt, g	335 ± 100^{e}	908 ± 78^{f}	678 ± 108^{f}	239 ± 41^{e}	0.001
Muscle(%)[h]	55.9 ± 2.1	49.5 ± 1.3	52.1 ± 2.8	56.4 ± 1.9	0.12
Bone(%)[h]	24.4 ± 3.0^{e}	16.5 ± 1.5^{f}	19.0 ± 1.2^{f}	27.7 ± 1.4^{e}	0.001
Total fat(%)[h]	19.7 ± 4.1^{e}	33.9 ± 1.5^{f}	28.9 ± 3.2^{f}	15.8 ± 1.7^{e}	0.001
Muscle:Bone	2.4 ± 0.3^{e}	3.0 ± 0.2^{f}	2.8 ± 0.2^{f}	2.1 ± 0.1^{e}	0.01
Muscle:Fat	3.1 ± 0.6^{e}	1.5 ± 0.1^{f}	2.0 ± 0.3^{f}	3.8 ± 0.6^{e}	0.002

[a] Animals slaughtered at d 1 (25 d after weaning).

[b] Animals fed ad libitum for 4 mo.

[c] Animals restricted for 2 mo followed by refeeding for 2 mo.

[d] Animals restricted for 4 mo.

[e,f,g] Means within a row with different superscripts differ ($P<0.05$).

[h] Tissue weight expressed as percentage of the 3-rib joint weight.

($P<0.05$) while that of the R4F0 group had decreased. Meanwhile, bone was steadily growing with no major treatment effect; also all the treatments were similar to the INIT group at the end of this period, indicating the relatively slow growth and development of this tissue.

When the tissue weights were expressed as proportions of the 3-rib joints, percent muscle was similar ($P>0.05$) in all the treatments. The change in the proportion of muscle with feed restriction is illustrated in Figure 3.9

The proportion of bone in the 3-rib joint of the R4F0 group was similar to the INIT group but was higher ($P<0.05$) than in the R0F4 and R2F2 groups. It can be seen that the proportion of bone in both the ad lib fed and 2-month restricted-refed animals had steadily fallen over this period, while that of the 4-month restricted animals was still significantly high (see Figure 3.10). Price (1976) found similar results in early and late maturing steers. In his study, a significant increase in percent bone during feed restriction was found. He noted that this suggested a relative stability of bone weight during undernutrition. This reasoning would well be applicable to the present study of heifers. As can be seen, the stability of bone is evidenced by the non-significance of the treatment effect on bone weight measurements to the end of both the first and second periods of the experiment.

Fat being the most variable tissue in the carcass (Seebeck, 1983), its proportion in the 3-rib joint had the greatest influence on the other two tissues. Over the second period of the experiment, percent fat in the ad lib fed animals increased by over 42% (from

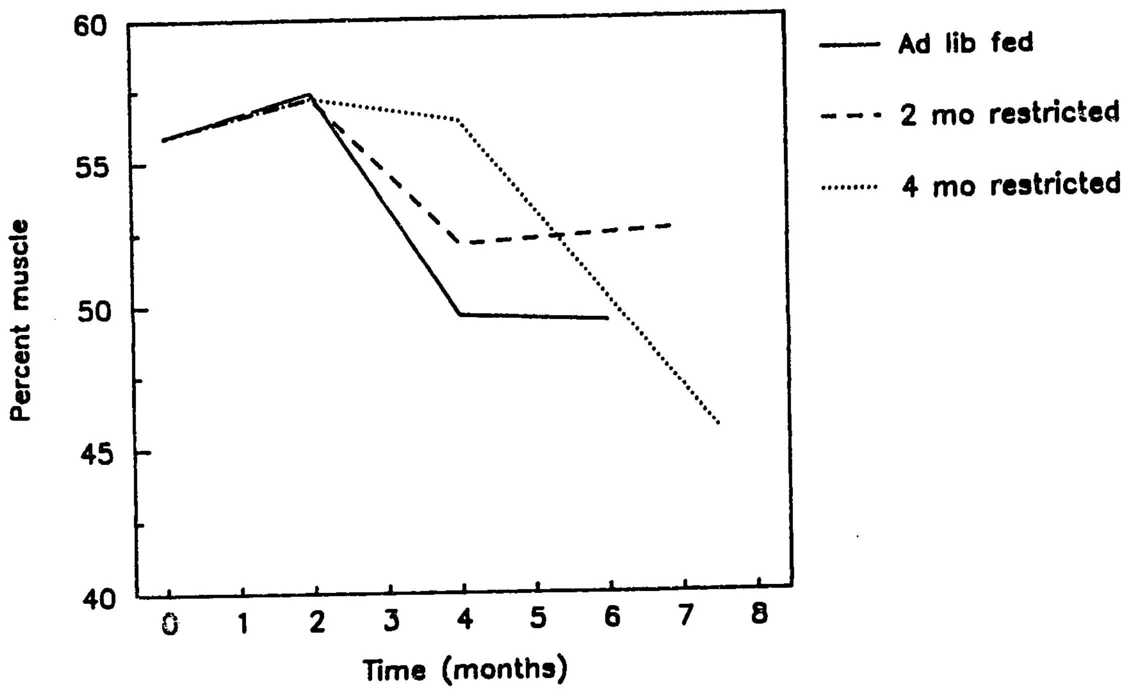

Figure 3.9. Change in the proportion of 3-rib joint muscle over time from ad lib, 2 mo and 4 mo feed restriction of heifers followed by refeeding to about 400 kg.

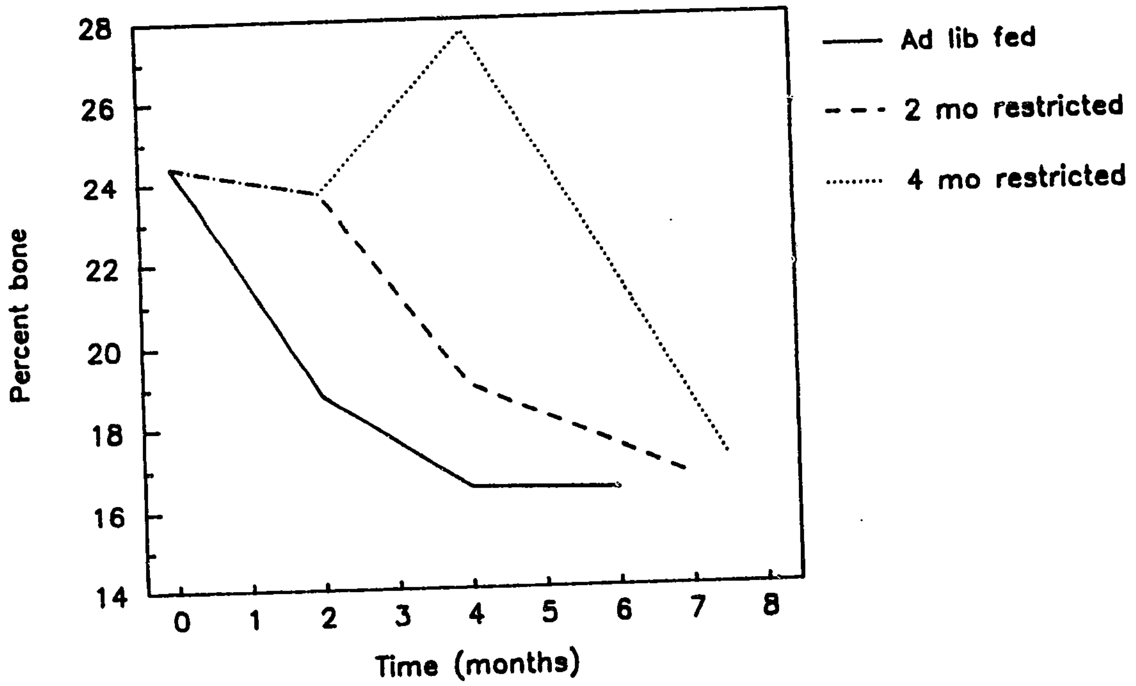

Figure 3.10. Change in the proportion of 3-rib joint bone over time from ad lib, 2 mo and 4 mo feed restriction of heifers followed by refeeding to about 400 kg.

23.8% to 33.9%) while that in the 2-month restricted-refed animals increased by over 51% (from 19.1 to 28.9%). Meanwhile the proportion of fat in the 3-rib joint of the 4-month restricted animals was not different from the point of origin (INIT animals). Figure 3.11 illustrates the changes in the proportion of fat in the 3-rib joint associated with the feeding regimes. Thus as percent fat in the 3-rib joint increased, percent muscle and percent bone decreased. Butterfield (1966) made similar conclusions in a study with steers.

The muscle to bone ratio in the 3-rib joint of the R0F4 and R2F2 groups was larger ($P<0.05$) than in the INIT and R4F0 groups. On the other hand, the muscle to fat ratio in the R0F4 and R2F2 groups was smaller ($P<0.05$) than in the INIT and R4F0 groups. Although muscle was increasing relatively faster in the 3-rib joint of the ad lib fed and 2-month restricted-refed animals than in the 4-month restricted animals, the former had also entered the fattening phase since the muscle to fat ratio was lower at this stage than at the beginning of the experiment and during the first 2 months.

At the final slaughter weight, the amounts of bone and fat in the 3-rib joint were similar in all treatments while that of muscle in the R4FM group was smaller ($P<0.05$) than that in the R2FM group; the amount of muscle in the R0FM group was, however, not significantly different from either treatment (Table 3.11). The significant difference in the 3-rib joint muscle between the R2FM and R4FM groups at final slaughter weight could be explained by examining the amount and proportion of fat. The R4FM animals were certainly accumulating fat at a faster rate than the R2FM animals during the

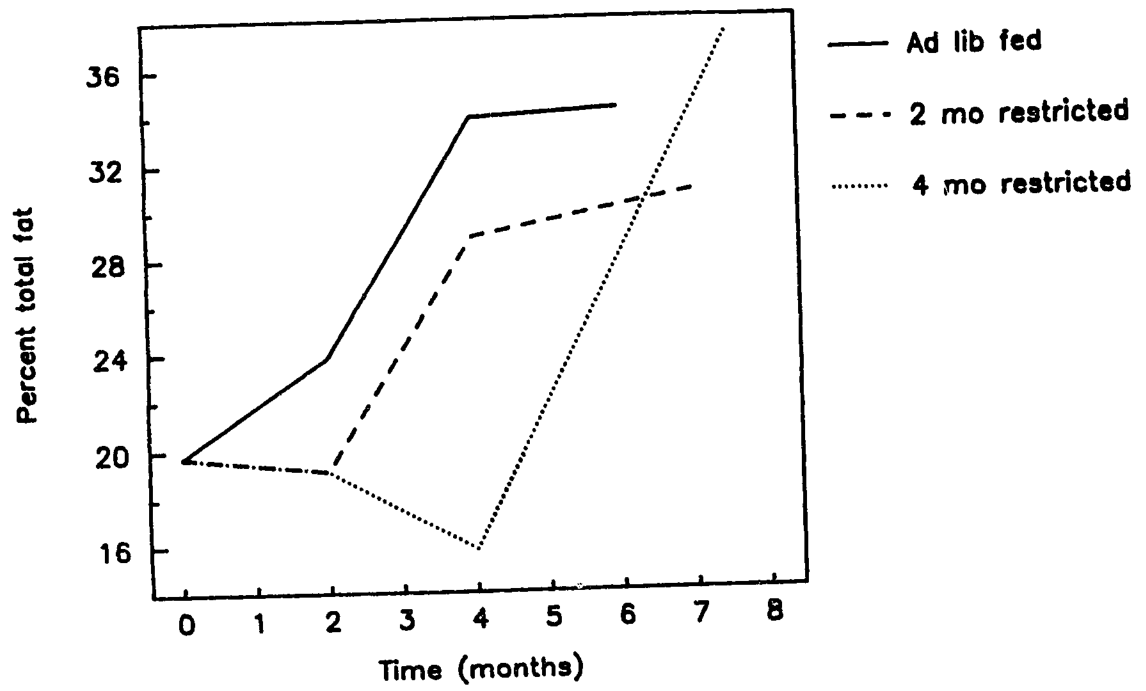

Figure 3.11. Change in the proportion of 3-rib joint fat over time from ad lib, 2 mo and 4 mo feed restriction of heifers followed by refeeding to about 400 kg.

TABLE 3.11. LEAST SQUARES MEANS ± STANDARD ERRORS OF THE MAJOR CARCASS TISSUE WEIGHTS AND PROPORTIONS IN A 3-RIB JOINT OF HEIFERS AT ABOUT 400 kg

Item	R0FM[a]	R2FM[b]	R4FM[c]	Probability
No. of animals	6	6	6	
Slaughter wt, kg	414 ± 19	419 ± 13	408 ± 13	0.88
3-Rib joint wt, g	3002 ± 118	3220 ± 160	2933 ± 102	0.45
Muscle wt, g	1477 ± 59[de]	1738 ± 144[d]	1328 ± 19[e]	0.02
Bone wt, g	492 ± 22	549 ± 39	500 ± 15	0.30
Total fat wt, g	1034 ± 81	1002 ± 80	1105 ± 104	0.71
Muscle(%)[f]	49.4 ± 1.9	52.6 ± 2.3	45.6 ± 2.0	0.10
Bone(%)[f]	16.4 ± 0.5	16.7 ± 0.9	17.1 ± 0.5	0.74
Total fat(%)[f]	34.2 ± 1.8	30.7 ± 2.8	37.3 ± 2.4	0.18
Muscle:Bone	3.0 ± 0.2	3.2 ± 0.2	2.7 ± 0.1	0.07
Muscle:Fat	1.5 ± 0.1	1.8 ± 0.2	1.3 ± 0.2	0.15

[a] Animals fed ad libitum throughout to final slaughter weight.

[b] Animals restricted for 2 mo followed by refeeding to final slaughter weight.

[c] Animals restricted for 4 mo followed by refeeding to final slaughter weight.

[d,e] Means within a row with different superscripts differ ($P<0.05$).

[f] Tissue weight expressed as percentage of the 3-rib joint weight.

refeeding period.

It therefore seems logical to use Joubert's (1954) explanation that "the rapid increase in weight which follows retardation may be, to a considerable extent, the replacement of the lost fat, and this process may take place more rapidly than true growth". Thus the R4FM animals, which exhibited very high growth rates during refeeding, were putting on fat at a faster rate than muscle. This is contrary to Berg and Butterfield's (1976) suggestion that realimentation results in an increase in muscle towards a point of normal muscle to bone relationship, while the recovery of fat is given lower priority. At least in the present study, those heifers that were restricted for 4 months and then refed, fat accumulation was not given low priority. However, Berg and Butterfield's (1976) statement seems to be applicable to those heifers that were restricted for 2 months and then refed (as is evidenced by the amount and proportion of fat).

This dilemma can be explained in terms of the severity and duration of the feed restriction. Obviously the 4-month restricted animals underwent a more severe feed restriction than the 2-month restricted animals. Therefore when the former were refed, a higher proportion of the feed was converted into fat compared to those restricted for 2 months. Butterfield (1966) postulated that if a very young animal is fed an inadequate diet, the normal development of the GIT and other viscera are less affected than later developing parts such as fat, muscle and bone. Therefore at the end of a period of poor nutrition, from say 1 - 2 months of age, an animal is produced which, at a chronological age of 2 months, has the viscera of a seven-week-old animal in a carcass of equivalent weight to that of a three-week-old animal. When maximum food intake is re-introduced the viscera can handle more nutritive intake than the underdeveloped musculature is capable of absorbing, and the surplus food metabolized then overflows into fat depots. Butterfield (1966) further suggested that cattle which undergo semi-starvation at more mature ages have a larger proportion of muscle to fat in their weight gain during recovery than have calves submitted to similar treatments.

Butterfield (1966) did not define exactly what a "younger" and "older" age in cattle meant, but if those that are weaned at the age of 6 months are still "young", then the heifers that were restricted for 4 months could be considered physiologically young. On the other hand, 2 months feed restriction did not cause as much physiological change in the body, particularly to the musculature. As a result when these animals were realimented, recovery of muscle and normal muscle to bone relationship resulted.

In terms of muscle to fat ratio, there was no difference ($P>0.05$) among treatments. These results are contrary to those in steers (Butterfield, 1966) in which there was a larger proportion of muscle in the weight gain of the recovering animals. Also the present findings do not agree with those of Meyer and Clawson (1964) who showed that more fat than protein was laid down in young rats (7 to 10 weeks of age) and young sheep (6 months of age) during catch-up growth than during ad lib feeding.

The results of bone weight and proportion in the 3-rib joint at the final slaughter weight were quite expected. As reported in other studies (Murray et al., 1974; Price, 1976), bone is almost unaffected by nutritional treatments, and the present study of heifers was not any different. Thus bone weight is more closely associated with age than with differences in plane of nutrition (Guenther et al., 1965). For example Murray et al. (1974) fed Angus steers such that they grew from 300 to 440 kg at three different rates: high (H=0.8 kg d^{-1}), low (L=0.4 kg d^{-1}) and high-maintenance (HM=0.8 kg d^{-1} followed by a period of zero growth). The steers were slaughtered at similar live weights (300, 330, 363, 400 and 440 kg) and comparison of the groups at the same dissected side weight revealed that muscle weights were comparable for the three groups but weight of bone was greater for the L and HM groups. This was because at constant weights, the L and HM animals were older than the H animals since the former obviously took longer to reach such weights than the latter.

In the present study, the animals slaughtered at 2 and 4 months of the experimental period were of the same age and therefore it is not surprising that bone weight in the 3-rib joint was similar in all treatments. However, at the final slaughter weight, the R2FM and R4FM animals were 28 and 49 days respectively older than the R0FM animals, and yet there was no difference in bone weight. The most probable explanation for this could be that because of the slow and steady growth of bone, the periods of 28 and 49 days were not long enough to show any significant growth in bone. Moreover, the animals were approaching maturity at that time, hence slowing down the growth of bone considerably.

The carcass composition results at the final slaughter weight can be explained more clearly by looking at the allometric growth coefficients that were calculated by regressing the weight of each carcass tissue on the weight of the respective 3-rib joint using Huxley's (1932) equation $y = ax^b$ in its linear form: $\log y = \log a + b.\log x$. Comparison of the allometric coefficients between the ad lib fed and 2-month restricted-refed animals, considered over the three periods, revealed that muscle was growing at a relatively faster ($P=0.04$) rate in the latter than in the former (Table 3.12 and Figure 3.12). However, considering the last two periods (refeeding of the 4-month restricted animals), the allometric coefficients showed that fat was accumulating at a relatively faster ($P<0.05$) rate in the 3-rib joint of the 4-month restricted-refed animals than in the ad lib fed and 2-month restricted-refed animals (Table 3.13 and Figure 3.13). These b values confirm the suggestion that the 2-month restricted-refed animals placed priority on rebalancing the muscle to bone relationship while the 4-month restricted-refed animals were accumulating more fat rather than putting on muscle.

Hironaka and Kozub (1973) in their study suggested that since the restricted steers consumed more feed per day than the ad lib fed animals of the same weight, the former presumably deposited fat at a faster rate, but the period of fat deposition was so shortened that total deposition tended to be less, leading to leaner animals. In the present study, although the effective period of fat deposition in the R4FM animals may have been shortened, this did not result in leaner animals presumably because of the relatively faster rate of fat deposition in heifers than in steers (Berg and Butterfield, 1976).

TABLE 3.12. LINEAR RELATIONSHIP OF THE TYPE: LOGy=LOGa+b.LOGx OF THE 3-RIB JOINT MAJOR CARCASS TISSUE WEIGHTS ON 3-RIB JOINT WEIGHTS OF TWO GROUPS OF HEIFERS

	Ad libitum fed[a] n = 16			2 months restricted[b] n = 16			
Item	*a*	*b*	R^2	*a*	*b*	R^2	Probability[c]
Log muscle weight	0.7	0.71±0.1	0.85	0.04	0.91±0.1	0.91	0.04
Log bone weight	0.4	0.66±0.1	0.72	0.80	0.56±0.1	0.78	0.23
Log total fat weight	-3.2	1.79±0.1	0.92	-2.40	1.55±0.2	0.88	0.13

[a] Animals fed ad libitum and serially slaughtered at 2 mo, 4 mo and final slaughter weight of about 400 kg.

[b] Animals restricted for 2 mo followed by refeeding and serially slaughtered at 2 mo, 4 mo and final slaughter weight of about 400 kg.

[c] Comparison of *b* values.

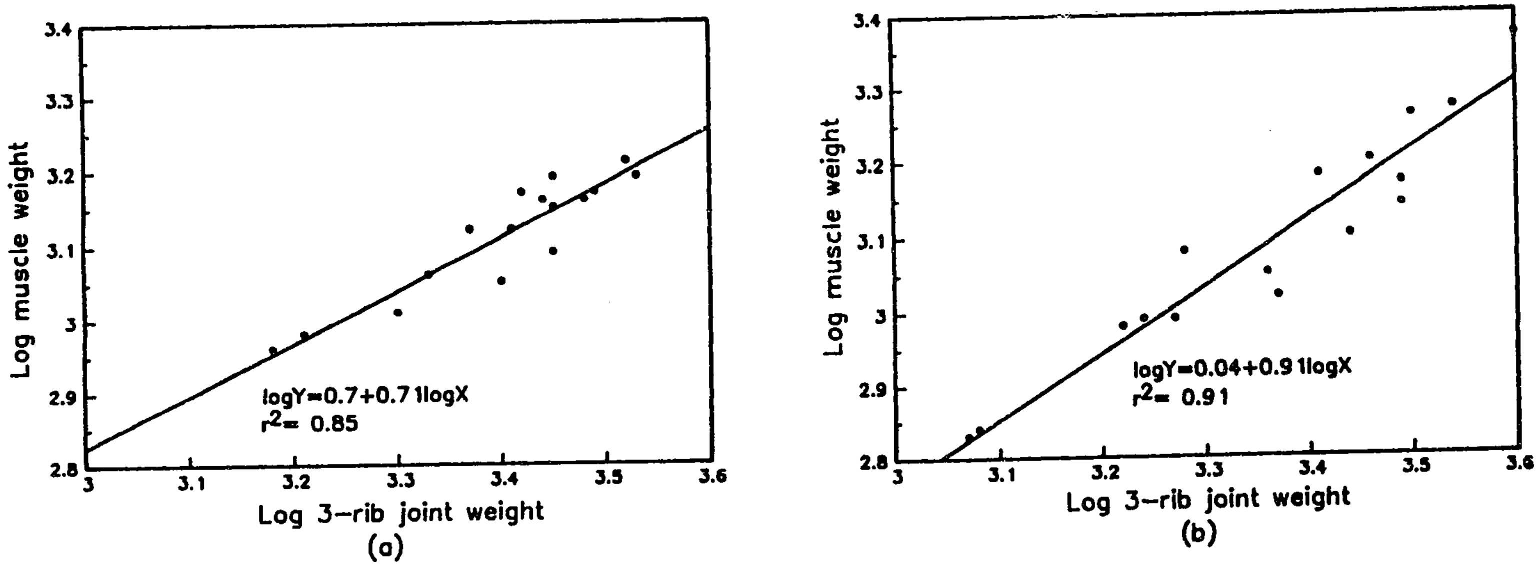

Figure 3.12. Linear relationship of the type: $\log y = \log a + b.\log x$ of 3-rib joint muscle weight on 3-rib joint weight of three slaughter groups from ad libitum (a) and 2-mo restricted-refed (b) heifers.

TABLE 3.13. LINEAR RELATIONSHIP OF THE TYPE: $LOGy = LOGa + b.LOGX$ OF THE 3-RIB JOINT MAJOR CARCASS TISSUE WEIGHTS ON 3-RIB JOINT WEIGHTS OF THREE GROUPS OF HEIFERS

Item	Ad libitum fed[a] n = 12			2 months restricted[b] n = 12			4 months restricted[c] n = 12			Probability[d]
	a	b	R^2	a	b	R^2	a	b	R^2	
Log muscle weight	0.2	0.80 ± 0.2	0.71	-0.3	1.00 ± 0.2	0.80	0.7	0.70 ± 0.1	0.92	0.33
Log bone weight	0.6	0.59 ± 0.2	0.44	0.7	0.57 ± 0.2	0.55	1.4	0.38 ± 0.1	0.70	0.60
Log total fat weight	-2.0	1.45 ± 0.2^{e}	0.81	-1.6	1.32 ± 0.2^{e}	0.64	-4.6	2.22 ± 0.1^{f}	0.97	0.02

[a] Animals fed ad libitum and serially slaughtered at 4 mo and final slaughter weight of about 400 kg.

[b] Animals restricted for 2 mo followed by refeeding and serially slaughtered at 4 mo and final slaughter weight of about 400 kg.

[c] Animals restricted for 4 mo followed by refeeding and serially slaughtered at 4 mo and final slaughter weight of about 400 kg.

[d] Comparison of b values.

[e,f] b values within a row with different superscripts differ ($P<0.05$).

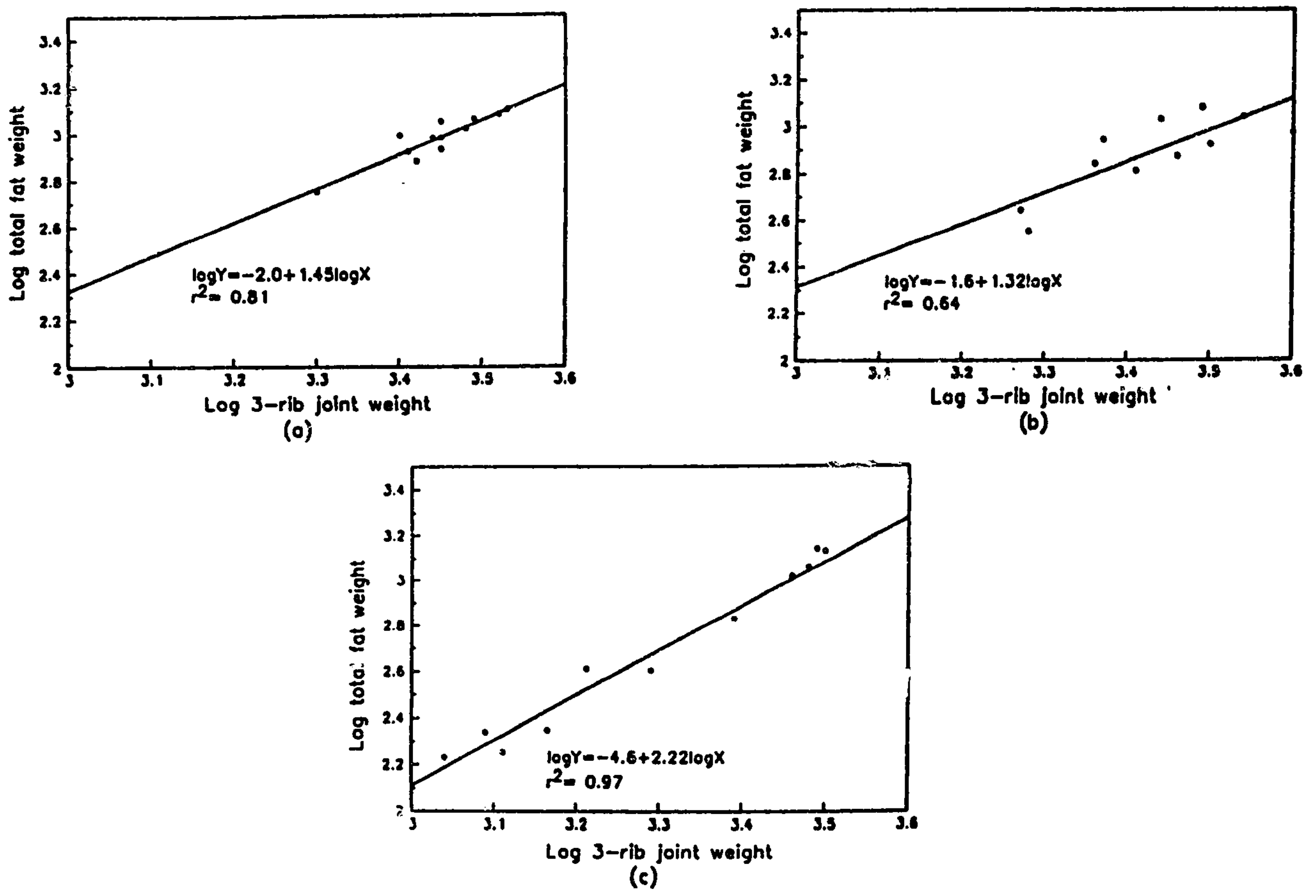

Figure 3.13. Linear relationship of the type: *log y = log a + b.log x* of 3-rib joint total fat weight on 3-rib joint weight of two slaughter groups from ad libitum (a), 2-mo restricted-refed (b) and 4-mo restricted-refed (c) heifers.

This, however, was not the case in the R2FM animals and, as suggested earlier, the most probable reason could be the difference in the severity and duration of the feed restriction.

3.3.6. Interactions

There were treatment by period interactions for the proportions of the major carcass tissues and muscle to bone ratio in the 3-rib joint. Percent muscle in the 3-rib joint of the ad lib fed and 2-month restricted-refed animals were similar (49.6% and 52.1% respectively) at the end of the second period and remained relatively constant in the third period. Percent muscle in the 4-month restricted-refed animals decreased from 56.4% at the end of the second period to 45.6% at the end of the experiment (final slaughter weight), although overall this ultimate proportion was not significantly different from the other treatments. Similarly, percent bone and percent fat in the 3-rib joint of the ad lib fed and 2-month restricted-refed animals were similar at the end of the second period and remained relatively constant up to the end of the experiment. On the other hand, percent bone was significantly higher and percent fat significantly lower in the 4-month restricted animals than in the ad lib fed and 2-month restricted-refed animals at the end of the second period. Percent bone and percent fat significantly decreased and increased respectively when the 4-month restricted animals were refed in the third period. The muscle to bone ratio also remained relatively constant in the ad lib fed and 2-month restricted-refed animals while there was a significant decrease in the 4-month restricted-refed animals during the third period.

3.3.7. The Fat Depots

The proportions of the fat depots in the 3-rib joint did not increase over initial values in the 2-month restricted heifers (Table 3.14). They did increase in the ad lib fed heifers but did not reach statistically significant differences compared to INIT or restricted groups. The non-significance of the treatment effect was probably due to small numbers of carcasses.

Four months feed restriction had a significant effect on both the absolute amounts and proportions of the fat depots in the 3-rib joint (Table 3.15). The amount of SCF in the 3-rib joint of R0F4 and R2F2 groups was greater ($P<0.05$) than that in the INIT and R4F0 groups. Similarly, the proportion of SCF was relatively higher ($P<0.05$) in the 3-rib joint of R0F4 and R2F2 groups than that in the INIT and R4F0 groups. Obviously SCF had accumulated significantly in the R0F4 and R2F2 animals over the second period while the accumulation in the R4F0 animals was checked. These results reflect, to a great extent, the results obtained from back fat measurements in live animals (see chapter 2).

The amount of IMF was significantly greater ($P<0.05$) in the 3-rib joint of the R0F4 group than that in the INIT and R4F0 animals. The R2F2 animals were not different from either the INIT or R0F4 group. However, IMF weight expressed as a proportion of the total fat weight in a 3-rib joint, was relatively higher ($P<0.05$) in the INIT and R4F0 groups than in the R0F4 and R2F2 groups. This was an opposite trend compared to the SCF depot.

From these results, taking the INIT group as the baseline, the

TABLE 3.14. LEAST SQUARES MEANS ± STANDARD ERRORS OF THE FAT DEPOT WEIGHTS AND PROPORTIONS IN A 3-RIB JOINT OF HEIFERS FED FOR 2 MONTHS

Item	INIT[a]	R0F2[b]	R2F0[c]	Probability
No. of animals	5	4	4	
Slaughter wt, kg	211 ± 17[d]	296 ± 23[e]	246 ± 12[e]	0.02
3-Rib joint wt, g	1637 ± 219	1900 ± 198	1447 ± 147	0.25
Subcutaneous fat, g	99 ± 39	160 ± 35	89 ± 18	0.24
Intermuscular fat, g	237 ± 71	304 ± 57	192 ± 31	0.34
Subcutaneous fat(%)[f]	27.2 ± 2.9	34.1 ± 2.6	31.7 ± 0.6	0.37
Intermuscular fat(%)[f]	72.8 ± 2.9	65.9 ± 2.6	68.3 ± 0.6	0.62

[a] Animals slaughtered at d 1 (25 d after weaning).

[b] Animals fed ad libitum for 2 mo.

[c] Animals restricted for 2 mo.

[d,e] Means within a row with different superscripts differ ($P<0.05$).

[f] Fat depot weight expressed as percentage of the 3-rib joint total fat weight.

TABLE 3.15. LEAST SQUARES MEANS ± STANDARD ERRORS OF THE FAT DEPOT WEIGHTS AND PROPORTIONS IN A 3-RIB JOINT OF HEIFERS FED FOR 4 MONTHS

Item	INIT[a]	R0F4[b]	R2F2[c]	R4F0[d]	Probability
No. of animals	5	6	6	6	
Slaughter wt, kg	211 ± 17^e	343 ± 4^f	314 ± 7^f	244 ± 12^e	0.001
3-Rib joint wt, g	1637 ± 219^e	2640 ± 153^f	2289 ± 143^f	1416 ± 122^e	0.001
Subcutaneous fat, g	99 ± 39^e	358 ± 29^f	264 ± 44^f	76 ± 18^e	0.001
Intermuscular fat, g	237 ± 71^e	544 ± 52^f	414 ± 73^{ef}	162 ± 27^g	0.001
Subcutaneous fat(%)[h]	27.2 ± 2.9^e	40.0 ± 1.4^f	38.7 ± 2.5^f	30.8 ± 2.8^e	0.05
Intermuscular fat(%)[h]	72.8 ± 2.9^e	60.0 ± 1.4^f	61.3 ± 2.5^f	69.2 ± 2.8^e	0.05

[a] Animals slaughtered at d 1 (25 d after weaning).

[b] Animals fed ad libitum for 4 mo.

[c] Animals restricted for 2 mo followed by refeeding for 2 mo.

[d] Animals restricted for 4 mo.

[e,f,g] Means within a row with different superscripts differ ($P<0.05$).

[h] Fat depot weight expressed as percentage of the 3-rib joint total fat weight.

proportion of SCF in the ad lib fed animals increased significantly during the first and second periods of the experiment while the IMF showed the trend of decreasing. On the other hand, the proportion of SCF in the 2-month restricted-refed animals did not increase significantly during the first period (reflecting the effect of feed restriction) while there was a significant increase during the second period (reflecting the effect of refeeding).

Percent IMF was relatively unaffected in the first period while it fell significantly in the second period. In the 4-month restricted animals, the change in the proportions of both SCF and IMF from the baseline was not significant during the 2 periods. However, when the change in terms of depletion of these depots . considered, it would appear that IMF suffered a greater percentage loss than SCF during feed restriction of the animals. SCF is a later maturing depot while IMF is an earlier developing depot (Berg et al., 1978b; Thompson and Barlow, 1981).

Fat depots are expected to follow an order of depletion during feed restriction, opposite to the direction of their development Butterfield, 1966); it would therefore be expected that the SCF depot would be affected more than IMF. One major reason why such a trend may not have occured in the present study is that feed restriction was imposed when the SCF was relatively too low. Therefore, depletion of IMF would be expected.

At the final slaughter weight, the amount of SCF in the 3-rib joint was greater ($P<0.05$) in the R4FM group than in the R0FM and R2FM groups (Table 3.16). Similarly, the proportion of SCF was higher

TABLE 3.16. LEAST SQUARES MEANS ± STANDARD ERRORS OF THE FAT DEPOT WEIGHTS AND PROPORTIONS IN A 3-RIB JOINT OF HEIFERS AT ABOUT 400 kg

Item	R0FM^{a}	R2FM^{b}	R4FM^{c}	Probability
No. of animals	6	6	6	
Slaughter wt, kg	414 ± 19	419 ± 13	408 ± 13	0.88
3-Rib joint wt, g	3002 ± 118	3220 ± 160	2933 ± 102	0.45
Subcutaneous fat, g	408 ± 38^{d}	468 ± 37^{d}	693 ± 68^{e}	0.003
Intermuscular fat, g	626 ± 50^{d}	534 ± 44de	412 ± 43^{e}	0.001
Subcutaneous fat(%)^{f}	39.3 ± 1.5^{d}	46.7 ± 1.0^{d}	62.7 ± 1.6^{e}	0.001
Intermuscular fat(%)^{f}	60.7 ± 1.5^{d}	53.3 ± 1.0^{d}	37.3 ± 1.6^{e}	0.001

[a] Animals fed ad libitum throughout to final slaughter weight.

[b] Animals restricted for 2 mo followed by refeeding to final slaught [illegible] ht.

[c] Animals restricted for 4 mo followed by refeeding to final slaugh[illegible]

[d,e] Means within a row with different superscripts differ (P<0[illegible]

[f] Fat depot weight expressed as percentage of the 3-rib joint total [illegible]

($P<0.05$) in the R4FM group than in the R0FM and R2FM groups. The amount of IMF was greater ($P<0.05$) in the 3-rib joint of the R0FM group than in the R4FM group while the amount in the R2FM group was not different from either treatment. The proportion of IMF was higher ($P<0.05$) in the R0FM and R2FM groups than in the R4FM group.

The overall changes in the proportion of the SCF and IMF depots are illustrated in Figures 3.14 and 3.15 respectively. It can be seen that the change in percent SCF in the third period of the experiment was not significant in the ad lib fed animals; it increased by about 27% in the 2-month restricted-refed animals, and increased by over 368% in the 4-month restricted-refed animals. The change in percent IMF was not significant in the ad lib fed and 2-month restricted-refed animals while there was an increase of 87% in the 4-month restricted-refed animals over the period.

It is clear from Figure 3.14 that the R4FM animals accumulated more SCF in the 3-rib joint than the other two groups during the period of refeeding. It was not surprising that there was such a large amount of SCF accumulation considering that the feed intake increased considerably during the refeeding of these animals. As discussed earlier, more feed was being converted into fat and being stored under the skin as SCF. Therefore, a large amount of total fat was SCF. The difference between the two restricted-refed groups (R2FM vs R4FM) in percent SCF was possibly due to the differences in the severity of feed restriction, the R2FM animals having been subjected to a milder restriction than the R4FM animals.

The overall trend in the accumulation of IMF was a steady

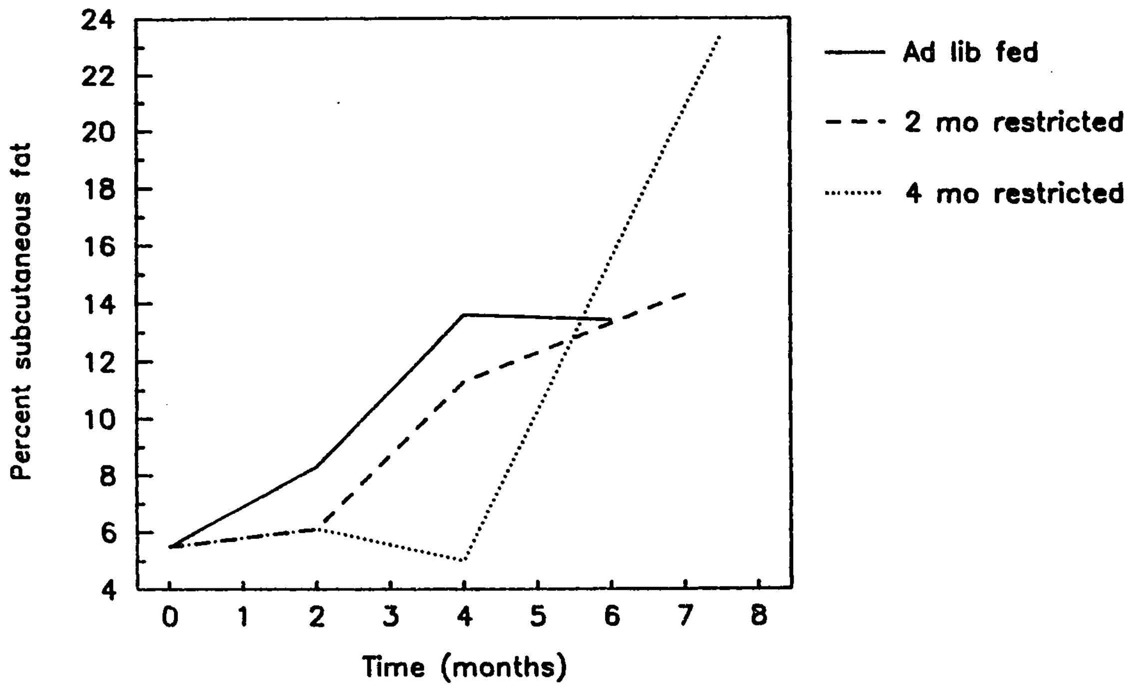

Figure 3.14. Change in the proportion of 3-rib joint subcutaneous fat over time from ad lib, 2 mo and 4 mo feed restriction of heifers followed by refeeding to about 400 kg.

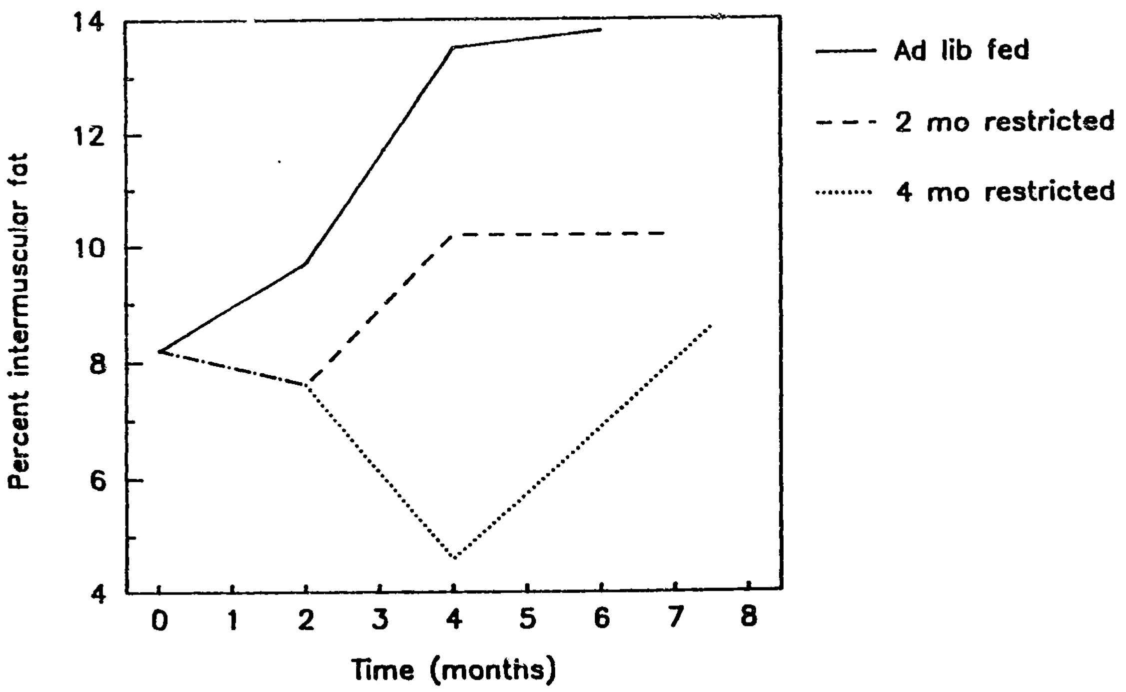

Figure 3.15. Change in the proportion of 3-rib joint intermuscular fat over time from ad lib, 2 mo and 4 mo feed restriction of heifers followed by refeeding to about 400 kg.

increase in the ad lib fed and 2-month restricted-refed animals while this depot did not catch-up in the 4-month restricted-refed animals. This may be attributed to local pressures described by Berg and Butterfield (1976). At that chronological age (i.e. third period), resistance was probably already building up in the IMF depot while it was becoming less in the SCF depot.

Relative deposition patterns of the two depots were examined using allometry. Over the refeeding periods of the 2-month restricted animals, there was no significant difference between the *b* values of the fat depots in the ad lib fed and 2-month restricted-refed animals (Table 3.17). However, during the refeeding of the 4-month restricted animals, comparison of the allometric coefficients, calculated for the weight of each depot versus total fat weight in the 3-rib joint showed that the SCF depot increased at a significantly higher ($P<0.05$) rate in the 4-month restricted-refed animals than in the ad lib fed animals (Table 3.18 and Figure 3.16). The 2-month restricted-refed animals were not different from either group. On the other hand, the IMF depot increased at a higher ($P<0.05$) rate in the ad lib and 2-month restricted-refed animals than in the 4-month restricted-refed animals (Table 3.18 and Figure 3.17).

It can also be seen that the fat depots within each treatment increased at different rates, causing their proportions to change as the heifers became fatter. For example in the R4FM animals, with increasing total fat weight in the 3-rib joint during refeeding, the proportion of SCF increased at a relatively higher rate than the proportion of IMF depot. Thus at final slaughter weight, there was

TABLE 3.17. LINEAR RELATIONSHIP OF THE TYPE: $\mathrm{LOG}y=\mathrm{LOG}a+b.\mathrm{LOGX}$ OF THE 3-RIB JOINT FAT DEPOT WEIGHTS ON 3-RIB JOINT TOTAL FAT WEIGHT OF TWO GROUPS OF HEIFERS

	Ad libitum fed[a] n = 16			2 months restricted[b] n = 16			
Item	a	b	R^2	a	b	R^2	Probability[c]
Log subcutaneous fat wt	-0.8	1.14±0.1	0.96	-1.1	1.24±0.1	0.96	0.14
Log intermuscular fat wt	-0.1	0.93±0.1	0.98	-0.2	0.85±0.1	0.97	0.08

[a] Animals fed ad libitum and serially slaughtered at 2 mo, 4 mo and final slaughter weight of about 400 kg.

[b] Animals restricted for 2 mo followed by refeeding and serially slaughtered at 2 mo, 4 mo and final slaughter weight of about 400 kg.

[c] Comparison of b values.

TABLE 3.18. LINEAR RELATIONSHIP OF THE TYPE: LOGy=LOGa+b.LOGX OF THE 3-RIB JOINT FAT DEPOT WEIGHTS ON 3-RIB JOINT TOTAL FAT WEIGHT OF THREE GROUPS OF HEIFERS

Item	Ad libitum fed[a] n = 12			2 months restricted[b] n = 12			4 months restricted[c] n = 12			Probability[d]
	a	b	R^2	a	b	R^2	a	b	R^2	
Log subcutaneous fat wt	-0.2	0.92 ± 0.1^{e}	0.86	-0.9	1.19 ± 0.1^{ef}	0.92	-1.5	1.41 ± 0.1^{f}	0.98	0.005
Log intermuscular fat wt	-0.4	1.05 ± 0.1^{e}	0.94	-0.2	0.86 ± 0.1^{e}	0.93	0.6	0.66 ± 0.1^{f}	0.95	0.001

[a] Animals fed ad libitum and serially slaughtered at 4 mo and final slaughter weight of about 400 kg.

[b] Animals restricted for 2 mo followed by refeeding and serially slaughtered at 4 mo and final slaughter weight of about 400 kg.

[c] Animals restricted for 4 mo followed by refeeding and serially slaughtered at 4 mo and final slaughter weight of about 400 kg.

[d] Comparison of b values.

[e,f] b values within a row with different superscripts differ ($P<0.05$).

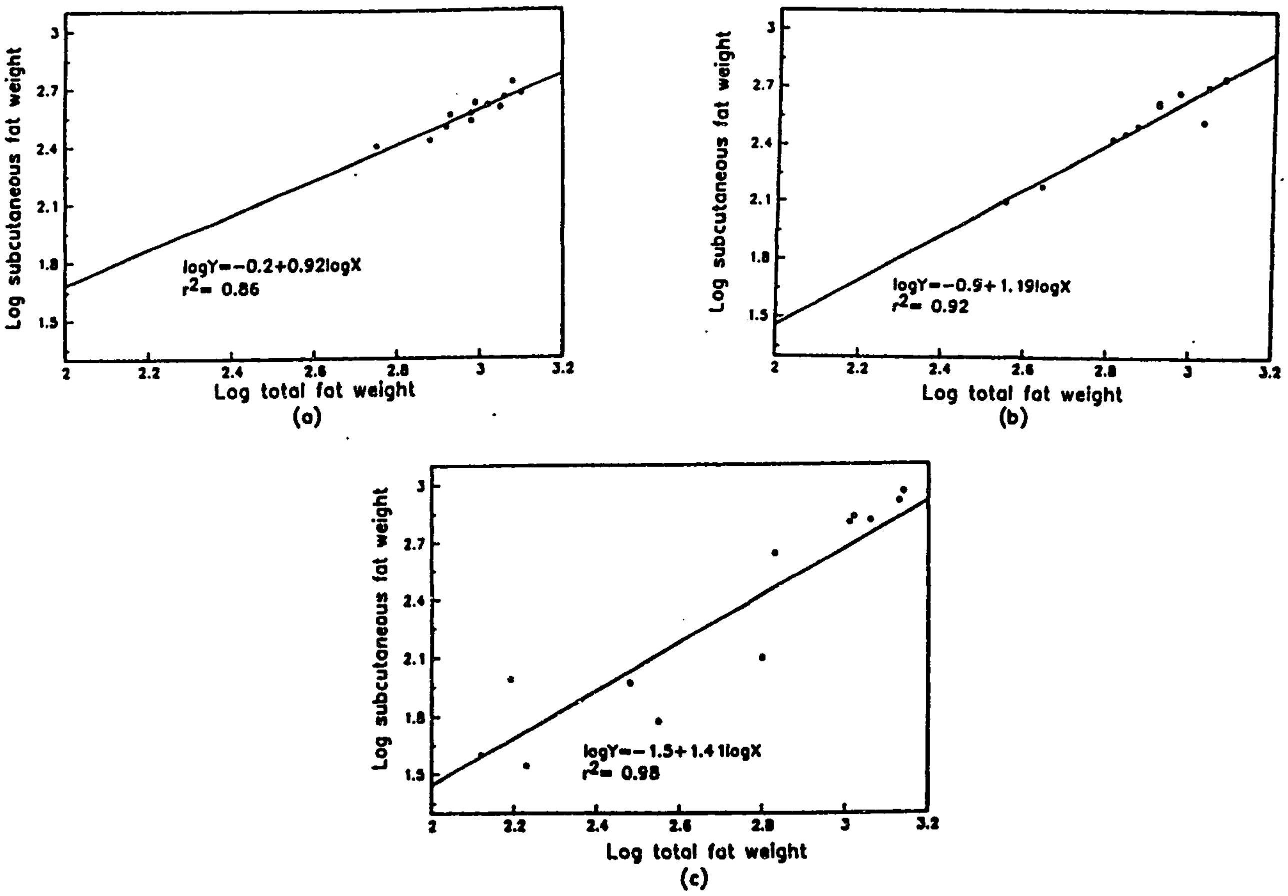

Figure 3.16. Linear relationship of the type: $log\ y = log\ a + b.log\ x$ of 3-rib joint subcutaneous fat weight on 3-rib joint total fat weight of two slaughter groups from ad libitum (a), 2-mo restricted-refed (b) and 4-mo restricted-refed (c) heifers.

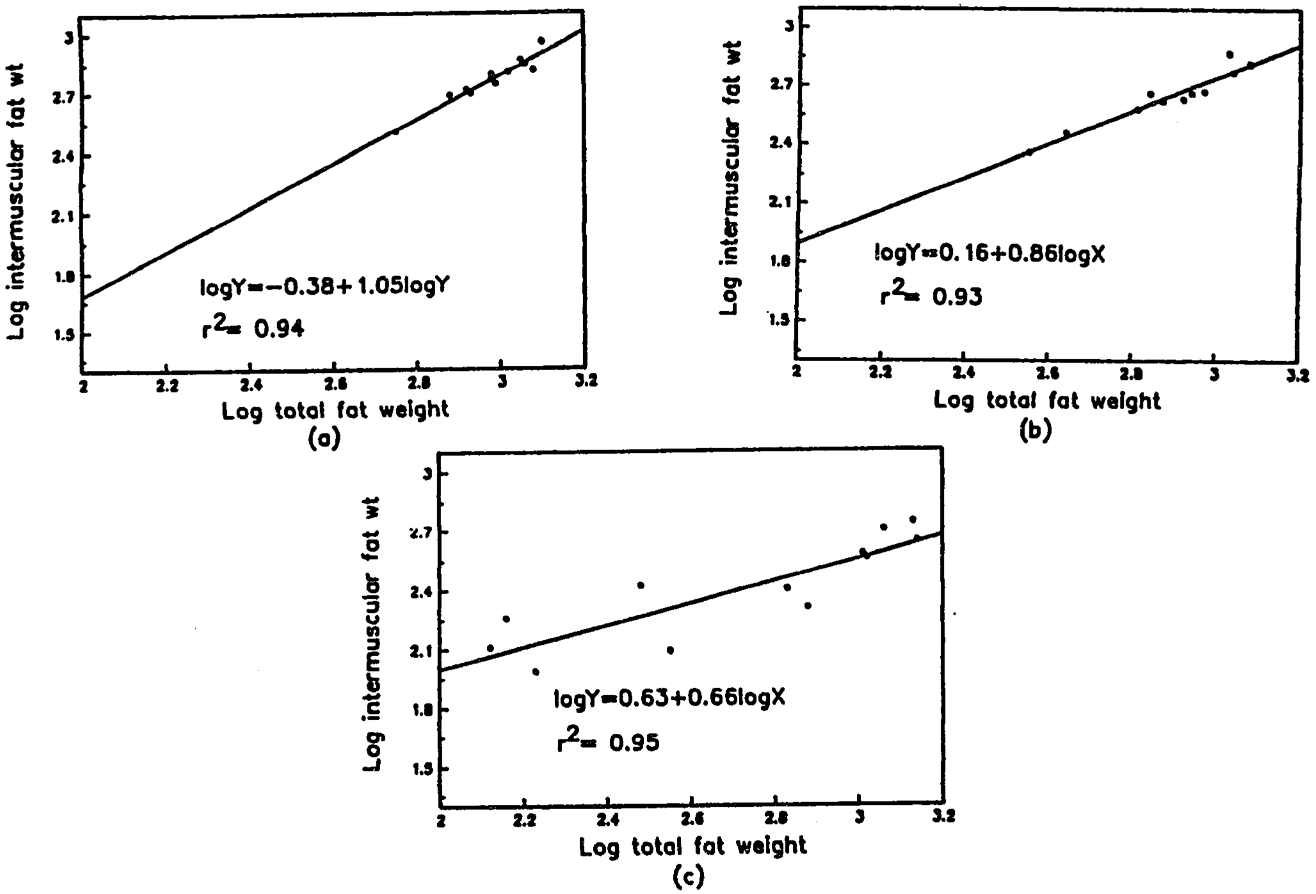

Figure 3.17. Linear relationship of the type: *log y -log a + b.log x* of 3-rib joint intermuscular fat weight on 3-rib joint total fat weight of two slaughter groups from ad libitum (a), 2-mo restricted-refed (b) and 4-mo restricted-refed (c) heifers.

more SCF than IMF in the 3-rib joint of the refed R4FM animals. In the R0FM and R2FM animals, the trend was opposite.

3.3.8. Interactions

Only the proportion of SCF showed a significant treatment by period interaction. Percent SCF, like total fat, was similar in both the ad lib fed and 2-month restricted-refed animals at the end of the second period and remained relatively constant during the third period of the experiment. In the 4-month restricted animals, percent SCF was significantly lower than in the other treatments at the end of the second period but increased significantly during the third period, exceeding that in the other treatments at the final slaughter weight.

3.3.9. Relationship between the propotions of the 3-rib joint and left side major carcass tissues and fat depots

Comparison of the proportions of the major carcass tissues and fat depots between 3-rib joints and left sides at the end of the second period (Table 3.19) and at the final slaughter weight (Table 3.20) showed that the 3-rib joint was not a good estimator of the side carcass composition of an animal. Although the overall correlations between the 3-rib joints and left sides showed that percent bone and percent total fat were significantly correlated (Table 3.21), the r^2 for these parameters was rather too low.

Hankins and Howe (1946), and later other workers (Marchello et al., 1979; Lunt et al., 1985), developed the 3-rib joint dissection technique as a cheaper method of determining carcass composition in beef animals. This is because of the huge costs involved in the dissection or chemical analysis of the entire animal carcass. All the above workers and several others have generally found that the standard 9-10-11th rib joint is highly correlated with the whole animal carcass in terms of the major carcass tissues (fat, muscle and bone). The correlations are especially high for the percentage of the total fat. The results from the present study show a similar trend with the general findings, but other workers have reported higher correlation coefficients than in this study.

Hankins and Howe (1946) found that in their first group of animals consisting of 53 steers and 24 heifers, the overall correlation coefficient for percent fat was 0.99. In the second group of animals consisting of 84 steers and 36 heifers, the authors

TABLE 3.19. COMPARISON OF THE PROPORTIONS OF THE MAJOR CARCASS TISSUES[a] AND FAT DEPOTS[b] BETWEEN 3-RIB JOINTS AND LEFT SIDE CARCASS DISSECTIONS OF HEIFERS AT 4 MONTHS

	R0F4[c]		R2F2[d]		R4F0[e]	
Item	3-Rib joint	Side	3-Rib joint	Side	3-Rib joint	Side
No. of carcasses	2	2	2	2	2	2
%Muscle	48.3	59.2	57.2	61.8	59.6	57.1
%Bone	15.2	15.6	21.6	20.2	24.8	30.7
%Total fat	36.5	25.2	21.2	18.0	15.6	12.2
%Subcutaneous fat	41.2	38.2	35.0	37.8	36.1	30.8
%Intermuscular fat	58.8	61.8	65.0	62.2	63.9	69.2

[a] Tissue weight expressed as percentage of either the 3-rib joint or side carcass weight.

[b] Fat depot weight expressed as percentage of either the 3-rib joint or side total fat weight

[c] Animals fed ad libitum for 4 mo.

[d] Animals restricted for 2 mo followed by refeeding for 2 mo.

[e] Animals restricted for 4 mo.

TABLE 3.20. COMPARISON OF THE PROPORTIONS OF THE MAJOR CARCASS TISSUES[a] AND FAT DEPOTS[b] BETWEEN 3-RIB JOINTS AND LEFT SIDE CARCASS DISSECTIONS OF HEIFERS AT ABOUT 400 kg

	R0FM[c]		R2FM[d]		R4FM[e]	
Item	3-Rib-joint	Side	3-Rib-joint	Side	3-Rib-joint	Side
No. of carcasses	2	2	2	2	2	2
%Muscle	55.0	60.0	53.6	57.7	46.9	55.9
%Bone	16.0	16.1	18.0	15.4	17.6	16.2
%Fat	29.0	23.9	28.3	26.9	35.6	27.8
%Subcutaneous fat	39.0	34.0	44.6	42.3	64.6	39.4
%Intermuscular fat	61.0	66.0	55.4	57.7	35.4	60.6

[a] Tissue weight expressed as percentage of either the 3-rib joint or side carcass weight.

[b] Fat depot weight expressed as percentage of either the 3-rib joint or side total fat weight.

[c] Animals fed ad libitum throughout to final slaughter weight.

[d] Animals restricted for 2 mo followed by refeeding to final slaughter weight.

[e] Animals restricted for 4 mo followed by refeeding to final slaughter weight.

TABLE 3.21. POOLED CORRELATIONS (R) OF THE PROPORTIONS OF THE MAJOR CARCASS TISSUES AND FAT DEPOTS BETWEEN 3-RIB JOINTS AND LEFT SIDE CARCASS DISSECTIONS OF HEIFERS[a]

Item	Correlation Coefficient (R)	Probability
%Muscle	0.40	0.10
%Bone	0.81	0.001
%Total fat	0.85	0.001
%Subcutaneous fat	0.36	0.12
%Intermuscular fat	0.36	0.12

[a] Heifers slaughtered at the end of 4 mo of feed restriction and final slaughter weight from: ad libitum fed, 2-month restricted-refed and 4-month restricted-refed animals.

reported overall correlation coefficients of 0.93, 0.85 and 0.83 for percent fat, percent muscle and percent bone respectively. When the heifers were considered separately, the correlation coefficients were respectively 0.88, 0.72 and 0.83 for the above tissues. Because of the relatively lower correlation coefficient for muscle, the authors questioned the use of the muscle content of the 3-rib joint for estimating that of the carcass for heifers. However, they found that the correlation for protein content was higher (0.77) and noted that the 3-rib joint could be used for estimating protein in carcasses of heifers.

In the present study, the standard 10-11-12th rib joint was used as the estimator of carcass composition. This 3-rib joint has been used in other studies (Arthur et al., 1989), and the major reason for using it instead of the usual 9-10-11th rib cut is that of the Canadian system of quartering beef carcasses (between 12th and 13th ribs).

Probably the relatively low correlation coefficients for the carcass components, particularly muscle, in this study can be attributed mainly to the small numbers of carcasses whose full sides were dissected.

CHAPTER FOUR

MUSCLE FIBER CHARACTERISTICS

4.1. LITERATURE REVIEW

4.1.1. Types of muscle fibers

There are several ways of classifying muscle fibers. One commonly used method is based on the ATPase activity of their myosin (Moody et al., 1980; Suzuki and Cassens, 1983; Arnold and Meyer, 1988). On this basis, three fiber-types can be identified; they are "red" (βR) fibers, "white" (αW) fibers and "intermediate" (αR) fibers.

Red fibers are physiologically slow and contain a high oxidative enzyme activity and low myosin ATPase activity (Moody and Cassens, 1968). They are thus adapted for repetitive contraction requiring continual energy production and therefore a constant source of oxygen, nutrients and waste removal (Ashmore et al., 1972). On the other hand, white fibers are glycolytic and have a high myosin APTase activity. They derive a greater proportion of their energy anaerobically from the metabolism of endogenous glycogen stores. The intermediate fibers have a mixed oxidative-glycolytic activity (White et al., 1978).

Each muscle in an animal has a characteristic proportion of each fiber-type (Guth and Yellin, 1971; Ashmore et al., 1972, 1974; Seideman and Theer, 1986). West (1974) showed that the type of muscle as well as location within a muscle can have a significant effect on fiber-type characteristics. Muscles perform different functions and depending on this, the proportion of fiber-types will differ from one muscle to another.

Regarding function per se, all muscles maintain a certain degree of tone at all times, yet some have to exert a continuous tension to maintain the animal in a standing position, while still others are only called into action to perform quick and powerful movements (Joubert, 1956; Ashmore et al., 1972). Muscles which are used to maintain posture, or which otherwise are used frequently by the animal, have a relatively higher proportion of βR fibers. Those that are less active contain relatively more αW fibers because such muscles are used only for explosive work. For example, Moody and Cassens (1968) reported that in pigs, the trapezius muscle has a much higher proportion of βR fibers than the longissimus muscle. They concluded that this is because the trapezius muscle has a more tonic function than does the longissimus muscle which is a typical white muscle with largely phasic function.

4.1.2. Muscle fiber transformations

Muscle fibers undergo a continual alteration throughout life as an adaptation to changing functional demands, and that "fiber-type" merely reflects the constitution of a fiber at any particular time (Guth and Yellin, 1971). From an agricultural point of view, this is particularly interesting since it suggests the existence of some degree of genetic or developmental plasticity in the fiber-type continuum.

Several factors influence the transformation of one fiber-type to another (Joubert, 1956; Johnston et al., 1981). The transformation of αR to αW fibers is particularly well established (Ashmore et al., 1972; Rahelic and Puac, 1981; Solomon et al., 1988). Transformation of βR to αW fibers has also been reported (Moody et al., 1980) although more work needs to be done on this. In cattle (Ashmore et al., 1972) and pigs (Rahelic and Puac, 1981), there is evidence that domestication is one such factor that has promoted the transformation of fibers from αR to αW. Rahelic and Puac (1981) showed that a relatively greater proportion of muscle fibers in wild pigs are red while a relatively greater proportion in domesticated pigs are white. Ashmore et al. (1972) concluded that domestication results in protection of animals from their natural enemies and removal of need to look for food and water; this reduces the requirement for muscular endurance and the result is a decrease in red fibers and an increase in white fibers.

Management practices (e.g. feeding systems, environment and stress) and genetic factors (e.g. breed, gender, age, live weight) have also been found to play a major role in fiber-type transformations (Joubert, 1956; Johnston et al., 1981; Rahelic and Puac, 1981). Those practices which tend to restrict muscular activity of meat-producing animals would be expected to increase the proportion of white fibers and conversely, practices which tend to promote muscular activity would increase the proportion of red fibers (Ashmore et al., 1972).

As an animal grows, the functional demands of muscles change. Thus as live weight increases, we would naturally expect muscle fiber transformations to take place in order to cope with the demands of the muscles. Evidence was provided by Moody et al. (1980) who observed a shift in the relative numbers of the different fiber-types as live weight increased in lambs. βR fibers became less numerous while αW fibers became more numerous. The authors suggested that this finding could in fact have important implications in muscle growth and development since it shows that APTase activity may not be fixed at birth. Holmes and Ashmore (1972) also obtained results that supported the hypothesis that increasing transformation of α fibers from αR to αW fibers is correlated with increasing muscularity.

Age which, under normal conditions is directly related to live weight change, also affects muscle fiber transformations. Holmes and Ashmore (1972) found that as calves age, the proportion of white fibers increases. On the contrary, Suzuki and Cassens (1983) showed in sheep that white fibers decreased greatly in proportion from birth to four weeks of age and were essentially unchanged during further growth of the animals. Red fibers increased in proportion from birth to four weeks, increased slightly from four to twelve weeks, and then underwent little further change.

Nutrition is another important factor influencing muscle fiber transformations. Type of feed and plane of nutrition have both been implicated in such transformations. For example, Johnston et al. (1981) observed that there were relatively fewer αR and αW fibers in the longissimus muscle of grain-plus-grass fed lambs. In general as energy level in the ration increased the percentage of

αR fibers decreased and that of αW increased. Moody et al. (1980) had earlier postulated that the available source of energy in lamb rations appeared to cause a physiological shift from αR to αW fiber-types. The workers had found that lambs fed pasture without creep had a higher percentage of αR fibers than lambs in drylot. Conversely, αW fibers were more numerous in the drylot group.

As far as plane of nutrition is concerned, several studies have shown that high plane of nutrition (ad lib feeding) increases the proportion of αW while restricted feeding increases the proportion of βR fibers (Moody et al., 1980; Reid et al., 1980; Solomon et al., 1988). Reid et al. (1980) found that underfed cows had relatively more βR fibers than ad lib fed cows while αW fibers were relatively less in the former than the latter. In pigs, Solomon et al. (1988) similarly observed that pigs with ad lib access to feed had fewer αR fibers and more αW fibers in the longissimus muscle compared with restricted pigs. The authors concluded that restricted feed intake reduced transformation from αR to αW fibers.

Given all this information, there is need to establish whether or not refeeding the underfed animals to the same levels as the ad lib fed animals can reverse the fiber transformations back to the "normal" situation.

4.1.3. Muscle fiber size

The size of an animal is a function of its cell size and cell number (Moody et al., 1980). It has been demonstrated that muscle fiber numbers remain unchanged from around birth throughout an animal's life (Joubert, 1956; Staun, 1963). Thus growth in animals after birth is the result of an increase in the size of cells present at that time. Hammond (1932) and Joubert (1956) measured the average diameter in different muscles in lambs and sheep. They found that the postnatal growth of muscles was largely due to an increase in the length and diameter of muscle fibers.

Any factor that decreases the hypertrophy of the muscle cells consequently decreases the amount of muscle on the animal. Several factors are associated with the size of muscle cells in an animal; these include breed, gender, live weight, age and nutrition (Joubert, 1956; Yeates, 1964). Joubert (1956) noted that there can be little doubt that the wide range of factors affecting growth in body weight have an equal bearing on the development of individual muscle fibers. For example, Reid et al. (1980) observed in dairy cows that as the body weight of the animals fluctuated, the muscle fiber diameter fluctuated accordingly.

Muscle fiber diameter also increases with age. Joubert (1956) reported that the mean muscle fiber diameter of the longissimus muscle in lambs was 9.3 μm at birth; at age 60 d, the mean diameter was 33.6 μm and in fully developed sheep the diameter was 49.2 μm. The author pointed out that chronological age afforded an adequate explanation in a homogenous population particularly in respect of "weight for age". Tuma et al. (1962) and Staun (1963) also found that the diameter of muscle fibers continued to increase with increasing age of the animals. Staun (1963) found in pigs that the greatest increase in fiber diameter occured during the growth period 15-30 kg where it was 1.21 µm per kg increase in live weight. During the period 30-60 kg the corresponding figure was 0.41 µm, and from 60-90 kg there was only 0.11 µm per kg gain in live weight.

Plane of nutrition also has a major influence on the size of muscle fibers. Joubert (1956) stated that it was reasonable to conclude that the effect of nutrition is primarily associated with quantitative, and only secondarily with qualitative aspects of meat. The producer's major concern is how much muscle is to be gained from improved nutrition and, conversely, what loss will result from inadequate nutrition.

In catch-up growth studies, one important thing that needs to be established is whether or not muscle fiber size can compensate fully during the refeeding period.

4.2. MATERIALS AND METHODS

4.2.1. Sampling from the longissimus muscle, fiber typing and fiber diameter measurement

On the day following slaughter, two samples (1 cm^3 each) were removed from the centre of the 11th rib portion of the longissimus muscle immediately after cutting the standard 10-11-12th rib joints from all the carcasses. These were used for fiber typing. A third sample (about 0.2 g), for fiber diameter determination, was cut from the same central location of the rib joint. The samples were put in small plastic bags and taken to the Histology Laboratory within an hour after removal.

The two 1 cm^3 samples from each rib joint were immediately mounted on cryostat chucks, with the muscle fibers oriented perpendicular to the cutting blade. They were encased in isopentane, frozen in liquid nitrogen at -179 C and stored overnight at -20 C.

The following morning, cross sections of 8 μm were cut, mounted on microscope slides (two slides per sample) and stored at room temperature for 30 minutes. The sections were fixed for five minutes in 5% formalin (Guth and Samaha, 1970). They were then pre-incubated in a $CaCl_2$ buffer (pH 10.4) for 15 minutes. They were rinsed in a solution of calcium chloride and incubated for 30 minutes at 37 C in a buffer (pH 9.4) containing ATP. They were placed in a $CoCl_2$ solution for three minutes during which a precipitate of cobalt phosphate was formed. The sections were then placed in a dilute solution of ammonium sulphide during which the cobalt phosphate reacted with the sulphide to form cobalt sulphide which appeared as a dark brown precipitate at the site of enzyme activity. The stained sections were rinsed in distilled water, dehydrated in graded (70%, 85%, 95% and 100%) ethanol, cleared in xylene and finally mounted in permount.

The following day, a single, randomly selected field from each slide was photographed at 10x magnification using a Nikon Leitz System camera (Wetzlar, W. Germany) mounted on a Leitz-Dialux 20 EB microscope (Wetzlar, W. Germany). From the photographs, all the fibers in the field were classified on the basis of color into one of the three fiber-types βR, αW and αR (see Figure 4.1).

The muscle samples for fiber diameter determination were immediately fixed in 10% formalin and stored at 4 C for later analysis. At analysis, each sample was placed in a 15 ml glass tube of 16 mm diameter. About 5 ml of physiological saline were added to the sample and homogenized (Hegarty and Naude, 1970) at 900 rpm for 5 to 10 seconds using a polytron homogenizer. The barrel of the homogenizer was washed in distilled water after each sample. Using a pasteur pipette, a drop of the homogenate was transferred to a hanging-drop slide with a 15 mm diameter well. The homogenate was covered with a slide cover slip and while still fresh, 50 random fibers had their diameters measured at their greatest width with an ocular micrometer.

4.2.2. Statistical analysis

The muscle fibers for each animal were counted and the number of each type expressed as the percentage of the total. Analysis of

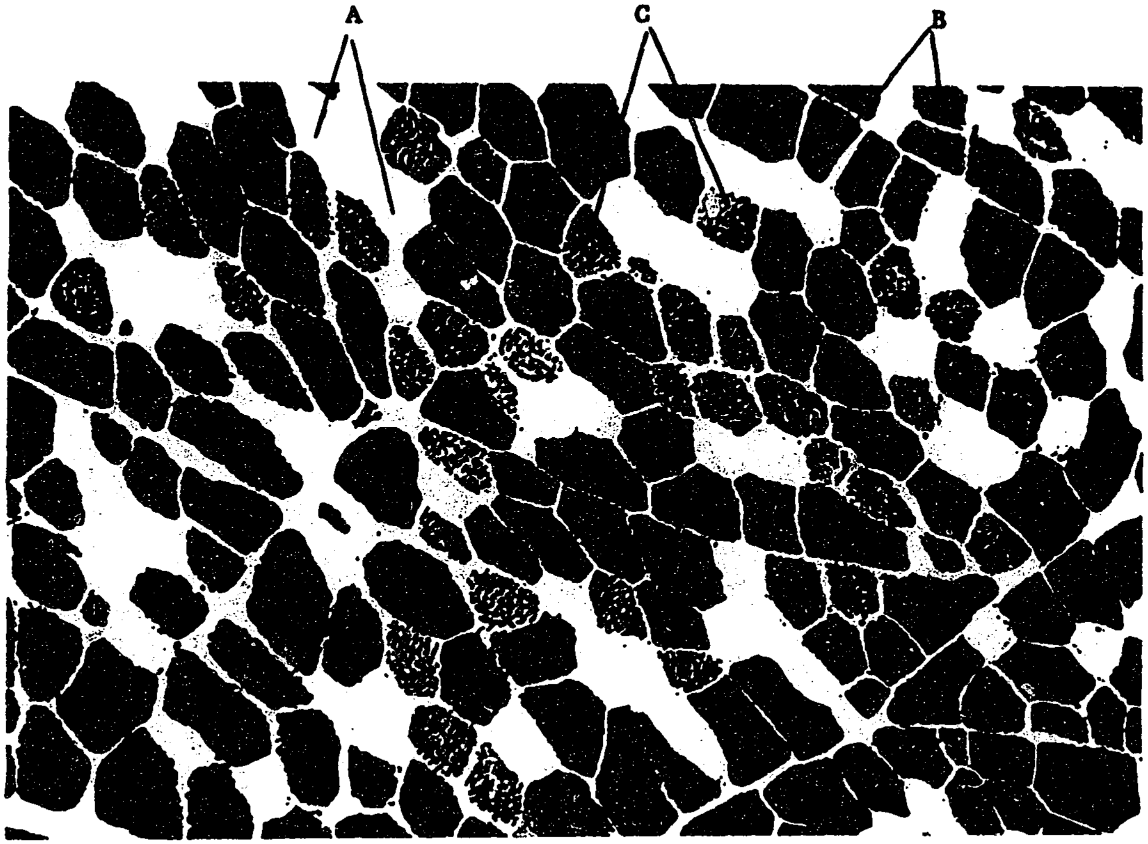

Figure 4.1. The three types of longissimus muscle fibers from heifers slaughtered at various times (see text): A-red fibers; B-white fibers; C-intermediate fibers.

variance for fiber-types and diameters was done according to the model described under section 2.2.3.

4.3. RESULTS AND DISCUSSION

Feed restriction for 2 months did not cause a significant change in the proportions of the muscle fiber-types in the longissimus muscle (Table 4.1). However, one surprising thing was that the R0F2 and R2F0 animals were both similar to the INIT animals. Assuming that the INIT group was the baseline of the whole population, it could then be stated that the proportions of the different muscle fiber-types did not change over the first 2 months. This was despite the significant increase ($P<0.05$) in the live weight of both the R0F2 and R2F0 groups from the INIT group. With this increase in the live weight, it would be expected that muscle fiber transformations would naturally take place to cope with the muscular functional demand.

Studies in sheep (Moody et al., 1980), cattle (Reid et al., 1980) and pigs (Solomon et al., 1988) have shown that ad libitum feeding is associated with an increased proportion of αW fibers while feed restriction is associated with an increase in the proportion of βR fibers. Such a trend was not evident in the present study of heifers, at least during the first 2 months of feed restriction. One of the most probable reasons for this could be that the feed restriction during this period was not severe enough to cause any significant change in the demands of the longissimus muscle. Of course other factors (environment, breed and gender) as suggested by Joubert (1956) and Rahelic and Puac (1981) may have played a role.

On the other hand, feed restriction for 2 months was associated with smaller ($P<0.05$) muscle fiber diameters in the longissimus

TABLE 4.1. LEAST SQUARES MEANS ± STANDARD ERRORS OF LONGISSIMUS MUSCLE FIBER-TYPE PROPORTIONS AND DIAMETERS OF HEIFERS FED FOR 2 MONTHS

Item	INIT[a]	R0F2[b]	R2F0[c]	Probability
No. of animals	5	6	6	
Slaughter wt, kg	211 ± 17[d]	296 ± 23[e]	246 ± 12[e]	0.02
Slaughter age, d	199 ± 4[d]	255 ± 5[e]	254 ± 5[e]	0.001
<u>Fiber proportions</u>				
%Red fibers (βR)	27.6 ± 1.1	28.2 ± 1.6	31.8 ± 2.3	0.25
%White fibers (αW)	44.4 ± 3.0	49.4 ± 2.3	46.4 ± 0.9	0.30
%Intermediate (αR)	28.0 ± 3.2	22.4 ± 1.5	21.8 ± 1.7	0.14
Fiber diameter, μm	38.2 ± 1.5[d]	68.5 ± 1.9[e]	46.0 ± 1.4[f]	0.001

[a] Animals slaughtered at d 1 (25 d after weaning).

[b] Animals fed ad libitum for 2 mo.

[c] Animals restricted for 2 mo.

[d,e,f] Means within a row with different superscripts differ ($P<0.05$).

muscle of the R2F2 group than in the R0F2 group; the INIT group had significantly smaller ($P<0.05$) muscle fiber diameters than the R2F0 group. This means that the mean fiber diameter in both the R0F2 and R2F0 animals increased significantly over the first period. This was not surprising since the R2F0 animals gained some weight during this period. Since the size of an animal is a function of its cell size (Moody et al., 1980), one would expect the R0F2 animals to have larger muscle fiber diameters than the R2F0 and INIT animals.

Four months feed restriction was associated with significant changes in muscle fiber-type proportions as well as fiber diameters (Table 4.2). The R4F0 group had relatively more ($P<0.05$) βR fibers in the longissimus muscle than the INIT group which in turn had relatively more ($P<0.05$) than in the R0F4 and R2F2 groups. Conversely, the proportion of αW fibers was higher ($P<0.05$) in the R0F4 and R2F2 groups than in the R4F0 and INIT groups. The proportion of αR fibers was higher ($P<0.05$) in the INIT group than in the other groups.

The changes that took place during the second period can be attributed to the plane of nutrition in the different treatments, age and live weight change of the animals. Under normal feeding conditions, the proportion of white fibers would be expected to increase as the animal gains weight, since the increase in muscle is associated with an increase in the proportion of white fibers. Holmes and Ashmore (1972) found that as calves age, the proportion of white fibers increases, although Suzuki and Cassens (1983) found otherwise in sheep. The findings of the present study agree with those of

TABLE 4.2. LEAST SQUARES MEANS ± STANDARD ERRORS OF LONGISSIMUS MUSCLE FIBER-TYPE PROPORTIONS AND DIAMETERS OF HEIFERS FED FOR 4 MONTHS

Item	INIT^{a}	R0F4^{b}	R2F2^{c}	R4F0^{d}	Probability
No. of animals	5	6	6	6	
Slaughter wt, kg	211 ± 17^{e}	343 ± 4^{f}	314 ± 7^{f}	244 ± 12^{e}	0.001
Slaughter age, d	199 ± 4^{e}	315 ± 4^{f}	317 ± 5^{f}	311 ± 5^{f}	0.001
<u>Fiber proportions</u>					
%Red fibers (βR)	27.6 ± 1.1^{e}	21.0 ± 0.6^{f}	23.9 ± 1.1^{f}	34.9 ± 1.1^{g}	0.001
%White fibers (αW)	44.4 ± 3.0^{e}	57.0 ± 2.3^{f}	55.4 ± 2.0^{f}	44.0 ± 0.8^{e}	0.001
%Intermediate (αR)	28.0 ± 3.2^{e}	22.0 ± 0.8^{f}	20.7 ± 1.4^{f}	21.1 ± 0.6^{f}	0.03
Fiber diameter , μm	38.2 ± 1.5^{e}	66.8 ± 0.9^{f}	77.0 ± 0.1^{g}	52.3 ± 0.2^{h}	0.001

[a] Animals slaughtered at d 1 (25 d after weaning).

[b] Animals fed ad libitum for 2 mo.

[c] Animals restricted for 2 mo followed by refeeding for 2 mo.

[d] Animals restricted for 4 mo.

[e,f,g,h] Means within a row with different superscripts differ ($P<0.05$).

Holmes and Ashmore (1972), but only for the R0F4 and R2F2 animals at the end of the second period. It can be seen from Figures 4.2 and 4.3 that there was a decrease in the proportion of βR fibers from 28.2% to 21.0% and from 31.8% to 23.9% and an increase in the proportion of αW fibers from 49.4% to 57.0% and from 46.4% to 55.4% in the ad lib fed and 2-month restricted-refed animals respectively. No significant changes were found in proportions of αR fibers in these two treatments. On the contrary, there was a significant increase in the proportion of βR fibers while the proportion of αW fibers remained relatively constant in the 4-month restricted animals. Thus the fiber transformations in the 4-month restricted animals did not go the "normal" way with age as in the ad lib fed and 2-month restricted-refed animals. Feed restriction, therefore, played a major role in the observed fiber transformations.

Exactly how and why feed restriction is associated with an increase in the proportion of βR fibers is not known. However, from the speculations of Ashmore et al. (1972), both behavioural and metabolic changes could be implicated. A good example is the comparison between domesticated and wild animals; while many muscles in domesticated animals are predominantly white, the same muscles in wild animals are predominantly red (Rahelic and Puac, 1981). Ashmore et al. (1972) speculated that domestication removes the need of animals to wander about in search of food and water. This, to a great extent, reduces the requirement for muscular endurance and the result is a decrease in the proportion of red fibers and an increase in the white fibers. Similarly, good management practices can result in animals being even "more domesticated" than otherwise. Feed restriction may change the behaviour of animals altogether. Whether confined or not, such animals would always want to search for food, thus keeping their muscles somewhat more active.

Metabolically, the white fibers are glycolytic while the red fibers are oxidative (Ashmore et al., 1972). Since feed restriction causes depletion of glycogen in bovine muscles (Crouse et al., 1984), it is possible that lack of this substrate can influence the changes in muscle fiber-type proportions.

In the present study, there is no evidence as far as the above speculations are concerned. But whether they are applicable or not, they should certainly be taken into account.

It appears from the present study (Figures 4.2, 4.3 and 4.4) that both the αR and βR fibers underwent transformations into αW fibers in the ad lib fed animals during the first two periods. However, it seems that relatively more βR than αR fibers underwent such transformations. The transformation of βR fibers into αW fibers is not well established, although it has been reported (Moody et al., 1980) in lambs. On the other hand, the transformation of αR fibers is well established (Ashmore et al., 1972; Suzuki and Cassens, 1983; Solomon et al., 1988). Why this "normal" trend did not occur to a large extent in the present study is not clear. Thus it can be concluded that nutrition appeared to have relatively less effect on the proportion of αR fibers.

The mean muscle fiber diameter in the longissimus muscle of the

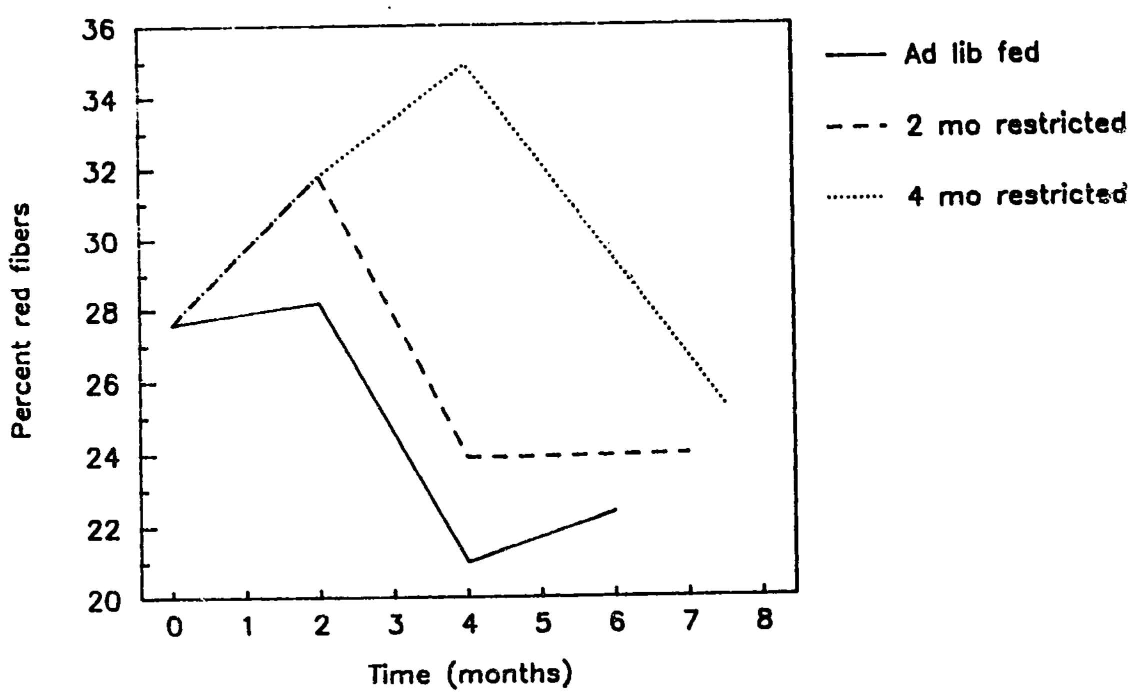

Figure 4.2. Change in the proportions of longissimus muscle red fibers over time from ad lib, 2 mo and 4 mo feed restriction of heifers followed by refeeding to about 400 kg.

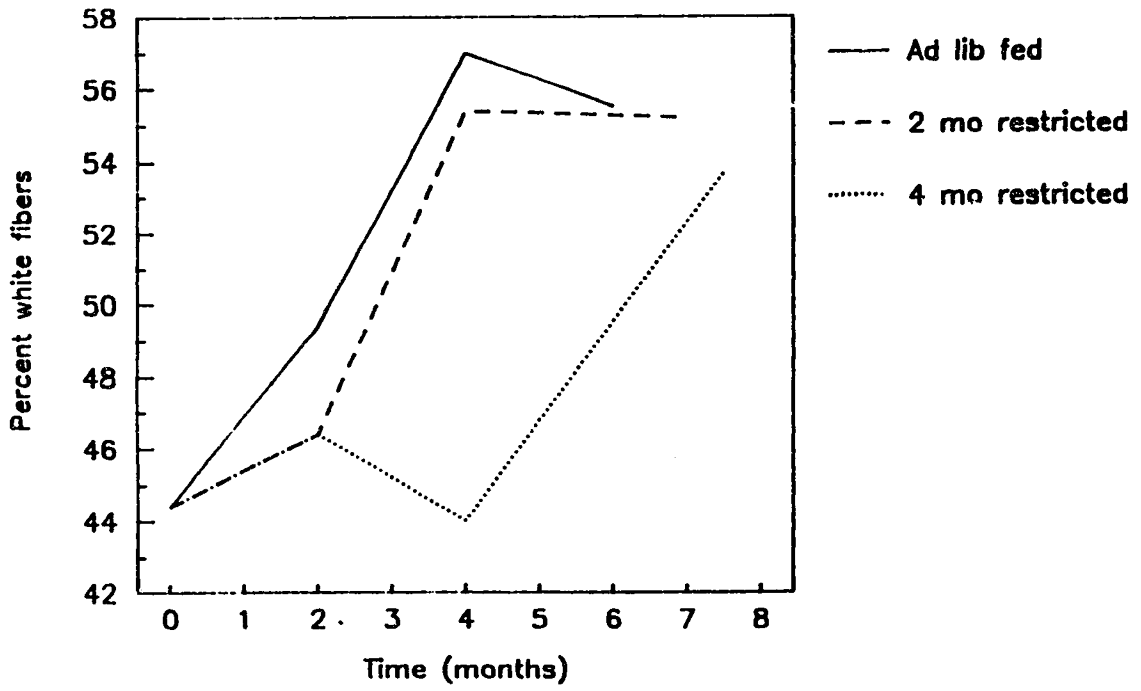

Figure 4.3. Change in the proportions of longissimus muscle white fibers over time from ad lib, 2 mo and 4 mo feed restriction of heifers followed by refeeding to about 400 kg.

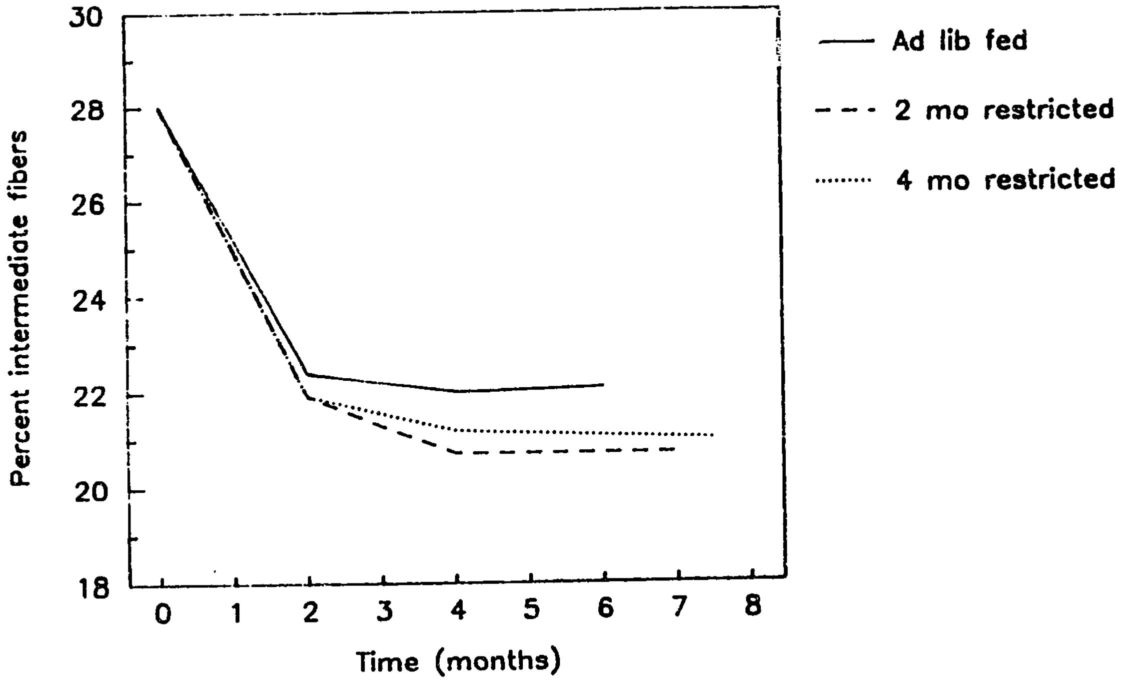

Figure 4.4. Change in the proportions of longissimus muscle intermediate fibers over time from ad lib, 2 mo and 4 mo feed restriction of heifers followed by refeeding to about 400 kg.

R0F4 group was larger ($P<0.05$) than in the R2F2 group which was in turn larger ($P<0.05$) than in the R4F0 group; this was in turn larger ($P<0.05$) than in the INIT group. As at the end of the first period, such differences in the mean muscle fiber diameters were quite expected since the size of the muscle under examination depended on the size (live weight) of the animals in each treatment. These results are in agreement with the findings of Reid et al. (1980) who observed that the changes in muscle fiber diameter in dairy cows appeared to be related to the changes in body weight. It can therefore be concluded that plane of nutrition, which caused the differences in the live weights was associated with the differences in the mean muscle fiber diameters.

When the animals were refed to final slaughter weight, complete catch-up took place and no significant differences were found among treatments in any of the muscle fiber-type proportions (Table 4.3). In the 4-month restricted-refed animals, there was a decrease in the proportion of βR fibers from 34.9% to 25.3% during the refeeding period; meanwhile there was an increase in the proportion of αW fibers from 44.0% to 53.7% during the same period. The proportion of αR fibers in these animals remained relatively constant. In the ad lib fed and 2-month restricted-refed animals, the proportions of all three muscle fiber-types remained relatively constant throughout the third period. Thus during catch-up growth, not only were changes taking place at the tissue and whole animal level, but also at the cellular level. It may therefore be concluded that refeeding of the restricted animals reversed the trend of muscle fiber transformations

TABLE 4.3. LEAST SQUARES MEANS ± STANDARD ERRORS OF LONGISSIMUS MUSCLE FIBER PROPORTIONS AND DIAMETERS OF HEIFERS AT ABOUT 400 kg

Item	R0FM[a]	R2FM[b]	R4FM[c]	Probability
No. of animals	6	6	6	
Slaughter wt, kg	414 ± 19	419 ± 13	408 ± 13	0.88
Slaughter age, d	373 ± 8[d]	401 ± 5[e]	422 ± 7[f]	0.001
<u>Fiber proportions</u>				
%Red fibers (βR)	22.4 ± 0.9	24.0 ± 1.4	25.3 ± 0.7	0.18
%White fibers (αW)	55.5 ± 1.0	55.2 ± 1.6	53.7 ± 1.2	0.60
%Intermediate (αR)	22.1 ± 1.0	20.7 ± 1.4	21.0 ± 1.4	0.74
Fiber diameter, μm	91.7 ± 3.3	84.0 ± 3.6	81.2 ± 3.0	0.10

[a] Animals fed ad libitum throughout to final slaughter weight.

[b] Animals restricted for 2 mo followed by refeeding to final slaughter weight.

[c] Animals restricted for 4 mo followed by refeeding to final slaughter weight.

[d,e,f] Means within a row with different superscripts differ ($P<0.05$).

to that of the ad lib fed animals.

There was no difference (P>0.05) in the mean muscle fiber diameters among treatments at the final slaughter weight. This means that during catch-up growth, the size of the muscle fibers in the longissimus muscle also made a quick recovery to catch-up with the "normal" muscle fiber size. However, the results at the final slaughter weight appear to be in line with those for rib eye areas (see chapter 3) in which there was lack of complete catch-up growth. It is logical that lack of complete catch-up growth in rib eye areas would be reflected at the cellular level since muscle size is a function of muscle fiber size. Although there were no differences in mean fiber diameters among treatments, the trend was that of lack of complete catch-up in the restricted animals.

Considering the whole experimental period, the increase in the mean muscle fiber diameter in the ad lib fed animals was at a high rate during the first 2 months of the experiment, slowing down increasingly as time progressed (Figure 4.5). As for the 2-month restricted-refed animals, the increase was slow during the first 2 months, increased at a very high rate during refeeding and then slowed down in the last phase of the experiment. In the case of the 4-month restricted animals, the increase was slow in the first 4 months and then increased more rapidly during the refeeding period.

Overall it may be concluded from the present study that recovery of animals during catch-up growth takes place at the cellular level, both in terms of muscle fiber proportions and muscle fiber size.

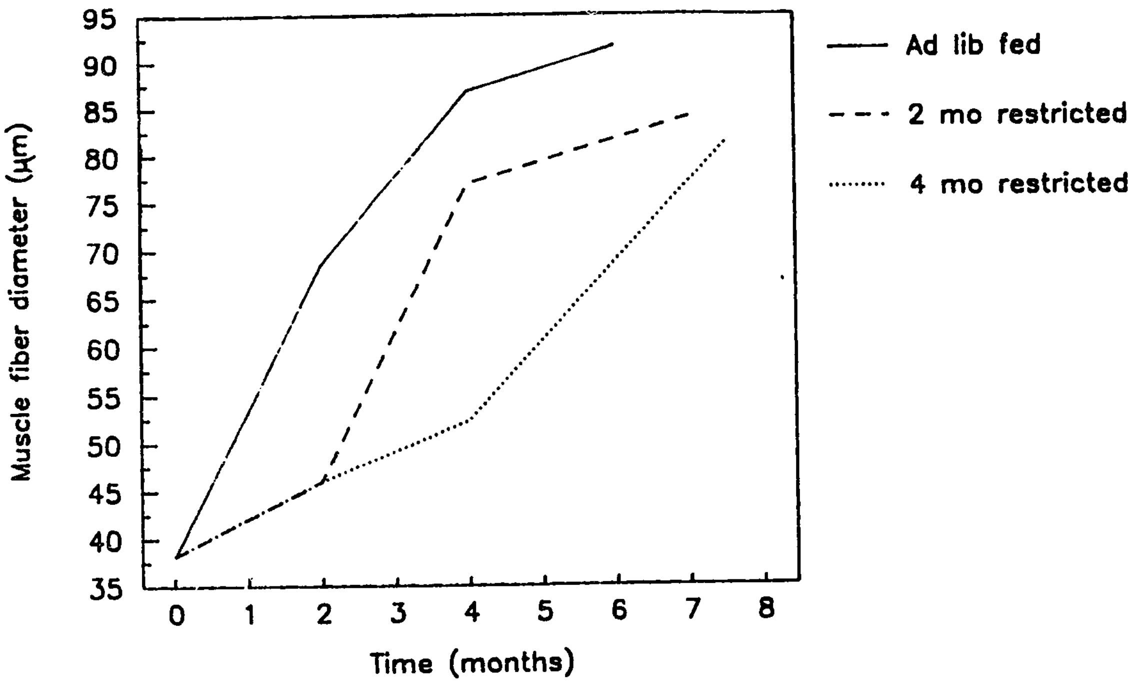

Figure 4.5. Change in the longissimus muscle mean fiber diameters over time from ad lib, 2 mo and 4 mo feed restriction of heifers followed by refeeding to about 400 kg.

4.3.1. Interactions

The proportions of βR and αW fibers and muscle fiber diameters were all affected by treatment by period interaction. At the end of the second period, the proportion of βR fibers was higher while that of αW fibers was lower in the 4-month restricted animals than in the ad lib fed and 2-month restricted-refed animals. During the third period, the proportion of βR and αW fibers respectively decreased and increased significantly in the 4-month restricted-refed animals, while the proportion of these muscle fibers remained relatively constant in the ad lib fed and 2-month restricted-refed animals. The result was a non-significanct treatmemnt effect in the proportions of these fiber-types at the final slaughter weight.

The mean muscle fiber diameters were all different among treatments at the end of the second period. During the third period the increase in the muscle fiber diameters was greater in the 4-month restricted-refed animals than in the 2-month restricted-refed animals which was in turn greater than in the ad lib fed animals. The result was closing up the gap, and at the final slaughter weight there were no significant differences.

CHAPTER FIVE

GENERAL CONCLUSIONS

The phenomenon of catch-up growth is real and whether or not the animals are destined for meat production, catch-up growth may be advantageous in certain situations. During times of feed scarcity, animals can be fed less without compromizing their capacity to recover. It must be borne in mind that the recovery of animals from a nutritional insult depends on several factors, as suggested by Wilson and Osbourn (1960) (see chapter 3, literature review). Therefore, in certain beef production systems, catch-up growth can be utilized to full advantage, particularly in terms of feed costs (e.g. pasture beef production) while it may not be totally advantageous in other systems (e.g. feedlot systems).

In the present study, the heifers which received a more severe feed restriction exhibited more catch-up growth during the refeeding period than those which received a less severe feed restriction. These results support the physiological model proposed by Mosier (1986) in which the brain set-point for body weight appropriate for age is responsible for the high growth rates exhibited during refeeding. There is a strong tendency for animals to reach a certain not necessarily be true. Many reported results on catch-up growth used steers and may not necessarily reflect the response that may be found with heifers. However, one important point to note is that in terms of feed costs, it is cheaper on pasture than feeding grain indoors. In the present study, the restricted-refed heifers ate more during refeeding than the ad lib fed animals but the total intakes at the end of the experiment were similar.

The animals restricted for 2 months took an extra 28 days while those restricted for 4 months took an extra 49 days to reach about 400 kg live weight. The time taken to reach final slaughter weight is obviously one big disadvantage of restricting animals, particularly if they are destined for meat production. The time taken to recover completely for those animals destined for the breeding herd may not be a serious factor, although this requires investigation.

Looking at the pattern of compensation of the carcass tissues, in general body fat which was the most affected tissue in the 3-rib joint during feed restriction, accumulated at a very high rate during refeeding. However, the 4-month restricted animals accumulated fat at a faster rate than the 2-month restricted animals, with the subcutaneous fat depot exceeding the latter and also the ad lib fed animals. The overall total fat was, nonetheless, not significantly different among treatments. Muscle, compared to fat, was less affected by feed restriction and during refeeding recovered completely in the 2-month and 4-month restricted animals. The amount of muscle in the 4-month restricted animals was, however, less than that in the 2-month restricted animals. Bone weight was almost entirely unaffected by any nutritional treatment, although of course its proportion was significantly affected. It appears that a more severe feed restriction was associated with more accumulation of fat during refeeding than building muscle to rebalance the muscle to bone relationship.

Other carcass characteristics investigated were rib eye area, fat cover and marbling. All these were significantly affected by feed restriction. At the final slaughter weight there was no difference among treatments in terms of fat cover and marbling. The rib eye areas in both the 2-month and 4-month restricted-refed animals did not, however, recover completely. Thus despite the similar amount of muscle in the 3-rib joint of the R2FM and the R0FM groups, the former had significantly smaller rib eye areas than the latter. The R4FM group had a lesser amount of muscle in the 3-rib joint than the R2FM group, and the smallest rib eye areas. It can therefore be concluded that feed restriction followed by refeeding to about 400 kg resulted in lack of complete catch-up growth in rib eye areas. From these results, it is also clear that the amount of muscle in the 3-rib joint is not closely associated with the rib eye area.

For non-carcass components, kidney weight did not seem to be affected by any nutritional treatment. Kidneys, though not "nutritional" organs like liver, are metabolically active and it would be expected that a significant change in the nutritional status of the animals would have affected their weight. But it certainly appears that kidneys, unlike liver, are less affected by plane of nutrition. These results are contrary to findings in pigs (Koong et al., 1985) and sheep (Ferrell et., 1986; Black, 1988) where significant effects have been reported. Being early developing organs, the periods of 2 and 4 months feed restriction were probably too short to test the hypothesis for cattle.

At the cellular level, proportions of muscle fiber-types in the longissimus muscle were not significantly affected by 2 months feed restriction while 4 months feed restriction did have a significant effect - an increase in βR fibers and a decrease in αW fibers. It appears from these results that it requires a more prolonged feed restriction for the transformation of muscle fibers to take place. Perhaps a short period of more severe feed restriction would have similar effects. As long as the functional demand of the muscle changes, there is a shift in the proportions of muscle fibers. However, nutrition seemed to have very little effect on the proportion of αR fibers. When the restricted animals were refed and slaughtered at about 400 kg, there was no difference in muscle fiber-type proportions among treatments. This was an indication that refeeding reversed the trend of muscle fiber transformations to the "normal" situation.

The muscle fiber diameters of the longissimus muscle were significantly affected by both 2 months and 4 months feed restriction. The size of muscle fibers is a reflection of the amount of muscle (Tuma et al., 1962), and this was reflected in the amount of muscle in the ad lib fed and restricted animals at the end of both the first and second periods. At the final slaughter weight the muscle fiber diameters were similar in all the treatments, although they showed a trend of lack of complete catch-up which was reflected in the rib eye areas. It would be concluded from these findings that muscle fiber diameters are more easily affected by feed restriction than muscle fiber transformations. Refeeding reverses the situation, showing that catch-up growth observed at the whole animal level takes place at the cellular level.

LITERATURE CITED

Alison, M. R., Ryan, C. J., Lee, C. A. and McDermott, K. 1986. Compensatory hyperplasia in the rat liver as a result of cytoplasmic atrophy. Br. J. Exp. Path. 67:901-908.

Allden, W. G. 1968. Undernutrition of the Merino sheep and its sequelae. 1. The growth and development of lambs following prolonged periods of nutritional stress. Aust. J. agric. res. 19:621-638.

Arm [illegible] Nour, A. Y. M., Thonney, M. L. and Stouffer, J. R. 1983. Changes in cooking losses and sensory attributes of Angus and Holstein beef with increasing carcass weight, marbling score or longissimus ether extract. J. Food Sci. 48:835-840.

Arnold, A. M. and Meyer, H. H. 1988. Influences of gender, time of castration, genotype, birthtype and feeding regimen on lamb longissimus muscle fiber type proportions. J. Anim. Sci. 66:2476-2483.

Arthur, P. F., Makarechian, M., Price, M. A. and Berg, R. T. 1989. Heterosis, maternal and direct effects in double-muscled and normal cattle: II. Carcass traits of young bulls. J. Anim. Sci. 67:911-919.

Asghar, A., Pearson, A. M., Magee, W. T. and Tahir, M. A. 1981. Effects of ad libitum, maintenance and submaintenance feeding and of compensatory growth on some biochemical properties of muscle from weanling rabbits. J. Nutr. 111:1343-1352.

Ashmore, C. R., Tompkins, G. and Doerr, L. 1972. Postnatal development of muscle fiber types in domestic animals. J. Anim. Sci. 34: 37-41.

Ashmore, C. R., Parker, W., Stokes, H. and Doerr, L. 1974. Comparative aspects of muscle fiber types in fetuses of the normal and "double-muscled" cattle. Growth 38: 501-506.

Ashworth, A. and Millward, D. J. 1986. Catch-up growth in children. Nutr. Rev. 44:157-163.

Baker, R. D., Young, N. E. and Laws, J. A. 1985. Changes in the composition of cattle exibiting compensatory growth and the modifying effects of grazing management. Anim. Prod. 41:309-321.

Bennet, D., Morley, F. H. W., Clark, K. W. and Dudzinski, M. L. 1970. The effect of grazing cattle and sheep together. Aust. J. Exp. Agric. Anim. Husb. 10:694-709.

Berg, R. T., Andersen, B. B. and Liboriussen, T. 1978a. Growth of bovine tissues. 2. Genetic influences on muscle growth and distribution in young bulls. Anim. Prod. 27:51-61.

Berg, R. T., Andersen, B. B. and Liboriussen, T. 1978b. Growth of bovine tissues. 3. Genetic influences on patterns of growth and distribution in young bulls. Anim. Prod.27:63-69.

Berg, R. T. and Butterfield, R. M. 1976. New Concepts of Cattle Growth. Sydney University Press.

Berg, R. T. and Walters, L. E. 1983. The meat animal: Changes and challenges. A review. J. Anim. Sci. 57:133-146.

Bergstrom, P. L. 1978. Sources of variation in muscle weight distribution. In: H. De Boer and J. Martin (eds). Patterns ofgrowth and development in cattle. pp91-132. Martinus and Nijoff. The Hague.

Black, J. L. 1983. Growth and development of lambs. In: W. Haresign (Ed.) Sheep production. pp21-58. Butterworths, London.

Black, J. L. 1988. Animal growth and its regulation. Biennial Symposium IV on current concepts of animal growth (Suppl. 3) 66:1-22.

Bohman, V. R. 1955. Compensatory growth of beef cattle: The effect of hay maturity. J. Anim. Sci. 14:249-255.

Buhain, W. J. and Brody, J. S. 1973. Compensatory growth of the lung following pneumonectomy. J. Appl. Physiol. 35:898-902.

Butterfield, R. M. 1966. The effect of nutritional stress and recovery on the body of cattle. Res. Vet. Sci. 7:168-179.

Butterfield, R. M. 1976. Beef carcass composition - Our knowledge to 1976. Beef Cattle Science Handbook. Vol. 13, p139.

Butterfield, R. M., Zamora, J., James, A. M. and Thompsom, J. M. 1983. Changes in body composition relative to weight and maturity in large and small strains of Australian Merino rams. 2. Individual muscles and muscle groups. Anim. Prod. 36:165-174.

Callow, E. H. 1948. Comparative studies of meat. II. The changes in the carcass during fattening and their relation to the chemical composition of the fatty and muscular tissues. J. Agric. Sci. (Camb.) 38:174-199.

Callow, E. H. 1961. Comparative studies of meat. VII. A comparison between Hereford, Dairy Shorthorn and Friesian steers on four levels of nutrition. J. Agric. Sci. (Camb.) 56:265-282.

Calvert, C. C., McMurty, J. P., Rosebrough, R. W. and Campbell, R. G. 1987. Effect of energy level on the compensatory growth response of broilers following early feed restriction. Poult. Sci. (Suppl.1) 66:75.

Carstens, G. E., Johnson, D. E. and Ellenberger, M. A. 1988. Energy metabolism and composition of gain in beef steers exhibiting normal and compensatory growth. In: Energy metabolism of farm animals. EAAP publication No. 43. pp131-134. Lunteren, Netherlands.

Cianzio, D. S., Topel, D. G., Whitehurst, G. B., Beitz, D. C. and Self, H .L. 1982. Adipose tissue growth in cattle representing two frame sizes: Distribution among depots. J. Anim. Sci. 55:305-312.

Clandinin, T. 1984. Understanding the composition of dietary fat. Meat Probe, Vol.1, No.3.

Coleman, S. W. and Evans, B. C. 1982. Can compensatory growth be used to your advantage. Oklahoma Agric. Exp. Sta. Bull. No. 824. pp67-70.

Coleman, S. W. and Evans, B. C. 1986. Effect of nutrition, age and size on compensatory growth in two breeds of steers. J. Anim. Sci. 63:1968-1982.

Coleman, S. W., Pate, F. M. and Beardsley, D. M. 1976. Effect of level of supplemental energy fed grazing steers on perfomance during the pasture and subsequent drylot period. J. Anim. Sci. 42:27-35.

Crouse, J. D., Smith, S. B. and Prior, R. L. 1984. Bovine muscle glycogen as affected by fasting and refeeding. J. Anim. Sci. 59:384-387.

Davies, A. S. and Pryor, W. J. 1977. Growth changes in the distribution of dissectable and intramuscular fat in pigs. J. Agic. Sci. (Camb) 89:257-266.

Davies, A. S., Pearson, G. and Carr, J. R. 1980. The carcass composition of male and female pigs resulting from two levels of feeding. J. Agric. Sci. (Camb.) 95:251-259.

Drennan, M. J. 1979. Compensatory growth in cattle. 1. Influence of feeding level during the first winter (9 to 14 months of age) on subsequent perfomance and carcass composition. Ir. J. Agric. Res. 18:131-143.

Drennan, M. J., Conway, A. and O'Donovan, R. 1982. Compensatory growth in cattle. 3. Effect of stocking rate at pasture in summer on animal performance at pasture and during the subsequent winter period. Ir. J. Agric. Res. 21:1-11.

Drew, K. R. and Reid, J. T. 1975. Compensatory growth in immature sheep. I. The effects of weight loss and realimentation on the whole body composition. J. Agric. Sci. (Camb.) 85:193-204.

Enser, M. and Wood, J. D. 1978. The development of adipose tissue in cattle. pp243-254. In: H. De Boer and J. Martin (eds). Patterns of growth and development in cattle. Martinus Nijhoff. The Hague.

Ferrell, C. L., Koong, L. J. and Nienaber, J. A. 1986. Effect of previous nutrition on body composition and maintenance energy costs of growing lambs. Br. J. Nutr. 56:595-605.

Folman, Y., Drori, D., Holzer, Z. and Levy, D. 1974. Compensatory growth of intensively raised bull calves. III. Restricted, refeeding and breed differences. J. Anim. Sci. 39:788-795.

Foot, J. Z. and Tulloh, N. M. 1977. Effects of two paths of live-weight change on the efficiency of feed use and on body composition of Angus steers. J. Agric. Sci. (Camb.) 88:135-142.

Fourie, P. D., Kirton, A. H. and Jury, K. E. 1970. Growth and development of sheep. II. NZ. J. Agric. Sci. 13:753-770.

Fox, D. G., Johnson, R. R., Preston, R. L., Dockery, T. R. and Klosterman, E. W. 1972. Protein and energy utilization during compensatory growth in beef cattle. J. Anim. Sci. 34:310-318.

Georgieff, M. K., Mills, M. M., Zempel, C. E. and Chang, P-N. 1989. Catch-up growth, muscle and fat accretion, and body proportionality of infants one year after newborn intensive care. J. Pediatr. 114:288-292.

Goss, R. J. 1978. The physiology of growth. Academic Press, New York.

Graham, W. C. and Price, M. A. 1982. Feedlot performance and carcass composition of cull cows of different ages. Can. J. Anim. Sci. 62:845-854.

Graham, N. M. and Searle, T. W. 1979. Studies of weaned lambs before, during and after a period of weight loss. 1. Energy and nitrogen utilization. Aust. J. Agric. Res. 30:513-523.

Guenther, J. J., Bushman, D. H., Pope, L. S. and Morrison, R. D. 1965. Growth and development of the major carcass tissues in beef calves from weaning to slaughter weight, with reference to the effect of plane of nutrition. J. Anim. Sci. 24:1184-1191.

Guth, L. and Samaha, H. J. 1970. Procedure for the histochemical demonstration of actomyosin ATPase. Exp. Neurol. 28: 365-367.

Guth, L. and Yellin, H. 1971. The dynamic nature of the so-called "fiber types" of mammalian skeletal muscle. Exp. Neurol. 31: 277-300.

Hammond, J. 1932. Growth and development of mutton qualities in the sheep. Oliver & Boyd, Edinburgh.

Hand, R. K., Gould, S. R., Basarab, J. A. and Engstrom, D. F. 1986. Condition score, body weight and hip height as predictors of gain in various breed crosses of yearling steers on pasture. Can. J. Anim. Sci. 66:837-842.

Hankins, O. G. and Howe, P. E. Estimation of the composition of beef carcasses and cuts. USDA bull. 926. pp1-20.

Harris, P. M. 1980. Changes in adipose tissue of the rat due to early undernutrition followed by rehabilitation. 1. Body composition and adipose tissue cellularity. Br. J. Nutr. 43:15-26.

Hegarty, P. V. J. and Kim, K. O. 1980. Changes in muscle cellularity in starved and refed young rats. Br. J. Nutr. 44:123-127.

Hegarty, P. V. J. and Naude, R. T. 1970. The accuracy of measurement of individual skeletal muscle fibers separated by a rapid technique. Lab. Prac. 19: 161-164.

Heinemann, W. W. and Van Keuren, R. W. 1956. The effect of wintering plane of nutrition on subsequent gains of beef yearling steers on irrigated pastures. J. Anim. Sci. 15:1097-1102.

Hermanussen, M., Geiger-Benoit, K. and Sippel, W. G. 1985. Catch-up growth following transfer from three times weekly im to daily sc administration of hGH in GH deficient patients, monitored by knemometry. Acta. Endocr. 109:163-168.

Hidiroglou, N, McDowell, L. R. and Johnson, D. D. 1987. Effect of diet on animal perfomance, lipid composition of subcutaneous adipose and liver tissue of beef cattle. Meat Sci. 20:195-210.

Hight, G. K. and Barton, R. A. 1965. The effects of undernutrition and realimentation on the Romney ewe. J. Agric. Sci. (Camb.) 64:413-424.

Hironaka,R. and Kozub,G.C. 1973. Compensatory growth of beef cattle restricted at two energy levels for two periods. Can. J. Anim. Sci. 53:709-715.

Holmes, J. H. G. and Ashmore , C. R. 1972. A histochemical study of development of muscle fiber type and size in normal and "double-muscled" cattle. Growth 36: 351-372.

Hood, R. L. and Thornton, R. F. 1979. The cellularity of bovine adipose tissue. Aust. J. Agric. Res. 30:153-161.

Huxley, J. S. 1932. Problems of relative growth. 2nd Ed. Dover Publication Inc. 1972. New York.

Johnson, E. R., Butterfield, R. M. and Pryor, W. J. 1972. Studies of fat distribution in the bovine carcass. 1. The partition of fatty tissues between depots. Aust. J. agric. res. 23:381-388.

Johnston, D. M., Moody, W. G., Boling, J. A. and Bradley, N. W. 1981. Influence of breed type, sex, feeding systems, and muscle bundle size on bovine fiber type characteristics. J. Food Sci. 46: 1760-1765.

Joubert, D. M. 1954. Influence of winter nutritional depression on the growth, reproduction and production of cattle. J. Agric. Sci. (Camb.) 44:5-65.

Joubert, D. M. 1956. An analysis of factors influencing postnatal growth and development of the muscle fiber. J. Agric. Sci. 47: 59-101.

Keenan, D. M., McManus, W. R. and Freer, M. 1969. Changes in the body composition and efficiency of mature sheep during loss and regain of live weight. J. Agric. Sci. 72:139-147.

Kempster, A. J. 1981. Fat partition and distribution in carcasses of cattle, sheep and pigs: A review. Meat Sci. 5:83-98.

Kempster, A. J., Cuthbertson, A. and Harrington, G. 1976. Fat distribution in steer carcasses of different breeds and crosses. 1. Distribution between depots. Anim. Prod. 23:25-34.

Kirtland, J. and Harris, P. M. 1980. Changes in adipose tissue of the rat due to early undernutrition followed by rehabilitation. 3. Changes in cell replication studied with tritiated thymidine. Br. J. Nutr. 43:33-43.

Koch, A. 1982. A kinetic model for growth as a function of time and nutritional status. Growth 46:74-87.

Koong, L. J. and Nienaber, J. A. 1985. Changes of fasting heat production and organ size of pigs during prolonged weight maintenance. In: Energy metabolism of farm animals. Eur. Assoc. Anim. Prod. 32:46-49.

Koong, L. J., Ferrell, C. L. and Nienaber, J. A. 1985. Assessment of interrelationships among levels of intake and production, organ size and fasting heat production in growing animals. J. Nutr. 115:1383-1390.

Lawrence, T. L. J. and Pearce, J. 1964. Some effects of wintering yearling beef cattle on different planes of nutrition. I. Liveweight gain, food consumption and body measurement changes during the winter period and subsequent grazing period. J. Agric. Sci. 63:5-21.

Ledin, I. 1983. Effect of restricted feeding and realimentation on compensatory growth, carcass composition and organ growth in lambs. Swedish J. Agric. Res. 13:175-187.

Lemon, P. W. R. and Nagle, F. J. 1981. Effects of exercise on protein and amino acid metabolism. Med. Sci. Sports Exercise 13:141-149.

Levy, D., Folman, Y., Holzer, Z. and Drori, D. 1971. Compensatory growth in intensively raised bull calves. J. Anim. Sci. 33:1078-1085.

Little, D. A and Sandland, R. L. 1975. Studies on the distribution of body fat in sheep during continuos growth, and following nutritional restriction and realimentation. Aust. J. Agric. Res. 26:363-374.

Lofgreen, G. P. and Kiesling, H. E. 1985. Effects of receiving and growing diets on compensatory gains of stressed calves. J. Anim. Sci. 61:320-328.

Lomax, M. A. and Baird, G. D 1983. Blood flow and nutrient exchange across the liver and gut of the dairy cow. Effects of lactation and fasting. Br. J. Nutr. 49:481-496.

Lunt, D. K., Smith, G. C., McKeith, F. K., Savell, J. W., Riewe, M. E., Horn, F. P. and Coleman, S. W. 1985. Techniques for predicting beef carcass composition. J. Anim. Sci. 60:1201-1207.

Malina, R. M. 1969. Exercise as an influence upon growth. Clin. Ped. 8:16-26.

Marchello, J. A., Wooten, R. A., Roubicek, C. B., Swingle, R. S. and Dryden, F. D. 1979. Realimentation of cull range cows. 3. Prediction of carcass composition.

Marple, D. N. 1983. Principles of growth and development. Proc. Of the Growth Management Conference. pp1-6.

May, M. L., Dikeman, M. E., and Schalles, R. 1977. Longissimus muscle histological characteristics of Simmental x Angus, Hereford x Angus, and Limousin x Angus Crossbred steers as related to carcass composition and meat palatability traits. J. Anim. Sci. 44: 571-580.