PROSPECTS OF COMPENSATORY GROWTH FOR SHEEP PRODUCTION SYSTEMS

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PROSPECTS OF COMPENSATORY GROWTH FOR SHEEP PRODUCTION SYSTEMS

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Kamalzadeh, A. 1996. Prospects of compensatory growth for sheep production systems. The dry (lean) season imposes a natural feed restriction in grazing animals that must be compensated for during the wet (lush) season. The nutrition physiological backgrounds governing the changes during growth retardation and higher gain during compensation are obscure. Immature male lambs were used to determine the effects of feed quality restriction, *i.e.* feeding grass straw, on the pattern of feed intake, feed efficiency and growth, and changes in the physiological state of the animals. During restriction and following realimentation, the grass straw intake of the restricted animals was significantly higher than of their controls. Maintaining gut capacity was the main reason of ingesting more low quality feed. The delay in growth during the restriction period was fully compensated after realimentation with a significantly lower total feed consumption, while the carcass of the realimented animals was leaner than of the controls. Higher grass straw intake, lower maintenance requirements, an increased feed efficiency and changes in the composition of gain were mechanisms supporting compensatory growth. During the dry season with limited amounts of good quality feed available, imposing feed quality restriction is a useful strategy. During the following recovery period, animals compensate through increased feed intake and a more efficient use of the nutrients. Modelling the implementation of a strategy of compensatory growth indicated the possibility of a reduction of the total concentrate input by 40% per animal compared to an intensive system. Compared to an extensive system, only 35% of the rangelands is required, thereby reducing the grazing pressure on the rangelands and allowing regeneration of the vegetation species.
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STATEMENTS

1 The general allometric law developed by Huxley (1932) is only valid for relatively short periods of growth under homogeneous conditions.

This thesis

2 Delayed growth during periods of feed quality restriction in small ruminants, can potentially be fully compensated and yield an even better carcass quality.

This thesis

3 Body reserves are an underexploited resource in improving the sustainability of ruminant production systems.

This thesis

4 Whether compensatory growth is an effective mean to overcome seasonal fluctuations in feed availability depends on the onset and duration of feed quality restriction.

This thesis

5 Longer term productivity of an animal production system benefits from a better matching of animals to the ecosystem's carrying capacity.

This thesis

6 The statement made by Oldham, J. D. & Tamminga, S. (1995) that "animal production systems should be much more closely tuned to efficient and environmentally sound production of desirable products than ever before", does not have general applicability.

7 Forbes (1995) stated that ruminants eat that amount of feed which leaves them with the most comfortable feelings. The inability to measure feelings considerably weakens this statement.

8 Sustainable developments constitute an investment for the future, aiming at improving the longer-term resilience of a system. Such developments have to be focused at continuity and optimization, at preservation of natural resources and appropriate recycling of nutrients, rather than at maximal output.
These statements by Van Bruchem, J & Zemmelink, G. (1995) are valid, if at least also economic considerations are taken into account.

9 Many new progress which man has made, is at the expense of the ecosystem, which he can not always repair.

10 To quantify the real importance of results of experiments with farm animals, it is necessary to evaluate these results in the longer term perspective of the production system.

11 There are aspects of life which are not always played fairly. Sometimes, during the game itself the rules are changed, without consulting the players.

Azizollah Kamalzadeh
Prospects of compensatory growth for sheep production systems.
Wageningen, 15 May 1996

In the name of God,
The compassionate, the merciful

Take knowledge from cradle to the grave.

(prophet of Islam, Mohammad PBUH)

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PREFACE

All my thanks to God for keeping me healthy and making me able to successfully finish this work.

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I am very much appreciate sharing office space with my colleague and friend Drs Henri G. D. Leuvenink, I enjoyed very much all those daily greetings, talks, discussions during working days, trips, seminars and social activities,... which made a pleasant environment for my study.

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I extend my appreciation to John Dierx, Marit van Bakel and all the colleagues and friends whose names are not mentioned here, both from Iran as well as from the Netherlands, who have supported me in one way or another.

It is certain that I never would have ventured this far all alone without the support of my wife Anahita, my children Zahra, Leila and Mohsen. You have painfully endured my frequent absence from home. Your patience and support all the way made it possible for me to advance with pleasure and comfort.

A. Kamalzadeh
March 21th, 1996

To Anahita, Zahra, Leila and Mohsen

CONTENTS

Chapter 1

GENERAL INTRODUCTION

GENERAL INTRODUCTION

Livestock production systems in most parts of the world, particularly in the developing countries, mainly depend on natural vegetation of the range and farm lands. Periods of drought are interspersed with periods of rainfall, making forage availability and quality very unpredictable. Seasonal variations in feed quantity and quality cause periods of live weight loss and gain in grazing animals. The productivity of the animals is low compared to performance of the same species in more favourable environments, but their ability to survive in bad periods is remarkable.

During periods with insufficient feed availability, *i.e.* during the dry and cold seasons, suitable feeding strategies need to be developed to minimize the adverse effect on livestock production.

Sheep production in Iran

In Iran, there is a wide spectrum of environmental conditions, from the areas of higher rainfall around the Caspian sea, high elevation in the north and west, the subtropical climates in the south, to the drier steppe and desert areas in the centre. Irrigated agriculture is important along the rivers but most agricultural lands are rainfed. Farms are generally small, with over 95% being less than 50 hectare and more than 70% less than 5 hectare. The main agricultural products are wheat, barley, rice, and milk and meat from small ruminants and cattle. Grain legumes are also grown, mainly in high rainfall and irrigated areas. In the villages, mixed crop-livestock systems are the main production systems, particularly in the drier areas. In the areas with less than 300 mm rainfall there are few alternatives to cereals and small ruminants are predominant. Livestock products are the main source of income and an important component of people's diets. Small ruminants (sheep and goats) constitute the major basis of livestock production (Table 1). Sheep alone account for about 60% of livestock population.

Table 1. Number of livestock in Iran.

Sheep	45,000,000
Goats	23,500,000
Cattle	6,900,000
Buffaloes	330,000
Camels	250,000

Source: FAO (1993).

Sheep and goats produce 70 percent of the red meat and 35-40% of the milk and milk products. Apart from the Zel breed which is found near the Caspian sea, the indigenous sheep breeds are of a fat-tailed type. In general the sheep are mainly bred for meat, milk and wool production, with the exception of the northern pelt breed of Karakul. Sheep and goat by-products such as hides, intestines, hair and related products constitute also parts of the country's exports.

Feed resources

Flocks of small ruminants are mainly managed under two different systems, namely, village and migratory. Both systems are extensive. Natural grasslands and farm lands are the main sources of livestock nutrition. Intensive systems of sheep production are employed in only a few cases.

The nomadic tribes depend for their existence almost exclusively on breeding of small ruminants. The flocks migrate annually from the lowland winter ranges to the higher mountain grazing areas in the summer. In the village system, the flocks are allowed on the natural communal grazing pastures, or irrigated farm lands, or even mountain ranges in summer.

The majority of the lambs is born in March/April. Usually the lambs are weaned in June/July. However, during the subsequent period the available feed does not fully meet the nutrient requirements for early growth. During this period of early growth, the lambs can potentially deposit 160 g protein per kg weight gain (McDonald *et al.,* 1988). For this purpose small intestinal digestible protein (SIDP) is required in excess of SIDP derived from the rumen microbes synthesized in the reticulo-rumen. With insufficiently high quality forage available, however, the extent and efficiency of microbial protein synthesis are low, and rumen by-pass protein more or less negligible. As a result, the young sheep cannot fully exploit their growth potential or may sometimes even loose rather than steadily gain weight. The problems dealing with the present animal production systems can be formulated as follow:

* Low-quality grasses.
* Lack of rain, little ratoon crops available due to low temperature and unsuitable raining intervals.
* Insufficient and inadequately balanced nutrients for early growth (pre-fattening phase).
* Live weight loss due to periodic restriction as a result of seasonal variation.
* Low extent and efficiency of rumen microbial protein synthesis and negligible rumen by-pass protein due to low-quality available forages.
* Less favourable protein to fat ratio in the carcass due to feeding high energy

and low protein concentrates in fattening farms.

* Insufficient knowledge about composition and potential of compensatory growth in relation to stage of growth.
* Lack of appropriate feeding strategies during periods with insufficient feed availability.

The present system of nutritional management which completely depends on natural vegetation, is unsatisfactory. The alternative, an intensive production system gives higher outputs, but it needs a large amount of concentrates. In the intensive system, the conversion of concentrate to live weight is low (7:1) compared to 2.5 to 3 kg concentrates which is needed to produce 1 kg poultry. But, the population interest to red (particularly sheep) meat is high, the price of sheep meat is 2 to 3 times more compared to poultry meat. By implementing a more suitable strategy the concentrates can be used more efficiently for the production of the red meat.

With the present conditions of overgrazing as a result of high stocking rates, there is little doubt that range improvement would be a very time-consuming programme and presumably, unsuccessful. In order to overcome present nutritional problems of poor ranges, sheep should be taken off the ranges as much as possible to reduce the grazing pressure on the vegetation and to allow regeneration of the range species. In recent years, on one side, there was more attention for increasing the amount of concentrates in order to overcome the nutritional problems of poor ranges. On the other side, the contribution of the fibrous crop residues and agricultural by-products as basal feed for ruminants have increased.

So, as to be able to take the sheep from the ranges, it is suggested that the present extensive system of production should be gradually changed to a more productive semi-intensive system. In this respect, the compensatory growth strategy could be of special importance and a suitable way to increase the efficiency of the available feed. With the implementation of such strategy less high quality feed is needed to supplement the low-quality feed and part of the year, animals can be taken off from the ranges. The delay in growth during the dry period is compensated by supplying supplementary (protein rich) feed at a proper time, resulting in a more efficient use of the scarce supplement. However, the growth could be delayed until the coming green season, but then it is presumably too late for animals to fully express their potential for compensatory growth. The potential of such production system largely depends on the intake of the low quality feed during periods of nutritional limitation.

Compensatory growth

The term 'compensatory growth' is used to describe the increase in the rate of growth commonly observed following a period of nutritional stress. In environments with seasonal fluctuation, the periodic restriction of feed supply is an important natural component of animal production systems. The nutrient deficiency can be overcome with supplementary feeding or alternatively, it can be incorporated as a normal part of the annual cycle of production. This is especially feasible when considering compensatory response of young animals when adequate nutrients are made available.

Following the period of realimentation, responses expressed by animals vary from a complete compensation (Graham & Searle, 1975; Thornton *et al.,* 1979; Allden, 1968b), a partial compensation (Butler-Hogg & Tulloh, 1982; Ryan *et al.,* 1993), no compensation (Allden, 1968a) or even reduced growth rate and reduced mature size (Allden, 1979). Complete compensation occurs when previously restricted animals show an enhanced growth rate that is maintained long enough to attain the same weight for age as animals not restricted. Partial compensation occurs when growth rate of the previously restricted animals is higher at the beginning of realimentation but does not persist long enough, so that they do not attain the same weight for age as those animals not being restricted. No compensation occurs when following recovery, the growth rate is the same for both restricted and unrestricted animals. In this case, the previously restricted animals can either stop growing at the same time as their counterparts and become stunted or they can continue growing for a longer time until they have reached the same mature size.

This discrepancy in the responses after realimentation implies that several factors may be involved in the rate and persistency of compensatory gain after a period of nutritional restriction. The most important factors are the age at which restriction is imposed (Morgan, 1972), the relative mature weight of the animal at the onset of restriction (Joubert, 1954), the severity and duration of restriction (Meyer & Clawson, 1964; Ryan, 1990) and the nature of the restriction (Wilson & Osbourn, 1960). Other factors involved are different levels of protein and energy in the diet, as well as breed (Iason *et al.,* 1992) and sex differences (Marais *et al.,* 1991).

Age at restriction and relative mature weight

Age can be a factor when it is considered in relation to the relative mature weight. It is well known that various breeds have different ages at weaning, puberty and maturity. Supplying high quality feed may increase rate of gain and cause earlier maturity. Some researchers, cited by Ryan (1990), reported that lambs and calves restricted soon after birth, are not likely to compensate. They may be permanently stunted or need a longer period to catch up weight compared to animals restricted at later stages of growth. The critical period for lambs when nutritional restriction does not result in compensatory growth seems to be between birth and three months of age.

Severity and duration of restriction

The extent and severity of restriction may vary from a mild restriction (reduced rate of gain), moderate restriction (at maintenance level), to severe restriction (loss of body weight). Ryan (1990), concluded that increasing the severity of restriction is likely to result in a prolonged period of compensatory gain. Scales & Lewis (1971) restricted steers at two levels, maintenance and sub-maintenance. During the winter, the maintenance and the sub-maintenance groups lost 0.08 and 0.23 kg/day respectively. During the grazing period the maintenance group showed compensatory growth for only 82 days. The sub-maintenance group compensated for 180 days before their growth curve ran parallel to that of the control group.

Extending the duration of the restriction may result in a higher growth rate after realimentation. Graham & Searle (1975), noted that sheep maintained at the same body weight for 6 months consistently grew faster than sheep that were maintained for 4 months.

Changes during compensatory growth

Compensatory growth may be associated with lower maintenance requirements during the recovery period (Fox *et al.,* 1972; Butler-Hogg & Tulloh, 1982), an increase in the growth efficiency (Ryan, 1990), an increase in feed intake (Graham & Searle 1979), changes in the body dimensions (Searle *et al.,* 1989) and organ size (Ferrell *et al.,* 1986), changes in the content of the digestive tract (Winter, 1971) and changes in the body composition (Kabbali *et al.,* 1992).

Maintenance requirements

The energy required to maintain an animal at energy balance can be estimated from the relationship between energy intake and energy retention. Similarly, from the relationship between intake of digestible organic matter (DOMI) and gain or nitrogen retention, the digestible organic matter (DOM) requirement at zero weight gain and zero nitrogen retention can be estimated. ARC (1980) estimated a value of 420-450 kJ ME.$kg^{-0.75}$.d^{-1} at zero energy retention and a value of 26 g DOMI.$kg^{-0.75}$.d^{-1} at zero weight gain for growing animals. However, after a period of weight stasis of 4 to 6 months, maintenance requirements of weaner sheep were estimated to be decreased to about 300 kJ ME.$kg^{-0.75}$.d^{-1} (Graham & Searle, 1975). Lower values of 275 kJ ME.$kg^{-0.75}$.d^{-1} (Gingins *et al.,* 1980) and 266 kJ ME.$kg^{-0.75}$.d^{-1} (Ryan, 1990) have also been reported for sheep. After realimentation, the reduced maintenance requirement temporarily resulted in comparatively higher energy for gain. The longer the reduced maintenance requirement persists after realimentation, the greater the contribution it will make to compensatory growth.

Feed efficiency

The efficiency of energy deposition may change during compensatory growth. ARC (1980) suggested a range of 0.32 to 0.55 for the feed efficiency in the continuous growing ruminants but, Parks (1982) reported a range of 0.17 to 0.64 for the efficiency of feed utilization for various species fed *ad libitum.* Thomson (1979) and Ledin (1983) suggested that particularly the efficiency of protein deposition may be increased during the initial period after realimentation. Allden (1970) reported that animals subjected to sustained periods of energy restriction achieved the same weight as controls without consuming significantly more feed. Kabbali *et al.* (1992) and Turgeon *et al.* (1986) also reported an increased feed efficiency during the recovery period.

It thus appears that nutrients energy may be used more efficiently, particularly during the early stages of realimentation.

Feed intake

Recently, various mechanisms controlling feed intake have been proposed. The physical intake mechanism, states that rumen holding capacity is the major determinant of voluntary feed intake. Bosch *et al.* (1992) suggested that fibrous feed intake in dairy cattle is restricted by the rate of passage of undigested particles from the rumen. However, rumen holding capacity appeared quite variable, particularly in relation to stage of lactation. Ketelaars & Tolkamp (1991) stressed that fibrous feed intake is not simply physically regulated. They suggested that the animals balance the costs and benefits of feed intake, in other words optimize the ratio between net energy (NE) and oxygen consumption, with the intention to minimize the harmful effect of oxygen radicals. While, Forbes (1995), postulated that ruminants eat that amount of feed which leaves them with the most comfortable feelings, these deriving from physical and chemical receptors in the wall of the digestive tract as well as unidentified receptors for metabolic balance in the body. Oosting *et al.* (1995), feeding ammoniated straw as a basal ration, showed that fibrous feed intake responded positively to protein availability from the small intestine. Hence, the environment, physiological status of the animal and nutrient availability may have an effect on rumen processing capacity.

There is an abundance of conflicting research results on amount of feed which animals consume following realimentation. The major feature of the response is its variability between animals. An increase in intake of realimented animals has been reported in some studies with sheep (Winter, 1971; Graham & Searle 1979; Allden 1968a). In contrast, Hogg (1977) and Foot & Tulloh (1977) found no difference in feed intake of realimented animals and their controls. In the study of Butler-Hogg & Tulloh (1982), realimented sheep had significantly lower intake than controls for the first 10 kg of live weight gain. Similarly, Drew & Reid (1975a) noted that it took 15 days for realimented sheep to achieve the same intake as their controls, while, Ryan *et al.* (1993) reported that it took approximately 100 days for both realimented sheep and cattle, before they consistently ate more than their controls.

It is commonly believed that the contents of the digestive tract are decreased when animals are under-nourished. However, when animals are restricted in quality rather than quantity, it is unlikely that the contents of the digestive tract decrease.

Body dimensions

In a number of studies, the changes in body dimensions have been identified by measuring the body surface on the live animals (*e.g.* Brody, 1927; Lawrence & Pearce, 1964; Searle *et al.,* 1989). Brody (1927) found that the weight and circumference of chest in dairy cattle was affected to about the same extent by the conditions of undernutrition. Lawrence & Pearce (1964) reported greater effects of nutrition on length than on height for beef cattle. However, Coleman & Evans (1986) reported that the growth of both height and length was suppressed by restricted feeding. The length of the forearm has been found to be the most accurate of the surface measurements (Hopkins & Tulloh, 1985). Further, there is a high correlation between sperm production and the weight and size of the testes (Hahn *et al.*, 1969). Size of the testes can be measured accurately in the live animals by scrotal circumference.

Body organs

Changes in the nutritional condition of the animals have a direct effect on the relative metabolic activities of organs. Internal organs, particularly liver, digestive tract, kidneys and heart are metabolically very active, accounting for about 40% of fasting heat production in spite of comprising only 10-15% of total live weight (Koong *et al.*, 1985). The greatest rate of protein synthesis occurs in the gut and the liver (Webster, 1980). The liver is essential in regulating metabolism. Plasma albumins (formed in the liver) and globulin serve important roles in body fluid balance. Periods of live weight loss (Winter *et al.*, 1976; Ferrell *et al.*, 1986; Wright & Russel, 1991) as well as live weight maintenance (Burrin *et al.*, 1988) caused a reduction in both the absolute weight and the proportions of the internal organs. The liver and small intestine showed the biggest changes and appeared to be most sensitive to nutritional restriction (Winter *et al.*, 1976; Koong *et al.*, 1985). Burrin *et al.* (1988) reported that the rate of blood flow to the liver and digestive tract of young sheep and their metabolic activities as measured by oxygen uptake, were rapidly reduced during starvation.

During compensatory growth, all internal organs showed an accelerated growth rate in sheep (Butler-Hogg, 1984). Winter *et al.* (1976) observed that the biggest changes in relative growth occurred in the liver and small intestine. While, Foot & Tulloh (1977) observed lower liver weight (3.5 kg) for realimented cattle compared to 4.4 kg for controls at the same live weight. In contrast, the digestive tract constituted 8.5% of live weight in realimented cattle compared to 7.9% for controls.

Body composition

The composition of gain usually differs between restricted/realimented animals and unrestricted animals. It is generally believed that protein gain in the carcass is increased during compensatory growth. Some studies (Drew & Reid, 1975a,b; Carstens *et al.*, 1991; Kabbali *et al.*, 1992) have shown that realimented animals were leaner than their unrestricted controls. However, there is also evidence to suggest that realimented animals were not leaner than their controls. Searle *et al.* (1979) noted that 1 kg gain during compensatory growth in sheep contained 170 g protein, while for control animals this figure was 160 g. While, Allden (1970) observed that fat tissue responded more readily than any other tissue to high nutrient intakes in the period immediately after rehalibitation. However, the composition of gain may be related to the composition of the diet (*i.e.* by pass protein, high energy, etc).

Ledin (1983) reported that at the end of a period of nutritional restriction in quantity, the carcasses of the restricted sheep were fatter and contained less water and protein than those of the *ad lib.* fed controls. After realimentation, however, the carcass of the previously restricted animals contained less fat but more protein and water. Cowan *et al.* (1980) and Butler-Hogg (1984) have also reported that water and protein were mobilized relatively faster and earlier than fat during nutritional restriction. Searle & Graham (1975) restricted 4 months old wether sheep at 20 kg live weight for either 4 or 6 months and then fed them *ad lib.*, found no difference in the body composition between realimented animals and controls at any given body weight above 32 kg. Although during the early stages of recovery, the compensating sheep gained more protein and fat and less water than their controls, but during the fattening phase, no differences occurred. Both Fox *et al.* (1972) and Ryan *et al.* (1993) noted that animals appear to deposit a greater amount of protein during the initial stages of realimentation.

Burrin *et al.* (1988) stressed that cell size rather than cell numbers was reduced during nutritional restriction. In internal organs, a large part of the recovery in weight is due to cell enlargement (hypertrophy). In muscle, this is through increases in cell number (hyperplasia) as well as hypertrophy. Hyperplasia may have some impact on the process of fattening, depending upon the physiological stages at which the nutritional stress occurred. It has been shown by Thornton *et al.* (1979) for sheep that in older animals (more than 50% mature) hyperplasia is essentially complete, and thus cell numbers are unchanged. In younger animals some hyperplasia may accompany hypertrophy, although hypertrophy is the major mechanism whereby fat depots increase in size (Hood & Thornton, 1979).

The various adipose tissue depots behave differently to both nutritional restriction and realimentation. According to Butler-Hogg & Johnsson (1986), during restriction the subcutaneous fat appears to be the first to be utilized and the internal depots fat follow. During recovery the opposite occurs. Hood & Thornton (1980) found that older sheep required longer to reach high rates of lipogenesis. Drew & Reid (1975b) and Butler-Hogg (1984), both found reduced rates of fat deposition in the early stages of compensatory growth. Probably at this time lipogenic capacity is reduced. Hood & Thornton (1980) reported that realimented sheep took between 50 to 100 days to reach similar levels of fatness as their unrestricted controls.

Growth curves and feed intake

In many studies (Brody, 1927; Searle *et al.*, 1989), growth in various species of animals has been determined from the relation between age and body weight or body measurements. The growth function [$y(t) = A.f(t)$], relates a body constituent y (dependent variable) at age t, to its asymptotic value (A) and f(t) which is some monotonic increasing or sigmoid function of t starting at 0 and having an asymptote of one for $t \rightarrow \infty$.

In some studies (*e.g.* Hammond, 1932; Parks, 1982), it has been realized that growth can also be determined from the relation between feed intake and body weight. Parks (1982) proposed a model to relate the body weight to cumulative feed intake. This enables to calculate feed efficiency from the relation between the ratio of daily weight gain over daily feed intake (dW/dF) and degree of maturity. However, all these approaches only apply when feed is available *ad libitum* and growth is not affected by environment and internal factors. Therefore, description of changes in growth paths or stages of development with different treatments is not possible with these models.

THIS STUDY

The present system of small ruminant (sheep and goats) production in Iran alike most parts of the world (sub(tropics)), Mediterranean areas, south and west Asia and Africa, mainly depends on vegetation ranges and farm lands. Overgrazing and as a consequence land degradation is high and the overall performance of animals is low. To be able to overcome these problems, suitable feeding strategies need to be developed to (1) reduce the adverse effects on agricultural production and (2) increase the efficiency of the available feed resources.

The aims of this study are:

(1) To determine the physiological changes during feed quality restriction and subsequent periods of compensatory growth in order to explain the possible mechanisms of compensatory growth and feed intake.

(2) To investigate whether after a period of feed restriction, the sheep are still

able to attain the weight of the control animals, and if so how the empty body composition has changed.

(3) To develop (new) models to measure the relative growth patterns and the efficiency of feed utilization under nutritional restriction and following compensation periods.

(4) To develop a flock growth model to evaluate the assessment of growth (productivity) and structure of sheep flock in different production systems.

(5) To evaluate the productivity of a sheep production system based on compensatory growth strategy compared to existing systems.

(6) To develop a more suitable strategy for small ruminant production systems with regard to the seasonal variations in the quality and availability of feed resources.

These aspects were studied by comparing a group of immature non-castrated male lambs restricted in feed quality by supplying low-quality roughage *ad lib.* for a period of 3 months, taking lambs fed *ad lib.* on low-quality roughage plus supplement as a control group. The comparison was made in terms of:

* Growth rate (body weight gain, empty body weight gain).
* Voluntary intake of low-quality roughage, efficiency of feed utilization, rumen retention time, digestibility and nitrogen balance.
* Growth curve of the individual organs and carcass weight/composition.
* Body dimensions changes.

OUTLINE OF THE THESIS

This thesis describes the results of a long-term experiment in which young lambs were subjected to a period of 3 months feed quality restriction from 3 to 6 months of age. Animals were Swifter (Flemish ♀ x Texel ♂) non-castrated male lambs born in March 1993 and weaned at ≈2 months age. The rations consisted of a basal grass straw (51 g crude protein per kg dry matter (DM)) and a concentrate mixture (173 g crude protein per kg DM).

Chapter 2 describes the effects of feed quality restriction and consequential compensatory effects on voluntary feed intake, digestion, gain and nitrogen balance. The voluntary low-quality feed intake during restriction and realimentation are discussed relative to the suggested mechanisms for feed intake regulation.

From the relation between digestible organic matter (DOMI), nitrogen balance, and gain, the maintenance requirements of DOMI were estimated. The efficiency of amino acid nitrogen deposition was estimated from the relation between nitrogen balance and amino acid nitrogen available for absorption.

Chapter 3 deals with the changes which occurred in the body dimensions as a result of feed quality restriction. A growth model was developed to identify the pattern of the changes in various body dimensions during restriction and following realimentation.

Chapter 4 describes the responses of various body organs to restricted feeding. The trend of changes during restriction and compensation was characterized by the growth function used in chapter 3.

In Chapter 5, the changes in body composition (water, protein, fat, ash) during restriction and compensatory growth were determined. The composition of loss and gain were measured. The growth model which was used in chapters 3 and 4, was also used to identify the pattern of changes in body composition.

Chapter 6 describes the changes in the pattern of feed intake, feed efficiency and growth. Two models were developed to measure feed efficiency from the relation between cumulative feed intake and body weight and the relation between feed intake and gain per unit of time.

In Chapter 7, the implementation of the compensatory growth strategy in sheep production system is presented. The productivity of a system based on compensatory growth approach is simulated and compared with the two existing systems. A flock growth model was developed to assess the growth or productivity of a sheep flock in different production systems.

Finally, in the General Discussion (Chapter 8) the major findings of Chapters 2-7 are discussed in an integrated manner.

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Chapter 2

Feed quality restriction and compensatory growth in growing sheep: feed intake, digestion and nitrogen balance.

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ABSTRACT

The effects of feed quality restriction on intake, digestion, nitrogen balance and performance of growing lambs were examined. A total of 56 crossbred Swifter (Flemish ♀ X Texel ♂) male lambs, born in March 1993 and weaned at ≈2 months old, were fed grass straw (51 g crude protein per kg dry matter (DM)) *ad libitum* and 35 $g.kg^{-0.75}.d^{-1}$ mixed concentrates (173 g crude protein per kg DM). At an age of 3 months, the animals were randomly divided into a restricted (R) and a control (C) group. Group R was restricted in feed quality by withholding concentrates from 3-6 months of age.

During restriction, the R animals lost weight and showed a slightly negative nitrogen (N) balance. Grass straw intake of the R animals gradually increased to a level significantly higher ($P < 0.001$) than of the C animals. The R animals showed a significantly ($P < 0.001$) higher rumen retention time (RRT).

Linear relationships were observed between digestible organic matter intake (DOMI), truly absorbed small intestinal amino acid nitrogen (AAN) and N balance. Regression of N balance on AAN resulted in an estimated marginal efficiency of utilization of AAN of 0.78. After realimentation, the R animals persisted in showing a higher ($P < 0.001$) straw intake, gained in weight significantly ($P < 0.001$) faster than the C animals and showed a significantly ($P < 0.001$) higher DOMI and N balance.

(*Key words:* sheep, feed intake, compensatory growth, digestibility, feed quality restriction)

INTRODUCTION

Livestock production systems in Iran, like most parts of the world, mainly depend on natural vegetation of range and farm lands. Feed availability fluctuates throughout the seasons and as a consequence, animals cope with periodical restriction in feed quality and quantity. During periods with insufficient feed availability, appropriate feeding strategies need to be developed to minimize the adverse effect on livestock production. The producers may choose for the option of nutrient restriction and delay of growth until an adequate good quality feed supply is available in the next wet season and benefit from compensatory growth. Weaning is towards the warm and dry season, when the fodder quality decreases and the available feed does not fully meet the nutrient requirements for early growth. During this period, lambs can potentially deposit approximately 165 g protein per kg gain (McDonald *et al.*, 1988), and small amounts of intestinal amino acid nitrogen are required in excess of that derived from the rumen microbes. With insufficiently high-quality forage available, however, the extent and efficiency of microbial protein production are low, and rumen by-pass protein negligible. As a result, the young sheep cannot fully exploit their growth potential or may sometimes even loose rather than gain weight.

According to Hoover (1986), supplementation of proteins to low-quality roughages, could increase the efficiency of microbial protein production. Egan (1977), Preston & Leng (1987) and Oosting *et al.* (1995) reported that ruminants may show higher roughage intake as a result of an increased small intestinal availability of amino acids. However, in other experiments this was not confirmed (Kellaway & Leibholz, 1983; Ketelaars & Tolkamp, 1991).

Accelerated (compensatory) growth is observed when adequate nutrients are offered to animals which have been previously restricted in nutrient intake. There has an abundance of seemingly conflicting research results been published on this issue (O'Donovan, 1984; Ryan, 1990; Hogg, 1992). Some researchers have shown that the response of animals after a period of deprivation depends on the severity and duration of the restriction (Meyer *et al.,* 1956), the nature of the restriction, the age at which the restriction is imposed (Morgan, 1972) and the relative mature weight of the animal (Joubert, 1954). Other factors involved are level of protein in the feed, as well as breed and sex (Iason *et al.,* 1992).

Compensatory growth may be associated with an increased feed intake (Graham & Searle, 1975), lower maintenance requirements brought about by feed restriction (Fox *et al.,* 1972; Butler-Hogg & Tulloh, 1982), an increased efficiency of nutrient utilization (Meyer & Clawson, 1964; Ryan, 1990), and changes in body composition. Thomson (1979) suggested that particularly the efficiency of protein deposition may be increased during the initial period after realimentation. Asplund *et al.* (1975), reported a higher efficiency in the metabolism of protein, whereas Keenan *et al.* (1969) reported an increase in water content of the gut.

The objective of this study was to quantify the effect of a period of feed quality restriction on intake, digestion, N balance, amino acid nitrogen availability for absorption and performance of growing lambs fed grass straw with/without concentrates.

Data of this paper are part of the results of a main experiment in which, the effects of feed quality restriction in immature sheep were investigated. Results on body dimensions changes are described (Kamalzadeh *et al.*, 1995). The results with regard to modelling feed efficiency, the development of body organs and analysis of body composition will be reported later.

MATERIAL

Animals

Intact male Swifter (Flemish ♀ X Texel ♂) lambs born in March 1993 were selected randomly from flocks in Wageningen/Swifterbant. Birth weight averaged ≈4 kg and average weight at weaning (approx. 10 weeks of age) was ≈25 kg. Thereafter, the lambs were adapted to the control diet. The lambs grew slowly, reaching a live weight of 27 kg at the age of approx. 14 weeks. From a total of 56 lambs, 8 were slaughtered at the onset of the experiment to determine initial body composition. A number of 28 lambs (14 per group) were housed in metabolism cages, whereas the remaining 20 (10 per group) were group housed with facilities for individual feeding. The data include measurements of 48 sheep (24 per group) at the beginning of the restriction, gradually reducing to 8 sheep (4 per group) at the end of the experiment due to slaughtering at intervals of three weeks.

Experimental groups

The control group (C) was fed low-quality roughage *ad libitum* and a concentrate supplement. The same diet was fed to the restricted group (R), however, between age of 3 to 6 months only low-quality roughage was fed *ad libitum* including a mineral mixture, but no concentrates.

Diets

The low-quality roughage consisted of chopped grass *(Festuca arundinacea)* straw (51 g crude protein per kg dry matter (DM)). Grass straw was offered at 70 $g.kg^{-0.75}.d^{-1}$, which was sufficient to keep the animals at maintenance level. Grass straw refusals approximated 40% of the amount offered. The supplement (173 g crude protein per kg DM) was offered at 35 $g.kg^{-0.75}.d^{-1}$, and consisted of a ground and pelleted mixture of sugar beet pulp (870 g/kg), potato protein (100 g/kg), a mineral mixture of (mervit 318), vitamin A, D and trace elements (14 g/kg), $NaH_2PO_4.2H_2O$ (9 g/kg), $FeSO_4.7H_2O$ (0.15 g/kg), and $MgSO_4.7H_2O$ (6 g/kg). The composition and the *in vitro* (Tilley & Terry, 1963) organic matter digestibility (OMD) of the diets are in Table 1. Concentrates were eaten completely at all times by all animals.

Table 1. *Composition of grass straw and of concentrate; dry matter (DM), organic matter (OM), crude protein (CP), ash and in vitro digestible organic matter (OMD).*

Diet	DM (g/kg)	composition (g/kg DM)			
		OM	CP	ash	OMD
grass straw	875	923	51	88	377
concentrate	869	924	173	78	615

Management

From weaning until the onset of the restriction period (14 weeks old), all lambs were kept together for a period of 3 weeks. The C and R animals were placed alternately, both in metabolism cages and ground pens. The ambient temperature was kept at ≈20°C. An artificial lighting regime was imposed of 12/12 h day/night to avoid seasonal effects of day length. Grass straw was offered at 07.00, 14.00 and 18.00 h, and concentrates at 07.00 and 18.00 h. Water and salt licking blocks were freely available. Grass straw residues were collected daily prior to the afternoon feeding.

During the experiment, 12 successive balance trials were conducted; four (1-4) trials were carried out in the period that the R animals were restricted and the other 8 (5-12), after the R animals had been realimented. Following the 8 lambs slaughtered at the onset of the experiment, every three weeks 4 (2 per group) were slaughtered leaving 8 lambs (4 per group) for slaughtering at the end of the experiment. Therefore, the data presented in this paper, include measurements of 28 lambs (14 per group) at the beginning of the experiment, gradually decreasing to 8 (4 per group) at the end of the experiment.

Animals were weighed weekly. Each balance trial had a duration of 3 weeks, and consisted of a preliminary period of 11 days and a collection period of 10 days. The amounts of offered feed were adjusted biweekly on the basis of metabolic weight. During each collection period, representative samples were taken from the straw and concentrates offered. Straw residues, faeces and urine were collected daily. A small amount of 30% formalin was added to the faeces container for preservation. Before starting the daily collection of urine, one litre water acidified by 20 ml (6N) HCl were put in the collection bucket, to prevent evaporation of ammonia. The feed residues, faeces and urine were pooled over each collection period, weighed, while representative samples were taken for chemical analyses.

The DM content of the offered feeds, refusals and faeces was determined by drying representative sub-samples to constant weight at 103°C, while organic matter (OM) was calculated as weight loss of the same sub-samples during ashing at 550°C. The nitrogen (N) content of the feeds, refusals, faeces and urine was determined according to the Kjeldahl method.

A total number of 8 animals (4 per group) were used to determine the mean residence time of the feed in the rumen (RRT) with an oral pulse dosage of Cr-NDF. On the 4th day of each collection period, 50 g of marker pellet with 7.5 g Cr-NDF was administered to the sheep. Subsequently, the following 5-day period, separate faecal samples of approximately 150 g were collected over 12-h periods. The rate of passage of the marker Cr-NDF was estimated from the descending part of the logarithmically transferred faecal Cr excretion curve (Grovum & Williams, 1973). The amount of amino acid nitrogen available for absorption in the small intestine (AAN) was estimated on the basis of microbial AAN synthesized in the rumen (AAN_m) and dietary N (AAN_d) escaping rumen degradation, as follows:

$$AAN_m = (A * B * C * D * DOMI) / E$$

in which:

A = 0.7 : partial digestion in the rumen (rumen degraded organic matter; RDOM).

B = 0.2 : efficiency of microbial protein synthesis (Oosting *et al.*, 1995), (to avoid overestimation, this value was set at 0.15 for the R group during the period of restriction).

C = 0.75 : true protein in microbial protein (van Bruchem *et al.*, 1985).

D = 0.85 : true small intestinal digestibility of microbial protein (van Bruchem *et al.*, 1985).

E = 6.25 : protein to N conversion factor.

DOMI : digestible organic matter intake ($g.kg^{-0.75}.d^{-1}$).

$AAN_d = F * G * N$

F = 0.5 : proportion of N escaping rumen degradation.
G = 0.8 : true digestibility in the small intestine.
N : nitrogen in feed ($g.kg^{-0.75}.d^{-1}$).

RESULTS

The difference in straw intake, at similar body weight (BW), is presented in Fig. 1. As the figure shows the straw intake of R group at a constant BW was increased remarkably and was significantly higher ($P < 0.001$) than C group. At the initial stage of realimentation, the straw intake of R sheep dropped, but remained significantly higher than C sheep. This difference became larger with increasing BW.

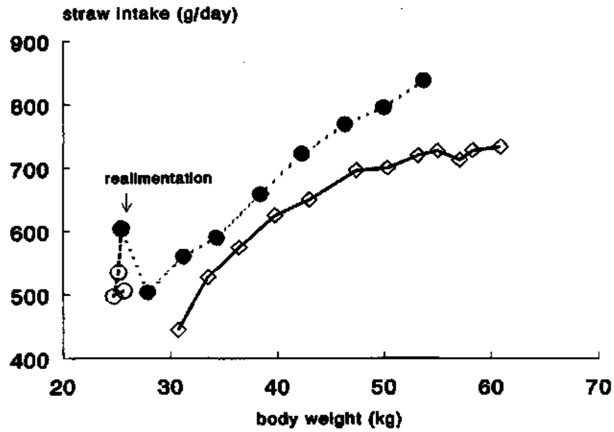

Figure 1. Straw intake (g/day) versus body weight (kg) from the onset of restriction to the end of experiment· (—◇—) C, (--O--) R during restriction, (··●··) R during realimentation.

Table 2 gives the values based on metabolic weight ($g.kg^{-0.75}.d^{-1}$) for intake of organic matter (OM) and nitrogen (N), amino acid nitrogen available for absorption (AAN), N balance, daily gain and rumen residence time (RRT/h). During restriction, R animals had a significantly ($P < 0.001$) lower whole diet organic matter intake (OMI), DOMI, nitrogen intake (NI) and AAN, and lost weight ($-0.7\ g.kg^{-0.75}.d^{-1}$), while C animals gained 8.4 $g.kg^{-0.75}.d^{-1}$. Surprisingly, the R animals showed a significantly ($P < 0.001$) higher RRT than the C animals.

Table 2. *Means and standard errors based on metabolic weight ($g.kg^{-0.75}.d^{-1}$) of straw and concentrate consumption, intake of organic matter (OM), digestible OM (DOM) and nitrogen (N), amino acid nitrogen (AAN), N balance, gain and rumen residence time (RRT/h), of the control (C) and the restricted (R) groups, the latter during restriction and during realimentation.*

	age, 14-28 weeks†				age, 28-52 week‡			
	C	se	R§	se	C	se	R‖	se
Intake ($g.kg^{-0.75}.d^{-1}$)								
Straw	36.90	0.51	48.45$^{'''}$	1.46	35.77	0.86	43.40$^{'''}$	1.20
Concentrate	35.00	0.00	0.00$^{'''}$	0.00	35.00	0.00	35.00	0.00
OM	60.28	0.50	45.45$^{'''}$	1.04	58.38	0.54	65.75$^{'''}$	0.74
DOM	37.02	0.29	20.92$^{'''}$	0.54	35.87	0.44	40.45$^{'''}$	0.60
N	1.18	0.01	0.49$^{'''}$	0.02	1.07	0.01	1.14$^{'''}$	0.01
AAN ($mg.kg^{-0.75}.d^{-1}$)								
-microbial	529	4.19	223$^{'''}$	5.80	512	6.23	578$^{'''}$	8.62
-feed	471	3.88	198$^{'''}$	7.32	429	2.23	454$^{'''}$	3.39
N-balance ($mg.kg^{-0.75}.d^{-1}$)	341	12.40	-98$^{'''}$	19.80	394	8.30	451$^{'''}$	7.10
Faecal excretion ($g.kg^{-0.75}.d^{-1}$)								
OM	23.43	0.35	24.56	0.62	22.45	0.34	25.30$^{'''}$	0.45
N	0.51	0.01	0.40$^{'''}$	0.01	0.47	0.01	0.50$^{''}$	0.01
Urinary N excretion ($g.kg^{-0.75}.d^{-1}$)	0.29	0.01	0.19$^{'''}$	0.01	0.21	0.00	0.18$^{'''}$	0.00
Gain ($g.kg^{-0.75}.d^{-1}$)	8.40	0.54	-0.72$^{'''}$	0.93	6.21	0.46	10.72$^{'''}$	0.44
RRT (h)	28.16	1.85	41.54$^{'''}$	4.01	28.26	1.43	25.03	0.84

†) means of 3 balance trials (number of observations 38 per treatment).
‡) means of 4 balance trials (number of observations 25 per treatment).
§) restriction; ‖) realimentation; $^{''}$) and $^{'''}$) indicate significant differences from C group ($P < 0.01$ and $P < 0.001$).

After realimentation of the R animals, with the grass straw supplemented by concentrates, they gained in weight significantly ($P < 0.001$) faster than the C animals did. The R animals persisted to show a significantly ($P < 0.001$) higher straw intake (SI), OMI, DOMI, NI and N balance than the C animals.

There was a linear relation between N balance and DOMI (Fig. 2; s.e. of estimate between brackets):

$$Y = -656\ (81.7) + 26.8\ (1.10) * X, \quad (n = 76 \text{ and } R^2 = 0.89)$$

in which: Y = N balance ($mg.kg^{-0.75}d^{-1}$)
X = DOMI ($g.kg^{-0.75}d^{-1}$)

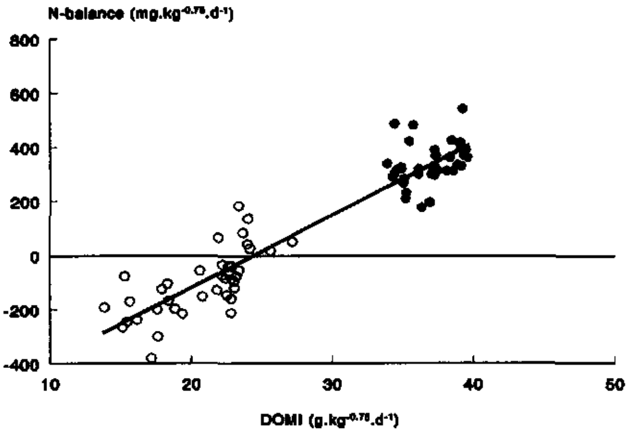

Figure 2. Relationship between N balance (mg.kg$^{-0.75}$.d^{-1}) and DOMI (g.kg$^{-0.75}$.d^{-1}), combined data of both C (●) and R (O) groups during restriction period.

The efficiency of AAN deposition was estimated by regression of N balance on AAN (Fig. 3; s.e. of estimates between brackets):

$$Y = -435\ (73) + 0.78\ (0.03) * X, \ (n = 76 \text{ and } R^2 = 0.91)$$

in which: Y = N balance (mg.kg$^{-0.75}$.d^{-1})
X = AAN (mg.kg$^{-0.75}$.d^{-1})

To present the relationship between N balance and BW, 63 individual animal data in 7 balance trials during whole experiment (14-52 week period) are used for C sheep. The data of R sheep divided to two parts: 38 observations during restriction (3 balance trials, 14-28 week period) and 25 observations during realimentation (4 balance trials, 28-52 week period). The differences between C and R sheep were tested by Student t-test. The average absolute value (g/day) of N balance for R sheep was significantly higher ($P < 0.001$, t-value = 4.14), at a body weight, during the 28-52 week period for the R treatment (5.4, se=0.11 *vs* 4.9, se=0.08).

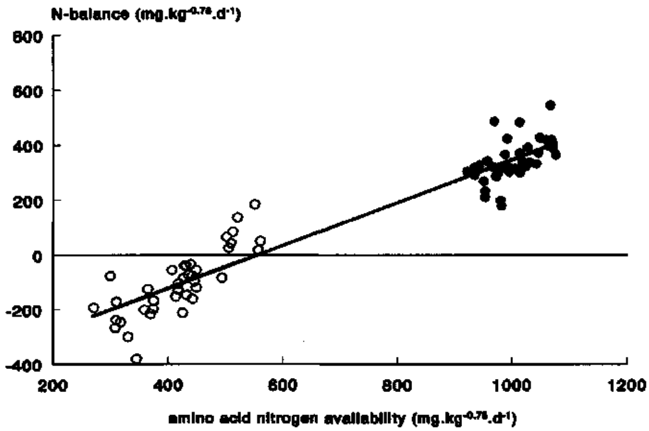

Figure 3. Relationship between N balance (mg.kg$^{-0.75}$.d^{-1}) and amino acid nitrogen availability (mg.kg$^{-0.75}$.d^{-1}), combined data of both C (●) and R (O) groups during restriction period.

The relationship between N balance and BW for the C sheep during whole experiment and for the R sheep during restriction (R†) and realimentation (R‡) is presented in Fig. 4. The following equations were found (s.e. of estimate between brackets).

C : Y = 4.21 (0.64) + 0.02 (0.01) * X (n=63 and R^2=0.06).
R† : Y = 4.53 (1.25) - 0.22 (0.07) * X (n=38 and R^2=0.20).
R‡ : Y = 4.03 (0.44) + 0.04 (0.01) * X (n=25 and R^2=0.33).

in which: Y = N balance (g/day)
X = BW (kg)

DISCUSSION

Fibrous feed intake during feed quality restriction

Part of the compensatory growth was brought about by a sustained increase in fibrous feed intake. Several mechanisms for feed intake regulation in ruminants have been proposed. According to Bosch *et al.* (1992), feed intake is determined by physical and metabolic factors. Physical factors, *i.e.* rumen capacity and turnover, have been suggested predominant with low-quality forages while metabolic factors play a more pronounced role with high-quality diets (Baile & Forbes, 1974).

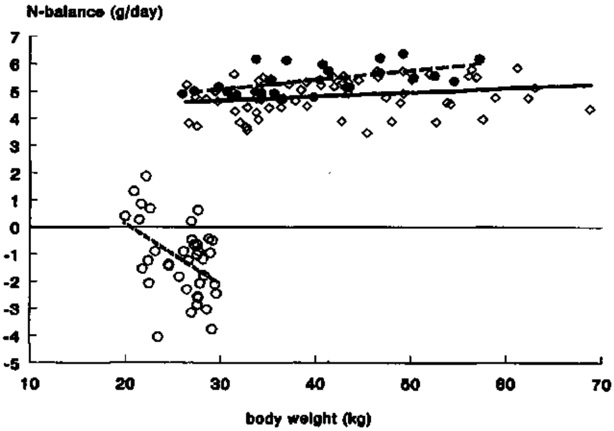

Figure 4. Relationship between N balance (g/day) and body weight (kg) for control (C) animals (◇), restricted animals during restriction (O) and during realimentation (●). The lines present the predicted values.

An alternative theory was formulated by Ketelaars & Tolkamp (1991). They proposed, that feed intake behaviour of animals is related to the physiological costs and benefits associated with intake, that the animal's aim is to minimize costs relative to benefits. They postulated that low-quality feed will result in a lower net energy intake (NEI) level, to minimize oxygen consumption per unit NEI (O_2 / NEI). Therefore, increasing the quality of a feed through supplementation could increase voluntary intake as a result of an increased NEI-level at minimal O_2 / NEI. However, the higher voluntary intake of grass straw by the R animals during restriction as observed in this experiment can not be explained by this theory. In fact, the animals partly substituted the lack of easily digestible concentrates by ingesting more straw, particularly during the last month of the restriction period. However, the data from slaughtering indicated that during restriction, when R animals lost BW, except for the small intestine, the weight of the other parts of the empty gastrointestinal tract (GIT) did not reduce (Kamalzadeh, unpublished results).

Hence, R animals managed to well develop GIT compartments in terms of weight and volume. This can be seen as a physiological adaptation of the digestive tract to ingest more low-quality roughages. As indicated in Table 2, the R animals managed to retain the low-quality feed longer in the rumen. Contrary to the present findings, Ryan (1990) reported that the weight of the digestive tract was reduced when both cattle and sheep were subjected to nutritional restriction. This is probably related to the type of restriction imposed. Restriction in feed quantity allows a reduction of the weight of the GIT.

The physical intake regulation mechanism is based on the assumption that, in the case of low-quality feed, the rumen is filled to its maximum capacity, and that an increased intake can only occur if rumen disappearance of particulate matter increases. The longer RRT of R animals during restriction shows that the physical regulation mechanism of feed intake does not hold for immature sheep fed low-quality fibrous feeds.

Another hypothesis, which has been proposed by Egan (1977), Preston and Leng (1987) and Oosting (1993), is that voluntary intake of low-quality feeds is related to the availability of protein to the tissues. However, the present results can not be explained by an increased small intestinal protein availability. The R animals increased intake of low-quality feed without protein supplementation. Hence, the results of this experiment suggest that under low plane of nutrition, physiological changes and as a consequence, metabolic changes in the body create a condition that animals can take benefit from ingesting low-quality feed.

Ørskov *et al.* (1976) fed two groups of lambs *ad libitum* low (120 g CP/kg dry matter) and high protein diets (200 g CP/kg dry matter), consisting of barley or a mixture of barley and fishmeal. They reported a lower intake of the animals which received the low protein diet, relative to those which received the high protein diet. These latter findings are not in line with the present results, most likely because a different type of feed restriction was imposed.

Compensatory intake of low-quality feed after realimentation

In literature, there is contradictory information with regard to the amount of feed which animals consume following feed restriction. Most of the available results on this issue, is related to the changes in feed intake following feed quantity restriction rather than feed quality deprivation. Fox *et al.* (1972) reported higher intake by realimented animals on high than on low energy diets. Hogg (1992) reported that feed intake increases largely up to 2 & 3 fold on the first day after realimention, followed by a drop on the second day, then followed by a slow but sustained increase. After protein deprivation, Ørskov *et al.* (1976) found lower intake of realimented sheep. Lower intake of realimented animals for the first 10 kg of live weight gain has also been reported by Butler-Hogg & Tulloh (1982). Ryan (1990) reported a delay of 70 to 90 days in increasing feed intake after realimentation. Higher intake of realimented sheep has been found by Winter (1971) and Graham & Searle (1979). However, Foot & Tulloh (1977), reported no difference in feed intake between realimented and control cattle.

In the present experiment, the higher DOMI and NI of R animals was the result of a higher straw intake. According to Zinn & Owens (1983), the proportion of dietary N escaping rumen degradation increased from 43.8 to 70.6% when intake was increased from 1.2 to 2.1% of BW. They found that with increasing intake, the endogenous N losses increased, while more AAN was available from the small intestine. Tamminga *et al.* (1979) reported similar results and showed that the response was also affected by the level of N in the diet. The higher N balance of realimented animals, probably relates to the higher NI from the diet and a higher proportion escaping rumen degradation.

Changes in feed intake over time are a function of the relative changes in energy storage and energy expenditure of the animal. Energy stored per unit of energy intake of the animal declines, as the animal matures. The greater gain of realimented animals suggests that these animals had a rapid increase in energy storage, or a slower rate of decrease in energy expenditure after realimentation. If under restricted feeding, no weight gain is possible, usually maintenance energy requirements decrease. Maintenance requirements of restricted animals can be reduced to a level that approaches their basal metabolic rate (Ryan, 1990). During restriction, the regression of daily weight gain (DWG) on DOMI suggested a zero DWG for DOMI of 22.1 $g.kg^{-0.75}.d^{-1}$ for the R animals. This value is considerably lower than the range reported in the literature for maintenance energy requirement of 25-30 $g.kg^{-0.75}.d^{-1}$. This indicates that R animals decreased their maintenance requirement as a result of feed quality restriction. After realimentation, the reduced maintenance requirement temporarily resulted in comparatively higher energy for growth.

Amino acid N availability and utilization

The regression equation of N balance on DOMI predicts a zero N balance at DOMI = 24.4 $g.kg^{-0.75}.d^{-1}$, lower than the maintenance energy requirements proposed by ARC (1980) of 26 g $DOMI.kg^{-0.75}.d^{-1}$. For mature Swifter sheep, fed wheat straw based diets, Oosting (1993) found a value of 29.7 $g.kg^{-0.75}.d^{-1}$ DOMI.

Ketelaars and Tolkamp (1991) observed a DOMI of 26.4 $g.kg^{-0.75}.d^{-1}$ in sheep, while Zemmelink *et al.* (1991), estimated a value of DOMI = 24.3 $g.kg^{-0.75}.d^{-1}$ for maintenance requirements of growing West African Dwarf goats. Most likely, growing sheep, after some time on a restricted diet, are able to maintain N balance beyond the level of DOMI where the energy balance becomes negative.

However, it is expected that N balance to vary with BW, but as the Figure 4 shows, from 30 kg BW, the N balance was constant for C sheep (slope = 0.02). For R sheep, N balance was significantly higher with an increasing slope (0.04), at a body weight, compared to C sheep after the lifting of the restriction (28-52 week period). The N balance during 14-28 week period of restriction was negative for R treatment.

The regression coefficient of N balance on AAN indicates a true utilization of absorbed AAN of 0.78. As Figure 3 shows, the fit is in line with both data of the C and R animals. ARC (1980) adopted a value of 0.75, while AFRC (1992) proposed a value of 0.80. Oosting (1993) found an efficiency of 0.54 in sheep of more than one year old, fed straw based diets. Rohr & Lebzien (1991) proposed a value of 0.65 as net efficiency of utilization of absorbed AAN in cattle. The utilization is amongst others determined by the supply of the most limiting essential amino acids. The estimates of the ARC (1980) and AFRC (1992) corresponded well with the value of 0.78 in this study. The lower values from the studies of Oosting (1993) and Rohr & Lebzien (1991), were estimated in animals aged more than one year and far from early growth stage. Therefore, the large variation among the literature sources probably relates to estimation of this value in animals of different ages.

The present equation implies a zero N balance at an AAN of 555 $mg.kg^{-0.75}.d^{-1}$. Ørskov (1982) proposed a value of 250-430 $mg.kg^{-0.75}.d^{-1}$ as net maintenance requirements for truly absorbed AAN, on the basis of the total urinary and faecal N excretion of animals fed on N free diets. The results of Rohr & Lebzien (1991) suggested a range of 380-620 $mg.kg^{-0.75}.d^{-1}$. Oosting *et al.* (1995) reported a value of 520 $mg.kg^{-0.75}.d^{-1}$ in sheep fed ammoniated wheat straw either supplemented with potato protein or casein. These large variations probably relates to estimation of this value in animals fed different feeds. Most likely, when the basal diet is consisted of low-quality roughage, this value ranges from 500 to 600 $mg.kg^{-0.75}.d^{-1}$.

CONCLUSIONS

The results presented in this experiment indicate that animals substitute the lack of concentrates (high protein content) by ingesting more low-quality roughage. Maintaining the gut in terms of capacity, is probably the main reason for allowing animals to ingest more low-quality roughage. It appears that this physiological change in the gut of immature sheep in response to feed quality restriction differ from feed quantity restriction.

The results of this experiment suggest that higher straw intake and a reduction in maintenance requirement resulted in a compensation in terms of higher N balance and gain.

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Chapter 3

Feed quality restriction and compensatory growth in growing sheep: modelling changes in body dimensions

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Feed quality restriction and compensatory growth in growing sheep: modelling changes in body dimensions

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ABSTRACT

A total of 56 crossbred Swifter (Flemish ♀ X Texel ♂) male lambs, born in March 1993 and weaned at age ≈2 months, were used to quantify effects of feed quality restriction with respect to growth rates of weight and dimensions of the body. The ration was gradually changed to the experimental control diet of grass straw (51 g crude protein per kg dry matter (DM)) *ad libitum* and 35 $g.kg^{-0.75}d^{-1}$ mixed concentrates (173 g crude protein per kg DM). At age of approximately 3 months, the animals were randomly divided into a restricted (R) and a control (C) group. Group R was subjected to feed quality restriction by withholding concentrates from 3 to 6 months of age. A growth model was developed to quantify effects of feed quality restriction and consequent compensation after realimentation.

Estimates of parameters clearly indicated retardation in growth after restriction and compensatory growth after realimentation. Feed quality restriction suppressed growth in weight and body dimensions. Effects of restriction varied among body dimensions. In general, bone length measures such as ulna length, body height and length, and chest depth were less affected than body weight. Width measures, such as shoulders and hips and body circumference showed a reaction similar to body weight, while testes showed earlier effect of restriction. At the end of the experiment, at age of ≈ 1 year, except width at hips, which was larger ($P<0.01$) in C group, there were no significant differences ($P>0.05$) in body measurements between groups. The results showed that after realimentation those, which were affected most during restriction, started to recover earlier compared to body weight and those which were less affected delayed their growth.

(*Key words:* sheep, growth model, compensatory growth, body dimensions, feed restriction)

INTRODUCTION

The growth of an organism in size and shape is based initially on hyperplasia, followed by hypertrophy and finally on cell differentiation (Brody, 1945). After birth, the growth of an animal is determined by cell enlargement and growth rates of different body components. Growth can be defined as an increase in size and shape, or as deposition of protein, fat, minerals and water. The size and shape of the body of an animal depends on the skeleton structure of the body, and any change in body tissues may be associated with the change of skeletal structure. Body conformation and growth rate are important criteria for selection of meat animals.

In many parts of the world, nutrient availability fluctuates throughout the seasons and induces in grazing animals alternating periods of live weight loss and compensatory growth. As a result of recurrent droughts and floods, animals may be subjected to prolonged periods of severe undernutrition. The retardation of growth in periods with insufficient feed availability, is therefore, an important factor in sheep production. Lambs are born in spring, weaning is towards the warm season when available feed mainly consists of low-quality roughage. Then, the immature animal is unable to achieve its full genetic potential for growth. However, young sheep may recover from insufficient nutrition by supplementary feeding, but may not always express compensatory growth, especially if starved at an early age.

Under a low plane of nutrition, priority of nutrient supply to each part of the body depends on its rate of development and metabolic rate (Palsson & Verges, 1952). The central nervous system has the highest priority, followed by the reproductive system, the skeleton, muscle and fat. The priority of nutrient supply to different body parts may change by feed restriction.

Body surface measurements on live animals were used in a number of studies (e.g. Brody, 1927; Joubert, 1954; Lawrence & Pearce, 1964; Gunn, 1967; Allden, 1979; Hopkins & Tulloh, 1985; Coleman & Evans, 1986; Searle *et al.*, 1989a; Ogink, 1993). Brody (1927) showed that the weight and circumference of chest in dairy cattle were affected to about the same extent by the conditions of undernutrition. The effect of adverse conditions on height, however, was relatively slight when compared to the effect on muscle parts and body weight. Lawrence & Pearce (1964) found for beef cattle larger effects of nutrition on length than on height. Coleman & Evans (1986) reported that restricted nutrition suppressed growth of both height and length of the body during the growing phase in cattle.

Joubert (1954) reported sooner recovery of skeletal dimensions relative to lean tissues and body weight after realimentation.

The length of some specific bones (e.g. forearm) can be easily measured externally. The length of the forearm has been found to be the most accurate of the surface measurements for predicting a skeletal dimension (Hopkins & Tulloh, 1985; Ogink, 1993). The results of Hopkins & Tulloh (1985), obtained by body surface measurements were supported by those obtained at dissection and radiographic measurements. Sperm production has been shown to be correlated highly with weight and size of the testes. Size of the testes can be measured accurately in the live animal by scrotal circumference (Boyd & VanDemark, 1957; Hahn *et al.*, 1969).

A research project was planned to quantify the effects of feed quality restriction in immature sheep after a 3-month period of moderate feed quality restriction by supplying low-quality roughage *ad libitum*. Sheep fed *ad libitum* on low-quality roughage plus supplement served as a control group. Changes in the skeletal and body dimension during restriction and subsequent compensatory growth are analyzed. Feed intake was recorded and animals were subjected to serial slaughtering for determination of body composition and analysis of organs growth, the results of which will be reported later. A linear growth function was developed to describe the effects of feed restriction and realimentation on body dimensions.

MATERIAL

Experimental design

A detailed description of the experimental design, animals, feed composition, housing and management, has been reported by Kamalzadeh *et al.* (1995). Briefly, fifty six intact male Swifter (Flemish ♀ X Texel ♂) lambs of approximately 3 months age, were randomly divided into two experimental groups. At the onset of the experiment, animals were randomly allotted to serial-slaughtering groups for the determination of body composition. Eight lambs were slaughtered at the beginning of the experiment. Half of the remaining animals (*i.e.* 24) was used as control (C) group and fed grass straw (51 g crude protein per kg dry matter (DM)) *ad libitum* and 35 $g.kg^{-0.75}d^{-1}$ mixed concentrates (173 g crude protein per kg DM). The other half was used as restricted (R) group and subjected to feed quality restriction. The R group was fed grass straw *ad libitum* with minerals from 3-6 months of age and thereafter the same feed as the C group. Twenty eight lambs (14 per group) were housed in metabolism cages, whereas the remaining 20 (10 per group) were housed in individual pens. The C and R animals were placed alternately.

Measurements

A series of body measurements was recorded on the live animal. The following is a list of body measurements and their abbreviations.

Body weight (BW)	:	weight recorded by a weighing scale at the same time of day.
Ulna length (UL)	:	distance between the elbow and the most distal point of the carpus joint. To measure ulna length, the right forearm of the animal was lifted, the foot limb below the carpus joint bent fully toward the radius, and kept tight against the body.
Trunk length (TL)	:	distance between the most distal point of the major tuberosity of the humerus and the sciatic tuber (pinbone).
Withers height (WH)	:	distance between the most developed spinous process of the thoracic vertebra (wither point) and the midlateral point of the coronet.
Chest depth (CD)	:	distance between the ventral surface of the sternum and the most dorsal point of the wither.
Hip width (HW)	:	distance between the two coxal tubers.
Shoulder width (SW)	:	distance between the lateral tuberosities of the humerus.
Chest girth (CG)	:	circumference of the chest just behind the forearms.
Testes girth (TG)	:	largest diameter of the testes and scrotum.

All body dimensions were measured weekly from birth till the second month of age, biweekly until 3rd month of age, and thereafter every three weeks. BW was recorded to the nearest 10 g, WH, TL and CG were measured to the nearest 0.5 cm. All other body dimensions were measured to the nearest 0.1 cm. CG was measured by tape, all other body dimensions were measured by vernier calliper. All measurements were taken by the same person.

METHODS

Growth model

To describe growth mathematically, there is a number of growth models available, such as Mitscherlich, Gompertz, Richards and logistic, which have been used to describe the relation between various body measurements and age. Gompertz and Mitscherlich models have been used by Searle *et al.* (1989a) to describe growth in sheep. The Gompertz growth function has been studied extensively by Laird *et al.* (1965).

A general form for a growth function is:

$$y(t) = A \,.\, f(t) \qquad [1]$$

where y(t) is a measurement of the body at age t, A is the asymptotic value of y, and f(t) is some monotonic increasing or sigmoid function of t starting at 0 and having an asymptote of unity for $t \rightarrow \infty$.

Most of the available growth functions assume *ad libitum* feeding and a constant environment. In many experiments these assumptions are not met. In this experiment at time of weaning there was a change in available feed and later on feed was restricted for one group, some existing growth function cannot be used. The general function [1], however, gives a possibility to account for deviations of the assumptions by taking a suitable expression for f(t). Based on the change in type of feed at time of weaning for the C as well as for the R group, and the restriction of feed quality for the R group, a suitable function for f(t) can be constructed by separating f(t) into three components:

$$f(t) = f_0(t) \,.\, f_w(t) \,.\, f_r(t) \qquad [2]$$

where:

- $f_0(t)$ describes the normal growth function, by replacing it by a Gompertz, Brody, logistic or other known growth function;
- $f_w(t)$ describes the effects of weaning and recovery after weaning, if not present function $f_w(t)$ should be unity for all t's;

$f_r(t)$ describes the effects of feed restriction and realimentation, if not present function $f_r(t)$ should be unity for all t's.

The final growth equation (eq [2] substituted in eq [1]) is:

$$y(t) = A \cdot f_0(t) \cdot f_w(t) \cdot f_r(t) \qquad [3]$$

Ratio for average measurements of restricted and control group

If animals randomly divided over the C and R group, the expectations for A, $f_0(t)$ and $f_w(t)$ are the same for both groups. In the ratio (R_y) of the averaged measurement for the restricted group over that average of the control group at time t, the components A, $f_0(t)$ and $f_w(t)$ cancel and the equation reduces to:

$$R_y(t) = \frac{y_{restricted}}{y_{control}}(t) = f_r(t) \qquad [4]$$

If no restriction is present expectation for R_y is unity for all t's.

Allometry

Allometry assumes a constant ratio between relative growth rates of two measures of the body. After integration, the well known allometric equation can be derived:

$$y(t) = \alpha . [x(t)]^{\beta} \qquad [5]$$

In which α is called the scale parameter, and β the allometric growth coefficient. Taking natural logarithms ($\log_e$) on both sides, this becomes a linear relation between measure y and measure x:

$$\log_e[y(t)] = \log_e[\alpha] + \beta . \log_e[x(t)] \qquad [6]$$

This equation is independent of age, as is assumed for an allometric relation.

Allometry during the restriction and realimentation period

If growth of the restricted group is expressed as the ratio to growth of the control group, the following equation can be used to analyze the effects of restriction and realimentation on allometry:

$$\log_e[R_y(t)] = a + b.\log_e[R_x(t)] \qquad [7]$$

In this equation the expected value for a is zero and for b is unity outside the period of restriction and realimentation. In other words, the allometric relation for normal growth is removed by using the ratio, and therefore, it offers the opportunity to study the allometric relation during periods of restriction and realimentation, independent of the allometric relation during normal growth. It is assumed that a is not influenced by restriction or realimentation, and will stay at zero level:

$$\log_e[R_y(t)] = b.\log_e[R_x(t)] \qquad [8]$$

To test constancy of b during restriction and during realimentation, the effect of time is included into the b term by defining the allometric coefficient as a sum of different functions of time:

$$\log_e[R_y(t)] = [b_0 + b_s.t_s + b_m.t_m + b_{sm}.t_s.t_m].\log_e[R_x(t)] \qquad [9]$$

In which t_s is the number of weeks after start of restriction and t_m is the number of weeks after start of realimentation. If b_s, b_m and b_{sm} are zero, the allometric relation during restriction and realimentation is constant and independent of time, b_0 is equal to b in eq [8]. BW is taken as the reference (x) measurement, because this measurement can be considered as the total of all other body dimensions. Also in the literature growth of body dimensions mostly are referred to growth of total body weight.

Statistical analysis

For the statistical analysis the averages of observations at each age and group were used. In total, averages at 22 ages were available for the analysis. Although averages are based on a different number of observations (serial slaughtering), no weighing procedures were used. Each average value is considered to be the best value to represent the mean of each age group combination, and weighing according to numbers would lead to results especially based on data from the earliest periods.

Equations [8] and [9] were used to estimate parameters in the allometric relations over periods of restriction and realimentation, and for testing of the effects of time in these relations. A stepwise linear regression procedure from the statistical program Statistix 4.0 (Analytical software, 1992) was used to estimate parameters. As a result of this choice, the same components are not always included in the model for various measurements. The best model was chosen according to minimal residual standard deviations. Parameters were tested to deviate from zero with a Student t-test. Durbin-Watson (DW) statistics were computed to test positive autocorrelation using Table A-6 in Neter *et al.* (1985). Significance in the tables is indicated by * ($P < 0.05$), ** ($P < 0.01$) and *** ($P < 0.001$). Predictions were made using equations [8] and [9], and are presented in Figure 3 for each measurement in relation to age and to body weight.

RESULTS

Means of body weight and body measurements for both groups at onset of restriction, end of restriction and end of experiment are listed in Table 1. At the onset of restriction, virtually the means of the body dimensions for both groups were similar. Feed quality restriction, suppressed growth in all body dimensions. At the end of the restriction period means of the R group differed significantly ($P < 0.001$) from the means of the C group for all measurements. BW of group R was only 0.65 of the weight of group C, whereas for TG this fraction was 0.58, UL 0.94, WH 0.93, CD 0.86, TL 0.88, CG 0.85, SW 0.79 and for HW 0.77. After the lifting of the restriction, the R group grow at a higher rate, at a similar live weight, compared to the C group (Fig. 1). Average daily weight gain (DWG) was significantly higher ($P < 0.001$) in both absolute amount (171.4 *vs* 123.2 g/day), and based on the metabolic weight (10.7 *vs* 6.1 $g.kg^{-0.75}.d^{-1}$) (Kamalzadeh *et al.*, 1995). At the end of the experiment, at the age of approx. one year, mean BW of the R group was 0.90 of the weight of C group, TG 1.06, SW 1.00, WH 0.97, UL 0.98, TL 0.97, CD and CG 0.99 and HW 0.89.

Table 1: *Means[1] and standard errors (s.e.) of body weight (kg) and body measurements[2] (cm) of the control (C) and restricted (R) groups at the start[3] of restriction (14 weeks age), at the end[3] of restriction (28 weeks age) and at the end[3] of experiment (52 weeks age).*

measure (y)	group	start of restriction		end of restriction		end of experiment	
		mean	s.e.	mean	s.e.	mean	s.e.
BW	C	26.9	0.75	39.1	1.30	61.3	2.94
	R	26.9	0.58	25.2***	0.62	55.1	1.35
UL	C	18.6	0.15	19.8	0.18	22.5	0.28
	R	18.7	0.12	18.5***	0.15	22.1	0.31
TL	C	59.8	0.53	66.7	0.59	80.3	1.08
	R	60.2	0.35	60.4***	0.58	78.0	1.06
WH	C	54.0	0.34	57.6	0.41	67.3	0.74
	R	54.2	0.33	53.6***	0.45	65.8	0.90
CD	C	22.2	0.22	24.8	0.19	29.2	0.53
	R	22.2	0.20	21.4***	0.23	28.8	0.76
HW	C	10.8	0.15	12.8	0.16	15.6	0.06
	R	11.0	0.14	9.9***	0.09	13.8**	0.19
SW	C	17.9	0.28	19.7	0.34	23.8	0.19
	R	17.7	0.26	15.4***	0.18	23.7	0.38
CG	C	66.8	0.65	75.6	1.24	96.3	1.14
	R	67.2	0.64	64.3***	0.56	95.0	0.50
TG	C	5.8	0.11	9.7	0.35	10.5	0.42
	R	6.1	0.12	5.6***	0.57	11.0	0.13

[1]) If mean of R group differs significantly from that of C group, significance level is indicated.

[2]) For abbreviations see text.

[3]) Numbers for each group at start of restriction are 24, at end of restriction 18, and at end of experiment 4.

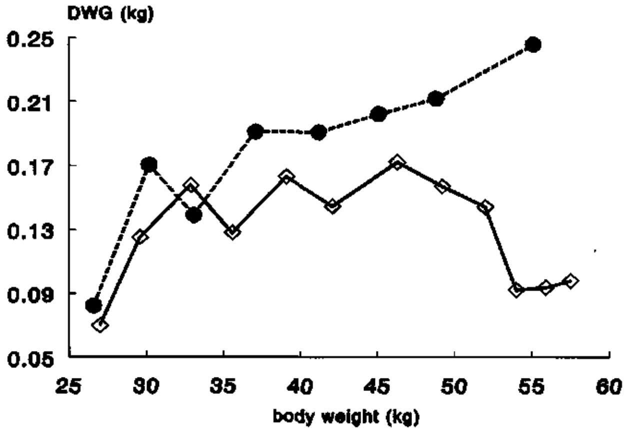

Figure 1. The relationship between daily weight gain (DWG) and body weight after lifting the restriction from restricted animals; (—◇—) control, (--●--) realimented.

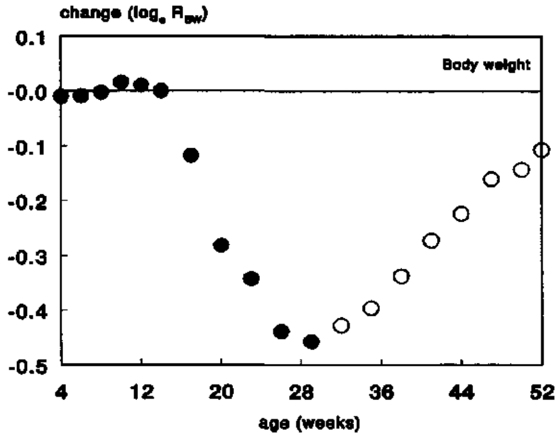

Figure 2. The pattern of the natural log of the body weight ratio ($\log_e R_{BW}$) of average of the restricted group over that of the control group versus age (weeks) during restriction (●) and realimentation (○) periods.

Figure 2 shows the pattern of the natural log of the body weight ratio ($\log_e R_{BW}$) during restriction and realimentation. Before week 14 (start of restriction), the observations are scattered around zero. Between week 14 and 28 (restriction period) there is almost a linear decrease, and after week 28 (realimentation period) there is almost a linear increase. It is expected that after week 52 there will be a trend asymptotically to zero.

The allometric relationship between the various corrected body measurements (ratio of average of the restricted group over that of the control group) and for corrected body weight, was described by equation [8], the relation including time of restriction and realimentation was described by equation [9]. Estimates of the parameters, residual standard deviations and DW statistics for fitted curves are presented in Table 2. In Figure 3, observations and predictions are presented for the natural log of the ratio of each measurement ($\log_e R_y$) against age (left side), and against the natural log of the ratio of body weight ($\log_e R_{BW}$) (right side).

Figure 3 and Table 2 show the results of application of the two models (equations [8] and [9]). The first model is the simple allometric relation, containing the allometric growth coefficient b. Without any restriction or realimentation, expectation for b is one. In the second model, the allometric growth coefficient is made dependent on time by including effects of time of restriction (b_s), time of realimentation (b_m) and the interaction (b_{sm}).

Goodness of fit characteristics (DW and resid. s.d.) show that equation [8] did not fit the measurements well. This fact is illustrated by the solid lines in Figure 3, they all do not predict the observations well. Equation [9] gave a good fit (no autocorrelations) for all measurements, autocorrelation with time removed completely; this is illustrated in Figure 3 by the dashed lines. In the final model UL, TL, WH and CD had lower resid. s.d. compared to HW, SW, CG and TG. This is explained by the fact that the first measures are bone measures and the others include bone, muscle and fat, and therefore, are more flexible and sometimes more difficult to measure.

Equation [8] assumes a complete relation between changes of body measures in relation to BW. It is expected that decrease after restriction follows the same line as the increase after realimentation. The solid lines in Figure 3 show that equation [8] gives an average description of the allometric relation between measures and BW. Growth coefficients average 0.27 for length, height and depth measures, and 0.53 for width and girth measurements, while TG had a very high coefficient of 0.81. Looking closer to Figure 3, changes in all measures do not follow the same line during restriction and realimentation. UL, TL, WH and CD delay their growth after restriction and realimentation compared to growth of BW. During restriction SW, HW and CG follow a same pattern of growth as BW, TG shows even an earlier effect of restriction compared with BW.

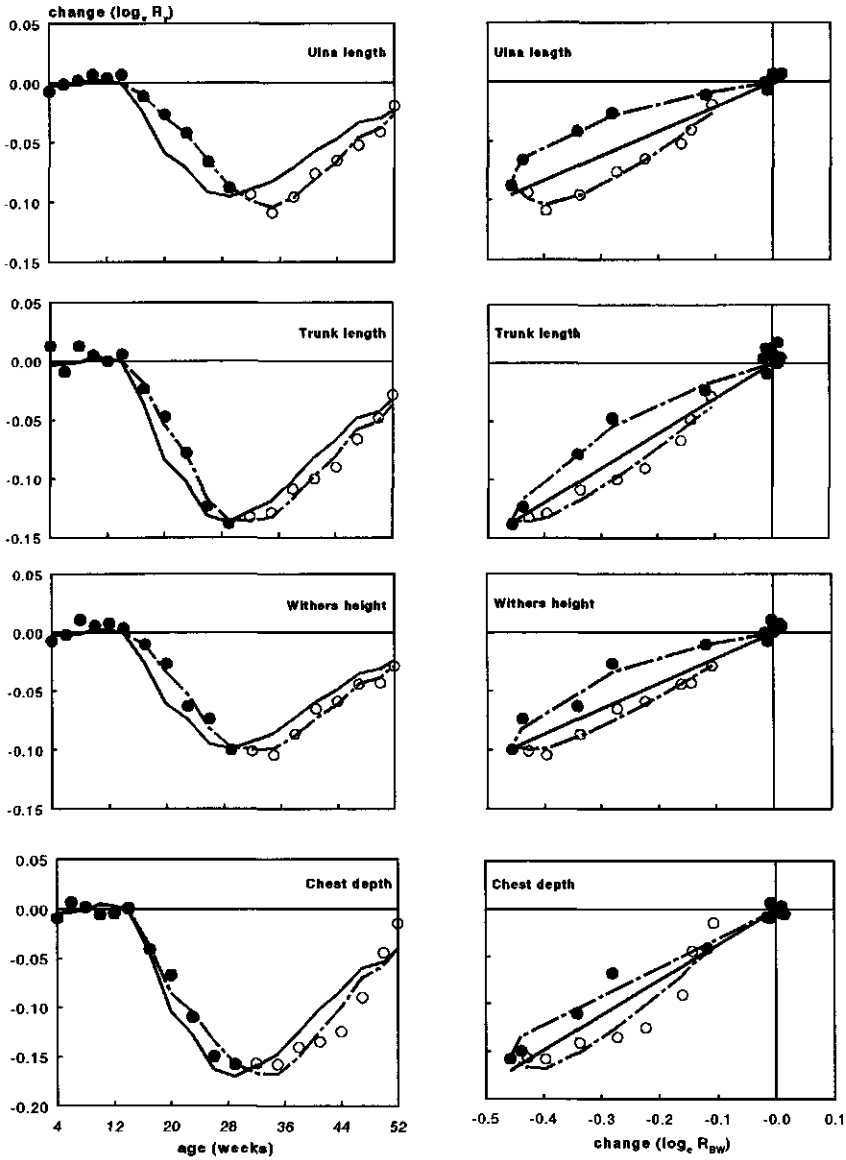

Figure 3. The relationship between the natural log of the ratio of each measurement ($\log_e R_y$) against age (weeks) (left side), and against the natural log of the body weight ratio ($\log_e R_{BW}$) (right side); (●) observation during restriction period, (○) observation during realimentation period, (———) prediction based on Eq. [8], (— - — -) prediction based on Eq. [9].

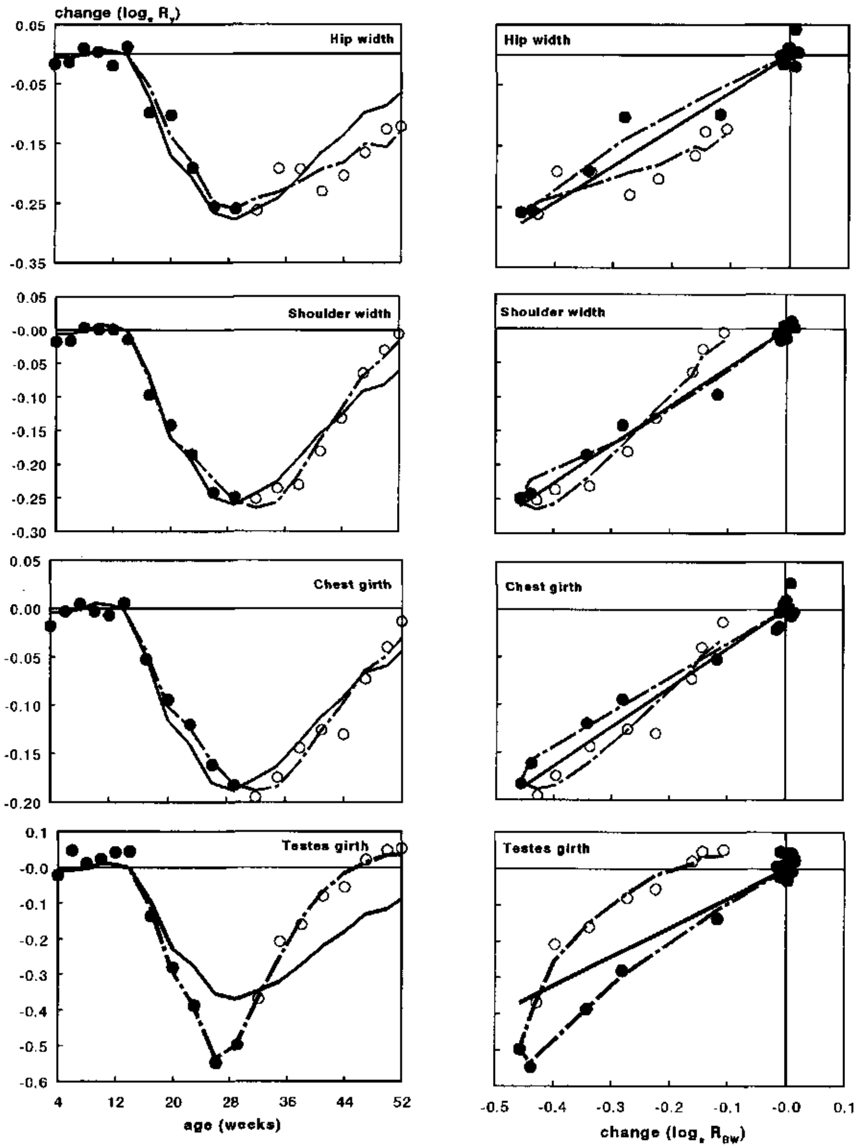
change (log$_e$ R$_y$)
Hip width
Shoulder width
Chest girth
Testes girth
age (weeks)
change (log$_e$ R$_{BW}$)
0.05
-0.05
-0.15
-0.25
-0.35
-0.00
-0.10
-0.20
-0.30
0.00
0.1
-0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
4
12
20
28
36
44
52
-0.5
-0.4
-0.3
-0.2
-0.1
-0.0
0.1

Table 2. *Estimates of parameters for two models[†], Durbin-Watson statistics (DW)[‡] and residual standard deviations (resid. s.d.) for all measurements[§].*

measure (y)	b	DW	resid. s.d.
	$\log_e(R_y) = b \, . \, \log_e(R_{BW})$		
UL	0.2077***	0.33***	0.0161
TL	0.2984***	0.66***	0.0146
WH	0.2158***	0.70***	0.0125
CD	0.3710***	0.67***	0.0185
HW	0.6041***	1.01***	0.0374
SW	0.5668***	0.62***	0.0228
CG	0.4102***	1.06***	0.0171
TG	0.8066***	0.30***	0.0998

measure (y)	b_0	b_s	b_m	b_{sm}	DW	resid. s.d.
	$\log_e(R_y) = (b_0 + b_s . t_s + b_m . t_m + b_{sm} . t_s . t_m) \, . \, \log_e(R_{BW})$					
UL	0.0567*	0.0076***	0.0179***	-0.0006***	1.72	0.0044
TL	0.1181***	0.0123***		-0.0002*	1.61	0.0084
WH	0.0525*	0.0112***		-0.0002**	2.06	0.0060
CD	0.3049***		0.0298***	-0.0007**	1.27	0.0130
HW	0.4093**	0.0133	-0.0439	0.0015*	2.42	0.0253
SW	0.6441***	-0.0116	0.0711***	-0.0019***	1.69	0.0141
CG	0.3590***		0.0332***	-0.0009***	1.67	0.0134
TG	0.8749***	0.0286	-0.1212***	0.0008***	1.78	0.0275

[†]) See for explanation of variables and parameters equations [8] and [9] in text. Significance levels are indicated for parameter estimates deviating from zero

[‡]) Test for positive autocorrelation with time. Significance level is indicated.

[§]) For abbreviations see text.

In equation [9] the growth coefficient is made time dependent. Parameter b_0 is now an estimate of the growth coefficient at start of the restriction. If b_0 is lower than b in equation [8], as for UL, this results in a line (Figure 3, right side) starting above the solid line, and ends below the solid line. If b_0 is higher then b, as for TG, the line starts below the line and ends above. Ranking for b_0's are similar to that for b's. Including b_s, b_m and b_{sm} into the allometric equation gave better fits, with positive b_s and b_m and negative b_{sm}. This model can be used to calculate the time where full compensation is expected. In equation [9] the left term is equal to zero, if $\log_e (R_{BW})$ is zero or if $(b_0 + b_s.t_s + b_m.t_m + b_{sm}.t_s.t_m) = 0$. This is a quadratic equation in t and roots of this equation can be calculated. Only the positive root is of interest because it gives information over the expectation of complete compensation. This root was 64, 96, 87, 67, 55, 62 and 45 weeks for UL, TL, WH, CD, SW, CG and TG. For HW no root could be calculated. This is in agreement with the expectations read from Figure 3, left side.

DISCUSSION

Understanding the relationship between growth stage and body shape needs an accurate description of growth of the body dimensions. Most of the available growth equations can be used in cases where internal and environmental factors are assumed constant. Weaning, onset of puberty and sexual maturity are the natural processes in animals which are affected by environmental factors. In ruminant species, feed type changes after weaning and development of the forestomachs, cause physiological changes during normal growth of animals and the partitioning of the available nutrients to the body components and functions.

Supplying low-quality feed had a great inhibiting effect on the normal development of live weight and body dimensions of R animals (weeks 14 to 28 of age). The results indicate that during weight loss the growth of body dimensions also ceased. In contrast to R animals, there was a continuous development in BW and all body dimensions of C animals. Differences between the two experimental groups (Table 1) were highly significant ($P < 0.001$).

The relationship between the various body measurements and BW is different for the C and R group (Figure 3). In fact, this difference is illustrated in different patterns of growth for various body measurements in C and R group. Reaction of feed quality restriction was for TG faster than for BW, dimensions HW, SW and CG showed a reaction similar to BW. UL, TL, WH and CD delayed their reaction compared to BW. UL, TL, and WH which are relatively the early maturing parts and their growth primarily related to bone growth, were least affected. The effect of restriction on the growth of skeleton was not presumably related to mineral deficiency, because during restriction period, low-quality diet was supplemented with a mineral mixture. These results confirm the findings of Palsson (1955), Lawrence & Pearce (1964) and Koops (1986). They found, that restricted nutrition had a retarding effect on the different parts of the animal's body in the direct order of their maturity. The early maturing parts; *e.g.* the central nervous system and bones are least affected and the latest maturing ones; *e.g.* muscle and fat are most affected. Width, depth and girth measurements, which are relatively late maturing parts, since they are composed of bone, muscle and fat. The reduction in these dimensions during feed restriction were related to the depletion of fat and muscle parts, and it seems that the skeleton part only stopped growing. Hammond (1955) reported that restricted nutrient supply during growth had a great inhibiting effect on the normal development of sexual characteristics. The present experiment showed that testes growth was completely suppressed by low-quality nutrition. This indicates that sperm production was reduced during restriction period.

After the period of nutritive restriction, when sufficient nutrients were made available to group R, different parts of the body competed for the newly available nutrients. The priority of nutrient supply, and as a consequence, compensation varied among different body dimensions. As can be seen from Figure 3, the effect of realimentation was very fast for TG; UL, TL, WH and CD started late, because of their delayed reaction, however this delay was compensated soon; SW and CG had a slow start but compensated even earlier than BW. The reaction of HW was different to all others, after a quick response on realimentation its growth delayed for about 10 weeks and seems to compensate very late.

As shown by Figure 3, right side, the widely used simple allometry model (Eq. 8) is inadequate for a detailed description of the studied dimensions. This model assumes that the allometric relation between two components is independent of time and estimating an average relation. In many experiments, the simple allometric equation showed a consistent overall pattern of the estimates. Searle *et al.* (1989b) found b values of 0.34 and 0.30 respectively for body length, and 0.19 and 0.16 for leg length in fed Corriedale and Dorset Horn sheep. In an earlier experiment, Searle *et al.* (1989a) estimated b values in wether sheep (Leicester X Merino) fed *ad libitum* or 1/2 *ad libitum* of 0.26 and 0.32, respectively, for body length and 0.15 and 0.23 for leg length. Brody (1945) found a stronger development of body trunk dimensions than leg lengths. He reported b values of 0.24 and 0.26, respectively, for height development in Jersey and Holstein cattle. Ogink (1993) estimated b values in castrated Saanen and West African Dwarf (WAD) goats fed *ad libitum* of 0.39 and 0.36 respectively for TL, 0.35 for CG and 0.23 for UL of both groups. These results of b values are confirmed with b values estimated from using equation [8] in this experiment.

Equation [9] gives an adequate description for the development of body dimensions relative to BW and time (Figure 3, right side). As the figure shows, almost all body dimensions behaved differently during restriction and during realimentation. Joubert (1954) reported that certain body measurements, especially those of height and length, recover sooner than body circumference and body weight. The results of this experiment showed that the trend of recovery after realimentation depended on the level of loss during restriction: those which were most affected, started to recover earlier. Those which had similar reaction as body weight during restriction, showed the same trend of growth as body weight during realimentation and those which were less affected, delayed their growth during realimentation. Allden (1968), in his work on Merino sheep, maintained sheep at 15 kg LW for up to 400 days and reported that there was no difference in body dimensions at 60, 260 and 460 days of age. Searle *et al.* (1989a) found that at equal BW, body length was similar in both *ad libitum* and restricted groups. The *ad libitum* group had wider shoulders, whereas the restricted group had larger leg and chest depth. In contrast, Hopkins & Tulloh (1985) found that restricted animals had wider shoulders and smaller width at hips. The results of the present experiment showed that at equal BW, R animals had larger testes girth, width at shoulders and chest girth compared to C animals. Ulna length, trunk length, height at withers and chest depth were similar in both groups while width at hips in R animals was smaller than C animals. It seems that any increase in the width of hips depended on the fat deposition.

CONCLUSIONS

The approach to describe the development of body dimensions during restriction and realimentation is different to other studies on this subject. By using the ratio of the measurements of the restricted group over the control group all disturbing effects are removed and the analysis is concentrated on pure effects of restriction and realimentation. This method gives the opportunity to show the different reactions of the body dimensions in greater detail.

The development of various body components of an animal is affected by the plane of nutrition. Various body dimensions of immature sheep react differentially under restricted nutritive quality and during realimentation when animals receive sufficient nutrients. In general, bone dimensions such as ulna length, height and body length are less affected than width, depth and body circumference. After realimentation, those parts which are most affected during restriction, show higher gain. Any change in body components of immature sheep related to the shape and size of the animals and any change in body size is primarily related to the skeletal structure of the body.

Bone measurements such as ulna length, trunk length and height at withers have a more stable character than body weight and other body dimensions. Ulna length (forearm) measure is the most accurate of the surface measurement. Body weight can show more fluctuations as a result of changes in gut fill. While width, depth and girth measurements can be influenced by lean and fat deposition.

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Chapter 4

Feed quality restriction and compensatory growth in growing sheep: development of body organs.

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Feed quality restriction and compensatory growth in growing sheep: development of body organs.

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ABSTRACT

The effects of feed quality restriction and the consequence compensatory growth on body organs development were measured in 56 crossbred Swifter (Flemish ♀ X Texel ♂) male lambs born in March 1993 and weaned at ≈2 months old. The ration was gradually changed into an experimental diet of grass straw (51 g crude protein (CP) per kg dry matter (DM)) *ad libitum* and 35 $g.kg^{-0.75}d^{-1}$ mixed concentrates (173 g CP per kg DM). At an age of 3 months, animals were randomly divided into a restricted (R) and a control (C) group. Group R was subjected to feed quality restriction by withholding concentrates from 3-6 months of age. The serial slaughtering procedure was used to determine the changes in body organs. At the onset of the experiment 8 lambs, thereafter every 3 weeks 4 lambs (2 per group), and finally 8 lambs (4 per group) were slaughtered.

A linear growth function was used. Estimated parameters clearly indicated retardation in body organs growth during feed quality restriction. Different organs behaved differently during restriction and realimentation. In general, the carcass showed an earlier effect of restriction and realimentation compared to body weight (BW), whereas, non-carcass components showed a delay in growth after restriction but, the same trend as BW after realimentation. At the end of experiment, the head was heavier in C group ($P<0.05$) and the weight of the small intestine was higher in R group ($P<0.05$). No significant differences ($P>0.05$) were observed for other organs between groups.

(*Key words:* sheep, growth function, compensatory growth, organ, restriction)

INTRODUCTION

Undernutrition and subsequent compensatory growth in which animals show higher growth rate and possible mechanisms involved in compensatory growth has been the subject of a number of studies (Allden, 1970; O'Donovan, 1984; Hogg, 1992). Physiological changes and different functional demands, such as growth, protein and energy metabolism, or milk production of the animals are associated with the activities of visceral organs. Visceral organs have different rates of growth and different metabolic rates compared to the other parts of the body.

Effects of restricted feeding and realimentation on organs weight have been found in sheep (Koong *et al.*, 1982; Burrin *et al.*, 1990; Ryan *et al.*, 1993), in cattle (Lawrence & Pierce, 1964; Ryan *et al.*, 1993), in pigs (Walstra, 1980; Koong *et al.*, 1982) in rabbits (Ledin, 1983), and in rats (Ferrell & Koong, 1986). Nutritional conditions of animals have a direct effect on the metabolic activities of organs (e.g. liver, gastrointestinal tract, heart and kidneys). Brody (1945) compared the relation between organ weights to total body weight and concluded that the metabolic rate during growth decreased as the ratio of visceral organs to body weight declines. Results reported by Foot & Tulloh (1977), Canas *et al.* (1982) and Ferrell & Koong (1986), with several species such as sheep, pigs and rats showed that a reduction in the plane of nutrition, declines the relative size of the internal organs.

The allometric growth model $y = ax^b$ or its logarithmic form ($ln\ y = ln\ a + b\ ln\ x$), has been generally used in studies on the relative growth patterns of the different tissues or organs to the weight of each other or to the whole weight of the animal. However, in many growth studies, *e.g.* in birds (Lilja, 1983; Kwakkel, 1994) and goats (Ogink, 1993), the simple allometric equation did not fit for whole body tissues and organs. The growth function suggested by Kamalzadeh *et al.* (1995a), offered possibilities for determining the effects of the restriction and realimentation on body organs development.

Data of the present paper were part of the results of a main experiment in which, the effects of feed quality restriction in immature sheep were investigated. Results on the development of body dimensions and feed intake are described (Kamalzadeh *et al.*,1995a and 1995b) and the results with regard to feed efficiency and body composition will be reported later.

The objective of this study is to describe the effects of a period of feed quality restriction on the body organs development. The data of the control group were used to describe the changes in body organs weight in relation to body weight during normal growth. Estimated parameters were used to compare control and restricted animals during restriction and after realimentation.

MATERIAL

Experimental design

A detailed description of the experimental design, animals, feed composition, housing and management, has been reported elsewhere (Kamalzadeh et al., 1995b). Briefly, fifty six intact male Swifter (Flemish ♀ X Texel ♂) lambs of approximately 3 months age, were randomly allotted to two experimental groups. At the onset of the experiment, animals were randomly allotted to serial-slaughtering. For determination of the initial body composition, eight lambs were slaughtered at the beginning of the experiment. Half of the remaining (24 animals) were used as control (C) group and fed grass straw (51 g crude protein (CP) per kg dry matter (DM)) *ad libitum* with 35 $g.kg^{-0.75}d^{-1}$ mixed concentrates (173 g CP per kg DM). The other half (24 animals) were used as restricted (R) group and subjected to feed quality restriction. The R group was fed grass straw *ad libitum* with minerals from 3-6 months of age and thereafter the same feed as group C. The C and R animals were placed alternately. Following the 8 lambs which were slaughtered at the onset of the experiment, every three weeks 4 lambs (2 per group) and finally 8 lambs (4 per group) were slaughtered. In this way, it was possible to study the continuous rate of loss and gain in body organs during restriction and realimentation.

Slaughtering procedures

Animals were shorn prior to slaughter, in the morning of the slaughter day, animals were weighed, shot with a captive bolt and bled by cutting the jugular vein. Blood was collected and weighed. After dressing, the full gastrointestinal tract (GIT) was taken out and weighed after removing the surrounding fat. The stomach complex (rumen, reticulum, omasum and abomasum), large and small intestines were separated and weighed full and empty. The empty body weight (EBW) was calculated as the body weight (BW) at slaughter minus the weight of the gastrointestinal tract contents. The other visceral organs (liver, lungs, heart, kidneys and spleen), pelt, head and feet were removed and weighed separately. The gall bladder was removed from the liver before weighing.

Depots fat (omental, mesenteric and peritoneal fat) was removed and weighed. The trachea, reproductive organs and urinary tract were combined, considered as 'rest' and weighed separately. Finally, after complete dissection, the carcass was weighed, all different parts and the carcass were packed separately in tight plastic bags and frozen at -20°C for subsequent mincing and chemical analysis. With lambs weighing over 40 kg, the carcass was split medially and the left side was sold; with lighter lambs the whole carcass was used for chemical analysis (protein, fat, water and ash).

METHODS

Growth model

The statistical procedures were based on the growth model described by Kamalzadeh *et al.* (1995a). Briefly, the average weight or measurement of the restricted group expressed as the ratio to the average weight or measurement of the control group. The following equation is used to analyze the effects of restriction and realimentation on allometry:

$$\log_e[R_y(t)] = a + b.\log_e[R_x(t)] \quad [1]$$

In which R_y is the ratio of the averaged measurement for the restricted group over that average of the control group and R_x is the averaged body weight for the restricted group over that of the control group at time t. During normal growth, the expected value for 'a' is zero and for 'b' is unity. By using the ratio, the allometric relation for normal growth is removed, and therefore, it gives the opportunity to study the allometric relation during periods of restriction and realimentation. It is assumed that 'a' is not influenced by restriction or realimentation, and will stay at zero level:

$$\log_e[R_y(t)] = b.\log_e[R_x(t)] \quad [2]$$

To test constancy of 'b' during restriction and during realimentation, the effect of time is included in the 'b' term by defining the allometric coefficient as a sum of different functions of time:

$$\log_e[R_y(t)] = [b_0 + b_s.t_s + b_m.t_m + b_{sm}.t_s.t_m].\log_e[R_x(t)] \quad [3]$$

In which t_s is the number of weeks during feed quality restriction period and t_m is the number of weeks during realimentation period. If b_s, b_m and b_{sm} are zero, the allometric relation during restriction and realimentation is constant and independent of time. BW is taken as the reference (x) measurement, because this measurement can be considered as the total of all other body organs and components.

Equations [2] and [3] were used to estimate parameters in the allometric relations over periods of restriction and realimentation, and for testing the effects of time in these relations. A stepwise linear regression procedure from the statistical program Statistix 4.0 (Analytical software, 1992) was used to estimate parameters. The best model was chosen according to minimal residual standard deviations. Parameters were tested to deviate from zero with a Student t-test. Durbin-Watson (DW) statistics were computed to test positive autocorrelation using Table A-6 in Neter *et al.* (1985). Significance in tables is indicated by * ($P < 0.05$), ** ($P < 0.01$) and *** ($P < 0.001$).

Predictions were made using equations [2] and [3], and are presented in figures in relation to age and to body weight.

RESULTS

During the 3 months of feed quality restriction, R animals lost weight from both carcass and non-carcass parts (Table 1). The trend of changes during restriction and realimentation for EBW, carcass, non-carcass and some organs are presented in Table 2. From the non-carcass components, the absolute weight of the empty gastrointestinal tract (GIT), liver, spleen, heart, kidneys, blood, pelt, head, feet, depots fat and 'rest' decreased toward the end of restriction period. There was no change in the absolute weight of the lung and wool. From the various components of the GIT, the absolute weight of the small intestine reduced, while, there was no change in the combined weights of the rumen, reticulum and omasum (RRO) and abomasum, the weight of the large intestine slightly increased.

Table 3 shows the weight of the different body organs of each group as proportions of BW from the onset till the end of the experiment. As can be seen

Table 1: *Means[†] and standard errors (s.e.) of body weight (kg) and body organs[‡] (kg) of the control (C) and restricted (R) groups at the start[§] of restriction (14 weeks age), at the end[§] of restriction (28 weeks age) and at the end[§] of experiment (52 weeks age).*

	start of restriction		end of restriction				end of experiment			
group:	C,R		C		R		C		R	
	mean	s. e.	mean	s. e.	mean	s. e.	mean	s. e.	mean	s. e.
BW	27.73	0.97	38.90	4.06	24.31***	1.73	60.80	3.23	55.10	1.59
EBW	21.36	0.82	29.51	3.05	16.22***	0.80	47.12	2.87	42.62	1.06
BW										
Carcass	12.28	0.48	16.25	1.74	8.28***	0.42	26.31	1.55	23.93	0.61
GIT(content)	6.37	0.27	9.39	1.00	8.09***	0.93	13.68	0.62	12.48	0.57
Non-carcass	9.08	0.34	13.26	1.00	7.94***	0.33	20.81	1.28	18.69	0.82
Non-carcass components										
Feet	0.75	0.02	0.75	0.03	0.60***	0.01	1.08	0.05	0.97*	0.02
Blood	1.16	0.05	1.55	0.04	1.07***	0.12	2.26	0.07	2.20	0.11
Pelt	1.80	0.11	2.86	0.26	1.25***	0.07	4.30	0.28	3.95	0.24
Head	1.58	0.05	2.05	0.26	1.49***	0.06	3.20	0.10	2.82	0.09
Wool	0.50	0.04	1.36	0.16	0.61***	0.08	3.58	0.35	2.98	0.28
Depots fat	0.27	0.04	0.75	0.29	0.23***	0.01	1.90	0.27	1.25	0.03
Rest	0.35	0.02	0.64	0.05	0.21***	0.04	0.84	0.05	0.81	0.04
Visceral organs	2.69	0.09	3.19	0.16	2.58***	0.05	3.65	0.18	3.74	0.17
Visceral organs components										
Liver	0.41	0.01	0.52	0.03	0.38***	0.03	0.65	0.05	0.64	0.03
Heart	0.13	0.01	0.15	0.01	0.11***	0.01	0.19	0.01	0.18	0.01
Kidneys	0.10	0.00	0.09	0.00	0.07***	0.00	0.11	0.00	0.11	0.00
Lungs	0.30	0.02	0.41	0.01	0.33***	0.06	0.42	0.03	0.38	0.06
Spleen	0.04	0.00	0.05	0.00	0.02***	0.00	0.06	0.00	0.06	0.00
GIT(empty)	1.71	0.05	2.02	0.13	1.59**	0.09	2.24	0.10	2.37	0.06
GIT components										
RRO	0.59	0.03	0.85	0.08	0.59***	0.04	1.09	0.10	1.11	0.04
Abomasum	0.12	0.01	0.15	0.02	0.12***	0.01	0.22	0.04	0.23	0.01
Small intestine	0.67	0.02	0.62	0.02	0.45***	0.04	0.50	0.03	0.62*	0.02
Large intestine	0.33	0.02	0.41	0.00	0.38	0.00	0.43	0.01	0.45	0.02

[†]) If mean of R group differs significantly from that of C group, significance level is indicated.

[‡]) For abbreviations see text.

[§]) Numbers for each group at start of restriction are 8, at end of restriction 2, and at end of experiment 4.

from the data of the C group, with increasing BW, the proportions of all of the visceral organs, feet, head and blood decreased. The proportions of wool, pelt, depots fat and 'rest' increased. Depots fat and wool had the largest rate of increase and visceral organs had the largest rate of decrease. Among the various components of the visceral organs, GIT showed the largest, while kidneys showed the smallest rate of decrease. The largest reduction for the components of the GIT

Table 2: *Age (week), number of animals[†], means of body weight (kg), empty body weight, carcass, non-carcass and means of some body organs[‡] (kg) of the control (C) and restricted (R) groups from the start of restriction to the end of experiment.*

age	no.animals	BW	EBW	car.	n-car.	liver	GIT	feet	depots fat
control (C):									
14	8[§]	27.7	21.4	12.3	9.1	0.41	1.71	0.75	0.27
20	2	31.2	23.1	13.0	10.1	0.43	1.85	0.68	0.41
23	2	34.1	23.8	13.3	10.5	0.44	1.91	0.72	0.52
26	2	37.0	26.4	14.8	11.5	0.49	1.92	0.72	0.51
29	2	38.9	29.5	16.3	13.3	0.52	2.02	0.75	0.75
32	2	41.6	29.0	15.5	13.5	0.54	2.03	0.84	0.87
35	2	47.2	33.5	18.6	15.0	0.57	2.14	0.92	1.27
38	2	49.5	37.0	20.9	16.1	0.62	2.18	0.98	1.37
41	2	54.1	41.5	23.7	17.8	0.62	2.27	1.03	1.71
44	2	56.6	43.8	24.3	19.5	0.65	2.32	1.11	1.99
47	2	58.9	46.7	26.7	19.9	0.62	2.34	1.15	1.64
52	4	60.8	47.1	26.3	20.8	0.65	2.24	1.08	1.90
restricted (R):									
14	8[§]	27.7	21.4	12.3	9.1	0.41	1.71	0.75	0.27
20	2	23.7	16.9	8.6	8.3	0.39	1.67	0.64	0.24
23	2	23.7	15.7	7.8	8.0	0.38	1.61	0.63	0.22
26	2	23.8	15.6	7.8	7.8	0.38	1.61	0.59	0.20
29	2	24.3	16.2	8.3	7.9	0.38	1.59	0.60	0.23
32	2	26.8	18.5	9.8	8.7	0.38	1.56	0.65	0.24
35	2	31.4	21.9	12.1	9.8	0.41	1.72	0.74	0.28
38	2	34.9	25.3	14.4	10.9	0.47	1.84	0.79	0.39
41	2	40.9	29.9	17.3	12.6	0.49	2.00	0.85	0.67
44	2	44.5	32.8	18.7	14.1	0.53	2.13	0.93	0.94
47	2	49.4	36.5	21.3	15.2	0.54	2.21	0.99	0.82
52	4	55.1	42.6	23.9	18.7	0.64	2.37	0.97	1.25

[†]) number of animals contributed to the means of body weights and body organs.

[‡]) for abbreviations see text.

[§]) means of 8 animals which slaughtered as initial group were used for both control and restricted treatments.

was associated with the small intestine, then RRO, large intestine, with the smallest for abomasum.

The allometric relationship between the corrected weight of the various body organs (ratio of average of the restricted group over that of the control group) and corrected body weight was described by equation [2]. The relation including time of restriction and realimentation was described by equation [3]. The first equation

Table 3: *Means of body organs[1] as proportion of body weight of the control (C) and restricted (R) groups at the start[‡] of restriction (14 weeks age), at the end[‡] of restriction (28 weeks age) and at the end[‡] of experiment (52 weeks age).*

	start of restriction	end of restriction		end of experiment	
group:	C,R	C	R	C	R
EBW	0.770	0.760	0.667	0.775	0.774
BW					
Carcass	0.443	0.418	0.341	0.433	0.434
GIT(content)	0.230	0.241	0.333	0.225	0.226
Non-carcass	0.327	0.341	0.327	0.342	0.339
Non-carcass components					
Feet	0.027	0.019	0.025	0.018	0.018
Wool	0.018	0.035	0.023	0.059	0.054
Blood	0.042	0.040	0.044	0.037	0.040
Pelt	0.065	0.074	0.051	0.071	0.072
Head	0.057	0.053	0.058	0.053	0.051
Depots fat	0.010	0.019	0.009	0.031	0.023
Rest	0.012	0.016	0.008	0.015	0.014
Visceral organs	0.097	0.082	0.110	0.060	0.067
Visceral organs components					
Liver	0.015	0.013	0.016	0.011	0.012
Heart	0.004	0.004	0.004	0.003	0.003
Kidneys	0.003	0.002	0.003	0.002	0.002
Lungs	0.011	0.010	0.015	0.007	0.007
Spleen	0.002	0.001	0.001	0.001	0.001
GIT(empty)	0.062	0.051	0.067	0.037	0.043
GIT components					
RRO	0.021	0.022	0.240	0.017	0.019
Abomasum	0.004	0.004	0.005	0.003	0.004
Small intestine	0.024	0.016	0.019	0.008	0.011
Large intestine	0.012	0.010	0.016	0.007	0.008

[1]) For abbreviations see text.

[‡]) Numbers for each group at start of restriction are 8, at end of restriction 2, and at end of experiment 4.

is the simple allometric model. Under normal conditions, b is expected to be one. The allometric growth coefficient (b) in eq [2] is made dependent on time in eq [3] by including effects of time of restriction (b_s), time of realimentation (b_m) and the interaction (b_{sm}).

Table 4. *Estimates of parameters for the first model[†] (eq [2]), Durbin-Watson statistics (DW)[‡] and residual standard deviations (resid. s.d.) for all measurements[§].*

measure (y)	b	DW	resid. s.d.
	$\log_e(R_y) = b \cdot \log_e(R_{BW})$		
BW			
EBW	1.144***	1.95	0.031
Carcass	1.270***	0.80**	0.064
Non-carcass	1.015***	0.56***	0.059
GIT (content)	0.470**	1.46	0.075
Non-carcass components			
Feet	0.520***	0.50***	0.050
Head	0.728***	0.43***	0.035
Blood	0.746***	0.63***	0.067
Wool	1.558***	0.73***	0.139
Pelt	1.502***	1.47	0.059
Rest	1.477***	0.74***	0.216
Depots Fat	2.870***	0.60***	0.214
Visceral organs	0.535***	0.78***	0.046
Visceral organs components			
Liver	0.673***	0.62***	0.056
Lung	0.645***	0.89**	0.070
Heart	0.707***	0.92**	0.046
Kidneys	0.489***	1.15	0.026
Spleen	0.958***	1.40	0.116
GIT	0.460***	0.42***	0.045
GIT components			
RRO	0.622***	0.92**	0.027
Abomasum	0.621***	0.78***	0.067
Small intestine	0.577***	0.26***	0.121
Large intestine	0.285**	0.48***	0.081

[†]) See for explanation of variables and parameters equation [2] in text.
Significance levels are indicated for parameter estimates which deviating from zero

[‡]) Test for positive autocorrelation with time. Significance level is indicated.

[§]) For abbreviations see text.

The estimated parameters, residual standard deviations and DW statistics for fitted curves are presented in Tables 4 and 5. Figures present the observations and predictions of using the two models which applied to the natural logarithm of the ratios ($\log_e R_y$) against age (left side), and against the natural log of the ratio of

Table 5. *Estimates of parameters for second model[†] (eq [3]), Durbin-Watson statistics (DW)[‡] and residual standard deviations (resid. s.d.) for all measurements[§].*

measure (y)	b_0	b_s	b_m	b_{sm}	DW	resid. s. d.
$\log_e(R_y) = (b_0 + b_s \cdot t_s + b_m \cdot t_m + b_{sm} \cdot t_s \cdot t_m) \cdot \log_e(R_{BW})$						
BW						
EBW	1.165***		0.0188	0.0030	2.30	0.031
Carcass	1.436***		0.0254	0.0073*	1.91	0.033
Non-carcass	0.471**	0.0365**	-0.0101	0.0011	1.65	0.030
GIT (content)	1.600***	-0.0925**	0.0813*	-0.0017	2.41	0.049
Non-carcass components						
Feet	0.017	0.0344***	-0.0033	0.0021*	3.15	0.012
Head	0.430**	-0.0186		-0.0001	1.97	0.040
Blood	-0.048	0.0572**	-0.1026***	-0.0086	1.61	0.026
Wool	0.348	0.0775**		0.0035	2.73	0.068
Pelt	1.825***	-0.0255		-0.0022	2.28	0.086
Rest	0.739	0.1185	-0.1099	0.0175	2.88	0.102
Depots fat	2.274***		-0.0223	-0.0171	1.99	0.104
Visceral organs	0.438	0.0047		-0.0004	1.68	0.048
Visceral organs components						
Liver	0.494*	0.0060		-0.0011	1.43	0.047
Lung	0.083	0.0323***	-0.0356*	-0.0001*	2.23	0.019
Heart	0.396*	0.0189		0.0001	2.19	0.029
Kidneys	0.470***		-0.0227	-0.0171	1.40	0.024
Spleen	-0.440	0.1432**	-0.1197*	0.0109	2.53	0.073
GIT	0.459***		-0.0706***	-0.0096***	1.74	0.024
GIT components						
RRO	0.620***	0.0056		0.0001	2.50	0.020
Abomasum	0.343**	0.0192	-0.0359**	-0.0034**	3.01	0.013
Small intestine	1.340**	-0.0428		-0.0000	1.18	0.070
Large intestine	0.060*		-0.0787***	-0.0150***	2.01	0.026

†) See for explanation of variables and parameters equation [3] in text.
Significance levels are indicated for parameter estimates which deviating from zero

‡) Test for positive autocorrelation with time. Significance level is indicated.

§) For abbreviations see text.

body weight ($\log_e R_{BW}$) (right side).

As the solid lines in the Figures 1 to 4 and the goodness of fit characteristics (DW and resid. s.d.) in the Table (4) show, the equation [2] did not fit the data well. Using Eq.[3], showed a good fit (no autocorrelations) for all of the measurements (dashed lines in Figures 1 to 4). The results showed that depots fat and 'rest' had the highest resid. s. d. compared to the other parts. This can be explained by the fact that these parts are combined from various parts. Depots fat is combined from omental, mesenteric and peritoneal fat, and 'rest' is combined from reproductive organs, urinary tract and trachea.

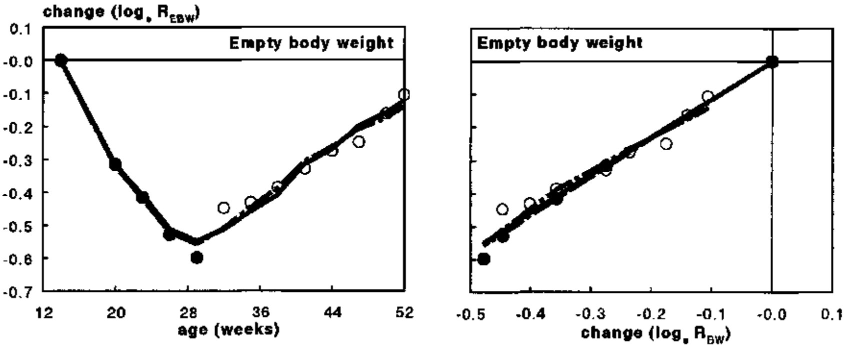

Figure 1. The relationship between the natural log of the ratio of empty body weight ($\log_e R_{ebw}$) against age (weeks) (left side), and against the natural log of the body weight ratio ($\log_e R_{BW}$) (right side); (●) observed during restriction, (O) observed during realimentation, (———) prediction based on Eq. [2], (— - — -) prediction based on Eq. [3].

Equation [2] presents an average description of the allometric relation between organs and BW. The expectation is that the decrease after restriction follows the same line as the increase after realimentation. The growth coefficients ranged from 0.4 to 1 for feet, head and all visceral organs, between 1 and 2 for carcass, wool, pelt and 'rest', while depots fat had a very high coefficient of 2.87. As figures show growth of all organs and components did not have the same trend during restriction and realimentation.

In equation [3], parameter b_0 is an estimate of the growth coefficient.at the start of the restriction. Higher value of b_0 than the b in equation [2], gives a line starting below and ends above the solid line, as for carcass (Figure 2, right side).

If this b_0 is lower, the line starts above and ends below, as for liver (Figure 3, right side). Ranking of b_0's are similar to that for b's. Including b_s and b_m into the allometric equation resulted in better fits.

After restriction, EBW reacted in the same way as BW (Figure 1), carcass showed an earlier effect of restriction, but there was a delayed effect of restriction on non-carcass (Figure 2). Among the various components of non-carcass, pelt, kidneys and GIT showed the same trend as BW. Feet, head, liver, lungs, heart, and

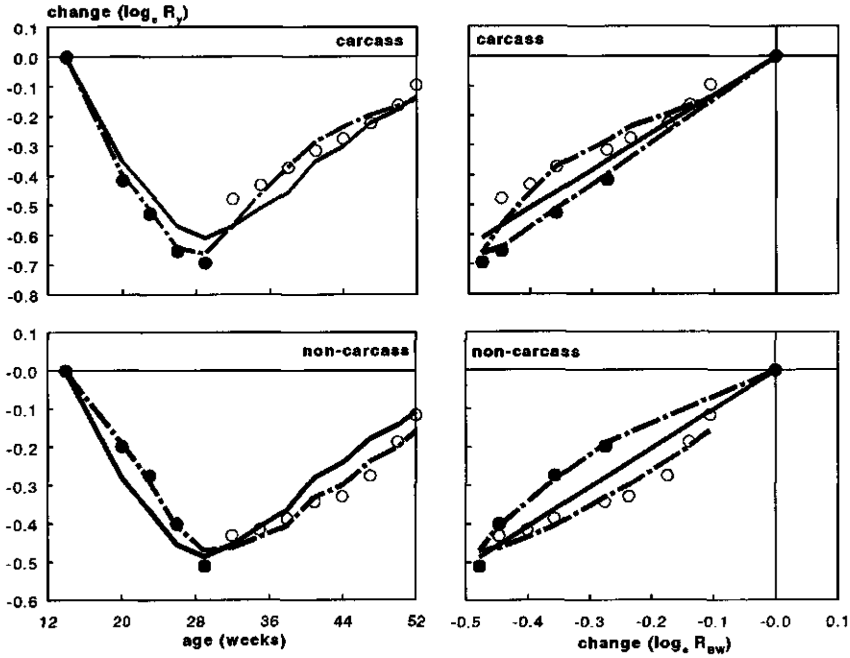

Figure 2. The relationship between the natural log of the ratio of carcass and non-carcass ($\log_e R_y$) *against age (weeks) (left side), and against the natural log of the body weight ratio* ($\log_e R_{BW}$) (right side); (●) observed values during restriction, (○) observed values during realimentation, (———) prediction based on Eq. [2], (— - — -) prediction based on Eq. [3].

depots fat delayed their weight loss (Figure 3), whereas, 'rest' and spleen showed a faster decrease. Among the various components of the GIT, RRO had the same trend as BW, while, abomasum and large intestine delayed their growth. In contrast, small intestine showed earlier effects of restriction (Figure 4).

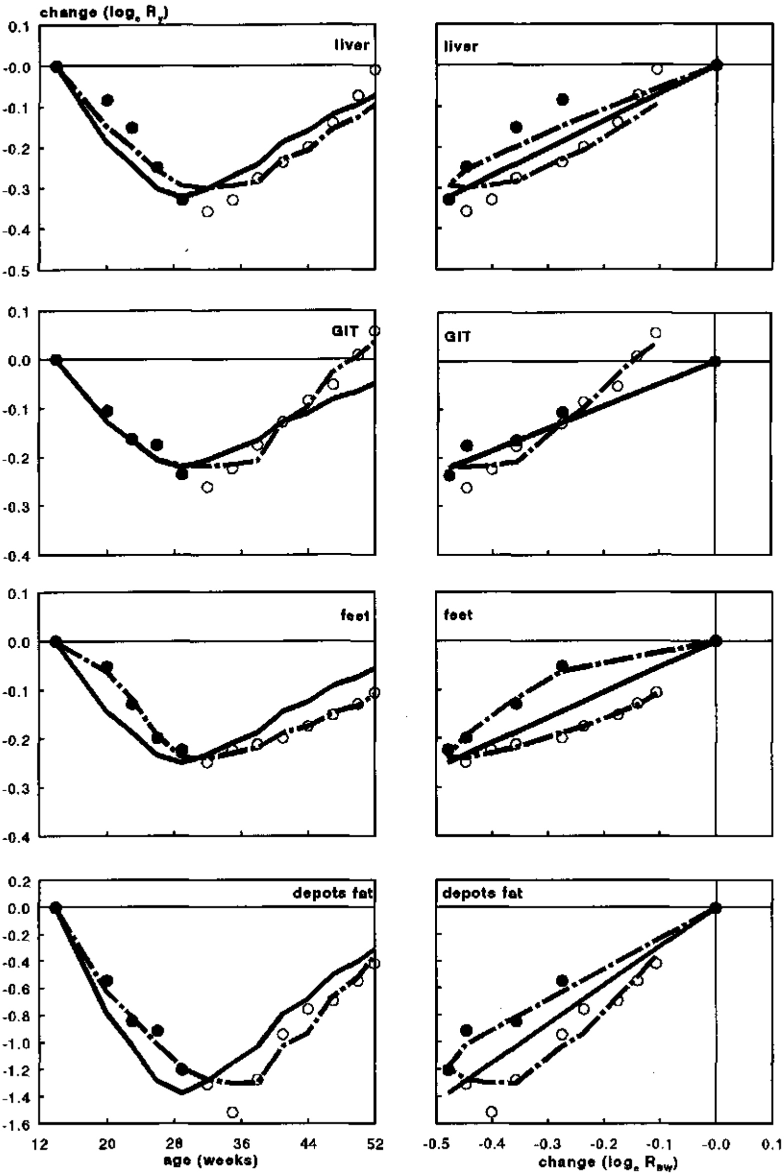

Figure 3. The relationship between the natural log of the ratio of each measurement ($\log_e R_Y$) against age (weeks) (left side), and against the natural log of the body weight ratio ($\log_e R_{SW}$) (right side); (●) observed during restriction, (○) observed during realimentation, (———) prediction based on Eq. [2], (— - — -) prediction based on Eq. [3].

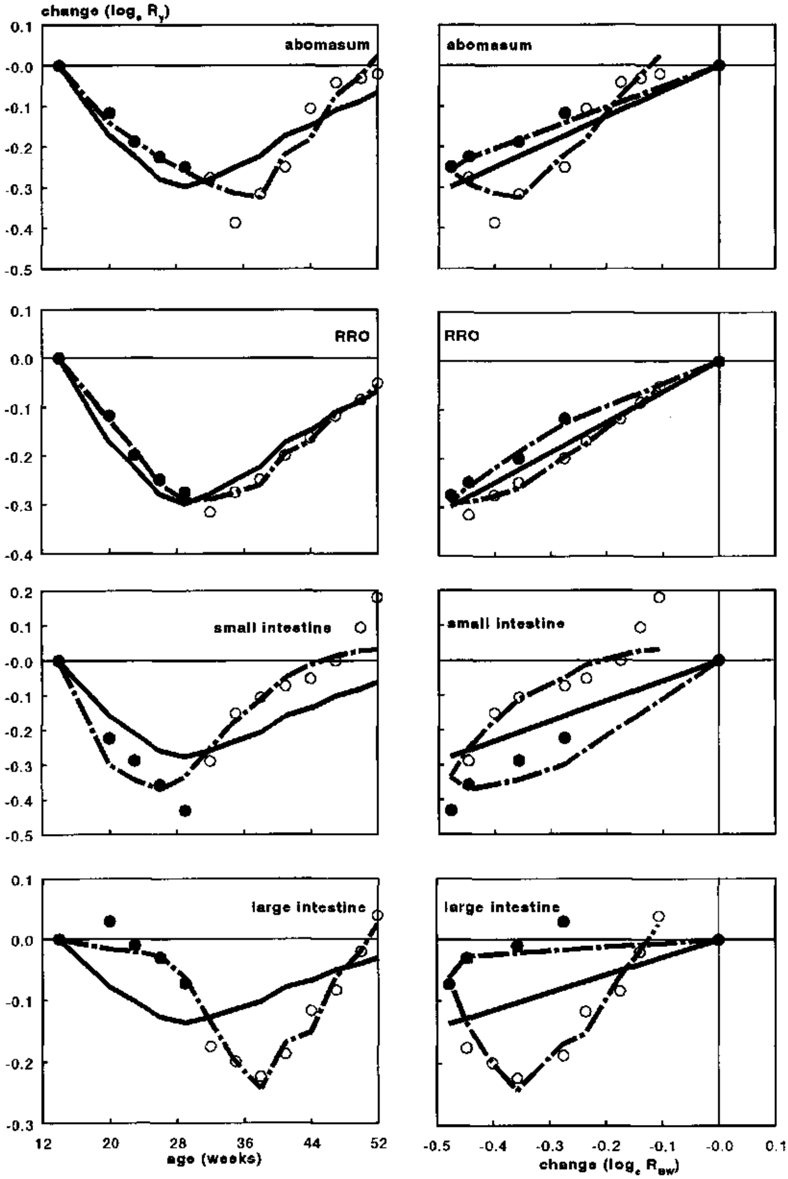

Figure 4. The relationship between the natural log of the ratio of the GIT components ($\log_e R_y$) against age (weeks) (left side), and against the natural log of the body weight ratio ($\log_e R_{BW}$) (right side); (●) observed during restriction, (○) observed during realimentation, (———) prediction based on Eq. [2], (— - — -) prediction based on Eq. [3].

After realimentation, EBW showed the same pattern of growth as BW (Figure 1). Carcass showed a faster growth rate than BW, while, non-carcass had the same trend of growth as BW (Figure 2). From the various components of the non-carcass, pelt and kidneys had the same pattern as BW. GIT had a slower trend of growth at the onset of realimentation, but later showed a very fast growth rate. Feet, head, wool, liver, lungs, heart, and depots fat delayed their growth compared to BW (Figure 3). Whereas, 'rest' and spleen showed a faster rate of growth. Among the various components of the GIT, small intestine showed the highest and large intestine had the lowest growth rate (Figure 4). At the end of experiment, head weight was higher ($P < 0.05$), and depots fat tended to be higher ($P < 0.1$) in C group compared to R group. In contrast, the weight of the small intestine was significantly ($P < 0.05$) higher in R group. No significant differences ($P > 0.05$) were observed for the other parts between groups (Table 1).

DISCUSSION

Effect of increasing body weight on the weight of organs

The data of the C group were used to describe the changes in the weight of body organs during increasing BW under normal condition. The correlation between EBW, visceral organs weight and the weight of the other body components with BW were differed as BW increased (Table 3). As proportions of BW, the empty body and carcass weights were on average 0.77 and 0.43. Thonney *et al.* (1987) found the average values of 0.80 for EBW and 0.41 for carcass as a proportion of the mature weight in Wiltshire Horn and Oxford Down sheep. They reported that the carcass proportion of the EBW increased from 0.56 to 0.59. In contrast to that, in this experiment, the proportion of the carcass weight was 0.58 of the EBW and decreased to 0.56 with increasing BW.

In general, the non-carcass components showed either early or late maturing patterns. The decreased proportions of the feet, head, blood and visceral organs with increasing BW, indicate the early maturing pattern of these parts. While, the increased proportions of wool, pelt, depots fat and 'rest' indicate a late maturing pattern. The early maturing pattern of the head is related to the development of brain and bones. The growth of feet is mainly related to the development of bone. Brain and bones are matured earlier than the other parts of the body (Palsson & Verges, 1952)

Blood was made up on average 0.04 of the BW and 0.054 of the EBW and declined to 0.048 at the end of the experiment. In line with this experiment, Butterfield *et al.* (1983) reported a decline from 0.046 when animals were 0.62 of the mature weight to 0.037 when animals were fully mature. Thonney *et al.* (1987) also reported a decline from 0.047 when animals were 0.40 of mature weight to 0.040 when animals were 0.76 of mature weight.

From the visceral organs, the proportion of the empty GIT made up 0.062 of the BW at 27.7 kg BW and decreased to 0.036 at 60.8 kg. The small intestine had the highest rate of decline relative to the other components of the GIT. This is in line with the data of Butterfield *et al.* (1983) which showed a decrease in the weight of the small intestine as the animals matured in BW beyond 60% in Merino sheep. Hammond (1932) also found a decrease in the absolute weight of the small intestine and as a proportion of BW, between 3 months and adult age in Suffolk rams. Burrin *et al.* (1990) found the same result for the forestomachs and large intestine. However in contrast, they reported that the weight of the small intestine increased with increasing BW. The GIT appeared to be an early maturing component and the small intestine appeared to be somewhat earlier matured than the other parts of the GIT.

As the GIT, the proportions of most of the other visceral organs (liver, lungs, kidneys and spleen) decreased with increasing BW, indicating early maturing pattern than BW. The liver comprised on average 0.015 of the BW at 27.7 kg and declined to 0.011 at 60.8 kg BW. The data of Kraybill *et al.* (1954), Butterfield *et al.* (1983) and Thonney *et al.* (1987) indicated the same pattern for liver during increasing BW.

The heart showed more stable characteristic with increasing BW and appeared to be much more dependent on the absolute weight of the body. The same has been reported in pigs (Mcmeekan, 1940) and in sheep (Palsson & Verges, 1952). Brody (1945) and Prothero (1979) reported a constant ratio between the weight of the heart and BW with increasing BW in several species.

Of the other components, the pelt was 0.065 of the BW, and increased to 0.071 with increasing BW, indicating a late maturing pattern. The findings of Hammond (1932) and Kirton *et al.* (1972) are not in line with these results. In the data of Hammond (1932), the feet were included in the pelt weight. As mentioned earlier, the feet showed early maturing pattern in this experiment. The data of Kirton *et al* (1972) were from the immediate post-natal period of growth. These might be the reasons of different conclusion for the growth of the pelt in their studies. The depots fat showed a late maturing pattern and its proportion increased with increasing BW. Similar results were reported by Kirton *et al.* (1972), Wood *et al.* (1980) and Butterfield & Thompson (1983) for omental and mesenteric fat.

The proportion of the contents of the GIT decreased with increasing BW, probably due to the decline in the straw intake (Kamalzadeh *et al.*, 1995b). Confirming results reported by Butterfield *et al.* (1983) and Thonney *et al.* (1987). Thompson & Parks (1983) also reported that the decline in the weight of the gut contents of Merino sheep as animals matured was related to the decline in feed intake. Blaxter *et al.* (1982) also reported a constant weight of the gut contents over a wide range of BW.

In general, the visceral organs have priority use for the available nutrients in the blood stream relative to the other parts of the body. Therefore, they grow faster at early age and are matured relatively earlier than whole body. The early maturing pattern of the visceral organs seems an essential process for their functional activities and further growth of the whole body.

Feed quality restriction

Supplying low quality feed had inhibiting effects on the normal development of the body organs. During feed quality restriction, R animals lost about 13% of their body weight. The reduction in the absolute weight of the carcass and most of the non-carcass components such as, feet, head, pelt, depots fat, GIT, liver, kidneys, spleen and 'rest' in this experiment is in line with the results reported by the other authors (*e.g.* Hogg, 1992; Ryan *et al.*,1993). Hogg (1992) concluded that the internal organs such as the liver, kidneys, heart and GIT were very sensitive to changes in nutrition, due to their high metabolic activity. Koong *et al.* (1982) and Ferrell *et al.* (1986) observed significant decreases in the weight of the liver, stomach and small intestine of sheep and pigs during 6-10 weeks of feed restriction. Ledin (1983), reported that the liver, small intestine and kidneys were most affected. Burrin *et al.* (1990) and Ryan *et al.* (1993) found the same for liver and digestive tract. Foot & Tulloh (1977), and Burrin *et al.* (1990) also reported the same for liver and the small intestine.

The above comparison of the results were mainly based on the absolute weight of the organs at the end of the restriction period. In general, evaluation of organ weights in absolute term, has little or no significance, they must be evaluated in relation to BW. Especially, under a low plane of nutrition, restricted animals have a different physiological status than controls which results in different reactions among various organs. Therefore, the effects of feed quality restriction on the size of various body organs of R animals were measured as proportions of the BW.

After restriction, with decreasing BW, the proportions of empty body and carcass weights decreased (Table 2). From the non-carcass components, the proportions of the GIT, lung and blood increased. The proportions of the liver, heart, kidneys, spleen and head, were stable. Whereas, of the pelt, feet, depots fat and 'rest' decreased. The proportion of the GIT was 0.067 of the BW at the end, compared with 0.062 at the onset of the restriction period. This indicates that the gut of R animals were well developed in terms of volume to ingest more straw. Among the various components of the GIT, the proportions of the RRO, abomasum and large intestine were higher, and of the small intestine was lower at the end of the restriction period. The proportion of the contents of the GIT increased, because of the higher straw intake.

The comparison of the relative organ weights between both groups showed that, as proportions of the BW, R animals had lighter empty body and carcass weight compared to C animals. From the non-carcass components, the proportions of the wool, pelt, 'rest' and depots fat were lower, whereas of the feet, head and all of the visceral organs were higher in R animals compared to C animals. The evaluation of the organ weights as proportions of the BW indicates that, under low plane of nutrition, the internal organs especially the highly active organs such as GIT, liver and heart are affected to a lesser extent than BW. This is different to the results reported earlier in this section, that the internal organs are most affected by feed restriction. This shows that the different way of evaluation of organ weights may lead to different conclusion for the development of organs. The results of this experiment showed that visceral organs had higher priority for the available nutrients during feed quality restriction. This can be explained by the fact that the functional activities of these organs were essential for the survival of the animals under a low plane of nutrition.

Realimentation

The delay in the organs growth of the R animals was compensated during the realimentation period. At the end of the experiment, in absolute terms, there were no significant differences between treatments except the head which was heavier in group C and the small intestine which was heavier in group R. Ryan *et al.*, (1993), also reported heavier heads for controls than realimented cattle. When, the organ weights of the R and C animals were compared based on the proportions of BW, carcass, lungs, heart, kidneys, spleen, feet, head, pelt, and 'rest' in the R animals had the same proportions of BW, compared with C animals (Table 3).

Whereas, the weight of the GIT in the R animals was higher and constituted 0.043 of BW, compared with 0.037 for C animals. The small intestine had the greatest differential weight, 0.011 of BW for R animals, compared with 0.008 for C animals. This result is in line with the results of Foot & Tulloh (1977), who reported that the digestive tract as a whole in the realimented cattle was 0.085 of BW, compared with 0.079 for control animals. The weight of the liver in R animals was 0.012 of BW, compared with 0.011 for C animals, indicating full compensation of the liver. In contrast, Foot & Tulloh (1977) reported that in cattle which lost about 15% of their initial BW, the weight of the liver was 3.5 kg in R animals compared with 4.4 kg in C animals at the same BW. The same result has been reported by Ledin (1983), who found that, the liver of the lambs fed 60% of their *ad libitum* feed intake for 52 days did not fully compensate after 73 days *ad libitum* feeding. Whereas, in line with the results of this experiment, Ryan *et al.*, (1993), reported lighter livers for controls in cattle.

Blood weight in R animals constituted 0.040 of the BW, compared with 0.037 for C animals. In contrast to the other components, the weight of the wool and depots fat were lower in R animals and constituted 0.054 and 0.023 of the BW compared with 0.059 and 0.031 for C animals.

Use of the growth model

The growth patterns of organs are generally defined by using simple allometric models or its logarithmic linear form. However, in many growth studies of various species this model did not hold for the whole weight range. The observed values in the experiments of Lilja (1983) and Kwakkel (1994) in birds and Ogink (1993) in goats led these authors to assume different phases in the growth of the various organs related to different body weight ranges. Some of the above mentioned studies described the growth phases in organs versus total BW, and some other interpreted the growth of organs based on a description against empty body weight or fat free empty body weight. According to Kamalzadeh *et al.* (1995a), the simple allometry model is based on the independency of time and estimating only an average relation between growth of component relative to BW. Therefore, this model can not give a proper description for a detailed growth study during restriction and realimentation. As the figures show, equation [2] predicted that the decrease after restriction follows the same line as the increase after realimentation (solid lines). Equation [3] resulted in a good fit of the observed patterns and an adequate description of the development of organs and components relative to BW.

In this equation, the size of b_0 indicates whether y is early ($b_0 < 1$) or late ($b_0 > 1$) maturing relative to x. The estimated b_0 values from using equation [3] in this experiment show that feet, head and all of the visceral organs are matured earlier than BW. Carcass, wool, pelt, and depots fat showed late maturing pattern. EBW showed the same pattern of growth as BW.

The slower rate of reduction in the weight of feet and head after restriction indicates that these organs are mainly composed of bone, during restriction the bone only stop growing rather than losing weight. Wool stopped growing during restriction probably due to the lack of protein. The delay in the reduction of depots fat indicates that during weight loss, animals mainly used the muscular fat and tissue protein as sources of energy rather than depots fat. The delay in the reduction of the weight of the liver, heart and lung indicates that these organs were affected to a lesser extent than BW, and had higher priority for the available nutrients during feed quality restriction. The faster rate of reduction in carcass, pelt, and 'rest' indicates that these parts were late maturing ones and affected earlier than the other parts during restriction. The faster rate of reduction in the weight of small intestine during restriction, mainly related to the low level of available nutrients for absorption. The stable growth pattern of RRO, abomasum and large intestine, related to the type of restriction imposed in this experiment (feed quality restriction), which resulted to a higher straw intake of the R animals during restriction period (Kamalzadeh *et al.*, 1995b).

The slower growth rate of the GIT at the onset of realimentation, indicates that there was a period of several days to adapt to the higher protein and energy intake. Hogg (1992), also reported an adaptation period of several days for internal organs at the onset of the recovery period. The very high growth rate of the GIT and specially the small intestine at the latter stage of realimentation can be explained by higher metabolic activities and the process of protein synthesis of these organs.

The different reactions of various organs and components after realimentation were mainly a reflection of their reactions during restriction. Some of the organs such as head, feet, liver, lungs, and heart which delayed their weight loss during restriction, showed also a slower rate of increase after realimentation, however at the end of experiment, except head, the other body organs compensated and there was no significant difference between groups. Most of the organs which had a faster rate of reduction during restriction, showed a faster growth rate after realimentation.

CONCLUSIONS

The growth model used in this experiment clearly shows the effects of feed restriction on body organs development. Various body organs react differently during restriction and after realimentation. In general, early maturing parts (head, feet and visceral organs) have high priority for use of the available nutrients in the blood stream and are affected less than the late maturing parts by feed restriction. After realimentation, the responses are mainly related to their reactions during restriction, *i.e.* the organs which are most affected and have the greatest retardation, respond quicker than those which are less affected.

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Chapter 5

Feed quality restriction and compensatory growth in growing sheep: changes in body composition.

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Feed quality restriction and compensatory growth in growing sheep: changes in body composition.

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ABSTRACT

Changes in the chemical composition (protein, fat, ash and water) of the empty body, carcass, gastrointestinal tract (GIT), liver and remainder of 56 crossbred Swifter (Flemish ♀ X Texel ♂) male lambs were measured by serial slaughter of animals following two different growth paths. Lambs were born in March 1993 and weaned at ≈ 2 months old. The ration was gradually changed into a grass straw based diet (51 g crude protein (CP) per kg dry matter (DM)) *ad libitum* and 35 $g.kg^{-0.75}.d^{-1}$ mixed concentrates (173 g CP per kg DM). At an age of 3 months, after an initial slaughter of 8 lambs, the remaining 48 animals were divided into a restricted (R) and a control (C) group. The R group was subjected to feed quality restriction by withholding concentrates from 3-6 months of age. At each three-week interval, 4 lambs (2 of each group) were slaughtered regularly, except for the last remaining 8 lambs (4 of each group), which were slaughtered six weeks after the previous slaughter date.

The chemical body composition of the R animals, after losing up to 24% of empty body weight over 3 months, in absolute term, was significantly ($P < 0.001$) lower than the C animals. But as proportion, relative to the C animals, the R animals contained less fat, more water and ash and the same amount of protein.

As proportion of the initial weight, the greatest loss was associated with fat, then protein, water, with the smallest for ash. The responses to feed quality restriction and to realimentation differed among body parts. Particularly the protein loss in the GIT and liver was compensated earlier than in the other parts of the body. At the end of experiment, the R animals were leaner and had significantly ($P < 0.01$) less fat in the empty body.

(*Key words:* body composition, restriction, compensatory growth, sheep, growth)

INTRODUCTION

The effect of restricted feeding and realimentation on body composition has been studied by various researchers but, with apparently conflicting results. Searle & Graham (1975) and Thornton *et al.* (1979) reported that realimented animals had a body composition similar to the controls, while Little & Sandland (1975) reported that realimented animals were leaner. In contrast, Wilson & Osbourn (1960) and Meyer & Clawson (1964) found more fat for rehabilitated animals. Allden (1970) suggested that fat tissue responds more rapidly than the other tissues to high nutrient intake immediately after realimentation. Ledin (1983) reported that after realimentation the carcass of the realimented sheep contained more protein and water when compared with controls in terms of actual weight. However, when the data expressed as percentage, the result was reversed and realimented animals contained more fat. Searle & Graham (1975) who restricted 4 months old wether sheep at 20 kg for either 4 or 6 months, and then fed *ad lib.*, found no difference in body composition between controls and previously restricted animals at any given weight above 32 kg. They reported that during the early stages of realimentation, the realimented animals retained less water and more protein and fat than the controls, but, during the fattening phase no differences occurred. Fox *et al.* (1972) reported that steers which were restricted at 260 kg body weight, showed a higher protein deposition than controls between the range 260-350 kg. This trend was reversed over the range 350-450 kg and previously restricted animals deposited more fat. However, finally both groups had the same body composition at 450 kg. Ørskov *et al.* (1976) and Black (1983) noted that the increase in growth rate following realimentation after a period of restriction was mainly related to the changes in the composition of gain.

Liver and digestive tract are very sensitive to nutritional changes, possibly because they are metabolically very active. Webster (1980) reported that the greatest rates of protein synthesis do not occur in muscle, but in tissues such as the liver and the digestive tract. Winter *et al.* (1976) noted that in the recovery period, the biggest changes in relative growth occurred in the liver and small intestine. Kamalzadeh *et al.* (1996) found that the biggest changes occurred in the small intestine during feed quality restriction and following recovery periods. Butler-Hogg (1984) also observed an accelerated growth rate of the visceral organs; the rate of protein gain in the visceral organs was doubled during compensatory growth compared to controls. Burrin *et al.* (1988) have shown that in the visceral organs cell size rather than cell numbers was reduced during feed restriction. This implies that a large part of the increase in the weight of the visceral organs during compensatory gain is due to hypertrophy rather than hyperplasia. Hypertrophy occurs through increase in protein gain, which in turn will be influenced by the availability of ribonucleic acid (RNA). According to Re & Thornton (1980), the changes in the activity of aspartate carbamoyl-transferase (ACT), which is the first step in the biosynthesis of pyrimidine required for RNA synthesis, follow the responses in weight. According to Hogg (1992), ACT activity was highest in the liver and small intestine. In immature sheep during compensatory growth, ACT levels were rapidly restored and tended to be 20-97% higher than in comparable control animals and were elevated for up to 130 days. This suggests that the enhanced regenerative (protein synthetic) capacity resumes for considerable time after realimentation.

The objective of this study is to describe changes in the body composition of immature sheep during nutritional restriction and subsequent compensatory growth, and compared with the changes in control animals. Changes in the composition of the empty body and its constituent parts (carcass, gastrointestinal tract, liver and remainder) are measured separately. The growth pattern of the body composition are described by the growth model outlined by Kamalzadeh *et al.* (1995a).

MATERIAL

Experimental design

A detailed description of the experimental design, animals, feed composition, housing and management, has been reported by Kamalzadeh *et al.* (1995b). Briefly, fifty six 3 months old non-castrated male Swifter (Flemish ♀ X Texel ♂) lambs, born in March 1993 were randomly allotted to two experimental groups. At the onset of the experiment, animals were randomly allotted to serial-slaughtering. Eight lambs were slaughtered to determine the initial body composition. Half of the remaining (24 animals) was designated as the control (C) group, fed a diet of grass straw (51 g crude protein (CP) per kg dry matter (DM)) *ad libitum*, supplemented by 35 $g.kg^{-0.75}.d^{-1}$ mixed concentrates (173 g CP per kg DM). The other half (24 animals), designated as the restricted group (R), was offered only grass straw *ad libitum* and concentrate restriction was imposed for a period of 3 months (3-6 months of age). Thereafter, that restriction was removed by offering the R animals the same ration as the C animals. The C and R animals were placed alternately and were housed in metabolism cages and individual pens. The ambient temperature was kept at about 20°C. An artificial lighting regime was imposed of 12/12 h day/night to avoid seasonal effects of day length.

Following the 8 lambs which were slaughtered at the onset of the experiment, 4 lambs (2 per group) were slaughtered regularly at three-week intervals, except for the last 8 remaining lambs (4 per group), which were slaughtered six weeks after the previous slaughter date. In this way, it was possible to study the trend of changes in body composition during restriction and realimentation.

Slaughtering procedures

A detailed description of the slaughtering procedures has been reported by Kamalzadeh *et al.* (1996).

Sampling procedures and chemical analysis

In total, chemical analyses were carried out for four different fractions including carcass, liver, gastrointestinal tract (GIT) and remainder (the summed of the head, pelt, feet, lungs, heart, kidneys, spleen, depots fat and 'rest'). All fractions were weighed frozen, cut into small pieces, roughly minced and homogenized thoroughly in the meat grinder fitted with a three fixed, rotating knife blades (Berkel BV, Rotterdam). Carcass, GIT and remainder were separately minced and about 1.5 kg was taken, placed in a sealed plastic container and frozen pending for chemical analyses. The liver was minced in the meat cutter and further treated by a (kitchen) blender (Kenwood). Because of the size, the liver was not sub-sampled and the entire liver was subsequently freeze-dried prior to chemical analyses.

The frozen samples of carcass, GIT and remainder were thawed overnight and before actually taking sub-samples for chemical analyses further homogenized with a high rotation sample mill (Tecator, Kjeltec 1095 sample mill). Samples from the remainder part that included head, feet and pelt contained small bone chips and pelt particles which prevented them being mixed mechanically either in the meet cutter or the homogenizer. Therefore, these samples of remainder were added by 500 g water and further treated by autoclave at 122°C, 1 bar (10^5 Pa, 750 mm Hg) for 10 h. Before sub-sampling, the samples were further homogenized by a (kitchen) blender (Kenwood).

The dry matter content of the fresh samples of carcass, GIT and remainder was obtained by drying representative sub-samples in a vacuum stove at 50°C, 10kPa (75 mm Hg) for 24 h, and subsequently to constant weight at 103°C. The dry matter content of the freeze-dried sample of the liver was obtained by drying to constant weight at 103°C. The ash content was determined by ashing to constant weight at 550°C. The nitrogen content was determined by the Kjeldahl method. The fat content was determined by ether extraction on freeze-dried subsamples of carcass, GIT, liver and remainder.

METHODS

Calculations were made of the weights of dry matter, water, crude protein, fat and ash in the carcass, liver, GIT and 'remainder'. The composition of these four body parts were pooled and designated as the composition of the empty body. The statistical procedures were based on the method outlined by Kamalzadeh *et al.* (1995a). A satisfactory fit to the data obtained by using this method to describe the changes in composition during restriction and realimentation. Equation [1] is used to analyze the effects of restriction and realimentation on allometry.

$$\log_e[R_y(t)] = a + b.\log_e[R_x(t)] \qquad [1]$$

In this equation, R_y is the ratio of the averaged chemical components for the R group over that average of the C group and R_x is the averaged weight of each body part (empty body, carcass, liver, GIT and 'remainder') for the R group over that of the C group at time t. During normal growth, the expected value for 'a' is zero and for 'b' is unity. By using the ratio, the allometric relation for normal growth is removed, and therefore, it gives the opportunity to study the allometric relation during periods of restriction and realimentation. It is assumed that 'a' is not influenced by restriction or realimentation, and will stay at zero level:

$$\log_e[R_y(t)] = b.\log_e[R_x(t)] \qquad [2]$$

To test constancy of 'b' during restriction and during realimentation, the effect of time is included into the 'b' term by defining the allometric coefficient as a sum of different functions of time:

$$\log_e[R_y(t)] = [b_0 + b_s.t_s + b_m.t_m + b_{sm}.t_s.t_m].\log_e[R_x(t)] \qquad [3]$$

Where, t_s is the number of weeks during feed quality restriction period and t_m is the number of weeks during realimentation period, b_s presents the effect of time of restriction, b_m shows the effect of time of realimentation and b_{sm} presents the interaction. If b_s, b_m and b_{sm} are zero, the allometric relation during restriction and realimentation is constant and independent of time. The weight of each body part is taken as the reference (x) measurement, for the composition (y) of that part.

Statistical analysis

Equations [2] and [3] were used to estimate parameters in the allometric relations over periods of restriction and realimentation, and for testing the effects of time in these relations. A stepwise linear regression procedure from the statistical program Statistix 4.0 (Analytical software, 1992) was used to estimate parameters. The best model was chosen according to minimal residual standard deviations. Parameters were tested to deviate from zero with a Student t-test. Durbin-Watson (DW) statistics were computed to test positive autocorrelation using Table A-6 in Neter *et al.* (1985). Significances in the tables are indicated by * ($P < 0.05$), ** ($P < 0.01$) and *** ($P < 0.001$).

Predictions were made using Equations [2] and [3], and are presented in figures in relation to age and to the weight of each body part separately.

RESULTS

Body composition changes

The mean weights of the chemical components of each body part at the onset of restriction, end of restriction and at the end of experiment for both C and R groups are given in Table 1. The trend of changes during restriction and realimentation for the components of empty body and carcass are presented in Table 2. At the end of the restriction period, the absolute weights of the chemical components of the R group were significantly ($P<0.001$) lower than C group. At the end of the experiment, despite different growth paths, only the absolute weight of fat was significantly lower in the empty body ($P<0.01$) and in the carcass ($P<0.05$) of the R group compared with C group. No significant differences were observed for the absolute weights of any of the other components between groups.

Table 1: *Means[†] and standard errors (s.e.) of weights (kg) of chemical water, protein, fat and ash in the empty body, carcass, gastrointestinal tract (GIT), liver and remainder of the control (C) and restricted (R) groups at the start[‡] of restriction (14 weeks age), at the end[‡] of restriction (28 weeks age) and at the end[‡] of experiment (52 weeks age).*

	start of restriction		end of restriction				end of experiment			
group:	C,R		C		R		C		R	
	mean	s. e.	mean	s. e.	mean	s. e.	mean	s. e.	mean	s. e.
Empty body										
water	14.42	0.40	20.25	0.62	12.24***	0.49	30.08	0.48	27.76	0.77
protein	4.45	0.13	5.21	0.08	2.90***	0.16	8.27	0.15	7.83	0.19
fat	1.46	0.23	2.86	0.97	0.22***	0.13	6.82	0.24	5.26**	0.13
ash	1.03	0.04	1.15	0.14	0.81***	0.00	1.96	0.08	1.78	0.07
Carcass										
water	8.34	0.25	11.14	0.35	6.41***	0.30	16.39	0.87	15.21	0.39
protein	2.37	0.08	2.72	0.03	1.37***	0.05	4.62	0.31	4.38	0.10
fat	0.94	0.16	1.76	0.55	0.08***	0.08	4.08	0.40	3.24	0.06
ash	0.64	0.02	0.68	0.03	0.44***	0.01	1.22	0.08	1.10	0.05
GIT										
water	1.47	0.05	1.68	0.08	1.38***	0.16	1.83	0.03	1.97	0.08
protein	0.20	0.01	0.24	0.00	0.19***	0.02	0.27	0.02	0.28	0.02
fat	0.03	0.01	0.07	0.01	0.01***	0.01	0.12	0.00	0.10	0.01
ash	0.015	0.00	0.018	0.00	0.01***	0.00	0.02	0.00	0.02	0.00
Liver										
water	0.31	0.01	0.40	0.00	0.30***	0.02	0.49	0.04	0.49	0.02
protein	0.08	0.00	0.10	0.00	0.07***	0.01	0.13	0.01	0.13	0.01
fat	0.01	0.00	0.01	0.00	0.01***	0.00	0.02	0.00	0.02	0.00
ash	0.005	0.00	0.01	0.00	0.01***	0.00	0.01	0.03	0.01	0.00
Remainder										
water	4.26	0.13	7.02	0.18	4.16***	0.02	11.37	0.51	10.09	0.87
protein	1.80	0.06	2.15	0.04	1.27**	0.08	3.25	0.20	3.05	0.14
fat	0.49	0.07	1.02	0.42	0.13***	0.04	2.61	0.19	1.90*	0.10
ash	0.37	0.03	0.45	0.11	0.35***	0.01	0.71	0.02	0.65	0.04

† If mean of R group differs significantly from that of C group, significance level is indicated.

‡ Numbers for each group at start of restriction are 8, at end of restriction 2, and at end of experiment 4.

Table 2: *Age (week), number of animals†, means of weights (kg) of chemical water, protein, fat and ash in the empty body, and carcass of the control (C) and restricted (R) groups from the start of the restriction to the end of experiment.*

		empty body				carcass			
age	no.animals	water	protein	fat	ash	water	protein	fat	ash
control (C):									
14	8‡	14.42	4.45	1.46	1.03	8.34	2.37	0.94	0.64
20	2	16.14	4.48	1.47	1.02	9.13	2.35	0.88	0.61
23	2	15.93	4.70	2.03	1.14	8.91	2.57	1.15	0.67
26	2	18.10	4.98	2.09	1.18	10.26	2.63	1.25	0.71
29	2	20.25	5.21	2.86	1.15	11.14	2.72	1.76	0.68
32	2	19.23	5.31	3.24	1.23	10.12	2.87	1.80	0.70
35	2	21.33	6.01	4.86	1.39	11.69	3.28	2.80	0.82
38	2	22.90	6.59	5.90	1.58	12.62	3.70	3.64	0.94
41	2	26.06	7.15	6.59	1.70	14.58	4.00	4.07	1.05
44	2	27.54	7.60	6.79	1.88	14.75	4.34	4.06	1.15
47	2	30.21	7.97	6.64	1.91	16.72	4.56	4.20	1.17
52	4	30.08	8.27	6.82	1.96	16.39	4.62	4.08	1.22
restricted (R):									
14	8‡	14.42	4.45	1.46	1.03	8.34	2.37	0.94	0.64
20	2	12.41	3.36	0.21	0.92	6.41	1.55	0.10	0.56
23	2	11.53	3.06	0.21	0.91	5.78	1.43	0.08	0.52
26	2	11.46	3.06	0.18	0.91	5.83	1.35	0.07	0.53
29	2	12.24	2.90	0.22	0.81	6.41	1.37	0.08	0.44
32	2	13.23	3.60	0.78	0.93	6.99	1.87	0.43	0.51
35	2	15.13	4.23	1.49	1.08	8.46	2.22	0.84	0.62
38	2	17.29	4.81	1.91	1.26	9.94	2.60	1.13	0.73
41	2	20.33	5.32	2.85	1.39	11.86	2.86	1.74	0.83
44	2	21.70	5.95	3.57	1.56	12.23	3.24	2.29	0.93
47	2	24.44	6.66	3.74	1.66	14.16	3.73	2.40	1.01
52	4	27.76	7.83	5.26	1.78	15.21	4.38	3.24	1.10

† number of animals contributed to the means of the chemical components.

‡ means of 8 animals which slaughtered as initial group were used for both control and restricted treatments.

The weights of the various chemical components as proportion of each body part are presented in Table 3. The results showed that at the end of restriction, R animals had a higher proportion of water and ash in the empty body and carcass compared to C animals. There were only miner differences in the percentages of water and ash in the GIT and liver. The proportion of protein was similar for each body part in C and R animals. But, the proportion of fat was much lower in all body

Table 3: *Weights of chemical water, protein, fat and ash as proportion of the weight of empty body, carcass, gastrointestinal tract (GIT), liver and remainder of the control (C) and restricted (R) groups at the start† of restriction (14 weeks age), at the end† of restriction (28 weeks age) and at the end† of experiment (52 weeks age).*

	start of restriction	end of restriction		end of experiment	
group:	C,R	C	R	C	R
Empty body					
water	0.675	0.687	0.757	0.638	0.651
protein	0.206	0.177	0.179	0.175	0.184
fat	0.068	0.097	0.014	0.145	0.123
ash	0.048	0.039	0.050	0.042	0.042
Carcass					
water	0.679	0.683	0.772	0.623	0.636
protein	0.193	0.167	0.165	0.175	0.184
fat	0.076	0.108	0.010	0.155	0.135
ash	0.052	0.042	0.053	0.046	0.046
GIT					
water	0.855	0.836	0.868	0.817	0.831
protein	0.116	0.119	0.119	0.121	0.118
fat	0.017	0.035	0.006	0.054	0.042
ash	0.009	0.009	0.008	0.010	0.009
Liver					
water	0.766	0.777	0.776	0.754	0.766
protein	0.190	0.187	0.184	0.194	0.195
fat	0.029	0.025	0.013	0.031	0.025
ash	0.012	0.013	0.013	0.014	0.013
Remainder					
water	0.619	0.660	0.704	0.634	0.643
protein	0.259	0.202	0.215	0.181	0.194
fat	0.070	0.096	0.021	0.145	0.121
ash	0.053	0.042	0.059	0.039	0.042

†) Numbers for each group at start of restriction are 8, at end of restriction 2, and at end of experiment 4.

parts of the R animals compared to C animals.

At the end of experiment, the proportion of water and protein in the empty body was higher for R group compared to C group. The proportion of ash was similar for both groups, while the proportion of fat was lower in R group compared to C group. The results showed the same trend for carcass and remainder. For GIT and liver, the proportions of protein and ash were similar in both groups, while of water was higher but, of fat was lower in the R group.

Composition of gain and loss

The absolute weights and the proportions of the chemical components in the total gain of the C group during the whole experiment, in the total loss of the R group during restriction and in the total gain of the R group during realimentation are shown in Table 4. Between start and end of the experiment, the C animals gained more fat than protein in the empty body, carcass, GIT and 'remainder', but the reverse was found for liver. The ratios of fat to protein in the gain for the C animals were 1.40:1 for both empty body and carcass, 1.29:1 for GIT, 1.46:1 for remainder, while 0.17:1 for liver.

Table 4: *The absolute (abs) weight (kg) and the proportion (%) of each chemical component in the empty body, carcass, gastrointestinal tract (GIT), liver and remainder gained (+) by control (C) group from start to the end of experiment, lost (-) by restricted group (R) during restriction and gained (+) during realimentation.*

	empty body		carcass		GIT		liver		remainder	
	abs	%	abs	%	abs	%	abs	%	abs	%
C:										
water	+15.66	60.8	+8.05	57.4	+0.36	68.3	+0.176	74.7	+7.11	64.5
protein	+3.82	14.8	+2.25	16.1	+0.07	13.3	+0.048	20.3	+1.45	13.2
fat	+5.36	20.8	+3.14	22.4	+0.09	17.1	+0.008	3.4	+2.12	19.2
ash	+0.93	3.6	+0.58	4.1	+0.01	1.3	+0.004	1.7	+0.34	3.1
R (restriction):										
water	-2.18	42.2	-1.93	48.4	-0.09	73.2	-0.019	55.9	-0.10	10.0
protein	-1.55	30.0	-1.00	25.1	-0.01	8.1	-0.008	23.5	-0.53	52.6
fat	-1.22	23.6	-0.86	21.6	-0.02	16.3	-0.007	20.6	-0.36	36.0
ash	-0.22	4.3	-0.20	5.0	-0.00	2.4	0.000	0.0	-0.02	2.0
R (realimentation):										
water	+15.52	58.7	+8.80	56.3	+0.59	75.6	+0.195	73.9	+5.93	60.6
protein	+4.93	18.6	+3.01	19.3	+0.09	11.5	+0.055	20.8	+1.78	18.2
fat	+5.04	19.1	+3.16	20.2	+0.09	11.3	+0.011	4.2	+1.78	18.2
ash	+0.97	3.7	+0.66	4.2	+0.01	1.3	+0.003	1.1	+0.30	3.1

Table 5, presents the absolute values and the proportion of each chemical component lost during restriction relative to the weight of that chemical component at the beginning of the restriction. In general, during restriction, the proportion of fat was reduced to a greater extent than protein, water and ash. In the empty body, fat lost 83.6% of its initial weight. This was 34.8% for protein, 21.4% for ash and 15.5% for water. The same trend was observed in carcass, where fat, protein, ash and water lost 91.5%, 42.2%, 31.3% and 23.1%, respectively. Different trends were observed in the other body parts. In the GIT, fat showed a greater proportion of depletion, followed by water, ash and protein. In the liver, again fat lost a higher proportion of its initial weight, followed by protein and water. There was no change in the proportion of ash in the liver by feed quality restriction. In the 'remainder' also fat lost a higher proportion of its initial weight, followed by protein and ash, while, water proportionally had a very small rate of reduction.

The composition of gain in the R animals after realimentation were different from the composition of gain between the start to the end of experiment by the C animals. In general, R animals had a higher rate of protein gain and a lower rate of fat gain than the C animals (Table 4).

The pattern of changes in body composition over time

The allometric relationship between the corrected weight of the various body composition (ratios of average values of the R group over that of the C group) and corrected weight of each body part was described by the simple allometric model (Eq.[2]). In this equation, the expected value for growth coefficient (b) is one under

Table 5: *The absolute (abs) weight (kg) and the proportion (%) of each chemical component in the empty body, carcass, gastrointestinal tract (GIT), liver and remainder lost by restricted group (R) during restriction period expressed as a proportion of that weight at the beginning of weight loss.*

	empty body		carcass		GIT		liver		remainder	
	abs	%	abs	%	abs	%	abs	%	abs	%
water	2.18	15.1	1.93	23.1	0.09	37.4	0.02	6.1	0.10	23.5
protein	1.55	34.8	1.00	42.2	0.01	5.1	0.01	10.3	0.53	29.4
fat	1.22	83.6	0.86	91.5	0.02	66.7	0.01	58.3	0.36	73.5
ash	0.22	21.4	0.20	31.3	0.003	20.0	0.00	0.0	0.02	5.1

normal condition. Eq. [3], described the relation including time of restriction and realimentation. In this equation, the growth coefficient (b) is made dependent on time by including effects of time of restriction (b_s), time of realimentation (b_m) and the interaction (b_{sm}).

The Figures 1, 2 and 3 present the observations and predictions based on the two models, plotting the natural logarithm of the ratios (relative chemical components, $\log_e R_y$) *v.* age (left side), and *v.* the natural log of the ratio of the weight of each body part ($\log_e R_x$) (right side) for empty body, carcass and GIT. Tables 6 and 7 present the estimated parameters, residual standard deviations (resid. s. d.) and Durbin-Watson (DW) statistics for fitted curves. Equation [2] did not fit the data well, this can be seen from the solid lines in the figures and the goodness of fit characteristics (DW and resid. s.d.) in Table 6. DW is significant (autocorrelation) for half of the measurements and resid. s. d. values are high. Eq.[3] gave lower resid. s.d. and no autocorrelations for all of the measurements compared to Eq. [2], (dashed lines in figures).

Eq. [2] presents an average description of the allometric relation between the weights of the chemical components and the weight of the body parts. This model predicts that the increase after realimentation follows the same line as the decrease after restriction. In general fat had the greatest growth coefficient in all body parts. Ranking of b's for the other chemical components (protein, water and ash) differed in each body part. In the empty body and carcass, protein showed a higher b value than water and water had a higher b value than ash. This trend was not consistent for the other body parts. In the GIT, ash had a higher b value than protein and water. In the liver, water showed a higher b value than ash and protein. In the 'remainder', water had a higher b value followed by protein and ash. As the Figures 1 to 3 show, development of all chemical components did not follow the same trend during restriction and realimentation.

Including b_s and b_m into the allometric equation resulted in better fits. In Eq. [3], parameter b_0 is an estimate of the growth coefficient at the start of restriction. Higher value of this b_0 than the b in Eq. [2], gives a line starting below and ends above the solid line, as for fat (Figures, right side). If this b_0 is lower, the line starts above and ends below, as for ash. Ranking of b_0's are similar to that for b's.

After restriction, in the carcass, water showed earlier effect of restriction (Figures). But, in the liver, protein showed earlier effect of restriction. Fat was affected more than the other components in all body parts and showed a rapid decrease. The changes in ash concentration by feed restriction differed among body parts. In the carcass there was a delay in the rate of ash loss, while, in liver and GIT, ash showed an earlier effect of restriction. There was a sharp increase in the deposition of particularly fat and protein during the initial stages of realimentation (Figures). Although, some variations was observed between body parts in the rates at which various chemical components were deposited. The trend of gain was different for each component in each body part. After the first sharp increase, the rates of protein and fat gain, maintained at a higher level compared

Table 6: *Estimates of parameters for the first model*[†] *(Eq. [2]), Durbin-Watson statistics (DW)*[‡] *and residual standard deviations (resid. s.d.) for all measurements.*

measure (y)	b	DW	resid. s.d.
	$\log_e(R_y) = b \cdot \log_e(R_x)$		
Empty body			
water	0.817***	1.28	0.027
protein	0.906***	1.02*	0.033
fat	3.826***	0.48***	0.427
ash	0.567***	1.52	0.029
Carcass			
water	0.787***	0.81**	0.029
protein	0.990***	1.17	0.030
fat	3.935***	0.59***	0.414
ash	0.565***	1.11	0.064
GIT			
water	0.881***	1.52	0.023
protein	1.186***	1.74	0.026
fat	6.282***	0.76**	0.610
ash	1.344***	1.14	0.057
Liver			
water	1.037***	0.64**	0.017
protein	0.785***	0.65**	0.048
fat	2.133***	0.55***	0.199
ash	0.850***	1.07	0.023
Remainder			
water	0.891***	1.39	0.025
protein	0.729***	0.95*	0.049
fat	3.302***	0.49***	0.506
ash	0.437***	1.16	0.021

[†] See for explanation of variables and parameters Eq. [2] in text.
Significance levels are indicated for parameter estimates which deviating from zero.

[‡] Test for positive autocorrelation with time. Significance level is indicated.

to water and ash for a considerable period of time. Then, the rate at which fat was gained fell back in all body parts, particularly in the GIT and liver.

Table 7: *Estimates of parameters for second model† (Eq. [3]), Durbin-Watson statistics (DW)‡ and residual standard deviations (resid. s.d.) for all measurements.*

measure (y)	b_0	b_s	b_m	b_{sm}	DW	resid. s. d.
---------- $\log_e(R_y) = (b_0 + b_s \cdot t_s + b_m \cdot t_m + b_{sm} \cdot t_s \cdot t_m) \cdot \log_e(R_x)$ ----------						
Empty body						
water	0.741^{***}	0.0097	-0.0191	0.0001	2.17	0.027
protein	0.965^{***}		-0.0129	0.0001	1.99	0.024
fat	7.274^{***}	-0.2168^{***}	-0.1049	0.0066^{**}	2.56	0.087
ash	0.202	0.0301^{*}	-0.0349	0.0002	3.16	0.019
Carcass						
water	0.842^{***}		-0.0518^{**}	0.0536^{*}	2.80	0.013
protein	1.123^{***}	-0.0100		0.0088	1.65	0.028
fat	6.175^{***}	-0.1387^{***}	-0.3022	0.4076	2.97	0.150
ash	0.039	0.0398		-0.0357	2.94	0.029
GIT						
water	0.676	0.0201	-0.0357	0.0003	2.09	0.026
protein	1.085^{***}		0.0472	-0.0012	1.73	0.026
fat	20.590^{***}	-0.9199^{***}		0.0163^{*}	2.01	0.253
ash	2.257^{**}	-0.0600		0.0012	1.25	0.051
Liver						
water	0.924^{***}		0.0655^{***}	-0.0687^{**}	2.79	0.006
protein	1.107^{***}		-0.2182^{***}	-0.2398^{***}	1.75	0.019
fat	5.647^{**}	-0.1914	-0.4702	0.7052^{*}	1.64	0.089
ash	0.987^{**}		-0.0747^{*}	0.0768	2.30	0.014
Remainder						
water	0.542^{***}	0.0282^{*}	-0.0607^{*}	0.0437	2.92	0.016
protein	0.638^{**}	0.0191	-0.0574	0.0243	3.29	0.026
fat	10.273^{***}	-0.4806^{***}	0.0161	0.4389^{***}	2.15	0.051
ash	0.679^{***}	-0.0167^{*}		0.0162	2.47	0.014

† See for explanation of variables and parameters Eq. [3] in text.
Significance levels are indicated for parameter estimates which deviating from zero

‡ Test for positive autocorrelation with time. Significance level is indicated.

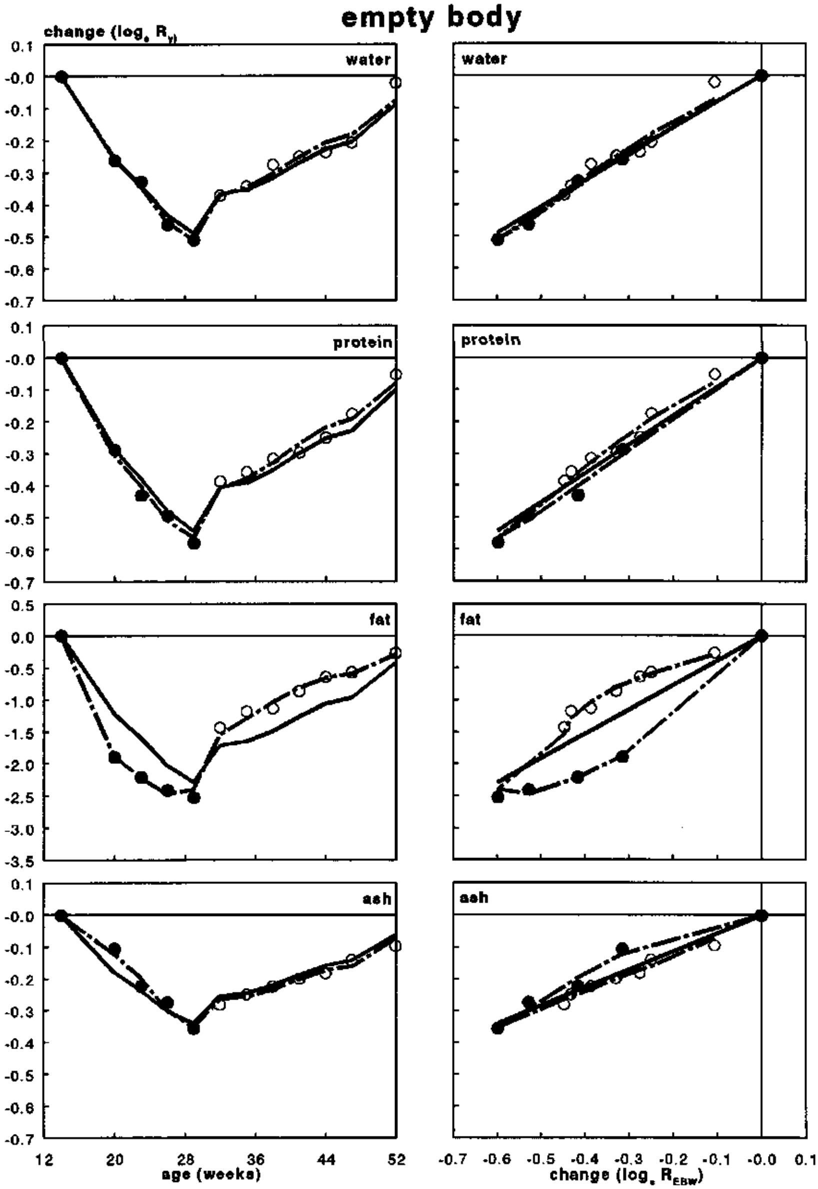

Figure 1. The relationship between the natural log of the ratio of chemical components ($\log_e R_y$) in empty body against age (weeks) (left side), and against the natural log of the empty body weight ratio ($\log_e R_{ebw}$) (right side); (●) observed during restriction, (○) observed during realimentation, (———) prediction based on Eq [2], (— · — ·) prediction based on Eq. [3].

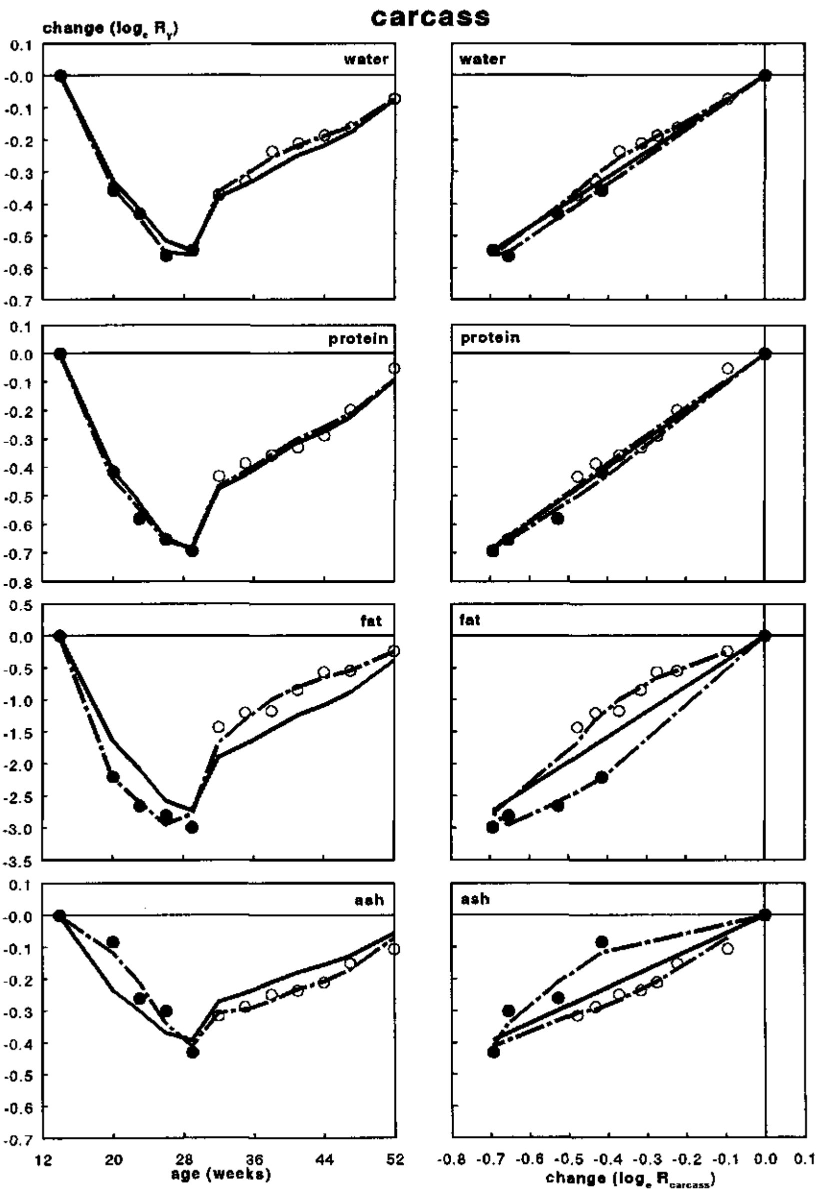

Figure 2. The relationship between the natural log of the ratio of chemical components ($\log_e R_y$) in carcass against age (weeks) (left side), and against the natural log of the carcass weight ratio ($\log_e R_{carcass}$) (right side); (●) observed during restriction, (○) observed during realimentation, (———) prediction based on Eq. [2], (— · — ·) prediction based on Eq. [3].

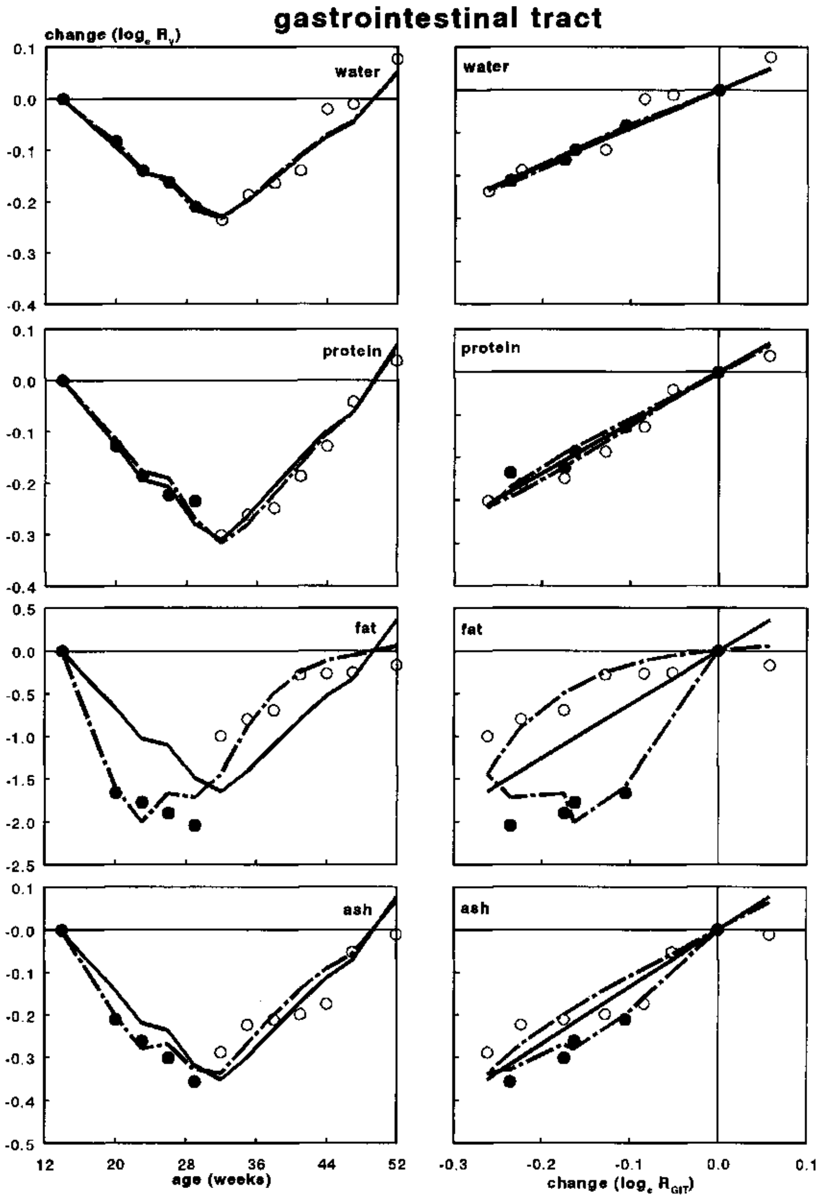

Figure 3. The relationship between the natural log of the ratio of chemical components ($\log_e R_y$) in GIT against age (weeks) (left side), and against the natural log of the GIT weight ratio ($\log_e R_{GIT}$) (right side); (●) observed during restriction, (○) observed during realimentation, (———) prediction based on Eq. [2], (— · — ·) prediction based on Eq. [3].

DISCUSSION

Body composition changes during restriction

During restriction, the total loss of the empty body was 5.17 kg or 24%. The loss in carcass was more than the loss in the non-carcass components (sum of liver, GIT and 'remainder'). The carcass lost 3.99 kg of its initial weight or 77% of the total empty body loss, whereas the loss from non-carcass was 1.17 kg of its initial weight or 23% of the total empty body loss. As Table 4 shows, water was the main part of the total loss (2.18 kg or 42.2%), protein (1.55 kg or 30%), fat (1.22 kg or 23.6%) and ash was 0.22 kg or 4.3%. The proportion of the total loss from water and ash in carcass were higher and those from protein and fat were lower compared to empty body. The total loss of the remainder, mainly was from the depletion of protein and fat rather than water and ash. In the liver, the total loss was from the depletion of water, then protein and fat. In the GIT, the main part of the total loss was water. Ryan *et al.* (1993), restricted 8 months old Merino wethers for 84 days and the animals lost 5 kg or 20.8% of their initial weight. They reported higher percentages of water loss (55.7%) and lower percentages of protein (20.3%), fat (21.8%) and ash (2.8%) compared to results of this experiment. In line with Drew & Reid (1975) and Butler-Hogg (1984), water had a large contribution to the changes in total weight of the empty body. But, when the composition of the loss was expressed as proportion of the initial weight of that composition at the beginning of restriction, fat was the major tissue lost during restriction (Table 5).

In general, despite variations in the rate of loss from each chemical component between various body parts, the greatest loss was associated with fat, then protein, water and ash. In agreement with the results of this experiment, Little & Sandland (1975) subjected wether sheep to nutritional restriction for 3 months and reported that body fat tissue was most affected. Kabbali *et al.* (1992) restricted weaned lambs to loose weight from 21 to 17 kg, also reported that fat was severely reduced by feed restriction.

The results of this experiment also support the observations made by Thornton *et al.* (1979), Marais (1991) and Ryan *et al.* (1993) with restricted sheep. They reported that considerable level of protein has been mobilized during restriction. The data of this experiment showed that the ratio of fat to protein mobilized in the empty body was 0.79:1. This ratio indicates relatively a high amount of protein mobilization during restriction, however not on energetic basis.

Ryan *et al.* (1993), reported a ratio of 1.1:1 for fat to protein mobilized in 8 months old Merino wether sheep. This ratio shows relatively higher level of fat mobilization than protein. This is because, animals used in their experiment were older and contained higher amounts of fat compared to the animals (3 months old) used in this experiment.

The results of this experiment are not supporting the observations made by Drew & Reid (1975) with wether lambs, Cowan *et al.* (1980) with lactating ewes and Butler-Hogg (1984) with Corriedale wether sheep that water and protein were mobilized relatively faster than fat. Except for the GIT, water lost a lower proportion of its initial weight compared to fat and protein. As restriction progressed, the rates of loss for different chemical components changed. These changes clearly can be seen from the figures (dashed-lines).

The pattern of changes in body composition over time

In growth studies, despite different growth paths between continuous growth, restricted growth and compensatory growth, the growth patterns of the body composition are often defined by using allometric relationships ($y = a + bx$). It incorporates the allometric growth coefficient (b), a parameter which is easy to compare between treatments. However, a simple allometric model did not hold for the whole weight range in many growth studies. In the study of Ogink (1993) with goats, the growth pattern of protein, water and ash were described by simple allometric relationships relative to fat free weight (FFW), and fat was described by a biphasic allometric model. In another study, Kwakkel (1994) used a biphasic allometric model to describe the growth patterns of protein, water, ash and fat as a function of empty body mass (EBM) or fat free empty body mass (FFEBM) in the restricted-realimented pullets. However, in contrast, Iason *et al.* (1992) reported a linear function and no evidence of a biphasic relationship for the growth of fat in mature Beulah and Welsh Mountain sheep. A simple allometric model is based on the independency of time, estimating only an average relationship between the growth of the body parts (Kamalzadeh *et al.,* 1995a). Therefore, this model [Eq.2] can not give an adequate description for growth during restriction and realimentation (Figures, solid lines). Using Eq. [3] resulted in a good fit of the data and an adequate description of the body composition changes.

Compensatory effects in body composition

Removing the restriction imposed by low quality feed had a remarkable effect on the rate of gain. Some lambs gained well in excess of 300 g/day, considerably more than any of the C animals from the start. This compensatory gain was not due to an increase in gut contents (Kamalzadeh *et al.* 1996). This very immediate effect on live weight gain has been observed before. Ørskov *et al.* (1976) found that some lambs gained 500 g/day, immediately after a change from a low to a high protein diet. They also reported that this fast rate of gain was not due to an increase in gut contents, nor was it due to an unusually high intake of feed. According to Allden (1970) and Wilson & Osbourn (1960), however, a high intake and an increase in gut contents has often been observed in association with compensatory gain following a period of restricted energy intake. Similarly, Wright & Russel (1991) reported that the initial enhanced proportion of protein and water in the empty body of cattle was independent of any increase in feed intake.

Ørskov *et al.* (1976) noted that the rates of accretion of protein and fat in lambs were more than doubled and of water was almost quadrupled immediately after the change from low to high protein diet. They found that the rates for protein and water fell as weight increased and approached the values for the controls. Wilson & Osbourn (1960) and Allden (1970) reported an increased rate of fat deposition during the initial stages of the recovery period. Drew & Reid (1975) showed that, water and protein made up the greater parts of early gain, but Butler-Hogg (1984) noted that the major changes occurred in the relative increase of fat and water, and lesser changes in protein. In contrast to that, Fox *et al.* (1972) and Ryan *et al.* (1993) postulated that animals appear to deposit a greater amount of protein during the initial period of realimentaion followed by a greater fat deposition at the later stages of realimentaion.

The different composition of gain in C and R animals was reflected in the ratio of fat to protein deposited in each body part. During realimentation, the average ratio of fat to protein in the empty body of R animals was 1.02:1, whereas this ratio for the C animals between the start and the end of the experiment was 1.4:1. In the carcass, GIT, liver and remainder, the ratios of fat to protein were 1.05:1, 1:1, 0.2:1 and 1:1 respectively for the R animals compared to 1.4:1, 1.29:1, 0.17:1 and 1.46:1 respectively for the C animals. If the proportion of energy deposited as protein increases, the gain in weight will be greater per unit of energy deposited, because, 3 to 4 units of water is retained with every unit of protein deposited. The differences in the ratio of fat to protein gain between R and C animals indicate that the energetic cost of gain was less for the R animals during realimentation. Therefore, more energy remained for growth.

At the end of the experiment, the delay in body tissue deposition was compensated. In general, the empty body, carcass, GIT, liver and 'remainder' of the

R animals contained more protein and water and less fat compared to C animals.

The results of this experiment support the observations made by (Drew & Reid, 1975; Carstens *et al.,* 1991; Ledin, 1983; and Kabbali *et al.,* 1992) that realimented animals were leaner than controls. The data of this experiment showed that 1 kg of carcass gain during compensation contained 0.184 kg protein compared to 0.175 kg protein for controls. In line with our findings, several reports (*e.g.* Searle *et al.,* 1979) showed that 1 kg of gain during compensatory growth in sheep contains 0.17 kg protein *v.* 0.16 kg for control animals.

In line with Butler-Hogg (1984) and Ryan *et al.* (1993), the delay in the protein gain in the GIT and liver compensated earlier than in the other parts of the body, implying rapid recovery of the liver and gut tissues. The enhanced rate of protein gain particularly in the GIT and liver resumed for some considerable time after realimentation. Similarly, Hogg (1992) reported that the regeneration (protein synthetic) capacity is enhanced for some considerable time after *ad libitum* feeding in immature sheep. According to Re & Thornton (1980) the longer time of protein regeneration during compensatory growth was related to the higher ACT activity in the liver and small intestine of realimented animals. The data of this experiment, together with those of Tulloh (1963), Thornton *et al.* (1979), Butler-Hogg (1984) and Kabbali *et al.*(1992) imply that the relationship between chemical body components and body weight is strong.

Reports on the body composition of the sheep which have undergone compensatory growth cover a wide spectrum of results, varying from increased protein and less fat (Drew & Reid, 1975; Little & Sandland, 1975; Ledin, 1983, Kabbali *et al.,* 1992), through to unchanged (Searle & Graham, 1975; Thornton *et al.,* 1979), to increased fat and less protein deposition (Wilson & Osbourn, 1960; Meyer & Clawson, 1964), relative to continuously grown controls. These variations may be depended to large variability in the experimental designs, variety in the conditions of nutritional restriction and realimentation as well as the degree of animals maturity during restriction and recovery periods.

CONCLUSIONS

During feed quality restriction and compensatory growth, the chemical components in each body part (empty body, carcass, GIT, liver and remainder) respond differently. The major changes occur in the relative loss and gain of fat and protein. The rate of gain of various body components during compensatory growth reflects the extent to which they have been depleted during preceding body weight loss. Those components which have greatest loss during body weight loss, show a faster response during the realimentation period.

The delay in growth after restriction is compensated during realimentation. The composition of gain in the realimented animals are different from controls. The realimented animals are leaner compared to controls. The growth model used in this experiment presents a detailed study of the responses of the body composition during restriction and the subsequent compensatory growth periods.

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Chapter 6

Feed quality restriction and compensatory growth in growing sheep: modelling changes in feed efficiency.

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Feed quality restriction and compensatory growth in growing sheep: modelling changes in feed efficiency.

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ABSTRACT

The effects of feed quality restriction on changes in the pattern of the feed intake, feed conversion efficiency and growth were examined. A total of 56 crossbred Swifter (Flemish ♀ X Texel ♂) male lambs born in March 1993 and weaned at ≈2 months old were fed grass straw (51 g crude protein (CP) per kg dry matter (DM)) *ad libitum* and 35 $g.kg^{-0.75}d^{-1}$ mixed concentrates (173 g CP per kg DM). At an age of approximately 3 months, animals were randomly divided into a restricted (R) and a control (C) group. Group R was restricted in feed quality by withholding concentrates from 3-6 months of age. Two models were developed to measure feed efficiency from (1) the relation between cumulative feed intake and body weight and (2) the relation between feed intake and gain per unit of time.

The shape and magnitude of the growth curve changed by feed quality restriction. The feed efficiency was negative for R animals during restriction. After realimentation, R animals were more efficient in converting feed to body weight compared to C animals. The delay in growth after restriction was compensated during realimentation though with lower total feed consumption.

(*Key words:* sheep, growth curve, compensatory growth, feed efficiency, restriction)

INTRODUCTION

In most parts of the world, livestock production systems mainly depend on natural vegetation of range and farm lands. Seasonal fluctuations cause a periodical restriction in feed quality and quantity. The majority of lambs is born in spring, while they are weaned towards the warm and dry season when the quality of the grass has gradually decreased to a level not sufficient for the immature animal to express its full genetic potential for growth. The adverse effects of nutrient restriction may be overcome by supplementary feeding. Alternatively, the growth may be delayed until an adequate feed supply is available in the next wet season and take benefit from compensatory effects in terms of feed intake and growth.

Compensatory growth is usually associated with reduced maintenance requirements, changes in body composition and an increased feed efficiency. Maintenance requirements are usually measured by fasting heat production. Changes in body composition are estimated by slaughtering procedures or energy and nitrogen balances. The improved feed efficiency during compensatory growth is not so clearly measured. Some studies (Turgeon *et al.,* 1986; Ryan, 1990; Kabbali *et al.,* 1992), reported higher feed efficiency for realimented animals compared to their controls. Butler-Hogg & Tulloh (1982) on the other hand, reported no difference in overall feed efficiency between realimented and controls. Parks (1982) suggested a range of 0.17 to 0.64 for the efficiency of feed utilization for various species (*i.e.* rat, chicken, pigs, sheep, cattle). Thompson *et al.* (1985) found a range of 0.25 to 0.27 for rams and a range of 0.27 to 0.31 for ewes. Thomson (1979) and Ledin (1983) suggested that particularly the efficiency of protein deposition may increase during the initial period after realimentation. Asplund *et al.* (1975) reported a higher efficiency in the metabolism of protein.

The objective of this research was to study the effect of feed quality restriction on feed intake and body development, and to quantify the effect of feed quality restriction in terms of improved feed efficiency. Two growth models were developed to measure feed efficiency from (1) the relation between cumulative feed intake and body weight and (2) the relation between feed intake and gain per unit of time.

MATERIAL

Experimental design

The experimental design, animals, feed composition, housing and management, have been reported in details by Kamalzadeh *et al.* (1995). Briefly, fifty six intact male Swifter (Flemish ♀ X Texel ♂) lambs of approximately 3 months age, were randomly allotted to two experimental groups.

At the onset of the experiment, animals were randomly allotted to serial-slaughtering for determination of body composition. Eight lambs were slaughtered at the beginning of the experiment. Half of the remaining (24 animals) were used as control (C) group and fed *ad libitum* grass straw (51 g crude protein (CP) per kg dry matter (DM)) with 35 $g.kg^{-0.75}d^{-1}$ mixed concentrates (173 g CP per kg DM). The other half was used as restricted group (R) and fed only grass straw *ad libitum* from 3-6 months of age and thereafter the same feed as the C group. The experimental lay-out is presented in Table 1. Following the 8 lambs slaughtered at the onset of the experiment, every three weeks 4 (2 per group) were slaughtered leaving 8 lambs (4 per group) for slaughtering at the end of the experiment. The number of animals, which contributed to the measurements are shown in Table 2. Animals were weighed weekly. The amount of offered feed was adjusted biweekly on the basis of metabolic weight.

Table 1. *Experimental lay-out.*

age (week)	diet	C	R
14-28	Straw (≈5 % CP)	ad libitum	ad libitum
	Concentrates (≈17 % CP)	35[†]	0
	Vitamin/minerals	1[†]	1
29-52	Straw (≈5 % CP)	ad libitum	ad libitum
	Concentrates (≈17 % CP)	35[†]	35
	Vitamin/minerals	1[†]	1

[†]) $g.kg^{-0.75}.d^{-1}$.

METHODS

Feed efficiency

Parks (1982) developed a method to compute feed efficiency based on the relation between cumulative body weight (W) and cumulative feed intake (F). He described the W-F relation with a diminishing return function.

$$W_t = W_0 + (A - W_0).(1 - e^{-AB.F_t/A}) \qquad [1]$$

In which:

W_t is body weight at time t,

W_0 is body weight at t = 0,

F_t is cumulative feed intake measured from t = 0,

AB is feed efficiency factor,

A mature body weight.

The result in terms of daily weight gain over daily feed intake (dW/dF) was a linear relation of dW/dF with degree of maturity (u), in which u is the ratio of actual weight to mature weight (A).

$$\frac{dW}{dF} \, . \, (u) = AB \, . \, (1 - u) \qquad [2]$$

Parks (1982) showed a reasonable constancy of AB over species. This result, however, is based on the choice of the function used by Parks, and is only applicable if feed is available *ad libitum* and animals are kept in a constant environment during the whole experimental period. In this experiment, feed restriction was imposed to one group, and therefore the method of Parks is impossible to use for this group and may use only for the data of the C group.

An alternative to describe W in relation to F is a broken line with a smooth transition (Koops & Grossman, 1993). This function is able to describe a large number of different curves, including equations [1] and [2].

$$W_t = W_0 + b_0 . F_t - (b_0 - b_1) . r . \ln(1 + e^{(F_t - F_i)/r}) \qquad [3]$$

In which the meaning of W_t, W_0 and F_t are the same as in equation [1] and:

F_i is the transition point of one straight line to another,

r is a smoothness parameter, large r means a smooth transition, small r means a sharp transition,

b_0 is an estimate of the feed efficiency in the range $F_t < F_i$,

b_1 is an estimate of the feed efficiency in the range $F_t > F_i$.

From equation [3] the first derivative of W with respect to F at time t is:

$$\frac{dW}{dF}(t) = b_0 - \frac{(b_0 - b_1)}{(1 + e^{-(F_t - F_i)/r})} \qquad [4]$$

In which the meaning of all variables and coefficients are the same as in equations [2] and [3]. This function represents a stair step curve with smooth transition from one step to another. Steps are the feed efficiency levels according to different periods of F. At each time t, there is a fixed relation between gain per unit time (dW/dt), feed efficiency (dW/dF) and feed intake per unit time (dF/dt):

$$\frac{dW}{dt}(t) = \frac{dW}{dF}(t) \cdot \frac{dF}{dt}(t) \qquad [5]$$

Substituting equation [4] into [5] results in:

$$\frac{dW}{dt}(t) = [b_0 - \frac{(b_0 - b_1)}{(1 + e^{-(F_t - F_i)/r})}] \cdot \frac{dF}{dt}(t) \qquad [6]$$

In which:

dW/dt is gain in body weight per unit time at time t,

dF/dt is feed intake per unit time at time t,

other variables and coefficients are the same as in equation [3].

Statistical analysis

Equations [3] and [6] are used to make estimates of the feed efficiency coefficients. Estimation is done using the nonlinear regression program NONLIN (Sherrod, 1992). Parameters were tested to deviate from zero with a Student t-test. Durbin-Watson (DW) statistics were computed to test positive autocorrelations using Table A-6 in Neter *et al.* (1985). Results are presented in graphs and tables. Significance levels of coefficients are indicated in tables by: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Parameters were expressed on the basis of both daily and cumulative digestible organic matter intake (DOMI) and protein intake (PI) instead of fresh feed intake, to correct for variation in the nutrient densities of straw and concentrates.

RESULTS

Means of cumulative weight (W), means of cumulative feed intake (DOMI, PI) (F) for C and R animals and the number of animals that contributed to these means are presented in Table 2. Table 3 shows the means of daily weight gain for

C animals (dW_c/dt) and for R animals (dW_r/dt), daily feed intake of C animals (dF_c/dt) and daily feed intake of R animals (dF_r/dt) during the whole experimental period. From the ratio of daily weight gain (dW/dt) over daily feed intake (dF/dt), the feed efficiency data (dW/dF) was calculated.

Equation [1] was fitted to the cumulative data of the both C and R groups. Estimates of the parameters, residual standard deviations and DW statistics for fitted curve of C group are presented in Table 4. The relation between cumulative DOMI (F) and (W) is presented in Figure 1. The pattern of the feed efficiency factor (AB) in relation to the degree of maturity (u) estimated by Eq. [2] for DOMI is presented in Figure 2.

Equation [3] was fitted to cumulative data of both the C and R groups. Estimates of the parameters, residual standard deviations and DW statistics for fitted curves are presented in Table 5. Figures 3 and 4 show the relation between W and F (DOMI, PI).

Table 2: *Age (weeks), number of animals (N)[†], means of body weight (W, kg) and means of cumulative digestible organic matter intake (DOMI) and cumulative protein intake (PI) (F, kg) for control (C) and restricted (R) groups from the onset to the end of experiment.*

				DOMI		PI	
age	N[†]	W_c	W_r	F_c	F_r	F_c	F_r
15	24	27.0	27.0	0.0	0.0	0.0	0.0
18	24	29.6	25.2	10.0	3.8	2.0	0.6
21	22	32.9	24.4	21.4	8.7	4.3	1.3
24	20	35.6	24.6	33.5	13.5	6.7	2.0
27	18	39.1	24.5	46.2	18.5	9.1	2.6
30	16	42.1	26.6	59.5	29.7	11.6	4.6
33	14	46.3	30.2	73.4	40.8	14.2	6.6
36	12	49.2	33.1	87.7	52.7	16.9	8.8
39	10	52.0	37.1	102.3	65.3	19.7	11.1
42	8	54.0	41.2	117.2	79.1	22.5	13.5
45	6	55.9	45.1	132.5	94.3	25.3	16.1
48	4	57.5	48.8	148.2	110.5	28.2	18.8
51	4	60.8	55.1	164.3	127.6	31.2	21.7

[†]) number of animals contributed to the measurements in each group.

Equation [6] was fitted to the daily data. The relation between feed efficiency (b) and F for DOMI is presented in Figure 5 and for PI is presented in Figure 6. Table 6 presents the estimates of the parameters, residual standard deviations (resid. s. d.) and DW statistics for fitted curves of Equation [6] fitted to the DOMI and PI data.

Table 3: *Age (weeks), means of daily weight gain (dW, kg), means of daily digestible organic matter intake (DOMI, PI) (dF, kg) and the efficiency of feed utilization (dW/dF) for both control (C) and restricted (R) groups from the onset to the end of experiment.*

age	dW_c	dW_r	dF_c	dF_r	dW_c/dF_c	dW_r/dF_r
DOMI:						
18	0.125	-0.086	0.477	0.183	0.263	-0.468
21	0.157	-0.038	0.543	0.231	0.290	-0.165
24	0.128	0.010	0.574	0.230	0.223	0.041
27	0.163	-0.005	0.605	0.236	0.269	-0.020
30	0.145	0.101	0.634	0.532	0.228	0.191
33	0.176	0.170	0.663	0.532	0.265	0.320
36	0.137	0.139	0.679	0.566	0.202	0.246
39	0.134	0.191	0.695	0.597	0.193	0.320
42	0.092	0.191	0.712	0.661	0.130	0.289
45	0.094	0.187	0.728	0.723	0.129	0.259
48	0.073	0.175	0.748	0.769	0.097	0.227
51	0.158	0.302	0.768	0.815	0.206	0.371
PI:						
18	0.125	-0.086	0.096	0.027	1.301	-3.138
21	0.157	-0.038	0.111	0.033	1.425	-1.163
24	0.128	0.010	0.113	0.033	1.135	0.292
27	0.163	-0.005	0.115	0.033	1.415	-0.147
30	0.145	0.101	0.119	0.094	1.212	1.081
33	0.176	0.170	0.124	0.096	1.420	1.780
36	0.137	0.139	0.128	0.103	1.077	1.350
39	0.134	0.191	0.132	0.110	1.014	1.735
42	0.092	0.191	0.133	0.116	0.696	1.643
45	0.094	0.187	0.134	0.122	0.703	1.530
48	0.073	0.175	0.139	0.130	0.525	1.346
51	0.158	0.302	0.144	0.137	1.099	2.202

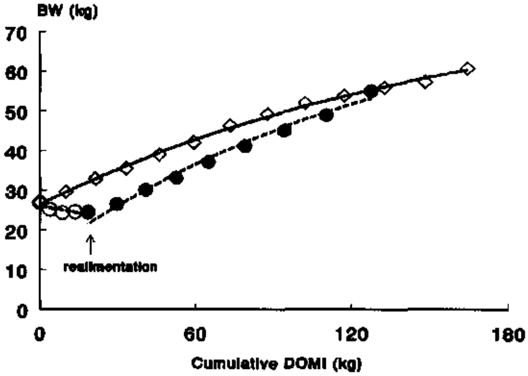

Figure 1. The relationship between cumulative digestible organic matter intake (DOMI) and body weight (BW), (◇) observed values for control group, (○) observed values for restricted group during restriction, (●) observed values for restricted group during realimentation, (——,---) predictions based on Eq. [1].

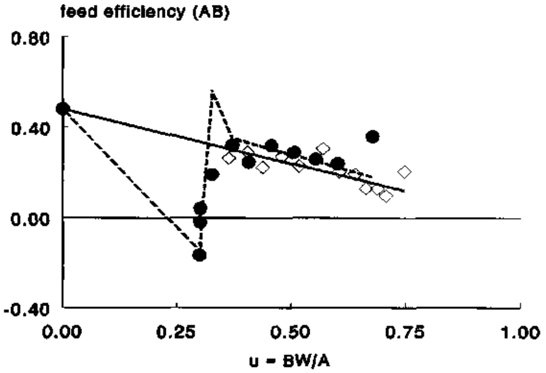

Figure 2. The relationship between degree of maturity (u) and feed efficiency factor (AB), (◇) observed values for control group, (●) observed values for restricted group, (——, ----) predictions based on Eq. [2] for digestible organic matter intake (DOMI).

Table 4. *Estimates[†] and their standard errors of parameters for the Eq. [1][‡], Durbin-Watson statistics (DW)[§] and residual standard deviations (resid. s.d.) for control (C) group during the whole experimental period.*

Parameter	DOMI[‖]	PI[‖]
A	81.28*** (4.32)	85.21*** (5.74)
AB	0.48*** (0.03)	2.38*** (0.19)
W_0	26.49*** (0.44)	26.39*** (0.48)
DW	1.28	1.13
resid. s.d.	0.61	0.66

†) If estimates are deviating from zero, significance levels are indicated.

‡) See for explanation of variables and parameters Eq. [1] in text.

§) Test for positive autocorrelation with time.

‖) For abbreviations see text.

Table 5. *Estimates[†] and their standard errors of parameters for the Eq. [3][‡], Durbin-Watson statistics (DW)[§] and residual standard deviations (resid. s.d.) for control (C) and restricted (R) groups from the start to the end of experiment.*

Parameter	DOMI[‖]	PI[‖]
C:		
W_0	27.09*** (0.25)	26.94*** (0.25)
b_0	0.26*** (0.01)	1.33*** (0.03)
b_1	0.13*** (0.01)	0.73*** (0.05)
F_i	88.96*** (4.43)	17.56*** (0.85)
r	5.00 (5.96)	0.71 (1.32)
DW	2.76	2.73
resid. s.d.	0.37	0.37
R:		
W_0	21.01 (27.08)	24.79*** (1.76)
b_0	-1.06 (2.26)	-4.49 (2.41)
b_1	0.29*** (0.01)	1.62*** (0.03)
F_i	2.02 (23.24)	0.92 (0.68)
r	7.68 (4.22)	1.00
DW	2.47	2.46
resid. s. d.	0.48	0.46

[†]) If estimates are deviating from zero, significance levels are indicated.

[‡]) See for explanation of variables and parameters Eq. [3] in text.

[§]) Test for positive autocorrelation with time.

[‖]) For abbreviations see text.

DISCUSSION

In general, feed efficiency is defined as the ratio of weight gain to feed intake (dW/dF), or as the inverse of this ratio. Feed efficiency can be calculated at any weight or stage of maturity. In some studies (Parks, 1982; Thompson *et al.*, 1985), feed efficiency called feed efficiency factor and is expressed by (AB), while in some others (Winter, 1976; Butler-Hogg, 1984), parameter (b) which is originally derived from the allometric relation between two structures (y = a + bx), is used to express feed efficiency.

Table 6. *Estimates[†] and their standard errors of parameters for the Eq. [6][‡], Durbin-Watson statistics (DW)[§] and residual standard deviations (resid. s.d.) for control (C) and restricted (R) groups from the start to the end of experiment.*

Parameter	DOMI[‖]	PI[‖]
C:		
b_0	0.26*** (0.02)	1.34*** (0.08)
b_1	0.14*** (0.02)	0.77*** (0.10)
F_i	94.74*** (10.24)	18.37*** (1.80)
r	7.37 (8.41)	1.00
DW	2.78	2.86
resid. s.d.	0.04	0.21
R:		
b_0	-2791 (5851)	-9.61 (5.58)
b_1	0.29*** (0.03)	1.57*** (0.15)
F_i	-92.37 (2451)	0.22 (0.77)
r	11.68* (4.57)	1.00
DW	2.45	2.09
resid. s. d.	0.07	0.41

[†]) If estimates are deviating from zero, significance levels are indicated.
[‡]) See for explanation of variables and parameters Equations [6] and [7] in text.
[§]) Test for positive autocorrelation with time.
[‖]) for abbreviations see text.

In the following paragraphs, the changes in feed efficiency from the relation between DOMI and weight will be described. The plots of W versus F (Figure 1) and of feed efficiency factor (AB) versus (u) (Figure 2) show that the methods outlined by Parks (1982) cannot adequately describe the relation between feed intake and weight. These models could only used for the C group, however, goodness of fit characteristics (DW and resid. s. d. in Table 4) show that the fit is not as good as Eq. [3]. To fit this model the data of the R group have to be divided into two parts (restriction and realimentation).

Figures 3 and 4 show that the relation between W and F can be described adequately by Eq. [3]. Durbin-Watson statistics and residual standard deviations show a good fit (no autocorrelations) for both groups (Table 5). The estimated values of W_0 were very close to the absolute data presented in Table 2. The lower

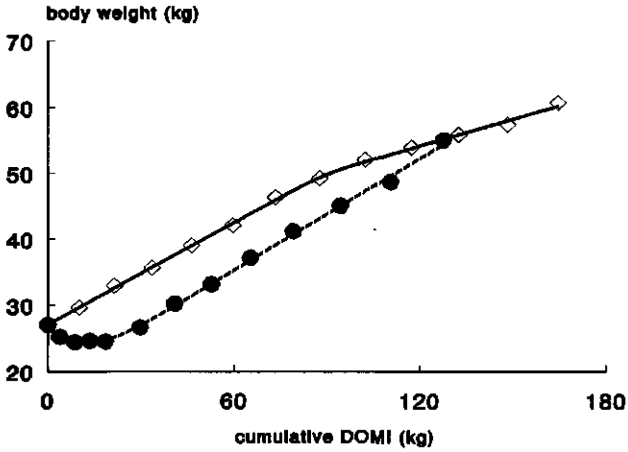

Figure 3. The relationship between cumulative digestible organic matter intake (DOMI) and body weight (BW), (◇) observed values for control (C) group, (●) observed values for restricted (R) group, (——, ----) predictions based on Eq. [3].

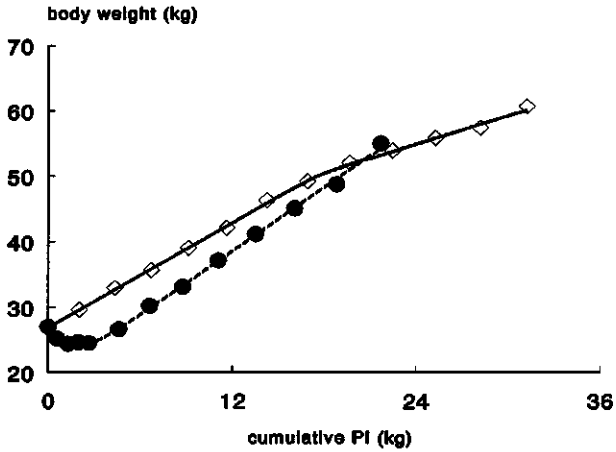

Figure 4. The relationship between cumulative protein intake (PI) and body weight (BW), (◇) observed values for control (C) group, (●) observed values for restricted (R) group, (——, ----) predictions based on Eq. [3].

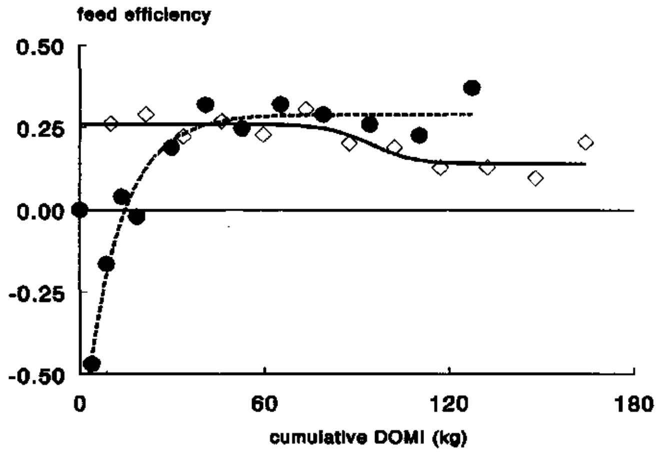

Figure 5. The relationship between cumulative digestible organic matter intake (DOMI) and feed efficiency (b), (◇) observed values for control (C) group, (●) observed values for restricted (R) group, (——, ----) predictions based on Eq. [6].

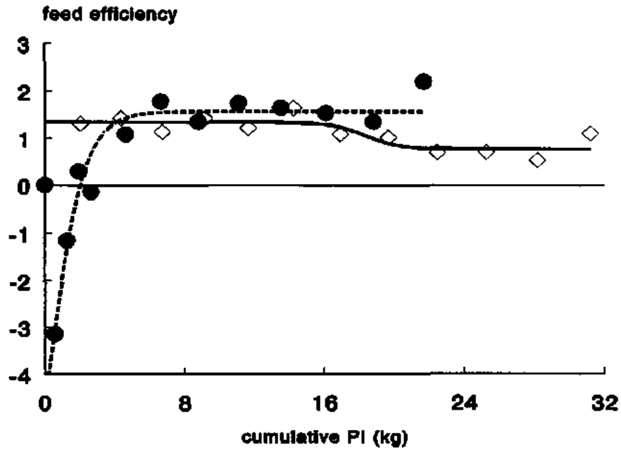

Figure 6. The relationship between cumulative protein intake (PI) and feed efficiency (b), (◇) observed values for control (C) group, (●) observed values for restricted (R) group, (——, ----) predictions based on Eq. [6].

value of W_0 for R group after realimentation was a reflection of the negative growth rate of this group during restriction. Ogink (1993) reported a similar response in goats which had a lower growth rate during the adaptation period to high quality diet.

Equation [3] showed that there is a change in the slope during growth for both the C and R groups. However, the transition point for R group is at the time of realimentation. Table 5 shows that the transition point (F_i) for C group was at 88.96 kg DOMI. This can be seen from the smooth transition of the solid curve in Figure 3. The smoothness parameter (r) was 5.00 with a larger standard error compared to the R group. The transition point for the R group estimated at the point 2.02 with a large standard error because of changes in feed composition at the time of realimentation. The smoothness parameter (r) was 7.68, with a smaller standard error compared to C group, because more data were available in the neighbourhood of the transition point.

Feed efficiency during the first phase (b_0) was 0.26 and during the second phase (b_1) was 0.14 for the C animals. The low quality diet caused a negative efficiency (b_0 = -1.06), with a large standard error for the R animals during restriction. The large standard error, implies that animals responded differently to feed restriction. During restriction, some animals lost about 30%, while some others lost only 5% of their initial live weight. During realimentation R animals showed a higher efficiency (b_1 = 0.29) compared to the feed efficiency for C animals either during the first phase (b_0 = 0.26) or during the second phase (b_1 = 0.14). This indicates that after realimentation, R animals were more efficient in converting feed into growth. To a considerable part, this can be related to increased nutrient intake, resulting in a more favourable ratio of nutrients for growth relative to maintenance.

Equation [6] showed a constant level of weight gain for group C during the first phase (Figures 5 and 6). During the second phase, the feed efficiency declined, probably because of changes in the ratio between protein and fat deposition (Kamalzadeh *et al.* 1996b). The estimated value for the feed efficiency during the first phase (b_0) was 0.26 and during the second phase (b_1) was 0.14 for group C. The growth rate of the R group was negative during the restriction period. But, as the Figures 5 and 6 (the pattern of the dashed line under the line drawn from zero) show, the efficiency of feed utilization in R animals increased during restriction. This indicates that the R group well adapted themselves to the low plain of nutrition. After initial weight loss, the average live weight of R animals was maintained at a constant level until the end of restriction period (Table 2). After realimentation, the feed efficiency value for R animals was 0.29 similar to the value estimated by Eq. [3]. For C animals, b_0 and b_1 were similar to those estimated by Eq.[3]. However, the F_i was estimated at 94.74 kg DOMI, higher but not significantly different than the value which was estimated by Eq. [3].

The same set of calculations was done for the data of PI. The results showed the same pattern as DOMI when the relation between cumulative PI and W was estimated (Figures 4 and 6). The parameters estimated from the data of PI were more precise compared to the estimated parameters derived from the data of DOMI (Tables 5 and 6) because of less variation in the intake of protein compared to DOMI between animals.

The results of this experiment support the observations made by Thomson (1979) and Ledin (1983) that the efficiency of protein deposition increased during the initial period after realimentation. During realimentation, the efficiency of both DOMI and PI were higher in the R group compared to the C group, but the relative efficiency of PI was higher than DOMI. This difference in the efficiency was reflected in the ratios of feed efficiency value (b_1) of R group during realimentation and the feed efficiency value (b_0) of C group during the first phase. The ratio for the relation between DOMI and W was 1.11 (b_1) : 1 (b_0), while the ratio for the relation between PI and W was 1.23 (b_1) : 1 (b_0). However, the efficiency for PI does not take into account the dynamics of N within the animal, which may increase the efficiency of PI.

The results of this experiment support the observations made by Turgeon *et al.* (1986), Ryan (1990) and Kabbali *et al.* (1992) with sheep that realimentaed animals showed higher feed efficiency. Butler-Hogg & Tulloh, (1982) reported a higher feed efficiency during the first 10 kg of weight gain. Ørskov *et al.* (1976), reported a substantial increase in feed conversion ratio of realimented sheep at the same live weight compared to controls which were fed high protein diet. Timon & Eisen (1970) also found higher feed efficiency for mice selected for high post weaning weight gain than controls. In the present experiment, the shape and the magnitude of the growth curve was affected by the quality of the feed. After realimentation, the realimented animals showed a greater feed efficiency than C animals. This high efficiency was not influenced by gut fill (Kamalzadeh *et al.*, 1996a).

Ogink (1993) measured the AB value on the basis of DOMI, and reported values of 0.26 and 0.17 in West African Dwarf goats fed *ad libitum* high-quality and low-quality diets. In most other studies in which feed efficiency was examined, values of AB are based on fresh feed. In order to be able to compare their results with the findings of this experiment, the values of AB from literature based on fresh feed, were converted to values based on digestible organic matter (DOM) content.

The AB values derived from the study of Thompson & Parks (1983), indicated values of 0.43 and 0.39 for *ad libitum* fed Dorset Horn rams and wethers, and values of 0.40 and 0.42 for *ad libitum* strains of Merino rams. The AB values derived from the study of Thompson *et al.* (1985) with Merino strains, ranged from 0.44 to 0.47 for rams and from 0.47 to 0.52 for ewes. Ogink (1993) computed AB values of 0.23 and 0.26 from the results of a long-term experiment of Blaxter *et al.* (1982), with crossbred sheep. Parks (1982), reported a range of 0.17 to 0.64 for the AB in various species during *ad libitum* feeding.

The estimated AB value of 0.48 for the C animals derived by Eq. [1] in this experiment, is in line with the estimates from the studies of Thompson & Parks (1983) and Thompson *et al.* (1985). According to Thompson *et al.* (1985), AB describes the feed efficiency of the animal if no feed were required for maintenance, *i.e.* AB is the true feed efficiency, free of the body weight component. But, from the data presented by Thompson *et al.* (1985) and the results presented by Figure 2 in this study, the estimated (AB) in the above studies show the estimation of the feed efficiency at the time that body weight or (u) has the value of zero (u = 0). In other words, AB shows the potential value for feed efficiency at time u = 0, which means the potential efficiency of an animal at the time of conception. Therefore, in contrast to the suggestion made by Parks (1970) and Thompson *et al.* (1985), AB is not the true growth efficiency. The value of 0.48 shows the value of AB for feed efficiency at u = 0 (Figure. 2). This value decreased at a constant rate with increasing body weight or (u).

Equations [3] and [6], both gave a good fit to the data. The estimated parameters and the calculated lines clearly show the transition point in feed efficiency with increasing body weight. As the Figures 5 and 6 show, the feed efficiency is not decreasing at a constant level with increasing body weight, but there is a breakpoint in the efficiency of feed utilization as body weight increased. At about 50 kg live weight, feed efficiency of C animals fell by about 50% (Tables 5 and 6). Most likely, this change in the efficiency is because of changes in the composition of gain as body weight increased (Kamalzadeh *et al.,* 1996b).

CONCLUSIONS

The models used in this study, give a good description of the relationships between the pattern of the cumulative feed intake in relation to body weight and feed efficiency. The estimates of the parameters clearly show the effects of feed quality restriction on feed intake and an improved efficiency of growth during compensation. The feed efficiency is significantly higher for realimented animals compared to controls, which will result to a higher growth rate. The results of this experiment suggest that lambs subjected to a considerable period of feed quality restriction achieve the same weight as controls with significantly lower total feed consumption.

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Chapter 7

Compensatory growth as a strategy for sheep production systems

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Compensatory growth as a strategy for sheep production systems

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ABSTRACT

Individual production traits, such as reproduction and mortality rates, are partial measures, but may be used to evaluate the performance of different systems by comparing the rate of flock growth and potential offtake. The productivity of two existing (extensive, intensive) sheep production systems was compared with an alternative option based on a compensatory growth strategy. The future flock sizes, offtakes and structures were predicted based on the age structure of the flock and age-specific reproduction, mortality and growth rates. The economic performance was evaluated by calculating the cash flow of the flock. Revenues were obtained from the sale of culled animals and milk. The profitability of the alternative system based on compensatory growth strategy was higher than the other systems.

(*Key words*: sheep, flock, system, productivity, compensatory growth)

INTRODUCTION

Livestock production forms a major part of agricultural activity in Iran. There are about 100 million units of livestock including sheep, goats, cows, buffalos and camel (Mirikhoozani, 1993). Sheep and goats constitute about 60% of the livestock population. Flocks of small ruminants (sheep and goats) are mainly managed under two different systems, namely, village and migratory. Both systems are extensive and the animals are mostly kept on natural vegetation of the range and farm lands with a little supplementary feeding. Intensive systems of sheep production are employed in only a few cases.

In the tribal migratory system, the flocks migrate annually from the lowland winter ranges to the higher mountain grazing area in the summer. In the village system, the flocks are allowed on the natural communal grazing pastures, or irrigated farm lands, or even mountain ranges in summer. The vegetation ranges provide part of the annual fodder requirements throughout the year.

Stocking rate on the natural ranges is not controlled and depends on the seasonal rainfall and conditions of the pastures. Overgrazing, drought and lack of protection during many decades have decreased the grazing capacity of the ranges.

Most parts of the year, the grazing animals are on a very low plane of nutrition. In the villages, supplementary feeding is practised during winter, when little or no feed remains on the communal grazing lands. Fattening feedlot units, where sheep are intensively fed for a certain period, could also be included in the category of supplementary feeding. In this respect, the commercially prepared pellets and concentrate mixtures are of special importance.

The effect of low-quality forages on animal production is accentuated by seasonal variation. The degree of seasonal variation varies with the climatic conditions. In most parts of the country, the growing season starts in March. Till June/July, forage (mainly grasses) is abundantly available. Part of the pastures in the lowlands are preserved for next autumn, when the nomads move from highlands to lowlands. In the course of June/July the dry season starts lasting till September/October. In the dry season, feed largely consists of grasses of which the fibre content is high and protein content low. In the summer, the stubble are used for maintenance of the sheep and goats flocks. In the course of autumn and winter, the nomads may use the preserved pastures of the lowlands which have a moderate quality or like in the villages, supplementary feeding is practised. The composition of the ration mainly consists of a straw diet, supplemented by barley.

At the beginning of the green season, the grasses contain on average 9-11% crude protein (CP), while the digestibility is about 60-65%. These values decrease gradually but nevertheless rapidly during the dry season. During a prolonged period of the year the protein content is only 4-5% and the digestibility between 40 and 50% (Fig. 1).

The present system of nutritional management, which largely depends on natural vegetation is unsatisfactory. On the one side, there is a sizeable gap between the actual and potential productivity of small ruminants. The data of World Bank (1983) showed a 17% lower yearly offtake and a 20% lower carcass yield in developing countries compared to developed areas. On the other side, lack of suitable feeding strategies resulted in inefficient use of the available feed resources. However, the completely intensive production system may give higher output, but it needs a large amount of high quality concentrate mixtures. The conversion of concentrate to live weight in the intensive system is low (each kg live weight gain needs about 7 kg concentrate) compared to 2.5 to 3 kg concentrates which is needed for the production of 1 kg poultry (Foroozesh, 1992). Therefore, at the present time, concentrates are more used for poultry, although, the price of red meat is about twice compared to poultry meat. Because of the consumers preference for red (sheep) meat, the demand for sheep meat is high.

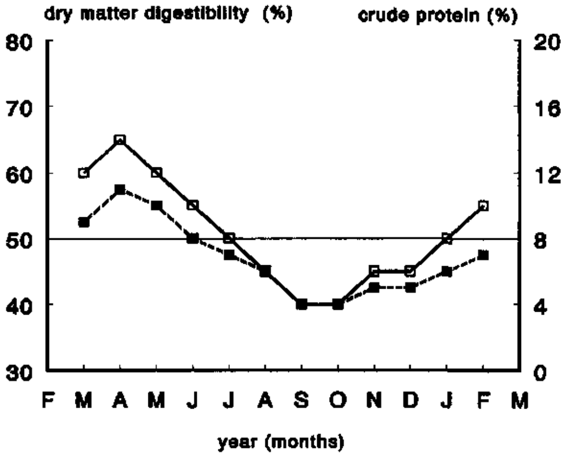

Figure 1. Seasonal variation in crude protein (cp) content (--■--) and digestibility (—□—) of pasture forage in Iran.

Therefore, more attention should be paid to the production of sheep meat at the lowest possible cost.

In order to overcome present nutritional problems of poor ranges, sheep should be taken off the ranges as much as possible to reduce the grazing pressure on the vegetation and to allow regeneration of the range species. Recently, more attention is paid to increase the available amount of concentrates in the country, to overcome the nutritional problems of poor ranges. Any increase in the number of animals should be prevented. More attention should be paid to the contribution of fibrous crop residues and agricultural by products as main basal feed resources.

With suitable feeding strategies, the output per each unit of feed intake will increase. The conversion of feed (concentrates) to live weight gain can decrease to 4:1 compared to 7:1 for the intensive system. In a longer term, this may lead to a reduction in the present number of animals without affecting the total productivity of the system. An alternative strategy is that both extensive and intensive systems of production gradually change to a semi-intensive system. In this respect, using a strategy of compensatory growth could be of special importance and a suitable way to increase the efficiency of the available low-quality feed. By using this strategy only part of the livestock feed requirements need to be produced to supplement the insufficient low-quality feed obtained from the ranges and farm lands. Efficient use of the available feed resources will result in higher output.

The objective of this paper is to simulate and evaluate the productivity of the three different systems in Iran, using a flock growth model. One of the systems is based on compensatory growth strategy, the two other systems are existing systems in Iran. The productivity of the system based on compensatory growth approach was evaluated under two situations with possible high and low outputs.

METHODS

Based on the model suggested by Upton (1993), a method was developed for building a 'flock growth model' from the knowledge of birth, mortality and production parameters (together known as 'production traits').

Systems

The productivity of a sheep flock was compared in the following production systems:

(I) Extensive system, animals are kept on natural vegetation of the range and farm lands, with minimal amounts of supplement during the cold period (pastoral migratory and village systems).

(II) Intensive system, animals are mainly kept in the stable, the diet consists of a basal low-quality roughage, supplemented with concentrates. These animals may feed from pastures during the green period.

(III) Semi-intensive system with respect to compensatory growth strategy. In this system, in the course of spring, the green forages are the main source of feed. Animals are kept on natural pastures and farm lands. In the dry period of summer, the feed largely consists of stubble and straw (animals are kept at maintenance level). In this way animals are imposed to a natural feed quality restriction. In the course of autumn and winter animals are taken off from the ranges, the feed consists of a basal low-quality diet (*i.e.* cereal straw), supplemented with concentrates. Based on productivity (birth rate, survival rate and level of offtakes), this system was evaluated for two situations with high (system III_a) and low (system III_b) outputs.

For comparison of the production performance of different systems, the economic benefits of each system were calculated.

Model description

The measurements were illustrated with reference to growth of a sheep flock of different age and sex in which replacement is completely done by own young lambs. The flock is in a so-called 'dynamic situation'. The young lambs which were produced may either be slaughtered for consumption or sold or retained as additions to the breeding stock, in other words for capital investment. Due to variations in age and size, the measurements were expressed in terms of livestock units (LSU). One LSU is equal to a sheep of 60 kg live weight. The conversion factors were based on the relative feed requirements per head, and were calculated based on the metabolic weight ($LW^{-0.75}$). It implies a non-linear relationship between LW and LSU (Table 1). The productive efficiency of each system was estimated from the relationship between the total output and the level of resources required:

* capital invested in the animal itself.
* feed consumed.
* labour.
* other costs (veterinary care, drugs, etc)

Table 1. *Live weight (LW) per age class and converted livestock unit (LSU) for each sheep production system.*

System:	I		II, III_a & III_b	
Sex and age category	LW	LSU	LW	LSU
Females and males aged up to 12 months	25	0.52	30	0.59
Immature females (aged 12 to 24 months)	45	0.81	50	0.87
Immature males (aged 12 to 24 months)	55	0.94	60	1.00
Females aged 2 years and above	60	1.00	65	1.06
Males aged 2 years and above	70	1.12	80	1.24

Season

Based on the seasonal conditions, the year has been divided into three periods:

* a first period of 3 to 4 months (March till June/July, green period). The lambs are mainly born in the first month and weaned in the third month of

this period (lambing to weaning)

* a second period of 3 to 5 months (June/July till September/October, dry and warm period).
* a third period of 5 to 6 months (September/October till March, wet and cold period).

Table 2. *The production traits for different systems.*

	age class						
	0	1	2	3	4	5	6
System I							
Lambing rate (%)			80	84	87	86	82
Mortality rate (%)	28	8	4	4	6	8	10
Milk yield per lactation (litre)			120	120	120	120	120
Milk offtake per lactation (litre)			20	20	20	20	20
Ratio of adult males to females (%)			10	10	10	10	10
System II							
Lambing rate (%)			90	95	103	97	93
Mortality rate (%)	15	3	2	3	4	6	10
Milk yield per lactation (litre)			150	150	150	150	150
Milk offtake per lactation (litre)			50	50	50	50	50
Ratio of adult males to females (%)			10	10	10	10	10
System III_a							
Lambing rate (%)			90	95	103	97	93
Mortality rate (%)	17	4	2	3	4	6	10
Milk yield per lactation (litre)			150	150	150	150	150
Milk offtake per lactation (litre)			50	50	50	50	50
Ratio of adult males to females (%)			10	10	10	10	10
System III_b							
Lambing rate (%)			87	92	99	94	90
Mortality rate (%)	21	5	3	4	5	7	10
Milk yield per lactation (litre)			140	140	140	140	140
Milk offtake per lactation (litre)			40	40	40	40	40
Ratio of adult males to females (%)			10	10	10	10	10

Performance

The main components of the 'production traits' which represent the performance, are reproduction, mortality and yield. Of these three main components of performance, the first two determine the size of the flock and possible offtake, while the last relates to the quantities of meat, milk and other outputs (*i.e.* hides, wool) produced by the animals.

The production traits were estimated on an age and sex specific basis. Age specific mortality rate quoted to express the mortality rates in different ages (Table 2). Reproductive performance of ewes increases to a maximum at an age of 5 to 6 years old (Gatenby, 1986). Thereafter a ewe's ability to produce lambs is likely to fall more as a result of poor body condition than specific reproductive disorders. Loss of teeth and lameness result in a ewe receiving inadequate nutrition. Assuming that the total replacement rate of adult ewes is 20% per year, the average reproductive life of a ewe is approximately 5 years, a value comparable to that of 4.3 (±25%) years observed for Rambouillet ewes in India by Tomar & Mahajan (1980). Reproductive rate was represented by lambing rate. The estimated lambing rates for different age classes in each system are presented in Table 2.

The flock growth model

General model

Based on the model suggested by Upton (1993) and a growth model for an age structured population (Crow, 1986), a flock growth model is constructed. The model is expressed in numbers of females per age class in time. The scale for age classes and time is years. The numbers are counted at time of birth and it is assumed that all births are at one fixed time in a year, within a short period (say one week). The growth of a population is determined by *birth rate* and *survival rate* of the female part of the population. It is assumed that females in age class 2 start to reproduce, and all females of 7 years are culled.

Birth rate (b_x) is defined as the number of females born from females of age x. Survival rate (p_x) is probability for a female to survive from age x to age x + 1. The schematic flow in time for females of different ages for this model is:

	age class (x)							
	0	1	2	3	4	5	6	7
time								
t	$n_{t,0}$	$n_{t,1}$	$n_{t,2}$	$n_{t,3}$	$n_{t,4}$	$n_{t,5}$	$n_{t,6}$	0
t + 1	$n_{t+1,0}$	$p_0n_{t,0}$	$p_1n_{t,1}$	$p_2n_{t,2}$	$p_3n_{t,3}$	$p_4n_{t,4}$	$p_5n_{t,5}$	0

The number of newborns at time t + 1 is calculated as:

$$n_{t+1,0} = b_2p_1n_{t,1} + b_3p_2n_{t,2} + b_4p_3n_{t,3} + b_5p_4n_{t,4} + b_6p_5n_{t,5}$$

Stable flock size

For a fair comparison between systems, the flocks should be about the same in size and stable in time. For a stable population the condition is: $n_{t,x} / n_{t+1,x} = 1$, for all x. In such a situation, the numbers for each class are stable over time and for further calculation time can be ignored, and the population structure in terms of n_0, p_x and b_x can be derived by developing the above scheme in time. The result is:

age class	number	expression
0	n_0	$n_0 = b_2n_2 + b_3n_3 + b_4n_4 + b_5n_5 + b_6n_6$
1	n_1	p_0n_0
2	n_2	$p_0p_1n_0$
3	n_3	$p_0p_1p_2n_0$
4	n_4	$p_0p_1p_2p_3n_0$
5	n_5	$p_0p_1p_2p_3p_4n_0$
6	n_6	$p_0p_1p_2p_3p_4p_5n_0$
7	n_7	0 (p_6 is 0)

Birth and Survival rates

Survival rate (p_x) contains two factors, mortality rate (m_x) and culling rate (c_x), and therefore: $p_x = (1 - m_x)(1 - c_x)$. Assuming that mortality happens during the year and culling is always at the end of the year. Mortality is a factor determined by the system, culling, however is a factor which can be used to manipulate the survival rates to reach a stable flock size in time. For each of the systems a culling strategy will be determined in a way that the flock is stable in time. To find culling rates for the different age classes some additional assumptions are necessary:

1. The number of females in the mature classes of age 2 and higher (N_m), is constant.
2. Within the mature classes a same fraction (c_m) of the females will be culled each year, and: $c_2 = c_3 = c_4 = c_5 = c_6 = c_m$.
3. Culling rates for the immature females are assumed to be equal: $c_0 = c_1 = c$.

Calculation of c and n_0 for a stable flock

From the formula for the number of newborns a value for p_0p_1 can be derived:

$$p_0p_1 = 1/[b_2 + b_3p_2 + b_4p_2p_3 + b_5p_2p_3p_4 + b_6p_2p_3p_4p_5] \quad [1]$$

Having values for p_0p_1 and for N_m, a value for n_0 can be computed:

$$n_0 = N_m / \{p_0p_1 [1 + p_2 + p_2p_3 + p_2p_3p_4 + p_2p_3p_4p_5]\} \quad [2]$$

Equation [1] offers the opportunity to calculate c from p_0p_1, because $p_0p_1 = (1 - m_0)(1 - c)(1 - m_1)(1 - c)$, and c can be solved:

$$c = 1 - \sqrt{\{p_0p_1 / [(1 - m_0)(1 - m_1)]\}} \quad [3]$$

Offtakes

In Table 3, the market prices of sheep and milk are given. These data will be used to evaluate the total annual offtake. However, the total revenue derived in this way is a poor measure of product output. No account of flock appreciation or depreciation was taken, and it is likely that the product outputs vary from year to year. Upton (1993) recommended that output should be measured as the total product offtake from a flock, which is assumed to be maintained at a constant size and structure, so that the flock depreciation or appreciation is zero. Because of differences in types of feed, culled animals in various systems had different live weights. The value of sheep is calculated based on the live weight of the culled animals, which is also given in Table 3 for the various systems. The price of sheep meat depends on the sex and age of the animals. Male and younger sheep have higher prices. The value of sheep will be calculated as the product of the average weight of a sheep from a specific age/sex class and the price per kg live weight.

Table 3. *Prices and average live weight (LW) for sheep, and average milk offtake per ewe.*

Item		average live weight (LW)			
	System:	I	II	III_a	III_b
Females:					
1 year old		35	45	45	43
2 years and older		45	55	55	53
Males:					
1 year old		40	50	50	48
2 years and older		60	70	70	68
		average milk offtake per ewe (kg)			
Milk		20	50	50	40

RESULTS

Assuming a culling rate (c_m) of 8%, and a constant number (N_m) of 200 for the mature females in the flock for all systems, the population is determined by the parameters as presented in Table 4. For the males the same survival rates (p_x) are taken as for the females, except c_0, which is assumed to be 90% for system I, 92.5% for systems II and III_a and 92% for system III_b, so that always 20 mature males are available in the flock. In Table 5, the numbers per age class are presented, with the number of animals that died and the number of animals culled. Numbers of culled animals at different ages are presented in Table 6.

Based on the data given in Tables 1 and 6, the flock in system I consisted of 362 and in the other systems of 411 LSU. The estimated feed intake data, the total amount of feed consumption and the rate of gain are given in Table 7.

Table 4. *Population parameters for the female part of the different systems. Derived values are in **bold italics**.*

parameter	system			
	I	II	III_a	III_b
b_2[†]	.400	.450	.450	.435
b_3	.420	.475	.475	.460
b_4	.435	.515	.515	.495
b_5	.430	.485	.485	.470
b_6	.410	.465	.465	.450
p_0[‡] (m_0, c)[§]	***.693*** (.278, ***.040***)	***.673*** (.154, ***.204***)	***.670*** (.172, ***.191***)	***.676*** (.208, ***.146***)
p_1 (m_1, c)	***.883*** (.080, ***.040***)	***.772*** (.030, ***.204***)	***.777*** (.040, ***.191***)	***.811*** (.050, ***.146***)
p_2 (m_2, c_m)	.883 (.040, .080)	.902 (.020, .080)	.902 (.020, .080)	.892 (.030, .080)
p_3 (m_3, c_m)	.883 (.040, .080)	.892 (.030, .080)	.892 (.030, .080)	.883 (.040, .080)
p_4 (m_4, c_m)	.865 (.060, .080)	.883 (.040, .080)	.883 (.040, .080)	.874 (.050, .080)
p_5 (m_5, c_m)	.846 (.080, .080)	.865 (.060, .080)	.865 (.060, .080)	.856 (.070, .080)
p_6 (m_6, c_m)	.000 (.100, 1.00)	.000 (.100, 1.00)	.000 (.100, 1.00)	.000 (.100, 1.00)
n_0[‖]	***84***	***95***	***95***	***92***

†) Birth rates (b_x) are 1/2 of the lambing rates in Table 2, assuming a sex ratio of 1 : 1.

‡) Survival rates (p_x) are derived from m_x and c_x.

§) Mortality rates (m_x) are from Table 2, culling rate (c_m) is assumed to be 8% and c is derived by Equation 3.

‖) The number of newborns (n_0) is a result of Equation 2, assuming a constant mature female number (N_m) of 200 in the flock.

For simplicity, feed intake data and rate of gains considered to be similar for systems III_a and III_b. In system I, low-quality roughage was the major part of the annual feed. The annual concentrate consumption in system II was 186.3 kg and in systems III_a and III_b 119.7 kg per LSU (Table 7), indicating about 67 kg per LSU lower concentrate consumption by animals in systems III_a and III_b compared to system II.

To be able to compare the productivity of various systems, it was assumed that the average live weight of the flock is 40 kg at the onset of dry period in all systems. The feed intake data (Table 7) were derived from the observed values by Kamalzadeh *et al.* (1995) in experiment with restricted/realimented Swifter sheep.

Table 5. *Numbers of females and males in a stable flock for different systems.*

	I		II		III_a		III_b	
	♀	♂	♀	♂	♀	♂	♀	♂
age class								
0	84	84	95	95	95	95	92	92
mortality	23	23	15	15	16	16	19	19
culled	3	55	16	74	15	73	11	67
1	58	6	64	6	64	6	62	6
mortality	5	0	2	0	3	0	3	0
culled	2	1	12	1	11	1	11	1
2	51	5	50	5	50	5	50	5
mortality	2	0	1	0	1	0	1	0
culled	4	0	4	0	4	0	4	0
3	45	5	45	5	45	5	45	5
mortality	2	1	1	1	1	1	2	1
culled	3	0	4	0	4	0	3	0
4	40	4	40	4	40	4	40	4
mortality	2	0	1	0	1	0	2	0
culled	3	1	4	1	4	1	3	1
5	35	3	35	3	35	3	35	3
mortality	2	0	1	0	1	0	2	0
culled	3	0	4	0	4	0	3	0
6	29	3	30	3	30	3	30	3
mortality	3	1	3	1	3	1	3	1
culled	26	2	27	2	27	2	27	2
7	0	0	0	0	0	0	0	0

During the dry period, animals in system II gained at a rate of 6.4 $g.kg^{-0.75}.d^{-1}$, quite comparable with the (sub) tropical areas. The rate of loss of the animals in systems I, III_a and III_b was set at -2.2 $g.kg^{-0.75}.d^{-1}$. A value of 20.1 $g.kg^{-0.75}.d^{-1}$ digestible organic matter intake (DOMI) was estimated for animals in system I, III_a and III_b on the low-quality feed during the dry period. Considering 26 $g.kg^{-0.75}.d^{-1}$ DOMI (ARC, 1980) for zero weight gain (maintenance requirements), the 20.1 $g.kg^{-0.75}.d^{-1}$ DOMI resulted in approximately 2.2 $g.kg^{-0.75}.d^{-1}$ weight loss in animals of systems I, III_a

Table 6. *Number of animals culled at different ages for various systems.*

System	Sex	Age (year)	
		1	2 and older
I	females	3	41
I	males	55	4
II	females	16	55
II	males	74	4
III_a	females	15	54
III_a	males	73	4
III_b	females	11	49
III_b	males	67	4

and III_b during dry period. During the cold period, the gain was estimated at rates of 3.7 and 4 $g.kg^{-0.75}.d^{-1}$ for systems I, II, respectively, and 8.2 $g.kg^{-0.75}.d^{-1}$ for both systems III_a and III_b (Table 7). At the end of year, the estimated live weight for animals in systems II, III_a and III_b was 65 kg compared to 48 kg for animals in system I (Fig. 2).

DISCUSSION

The productivity of a system can be measured in different ways, depending how inputs and outputs are quantified (Upton, 1989; Bosman, 1995). To be able to select a suitable system, the productivity of alternative systems has to be quantified. This can be done by comparing the economic return of various systems. However, in the areas with wide seasonal variation, animal productivity estimates are subject to large errors. This is reflected by the differences in flock structures and production traits among animals (Cossins & Upton, 1988). Despite of such errors, defining a suitable measure of performance is of great importance.

Table 7. *Initial and final live weight, live weight gain, feed intake (low-quality roughage and supplement) and intake of digestible organic matter (DOMI) from low-quality roughage[1] and supplement[2] during dry and cold periods in different systems*

	dry period (90 days)			cold period (180 days)		
	I	II	III_a & III_b	I	II	III_a & III_b
Initial live weight (kg)	40	40	40	37	50	37
Final live weight (kg)	37	50	37	48	65	65
Live weight gain (g/day)	-33	111	-33	61	83	156
Live weight gain ($g/kg^{-0.75}.d^{-1}$)	-2.2	6.4	-2.2	3.7	4	8.2
Intake (DOMI, g/day)						
low-quality roughage	310	255	310	332	275	360
supplement	0	370	0	220	445	404
Intake (DOMI, $g/kg^{-0.75}.d^{-1}$)						
low-quality roughage	20.1	14.7	20.1	19.9	13.2	18.9
supplement	0	21.3	0	13.2	21.3	21.2
Total intake (DOMI, kg/LSU)						
low-quality roughage	27.9	22.3	27.9	59.8	49.5	64.8
supplement	0	33.3	0	39.6	80.1	72.7
Intake (g/day)						
low-quality roughage	850	700	850	910	750	800
supplement	0	610	0	350	730	665
Intake ($g/kg^{-0.75}.d^{-1}$)						
low-quality roughage	53.4	40.3	53.4	53.2	37.3	44.5
supplement	0	35.0	0	21.0	35.0	35.0
Total intake (kg/LSU)						
low-quality roughage	76.5	63.0	76.5	163.8	135.0	144.0
supplement	0	54.9	0	63.0	131.4	119.7

[1]) low-quality feed contains about 50 g/kg dry matter crude protein, *ad libitum*.

[2]) supplement contains about 170 g/kg dry matter crude protein, ≈30 $g/kg^{-0.75}.d^{-1}$.

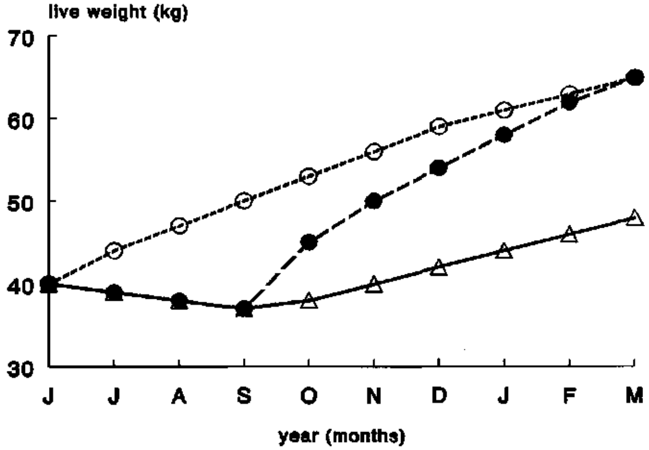

Figure 2. The annual growth patterns for different sheep production systems; (△) extensive, (○) intensive, (●) based on compensatory growth strategy.

Choice of models

Various livestock models (Knipscheer *et al.*, 1984; Wilson *et al.*, 1985; Upton, 1989, 1993; Bosman, 1995) have been proposed to evaluate the productivity of production systems under sub(tropical) and semi-aried climates. The models (Wilson, 1983; Knipscheer *et al.*, 1984; Bosman, 1995) used to assess the productivity of small ruminants in terms of production per individual animal or per flock. While, the models suggested by Peacock (1987), Ndamukong *et al.*, (1989) were used to evaluate the productivity of animals in terms of net production per flock.

Animal production in many parts of the world, particularly in the sub (tropics) and semi-arid areas are usually dynamic. The detailed and complex models which consider a large numbers of assumptions are not suitable and may not necessarily lead to better results. Many available models are affected by constraints imposed on animals (*i.e.* nutrient restriction). The input data in the model should be easily obtainable. Those that consider important traits and relatively offer an easier way for estimation of the parameters are more feasible. The herd growth model proposed by Upton (1989, 1993) for assessing livestock productivity is modified to a stable model, and offers a quick way to achieve reasonable estimates. The model used in Upton's study was not affected by feed quality restriction imposed to the animals during dry period.

Production traits

The production traits which are given in Table 2 are based on the observations from pastoral and intensive sheep production in the southern part of Iran and from literature (Goddard, 1982; White *et al.*, 1983; Devendra & Burns, 1983; Gatenby, 1986). The lambing rate is the number of lambs born per year per number of mature female sheep. In cattle, usually only one calf is born at a time, therefore, the calving rate ranges between 70-80 percent of the mature females, while in small ruminants twins and triplets are more common. For lambing rate a range of 97% to 118% in ewes under high (8 head per hectare) to low (2 head per hectare) stocking rate has been found by White *et al.* (1983). A range of 80 to 112 percent has been observed for sheep under extensive and intensive production systems in the Animal Husbandry Research Centre in Iran. In this study, a value of 84% has been set for system I, a value of 95% for systems II and III_a and a value of 92% for system III_b (Table 2).

Milk production depends on the lambing interval and milk offtake per lactation. The average lambing interval is 12 months, while the gestation period is 5 months. The milk production has been set to 120 litre and 150 litre per lactation (120-150 days) for various systems. For milk production, a range of 0.3 (Akinsoyinu *et al.*, 1977), 1.5 kg per day (Goddard, 1982) to 2.1 kg per day (Raats, 1983) has been proposed. Part of the milk (20-50 litre/ewe) is considered as offtake. Weaning can be based on age or weight, here weaning is set at an age of 90 days.

The rate of mortality varies between age classes, in young animals mortality rate is generally higher than in older animals. The mortality rate is higher under a low plane of nutrition than a high plane of nutrition. Different mortality rates have been chosen for various systems. In general, the mortality rates for system I were set at higher rate than the other systems due to the annual moving from one place to the other place and lack of adequate nutrition during most parts of the year. The data reported by White *et al.* (1983) indicated that the lambs mortality rates during the pre-weaning period varied between ewes under low and high planes of nutrition. A range of 3 to 20 percent mortality rate has been derived from the data reported by White *et al.* (1983) during pre-weaning period in pastures of high to low plane of nutrition.

The males are often slaughtered or sold as they reach maturity, or earlier, since a fewer males are needed for breeding. For replacement of the breeding animals a specific culling rate was adopted.

Systems productivity

Part of the higher gain of animals during the cold period in systems III_a and III_b compared to animals in system II was related to the higher low-quality roughage intake (Kamalzadeh *et al.,* 1995). The natural feed quality restriction imposed during the dry period, resulted in a lower maintenance requirements of the animals. This lower maintenance requirement persisted during the initial part of the cold period and as a consequence more net energy was available for growth when sufficient nutrients were made available for the animals in systems III_a and III_b.

During the cold period, the pastures preserved for the nomads in the lowlands have a relatively moderate quality. In the villages, hand feeding with limited supplement is practised. The moderate quality of the ranges and the little supplementary feeding resulted to a rate of approximately 3.7 $g.kg^{-0.75}.d^{-1}$ weight gain for animals in system I. The rate of gain in system II was set at 4.0 $g.kg^{-0.75}.d^{-1}$ lower than the value of 6.4 $g.kg^{-0.75}.d^{-1}$ for the dry period. This is because of changes in the composition of gain and reduction in the efficiency of growth with increasing body weight (Thompson *et al.,* 1985; Kamalzadeh *et al.,* 1996a,b).

Applying sufficient nutrients for animals in systems III_a and III_b during the cold period had a remarkable effect on the rate of gain. This is illustrated by 8.2 $g.kg^{-0.75}.d^{-1}$ gain in Table 7, indicating exhibition of compensatory growth. During compensatory growth the efficiency of feed utilization may change. ARC (1980) suggested a range of 0.32 to 0.55 for the efficiency of growth in the continuously growing ruminants. While, Gingins *et al.* (1980) reported a value of 0.75 for compensating animals. Ryan (1990) also reported a similar value (0.72) in sheep based on feed intake data and changes in body composition. According to Thomson (1979) and Ledin (1983), the efficiency of protein deposition may increase during the initial phase of the recovery period. Allden (1970), Turgeon *et al.* (1986) and Kabbali *et al.* (1992) also reported an increased feed efficiency during the recovery period. Ørskov *et al.* (1976) restricted animal in the quality of feed by supplying low-protein diet and reported that the higher live weight gain when animals were changed from a low to a high protein diet, was mainly related to the changes in the composition of gain. One possible reason can be a change in the rate of protein turnover. If protein synthesis increases or the rate of protein degradation decreases, there will be a reduction in the energetic cost of protein deposition and an increase in efficiency. Possible mechanisms responsible for compensatory growth of animals in system III were higher intake of low-quality feed, lower maintenance requirements, an increased feed efficiency and changes in the composition of gain.

Table 8. *Annual resource requirements and production per flock for four sheep production systems.*

		Production systems			
		I	II	III_a	III_b
Production	Unit				
Females culled, 1 year old	kg LW	105	720	675	473
Females culled, 2 years and older	kg LW	1845	3025	2970	2597
Males culled, 1 year old	kg LW	2200	3700	3650	3216
Males culled, 2 years and older	kg LW	240	280	280	272
Milk	l	3360	9400	9400	7360
Resource requirements	unit				
Land, pasture	ha	352	54	120	120
Capital invested in herd	LSU	362	411	411	411
Labour	manyear	2	5	3	3
Current inputs					
Concentrates	kg	22806	76569	49196	49196
Veterinary cost, etc	1000 Rls	500	1000	700	700

Economic performance

Comparison of the resource requirements for the three systems (Table 8) shows that the major differences are in the feeding strategy, *i.e.* the combination of land for grazing and concentrates. The systems I and II are the extremes, with 352 hectares providing the main part of the feed and 54 hectares providing just basal feed requirements respectively. Because, the poor quality grasses and stubles are the main feed resources in system I, therefore, the flock in this system needs an extensive area for grazing. System III is intermediate, as it requires approximately 60 hectares of pastures or farm land during the green and dry periods, and another 60 hectares to provide basal feed (straw) during the cold period. Other resource requirements as well as the physical production follow the same pattern, with the intensive system II requiring most resources and producing the highest output.

Valuation of the production according to actual market prices and the resources according to estimated market prices results in profits or returns to the herd owners (Table 9). Under the stated prices for products and resources the systems III_a and III_b result in profits which are substantially above those of either

Table 9. *Production value, estimated cost of production factors and profit per flock for four sheep production systems.*

	Production systems			
	I	II	III_a	III_b
Production value (Rls 1000)				
Females culled, 1 year old	368	2520	2363	1656
Females culled, 2 years and older	4613	7563	7425	6493
Males culled, 1 year old	7700	12950	12775	11256
Males culled, 2 years and older	720	840	840	816
Milk	1008	2820	2820	2208
Total	14408	26693	26223	22428
Resource costs (Rls 1000)				
Land				
estimated at Rls 5000/ha	1760			
estimated at Rls 10 000/ha		540	1200	1200
Capital invested in herd				
estimated at 5% of herd value	1305	1585	1585	1529
Labour				
estimated at Rls 500 000 per man/year	1000	2500	1500	1500
Current inputs				
Concentrates at Rls 250/kg	5702	19142	12299	12299
Veterinary cost, etc., estimated	500	1000	700	700
Total	10267	24767	17284	17228
Profit or return to herd owner	4142	1925	8939	5200

system I or system II. Because the combinations of land resources with concentrates form the main differences between the management systems, the influence of price changes in land and in concentrates on the profit were studied, Figures 3 and 4. For the land prices a fixed price ratio of 1:2 between the land for extensive grazing, and the more nearby the villages situated land for the other systems is assumed. Fig. 3 shows that changes of land prices over a wide range ,Rls 2000 to Rls 10000 per ha, do not affect the profitability ranking of the three systems: systems III_a and III_b remain superior. Fig. 4 shows that system II is seriously affected by a relatively small increase in concentrate prices: a price increase of 10% from Rls 250 to Rls 275/kg results in a reduction of the profits to zero, while the other systems remain profitable. At a price level of Rls 432/kg, the

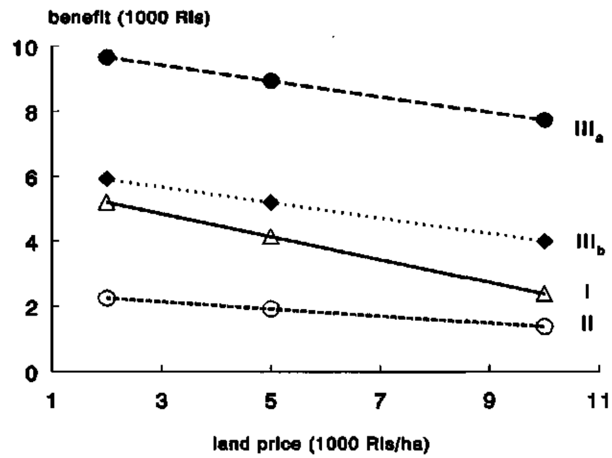

Figure 3. The effect of price changes in land on benefit for four sheep production systems; (I) extensive, (II) intensive, (III_a and III_b) based on compensatory growth strategy with high and low outputs.

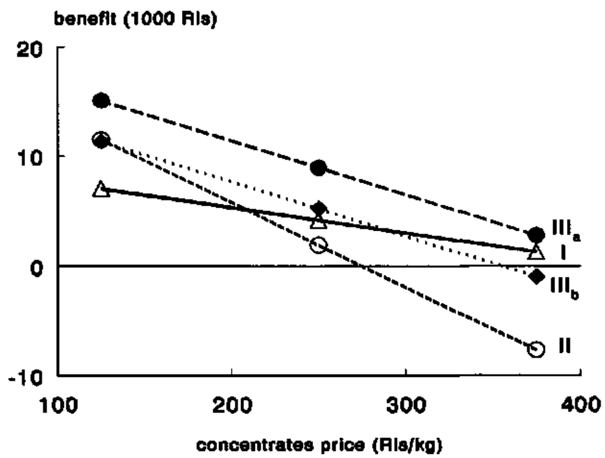

Figure 4. The effect of price changes in concentrates on benefit for four sheep production systems; (I) extensive, (II) intensive, (III_a and III_b) based on compensatory growth strategy with high and low outputs.

systems I and III_a just break even while the other systems are loss making. A price reduction to Rls 130/kg results in equal profitability levels for systems II and III_b, with system III_a at a higher and system I at a lower level of profitability. This sensitivity analysis shows that systems III_a and III_b are more profitable than either the extensive system I or the intensive system II under a wide range of prices for land and concentrates.

The continuous grazing of the flock in system I will seriously deteriorate 352 hectares of the pastures. In system III_a and III_b pasture requirements are reduced to about 120 hectares. Such a reduction enables either less intensive grazing on presently used lands or rotational grazing and possibilities for range improvement programmes. At system level, this means animals are taken off from about 65% of the ranges. The annual concentrate consumption in system II was 48.5% and in systems III_a and III_b was 35.2% of the total annual feed consumption. The conversion ratio (gain/concentrate) in system II was 1:7.5 compared to 1:4.4 for system III.

CONCLUSIONS

Livestock productivity may be assessed as output per livestock unit. The flock growth model used in this study provides estimates of flock size and structure, together with offtakes of animals and milk. These are derived by applying the average production traits (*i.e.* birth and survival rates) and given offtake rates. The flock structure and offtake rates are determined by the need to maintain constant animal numbers in each age/sex class and the given production traits. This model is readily adapted for assessing growth or productivity of small ruminant flock or cattle herds. Results are converted on an annual basis to give comparative figures per livestock unit.

Implementation of a strategy of compensatory growth relative to intensive system, enable a reduction of the concentrate input of 40% per livestock unit, and results in increased profitability. This indicates that animals on a discontinuous growth path, require a smaller input of feed than animals on a continuous growth path to achieve the same live weight. The delay in growth during the dry period is compensated during the cold period. An efficient use of the available feed results in higher profitability levels at a wide range of prices for land and concentrates.

A change from the currently widespread system I to systems IIIa and IIIb would mean a serious reduction of the land requirements per kg sheep meat produced. In sofar the reduced land requirements per kg are not offset by increased land requirements for an overall production increase, the pressure on grazing land would diminish. Such would open perspectives for range improvement programmes.

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Chapter 8

GENERAL DISCUSSION

GENERAL DISCUSSION

In the general introduction, the major constraints of livestock production, in particular small ruminants, in (sub)tropical areas were formulated. The general aims of this study were (1) to investigate the impact of feed quality restriction on the physiological state of the animals, in support of (2) the development of a more suitable strategy for sheep production in Iran, with no adverse effect on the environment.

The dry (lean) season imposes in grazing animals a natural feed restriction in quality and quantity that must be compensated for during the wet (lush) season. In such situation, compensatory growth after a period of undernutrition is a common feature. Even though the literature on this subject is quite extensive, the physiological background of the changes during growth retardation and higher gain during compensation is still obscure.

The effects of feed quality restriction on voluntary intake, digestibility, N balance, feed utilization efficiency, and changes in body dimensions, organs and chemical composition will be described first. Secondly, new approaches for the evaluation of the patterns of feed intake, feed utilization efficiency and growth, and changes in the physiological state of the animal will be explained. Further, a model is presented for assessing growth and productivity of small ruminant flocks.

Feed intake and digestibility

Recently, the mechanisms controlling fibrous feed intake have been reviewed by Forbes (1995). Several mechanisms have been proposed for the regulation of feed intake in ruminants (Chapter 2). The physical mechanism states that rumen throughput (*i.e.* holding capacity and turnover) is one of the major determinants of voluntary intake. However, the longer rumen retention time observed during feed quality restriction cannot be explained by such physical mechanism. Physiological mechanisms regulating feed intake are also related to the balance of ketogenic, glucogenic and aminogenic nutrients (Preston & Leng, 1987; Oosting, 1993), and blood borne factors, *e.g.* metabolites and hormones (Leuvenink *et al.*, 1994).

The higher voluntary intake of grass straw by the restricted animals during restriction shows that simple theories of feed intake may not hold under all sorts of conditions. During restriction, physiological changes at systemic level apparently create a condition that animals are capable to increase the intake of low quality feeds. This may in combination with an increased rumen retention time will inevitably lead to an increased pool size of feed particles in the rumen (Chapter 4), as was also found by Marais *et al.* (1991). During restriction, the daily grass straw intake gradually increased (Chapter 2). After realimentation, with the grass straw supplemented by concentrates, voluntary straw intake dropped, but remained significantly higher than the controls. It seems that the intake of the sheep after realimentation also depends on the animal's nutritional history in terms of quantity and/or quality of the available feed.

After feed restriction in quantity, there appears to be a period of 3-4 weeks of adaptation before feed intake of the realimented animals becomes as high as that of the controls (Ledin, 1983). However, after realimentation following feed quality restriction, only part of the increment in low quality feed intake substituted by concentrates (Chapter 2), in fact meaning that voluntary intake of low quality feed showed a sustained increase.

Weston (1979) suggested that the intake of low quality feeds is likely to be limited by the physical size of the digestive system, particularly the reticulo-rumen. The higher grass straw intake of the restricted animals is not in agreement with this suggestion. Depending upon the digesta load, retention and transit times there may also be changes in the digestibility of the diet. A digestibility depression may occur with increasing intake (Ledin, 1983). According to Van Soest (1982), such depression is a function of the rates of digestion and passage. As explained in Chapter 2, the longer rumen retention time during restriction presumably resulted in a slightly improved digestibility of grass straw.

During restriction, the regression of daily weight gain (DWG) on digestible organic matter intake (DOMI) suggested a zero DWG for DOMI at 22.1 $g.kg^{-0.75}.d^{-1}$ for the restricted animals, significantly lower than the range of 25-30 $g.kg^{-0.75}.d^{-1}$ for maintenance energy requirements, as reported in literature (ARC, 1980; Oosting, 1993). This indicates that the maintenance requirements of restricted animals must have decreased following feed quality restriction. During the early stages of realimentation, the reduced maintenance requirements may have resulted in comparatively higher energy for growth.

In conclusion, during feed quality restriction, animals partly substitute the lack of concentrates by ingesting more grass straw. Increased straw intake and an increased rumen residence time suggest an increased rumen fill. After realimentation, a higher straw intake and a reduction in maintenance requirements resulted in a compensation in terms of higher nitrogen retention and gain.

The evidence presented in this study together with results from literature show that no single mechanism governs the amount of fibrous feed consumed by ruminants. Obviously, voluntary feed intake must be considered as a multifactorally regulated process. The extent to which higher levels of feed intake persist, seems related to the previous type of restriction and also to the rate at which the homeostatic mechanisms of the animals have adjusted to the feed situation. It appears that the responses to feed quality restriction differ from those to feed quantity restriction.

Amino acid N availability and utilization

A zero N balance at DOMI = 24.4 $g.kg^{-0.75}.d^{-1}$ was predicted from the regression equation of N balance on DOMI (Chapter 2), quite in line with the value obtained for the zero energy balance. In mature Swifter wethers, fed wheat straw based diets, Oosting (1993) observed a value of 29.2 $g.kg^{-0.75}.d^{-1}$ DOMI. The lower value for zero N balance suggests that, most likely, immature lambs, after some time on a restricted diet, are able to maintain N balance beyond the level of DOMI where the energy balance becomes negative.

A value of 0.78 was predicted for the efficiency of the utilization of absorbed amino acid nitrogen (AAN) from the regression equation of N balance on AAN. This value is quite in line with the values of 0.75, adopted by ARC (1980) and of 0.80, as proposed by AFRC (1992). The regression equation of N balance on AAN indicated a zero N balance at an AAN of 555 $mg.kg^{-0.75}.d^{-1}$, quite in agreement with Oosting *et al.* (1995) who found a value of 520 $mg.kg^{-0.75}.d^{-1}$ in mature sheep.

Efficiency of feed utilization

There was a transition in the slope of feed efficiency (gain to feed ratio) of control animals with increasing body weight (Chapter 6). The response of control animals changed at $\approx$90 kg cumulative digestible organic matter intake (DOMI). This transition, allowed the calculation of an optimum rate of gain per unit of feed intake. The feed efficiency during the first phase was 0.26 and reduced to 0.13 with increasing body weight. This change in feed efficiency represents the decrease in protein deposition and the associated increase in lipid accretion.

Feed quality restriction resulted in a negative efficiency of feed utilization. After realimentation, the animals showed a significantly higher efficiency compared to controls, *i.e.* the realimented animals required less feed per kg gain than controls. The background for that was a combination of lower maintenance requirements (Chapter 2), higher feed utilization efficiency (Chapter 6) and difference in the composition of gain (Chapter 5). In realimented animals, a relatively greater part of the aminogenic nutrients was used for protein deposition. Because of the higher amount of associated water, the energy density of gain was less, while gain and gain to feed ratio were greater than in the controls.

Body dimensions

The development of different body dimensions was affected by feed quality restriction. During restriction, bone dimensions such as ulna length, height and body length were less affected than body circumference. The restriction effect on the skeleton cannot presumably be attributed to mineral deficiency, because during restriction period, low-quality diet was supplemented with a mineral mixture. After realimentation, those parts which were first and most severely affected by nutritional restriction started to recover earlier. Any change in the body shape and size of the animals was primarily related to the skeletal changes.

Development of body organs

As proportion of body weight, the empty body and carcass weights of restricted animals were lighter compared to controls (Chapter 4). However, the internal organs, in particular the highly active organs, *e.g.* gastrointestinal tract and liver, were affected to a lesser extent than body weight. When the comparison was made based on absolute weights, the internal organs were most severely affected. This discrepancy illustrates that different ways of evaluation of organ weights may lead to different conclusions. However, the results do show that the internal organs had a higher priority for the available nutrients during restriction.

After realimentation, the delay in the development of organs was fully compensated. The GIT, in particular the small intestine (Chapter 4), and the testes as presented in Figure 1, showed overcompensation. Similar responses have been reported by Ferrell *et al.* (1986) and Butler-Hogg (1984).

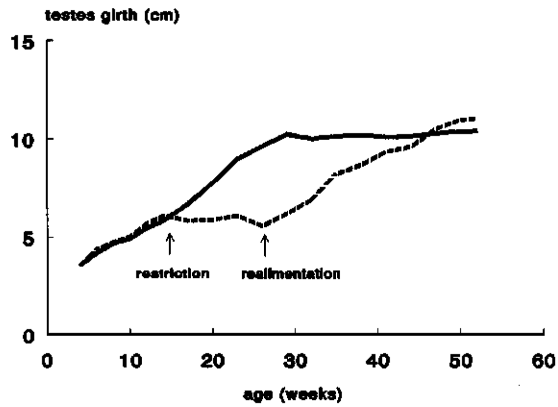

Figure 1. The development of sexual organs (testes) in control (——) and restricted/realimented (----) sheep.

Changes in body composition

The chemical components, *i.e.* water, protein, fat and ash, of the carcass and non-carcass were affected by restricted feeding in different ways. The rates of loss for the carcass components were considerably higher than those of the non-carcass. In an absolute manner, water made the largest contribution to the change in weight of the carcass and non-carcass components. This result agrees well with other studies with lambs (Drew & Reid, 1975; Butler-Hogg, 1984). However, with the composition of the loss expressed as proportion of the weights at the onset of restriction, fat was the major tissue lost during restriction.

The rate at which chemical components were lost from the various parts of the body changed with continuing nutritional restriction. Fat was mobilized from the onset of restriction onwards at a faster rate than the total loss of all parts of the body. The rate of fat depletion increased with continuing restriction. The rate at which water was lost, slightly increased at the last stages of the restriction period. This result does not support the suggestion of Butler-Hogg (1984), that the rate of water mobilization decreased with continuing nutritional stress. In the GIT, water was lost at the same rate as the total loss of GIT, while relative to the total loss of liver, water was mobilized to a lower extent. Despite variation in the rates of weight losses of different tissues, the greatest loss was associated with fat, then protein, water and finally ash. This is in agreement with earlier studies in sheep (Little & Sandland, 1975; Kabbali *et al.*, 1992), who also reported that body fat tissue was affected most.

After realimentation, the animals showed a significantly higher weight gain (Figure 2). This compensatory gain was not due to an increase in gut contents, but in part with increased protein deposition and the associated water. Therefore, at the end of the experiment, realimented animals contained more protein and water and less fat compared to their controls. This result agrees well with other studies with sheep (Drew & Reid, 1975; Carstens *et al.*, 1991; Ledin, 1983; Kabbali *et al.*, 1992). The results of the present study together with the above evidence from literature indicate that sheep do have the capacity to recover from considerable periods of nutritional restriction.

Compensatory growth strategy for sheep production systems

The current extensive sheep production systems in Iran, like in many developing countries, mainly depend on natural vegetation of range lands. The low plane of nutrition during most parts of the year results in a poor performance and degradation of the ecosystem. In an alternative manner, in urban regions, intensive sheep production systems are practised, with access to the market of scarce and expensive supplementary feeds. In Chapter 7, an alternative production system was designed combining feed quality restriction and compensatory growth. Following this strategy, sheep could be taken off from the ranges for part of the year and fed low quality feeds, *e.g.* cereal straws. During the dry period, animals are imposed to feed quality restriction. During the subsequent realimentation period, the conversion of supplement into gain increases (Van Bruchem & Zemmelink, 1995).

Following the strategy of compensatory growth resulted in a more efficient utilization of scarce supplements and per head a calculated net benefit of 2.7-4.6 times higher than the intensive system. So on the whole, there seems to be scope for a more efficient use of the scarce supplements. Relative to the extensive system, the grazing pressure on the vegetation ranges could be reduced for about 6 months annually. In theory, animals could be taken off from about 65% of the ranges. In conclusion, the compensatory growth strategy could give a more satisfactory result compared to the other two (extensive and intensive) systems. However, further in-depth research is needed on the seasonal availability and quality of the local feed supplements, the access to these materials, and options to improve the local feed resource base. Further research is also needed for a better tuning of the number of sheep to the ecosystem's carrying capacity. Lowering the number of sheep may increase feed utilization efficiency and the output of physical products, while alleviating the burden for the environment (Van Bruchem & Zemmelink, 1995).

Growth model during feed restriction and compensatory gain

Various growth models have been used to describe the relation between various body measurements and age, *e.g.* Gompertz, Mitscherlich, Richards and logistic (Chapters 3, 4 and 5). Unfortunately, most of these growth functions can only be used under conditions that feeding is *ad lib*, the environment constant and internal factors are not affecting growth. Under most circumstances, particularly in long-term experiments, controlling the environment is complicated and usually costly. Effects of feed type changes around weaning, development of the forestomachs in ruminants, onset of puberty and sexual maturity (Figure 1), all are natural process in the life time of animals. The data of this experiment (Figure 2) and the data presented by Malik & Acharya (1972) clearly show the change in the pattern of growth after weaning. These processes cause changes in growth and partitioning of nutrients over organs and tissues. Therefore, existing growth models cannot be used to explain the changes in advancing time or changes caused by constraints.

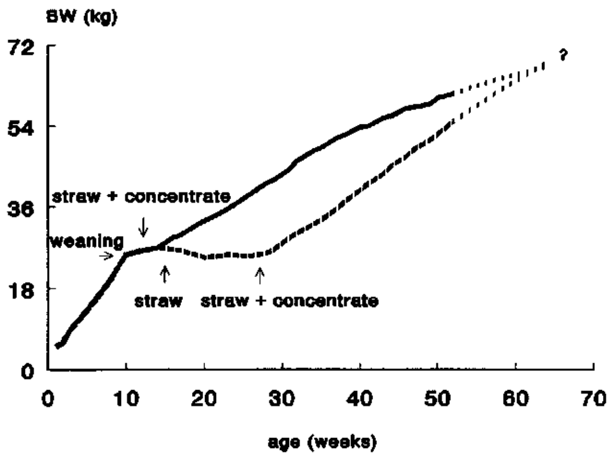

Figure 2. The relationship between body weight and age in control (——) and restricted/realimented (----) sheep.

The allometric growth model ($y = a.x^b$) has been generally used in studies of relative growth. However, in many growth studies (Chapter 3), the simple allometric model does not fit the body tissues and organs. Multiphasic growth curves may improve the insight in growth patterns of body weight or other measures and can be used to determine the stages of physiological development (Koops, 1989). Allometric models, however, are based on the independency of time and estimate only an average relation between the growth of two structures.

For these reasons, a new growth model was developed to quantify the effects of feed quality restriction and subsequent compensatory growth. The growth rates of restricted animals were expressed as the ratio to those in the controls. The allometric relation during normal growth was removed by taking the ratio, offering the opportunity to test the allometric relation during periods of nutritional stress and subsequent recovery. The effect of age was included in b (growth coefficient).

Modelling feed efficiency

Based on the relation between cumulative body weight (W) and cumulative feed intake (F), Parks (1982) developed a method to compute feed efficiency. He described the W-F relation with a diminishing return function. This model results in a linear relation between dW/dF, *i.e.* daily weight gain over daily feed intake, and degree of maturity (u), in which u is the ratio of the actual weight to mature weight (A) (Chapter 6). However, this model is only applicable if feed is available *ad lib* and animals are kept in a constant environment during the whole experimental period. In the present experiment, feed quality restriction was imposed to one of the groups, and therefore, the method of Parks could not be used. Instead, the change in the relationship between W and F was described by a broken line with a smooth transition (Koops & Grossman, 1993). This function is able to accurately describe a large number of curves, including the equations proposed by Parks.

Flock growth model

Reproduction and mortality rates are partial measures, but may be used as indicators of the productivity of a flock. Additionally, flock growth and potential offtake may be used to compare the productivity of different systems. Selection of the most appropriate one can be done by comparison with the characteristics of alternative systems. Various livestock models (*e.g.* Knipscheer *et al.*, 1984; Upton, 1993; Bosman, 1995) have been proposed to describe the productivity of dynamic production systems under (sub)tropical conditions. Based on the herd growth model proposed by Upton (1993), a flock growth model was developed. This model is able to estimate a stable number of different sex/age classes in the flock and offers a quick way to achieve reasonable estimates and predictions. This model provides estimates of flock size and structure, together with offtakes of animals and milk. The model was successfully adapted for assessing growth and productivity of small ruminants flocks.

Conclusions

The following conclusions can be drawn based on the results described in this thesis.

Maintaining the gut, particularly the reticulo-rumen, in terms of capacity is probably the main reason of ingesting more low quality roughage, despite an increased rumen residence time. This physiological change in the digestive tract of immature sheep in response to feed quality restriction differs from feed quantity restriction.

Voluntary feed intake in ruminants must be considered as a multifactorally regulated process. No single mechanism governs the amount of feed consumed by ruminants. Fibrous feed intake is related to the animal's nutritional history and physiological stage.

The responses of various body dimensions of immature sheep differ under restricted feeding and the following recovery period. In general, bone dimensions such as ulna length (forearm), trunk (body) length and height are less affected than width, depth and body circumference. Any change in shape and size of the body is primarily related to the skeletal structure, and any change in body components of immature sheep related to the shape and size of the animals. Bone measurements have a more stable character than other body dimensions and body weight. These dimensions, particularly ulna length, are the more accurate of the body surface measures. This is especially important in studies of growth stage and body shape of the animals.

While body weight can show considerable fluctuations as a result of changes in gut fill, width, depth and circumference measures can be influenced by lean meat and fat depositions.

The restricted nutrient supply in immature animals has a great inhibiting effect on the development of sexual characteristics, *e.g.* testes growth. Testes growth are most affected by nutritional restriction. However, the effect of realimentation is very fast for testes and at the initial stages of realimentation, the testes have fully compensated.

The hypothesis, proposing a constancy of the allometric growth coefficient based on the allometric law of Huxley, was not supported by present results.

The growth model presented in this study (Chapters 3, 4 and 5) to describe the development of body dimensions, organs and chemical body components during restriction and realimentation are different with other studies on these subjects. All disturbing effects during the process of growth are removed by using the ratio of the measurements of the restricted group over the control group. By using this model, the different responses and the patterns of the reactions in body dimensions, organs and body compositions can be study in greater detail.

Body organs react differently during feed restriction and realimentation. The internal organs, particularly the liver and gut, always have a high priority for use of the available nutrients either during restriction or during realimentation.

Various chemical components in each body part, *e.g.* carcass, digestive tract and liver respond differently to feed restriction and realimentation. The major changes occur in the relative loss and gain of fat and protein. The rate of gain of various body parts during compensatory growth reflect the extent to which they have been depleted during the phase of body weight loss. The composition of gain in the realimented animals is different from controls. The realimented animals are leaner and have a lower proportion of fat in the body compared to controls.

The feed efficiency model developed in this thesis gives an accurate explanation for the relationship between the pattern of the cumulative feed intake in relation to body weight and feed efficiency.

The delay in growth during the restriction period is compensated after realimentation with a better carcass quality. Higher intake of low quality feeds, lower maintenance requirements, an increased feed efficiency and changes in the composition of gain are contributed to compensatory growth.

The flock growth model developed in this study provides estimates of flock size and structure together with offtakes of animals and milk by the need to maintain constant numbers in each age/sex category and the given production traits.

Including the strategy of compensatory growth in the system show a reduction of 50 to 70 kg concentrate input per sheep compared to the intensive urban system, which would result in a 2.7-4.6 fold increase of net annual income. Compared to the extensive system, animals could be taken off from about 65% of the ranges, thereby reducing the grazing pressure on the vegetation and allowing regeneration of the range species.

A more efficient use of the available supplementary feed resources could result in an increased output of physical products, even though if the number of animals would be better tuned to the regional carrying capacity.

Prospects and future priorities for research

This study has shown that the potential nutritive value of a feed does not give insight in its potential value in the perspective of an animal production system. The approaches cited in the literature apply mainly to *ad libitum* fed animals in a controlled environment. The results may not be extrapolated as such to grazing animals which are always subjected to some degree of nutritional stress. The present study was designed taking into account the conditions prevailing in Iran. The insight in the growth pattern of various organs during/after nutritional stress was improved. Feeding strategies are needed taking into account the development of the various parts of the body and the physiological state of the animals. Maintaining body weight during the lean period largely depends on the animal's fibrous feed intake capacity. Future work should therefore aim at a better understanding of hormonal responses to feed quality restriction and subsequent compensatory growth, *i.e.* partitioning of nutrients and body tissue synthesis.

During the dry season with limited amounts of good quality feed available, feed quality restriction is a more useful strategy, rather than pursuing supplementation during the dry season. During the subsequent lush season, during realimentation, supplements are used more efficiently, and may animals benefit from compensation through increased low quality feed intake and a more efficient nutrient utilization. Suitable feeding strategies and a stocking density in balance with the ecosystem's carrying capacity may lead to an increased output of physical products. It is clear that to attain at an ecologically sustainable situation, any further increase in the present number of animals should be prevented. In a longer term, the productivity of the system may be optimized by reducing the number of animals, unless the high quality feed resource base can be significantly improved.

Last but not least, future efforts should be directed towards validation of these models under conditions in Iran, supported by an effective dissemination of the results amongst the small-scale subsistence farmers in the rural areas of Iran.

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SUMMARY

SUMMARY

In most parts of the world, livestock performance shows a seasonal pattern, related to the quantity and quality of the available feed resources. In Iran, like most parts of the world, animals are mainly kept on natural vegetation of range and farm lands, with only limited supplementary feeding. Overgrazing and consequently land degradation is high. Seasonal fluctuations cause periodic live weight loss and gain in grazing animals. The productivity of the animals is low compared to performance of the same species under more favourable conditions.

In order to overcome these problems, suitable strategies need to be developed (1) to minimize the adverse effects on livestock production and vegetation range lands and (2) to increase the efficiency of utilization of the available feed resources, particularly the limited amounts of high quality feed.

Small ruminants produce meat, milk and other products (wool, skin, etc). Also as a form of investment, small ruminants have many advantages. One or more animals can be readily sold for cash. The flock requires few inputs, and can give an acceptable return. The reproductive rate is high compared with that of larger ruminants so that if there is a disaster (such as a drought or epidemic disease), the number of animals can be quickly built up again.

In Iran, sheep and goats produce about 70 percent of the red meat and 35-40 percent of the milk and milk products. In most parts of the country, the growing season starts in March, and till May forage (mainly grass) is abundantly available. In the course of June the dry season starts lasting till September/October. In the dry season, the feed consists largely of grasses of which the fibre content is high and the protein content low. Usually, from October the rain starts but the temperature has then become too low for grass regrowth. Crop residues *e.g.* wheat, barley and rice straw, are commonly used roughages for small ruminants in the summer. Lambs are born in spring and weaned towards the summer when the quality of the available grass has decreased to a level hardly sufficient for maintenance requirements. This natural restriction in feed quality may be overcome by supplementary feeding during the dry season. Alternatively, imposing feed quality restriction during the dry season, may be a more appropriate strategy. The delay in growth during the dry period can be compensated by supplying supplements at a later stage and/or at the onset of the lush season, resulting to increased feed intake and a more efficient conversion of nutrients.

Compensatory growth is defined as a growth observed in animals fed sufficient

nutrients after a period of restriction in nutrient intake. Animals may respond in different ways following feed restriction. Compensatory growth may be caused by lower maintenance requirements during the recovery period, an increase in feed intake, an increase in feed utilization efficiency and changes in composition of gain.

The major aims of this study were:

(1) To determine the physiological changes during feed quality restriction and subsequent period of compensatory growth.
(2) To investigate whether after a period of feed restriction, the sheep are still able to attain the weight of the control animals, and if so how the empty body composition has changed.
(3) To develop (new) models to measure the relative growth patterns and the efficiency of feed utilization under nutritional restriction and following compensation periods.
(4) To develop a flock growth model for the assessment of growth (productivity) and structure of the sheep flock in different production systems.
(5) To evaluate the productivity of three sheep production systems applicable in Iran, using a flock growth model, comparing the performance of a simulated system based on compensatory growth strategy with the two existing (extensive and intensive) systems.
(6) To develop a more suitable strategy for small ruminant production systems with regard to the seasonal variations in the quality and availability of feed resources.

Crossbred Swifter (Flemish ♀ x Texel ♂) ram lambs, born in March, were selected and weaned at an age of approximately 2 months. The ration was gradually changed into the control diet of grass straw *ad libitum*, and 35 $g.kg^{-0.75}.d^{-1}$ mixed concentrates. At an age of approximately 3 months, animals were randomly divided into a restricted (R) and a control (C) group. By withholding concentrates, the R group was subjected to feed quality restriction from 3 to 6 months of age.

Feed (digestible) organic matter intake (OMI, DOMI), nitrogen (N) balance and gain were monitored (Chapter 2). During restriction, the R animals lost weight and showed a slightly negative N balance. The straw intake of the R animals increased, particularly during the last month of restriction. Retention time of the feed in the rumen also increased. After realimentation of the R animals, with the grass straw supplemented with concentrates, the animals persisted in ingesting more grass straw, while gain and N balance were higher than in the C animals. The evidence presented in this study (*e.g.* higher straw intake of R animals, increased rumen retention time) show that the current theories of feed intake regulation may not hold under all sorts of conditions. The physiological changes at systemic level apparently created a condition that animals were capable to increase low quality feed intake. This in combination with increased rumen retention time inevitably leads to an increased rumen pool size.

During restriction, the regression of daily weight gain (DWG) on digestible organic matter intake (DOMI) suggested a zero DWG for DOMI of 22.1 $g.kg^{-0.75}.d^{-1}$ for the R animals, lower than the maintenance energy requirements of 25-30 $g.kg^{-0.75}.d^{-1}$ reported in the literature. This indicates that R animals decreased maintenance energy requirements as a result of feed quality restriction. During the recovery period, the reduced maintenance requirement temporarily resulted in comparatively higher energy for growth. Linear relationships were observed between DOMI, the estimated truly absorbed small intestinal amino acid nitrogen (AAN) and N balance. Regression of N balance on AAN resulted in an estimated marginal efficiency of AAN utilization of 0.78.

A series of body measurements (body weight (BW), ulna length (UL), trunk length (TL), withers height (WH), chest depth (CD), hip width (HW), shoulder width (SW), chest girth (CG) and testes girth (TG)) was recorded on the live animal (Chapter 3). A growth model was developed to quantify the effects of feed quality restriction and consequent compensation. Estimated parameters clearly indicated retardation in growth after restriction and compensatory growth after realimentation. The effect of restriction varied among body dimensions. In general, bone dimensions such as ulna length, body height and length and chest depth were less affected than body weight. Width measures, such as shoulders and hips and body circumference showed a reaction similar to body weight, while testes showed an earlier effect of restriction. At the end of experiment, at an age of about 1 year, except for width at hips, no significant differences ($P > 0.05$) were observed between groups.

A serial slaughtering procedure was used to determine the changes in body organs and composition. Various organs (liver, gastrointestinal tract (GIT), lungs, heart) behaved differently during restriction and realimentation (Chapter 4). In general, the carcass showed an earlier effect of restriction and realimentation than body weight. Non-carcass (*e.g.* internal organs, head, feet, etc) showed a delay in growth after restriction, but a similar trend of growth as BW after realimentation. At the end of the experiment, the weight of the small intestine was significantly higher in R animals, though no significant differences were observed for other parts. Early maturing parts (visceral organs, head and feet) had higher priority for use of the available nutrients and were affected less than the later maturing parts.

During restriction, the R animals lost about 24% of the initial empty body weight (Chapter 5). The loss in carcass was more than the loss in the non-carcass parts (*e.g.* GIT and liver). The greatest loss was for fat, then protein, water, with the smallest for ash. Removing the restriction imposed by low quality feed had a remarkable effect on the rate of gain. Some lambs gained in excess of 300 g/day, considerably more than any of the C animals. This compensatory gain was not related to increase in gut contents. The responses to feed quality restriction and realimentation differed among body parts. The protein loss in the GIT and liver was compensated earlier than in the other parts of the body. The composition of gain in the R animals was different from that in controls. The realimented animals were leaner compared to their controls.

The approach to describe the pattern of development in body dimensions (Chapter 3), body organs (Chapter 4) and the pattern of changes in the chemical composition (Chapter 5) during restriction and realimentation differed from other studies on these subjects. Most of the available growth functions assume *ad libitum* feeding and a constant environment. In many conditions, these assumptions are not valid. By using the ratio of the measurements of the restricted group over that of the control group, all disturbing effects were removed and the analysis concentrated on pure effects of restriction and realimentation.

Two models were developed to measure feed efficiency from the relation between cumulative feed intake and body weight (1) and the relation between feed intake and gain per unit of time (2) (Chapter 6). These models gave a good description of the cumulative feed intake pattern in relation to body weight and feed efficiency. The slope and magnitude of the growth curve changed by feed quality restriction. After realimentation, R animals were more efficient in converting feed to body weight compared to their controls.

Individual production traits, such as reproduction and mortality rates may be used to evaluate the productivity of production systems, by comparing the rate of flock growth and potential offtake (Chapter 7). The productivity of a simulated system based on compensatory growth strategy was compared with two existing (extensive and intensive) sheep production systems. A population growth model was developed to estimate the flock size and structure, together with offtakes of animals and milk. These were derived by applying the average production traits (*i.e.* birth and survival rates) and given offtake rates. The flock structure and offtake rates were determined by the need to maintain constant animal numbers in each age/sex class. The economic performance was evaluated by calculating the cash flow of the flock. Financial revenues were obtained from the sale of culled animals and milk. The model can be readily adapted for assessing growth or productivity of flocks of small ruminants. Results are converted on an annual basis to give comparative figures per livestock unit. The productivity of the system based on compensatory growth was higher than that of the other systems. Implementing a strategy of compensatory growth in the system, enabled a reduction of the total concentrate input of 40% per livestock unit compared to the intensive system. By replacing the extensive system with the alternative system, only 35 % of the rangelands is required, thus reducing the grazing pressure on the vegetation and allowing regeneration of the range species.

SUMMARIZING CONCLUSIONS

* Maintaining gut capacity and an increased rumen retention time are probably the main reasons of ingesting more low quality roughage.
* The physiological changes in the digestive tract of immature sheep in response to feed quality restriction differs from those after feed quantity restriction.
* Voluntary feed intake in ruminants must be considered as a multifactorally regulated process.
* Bone dimensions of immature sheep are less affected than width, depth and body circumference by feed restriction.
* The restricted nutrient supply in immature sheep has a great inhibiting effect on the development of sexual characteristics, *e.g.* testes growth. However, after realimentation, the testes are fully compensated at the initial stages of realimentation.
* Body organs and chemical body components (water, protein, fat and ash) in each

part of the body (carcass, digestive tract, liver) respond differently during restriction and the subsequent period of compensatory gain.

* The major changes occur in the relative mobilization and deposition of fat and protein. The composition of gain in the realimented animals is different from the controls. The realimented animals are leaner compared to their controls resulting in better carcass quality.
* Higher intake of low-quality feed, lower maintenance requirements, an increased feed efficiency and changes in the composition of gain all contribute to compensatory growth.
* During the dry season with limited amounts of good quality feed, imposing feed quality restriction could be a useful strategy. During the following recovery period, animals can compensate through maintaining a higher low-quality feed intake and a more efficient use of the scarce high quality feeds.
* Modelling the implementation of the strategy of compensatory growth indicated a reduction of the concentrate input by 40% per animal compared to the intensive system. Compared to extensive system, the animals could be taken off till about 65% of the ranges, thereby reducing the grazing pressure on the vegetation.
* On the longer term, the productivity of such a system could be further increased by a better tuning of the number of animals to the ecosystem's carrying capacity.

SAMENVATTING

SAMENVATTING

In grote delen van de wereld vertoont de dierlijke produktie een seizoensgebonden patroon, in samenhang met de hoeveelheid en de kwaliteit van het beschikbare voer. In Iran, evenals in vele andere landen, worden grazers, zoals schapen en geiten, voor een belangrijk deel gehouden op de natuurlijke weidegronden, met slechts een geringe beschikbaarheid van hoogwaardig supplement. Overbegrazing en landdegradatie zijn het gevolg. De invloed van de seizoenen veroorzaakt bij de dieren afwisselende perioden van gewichtsverlies en groei. Vergeleken met een situatie waarin voldoende voer van hoge kwaliteit beschikbaar is, is de produktie beduidend lager.

Om het hoofd te bieden aan deze problemen is er behoefte aan een aangepaste strategie met als doel (1) het nadelige effect op zowel de dierlijke produktie als de weidegronden tot een aanvaardbaar niveau te beperken, en (2) de beschikbare voedermiddelen optimaal te benutten, in het bijzonder die van de beperkte hoeveelheid hoogwaardig supplement.

Naast melk en vlees produceren kleine herkauwers andere produkten, zoals wol, haar en leer. Ook zijn kleine herkauwers uiterst geschikt als vorm van belegging van kapitaal. Bij behoefte aan vlottende middelen kunnen één of meer dieren te gelde worden gemaakt. Een kudde schapen/geiten vergt bovendien beperkte externe inputs en geeft voldoende rentabiliteit. Daarnaast is het aantal jongen groter dan bij rundvee. Dit is vooral van belang na calamiteiten, zoals na een lange periode van droogte of na een epidemie, zodat de omvang van de kudde zich vrij snel kan herstellen.

Schapen en geiten produceren in Iran ongeveer 70% van het rode vlees en 35-40% van de melk(produkten). In de meeste regio's begint het groeiseizoen in maart. Tot eind mei is er voldoende gras van aanvaardbare kwaliteit beschikbaar. Medio juni begint het droge seizoen dat duurt tot september/oktober. In deze periode bestaat het voer in hoofdzaak uit volgroeid gras (hooi op stam) met een hoog gehalte aan ruwe celstof en een laag eiwitgehalte. In oktober is er doorgaans weer sprake van enige neerslag van betekenis, maar dan vormt de temperatuur een beperkende factor voor de grasgroei. Naast het laagwaardige gras worden in deze periode gewasbijdrodukten gebruikt als ruwvoer, bv. tarwe-, gerst- en rijststro. De lammeren worden in het voorjaar geboren. Zij worden gespeend in de voorzomer in een periode dat de kwaliteit van het gras is gedaald tot een niveau dat nauwelijks toereikend is om de onderhoudsbehoefte te dekken. Deze situatie zou in principe kunnen worden verbeterd door het verstrekken van hoogwaardig supplement. In alternatieve zin zou echter gekozen kunnen worden voor een

van de ruwvoeropname en een efficiëntere benutting van de nutriënten.

Compensatoire groei kan optreden na een periode van beperkt voeren. Dieren kunnen op verschillende manier reageren. Compensatoire groei kan het gevolg zijn van een lagere onderhoudsbehoefte in de herstelperiode, een verhoogde voeropname, een efficiëntere benutting van de voedingsstoffen en een verandering in de samenstelling van de lichaamscomponenten.

De doelstellingen van dit onderzoek laten zich als volgt formuleren:

(1) vaststellen van voedingsfysiologische parameters gedurende een periode van kwalitatieve voerrestrictie en de daaropvolgende periode van compensatoire groei.

(2) onderzoeken of jonge schapen na een periode van kwalitatieve voerrestrictie nog steeds in staat zijn het eindgewicht van de controledieren te bereiken, en of deze strategie consequenties heeft voor de karkassamenstelling

(3) ontwikkelen van (nieuwe) modellen ter interpretatie van relatieve groeipatronen en benutting van nutriënten gedurende de periode van kwalitatieve voerrestrictie en de daaropvolgende periode van compensatie

(4) ontwikkelen van een model dat de dynamiek van een schaapskudde beschrijft met als doel een indruk te krijgen van de produktiviteit en de opbouw van de schaapskudde in verschillende produktiesystemen

(5) met behulp van dit model evalueren van de output van produktiesystemen passend onder de condities van Iran, door de output van een gesimuleerd produktiesysteem waarin de 'compensatoire groei' strategie is opgenomen te vergelijken met bestaande extensieve en intensieve systemen

(6) ontwerpen van een optimale strategie voor produktiesystemen voor kleine herkauwers rekening houdend met de seizoensgebonden variatie in de kwaliteit en kwantiteit van het beschikbare voer.

In maart geboren kruisling Swifter (Vlaams melkschaap ♀ * Texelaar ♂) ramlammeren werden gespeend op een leeftijd van omstreeks 2 maanden. Het rantsoen werd geleidelijk aangepast tot het positieve controle rantsoen, per dag bestaand uit *ad libitum* graszaadstro en per eenheid metabolisch gewicht ($kg^{0.75}$) 35 g krachtvoer. Op een leeftijd van ongeveer 3 maanden werden de dieren *at random* verdeeld over twee groepen, respectievelijk een 'beperkte' (R) en een controle (C) groep. Door het onthouden van het krachtvoersupplement werd de R groep onderworpen aan een periode van kwalitatieve voerrestrictie gedurende een periode van 3 maanden, over een leeftijd van 3-6 maanden.

Bepaald werden de opname van verteerbare organische stof (vos), de stikstof

(N) balans en de ontwikkeling van het lichaamsgewicht (Hfdstk 2). Gedurende de periode van restrictie verloren de dieren gewicht en vertoonden een licht negatieve N balans. De graszaadstro-opname nam evenwel toe, in het bijzonder in de 3e en laatste maand van kwalitatieve voerrestrictie. Ook de verblijfsduur van het voer in de pens-netmaag nam toe. Na re-alimentatie, met naast graszaadstro weer de beschikking over krachtvoer, bleef de opname aan graszaadstro per eenheid metabolisch gewicht hoger. In vergelijking met de controledieren waren ook de groeisnelheid en de N retentie hoger. Op basis van deze bevindingen, bv. hogere graszaadstro-opname gedurende restrictie en verhoogde verblijfsduur in de pens-netmaag, werd geconcludeerd dat gangbare voederopname theorieën niet zonder meer geëxtrapoleerd mogen worden naar andere condities. De gewijzigde fysiologische omstandigheden op centraal niveau creëerden een conditie waarin de dieren in staat bleken de opname aan laagwaardig voer te verhogen. Dit moet in combinatie met de gestegen verblijfsduur in de pens-netmaag onvermijdelijk geresulteerd hebben een aanzienlijk toegenomen inhoud van de pens-netmaag.

Op basis van de regressie van groei ($kg^{-0.75}$) op de vos opname ($kg^{-0.75}$) werd tijdens restrictie een onderhouds energiebehoefte vastgesteld van 22.1 g vos $kg^{-0.75}$, aanzienlijk lager dan de doorgaans in de literatuur vermelde waarden in de range 25-30 g vos $kg^{-0.75}$. Dit duidt er op dat de R dieren kans zagen te besparen op onderhoud. In het begin van de herstelperiode heeft deze lagere onderhoudsbehoefte vermoedelijk bijgedragen aan een extra hoeveelheid nutriënten voor groei. Daarnaast werden lineaire relaties gevonden tussen DOMI en de berekende hoeveelheid darmverteerbare eiwit-N met de N balans. Regressie van de N balans op darmverteerbare eiwit-N resulteerde in een marginale benutting van 0.78.

Ook werd een aantal lichaamsmaten gevolgd, lichaamsgewicht, lengte van de ellepijp, romplengte, schofthoogte, borstdiepte, heupbreedte, schouderbreedte, borstomvang en de omvang van de testes (Hfdstk 3). Een groeimodel werd ontwikkeld om de effecten van kwalitatieve voerrestrictie en de daaropvolgende compensatie in kaart te brengen. Parameterschattingen toonden een duidelijke groeivertraging. Het effect van restrictie varieerde echter tussen lichaamsmaten. Afmetingen van het skelet, bv. lengte van de ellepijp, lichaamslengte en -hoogte, en borstdiepte werden minder sterk beïnvloed dan het lichaamsgewicht. Breedtematen, ter hoogte van de schouders en de heupen, en borstomvang vertoonden een reactie die sterk overeen kwam met die van het lichaamsgewicht. De omvang van de testes reageerde echter verreweg het sterkst. Met uitzondering van de heupbreedte werden aan het eind van het experiment, op een leeftijd van ongeveer een jaar, werden aan het eind van het experiment, op een leefijd van ongeveer een jaar, geen significante verschillen meer waargenomen.

Bij dieren geslacht in de loop van het experiment kon de ontwikkeling van organen en de lichaamssamenstelling worden gevolgd. Het effect van kwalitatieve voerrestrictie en re-alimentatie verschilde tussen organen, nl. lever, maagdarmkanaal, longen en hart (Hfdstk 4). Over het geheel reageerde het karkas scherper dan het lichaamsgewicht, zowel tijdens restrictie als na re-alimentatie. De overige lichaamsdelen, zoals interne organen, kop en poten, vertoonden ten opzichte van het lichaamsgewicht een extra groeivertraging, doch volgden de lichaamsgewicht trend na re-alimentatie. Aan het einde van het experiment, bleek het gewicht van de dunne darm significant hoger bij de R dieren, terwijl niet langer significante verschillen aantoonbaar waren tussen de overige delen van het lichaam. De vroegrijpere delen van het lichaam, bv. inwendige organen, kop en poten, hadden wat betreft de beschikbaarheid over nutriënten, een zekere prioriteit boven de laatrijpere delen.

Gedurende de voerrestrictie verloren de dieren ongeveer 24% van hun lichaamsgewicht (Hfdstk 5). De daling van het karkasgewicht overtrof dat van de niet-karkas delen, bv. lever en maagdarmkanaal. Qua chemische componenten werd de grootste daling aangetoond in het vet, gevolgd door eiwit en water, en de kleinste in de ascomponent. Het opheffen van de restrictie had een opmerkelijk effect op de groeisnelheid. Sommige dieren namen per dag meer dan 300 g in gewicht toe, aanzienlijk meer dan enig positief controledier. Deze compensatoire groei was niet gerelateerd aan een toename van de inhoud van het maagdarmkanaal. Qua chemische componenten verschilde de reactie op voerrestrictie en re-alimentatie tussen lichaamsdelen. Het eiwitverlies in lever en maagdarmkanaal werd sneller gecompenseerd dan in de overige lichaamsdelen. De samenstelling van de groei bij R dieren verschilde van die bij de controledieren. In relatieve zin zetten de R dieren minder vet aan.

De wijze waarop het ontwikkelingspatroon van de lichaamsmaten (Hfdstk 3), de organen (Hfdstk 4) en de wijziging in chemische samenstelling (Hfdstk 5) in dit proefschrift zijn beschreven, wijkt af van andere studies op dit gebied. De beschikbare groeifuncties veronderstellen *ad libitum* voeren en een constante omgeving. Aan deze condities kan doorgaans niet worden voldaan. Door de waarnemingen in de R groep uit de drukken in relatie tot die van de positieve controlegroep, konden alle storende invloeden worden geneutraliseerd en de analyse zich toespitsen op de zuivere effecten van restrictie en re-alimentatie.

Twee modellen werden ontwikkeld ter bepaling van de voerefficientie, (1) als afgeleide van de relatie tussen cumulatieve voeropname en lichaamsgewicht, en (2) de relatie tussen groei en voeropname per eenheid tijd (Hfdstk 6). Deze modellen gaven een betrouwbare beschrijving van het cumulatieve voeropnamepatroon in relatie tot het lichaamsgewicht en de voederconversie. Zowel de helling als de hoogte van de groeicurve veranderden in reactie op de kwalitatieve voerrestrictie. Na re-alimentatie bleken de R dieren voer efficienter om te kunnen zetten in groei.

Individuele karakteristieken, bv. van sterfte en voortplanting, kunnen gebruikt worden ter evaluatie van de produktiviteit van een produktiesyteem, door de berekende toename van het aantal dieren af te wegen tegen de potentiële afzet (Hfdstk 7). De produktiviteit van een gesimuleerd produktiesysteem, gebaseerd op de strategie van kwalitatieve voerrestrictie en compensatoire groei, werd vergeleken met twee bestaande, nl. extensieve en intensieve, produktiesystemen voor schapen. Een populatiegroeimodel werd ontwikkeld ter schatting van de omvang en opbouw van de schaapskudde, met daarnaast de produktie aan dieren en melk. Deze opbrengsten werden afgeleid van bekende produktiekarakteristieken, bv. het aantal geboren/gespeende dieren. De samenstelling van de kudde en de produktiviteit vooronderstelden een constant aantal dieren in iedere leeftijds/sex klasse. De rentabiliteit werd bepaald aan de hand van de *cash* opbrengsten. De inkomsten werden afgeleid van de verkoop van dieren en melk. De resultaten worden uitgedrukt op jaarbasis en per diereenheid. De produktiviteit van het produktiesysteem gebaseerd op 'compensatoire groei' was hoger in vergelijking met de beide bestaande systemen. Per diereenheid resulteerde deze strategie in een daling van de krachtvoerinput met 40%, relatief ten opzichte van het intensieve systeem. Door het extensieve systeem te vervangen door het 'compensatoire groei' produktiesysteem, lijkt het mogelijk om de begrazingsdruk van de natuurlijke weidegronden met 65% te verlagen, hetgeen zou kunnen resulteren in een regeneratie van bepaalde grassoorten.

RESUMEREND

* Handhaving van de capaciteit van het maagdarmkanaal en een toegenomen verblijfsduur in de pens-netmaag vormen waarschijnlijk de hoofdredenen van een toegenomen opname en mogelijk betere benutting van laagwaardig ruwvoer.
* Fysiologische aanpassingen in het maagdarmkanaal van onvolwassen schapen in respons op kwalitatieve voerrestrictie verschillen van die op een restrictie in kwantiteit.

* Voeropname bij herkauwers moet beschouwd worden als een multifactorieel gereguleerd proces.
* Skeletafmetingen van onvolwassen schapen reageren minder sterk op kwalitatieve voerrestrictie dan maten voor lichaamsbreedte, -diepte en -omvang.
* Beperkte voorziening van nutriënten heeft een sterk remmende werking op de sexuele ontwikkeling, bv. de groei van de testes; na re-alimentatie wordt de achterstand snel en volledig gecompenseerd.
* Organen en de chemische componenten water, eiwit, vet en as in delen van het lichaam, bv. karkas, maagdarmkanaal en lever, reageren verschillend op kwalitatieve voerrestrictie en de daaropvolgende periode van compensatoire groei.
* De grootste verschillen treden op in de relatieve mobilisatie en depositie van vet en eiwit. Ook de samenstelling van de groei wordt beinvloed door voerrestrictie en compensatoire groei, uiteindelijk resulterend in een karkas met een gunstiger eiwit/vet verhouding.
* Een gestegen opname van laagwaardig voer, een lagere onderhoudsbehoefte, een verbeterde voederconversie en een gewijzigde lichaamssamenstelling dragen alle bij aan compensatoire groei.
* Het blootstellen van groeiende dieren aan kwalitatieve voerrestrictie in het droge seizoen lijkt een passende strategie. Gedurende de daaropvolgende herstelperiode, kunnen de dieren dit compenseren door een hogere opname van laagwaardig voer en een efficiëntere benutting van schaarse supplementen.
* In vergelijking met het gangbare intensieve systeem, kwam een modelmatige analyse van het effect van compensatoire groei uit op een daling van de krachtvoerinput per diereenheid met 40%. In vergelijking met het gangbare extensieve systeem zou de begrazingsdruk van de natuurlijke weiden met 65% kunnen worden gereduceerd.
* Op langere termijn kan de produktiviteit van dit aangepaste produktiesysteem verder worden verhoogd door het aantal dieren beter af te stemmen op de draagkracht van het regionale ecosysteem.

PERSIAN SUMMARY

کیفیت و افزایش ضریب تبدیل غذا با استفاده از پدیدهٔ رشد جبرانی، کاهش در رشد در طول دوره خشک را جبران می‌نمایند.

* با کاربرد روش رشد جبرانی در سیستم تولید، مصرف مواد متراکم به میزان ۴۰ درصد نسبت به سیستم بسته کاهش می‌یابد. در مقایسه با سیستم چرای آزاد، فقط ۳۵% از مراتع مورد نیاز است، در بقیهٔ اراضی،می‌توان برنامه های توسعه و احیاء مراتع را اجرا نمود.

* در دراز مدت،با کاربرد چنین سیستمی تعداد دام کاهش یافته در حالیکه بهره دهی هر واحد دامی افزایش می‌یابد و در نتیجه تعداد دام موجود با منابع علوفه ای موجود بهتر تنظیم خواهد شد.

* تغییرات فیزیولوژیکی در دستگاه گوارش دام در حال رشد در زمان محدودیت کیفی غذایی، با تغییرات فیزیولوژیکی ناشی از محدودیت کمی غذایی متفاوت است.

* میزان مصرف اختیاری غذا در نشخوارکنندگان تنها به یك عامل بستگی نداشته، عوامل متعددی در مصرف اختیاری غذا دخالت دارند.

* ابعادی از بدن که از استخوان تشکیل شده اند کمتر از ابعاد عرضی، عمقی و محیطی بدن تحت تأثیر محدودیت غذائی قرار می‌گیرند.

* محدودیت غذایی اثر منفی زیادی در رشد دستگاه تولید مثل (بیضه ها) دارد. با فراهم شدن غذای مورد نیاز، بیضه ها رشد جبرانی زیادی خواهند داشت و در مدت کوتاهی رشد کامل خود رابدست می‌آورند.

* اثرات محدودیت غذایی در میزان رشد ارگانها و ترکیبات شیمیائی بدن یکسان نمی‌باشد.

* اثرات غذا دهی مجدد نیز در میزان رشد ارگانها و ترکیبات شیمیائی بدن متفاوت می‌باشد.

* چربی و پروتئین تغییرات بیشتری نسبت به ترکیبات دیگر دارند. ترکیبات شیمیائی در قسمتهای مختلف بدن دامی که مدتی تحت محدودیت غذایی قرار داشته و مجدداً" غذای کافی دریافت نموده با ترکیبات بدن دام شاهد متفاوت است. دامی که مدتی تحت محدودیت غذایی بوده و بعداً" رشد جبرانی داشته،دارای لاشه ای با پروتئین بیشتر و چربی کمتر و در نتیجه کیفیت بهتری است.

* مصرف بالای غذای کم کیفیت، کاهش در مقدار جیرهٔ مورد نیاز برای حالت نگهداری، افزایش ضریب تبدیل غذا و تغییرات در ترکیبات شیمیائی بدن،عواملی هستند که در رشد جبرانی دخالت دارند.

* در طول دورهٔ خشك با محدود منابع غذایی خوب و مناسب، ایجاد محدودیت غذایی روش مناسبی است، بعد از پایان دورهٔ محدودیت غذایی، دامها با افزایش مصرف غذای کم

دو مدل جدید برای اندازه گیری ضریب بازدهی غذا از: ۱- ارتباط بین مقدار کل غذای مصرف شده و وزن زندهٔ دام و ۲- ارتباط بین مقدار مصرف غذای روزانه و اضافه وزن روزانه، ارائه گردید. این مدلها بخوبی همبستگی بین مقدار کل غذای مصرف شده با وزن بدن و ضریب تبدیل غذا را توضیح می‌دهند. ضریب همبستگی و شکل منحنی رشد در اثر محدودیت غذایی ایجاد شده تغییر نمود. در طول دورهٔ غذادهی مجدد، ضریب تبدیل غذا برای گروه آزمایشی بیشتر از گروه شاهد بود.

از ویژگیهای فردی مختص تولید، از قبیل درصد تولید مثل و درصد مرگ و میر، و مقایسهٔ میزان رشد و میزان تولید بالقوه در گلهٔ دام، ممکن است جهت تعیین مقدار عملکرد سیستمهای پرورش دام استفاده گردد (فصل ۷). عملکرد یك سیستم پرورش دام بر اساس روش رشد جبرانی با عملکرد دو سیستم موجود (پرورش دام به روش باز و بسته) مقایسه گردید. با توسعهٔ یك مدل اندازه گیری رشد جمعیت و خصوصیات فردی دامها و مقدار تولید گوشت و شیر، اندازه و ترکیب گله تخمین زده شد. ترکیب و اندازهٔ گله و مقدار تولید برای حالتی در نظر گرفته شده است که تعداد دامها در گله همیشه در حالت ثابت باقی بماند. مقایسهٔ اقتصادی سیستم ها فقط بر اساس میزان درآمد نقدی در هر سیستم می‌باشد. درآمد از محل فروش بره ها، دامهای حذفی و شیر اضافه بر مصرف بره ها حاصل می‌گردد. روش مذکور بخوبی می‌تواند جهت تعیین میزان عملکرد گله های گوسفند و بز بکار رود. نتایج بدست آمده در این روش برای یك دورهٔ یکساله تعیین گردیده تا بتوان میزان تولید برای هر واحد دامی را تعیین نمود. نتایج بدست آمده از این مطالعه نشان داد که عملکرد سیستم پیشنهادی بر اساس رشد جبرانی بیشتر از دو سیستم موجود است. در روش رشد جبرانی، مواد متراکم مورد نیاز به مقدار ۴۰ درصد نسبت به سیستم بسته کاهش یافت. نسبت به سیستم باز یا چرای آزاد، فقط ۳۵ درصد از مراتع مورد نیاز است.

خلاصهٔ نتایج

* ثابت ماندن حجم شکمبه در طول دورهٔ محدودیت غذایی و بعد از آن (دورهٔ غذادهی مجدد) و افزایش مدت توقف غذا در شکمبه به احتمال زیاد، دلایل اصلی افزایش مصرف غذای دارای کیفیت پائین (کاه) است.

هفته ذبح گردیدند. اثرات دورهٔ محدودیت غذایی و دورهٔ غذا دهی مجدد برای همهٔ ارگانهای داخلی یکسان نبود (فصل ۴). بطور کلی، اثر محدودیت غذایی در لاشه زودتر از دیگر قسمتهای بدن نمایان گردید. بعد از سپری شدن دورهٔ محدودیت غذایی و فراهم نمودن غذای مجدد، لاشه رشد سریعتری نسبت به دیگر قسمتهای بدن داشت. در پایان آزمایش، وزن رودهٔ کوچك در گروه آزمایشی بطور معنی داری بیشتر از گروه شاهد بود، در حالیکه برای قسمتهای دیگر اختلاف بین گروهها معنی دار نبود.

در طول دورهٔ محدودیت غذایی، گروه آزمایشی بطور متوسط حدود ۲۴ درصد از وزن بدن (منهای محتویات دستگاه گوارش) را از دست داد (فصل ۵). مقدار کاهش در لاشه بیشتر از قسمتهای دیگر بود. بیشترین مقدار کاهش در وزن لاشه به ترتیب در اثر کاهش در مقدار چربی، پروتئین و آب بود. رفع محدودیت غذایی و استفاده از مواد متراکم اثر قابل ملاحظه ای در افزایش وزن روزانه داشت. اضافه وزن در بعضی از بره های گروه آزمایشی بیش از ۳۰۰ گرم در روز بود. این افزایش بسیار بیشتر از افزایش وزن روزانهٔ دامهای گروه شاهد از ابتدا تا پایان آزمایش بود. افزایش وزن در دامهای گروه آزمایشی در اثر افزایش محتویات دستگاه گوارش نبود بلکه،در اثر رشد جبرانی در قسمتهای مختلف بدن بود. چگونگی و میزان رشد جبرانی در قسمتهای مختلف بدن متفاوت بود. ترکیبات بدن در گروه آزمایشی در طول دورهٔ غذا دهی مجدد با ترکیبات بدن در گروه شاهد در طول آزمایش متفاوت بود. در پایان آزمایش، لاشهٔ دامهای گروه آزمایشی در مقایسه با گروه شاهد دارای پروتئین بیشتر و چربی کمتری بود.

نظریه ای که در این مطالعه برای بررسی روند رشد و توسعه در ابعاد بدن (فصل ۳)، اعضاء و ارگانهای بدن (فصل ۴) و تغییرات در ترکیبات شیمیائی بدن (فصل ۵) در طول دورهٔ محدودیت غذائی و دورهٔ غذادهی مجدد ارائه گردیده است با دیگر نظریه های ارائه شده در این زمینه متفاوت است. در اکثر نظریه های موجود در زمینهٔ رشد، فرض بر این است که غذا بصورت آزاد در اختیار دام قرار داده شده و تغییراتی در محیط وجود ندارد. در مواقع بسیاری چنین فرضیاتی معتبر نیست. با بکار بردن نسبت بین مقادیر اندازه گیری شده مربوط به گروه آزمایشی به مقادیر اندازه گیری شده در گروه شاهد،از تأثیر موارد جنبی مثل اثر محیط، اثر از شیرگیری، اثر بلوغ و غیره جلوگیری به عمل آمده و تجزیه و تحلیل نتایج فقط بر اساس اثرات خاص مربوط به دورهٔ محدودیت غذایی و دورهٔ غذادهی مجدد میباشد.

صادق نیست. این آزمایش نشان داد که بر خلاف نظریه های موجود، تغییرات فیزیولوژیکی در بدن شرایطی را ایجاد می‌نماید که دام قادر به افزایش مصرف اختیاری غذایی که دارای کیفیت پائینی است می‌باشد. این تغییرات فیزیولوژیکی به همراه افزایش مدت توقف غذا در شکمبه باعث افزایش گنجایش شکمبه می‌گردد.

در طول دورهٔ محدودیت غذایی، رابطهٔ رگرسیون بین مقدار اضافه وزن روزانه و مقدار مصرف مواد آلی قابل هضم نشان داد که دام در حالت نگهداری احتیاج به ۲۲/۱ گرم مواد آلی قابل هضم به ازاء هر کیلو وزن متابولیکی دارد. این مقدار کمتر از مقادیری (۲۵ تا ۳۰ گرم به ازاء هر کیلو وزن متابولیکی) است که تاکنون در دیگر منابع علمی ذکر گردیده است. این کاهش در مقدار احتیاجات نگهداری در طول دورهٔ غذا دهی مجدد نیز ادامه داشته و در نتیجه مقدار بیشتری از انرژی موجود در غذای مصرف شده برای رشد یا افزایش وزن روزانه اختصاص یافته است. ارتباط مستقیمی بین تعادل ازتی با مقدار مصرف مواد آلی قابل هضم و با مقدار اسیدهای آمینه ازتهٔ جذب شده از رودهٔ کوچك وجود داشت. از رابطهٔ بین تعادل ازتی و اسید های آمینه ازتهٔ جذب شده، ضریب ۰/۷۸ برای بازدهی اسیدهای آمینه ازته بدست آمد.

وزن زندهٔ دامها بطور هفتگی ثبت گردید، طول ساعد (زند زبرین)، طول و ارتفاع بدن، عمق سینه، عرض رانها، عرض شانه ها، دور سینه و قطر بیضه ها در دام زنده اندازه گیری شد (فصل ۳). يك مدل جدید برای تعیین میزان و چگونگی اثرات دورهٔ محدودیت غذایی و دورهٔ غذا دهی مجدد در رشد دام ارائه گردید. پارامترهای بدست آمده به روشنی تأخیر در رشد در طول دورهٔ محدودیت غذایی و رشد جبرانی در دورهٔ غذا دهی مجدد را نشان دادند. اثرات محدودیت غذایی در رشد ابعاد مختلف بدن متفاوت بود. بطور کلی، ابعادی که از استخوان تشکیل شده اند مثل طول ساعد، طول و ارتفاع بدن و عمق سینه کمتر از وزن بدن تحت تأثیر قرار گرفته،در صورتیکه، اثرات محدودیت غذایی برای ابعاد عرضی مثل شانه ها، رانها و دور سینه به اندازهٔ اثر در وزن بدن بود. اثر محدودیت غذایی در رشد بیضه ها زودتر از دیگر قسمتهای بدن نمایان گردید. در پایان آزمایش، در سن حدود يك سالگی،بجز عرض رانها،اختلاف معنی داری بین دو گروه برای دیگر ابعاد اندازه گیری شده وجود نداشت ($P>0/05$).

برای تشخیص و بررسی تغییرات حاصل در ارگانهای داخلی (جگر، دستگاه گوارش،...) و ترکیبات شیمیائی (پروتئین، چربی، آب و خاکستر) بدن، بره ها بطور متداول به فاصله هر سه

۴- ابداع یك مدل جدید برای بررسی میزان رشد و عملکرد یك گله دام سبك (گوسفند و بز) در سیستمهای مختلف تولید و پرورش دام.

۵- بررسی مقدار تولید و عملکرد سه سیستم تولید و پرورش دام در ایران با بکارگیری مدل جدید تعیین میزان رشد در گله. عملکرد یك سیستم براساس نتایج بدست آمده در این مطالعه با دو سیستم موجود به روشهای چرای آزاد (گسترده) و بسته (مبنی بر علوفه دستی) مقایسه می‌گردد.

٦- ارائه یك روش بهتر برای پرورش دام با توجه به تغییرات فصلی در کیفیت و کمیت منابع غذائی.

در این تحقیق از بره های نر دو رگه از نژاد سویفتر که در اواخر اسفند ماه متولد شده و در حدود دو ماهگی از شیر گرفته شده اند،استفاده شده است. بره ها بتدریج به جیرهٔ دورهٔ آزمایش، مرکب از کاه علف (بصورت آزاد) و ۳۵ گرم مواد متراکم به ازاء هر کیلو وزن متابولیکی (وزن زنده به توان ۰/۷۵) عادت داده شدند. در سن حدود سه ماهگی، بره ها به طور کاملاً تصادفی به دو گروه آزمایشی و شاهد تقسیم شدند. از سن ۳ تا ٦ ماهگی، مواد متراکم از جیرهٔ غذائی گروه آزمایشی حذف و بدین ترتیب گروه مذکور تحت محدودیت کیفی غذایی قرار گرفت.

مصرف مواد آلی و مواد آلی قابل هضم، مقدار جذب ازت و تعادل ازتی و مقدار اضافه وزن روزانه اندازه گیری شد (فصل ۲). در طول دوره محدودیت غذایی، میانگین وزن اولیهٔ گروه آزمایشی کاهش یافت، در حالیکه تعادل ازتی نیز منفی بود. مصرف اختیاری کاه در گروه آزمایشی نسبت به گروه شاهد بیشتر بود (P<۰/۰۰۱) و با ادامهٔ دورهٔ محدودیت غذایی افزایش یافت. مدت توقف غذا در شکمبه نیز برای گروه آزمایشی بیشتر از گروه شاهد بود (P<۰/۰۰۱). بعد از اینکه دورهٔ محدودیت غذایی برای گروه آزمایشی با فراهم نمودن مواد متراکم (دورهٔ غذا دهی مجدد) سپری گردید، مصرف اختیاری کاه در گروه مذکور در سطح بالاتر از گروه شاهد باقی ماند (P<۰/۰۰۱). میانگین اضافه وزن روزانه و جذب ازت در گروه آزمایشی بیشتر ازگروه شاهد بود (P<۰/۰۰۱). نتایج بدست آمده از این مطالعه از قبیل مصرف اختیاری کاه بیشتر و افزایش مدت توقف غذا در شکمبه برای گروه آزمایشی، نشان داد که نظریه های موجود در مورد مکانیزم های مسئول در مصرف اختیاری غذا بوسیله دام، همیشه

احتیاجات دام در حالت نگهداری می‌باشد. اکثر دامها مقداری کاهش وزن دارند. کاهش وزن دامها را می‌توان با اضافه نمودن مواد متراکم به جیرهٔ غذایی رفع نمود و یا اینکه در طول فصل خشك فقط جیرهٔ نگهداری دام را تأمین نمود و بعد از پایان فصل خشك (دورهٔ محدودیت غذایی) با فراهم نمودن مواد متراکم یا علوفهٔ مناسب در فصل بعدی (دورهٔ غذا دهی مجدد) با استفاده از پدیدهٔ رشد جبرانی، ضریب تبدیل غذا را افزایش داده تا حداکثر بهره برداری از منابع علوفه ای موجود حاصل گردد. بدین ترتیب تأخیر در رشد در طول دورهٔ محدودیت غذایی با تأمین مقدار نسبتا" کمی از مواد متراکم یا علوفه مناسب در دورهٔ غذا دهی مجدد جبران می‌گردد.

رشد جبرانی، رشد یا اضافه وزنی است که در اثر فراهم نمودن غذای مورد نیاز دام بعد از یك دورهٔ محدودیت غذایی، مشاهده می‌گردد. رشد جبرانی معمولا" از مقدار رشد در حالت معمولی بیشتر است. اثر محدودیت غذایی در همهٔ دامهای یك گروه (گله) یکسان نمی‌باشد. رشد جبرانی ممکن است در اثر کاهش مقدار احتیاجات دام در حالت نگهداری باشد، یا در نتیجهٔ افزایش مصرف غذا و یا افزایش ضریب تبدیل غذا و یا اینکه تغییر در مقدار ترکیبات شیمیائی (پروتئین، چربی، آب و خاکستر) بدن باشد. دامی که تحت دوره ای از محدودیت غذایی قرار گرفته دارای احتیاجات نگهداری کمتری می‌باشد. این دام در طول دورهٔ غذا دهی مجدد خصوصا" اوایل دورهٔ مذکور نیز دارای احتیاجات نگهداری کمتری در مقایسه با دامی که تحت دورهٔ محدودیت غذائی قرار نداشته، می‌باشد.

اهداف اصلی این مطالعه عبارتند از:

۱- بررسی و تشخیص تغییرات فیزیولوژیکی در بدن دام در طول دوره محدودیت کیفی غذا و دورهٔ رشد جبرانی بعدی.

۲- بررسی اینکه آیا بعد از یك دورهٔ محدودیت غذایی، گوسفند قادر است از نظر وزنی و ترکیبات شیمیائی بدن به دامی که رشد معمولی داشته و تحت محدودیت غذایی نبوده برسد.

۳- ابداع مدلهای جدید برای اندازه گیری روند رشد و ضریب تبدیل غذا در طول دورهٔ محدودیت غذایی و دورهٔ غذا دهی مجدد.

بسم الله الرحمن الرحيم

خلاصـــــه

با توجه به مقدار و کیفیت منابع علوفه ای موجود، پرورش دام در اکثر نقاط دنیـــا دست خوش تغییرات فصلی است۰ در ایران مانند اکثر مناطق دنیا، پرورش دام عمدتا" متکی بر منابع طبیعی و پس مانده های کشاورزی می‌باشد۰ مواد متراکم (کنسانتره) سهم کمی در تغذیه گوسفند و بز را دارا می‌باشند۰ در اثر چرای بی‌رویه و زودرس، فرسایش خاك بسیار بالاست۰ تغییرات فصلی متناوبا" موجب کاهش و افزایش در وزن زنده دام می‌گردد۰ بهره دهی دامها در مقایسه با مناطق دیگر دنیا که دارای منابع تغذیه ای بهتری می‌باشند، بسیار کمتر است۰

برای رفع مشکلات موجود، روشهای مناسبی با توجه به وضعیت منابع علوفه ای و مراتع کشور باید توسعه یافته تا:

۱-از تخریب مراتع و فرسایش خاك جلوگیری گردد و ۲- بهره دهی منابع علوفه ای موجود خصوصا" محدود منابع علوفه ایی که دارای ارزش غذایی بالایی هستند از قبیل مراتع درجه یك و مواد متراکم، افزایش یابد۰

نشخوار کنندگان کوچك (گوسفند و بز) عمده ترین منابع تولید گوشت قرمز، شیر و مواد دیگر از قبیل پشم، پوست می‌باشند بر اساس آمارهای موجود، گوسفند و بز حدود ۷۰ درصد از گوشت و ۳۵ درصد از شیر و فرآورده های شیری کشور را تأمین می‌نمایند۰ در اکثر نقاط کشور، وضعیت مراتع در فصل بهار نسبتا" مناسب است و علوفه مورد نیاز دامها تقریبا" تأمین است۰ از اوایل خرداد،فصل خشك شروع و تا اواسط پائیز ادامه دارد۰ در این مدت، علوفه موجود دارای مواد سلولزی زیاد و مواد پروتئینی کم و در نتیجه ارزش غذایی کمی می‌باشد۰ ضایعات و پس مانده های کشاورزی از قبیل کاه گندم و جو منابع اصلی غذای دامها را در فصل تابستان تشکیل می‌دهند۰ معمولا" از اواسط پائیز، بارندگی شروع ولی بدلیل کاهش درجه حرارت،رویش دوباره دانه های علوفه ای میسر نیست۰

زایش دامها در اوایل بهار است و زمان شیرگیری بره ها معمولا" سه ماه بعد یعنی اول تابستان است۰ در این زمان، علوفه موجود دارای ارزش غذایی کمی است و بسختی جوابگوی

Curriculum vitae

Azizollah Kamalzadeh was born in a farmer family in Seevand, a village located near to Shiraz, the centre of Fars, a southern province of Iran on March 21th, 1957. After receiving the High School Diploma in mathematics, he entered the faculty of Animal Husbandry in Oroumih University in Iran. In September 1979, he obtained his degree of agricultural engineer in the field of animal production. After that, he immediately joined the Ministry of Jahad-e-Sazandegi (reconstruction crusade) which established in post-revolution for supporting rural poor, in the Fars province, performing managerial tasks in the field of rural development. From 1990-1992 he completed a MSc in animal science from the Wageningen Agricultural University, in the Netherlands. From October 1992 till June 1996 he worked for his Ph.D degree majoring animal nutrition and physiology with the cooperation of the Departments of Human and Animal Physiology, Animal Production Systems and Animal Nutrition at the Wageningen Agricultural University, in the Netherlands.