THE REGULATION OF THE VOLUNTARY INTAKE OF FOOD BY SHEEP

A thesis presented in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Animal Science at Massey University

by

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ABSTRACT

Experiments were conducted with the main objectives of studying:

1. the extent to which the voluntary food intakes of sheep receiving diets, differing in physical form and digestible energy concentration, change with an increase in energy demand of the sheep
2. the effect of differences in body condition and an increase in energy demand on the voluntary food intake of sheep
3. the effect of an increase in the energy demand of sheep on measurements such as the retention time of food residues, alimentary tract fill and weight of alimentary organs
4. the extent to which increases in the energy intake of sheep equate with increases in energy demand.

The increase in energy demand was achieved by shearing Romney sheep, held at an ambient temperature of 13°C.

A section of the work also compared the retention times of food residues using various diets stained with safranine, treated with radiocerium ^{144}(Ce), or potassium permanganate (Mn). There were considerable differences in mean retention times depending on the method used. Because the variation in mean retention time was lower within and between sheep for ^{144}Ce than for the other methods, and because retention times could be determined rapidly with ^{144}Ce, the decision was made to use it in subsequent experiments.

Following shearing, there was a consistent increase in the voluntary intakes of sheep receiving chopped hay or ground hay of low digestible energy concentration. The increase in voluntary intake, with the exception of that for a hay of low protein content in one experiment, to a considerable extent met the increased energy expenditure when the sheep were shorn.

An increase in the amount of dry matter in the reticulorumen and a decrease in mean retention time was observed with sheep receiving chopped hay and ground hay. Evidence was also obtained of hypertrophy of the gut, measured as an increase in weight of the empty alimentary organs, when sheep receiving chopped hay or ground hay were shorn. No evidence was obtained of cause and effect, but it appeared that increases in intake were accomplished through a range of physical changes.

Evidence was also obtained that reticulorumen fill, in terms of the amount of dry matter, was unimportant in limiting the intake of chopped hay.

Following shearing, the increase in the voluntary intake of sheep receiving ground hay was greater than that of sheep receiving chopped hay. The increase in the intake of sheep receiving ground hay more than met the increase in energy expenditure following shearing. The result is consistent with the postulation that the rate of removal of dry matter from the reticulorumen imposed a limitation on the voluntary intake of sheep receiving chopped hay. This observation was further supported by the greater amount of dry matter caudal to the reticulorumen, with the shorn sheep receiving ground hay, than that of the unshorn sheep.

Voluntary intakes were invariably higher with sheep receiving foods of high digestible energy concentration, than with those receiving foods of low concentration, but the response in terms of changes in voluntary intake following shearing were variable.

In some of the experiments, increases in the voluntary intakes of sheep receiving dried grass were small, after shearing. However in an experiment which compared the effects of body condition, and of shearing on voluntary intake, fat sheep increased their energy intake of dried grass following shearing to about the same extent as the increase in energy expenditure. In the same experiment, the greatest increase in intake following shearing occurred with the thin sheep, and it appeared that the effects of shearing, in increasing voluntary intake, were reinforced by the condition of thinness.

The voluntary intakes of unshorn sheep receiving dried grass decreased as the experiments progressed. Physical restriction of the abdominal cavity by fat did not appear to be the cause of the decrease.

Measurements of oxygen consumption in two experiments (values converted to heat production) were obtained before and after shearing, with Romney wethers receiving dried grass or ground hay. Heat production increased after shearing, the increase being greater for the sheep receiving dried grass than for those receiving ground hay. The evidence obtained showed that, particularly with sheep receiving hay in the intake experiments, the increase in intake following shearing would have met the increase in energy expenditure in many cases. Changes in feeding behaviour and activity of the sheep occurred

following shearing. The effects of these changes on energy expenditure were discussed.

It was concluded that, even where voluntary intake is predominantly limited by physical factors, these can be overriden by changes in energy demand.

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PREFACE

The amount of food consumed by animals largely determines their productive output, and an understanding of how they regulate voluntary food intake is of fundamental importance in the field of animal nutrition.

The factors controlling food intake are complex and are not fully understood. The problem is not made simpler in the ruminant, with its close integration with the microbial population of the reticulorumen. The multifactorial nature of voluntary food intake presents many difficulties, in attempts to synthesise a system. Experimental approaches aimed at eliminating one control, in an attempt to understand the system, have often shown that the eliminated control is dispensable and that other control mechanisms are invoked to maintain food intake.

In both monogastrics and ruminants much of the research into the control of food intake has been concerned with the nature of the stimuli which signal the nervous system, in response to the ingestion of food. Many investigations have been directed towards establishing relationships between the amount of food consumed and the amount of digesta in the alimentary tract, or between food consumed and changes in the products of digestion in the alimentary tract and in the blood. The interpretation of these relationships is often difficult because of the inability to distinguish between cause and effect. In further efforts to understand the mechanisms involved, techniques such as the intravenous and intraruminal administration of various energy metabolites have been used. Generally, the response measured has been a decrease in voluntary intake, the interpretation of which could be complicated by the fact that, possibly the first symptom of metabolic stress is a decline in food intake.

Whilst the nature of the mechanisms controlling food intake remain unclear, there is considerable evidence to show that with roughage diets, in the long form, and of low digestible energy concentration, voluntary intake is controlled in ruminants by factors related to the capacity of the alimentary tract. In contrast, with foods of high digestible energy concentration, voluntary intake is related to the energy demand of the animal and the levels of the products of digestion.

It was considered that worthwhile advances towards understanding factors controlling food intake could be made under conditions where the energy demand of animals varied widely. This was achieved by shearing sheep, held at an environmental temperature of 13°C, which, from available evidence, was considerably below the critical temperature of shorn sheep.

The questions posed in this thesis were:

1. What effect would changes in the energy demand of sheep have on their voluntary intakes, when they were offered foods differing in physical form, and digestible energy concentration?

2. What effect would changes in the energy demand of sheep have on measurements (such as the retention time of food residues and alimentary tract fill) associated with the physical control of food intake?

3. To what extent would the change in the energy intake of sheep equate with the change in heat production, when they were shorn?

All experiments were carried out at the Animal Physiology Unit, Massey University.

CHAPTER 1

THE CONTROL OF VOLUNTARY FOOD INTAKE - A REVIEW

1.1 INTRODUCTION

The review begins with a brief outline of the neural basis of the control of food intake in mammals, and then considers how voluntary intake is controlled in the ruminant. Following this, a hypothetical model which attempts to integrate factors controlling voluntary intake is introduced. The review closes by considering a technique for investigating factors affecting voluntary food intake, based on the increase in energy expenditure of sheep, when they are shorn.

That mechanisms controlling voluntary intake exist is indicated by the balance between food intake and energy expenditure, which can be maintained in most animals over long periods, despite considerable variations in the nature of the diet, and the level of energy demand (Hervey, 1969). A distinction needs to be made between short term control in the initiation and cessation of feeding, and the long term control of food intake. Errors of adjustment in the control of food intake over a short period of time can be large, but the correlation between input and output improves if a longer period is considered (Widdowson, Edholm & McCance, 1954; Edholm, Fletcher, Widdowson & McCance, 1955 and review by McCance, 1972). It is apparent that a precise level of control must be maintained in the long term, if energy balance, or a set rate of change in energy balance is to be maintained.

1.2 THE NEURAL BASIS OF THE CONTROL OF FOOD INTAKE

There is considerable experimental evidence to support the contention that the central nervous system plays a major role in the ultimate control of food intake in mammals. Reviews on the subject have been provided by Brobeck (1960); Anand (1961 and 1967); Kennedy (1966); Baile & Mayer (1970) and Bell (1971).

It seems likely that neural control of food intake operates through a hierarchal organisation (Anand, 1961 and 1967) involving various integrated levels of nervous control through a complex of reflexes.

At the lowest level, the spinal cord and brain stem are most directly concerned with the control of feeding behaviour (Brobeck, 1960), and reflexes are put into effect by sensory stimuli that make the animal aware of the presence of food.

At the next highest level, the reflexes are facilitated by influences from the feeding centre in the lateral hypothalamus, and inhibited from the satiety centre in the region of the ventromedial nuclei of the hypothalamus. Much of the evidence on the role of the hypothalamus and the control of food intake has been gained with monogastric animals, mainly rats and mice. Stimulation in the region of the ventromedial nuclei (the satiety centre) produces hypophagia, and lesions produce hyperphagia and obesity. Stimulation of the lateral hypothalamus (the feeding centre) results in hyperphagia, and lesions cause aphagia (Mayer, French, Zighera & Barnett, 1955; Morgane, 1961, and reviews by Baile & Mayer, 1970 and Bell, 1971). The presence of hypothalamic feeding and satiety centres have also been demonstrated in ruminants (Larsson, 1954; Baile, Mahoney & Mayer, 1968), but Baile & Mayer (1970) stated that it was not a foregone conclusion that the ventromedial nuclei of the hypothalamus of ruminants has the same depressing effect on feeding as it does in rats.

At the highest levels, cerebral structures of the limbic system and the neocortex are probably involved in the control of food intake. Anand (1961) reviewed the evidence for higher levels of control and stated that cerebral influences are mainly of a discriminative character and may override control at lower levels. In summary, it appears likely that the hypothalamus contains areas of special activity for the control of food intake, and that these areas are integrated with lower and higher neural elements, to form a highly complex system.

In both monogastrics and ruminants much of the research into the control of food intake has been concerned with the nature of the stimuli which signal the nervous system in response to the ingestion of food. The main concern of the following sections will be to discuss how such stimuli might be provided, particularly as applicable to the ruminant.

1.3 THE CONTROL OF FOOD INTAKE IN RUMINANTS

1.3.1 Introduction

There are several important anatomical differences between ruminants and monogastrics which need to be considered. Some of these differences are listed as follows:-

1. the large size of the forestomach in ruminants compared with monogastrics
2. the fermentation of food in the reticulorumen by micro organisms, with volatile fatty acids as a major end-product of digestion in the ruminant
3. the ease with which adult ruminants fatten (This questions the validity of assuming that the primary activating mechanism in the control of food intake is energy balance, and it suggests an unusual adjustment of caloric intake and energy expenditure, possibly arising from the nature of the end-products of digestion).
4. the digestible energy (DE) concentration of ruminant diets is often low and the food is bulky. (This means that physical factors such as alimentary tract distension, and the rate at which food residues are removed from the tract may inhibit voluntary food intake to such an extent that the animal is in negative energy balance, or will not reach its maximum potential production).

1.3.2 Voluntary intake of foods of high DE concentration

That monogastric animals attempt to eat to a constant energy intake (Adolph, 1947), whereas the reverse is thought to be true for ruminants, is a well known generalisation. Blaxter (1962) stated that

> "the intake of a food by ruminants increases with the quality of the food they are offered, where quality is defined as the energy they obtain from food per unit of its weight".

There is now considerable evidence that food consumption in ruminants is reduced, when energy demand is satisfied, when foods of high DE concentration are offered. Depressed DM intakes have been reported with ruminants receiving diets of high apparent digestibility such as concentrates (Weir, Meyer, Garrett, Lofgreen & Ittner, 1959;

Freer & Campling, 1963). Instances have been reported with sheep (Harris & Raymond, 1963), and with dairy cattle (Hutton, Hughes, Newth & Watanabe, 1964) of a poor relationship between the digestibility of highly digestible leafy pasture and intake. Evidence that the intake of the pasture was not limited by physical factors was also obtained by the latter workers in that they observed a linear relationship between voluntary intake and the weight of DM in the reticulorumen.

Conrad, Pratt & Hibbs (1964), summarising data from a large number of experiments with lactating cows receiving diets ranging in apparent digestibility from 52 to 80%, concluded that DM intake decreased with rations varying between 67 and 80% in apparent digestibility. Food intake was related to body weight and to DM digestibility below 67% digestibility, but beyond this, (approximately 2.9 kcal DE/g DM) intake was dependent on metabolic size ($LW^{0.75}$) and milk production. The results were interpreted as indicating that at low apparent digestibilities, food intake was governed by "physical" means so that the level of milk production was determined by the animal's capacity and the rate at which undigested food could be moved along the tract. At higher levels of apparent digestibility, food intake was regulated by "physiological" means. The results obtained by Conrad, Pratt & Hibbs (1964) therefore illustrate an important departure from the generalisation given above (Blaxter, 1962).

Whilst it is convenient to separate physical and physiological mechanisms, the division is arbitrary as the mechanisms are not independent. In addition all mechanisms are "physiological", in that they have a neural basis, so that the term "physical" should not be taken too literally. For convenience, in the discussions that follow, the control of food intake exercised largely through the ability of the alimentary tract to accommodate food residues will be referred to as "physical" control, and control exercised through the absorbed products of digestion, occurring largely with foods of high DE concentration, will be referred to as "metabolic" control.

The dual concept of the control of food intake in ruminants, first developed by Conrad, Pratt & Hibbs (1964), was later confirmed by Montgomery & Baumgardt (1965a). They fed four pelleted rations containing increasing ratios of ground maize to lucerne meal to dairy heifers and to lambs. The diets ranged in apparent digestibility from 54 to 69%. Daily DM intake decreased as the energy concentration of the diets increased, but the daily consumption of DE was similar for all diets. They proposed the general relationship shown in Fig.1.1 to describe the regulation of food intake. With rations on the distension side (Fig. 1.1), DM and energy consumption increase with nutritive value, and reticulorumen load and distension was postulated as the mechanism limiting food intake. Most roughage rations probably fall into this category. With an increase in nutritive value, DM intake decreases and energy intake remains constant and the animal is able to consume enough DM to satisfy the physiological demand for energy. Chemostatic or possibly thermostatic mechanisms would appear to be operational at these higher levels of nutritive value. The term nutritive value was used by the authors rather than digestibility, as they maintained that factors such as the physical form and density of the ration may also determine the level at which mechanisms controlling food intake alter. On the basis of the results obtained by Conrad, Pratt & Hibbs (1964) and Montgomery & Baumgardt (1965a)it can now be stated that ruminants attempt to eat to a constant energy intake, but this can only be achieved with foods of high DE concentration.

The level of DE concentration at which DM intake decreases and DE intake remains constant is not likely to be fixed. This possibility is examined in the following section in relation to the physiological state of the animal.

1.3.3 The effect of the physiological state of the animal on voluntary intake

Changes in physiological state are reflected in changes in food intake, as the long term control of food intake is maintained by mechanisms which attempt to secure energy balance. There is ample evidence that this occurs. Lactating cows consumed 53% more pasture than dry cows (Hutton, 1963), lactating ewes consumed 42% more than dry ewes (Arnold & Dudzinski, 1967) and the intake of dried grass cubes was 80% higher in ewes suckling twins and 60% higher in ewes with single lambs, compared with dry ewes (Hadjipieris & Holmes, 1966). However, the latter authors observed that the food intake of lactating ewes receiving a medium quality hay was less than 10% greater than dry sheep receiving the same food. On the other hand,Campling (1966a)observed an increase of 29% in the consumption of a high quality hay by lactating

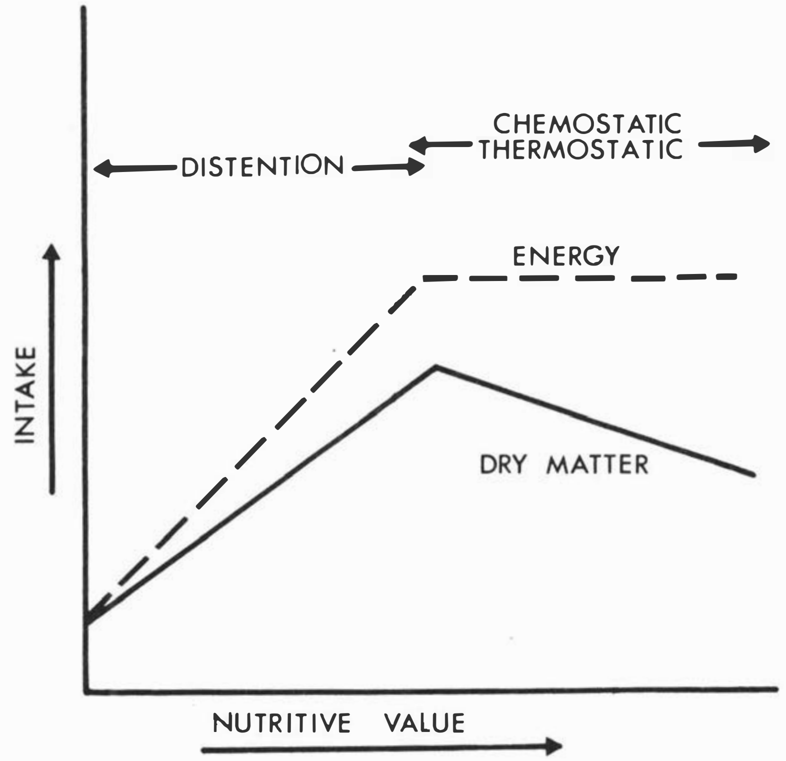

FIGURE 1.1 Probable relationships between energy and food intake and controlling mechanisms. From Montgomery and Baumgardt (1965a)

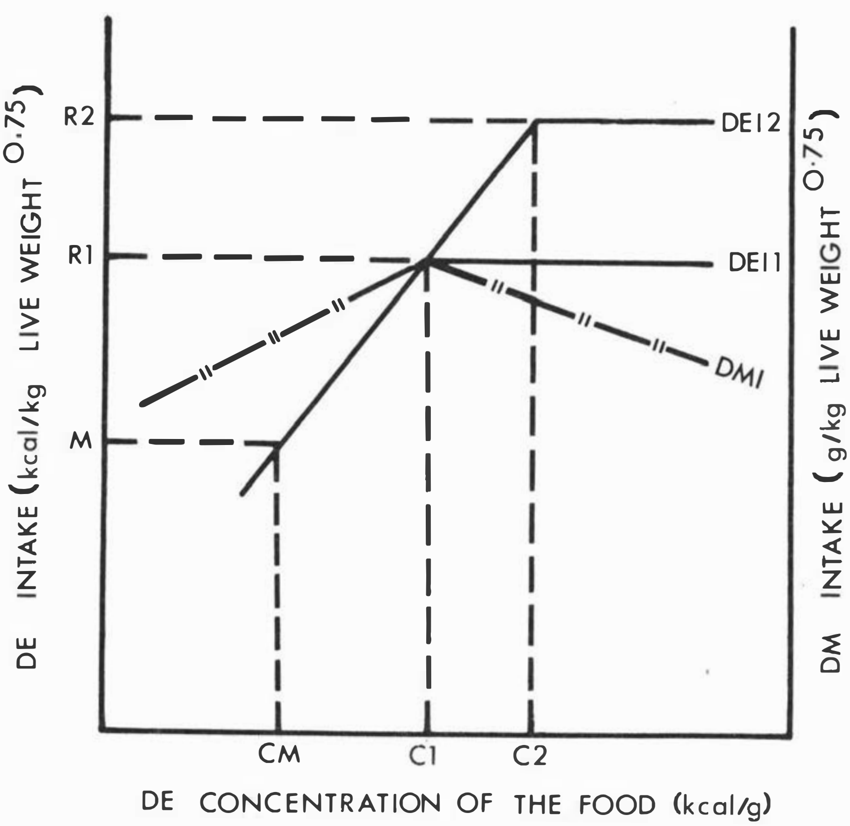

FIGURE 1.2 Relationships between the voluntary intake of digestible energy (DEI) and dry matter (DMI) and the digestible energy concentration of the food for ruminants requiring a lower (R1), and a higher (R2) level of digestible energy to maximize their production. From Bines (1971).

cows compared with dry cows, although the increase was only 8% with concentrates. Voluntary intake of the concentrates was higher than the hay but the reason for the small increase in concentrate intake is not known. In none of this work are results given which help to explain the effects observed. However, other reports offer a limited explanation. Thus Tulloh & Hughes (1965) and Tulloh (1966) observed an increase in the capacity of the reticulorumen and lower tract in lactating cows compared with dry cows. Similar results have been observed with lactating rats (Fell, Smith & Campbell, 1963) and in sheep (Fell, Campbell & Boyne, 1964). This is evidence that some integration of physical capacity with long term regulation of food intake can occur.

In the experiments of Montgomery & Baumgardt (1965a) it was shown that DE intake remained comparatively constant as the DE content of the diet rose above about 2.6 kcal/g DM. Subsequent work by Dinius & Baumgardt (1970) confirmed these results and the authors pointed out that their results were obtained with animals which were past their rapidly growing phase. Baumgardt & Peterson (1971) extended the observations to young lambs with an estimated energy demand of 266 kcal DE/kg $^{0.75}$/24 h., compared with an estimated demand of 206 kcal made with older lambs by Dinius & Baumgardt (1970). Their conclusions were that diets must contain at least 2.9 kcal DE/g DM for young lambs and 2.6 kcal/g DM for older lambs for energy demand to be satisfied.

Relationships between the voluntary intake of DM, DE concentration of the diet, and energy demand are illustrated in Fig.1.2 (from Bines, 1971). The relationships are shown for ruminant animals requiring a lower (R1) and a higher (R2) level of DE to maximize their production. M is the DE requirement for maintenance and CM, C1 and C2 are the minimum DE concentrations in the diet that will enable these various requirements to be met, and hence they are the points at which the mechanism of regulation of food intake changes in nature from physical to metabolic.

1.3.4 Factors involved in the control of voluntary food intake by physical means

Factors to be considered are the size and capacity of the alimentary organs, and of the abdominal cavity, alimentary tract fill, the rate at which the alimentary tract load is reduced; which is a function of the rate of digestion, rate of absorption, and rate of breakdown of food particles, particularly in the reticulorumen, rate of passage of food residues and motility of the alimentary organs.

All compartments of the alimentary tract can be considerably stretched when removed from the animal (Mäkelä, 1956) and the animal's ability to fill the alimentary organs with food is probably limited by the capacity of the body cavity rather than the organs themselves. The space occupied by the alimentary tract is limited to varying degrees by the uterus and abdominal fat, and Tayler (1959) obtained significant negative relationships between the amount of abdominal fat and faecal DM output in grazing cattle, suggesting that the degree of fatness of the animal can have an effect in physically limiting food intake. A reduced food intake by ewes during the last weeks of pregnancy was observed by Reid (1961), the effects being greater with ewes carrying twins. The experiments of Forbes (1968) are of considerable interest in this context, where photographic sections of frozen ewes showed extensive upward displacement of the ventral rumen by the uterus, as pregnancy advanced. The voluntary intake of the ewes fell in the latter stages of pregnancy, but at a rate less than the decrease in the volume of the reticulorumen contents (Forbes, 1970). This discrepancy may be explained by an increase in the rate of passage of food residues, as Graham & Williams (1962) observed a faster rate of passage in sheep in late pregnancy. This would help to offset the increase in the space occupied by the uterus.

Evidence that food intake is limited by physical factors is provided by experiments involving the addition or removal of food materials from the reticulorumen. Removal of swallowed hay as it entered the reticulorumen over the first 3 h. of a meal increased the amount of hay consumed by cows, and the addition of digesta from recently ingested hay resulted in a decrease in the hay consumed (Campling & Balch, 1961). The addition of food or sawdust to the rumen of sheep by Weston (1966) resulted in a compensatory drop in food intake, except on the first day of intraruminal feeding, but the addition of finely ground polyvinyl chloride had a much smaller effect on food intake, which Weston attributed to its rapid passage out of the reticulorumen. The above evidence provides support for a hypothesis of physical limitation of voluntary intake by ruminants receiving roughages, with the existence of a maximum critical level of fill of the reticulorumen which is reached at the end of a period of food consumption, which then presumably signals the end of eating. Further support for the hypothesis is seen with ruminants given diets such as dried grass or hay where they eat to a constant fill of the reticulorumen (Blaxter, Wainman & Wilson, 1961; Ulyatt, Blaxter & McDonald, 1967; Freer & Campling, 1963). In contrast to these results, Campling, Freer & Balch (1961) observed that when cows were given hay or straw ad libitum, they consumed more than twice as much hay as straw. Immediately after the meal the dry weight of the digesta in the reticulorumen was 35% greater with the hay than with the straw. Dry matter as such is probably not a good measure of the space filling characteristics of foods, and factors such as the density of the food and total wet weight of the digesta may be more useful criteria. Using diets with a range of apparent digestibilities fed to lambs, Montgomery & Baumgardt (1965a) observed that the calculated DM fill of the alimentary tract was not constant between diets but was lowest with the diets of lowest apparent digestibility, and Bines & Davey (1970) obtained a significant negative relationship between the total amount of digesta in the reticulorumen of cows after feeding, and the apparent digestibility of the diet. Further evidence for variations in reticulorumen fill following feeding was also provided by Egan (1970), who fed sheep on diets differing in apparent digestibility and protein content. When protein supplements were given via the duodenum, food intake and the amount of digesta in the reticulorumen increased. The amount of digesta in the reticulorumen was greatest with the foods of highest apparent digestibility and crude protein content, and the quantity of digesta increased as intake increased. It was concluded by Egan that the level of fill is not constant between diets, but is influenced by other factors, one being the protein status of the animal.

In further work involving the addition of inert material, or the food itself, or water filled bladders to the reticulorumen of sheep receiving foods of high and low apparent digestibility, Egan (1972) stated that his results indicated that sensitivity to indigestible material can limit the intake of a roughage even though the amount of digesta in the reticulorumen is not necessarily at the maximum physically permissible. He stated that relationships exist between the nutritive value of the diet, the nutrient status of the animal and its ability to accommodate indigestible material. The results reported by Egan (1970, 1972) support the hypothesis that mechanisms exist which override fill, or involve a resetting of the fill threshold at a different level.

If alimentary tract distension, or more particularly distension of the reticulorumen, is important in limiting intake, then factors that will result in a decrease in fill or load will, by providing more space, allow the animal to increase its intake of food. Close positive relationships between the voluntary intake of roughages and their apparent digestibility have been demonstrated by many workers (Blaxter, Wainman & Wilson, 1961; Minson, Harris, Raymond & Milford, 1964) but as apparent digestibility of the ration is only indirectly related to the rate at which the rumen load is reduced, poor relationships between these variables have been observed (Weston, 1967). In addition Baumgardt (1970) has pointed out that the physical form of the diet will affect the relationship and states that the density of the ration and its space-filling characteristics may be important and suggests that foods be expressed in terms of DE per unit volume.

The two avenues for removal of organic matter (OM) from the reticulorumen are by absorption and eructation, and propulsion to the omasum (see Fig.1.3). The higher the OM digestibility in the reticulo-rumen, the more rapidly will OM be removed from the organ, providing other factors remain constant. The voluntary intakes of roughages low in nitrogen can be improved by the addition of nitrogenous compounds, which by increasing the rate of microbial digestion, hasten the removal of OM from the rumen (Campling, Freer & Balch, 1962; Hemsley & Moir, 1963; Weston, 1967). The reverse effect is seen with antibiotics which depress microbial activity and reduce intake (Bell, Whitehair & Gallup, 1951, Oyaert, Quin & Clark, 1951).

The reduction of particle size by mastication, or by presenting the food in a ground form and thus allowing particles to be removed at a greater rate through the small reticulo-omasal orifice, are important factors affecting the rate of removal of OM from the reticulorumen (Fig. 1.3). The significance of rumination has been studied by Pearce & Moir (1964) where muzzling of sheep to prevent rumination increased the retention time of food residues in the reticulorumen. By contrast, the retention time was decreased when a ground roughage ration was fed, instead of a chaffed ration. Evidence that grinding of roughages increases voluntary food intake is provided by Minson (1963), and Campling, Freer & Balch (1963), with some evidence that the increased

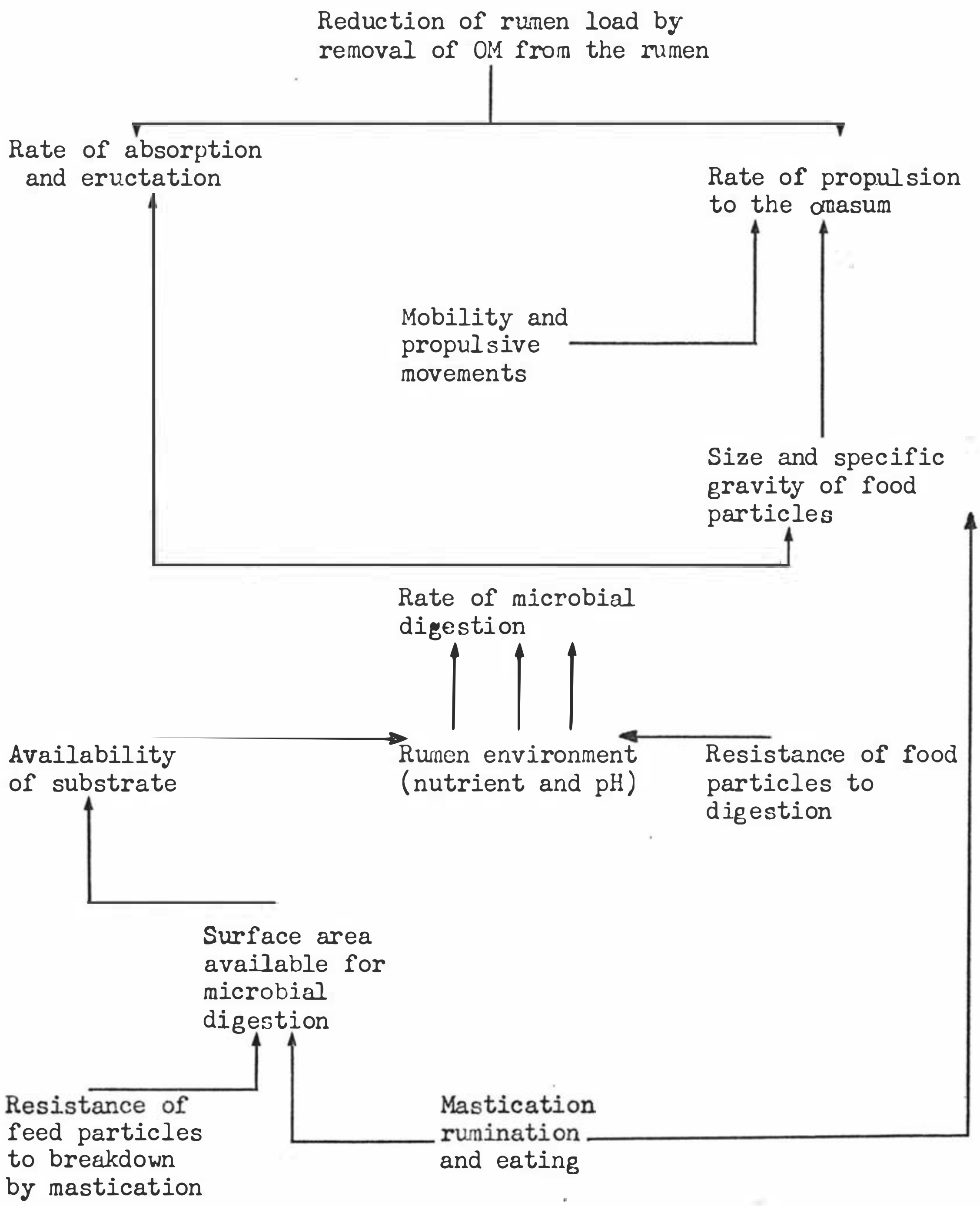

FIG:1.3 Factors affecting the removal of organic matter (OM) from the reticulorumen (adapted from Weston, 1967) intake with grinding is greater with poor foods (oat straw), compared with foods of higher quality (hay and dried grass), (Campling & Freer, 1966; Campling, Freer & Balch, 1963). However, Hogan & Weston (1967) found that the percentage increase in intake of sheep receiving wheaten hay or lucerne hay following grinding was similar, although larger total amounts of the latter food were eaten. As a result of the relationship between voluntary food intake and rate of removal of OM from the reticulorumen, there is an inverse relationship between the retention time of undigested food residues and voluntary intake (Blaxter, Wainman & Wilson, 1961; Campling, 1966b). Causal relationships are not known with certainty, although the grinding of roughages, in that it increases the rate at which food particles leave the reticulorumen, is associated with increased voluntary intake (Minson, 1963).

Most attention has been directed to the reticulorumen, but the capacity of the tract caudal to this organ and its effect on the flow of digesta from the reticulorumen may limit food intake. Distension of the abomasum inhibits contractions of the reticulorumen (Titchen, 1958, 1960) and omasal outflow (Ash, 1962), and thus could be expected to reduce the flow from the reticulorumen. There is evidence to suggest that where the flow of digesta out of the reticulorumen is enhanced by finely grinding roughage, the amount of material in the abomasum and intestines may limit food intake (Campling & Freer, 1966).

With many of the studies relating to the physical capacity of the alimentary tract, conclusions have been based on amounts of DM or OM, and the contribution that the liquid mass makes to fill has been neglected. As water accounts for approximately 90% of the weight of the digesta in the reticulorumen (Reid, Bailey & Glenday, 1967), it could make a considerable contribution to the effects of distension. However, the addition of large volumes of water to the reticulorumen has little effect on food intake (Campling & Balch, 1961) probably because of the rapid absorption and exit of this excess water. This may not be true of water held within the mass of the digesta, but evidence is lacking.

1.3.5 Factors involved in the control of voluntary food intake by metabolic means

As was shown in Fig.1.1 and discussed in section 1.3.2, there is evidence of regulation of food intake in ruminants in proportion to their energy expenditure, where food intake is not governed primarily by the capacity of the alimentary tract to accommodate food residues.

The digestion, absorption, and metabolism of nutrients results in changes in the levels of metabolites in the alimentary tract or body fluids and changes in heat production, which may act as feedbacks, which stimulate or inhibit food intake. Three main theories have been proposed to explain the relationship between food intake and energy expenditure in animals, resulting from metabolic changes. These theories attempt to identify the signals involved and are enumerated as follows:-

1.	the thermostatic theory	)	short-term control
2.	the chemostatic theory	)	of food intake
3.	the lipostatic theory	-	long-term control

The thermostatic theory proposed by Brobeck (1960) was based on observations that the food intake of animals increased in the cold and decreased at high temperatures and that food intake may be controlled by changes in body heat production, with the suggestion that temperature receptors in the anterior hypothalamus stimulate or inhibit feeding. The theory received some support, as far as ruminants are concerned, when Andersson & Larsson (1961) observed that cooling the hypothalamus of goats increased, and warming decreased food intake. The temperature changes at the hypothalamus in these experiments were considered higher than was physiologically possible by Baile (1968), and work by Baile, Mahoney & Mayer (1968); Baile & Mayer (1968) and Dinius, Kavanaugh & Baumgardt (1970) showed that hypothalamic temperature changes were not related to changes in food intake. Baile & Mayer (1968) concluded that temperature changes resulting from the ingestion of food were not important feedbacks in the regulation of food intake. Certainly animals adjust their food intake in response to changes in environmental temperature (eg. Appleman & Delouche, 1958), but the food intake response is probably secondary to a change in energy balance or the rate of heat loss, or both, rather than a response to a change in hypothalamic temperature.

The chemostatic theory proposed by Mayer (1955) is based on evidence that the availability and utilization of glucose acts as a feedback in the control of food intake by monogastrics, although it is not likely to be an important feedback component in ruminants (Baile &

Mayer, 1970) and intravenous infusions of glucose into ruminants do not depress food intake (Manning, Alexander, Kreuger & Bogart, 1959). The possibility that volatile fatty acids (VFA) produced in the reticulo-rumen act as components of a feedback system (chemostatic control) has received considerable attention. The VFAs have several characteristics that make it probable that they play a part in the control of food intake in ruminants. They are an important source of energy to the ruminant and are largely produced in, and absorbed from the reticulo-rumen, and their rates of production and absorption are related to feeding (Simkins, Suttie & Baumgardt, 1965). Intraruminal infusions of VFAs can decrease the voluntary intake of cattle (Rook, Balch & Campling, 1960; Rook, Balch, Campling & Fisher, 1963; Montgomery, Schultz & Baumgardt, 1963) and sheep, (Baile & Pfander, 1966; Ulyatt, 1965; Weston, 1966).

In these experiments acetic acid reduced food intake most consistently, although propionic and butyric acids have also caused reductions. Intravenous infusions of VFAs have given variable results. Thus Dowden & Jacobson (1960) observed that intravenous infusions of acetic and propionic acid into cattle reduced food intake, whereas Holder (1963) found that intravenous infusions of acetate into sheep, which resulted in higher than normal post-prandial blood acetate levels, did not affect food intake. Baile & Mayer (1968) demonstrated that acetate and propionate injections into the rumen of goats were more effective in depressing food intake than were injections of acetate, at the same rate, into the jugular vein. It was suggested that possible receptors were located on the lumen side of the rumen wall for both these acids. The above approach, involving a comparison of the effects of intraruminal and intravenous infusion appears to be a more satisfactory attempt at defining components of the feedbacks and their location. Subsequent work (see Baile & Mayer, 1970), indicated that changes in propionate concentration may be sensed in the portal system as well as in the rumen. Great care is needed in the interpretation of the results of experiments where concentrations of metabolites are infused into animals, as possibly the first sympton of metabolic stress is a depression in food intake.

Hervey (1969) pointed out that it is difficult to see how either the thermostatic or chemostatic theories account for the quantitative accuracy of the regulation of energy balance in the long term. Disturbances of body temperature, or of glucose or other metabolites are shortlived, and are rapidly corrected by specific regulatory mechanisms, and there is no evident means by which past changes can be integrated over a period of time. The long term balance of energy implies a memory system or reference input. This could be supplied by the size of the fat depots. Kennedy (1953) in his lipostatic theory postulated that feedbacks consisting of circulating metabolites, released in proportion to the size of the fat depots of the animal, might be involved in the long term control of food intake and energy balance. In support of this theory, Hervey (1971) stated that the amount of fat in the body provides an integrated record of the total of all past gains and losses of energy, and it is difficult to see what physiological quantity, other than fat depots, could act in this way.

Indirect evidence for the long term control of food intake and changes in the set-point of the reference input is provided by Schinckel (1960) with sheep, and Hutton (1963) with non-lactating cattle, each of whom observed a progressive decline in voluntary intake by their animals until finally food intake was reduced to a level sufficient to maintain these animals in a fat state. However it is possible, as discussed in section 1.3.4, that a reduction in the food intake of fat animals could be brought about by the physical restriction of abdominal fat within the body cavity, although Bines, Suzuki & Balch (1969) observed that the intake of concentrates was reduced in fat compared with thin cattle and it is possible that a lipostatic mechanism as postulated by Kennedy (1953) may have been involved.

An important factor in the validation of the lipostatic theory would be the identification of the satiety signals involved. Plasma free fatty acids (FFA) have been found to be useful predictors of subsequent food intake in lactating sheep (Thye, Warner & Miller, 1970). A reciprocal relationship between FFA and glucose utilization has been observed in humans (Van Itallie & Hashim, 1960), and FFA increase and decrease with feeding, and changes in energy balance. That insulin and growth hormone also play a role has been suggested by Kennedy (1966), but it must be concluded that there is no evidence that any one hormone or metabolite acts as the signal from the fat depots. In conclusion, as Kennedy (1966) suggested, it may be incorrect to see the long term and short term control of food intake as independent systems. What is certain is that the control of food intake is multi-factorial, with no sharp division between one form of control and another, and that the effects cannot be explained by any one mechanism.

1.3.6 Integration of factors controlling voluntary food intake

A hypothetical scheme which summarises some of the components thought to function in the control of voluntary food intake is illustrated in Fig.1.4. It is a modification of the schemes of Baile (1968) and Baumgardt (1970) and is a simplification of a highly complex system. The scheme is based on the assumption that energy balance is the regulated component, with food intake as a component of the control system. Energy balance is determined by the input of energy as food, which is partitioned to various metabolic pathways, and energy output, which is dependent on the physiological state of the animal. A negative energy balance is induced by a decrease in energy intake or an increase in energy output, without a concomitant increase in intake. Provided energy intake is not inhibited by limiting factors such as metabolic disturbances (Krebs, 1966) or sensory factors, (Morgane & Jacobs, 1969) or capacity of the alimentary tract, then food intake increases with an increase in energy output. With the consumption of food, digestion, absorption and metabolism results in physical and metabolic changes in the animal which act as feedback signals, which stimulate or inhibit food intake. The changes that occur and their effect on voluntary intake were discussed in detail in sections 1.3.3 and 1.3.4.

The feedback control system consists of receptors for detection, and a controlling centre (the brain), which also contains a memory or reference element. Feedback inputs resulting from short term and long term signals are relayed to the hypothalamus which integrates the inputs so that energy balance is maintained. A problem of central importance has been to understand the signals involved and their receptor sites. The information is not precise, but a number of theories discussed in section 1.3.5 have been proposed for what is a complex system.

The control of voluntary intake by physical and metabolic means were discussed separately in sections 1.3.4 and 1.3.5 respectively. Whilst it was convenient to discuss these factors separately, as already noted, they are not independent and the statement made by Egan (1970)

"that a complex of interacting physical and metabolic

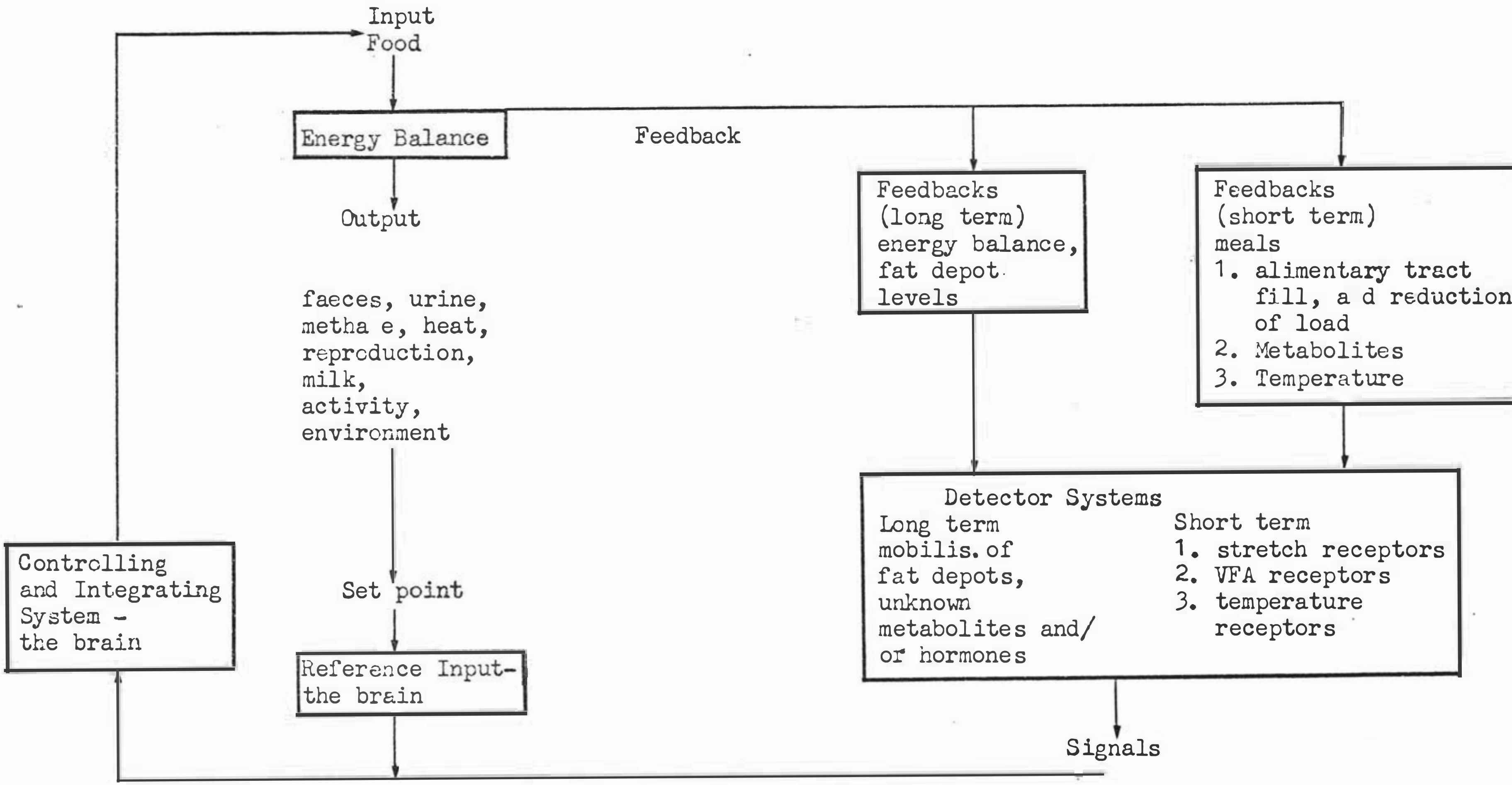

FIG:1.4 A hypothetical scheme showing some of the interrelationships of the system regulating food intake and energy balance in ruminants

> factors may be involved throughout the whole range of diets utilized by ruminants, and that there is not simply a switch-over to metabolic regulation at a point where disposal of indigestible bulk is no longer an embarrassment or a limitation to the total digestible energy intake",

illustrates an important concept that forms the underlying basis of this study.

1.4 INCREASING THE ENERGY EXPENDITURE OF SHEEP BY SHEARING, IN ORDER TO INVESTIGATE FACTORS AFFECTING VOLUNTARY FOOD INTAKE

When sheep are shorn, increases have been observed in heat production, (Armstrong, Blaxter, Graham & Wainman, 1959; Farrell, Leng & Corbett, 1972), fasting heat production, (Farrell & Corbett, 1970) and in heart rate (Webster & Lynch, 1966; Wodzicka-Tomaszewska, 1963). Armstrong, Blaxter, Graham & Wainman (1959) fed their sheep dried grass at three levels; 600, 1200 and 1800 g DM per day. The sheep were closely clipped to give a fleece length of 0.1 cm and heat production increased by 8 to 900 kcal/24 h. at the high level of feeding, 1100 kcal/24 h. at the medium level of feeding, and about 13 to 1400 kcal/24 h. at the low level of feeding. The above values were estimated from graphed results for an environmental temperature of 13°C, which was the temperature used in the experiments described in the following Chapters. Farrell & Corbett (1970) measured fasting heat production of the sheep soon after they were removed from pasture. The maximum increase in fasting heat production after sheep were shorn was 44%, and a return to pre-shearing values was not observed until day 135 following shearing. Heart rate increased immediately after shearing (Wodzicka-Tomaszewska, 1963), which is indirect, if rather imprecise evidence (CSIRO, 1960), that heat production had increased. The above evidence therefore indicates that a considerable increase in energy expenditure occurs when sheep are shorn.

A number of workers have shown that the food intake of sheep increases when they are shorn. Wheeler, Reardon & Lambourne (1963) observed increases in food intake of 42 to 62% following shearing, with sheep grazing pasture. The mean minimum temperature after shearing ranged from 7° to 11°C, the corresponding maximum temperatures being 19 to 20°C. Wodzicka-Tomaszewska (1963) studying sheep fed a diet of hay and a pelleted concentrate mixture, obtained increases in food intake following shearing of 50%, with air temperatures ranging from about 7 to 12°C. In neither of the above experiments were unshorn control sheep used. In a further experiment, this time using unshorn control sheep as well as shorn sheep, Wodzicka-Tomaszewska (1964) obtained increases in food intake (hay and pelleted concentrates) of 19 to 43% (mean 32%) at environmental temperatures of 10° to 13°C. In all of these studies, the diets could be described as being of good quality, and limitations of food intake by physical factors or sub-optimal levels of protein may not have been expected to be of importance. In none of these experiments were measurements made which would help to explain mechanisms controlling food intake.

Conrad, Pratt & Hibbs (1964) concluded that when the DM digestibility of the diet was greater than about 67%, the primary determinant of food intake was the physiological state of the animal, so that an increase in energy output would result in a concomitant increase in voluntary food intake. The considerable increases in voluntary intake observed by Wheeler, Reardon & Lambourne (1963) and Wodzicka-Tomaszewska (1963) when sheep were shorn is compatible with the findings of Conrad, Pratt & Hibbs (1964).

When the present series of experiments were begun in 1968, there had been no studies made on changes in food intake of sheep receiving food of low apparent digestibility, following shearing. With this type of food, voluntary intake would be limited mainly by physical means, such as the rate at which food residues are removed from the reticulo-rumen, so that the scope for increasing food intake might be expected to be small, in response to an increase in energy expenditure, following shearing.

Hypotheses based on evidence discussed in the review, are introduced in the next section. These hypotheses form the basis of the series of experiments, reported in subsequent Chapters.

1.5 THE MAIN OBJECTIVES OF THE THESIS AND EXPERIMENTAL PATTERN

The main objectives of the experiments to follow were to examine the following hypotheses:-

1. that an increase in energy expenditure, induced by shearing, would result in a minimal increase in the voluntary intake of

of sheep receiving food of low apparent digestibility, and that the intake of sheep receiving food of high apparent digestibility would increase to meet the increase in energy expenditure

2. that a change in the physiological state of sheep, induced by shearing, would affect values such as the retention time of food residues and amounts of food residues in the alimentary tract, concerned with the physical regulation of voluntary food intake.

The shearing of sheep was thus used as a convenient method to change the animal's energy demand readily, and to use this as a model to investigate relationships between the DE concentration of diets and voluntary food intake. A number of questions were raised and problems encountered, as the work progressed, and the experiments were designed in an attempt to answer some of these questions as they arose. In the experiment reported in Chapter 3, the voluntary intakes of sheep receiving chopped hay or a concentrate-oat husk mixture were compared, before and after shearing. The day to day variation in the voluntary intakes of the sheep receiving the concentrate-oat husk mixture was so high that its use was abandoned, and was replaced in subsequent experiments (Chapter 4 and 5) by dried grass, as the food of high DE concentration.

The results of further work suggested that the amount of digesta in the reticulorumen may not have been the main factor limiting the voluntary intake of chopped hay. Rather it may have been the rate at which food residues were able to leave the reticulorumen, so that in some of the experiments reported in Chapter 4, the change in voluntary intakes of sheep receiving ground hay were measured, before and after shearing. It was noted in some of the experiments that the voluntary intakes of unshorn sheep receiving dried grass decreased with time, and it was postulated that the body condition of the animals may have been associated with this effect. Accordingly in Chapter 5, an experiment is reported which compared the changes in voluntary intake when fat and thin sheep receiving dried grass were shorn.

In most of the experiments dealing with the effect of shearing in changing voluntary intake, it was difficult to reconcile the extent of these changes with published results on the increase in heat production that occurs when sheep are shorn. For this reason, experiments were carried out (Chapter 6) to determine the change in heat production following shearing with sheep held under the same conditions as those in the main experiments on intake.

Following the completion of much of this work, two papers have been published with similar objectives by Weston (1970), and Minson & Ternouth (1971). Weston used a wheaten hay of low apparent digestibility and varied ambient temperatures, whereas Minson & Ternouth used hays of different apparent digestibilities, with fluctuating ambient temperatures. In the series of experiments that follow, ambient temperatures were held constant at 13°C and various measurements, not carried out by the above workers, such as reticulorumen fill, apparent digestibility in the reticulorumen, retention time of food residues, eating behaviour and responses of fat and thin sheep following shearing, were studied.

Whilst the main theme of the work in this thesis was concerned with factors controlling food intake, a series of experiments (Chapter 2) were conducted with the objective of comparing methods of measuring the retention time of food residues in the alimentary tract of sheep. This work was considered necessary because of the projected intensive use of this measurement in the main intake experiments.

CHAPTER 2

A COMPARISON OF METHODS OF MEASURING THE TIME OF RETENTION OF FOOD RESIDUES IN THE ALIMENTARY TRACT OF SHEEP

S U M M A R Y

Retention times of food residues in the alimentary tract of sheep were compared using three markers, Mn, ^{144}Ce, and food stained with safranine.

The foods used were chopped hay and ground hay, chopped dried grass, and a concentrate-oat husk mixture. The sheep were fed both ad libitum and at restricted levels in the various experiments.

When chopped hay and dried grass were fed ad libitum, mean retention times with ^{144}Ce were significantly less ($p < 0.05$) than those obtained with stained food. When the above foods were fed at restricted levels, there were no differences in mean retention times between the two methods. In the one experiment with ground hay fed at restricted levels, there were no differences in retention times between food treated with ^{144}Ce and stained food.

With the concentrate-oat husk mixture, mean retention times with ^{144}Ce were considerably less than those obtained with stained food. Possible reasons for this difference were examined, the most likely was the migration of ^{144}Ce from particulate matter into solution.

The variation in mean retention times within and between sheep was less with ^{144}Ce than with stained particles and was an important factor in the decision to use ^{144}Ce in subsequent experiments. The rapidity with which retention times can be determined using ^{144}Ce is an advantage where resources are limited, although the need for safety precautions limits its wide application.

Because of variations in background levels, Mn was unsatisfactory as a marker.

2.1 INTRODUCTION

In studies of the utilisation of foodstuffs by ruminants, information on the flow of particulate matter along the alimentary tract is of value in the interpretation of factors affecting voluntary intake, in that it is related to the reduction of alimentary tract fill.

The most widely used method for determining the flow of particulate matter is that described by Balch (1950) where stained foods were fed, and the stained particles in sieved faeces were counted. The method is time consuming, and Ellis & Huston (1967) have questioned the validity of results where an extractive process,involving the sieving of faeces, is used in the counting of the stained particles. The use of a radioactive marker was therefore considered in the hope that it would add convenience and precision to the measurement of the retention time of food residues in the alimentary tract of sheep.

It is necessary that the marker used must be closely associated with the food residues it is marking, and that it should not be absorbed from the alimentary tract. Radiocolloidal concentrations of radiocerium (^{144}Ce) adsorb strongly onto particulate matter, (Ellis, 1968; Ellis & Huston, 1968), and is not absorbed to any extent from the alimentary tract, according to Garner,Jones & Ekman (1960), who first suggested its use as a marker. Huston & Ellis (1968), and Ellis & Huston (1968) evaluated ^{144}Ce as a marker in digestion studies for ruminants, and their *in vivo* and *in vitro* results suggested that it remained in close physical association with indigestible food residues during passage through the alimentary tract. This close association was maintained by continued adsorption to indigestible particles or by readsorption to other particles.

A disadvantage of radioactive markers is the care needed in their handling and disposal. An alternative marker that would remain closely associated with indigestible food residues in the alimentary tract and which could be readily and precisely determined in faeces, was investigated. Potassium permanganate has a strong affinity for lignin (Van Soest & Wine, 1968) and it was considered that the Mn in this compound might prove useful as the alternative marker.

A number of experiments were therefore carried out comparing the mean retention times of various foods stained with safranine or treated with ^{144}Ce or potassium permanganate (Mn).

2.2 MATERIALS AND METHODS

2.2.1 Plan of experiments

The experiments carried out to compare mean retention times of food residues in the alimentary tract of sheep, using various markers, are summarised in Table 2.1. The experiments in which feeding was *ad libitum* were part of a number of investigations into the effects of shearing on the voluntary food intake of sheep. In these experiments there were large variations in voluntary food intake between sheep and in experiments 1(a), 2 and 4(a) food intakes increased in Period 2 when the sheep were shorn. Although the effects of shearing on food intake were examined in experiments 1(c) and 3(a), mean retention times, obtained by the different methods, were determined in the pre-shearing period only (Period 1).

TABLE 2.1 Plan of the experiments to compare different methods of measuring the retention time of food residues in the alimentary tract of sheep

Expt no.	Food	No. of sheep	No. of periods	Feeding level	Markers compared
1 (a)	Chopped hay	3	2	*ad libitum*	^{144}Ce, S.F.,* Mn
1 (b)	"	3	1	restricted	^{144}Ce, S.F., Mn
1 (c)	"	4	1	*ad libitum*	^{144}Ce, S.F.
1 (d)	"	3	3	restricted	^{144}Ce, S.F., PEG
2	Ground hay	3	2	restricted	^{144}Ce, S.F.
3 (a)	Dried grass	4	1	*ad libitum*	^{144}Ce, S.F.
3 (b)	" "	3	2	restricted	^{144}Ce, S.F.
4 (a)	Concentration-oat husk mixture	3	2	*ad libitum*	^{144}Ce, S.F., Mn
4 (b)	" "	3	1	restricted	^{144}Ce, S.F., Mn
4 (c)	" "	3	1	restricted	^{144}Ce, S.F.

* S.F: Food stained with safranine

To further assist in the interpretation of results, experiments with unshorn sheep, and independent from the intake experiments were also carried out at restricted levels of intake, so that food intake was held as constant as possible between sheep. These experiments (Expts 1(d) and 3(b)) were extended into three and two periods respectively with food intakes held constant between sheep and periods. The data on mean retention time were analysed by analysis of variance for differences between sheep, methods, and where applicable, periods. The foods used were chopped hay and ground hay, chopped dried grass, and a pelleted concentrate-oat husk mixture (barley-meal 60%, linseed meal 15% and oat husks 25%), and were those used in the main experiments investigating the effects of shearing on voluntary intake.

In an effort to explain the large differences in mean retention times between ^{144}Ce and the stained food methods, when the concentrate-oat husk mixture was used, the fresh faeces collected in Expt 4(c) were separated into fine and coarse particle fractions through wire mesh sieves, using a jet of water. Fine particles were those passing through a sieve aperture of 0.14 mm square, and coarse particles were those retained by a sieve with apertures 0.42 mm square. The resulting fractions were dried and assayed for radioactivity.

To obtain an indication of the extent to which ^{144}Ce remained in association with food residues, samples of the hay and concentrate-oat husk mixture, treated with ^{144}Ce, were incubated with rumen contents using the in vitro digestibility technique of Tilley & Terry (1963). After 48 h. incubation with rumen liquor at pH 6.8 to 7.0 (Stage 1), the samples were centrifuged at 3000 g for 15 min. and filtered. The supernatants were then assayed for radioactivity. Supernatants were also assayed after a further 48 h. of acid-pepsin incubation at a pH of approximately 1.4 (Stage 2). Eight Stage 1 and eight Stage 2 incubations were carried out for each food.

To examine the possibility that centrifugation may have influenced the movement of ^{144}Ce into the liquid phase, 12 Stage 2 incubations were carried out with hay and with the concentrate-oat husk mixture treated with ^{144}Ce, and centrifugation and filtration were compared with filtration alone in the preparation of the samples for radioassay.

2.2.2 Animals

Castrated Romney male sheep (wethers) with rumen fistulae were used in all experiments. The sheep were kept in individual crates in controlled temperature rooms at 13°C ± 1°C. Water was available at all times and 5 g of a commercial vitamin and mineral mixture was given to the sheep daily.‡ The sheep received regular treatment with anthelmintics. Where sheep were fed *ad libitum* they were fed twice daily; approximately 60% of the day's food at 0900 h. and 40% at 1600 h. The sheep fed at restricted levels of intake were offered food once daily at 0900 h. The apparent digestibility of the DM of the foods was determined by total collection of faeces over 14 days where sheep were fed *ad libitum* or over 10 days where food was restricted.

2.2.3 Markers

Foods for staining were treated with a 0.01% solution of safranine, which was fixed with hot water at approximately 95°C and then repeatedly washed with hot water. Samples of faeces were homogenised in a blender and stained particles were counted using the method of Balch (1950). Radiocerium (^{144}Ce solution of cerous chloride in IN HCl, Radiochemical Centre, Amersham, England) was adsorbed on to samples of foods using the method of Ellis & Huston (1968). The dose rate was approximately 15 µ Ci. ^{144}Ce per sheep. Samples of faeces were dried, ground (2 mm sieve), and prepared for counting by filling tubes to a similar height and, as far as possible, to a similar degree of compaction. The faecal samples were counted in a Phillips gamma radiation counter, equipped with a well-type crystal. Foods for treatment with Mn were steeped in a solution of $KMnO_4$ for 2 h. and surplus $KMnO_4$ removed with copious washings with water. Manganese was extracted from the faeces using the method of Timperley, Brooks & Peterson (1970) and was measured by atomic absorption spectrophotometry. Separate samples of the foods were treated with the markers. In Expt 1(d) samples of fresh faeces (approximately 40 g) were mixed with 150 ml distilled water in a blender and the concentration of polyethylene glycol (PEG) determined by the turbidimetric method of Hydén (1956) with modifications by Smith (1959) and Ulyatt (1964).

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‡ The vitamin and mineral mixture supplied the following (/sheep/day): 3,000 i.u. vitamin A, 300 i.u. vitamin D_3, 60 i.u. vitamin E, 0.6 g Mg, 0.04 g Fe, 0.07 g Zn, 0.05 g Mn, 0.1 mg I_2, 0.3 mg Co, 2.5 g bone flour, 1.5 g NaCl.

2.2.4 Administration of markers and expression of results

Approximately 40 g of each of the treated foods were administered via the rumen fistulae and were well mixed with the rumen contents. In Expt 1(d) a dose of approximately 10 g PEG (M.W.4000) was dissolved in 250 ml water and was administered via the rumen fistulae and mixed with the digesta.

Samples of faeces were collected 10 h. after marker administration, then subsequently at 4 h. intervals on the first day, 6 h. intervals on the second day, followed by 12 h. intervals for the remainder of the collection period. The amount of marker (number of coloured particles, counts/min for ^{144}Ce, or mg of PEG) appearing in the faeces between the time of giving the stained food and any subsequent time was expressed as a percentage of the total number of units excreted during a particular experiment. The percentage figures were then plotted against time to obtain a cumulative excretion curve. Mean retention times were calculated from the cumulative curves by the method of summing excretion times at 10% intervals between the 5% and 95% times and dividing by 10, as proposed by Castle (1956).

2.3 RESULTS

Comparisons of the mean retention times for different markers, estimated with sheep receiving chopped hay and ground hay, are summarised in Table 2.2. In Expt 1(a) and 1(c), (ad libitum feeding), mean retention times obtained with food treated with ^{144}Ce were significantly less ($P < 0.05$) than times obtained with stained food. Differences between periods in mean retention times for both methods were highly significant ($P < 0.01$) in Expt 1(a), the shorter times in Period 2 being associated with an increase in DM intake of the sheep following shearing. Food intakes varied between sheep in both Expt 1(a) and 1(c) but despite this, differences in mean retention times between sheep were not significant. There were no significant differences in mean retention times between ^{144}Ce treated and stained hay in Expts 1(b) and 1(d)(restricted feeding), but both differed significantly ($P < 0.01$) from the mean retention times for Mn in Expt 1(b) and PEG in Expt 1(d).

Despite the similar DM intakes, both between sheep and periods in Expt 1(d), differences in mean retention times between sheep with both methods were highly significant ($P < 0.01$). In this experiment one sheep

TABLE 2.2 Comparison of mean retention times using different markers by sheep receiving varying amounts of chopped hay (Expt 1 a,b,c,d) and ground hay (Expt 2)

Expt	Period	Mean retention time (h.) ^{144}Ce	Stained food	Mn	PEG	S.E.means of methods	Mean intake (g DM/24 h.)
1 (a)	1	36.9	44.5	33.9			749
	2	31.7	35.3	27.5			1085
	Mean	34.3^{ABa}	39.9^{Bb}	30.7^{Aa}		1.5	
	Coeff.of Var	12.2	15.0	18.4			
1 (b)		40.0^{a}	40.3^{a}	53.8^{b}		2.5	1001
1 (c)		36.4^{a}	44.9^{b}			1.3	913
1 (d)	1	48.4	47.4		32.7		652
	2	49.3	48.0		32.3		589
	3	49.1	50.3		31.1		619
	Mean	48.9^{a}	48.5^{a}		32.0^{b}	0.7	
	Coeff.of Var	11.6	10.1		6.9		
2	1	40.7	34.0				652
	2	39.5	50.5				661
	Mean	40.1^{a}	42.3^{a}		1.7		
	Coeff.of Var	13.6	23.2				

The Coefficients of variation includes sheep and period variation

Means with dissimilar superscripts are significantly different, upper case ($P < 0.01$) lower case ($P < 0.05$)

had consistently higher retention times than either of the other two sheep with both ^{144}Ce and stained feed, in all periods. The retention times of the three sheep were similar with PEG used as a marker, resulting in a significant Sheep X Method interaction, ($P < 0.05$). Results using Mn in Expt 1(a) were in reasonable agreement with the other two markers, but in Expt 1(b) retention times using Mn showed considerable divergence from those obtained using ^{144}Ce or stained food. Further investigation showed that diurnal variations occurred in background levels of Mn in both food and faeces and limited its usefulness as a marker.

With ground hay (Expt 2, Table 2.2) there were no significant differences between mean retention times for methods, but differences between periods were significant ($P < 0.05$) despite the similar DM intakes between periods. A significant Methods X Period interaction ($P < 0.05$) was observed largely because of the unexplained low retention times obtained in Period 1 with the stained food, but not with the hay treated with ^{144}Ce. Retention times using ^{144}Ce were more consistent throughout the experiment, with coefficients of variation of 13.6 and 23.3% for ^{144}Ce and stained feed respectively.

Results of the experiments using dried grass are summarised in Table 2.3. Mean retention times using ^{144}Ce were significantly less ($P < 0.05$) than those obtained with stained food in Expt 3(a), but when the comparisons were repeated (Expt 3(b)) with the dried grass fed at a constant intake (restricted) over two collection periods, retention times with ^{144}Ce were higher than those obtained with stained feeds, although the differences were not significant. Results using ^{144}Ce were less variable (see Table 2.3). The sheep that had high retention times in Expt 1(d) also gave high values in Expt 3(b) with ^{144}Ce, but unlike the earlier experiment, high retention times were not obtained with this sheep with stained food.

Results using the concentrate-oat husk mixture are summarised in Table 2.4. In all experiments, mean retention times obtained with the stained concentrate-oat husk mixture were considerably longer than either the values obtained with ^{144}Ce or with Mn. In Expt 4(a), retention times using the stained food in Period 1 were not obtained because of secondary staining. Retention times with fine and coarse faecal particles from food treated with ^{144}Ce did not differ from each other, or to any extent, from the times obtained with unsieved faeces (see Table 2.4).

TABLE 2.3 Comparison of mean retention times using radiocerium and stained food by sheep receiving varying amounts of chopped dried grass

Expt	Period	Mean retention time (h.) ^{144}Ce	Stained food	SE of means of methods	Mean intake (g DM/24 h.)
3 (a)		34.3^{a}	44.0^{b}	1.7	1092
3 (b)	1	56.1	48.1		659
	2	57.5	51.9		667
	Mean	56.8^{a}	50.0^{a}	2.7	
	Coeff. of Var.	10.8	16.2		

Means with dissimilar superscripts are significantly different ($P < 0.05$)

TABLE 2.4 Comparison of mean retention times using different markers by sheep receiving varying amounts of a concentrate-oat husk mixture

Expt	Period	Mean retention time (h.) ^{144}Ce	Stained Food	Mn	SE of means of methods	Mean Intake (g DM/24 h.)
4 (a)	1	55.4	N.D.	63.6		1161
	2	31.6^{A}	79.3^{B}	35.0^{A}	5.2	1647
	Mean	43.5		49.3		
4 (b)		51.6^{A}	88.6^{B}	58.8^{A}	3.6	1033
4 (c)		78.7	121.0			515
	Fine Particles	82.2				
	Course Particles	81.0				

Means with dissimilar superscript are significantly different

Upper case ($P < 0.01$) Lower case ($P < 0.05$)

N.D. = not determined

Results obtained when ground hay and the concentrate-oat husk mixture treated with ^{144}Ce were incubated with rumen liquor are shown in Table 2.5. The results show that there was considerable movement of ^{144}Ce from particulate matter to the supernatant with hay, and an even greater movement with the concentrate-oat husk mixture during the Stage 2 incubation. The comparison between centrifugation and filtering, with filtering alone, in the preparation of samples is also summarised in Table 2.5.

TABLE 2.5 The percentage radiocerium in the supernatant following in vitro incubation of a concentrate-oat husk mixture or ground hay, treated with ^{144}Ce

	% ^{144}Ce in the supernatant			
	Stage 1 incubation		Stage 2 incubation	
	Hay	Concentrate-oat husk mixture	Hay	Concentrate-oat husk mixture
	1.1	2.4	24.6	41.0
Filtered only			18.5 $\pm$ 0.9	32.9 $\pm$ 1.3
Centrifuged + filtered			22.4 $\pm$ 0.8	38.9 $\pm$ 1.6

Highly significant differences ($P < 0.01$) were obtained between the two methods of separation with the percentage radioactivity being lower in the samples that were filtered only.

Mean digestibilities for the chopped hay, ground hay, dried grass and the concentrate-oat husk mixture were 56.6, 57.6, 76.4 and 69.6% respectively.

2.4 DISCUSSION

The results of these experiments provided evidence that ^{144}Ce could be used as a marker to determine the mean retention time of food residues in the alimentary tract of sheep. Presumably because of variations in the Mn content of the feedstuffs used, duirnal variations in background levels of Mn in the faeces reduced the accuracy of the results obtained and made their interpretation difficult. For these reasons Mn was considered an unsatisfactory marker for the particular foods used.

In two experiments with chopped hay, mean retention times found with ^{144}Ce were less than those obtained with stained food. Both of these experiments involved ad libitum feeding. When intakes of chopped hay were kept constant there were no differences in mean retention times between ^{144}Ce and stained food. A similar situation occurred with dried grass in that mean retention times obtained with ^{144}Ce were lower than those with stained food when food was given ad libitum, but there were no differences when food intake was kept constant. The evidence obtained in the experiments where food intake was restricted, with both chopped hay and dried grass, and where there was good agreement between methods, were reinforced by repetition in two or more periods. In one experiment with ground hay there was close agreement in mean retention times between ^{144}Ce and stained feed, but individual retention times derived from the use of stained food varied widely between sheep and periods.

Lower mean retention times obtained with ^{144}Ce compared with stained food might be explained on the basis that some of the ^{144}Ce may have entered the liquid phase and therefore flowed at a faster rate than the particulate matter. That this may have occurred is shown in the results obtained in Expt 1(d) where mean retention times for PEG, which moves with the liquid phase, were considerably less than those obtained with ^{144}Ce or stained food. The evidence obtained from the incubation studies using ground hay or the concentrate-oat husk mixture showed that appreciable amounts of ^{144}Ce moved into the liquid phase in the Stage 2 incubation. However, the acid conditions of Stage 2 are akin to those found in the abomasum and movement of ^{144}Ce into the liquid phase at this stage may have had a small effect on mean retention times. The method of incorporating markers with the foods may also have been a factor influencing mean retention times. Food for staining is subjected to repeated washings with hot water to avoid the possibility of secondary staining. This results in the loss of small particles and soluble material from the food. The ^{144}Ce was incorporated by steeping the food in a solution containing ^{144}Ce at room temperature for 30 min, followed by drying, with a minimum loss of material. It is possible that the greater mean retention times observed in some experiments with stained food may have been caused by the slower passage of coarser more insoluble material resulting from the preparation process. None of the above observations explain why there were no differences between ^{144}Ce and stained food in the experiments where intakes were restricted.

Mean retention times obtained with ^{144}Ce were invariably well below those with stained food in the experiments where the concentrate-oat husk mixture was fed. The technique used to determine the extent of labelling or staining in faecal samples varies greatly between the two methods, and was thought to be a source of variation. Thus the activity of ^{144}Ce is determined on the complete range of particles in faeces, whereas the sieving technique used to count stained particles, means that the smaller particles are not included in the determination. With the concentrate-oat husk mixture, the stained particles available for counting consisted almost solely of the oat husk fraction of the food. The work of Ellis & Huston (1967) showed that sieve size was important in determining the number of coloured particles in faecal samples. However this possibility was not supported by the evidence obtained in Expt 4(c) where mean retention times for fine and coarse particles were similar to each other, and to the unsieved faeces. Movement of ^{144}Ce into the liquid phase was much greater with the concentrate-oat husk mixture than with hay, and appears to be the most likely factor contributing to the large differences in mean retention times between the ^{144}Ce and stained feed methods, particularly with the concentrate-oat husk mixture.

The apparent digestibility of the foods did not appear to be a factor contributing to differences between the methods as best agreement was obtained with the hays which were of low apparent digestibility and with the dried grass of high apparent digestibility. Miller & Byrne (1970) observed that an average of 5% of ^{144}Ce was removed from ingesta by repeated washing and centrifugation. Ellis & Huston (1968) noted that excretion curves were almost identical for ^{144}Ce

initially absorbed onto hay or starch. This indicated that the ingesta particulate matter onto which the ^{144}Ce was absorbed following its release from starch, flowed through the tract in a similar way to the ^{144}Ce originally absorbed onto hay particles. In the present experiment the evidence suggests that the extent of binding of ^{144}Ce onto food residues was in fact less than that observed by Miller & Byrne (1970) and Ellis & Huston (1968).

Because of this and the possibility of secondary labelling of food residues from several meals, the results would not correspond to retention times as determined by the stained particle technique of Balch (1950). There is no reason why the stained particle technique, as used in the present experiment, would give a more valid measure of retention times than would ^{144}Ce, particularly as soluble material and small particles would be lost to a greater extent in the preparation of stained food compared with the food treated with ^{144}Ce.

The variation in mean retention times within and between animals was less with ^{144}Ce than with the stained particles and was considered an important factor in the decision to use ^{144}Ce in the experiments described in the following chapters. In addition the determination of mean retention times with ^{144}Ce can be carried out rapidly, and in the experiments to follow, these values could not have been determined as frequently, with the resources available, if the stained particle technique had been used. For safety reasons, additional care is needed in the use of ^{144}Ce, which limits its wide application, although the use of neutron activation analysis (Olbrich, Martz, Vogt & Hilderbrand, 1971) would overcome this problem.

CHAPTER 3

THE EFFECT OF SHEARING ON VOLUNTARY FOOD INTAKE, AND ON THE DIGESTION OF A PELLETED CONCENTRATE-OAT HUSK MIXTURE OR CHOPPED HAY FED TO SHEEP

SUMMARY

1. Eighteen Romney wethers receiving either a concentrate-oat husk mixture or chopped hay were used to study the effects of shearing on voluntary food intake.

2. There was a significant increase in dry matter intake ($P < 0.10$) of the sheep receiving the concentrate-oat husk mixture over the week when the response to shearing was at a maximum, but there was no significant increase in digestible energy intake following shearing. Variability in food intake within sheep, between weeks was high and limited the value of the results obtained, with the concentrate-oat husk mixture.

3. A highly significant increase ($P < 0.01$) in the dry matter intake of sheep receiving chopped hay occurred following shearing. Over the week of maximum response following shearing, the dry matter intake increased by 27%, compared with the pre-shearing values. The apparent digestibility of the chopped hay was depressed by approximately 5 percentage units following shearing. Digestible energy intakes of the sheep receiving the chopped hay were depressed in the first week following shearing. This was followed by an increase in digestible energy intake, which reached significance ($P < 0.05$) at the time of maximum response. The sheep receiving the chopped hay lost weight at a faster rate following shearing, which indicated that the increase in digestible energy intake was insufficient to meet the greater energy demands of the post-shearing period.

4. It was also found with six rumen fistulated sheep that: (i) there was less DM ($P < 0.01$) in the reticulorumen of the sheep fed chopped hay, compared with those receiving the concentrate-oat husk mixture (ii) there was a significant increase ($P < 0.05$) in the amount of DM in the reticulorumen of the sheep receiving

chopped hay, following shearing (iii) there was a greater amount of wet digesta in the reticulorumen of the sheep fed chopped hay compared with those receiving the concentrate-oat husk mixture (iv) retention times of food residues were lower following shearing with both foods (v) the total amount of DM digested in the reticulorumen was considerably higher with the sheep fed the concentrate-oat husk mixture compared with those receiving the chopped hay, but the amount of DM passing from the reticulorumen and voided as faeces was similar for both foods, with an increase in both these values following shearing (vi) the results from intraruminal feeding of the two foods indicated that palatability was probably unimportant in affecting voluntary food intake in this experiment (vii) the total time spent chewing was longer for the sheep receiving chopped hay than those receiving the concentrate-oat husk mixture.

Indications from the results were that physical factors appeared to limit the intake of chopped hay, although the increased intake which occurred after shearing indicated that metabolic factors were probably involved. The controlling factor with chopped hay did not appear to be the amount of DM in the reticulorumen, but may have been the amount of wet digesta, and the rate at which dry matter was able to pass from the reticulorumen. The possibility that the voluntary intake of sheep receiving chopped hay may have been limited partly by oropharyngeal mechanisms, and the protein level of the diet, was discussed.

The results obtained on the changes in voluntary intake of sheep receiving the concentrate-oat husk mixture were inconclusive, because of the variability of the intake data, and the small number of sheep used.

3.1 INTRODUCTION

The objective of the experiment described in this Chapter was to carry out a preliminary examination of the hypotheses proposed at the conclusion of the review of literature (Section 1.5). This was achieved, for the first hypothesis, by measuring the change in voluntary food intake when sheep receiving two foods, differing in apparent digestibility, were shorn. The foods offered were chopped hay or a concentrate-oat husk mixture.

To examine the second hypothesis, measurements concerned with the physical control of food intake were obtained before and after the sheep were shorn. These were the amount of digesta in the reticulorumen, apparent digestibility of the foods in the reticulorumen, and retention time of food residues. Measurements were also made of the feeding behaviour of the sheep and their respiration rates, before and after shearing, and the response in terms of a change in voluntary intake to the intraruminal addition of diets.

3.2 MATERIALS AND METHODS

3.2.1 Plan of experiment

Eighteen, 18-month old Romney wethers were held in crates in controlled temperature rooms at an ambient temperature of $13^{o} \pm 1^{o}C$. Six of the sheep were fitted with rumen cannulae (internal diameter 5 cm) and the remainder of the sheep were left intact. Each of the above categories of sheep were divided at random into two groups and were fed either a pelleted concentrate-oat husk mixture or chopped pasture hay. A training period of one month for the intact sheep, and two months for the fistulated sheep, in the crates, was followed by two weeks *ad libitum* feeding (Period 1), when the voluntary intakes of all sheep were recorded. The apparent digestibility of the foods, retention times of food residues, the amount of digesta in the reticulorumen, feeding behaviour and respiration rates were determined with the fistulated sheep during this period. All fistulated sheep were then shorn and continued receiving their diets *ad libitum* for a further four weeks (Period 2). At the same time, six of the intact sheep were shorn and six were left unshorn as controls, and feeding continued as for the fistulated sheep. The detailed measurements made in Period 1 were repeated in the last two weeks of Period 2, with the fistulated sheep.

At the completion of the shearing experiment, the effects of intraruminal feeding of 180 g dry matter (DM) of either the concentrate-oat husk mixture or chopped hay on the voluntary intake of the fistulated sheep were studied. Intraruminal feeding was carried out over six consecutive days.

3.2.2 Diets and management

The composition of the pelleted concentrate-oat husk mixture was (in parts), ground barley 60, linseed meal 15 and oat husks 25. The hay was coarsely chopped through a hammer mill with a 5 cm screen.

All sheep received 5 g of a vitamin and mineral mixture (see Section 2.2.2 for details) once daily, and were treated with anthelmintics at regular intervals. Water was freely available.

3.2.3 Voluntary intake

The sheep were fed twice daily; approximately 60% of the day's food at 0900 h. and 40% at 1600 h. Samples of the food and food refusals were taken daily and were dried at 90°C for 24 h. The amount of food offered was adjusted so that the refused portion was about 15% of the amount offered. The digestible energy (DE) intakes of all sheep were calculated using the digestibility data determined directly for the fistulated sheep.

3.2.4 Live weight and fleece length after shearing

The sheep were weighed before feeding in the morning; at the beginning of the experiment, on the day they were shorn, and at the end of the experiment. Liveweights included the weight of the fleece, as the control sheep were not available for shearing at the end of the experiment. The length of the wool remaining after shearing was measured on each sheep at nine points, three on the dorsal mid-line and three on each side.

3.2.5 Apparent digestibility, chemical methods and density of the foods

The apparent digestibilities of the foods were determined by collection of faeces over 10 days from the fistulated sheep. Faeces were dried at 90°C for 48 h. Digestion in the rumen was estimated by the lignin-ratio technique (Balch, 1957). Samples of digesta for lignin determination were taken from the rumen three times daily over five days and were bulked, dried at 90°C for 24 h. and sampled for analysis. The tips of sponge forceps were modified to form two opposing spoons and were used to take samples of digesta from a point close to the reticulo-omasal orifice. The food, faeces and rumen digesta were analysed for lignin by the method of Van Soest (1963). Digestibility coefficients in the rumen were calculated as follows:

$$\text{Digestibility in the rumen \%} = 100 - \left(100 \times \frac{\text{\% lignin in food}}{\text{\% lignin in rumen digesta}}\right)$$

Recoveries of lignin in the faeces with the concentrate-oat husk mixture were low, and the possibility that the method of drying samples may have been responsible, was examined in a later experiment as follows: Two sheep were fed the concentrate-oat husk mixture and the food, faeces and rumen digesta were dried in an oven at 90°C, or were freeze-dried prior to the determination of lignin.

The foods were analysed for ether extract, crude protein and ash (AOAC, 1965), and acid detergent fibre, (Van Soest, 1963). The gross energy of the foods and faeces were determined with an adiabatic bomb calorimeter. The density of samples of the food were determined by the method of Montgomery & Baumgardt (1965b).

3.2.6 Mean retention time of food residues in the alimentary tract

Approximately 40 g of the chopped hay or concentrate-oat husk mixture treated with ^{144}Ce, and 40 g stained with safranine (see Section 2.1.3) were thoroughly mixed with the rumen contents through the fistulae.

Samples of faeces were dried and counted with a Philips gamma ray counter for ^{144}Ce (see Section 2.1.3), and wet faeces were used to count coloured particles using the method of Balch (1950). Mean retention times of food residues were calculated using the method of Castle (1956) (see Section 2.1.3).

3.2.7 Amount of digesta in the reticulorumen

The total weight of digesta DM in the reticulorumen was determined by emptying the reticulorumen of the fistulated sheep on two consecutive days at the end of Periods 1 and 2. Emptying began at 1300 h. each day. The animals were strapped to a hinged table top which was raised to facilitate removal of the contents. Food was available from 0900 h.

until emptying.

3.2.8 Feeding behaviour

The times spent eating and ruminating were measured by recording pressure changes from balloons fitted to the lower jaws of the sheep. Recordings were made over 48 h. at the end of Periods 1 and 2.

3.2.9 Respiration rate

Respiration rates were measured by observing flank movements on 6 consecutive days at the end of Period 1, and the beginning of Period 2 with the fistulated sheep. The measurements were made at 1400 h. each day.

3.2.10 Statistical analysis

Because of the large difference in mean voluntary intake between treatments in Period 1, the change in voluntary intake (y - x) between the mean intake for Period 1 (x) and for separate weeks or the mean of the four weeks in Period 2 (y) were analysed by analysis of variance, rather than the analysis of covariance technique (Snedecor & Cochran, 1967). Because of the limited number of fistulated sheep available, all were shorn, leaving no unshorn fistulated sheep as controls. The unshorn intact sheep, data from which were obtained at the same time under identical conditions, were therefore used as the control group for the fistulated sheep.

In the intraruminal feeding experiment, voluntary intake over the six days prior to treatment was used as the independent variable in analysis of covariance. Differences between periods for reticulorumen digestion, apparent digestibility, and retention time of food residues were analysed by analyses of variance. The DM intakes of the fistulated sheep over 9 days covering the period of faecal collection, and over 7 days prior to emptying the reticulorumens were analysed by analysis of variance for differences between sheep and periods.

Live weight changes of the intact and fistulated sheep were analysed together, but separately for the two foods, by analysis of variance. The main interest lay in comparisons between periods within sheep.

3.3 RESULTS

3.3.1 Chemical composition, density and apparent digestibility of the foods

The chemical composition, density and apparent digestibility of the energy of the foods are summarised in Table 3.1. Differences in chemical composition of the foods between periods were small, except that the crude protein content of the chopped hay was higher in Period 2 than Period 1. The apparent digestibility of the concentrate-oat husk mixture was similar for both Periods 1 and 2, but there was a considerable depression in the apparent digestibility of the chopped hay in Period 2. The metabolizable energy (ME) content of the rations was estimated from DE x 0.82 (Blaxter, Clapperton & Martin, 1966). The weight per unit volume of the concentrate-oat husk mixture was three times that of the chopped hay.

TABLE 3.1 Chemical composition (g/100 g DM), apparent digestibility of the energy, and density of a concentrate-oat husk mixture and chopped hay, fed to sheep, before and after shearing

Measurements	Concentrate-oat husk mixture		Chopped hay	
	Period 1 Unshorn	Period 2 Shorn	Period 1 Unshorn	Period 2 Shorn
Crude protein	13.7	14.3	7.6	8.1
Ether extract	2.9	3.0	3.6	3.3
Acid detergent fibre	18.2	18.7	33.6	33.6
Lignin	4.0	4.6	6.2	6.3
Ash	3.7	4.6	6.1	6.2
Gross energy (kcal/g DM)	4.43	4.41	4.33	4.41
Digestible energy (%)	69.0	68.4 ± 0.6 N S	52.3	47.1 ± 0.4**
Digestible energy (kcal/g DM)	3.06	3.02	2.26	2.08
Estimated metabolizable energy (kcal/g DM)	2.51	2.48	1.85	1.71
Density (g DM/ml)	6.5		2.2	

NS , non significant

** , ($P < 0.01$)

3.3.2 Fleece weights and length of wool following shearing

Mean air-dry fleece weights were 3.41 and 4.12 kg for the fistulated sheep receiving the concentrate-oat husk mixture and chopped hay respectively. Corresponding fleece weights for the intact sheep were 5.68 and 5.51 kg. The length of wool remaining immediately following shearing ranged from 1.5 to 2.0 mm.

3.3.3 Voluntary intake and live weight change

The changes in voluntary intake, expressed as the highest weekly mean intake for Period 2 minus the mean intake for Period 1, for both DM and DE, are summarised in Table 3.2.

TABLE 3.2 Change in voluntary intake (highest weekly mean intake for Period 2 minus mean for Period 1) by sheep receiving a concentrate-oat husk mixture or chopped hay

Voluntary intake	Treatment	Concentrate-oat husk mixture Intact	Concentrate-oat husk mixture Fistulated	Chopped hay Intact	Chopped hay Fistulated
Change in DM intake (g/24 h.)	Shorn	595	518	308	222
		± 142+	± 159 NS	± 27**	± 26**
	Control	260	260	32	32
Difference		335	258	276	190
Change in DE intake (kcal/24 h.)	Shorn	1748	1500	499	315
		± 432NS	± 444NS	± 77*	± 63+
	Control	735	735	111	111
Difference		1013	765	388	204
Difference in ME intake (kcal/24 h.)		831	627	318	167

S.E. = Standard error of treatment means
NS , Non significant
+ , $P < 0.10$
* , $P < 0.05$
** , $P < 0.01$

The levels of significance refer to differences in the change in voluntary intake between shorn and unshorn sheep. Mean daily voluntary intakes of DM and DE are also illustrated in Fig.3.1. The levels of significance in Fig.3.1 refer to differences in the change in voluntary intake between shorn and unshorn sheep.

There was a significant increase in DM intake ($P < 0.10$) in the second week of Period 2 for the intact sheep receiving the concentrate-oat husk mixture, and in the fourth week ($P < 0.10$) for the fistulated sheep. There were no significant increases in DE intake following shearing by both the intact and fistulated sheep receiving the concentrate-oat husk mixture. The considerable between animal and between weeks variability in the intake of this food, together with the increased intake of the control animals as the experiment progressed, and the small number of animals used, meant that any increase in intake following shearing needed to be large to reach significance. Coefficients of variation for voluntary food intake were derived from daily and mean weekly intakes for the control animals over the four weeks of Period 2. For the sheep receiving the concentrate-oat husk mixture, coefficients were 17% between days and 11% between mean weekly intakes. Corresponding values for the sheep receiving hay were lower at 11% and 5%.

The mean increase in DM intake following shearing, over the whole of Period 2, was significant ($P < 0.05$) for both the intact and fistulated sheep receiving hay. The increase in DE intake was proportionately less than the increase in DM intake following shearing, reflecting the depression in apparent digestibility of the hay in Period 2. A depression in the DE intake of the sheep receiving the chopped hay was noted in the first week following shearing.

Live weight changes of the sheep receiving both foods are summarised in Table 3.3. From the results obtained when the reticulorumen of the fistulated sheep were emptied, and from slaughter data obtained in Chapter 4, where the ratio between the weight of the reticulorumen contents and whole contents of the alimentary tract was approximately 1 to 1.5, an estimate was made of the increase in the contents of the tract with the increase in voluntary intake following shearing. These estimates were 1.2 kg for the shorn, and 0.5 kg for the control group of sheep receiving the concentrate-oat husk mixture. With the sheep fed the chopped hay, the estimates were 1.5 kg for the shorn group, with a negligible increase for the control group. Accordingly, the mean

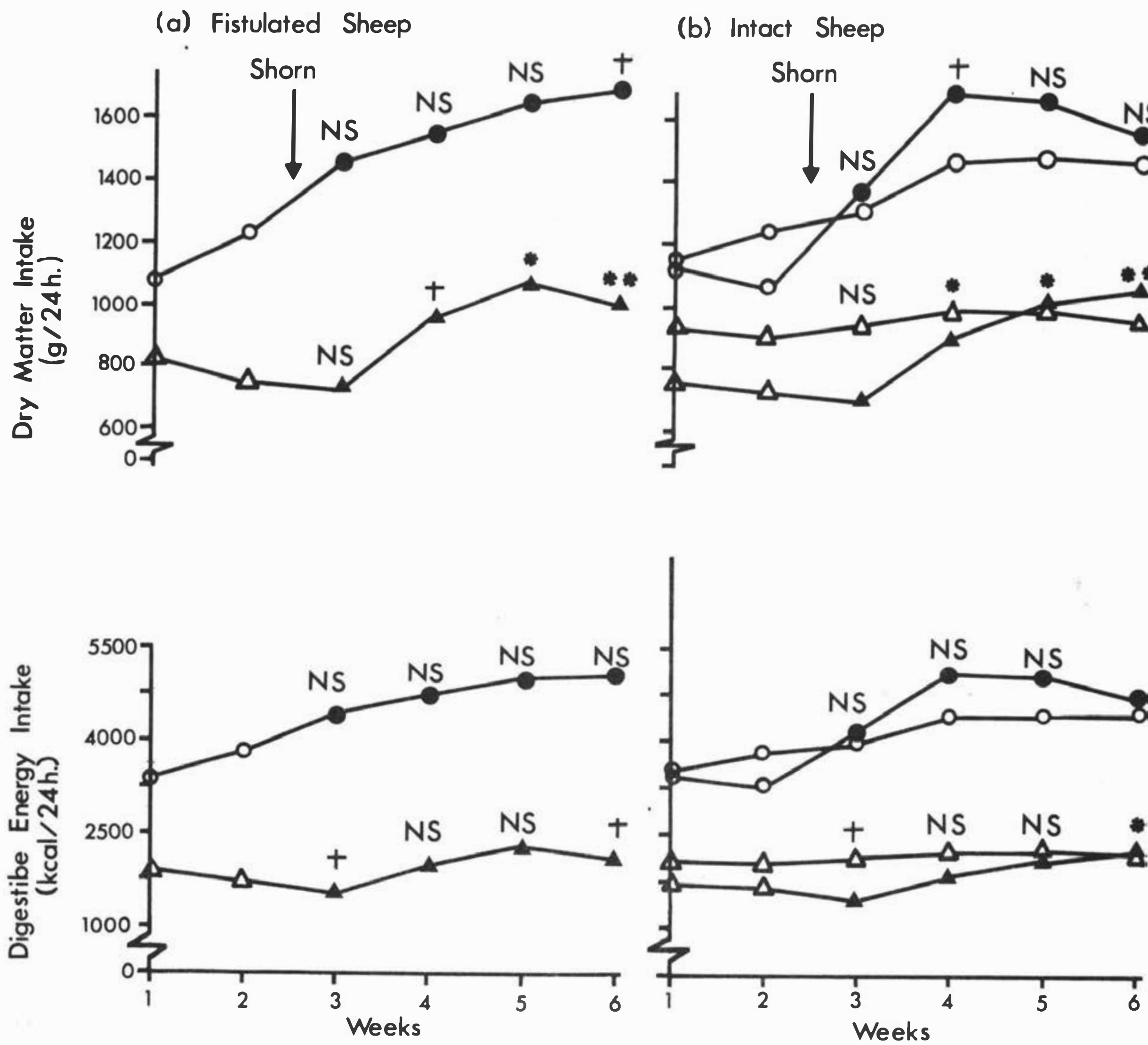

FIGURE 3.1 Mean daily voluntary intake by sheep, before and after shearing:
● concentrate–oat husk mixture, shorn;
○ concentrate–oat husk mixture, unshorn;
▲ chopped hay, shorn; △ chopped hay, unshorn.
N.S. Non significant; †, $P<0.10$, *, $P<0.05$; ** $P<0.01$.

TABLE 3.3 Live weight changes of sheep receiving a concentrate-oat husk mixture, or chopped hay, before (P_1) and after (P_2) shearing (S = Shorn, C = Unshorn)

Live weight		Concentrate-oat husk mixture				Chopped hay			
		Intact		Fistulated		Intact		Fistulated	
		P1	P2	P1	P2	P1	P2	P1	P2
Live weight change (g/24 h.)	S	115	121	50	118±45	-85	-118	-79	-208±20
	C	133	205			-45	+ 52		
Live weight change adjusted for differences in gut contents (g/24 h.)	S	115	77	50	74	-85	-174	-79	-264
	C	133	186			-45	+ 52		

live weight changes for the sheep were adjusted by these estimated changes in alimentary tract contents. Analysis of the unadjusted live weight changes for the sheep receiving the chopped hay showed that the live weight loss was significantly greater ($P < 0.01$) for the fistulated sheep in Period 2, after they were shorn, compared with Period 1. The corresponding live weight loss for the shorn intact sheep receiving chopped hay was not significantly greater in Period 2 compared with Period 1, although there was a highly significant difference ($P < 0.01$) in live weight change between the unshorn and shorn sheep in Period 2. Adjustment of live weight changes for differences in alimentary tract contents resulted in substantial increases in the live weight loss of both the intact and fistulated sheep receiving chopped hay, and which were shorn in Period 2. The unadjusted live weight gains for the sheep receiving the concentrate-oat husk mixture were too variable to show significant differences. Where live weight gains were adjusted for variations in alimentary tract contents, the differences between the shorn and unshorn sheep were greater, although based on the standard error obtained with the unadjusted data, the differences would still have not reached significance.

Various relationships between DE intake (Y) and live weight (X) were examined by regression analyses. There were no significant relationships between DE intake and live weight or the logarithms of these variables with either the shorn or unshorn sheep, whether receiving chopped hay or the concentrate-oat husk mixture.

Parameters describing the relationships between DE intake (Y) and live weight change (X) are given in Table 3.4. Relationships between DE intake and live weight change were not significant for the shorn sheep receiving chopped hay so that no comparison of intercepts of Y at X = 0 was possible, between the shorn and unshorn sheep. With the sheep receiving the concentrate-oat husk mixture, the significant relationship between DE intake and live weight change for both the shorn and unshorn sheep enabled a comparison to be made of the intercepts of Y at X = 0 (Table 3.4). The intercept was higher by 1106 kcal DE or 887 kcal estimated ME/24 h. for the shorn sheep, compared with the unshorn sheep.

TABLE 3.4 Regression of DE intake (Y,kcal/24 h.) on live weight gain (X, g/24 h.) for sheep receiving a concentrate-oat husk mixture or chopped hay

Diet	Treatment	df.	b.	SEb.	sy.x	Sig. of regression	Y at X=0 DE (kcal /24h.)	Y at X=0 Live Weight (kg)
Concentrate-oat husk mixture	unshorn	10	6.74	1.82	135	**	2891	44.9
	shorn	4	7.56	2.23	193	*	3997	46.3
Chopped hay	unshorn	10	3.45	0.97	59	**	2058	43.9
	shorn	4	1.52	1.61	91	NS		39.3

3.3.4 Digestion and alimentary tract measurements

Measurements concerned with digestion, obtained with the six fistulated sheep, are summarised in Table 3.5. With both foods, DM intakes were significantly higher ($P < 0.01$) in Period 2 when the sheep were shorn, compared with Period 1, both during the period of faecal collection and also over the 7 days prior to emptying of the reticulorumens. The changes in apparent digestibility in the reticulorumen between periods followed a similar pattern to those for total apparent digestibility, ie. a depression in apparent digestibility with the chopped hay, but not with the concentrate-oat husk mixture. Most of the difference in total apparent digestibility between the chopped hay and the concentrate-oat husk mixture occurred in the reticulorumen.

TABLE 3.5 Measurements relating to the digestion of a concentrate-oat husk mixture or chopped hay by rumen fistulated sheep, before and after shearing

Measurements	Concentrate-oat husk mixture		Chopped hay	
	Period 1 unshorn	Period 2 shorn	Period 1 unshorn	Period 2 shorn
DM intake during balance (g/24 h.)	960	1561 ± 66 **	838	1040 ± 25 **
DM digestibility in rumen (%)	49.2	50.5 ± 2.0 NS	34.0	25.8 ± 1.6 *
DM digestibility in hind gut (%)	19.5	17.0 ± 1.3 NS	19.3	21.8 ± 1.1 NS
DM digestibility in rumen as % of total digestibility	70	74	62	52
DM digested in reticulorumen (g/24 h.)	472	788 ± 129 +	285	268 ± 14 NS
DM passing from reticulorumen (g/24 h.)	488	773	553	772
Wt of faecal DM voided (g/24 h.)	272	508 ± 55 **	388	556 ± 74 **
DM intake, mean of 7 days prior to emptying of reticulo-rumen (g/24 h.)	1187	1563 ± 64 **	731	1013 ± 29 **
DM intake day before emptying of reticulo-rumen (g/24 h.)	1211	1462 ± 144 NS	767	1000 ± 39 **
DM content of digesta (%)	21.4	22.0 ± 0.6 NS	9.9	11.3 ± 0.4 +
Digesta in rumen(g)	4449	5259 ± 184 *	5803	6898 ± 395 +
DM in the reticulorumen (g)	1042	1172 ± 49 NS	608	792 ± 47 *
DM in reticulo-rumen (g/kg LW)	22	25 ± 1.0 NS	14	21 ± 1.3 *
Mean retention times(h.)				
^{144}Ce	55.4	31.6 ± 3.0 **	36.9	31.7
Stained food	-	79.3	44.5	35.3
Mean			40.7	33.5 ± 1.3 **

NS, non significant
+ $P < 0.10$
* $P < 0.05$
** $P < 0.01$

Mean recoveries of lignin were 103% for the chopped hay, and 79% for the concentrate-oat husk mixture. In the experiment where freeze drying was compared with oven drying, in the preparation of samples for lignin determination, the recovery of lignin was improved (95%), and rumen digestibility was 4% higher than the digestibility determined from oven-dried samples. Using the apparent digestibility figures derived from the freeze-dried faeces, changed the values for the DM of the concentrate-oat husk mixture apparently digested in the reticulorumen from 472 g to 511 g in Period 1, and from 788 g to 851 g in Period 2. Corresponding changes for DM passing from the reticulorumen were 488 g to 449 g in Period 1, and 773 g to 710 g in Period 2. These changes did not alter the interpretation placed on the results.

Greater amounts of DM were apparently digested in the reticulorumen of the sheep receiving the concentrate-oat husk mixture compared with those receiving chopped hay, but the amounts of DM passing from the reticulorumen and voided as faeces were similar, within periods, for the two foods.

There was more digesta DM in the reticulorumen of the sheep receiving the concentrate-oat husk mixture ($P<0.01$) than in those receiving chopped hay. There was a significant increase ($P<0.05$) in the amount of DM in the reticulorumen of the sheep receiving chopped hay following shearing. Variation in the amount of DM in the reticulorumen between sheep receiving the chopped hay was much less in Period 2 (SE of the mean $\pm$ 24 g DM), compared with those fed the concentrate-oat husk mixture (SE of the mean $\pm$ 135 g DM). There were no significant differences between days in the amount of DM in the reticulorumen with either food. Values for DM in the reticulorumen, as a proportion of body weight, showed a considerable increase ($P<0.05$) for the chopped hay in Period 2, which was partly an effect of the decrease in live-weight of these animals as the experiment progressed. The lower DM content of the digesta of the sheep receiving the chopped hay was reflected in the greater amount of wet digesta in the reticulorumen of these sheep, compared with those receiving the concentrate-oat husk mixture.

The mean retention times of food residues in the alimentary tract of the sheep are given in Table 3.5. Retention times for the stained concentrate-oat husk mixture were not obtained in Period 1 because of secondary staining. A mean retention time of 88.6h. was obtained at a later date with the same three sheep fed the concentrate-oat husk mixture, at a similar level of intake. Whilst mean retention times, particularly for the concentrate-oat husk mixture may not have been absolute, retention times for both foods decreased substantially following shearing.

Relationships between DM intake (mean of three days prior to emptying, x) and DM and wet matter in the reticulorumen (y) were not significant for both the shorn and unshorn sheep receiving chopped hay. The relationships were not significant for the unshorn sheep receiving the concentrate-oat husk mixture, but were highly significant ($P < 0.01$) for the shorn sheep.

3.3.5 Feeding behaviour and respiration rates

A summary of the time spent eating and ruminating is given in Table 3.6. The sheep receiving the chopped hay spent more time eating and ruminating ($P < 0.01$) than the sheep receiving the concentrate-oat husk mixture. Only time spent eating the chopped hay changed when the sheep were shorn. Respiration rates were higher for the sheep receiving the concentrate-oat husk mixture ($P < 0.01$) than those receiving chopped hay, before shearing. A considerable reduction in respiration rate ($P < 0.01$) occurred with both groups of sheep, following shearing.

TABLE 3.6 Mean daily time spent eating and ruminating, and respiration rates with sheep fed a concentrate-oat husk mixture or chopped hay, before and after shearing

Feeding behaviour and respiration rate	Concentrate-oat husk mixture		Chopped hay	
	Unshorn	Shorn	Unshorn	Shorn
Eating time (min./24 h.)	226	204 ± 13 NS	261	336 ± 11 **
Eating ratio (min./g DM intake)	0.19	0.22 ± 0.01 NS	0.31	0.32 ± 0.02 NS
Ruminating time (min./24 h.)	337	382 ± 28 NS	585	614 ± 68 NS
Ruminating ratio (min./g DM intake)	0.28	0.35 ± 0.69 NS	0.69	0.59 ± 0.08 NS
Respiration rate (/min.)	100	25 ± 8 **	58	20 ± 7 **

NS, non significant

**, $P < 0.01$

A proportion of the animals shivered during the first week following shearing. This was observed with all sheep receiving the chopped hay, and with one sheep receiving the concentrate-oat husk mixture.

3.3.6 Intraruminal feeding

The mean daily DM intake over the six days prior to the intraruminal feeding of 180 g DM per day, for the sheep receiving the concentrate-oat husk mixture, was 1440 g, with a mean DM intake of 1300 g ± 39 ($P<0.10$) over the six days of intraruminal feeding. Corresponding figures for the sheep fed the chopped hay were 971 g and 750 g ± 29 g ($P<0.01$). Thus DM intakes were reduced significantly by 140 g for the sheep receiving the concentrate-oat husk mixture, and by 220 g for those fed the chopped hay.

3.4 DISCUSSION

The first hypothesis tested in this experiment was that an increase in energy expenditure, induced by shearing, would result in a minimal increase in the voluntary intake of sheep receiving chopped hay, where physical factors controlling food intake would be predominant. With sheep receiving a concentrate-oat husk mixture, where physical factors were of lesser importance, voluntary intake would increase to meet the increase in energy expenditure, when sheep were shorn. The results obtained did not support this hypothesis in that an appreciable increase occurred in the DM intake of sheep receiving the chopped hay following shearing, while the results were inconclusive with the concentrate-oat husk mixture. At the time of maximum response, the net increase in the intake of chopped hay (% increase in intake of shorn sheep - % increase in intake of control sheep) was 32 and 23% for the intact and fistulated sheep respectively. The corresponding net increases in DE were 24 and 13% for the two groups of sheep. Results obtained with the sheep receiving the concentrate-oat husk mixture were unsatisfactory because of the large variation in response between sheep, and within sheep between weeks, and because there was an increase in intake of the unshorn control sheep as the experiment progressed. This latter effect was thought to have occurred because the food intakes of the sheep had not stabilised prior to shearing.

Judging from the results of Wodzicka-Tomaszewska (1963 and 1964), increases in food intake of the order of 30 to 40% were expected with sheep receiving the concentrate-oat husk mixture, and with an expected coefficient of variation in food intake per animal of 10 to 15% (Heaney, Pritchard and Pigden, 1968), six sheep in the shorn group, and three controls were expected to have provided sufficient numbers of animals for significance (Cochran & Cox, 1950). To examine the possibility that the training period for the animals was too short, a further experiment was begun with eight sheep receiving the concentrate-oat husk mixture, and to study the effects of changes in ambient temperature, and of shearing on voluntary food intake. Even after a period of six weeks feeding of the concentrate-oat husk mixture, under controlled conditions, the coefficient of variation per day was 33% and for mean weekly intakes it was 17%. It appeared that a high coefficient of variation for voluntary intake was a characteristic of this diet and as there seemed to be no indication that the variation could be reduced any further, the experiment was abandoned, as resources did not allow for the use of more than four sheep per treatment.

The mean increase in voluntary intake of the sheep receiving chopped hay, following shearing, was similar in extent to that observed by Weston (1970) with sheep receiving wheaten hay, and by Minson & Ternouth (1971) with hays, although the latter workers observed that the increase in food intake of sheep, following shearing and receiving a high quality lucerne hay with an apparent digestibility of over 70%, was almost negligible. Whilst increases in intake following shearing were similar to those obtained by Weston (1970) and Minson & Ternouth (1971), they were considerably less than the 30 to 50% increase in the intake of sheep receiving a mixed hay and pelleted food following shearing, obtained by Wodzicka-Tomaszewska (1964), or the 40 to 60% increase noted by Wheeler, Reardon & Lambourne (1963) when sheep grazing pasture were shorn. The foods used by these workers were of a higher digestibility than the chopped hay used in the present experiment, and the responses obtained were of the order that had been expected for the concentrate-oat husk mixture.

A decreased DE intake of the chopped hay, but not the concentrate-oat husk mixture was noted in the first week following shearing. Delays or depressions in intake in response to cold exposure in the first week following shearing have been noted by Wheeler, Reardon & Lambourne (1963), Wodzicka-Tomaszewska (1963 & 1964), Minson & Ternouth (1971), and

Weston (1970). These depressions or delays in intake occurred, irrespective of the digestibility of the foods, whereas in the present experiment only the intake of the chopped hay was depressed. It has been suggested, (Wodzicka-Tomaszewska, 1963 & 1964) that cold stress may have been responsible for this delayed increase in intake. This is consistent with observations made in the present experiment, in that shivering was more frequent and pronounced with the sheep receiving the chopped hay. It is also possible that time is needed for the digestive tract to accommodate extra food such as chopped hay, where bulk is important, although this would not account for a depression in intake. In contrast, Minson & Ternouth (1971) observed that the depression in intake following shearing was greatest with the food of highest apparent digestibility, and Sykes & Slee (1969) noted that depressions in food intake when sheep were cold exposed occurred with the animals on a high plane of nutrition, rather than those on a low plane. The bases of these early responses to cold exposure require clarification.

The DE intakes of the sheep receiving the concentrate-oat husk mixture were more than double those of the sheep receiving the chopped hay, which is in agreement with the general positive relationship between voluntary intake and apparent digestibility, noted by many workers (Blaxter, Wainman & Wilson, 1961; Minson, Harris, Raymond & Milford, 1964). The level of DE intake of the sheep receiving the concentrate-oat husk mixture was similar to DE intakes observed with sheep receiving foods of a similar DE concentration, in a number of experiments cited by Baumgardt (1970). However DE intakes of the sheep receiving the chopped hay, in the present experiments, were consistently below the DE intakes cited by Baumgardt for foods of comparable DE concentration. Evidence gained by Blaxter & Wilson (1963) suggested that a minimum of 8.5% crude protein was needed to ensure maximum voluntary intake of sheep receiving hay. Elliott & Topps (1963) also suggested that a similar level of crude protein was required for maximum voluntary intake. Increased voluntary food intake resulted when casein was included in the diet of sheep, or was administered via the duodenum by Egan (1970), with sheep receiving a hay with a crude protein content of 5.6%. It is therefore possible that the intake of the chopped hay used in the present experiment (mean crude protein content 7.8%) may have been limited by the amount of protein available to the sheep. With rats fed low protein diets, deficient in some amino-acids, cold exposure increased total food intake and thus increased the nitrogen status of the rats to such an extent that they increased their live weight gain in the cold (Meyer & Hargus, 1959; Klain, Vaughan & Vaughan, 1962). This phenomenon did not appear to occur with the sheep in the present experiment. The rat diets were finely ground and were hardly comparable to the chopped hay used, as the rate at which food particles were broken down may have been the dominant factor limiting food intake.

The sheep receiving chopped hay lost weight at a greater rate following shearing. This is an indication that the increase in DE intake following shearing was insufficient to compensate for the increased energy expenditure.

The regression relationships, summarised in Table 3.4, enable comment to be made on differences in energy expenditure between the shorn and unshorn sheep receiving the concentrate-oat husk mixture. The difference in the intercept of Y (DE intake, kcal/24 h.) at X = 0 of 1106 kcal (887 kcal ME), in favour of the shorn sheep, is an indication of the increase in energy expenditure following shearing. No reliance can be placed on the absolute value of the difference between the intercepts, because of the errors involved (Table 3.4), and the degree of extrapolation needed in deriving the value. The difference could be as low as 270 kcal DE/24 h. if the lower confidence level of the shorn sheep was compared with the upper confidence limit of the unshorn sheep. There was no significant relationship between DE intake and live weight loss for the shorn sheep receiving chopped hay so that a similar comparison to that made for the concentrate-oat husk mixture was not possible. The considerable decrease in the apparent digestibility of the chopped hay following shearing, but not of the concentrate-oat husk mixture, is consistent with the statement of the Agricultural Research Council (1965) that the effect of level of feeding in depressing apparent digestibility is greater for foods of low digestibility than those of high digestibility. Blaxter (1961) calculated that increasing the intake of a roughage in the long form similar to the chopped hay used in the present experiment, from maintenance to twice maintenance, would result in a depression of apparent digestibility of approximately 5 percentage units. What is surprising is that a similar depression in apparent digestibility was obtained with the chopped hay for a moderate increase in intake, in the present experiment. A small decrease in the apparent digestibility of a mixed hay and pelleted diet from 62.5 to 59.2% was noted by Wodzicka-Tomaszewska (1964) when sheep were shorn, and Minson & Ternouth (1971) obtained a significant fall in the apparent digestibility of one of their poorer hays from 54.8 to 51.9% following shearing, although no increase in intake occurred with this food. A small depression in apparent digestibility of the concentrate-oat husk mixture occurred in the present experiment following shearing, but the change was not significant. The fall in the apparent digestibility of the chopped hay following shearing lowered its ability to meet the increased energy demand of the sheep.

The second hypothesis tested in the present experiment was that a change in the physiological state of sheep, induced by shearing, would affect measurements concerned with the physical regulation of voluntary food intake. The results obtained supported this hypothesis, in that there were greater amounts of digesta DM in the reticulorumen of the sheep receiving chopped hay, after they were shorn, and retention times of food residues were lower following shearing with both foods. The amounts of DM passing from the reticulorumen and voided as faeces over a 24 h. period increased with both foods after the sheep were shorn.

A problem in the interpretation of the data relating to digestion, particularly with respect to that for the amount of DM in the reticulorumen, was the lack of unshorn control animals so that comparisons between unshorn and shorn animals were separated in time. However measurements of DM in the reticulorumen were carried out over two days, both before and after shearing, and the lack of significant differences between days allows some confidence to be placed in the results. Subsequent results from slaughter work supported the evidence that an increase occurs in the amount of DM in the reticulorumen following shearing.

Investigation of the relationships between voluntary intake and the amount of wet matter or DM in the reticulorumen contributed little towards interpretation of the results. The significant relationships obtained with the sheep receiving the concentrate-oat husk mixture may have indicated that the amount of wet matter or DM in the reticulorumen was unimportant in limiting intake. With the sheep receiving chopped hay the lack of a relationship probably arose more because of the narrow range in intakes of these sheep.

If with chopped hay, reticulorumen capacity limited food intake prior to shearing, then the indications are that a new threshold to reticulorumen capacity was set in response to an increased energy demand. However the amount of DM in the reticulorumen of the sheep receiving the chopped hay was considerably less than that observed with the sheep receiving the concentrate-oat husk mixture and thus observations of Blaxter, Wainman & Wilson (1961); Ulyatt, Blaxter & McDonald (1967) that sheep eat to a constant distension of their alimentary tracts and in the case of the latter workers, the reticulorumen, does not apply in the present experiment, where foods of different physical form and digestibility were used. Because steady state conditions were not obtained, and because feeding occurred at irregular intervals, no valid measure of digestive tract fill, as determined by the method of Blaxter, Graham & Wainman (1956) could be obtained. It is possible that fill in the whole tract may have been a more useful measure, although there is evidence that there is a close relationship between the amount of digesta in the reticulorumen and the amount in the rest of the tract (Mäkelä, 1956).

Montgomery & Baumgardt (1965b)observed that the calculated fill of the digestive tract was lower for diets of low apparent digestibility than for those of high digestibility, and Campling, Freer & Balch (1961) and Egan (1970) found lower levels of DM in the reticulorumen of cows and sheep respectively, with foods of low apparent digestibility, compared with those of higher apparent digestibility. The lower amount of DM in the reticulorumen of the sheep receiving the chopped hay therefore indicates that absolute reticulorumen fill may not be a controlling factor limiting food intake but, as suggested by Egan (1972), a critical fill may be set at levels determined by other factors, such as the rate at which food particles are broken down and removed from the reticulorumen. It may be of significance that the amounts of DM passing from the reticulorumen, and the amounts of faeces voided were similar for both foods, indicating that the removal rate of DM might be one of the factors involved. The amount of wet digesta in the reticulorumen was higher for the chopped hay, and may also have contributed towards a filling factor which limited food intake.

Eating and ruminating times probably reflected the degree of comminution needed to reduce the two foods to a given particle size, and the considerably longer time spent by the sheep chewing the hay compared with the concentrate-oat husk mixture is probably a reflection of their different physical forms. Forage quality is also a factor affecting rumination time. Welch & Smith (1969) obtained rumination ratios of 0.45 and 0.79 min./g DM intake with high quality lucerne and oat straw respectively which are similar to those obtained in the present experiment with both foods. Dry matter intakes were depressed during the recordings taken with the shorn sheep receiving the concentrate-oat husk mixture so the effects of shearing on their behaviour cannot be assessed. Despite an increase in voluntary intake, the time spent ruminating by the sheep receiving chopped hay did not increase following shearing. Gordon (1965) has shown that rumination time increases with increasing hay intake at lower levels of intake, but that there is a levelling off at higher levels. In discussing his results, he states that there is a point reached where limits to rumination are set by factors such as the time available to the animal for eating, or tiring of the animal. The length of time spent ruminating may have contributed, in part, to a limitation of the intake of the chopped hay in the present experiment. It is worth noting that the extra time spent ruminating the chopped hay, compared with the concentrate-oat husk mixture would result in somewhat greater energy expenditure. From evidence gained in Chapter 6 this would amount to about 70 kcal/24 h. The amount is small, but it is a further negative effect contributing to inability of the chopped hay to supply the animal's needs.

Palatability as a factor influencing food intake can probably be discounted, as the introduction of foods through the fistula was associated with a corresponding decrease in food intake by mouth, although Greenhalgh & Reid (1971) point out the possibility that the process of introducing feed through the fistula may in itself depress oral intake by its effect in reducing digestion in the reticulorumen.

3.5 CONCLUSION

The increase in voluntary intake following shearing of sheep receiving chopped hay was probably a response to an increase in energy demand. It appeared that the sheep were able to accommodate the increase in intake partly through an increase in the amount of DM held in the reticulorumen, and partly through a decrease in the retention time of food residues in the alimentary tract. It is obvious that strong factors limited the intake of the unshorn sheep, to the extent that they lost weight, but that these factors were overidden by the change in energy demand, so that intake increased. Thus even with a food of low DE concentration, intake cannot be regarded as a constant attribute of the diet.

The results obtained on the changes in the intake of sheep receiving the concentrate-oat husk mixture were inconclusive. The high within and between sheep variability in the voluntary intake of this food would necessitate the use of a greater number of animals than it was possible to use in the present experiment, and comparisons would probably be best made between foods of similar characteristics (e.g. physical form and density), but differing widely in apparent digestibility. For this reason comparisons in subsequent experiments have been made between chopped dried grass and hay.

There were a number of reasons why the sheep were held at an ambient temperature of 13°C throughout the present experiment. It meant that one of the variables known to affect food intake was held constant. The level was also chosen to be sufficiently below the critical temperature of shorn sheep, as determined by Armstrong, Blaxter, Graham & Wainman (1959) so that a definite response to shearing could be expected. The environmental temperature was also chosen with the thought that too great a heat load would not be imposed on the unshorn sheep, resulting in an inhibition of food intake. A definite response was obtained with the sheep receiving chopped hay, and it was decided that the sheep would be kept at an ambient temperature of 13°C in future experiments.

CHAPTER 4

THE EFFECT OF SHEARING ON THE VOLUNTARY FOOD INTAKE OF SHEEP RECEIVING DRIED GRASS, CHOPPED HAY OR GROUND HAY

S U M M A R Y

1. Romney wethers were used in four experiments to determine the effects of shearing in changing the voluntary intake of sheep receiving dried grass, chopped hay or ground hay. Romney ewes as well as wethers were used in a fifth experiment, designed specifically to study the effects of shearing on the alimentary tract and its contents, determined at slaughter.

2. In Expt 1(a), eight sheep, four on each food, were fed dried grass or chopped hay. The voluntary intakes of sheep receiving both foods increased following shearing, although the results were affected by an attempt to empty the reticulor-rumen of the sheep.

In Expt 1(b), with four sheep receiving the same foods as in Expt 1(a), the voluntary intake of dried grass declined, whilst that for chopped hay increased following shearing.

3. In Expt 2, 18 Romney wethers, six on each food, were fed dried grass, chopped hay or ground hay. There was no significant increase in the voluntary intake of dried grass following shearing, and a progressive decline in the voluntary intakes of the unshorn sheep receiving dried grass was observed. The voluntary intakes of sheep receiving chopped hay increased following shearing ($P < 0.10$), but a greater increase occurred in the intake of ground hay ($P < 0.05$).

4. In Expt 3, eight Romney wethers were fed ground hay. An increase in voluntary intake occurred following shearing to about the same extent as that noted with the ground hay in Expt 2. The sheep in this experiment were slaughtered to provide data on alimentary tract fill.

5. In Expt 4, four Romney wethers and four ewes were fed chopped hay. There was no significant increase in DM intake following shearing, probably because the preliminary period was too short.

The main interest in this experiment was with the data obtained at slaughter.

6. The rate of breakdown of cotton threads, determined in Expt 1(a) only, was faster with the dried grass than the chopped hay. There was no apparent effect of shearing on the rate of breakdown.

7. With the ground hay and chopped hay (Expt 3 and 4 respectively), both the wet and dry contents of the alimentary organs were greater in the shorn than the unshorn sheep. Evidence was also obtained, particularly with the sheep fed ground hay, of a considerable increase in the weights of the empty alimentary organs following shearing.

8. The experiments showed that the response to shearing, in terms of a change in voluntary intake, varied with the type of food, and with hay, its physical form. With the ground hay, but not the chopped hay, the increased intake following shearing probably met most of the increase in energy expenditure as indicated by changes in live weight gains. The results indicated that mechanisms controlling the voluntary intake of sheep receiving dried grass were different from those controlling the intake of sheep receiving chopped hay or ground hay.

4.1 INTRODUCTION

In an earlier experiment (Chapter 3), the effects of shearing on the voluntary food intake of sheep receiving a pelleted concentrate-oat husk mixture or chopped hay were studied. With the sheep receiving the chopped hay there was an appreciable increase in DM intake following shearing, although a delay in the intake response, and a depression in apparent digestibility following shearing, decreased the size of the response, in terms of DE intake. The increase in DE intake following shearing was insufficient to meet the increase in energy expenditure when the sheep were shorn, because they lost weight at a greater rate than before they were shorn. It was suggested that one of the controlling factors governing the intake of the chopped hay may have been the rate at which it was able to be removed from the reticulo-rumen. Thus the possibility that increases in voluntary intake of sheep receiving chopped hay were limited by the rate at which food particles are broken down to a size small enough to pass from the reticulorumen was investigated in two of the experiments to be described, using ground hay as the diet.

Because it was considered possible that the hay used in Chapter 3 did not supply sufficient protein for maximum voluntary food intake of the sheep, hays of a higher protein content were selected for use in the present series of experiments.

Results in terms of changes in the voluntary intake of the concentrate-oat husk mixture (Chapter 3) were unsatisfactory, mainly because of the large coefficient of variation for intake, which appeared to be a characteristic of this food, and the small numbers of animals used. As part of the objective of the present study was to compare voluntary intakes of sheep receiving food differing widely in apparent digestibility, it was considered that this would be achieved by using hay and dried grass, thus avoiding the problems associated with the concentrate-oat husk mixture.

In the work reported in Chapter 3 it was observed that the voluntary intakes of the unshorn control sheep continued to increase as the experiment progressed, which was noticeable particularly with the sheep receiving the concentrate-oat husk mixture. It was thought that this may have resulted from too short a preliminary period so that voluntary food intake may not have stabilized, prior to the start of the experimental period. To avoid this possibility, where possible, longer preliminary periods were employed in the following experiments.

In the first experiment, (Expt 1(a)) the rate of cellulose digestion was measured and an estimate made of DM in the reticulorumen using polyethylene glycol. These measurements were not carried out in the other experiments as the work involved limited the replication possible. It was considered that more useful information would be obtained by regarding voluntary intake as the major measurement in experiments designed to examine the hypotheses proposed in Section 1.5. In two of the experiments, data on the alimentary tract and alimentary tract fill were obtained at slaughter, and although this had the limitation that only single measurements were possible at the end of the experiments, they had the advantage of being direct measurements, and would provide additional information on weights of organs and fill in various parts of the tract.

4.2 MATERIALS AND METHODS

4.2.1 Plan of experiments

A total of 34 Romney wethers were used in four experiments, and in a further experiment, four Romney ewes and four wethers were used, specifically to obtain alimentary tract measurements determined at slaughter. All sheep were held in crates in controlled temperature rooms at an ambient temperature of 13°C ± 1°C. Feeding was ad libitum at all times, water was freely available, and the sheep were given 5 g of a vitamin and mineral mixture once daily (see Section 2.2.2) and received anthelmintics at regular intervals. Details of the various experiments are given in Table 4.1

TABLE 4.1 Plan of the experiments showing the number of sheep in each experiment, their age and live weights at the beginning of the experiments, and length of the experimental periods.

Expt No.	Food	No. of sheep	Age of sheep	Weight (kg)	Length of Period (wks) Period 1	Period 2	Remarks
1(a)	Dried grass	4	25 mo	47.7 ± 2.2	5	8	
	Chopped hay	4		49.1 ± 1.8			
1(b)	Dried grass	2	27 mo	56.7	3	3	Control sheep from Expt 1(a)
	Chopped hay	2		43.2			
2	Dried grass	6	20 mo	40.3 ± 1.8	5	4	
	Chopped hay	6		36.1 ± 1.4			
	Ground hay	6		37.6 ± 1.8			
3	Ground hay	4	20 mo	41.6 ± 3.5	4	4	slaughtered
		4		43.1 ± 1.1			
4	Chopped hay	4	38 mo	51.7 ± 2.5			
		4		56.2 ± 2.6	2	3½	slaughtered

In Expt 1(a), 1(b) and 2, feeding took place twice daily at 0900 and 1600 h. and in Expt 3 and 4, the sheep were fed once daily at 0900 h. The sheep were weighed once weekly, before the morning feed. Each experiment was divided into a pre-shearing period (Period 1), and a post-shearing period (Period 2). In all except Expt 1(b), half the sheep on each feed were shorn and half were left unshorn as controls. The sheep were allocated at random to treatments. The sheep in Expt 1(a) and 1(b) were fitted with rubber rumen cannulae (internal diameter 5 cm). An attempt was made to determine reticulorumen fill at the end of Period 1 in Expt 1 (a) by manually emptying the reticulorumens of four sheep, two on each feed. This resulted in a considerable depression in food intake, which continued for over three weeks following emptying. The procedure was therefore abandoned and was replaced by an indirect method of estimating reticulorumen fill, using polyethylene glycol (PEG).

In Expt 2, of the six sheep receiving each feed, three were shorn and three were left unshorn at the end of Period 1. In Expt 3 there was one heavy animal (51.2 kg) in the shorn group, which was well above the live weights of the other sheep. Expt 4 was specifically set up to examine the effects of shearing on alimentary tract fill, from feeding chopped hay. Ewes were included because of the unavailability of wethers. Two wethers and two ewes were shorn, and two of each sex were left unshorn as controls. The periods in Expt 4 were restricted in length because of the limited supply of the chopped hay used in previous experiments.

4.2.2. Diets

The hay was chopped through a hammer mill with a 5 cm screen and the ground hay was milled through the same machine, using a 2.5 mm screen. The chopped dried grass, consisting mainly of ryegrass species, was supplied by the N.Z. Grassmeal Ltd., Tahuna.

The physical nature of the foods was determined by methods devised by the American Society of Agricultural Engineers (1967). Sieves with apertures of 210 μ 1000 μ and 2000 μ were used to sieve the foods. The foods were then rated according to a modulus of uniformity and fineness. In addition, the length of approximately 150 particles of each of the foods retained on the coarsest sieves was determined. The chemical composition of the foods were determined as described previously (Section 3.1.5). The density of samples of dried grass and hay were determined by the method described by Montgomery & Baumgardt (1965b).

4.2.3 Voluntary food intake, apparent digestibility, time of retention of food residues and nitrogen balance

Samples of the food and food refusals were taken daily and were dried at 90°C for 24 h. for the measurement of voluntary DM intake. The amount of food was adjusted so that the refused portion was about 15% of the amount offered.

The apparent digestibilities of the diets were determined by collection of faeces for 14 days. The faeces were dried at 90°C for 48 h. and the energy content determined using an adiabatic bomb calorimeter. The time of retention of the food residues was measured by using ^{144}Ce,with retention times calculated by the method of Castle (1956), (see Section 2.1.3).

Apparent digestibility and time of retention of food residues were measured with all sheep in both periods in Expt 1(a) and 1(b) and on 12 sheep, two on each treatment,in Expt 2. Apparent digestibilities were determined with all sheep in Expt 3 and with the wethers in Expt 4. In Expt 2, nitrogen balances were determined in Period 2 on 12 sheep, two in each treatment. The nitrogen contents were determined on fresh faeces and acidified urine by the Kjeldahl method (AOAC,1965).

4.2.4 Digestion of cellulose in the rumen

The cotton-thread technique described by Campling, Freer & Balch (1961) was used to obtain an index of the rate of digestion of cellulose in the reticulorumen in Expt 1(a) and 1(b).

4.2.5 Indirect estimate of the amount of DM in the reticulorumen

In Expt 1(a), the amount of DM in the reticulorumen was determined using PEG. A dose of approximately 15 g of PEG (Mol.wt.4000) in 250 ml of water, was administered via the rumen fistula, using a 50 ml syringe and directing the solution into various regions of the reticulorumen. Liquor was taken from various parts of the reticulorumen using a syringe provided with a two-way valve, at 0, (11 30 h.) 1.5, 3, 6, 12 and 24 h. after dosing with the marker. Determinations were made on three consecutive days at the end of Periods 1 and 2. The concentration of PEG in rumen liquor was determined by using the method of Hydén (1956), with modifications by Smith (1959) and Ulyatt (1964). Samples of digesta were taken from various parts of the reticulorumen at the time of dosing (11 30 h.) and were dried in an oven at 90°C for 24 h. to obtain the DM content of the digesta. Sampling of the contents of the reticulorumen was facilitated by the large diameter of the cannulae.

The natural logarithms of marker concentration were plotted against time, the line being extrapolated back to zero time by linear regression. This provided an estimate of marker concentration at the time of dosing. Reticulorumen water volume (V) was calculated as follows:-

$$V = \frac{P}{C_1 - C_2}$$

where P is the amount of marker administered, and C_1 and C_2 are marker concentrations in the reticulorumen before and after dosing. The amount of digesta DM in the rumen at the time of dosing was then calculated, using the data obtained on the DM content of the digesta.

4.2.6 Slaughter

The sheep in Expt 3 and 4 were slaughtered at the end of Period 2. All sheep received food and water to within 2 h. of slaughter, which took place from 1300 h. on each of two days. Immediately after slaughter, the alimentary tracts were removed and the various organs were tied off. An estimate of the volume of the reticulorumen was obtained by water displacement and weights of the empty reticulorumen, omasum, absomasum, intestines and weights of the omental, mesenteric, and kidney fat were obtained. The empty organs were dried with a towel before weighing. The wet contents of the organs were weighed and the dry weights of the contents of the reticulorumen and whole tract were determined by drying samples at 90°C for 48 h.

4.2.7 Feeding behaviour

The times spent eating and ruminating were measured by recording pressure changes from balloons fitted to the lower jaws of the sheep. Recordings were made over 72 h. at the end of Periods 1 and 2 with eight sheep, four on each food in Expt 1(a); on the four sheep in Expt 1(b) and on six sheep, three receiving chopped hay, and three ground hay in Expt 2.

4.2.8 Statistical analysis

Expt 1(a): Because of the large differences in mean voluntary intake between treatment groups in Period 1, the change in voluntary intake (Y - X) between the mean intake for Period 1 (X) and the mean for Period 2 (Y) were analysed by analysis of variance rather than the analysis of covariance technique (Snedecor & Cochran, 1967).

Expt 2, 3 and 4: The effect of shearing on voluntary food intake was analysed by analysis of covariance using the data obtained in Period 1 as independant variables. The data for each diet were analysed separately for separate weeks or combinations of weeks following shearing. There were insufficient data to test for differences in feeding behaviour between shorn and unshorn animals in Expt 2. One of the control animals receiving dried grass in Expt 2 refused food, lost weight and was removed from the experiment. A missing plot was used in the analysis of these results.

TABLE 4.2 Chemical composition and physical characteristics of dried grass, chopped hay and ground hay

Experiment Diet		Crude Protein (% of DM)	Ether Extract (% of DM)	Acid detergent fibre (% of DM)	Ash (% of DM)	Gross Energy (kcal/ g DM)	Digestible energy (kcal/ g DM)	Modulus of fineness	Modulus of uniformity
Expt 1									
Dried grass	P_1	16.5	5.0	20.8	9.9	4.37	3.24		
	P_2	16.8	5.8	20.6	9.3	4.35	3.18		
Chopped hay	P_1	10.0	3.3	31.6	7.4	4.33	2.60		
	P_2	10.8	3.6	31.1	7.3	4.34	2.49		
Expt 2									
Dried grass	P_1	18.7	5.4	22.6	9.9	4.41	3.22	4.5	6:3:1
	P_2	19.2	5.1	22.5	9.4	4.44	3.28		
Chopped hay	P_1	10.6	3.4	29.2	8.1	4.38	2.45	4.8	6:3:1
	P_2	10.4	3.4	29.2	8.0	4.31	2.27		
Ground hay	P_1	8.9	3.8	30.7	6.8	4.36	2.18	2.6	0:5:5
	P_2	9.4	3.6	31.5	6.5	4.38	2.12		
Expt 3									
Ground hay	P_1	9.8	3.1	31.3	7.0	4.37	2.26		
	P_2	10.2	3.2	31.6	7.5	4.34	2.26		
Expt 4									
Chopped hay		9.9	3.6	31.5	8.0	4.37	2.40		

P1 = Period 1 P2 = Period 2

4.3 RESULTS

4.3.1 Chemical composition and physical characteristics of the foods

The chemical composition and physical characteristics of the foods used in the various experiments are given in Table 4.2. The foods were similar between periods for most constituents, although there were some differences in crude protein. The crude protein of the ground hay was less than that for the chopped hay in Expt 2, and the acid detergent fibre was slightly higher. These differences are difficult to explain, except through a variation in sampling. The density of the dried grass was 2.8 g/ml and for the hay it was 2.2 g/ml.

The modulus of fineness expresses the fineness of grinding, with very finely ground material having a modulus of 1.0. The modulus of uniformity expresses the proportion of coarse, medium and fine particles in 10 parts of the food and indicates the uniformity of particle size distribution. Linear measurements made on samples of the larger particles were as follows:-

dried grass on 66.6% of the sample	2.2 ± 1.1 cm
chopped hay on 60.5% of the sample	2.8 ± 1.8 cm
ground hay on 50.2% of the sample	0.4 ± 0.1 cm.

4.3.2 Fleece weights

Mean fleece weights for the shorn sheep were 4.5 and 5.0 kg for the sheep fed hay and dried grass respectively in Expt 1; 6.8, 5.9, and 6.4 kg for the sheep fed dried grass, chopped hay and ground hay in Expt 2, and 4.0 kg for the sheep fed ground hay in Expt 3. In Expt 4, the mean fleece weights of the ewes was 2.2 kg and for the wethers it was 4.6 kg, the lower fleece weights of the ewes reflecting the shorter time (6 mo) since they were last shorn.

4.3.3 Voluntary food intake

Expt 1(a) and 1(b): Mean daily voluntary intakes of DE are shown in Fig. 4.1 for both experiments. The change in DE intake between Periods 1 and 2 in Expt 1(a) are summarized in Table 4.3, and mean daily DE intakes obtained in Expt 1(b) are given in Table 4.4.

In Expt 1(a) the intakes of the shorn sheep receiving dried grass showed a large increase which continued into the second 4 weeks of Period 2. With sheep receiving chopped hay the pattern was similar,

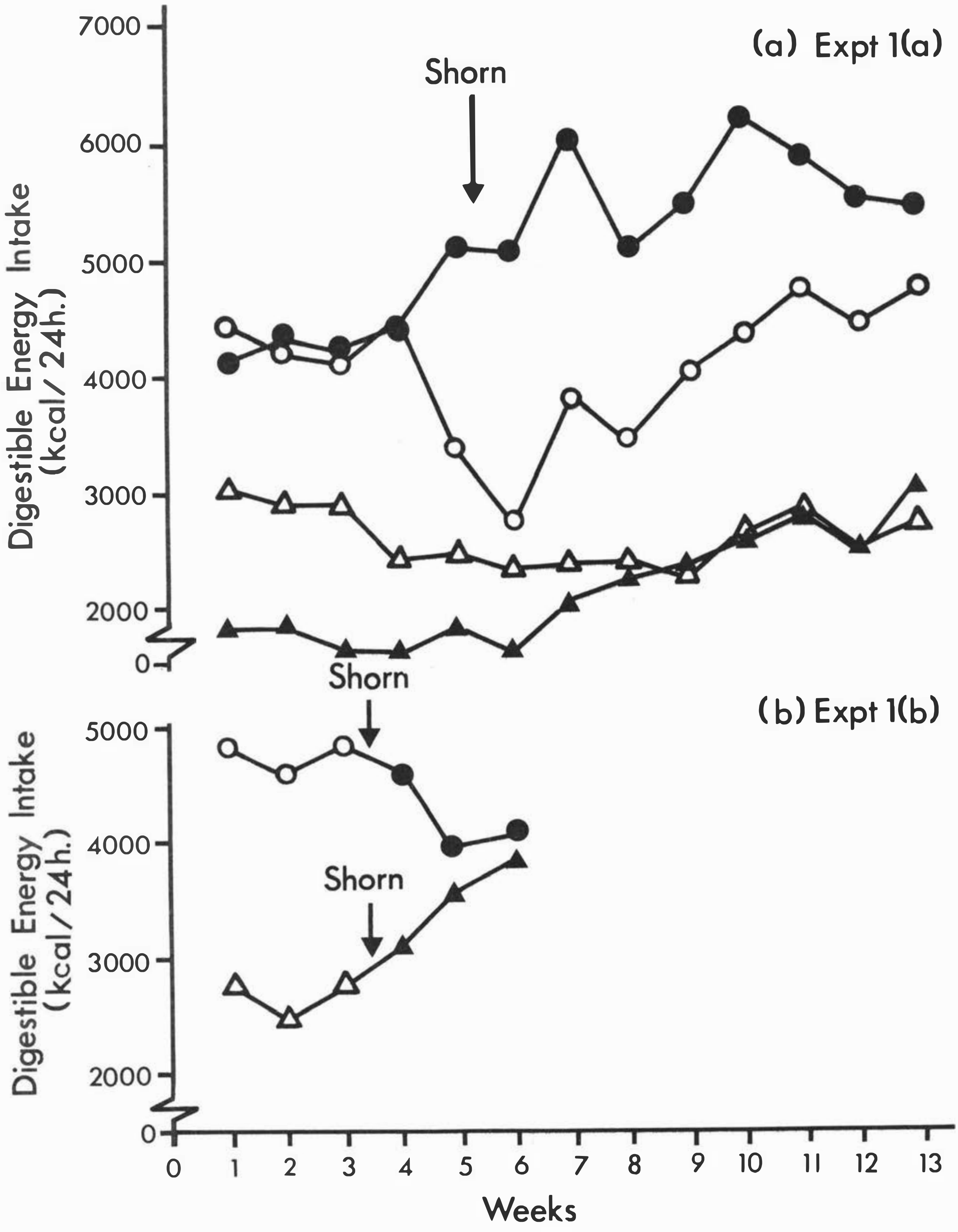

FIGURE 4.1 Experiment 1(a) and 1(b). Mean daily voluntary intake by sheep, before and after shearing:
● dried grass, shorn; ○ dried grass, unshorn;
▲ chopped hay, shorn; △ chopped hay, unshorn.

although the increase in intake was not as great as with the dried grass. Intakes of the unshorn sheep receiving both the dried grass and the chopped hay decreased in Period 2.

The voluntary intakes of a number of sheep in this experiment fell for over three weeks, following an attempt at emptying the reticulo-rumens, and the results therefore need to be treated with caution.

In Expt 1(b), the voluntary intakes of the sheep receiving dried grass decreased as the experiment progressed, although the effect was not significant. Intakes of the sheep receiving the chopped hay showed a considerable increase when the sheep were shorn.

TABLE 4.3 Expt 1(a). Change in digestible energy intake (mean of P_2 - mean of P_1) of sheep receiving dried grass or chopped hay, before and after shearing

Period	Treatment	Dried grass(kcal/24 h.)		Chopped hay(kcal/24 h.)	
1st 4 weeks of Period 2	shorn	1038	± 319 **	350	± 133 **
	unshorn	-638		-438	
2nd 4 weeks of Period 2	shorn	1308	± 177 **	976	± 171 **
	unshorn	411		-109	

TABLE 4.4 Expt 1(b). Mean daily digestible energy intake of sheep receiving dried grass or chopped hay before (P_1) and after shearing (P_2)

Diet	P_1 unshorn	P_2 shorn	SE	Sig. of difference
Dried grass (kcal/24 h.)	4708	4200	216	NS
Chopped hay (kcal/24 h.)	2603	3491	67	**

Expt 2: Changes in mean daily voluntary intake are shown in Fig.4.2, and mean daily voluntary intakes for Period 1, and mean intakes for the third and fourth weeks of Period 2, adjusted by analyses of covariance, are given in Table 4.5. The main points of note are the large increases

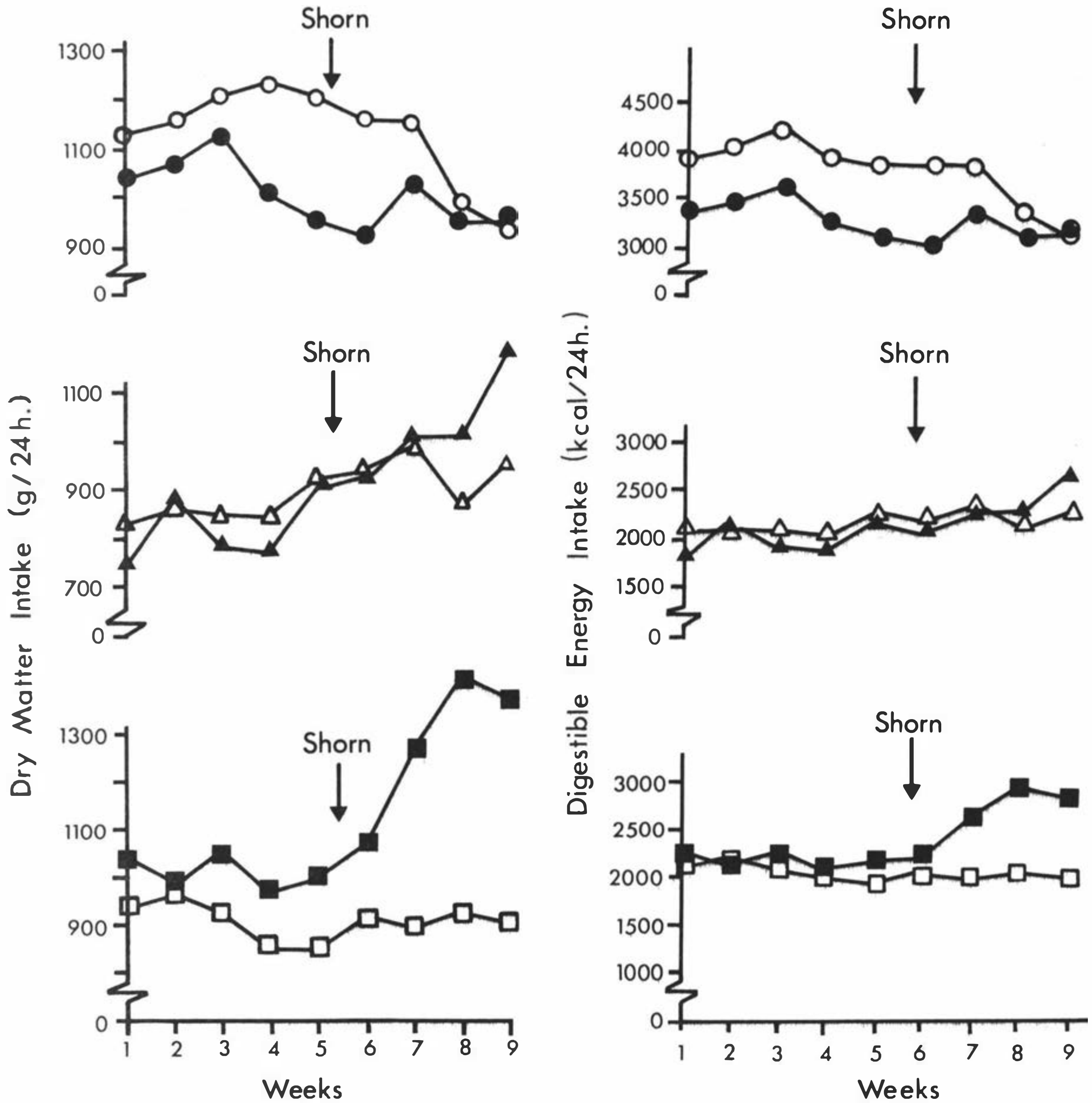

FIGURE 4.2 Experiment 2. Mean daily voluntary intake by sheep, before and after shearing:
● dried grass, shorn; ○ dried grass, unshorn;
▲ chopped hay, shorn; △ chopped hay, unshorn;
■ ground hay, shorn; □ ground hay, unshorn.

TABLE 4.5 Expt 2. Mean daily voluntary intake of sheep receiving dried grass, chopped hay or ground hay before (P_1) and after (P_2) shearing

Feed	Treatment	Period 1	Period 2	SE	Significance of difference
		DM intake (g/24 h.)			
Dried grass	shorn	1040	994	89	N.S.
	unshorn	1148	817		
Chopped hay	shorn	815	1117	70	+
	unshorn	858	900		
Ground hay	shorn	1010	1337	72	*
	unshorn	907	976		
		DE intake (kcal/24 h.)			
Dried grass	shorn	3377	3212	239	N.S.
	unshorn	3674	2789		
Chopped hay	shorn	1977	2494	182	+
	unshorn	2111	2063		
Ground hay	shorn	2161	2786	120	*
	unshorn	2013	2105		
		DE intake (kcal/kg $^{0.75}$/24 h.)			
Dried grass	shorn	211	187	13	N.S.
	unshorn	238	170		
Chopped hay	shorn	138	171	10	*
	unshorn	135	138		
Ground hay	shorn	140	177	6	**
	unshorn	133	141		

Means for voluntary intake in Period 2 have been adjusted by analysis of covariance

SE = Standard error of the difference between adjusted means

NS , Non significant

+ , $P < 0.10$

* , $P < 0.05$

** , $P < 0.01$

in voluntary intake following shearing of the sheep receiving ground hay, and the apparent lack of response to shearing of the sheep receiving dried grass, although Fig. 4.2 shows that a decline in intake appeared to be arrested following shearing. As shown in Fig. 4.2, the voluntary intakes of the unshorn control sheep receiving dried grass declined at a greater rate than the shorn sheep, although the effect was not significant. Digestible energy intake increased by 287 kcal/24 h. (235 kcal ME) over the whole of Period 2 for the sheep receiving chopped hay, and by 481 kcal DE/24 h. (394 kcal ME) at the time of greatest response. Corresponding increases for the sheep receiving ground hay were 469 (385 kcal ME) and 698 kcal DE/24 h. (572 kcal ME).

Expt 3: The voluntary intakes of sheep receiving ground hay are summarised in Table 4.6 and are illustrated in Fig. 4.3. The means for voluntary intake in Period 2, given in Table 4.6, have been adjusted by analysis of covariance and are the means for the whole of Period 2. The levels of significance refer to the differences between the adjusted mean voluntary intakes of the shorn and unshorn sheep.

TABLE 4.6 Expt 3. Mean daily voluntary intake of sheep receiving ground hay before (P_1) and after (P_2) shearing

Voluntary intake	Treatments	Period 1	Period 2	SE	Significance of differences
DM intake (g/24 h.)	shorn	1147	1412	48	**
	unshorn	1110	1175		
DE intake (kcal/24 h.)	shorn	2560	3151	146	*
	unshorn	2524	2672		
DE intake (kcal/kg $^{0.75}$/24 h.)	shorn	170	189	10	NS
	unshorn	156	170		

Means for voluntary intake in Period 2 have been adjusted by analysis of covariance

SE = Standard error of differences between adjusted means

NS, non significant

*, $P < 0.05$

**, $P < 0.01$

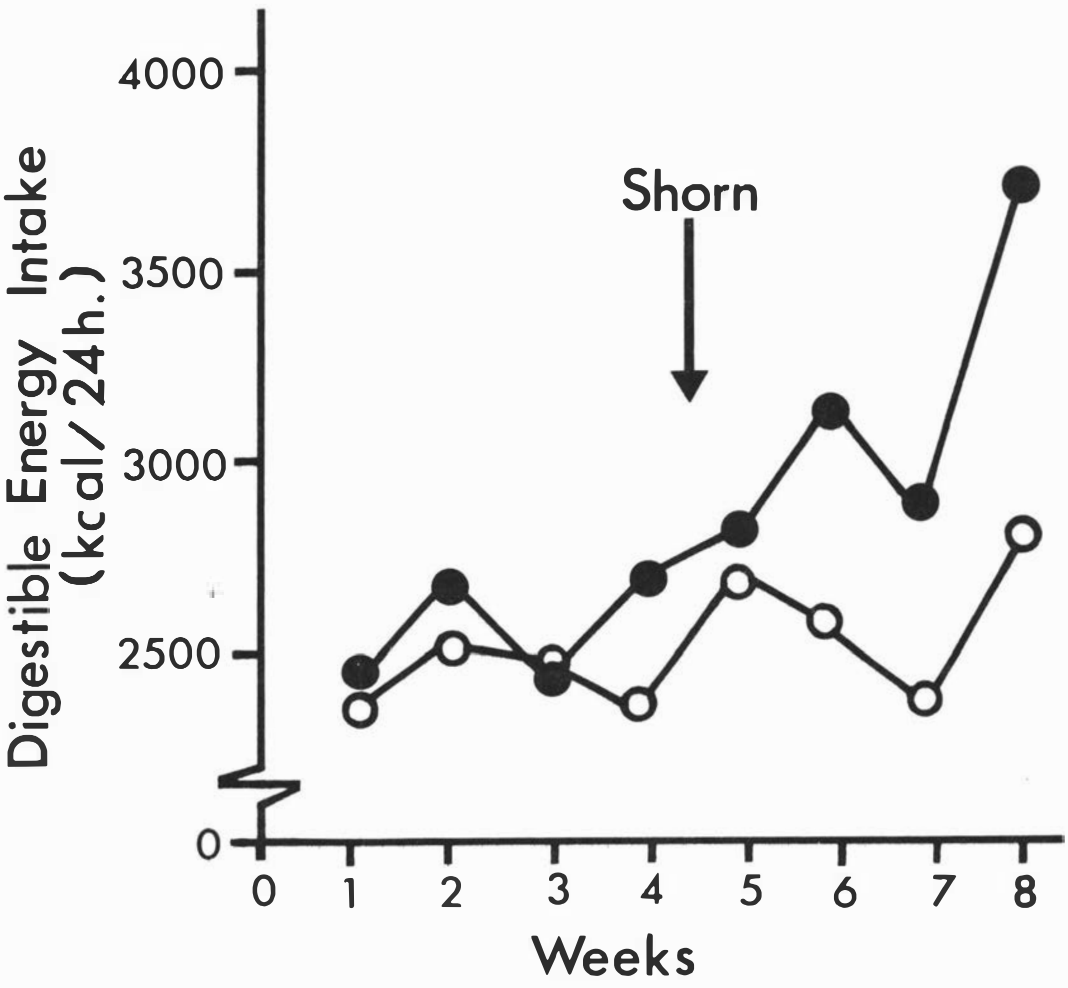

FIGURE 4.3 Experiment 3. Mean daily voluntary intake by sheep receiving ground hay, before and after shearing.
● shorn; ○ unshorn.

A mean increase of 610 kcal DE/24 h. (unadjusted mean for P_2 - mean for P_1) occurred with the shorn sheep over the four week period following shearing. The mean daily increase for the control sheep over the same period was 130 kcal/24 h. giving a net increase of 480 kcal DE or 393 kcal ME/24 h. Corresponding increases in DE intake for the fourth week of Period 2 (i.e. time of maximum response), compared with the mean for Period 1 were 1159 kcal for the shorn sheep and 346 kcal/24 h. for the control sheep, giving a net increase of 813 kcal DE or 667 kcal ME/24 h. The sheep took approximately one week longer to reach peak intakes, compared with the sheep receiving ground hay in Expt 2. Differences in intake between the shorn and unshorn sheep decreased when intake was expressed as a proportion of metabolic size, probably because of the increased gut fill of the shorn sheep.

Expt 4: There were no significant differences in mean DM intakes in Period 2 between the shorn and unshorn sheep receiving chopped hay. Mean DE intakes were 122 kcal DE/kg$^{0.75}$/24 h. and 164 kcal for the unshorn and shorn sheep respectively. Variability in intake between sheep was high, and control animals continued to increase their intake as the experiment progressed, probably because of the short preliminary period. The main objective of this experiment was to obtain data on the alimentary tract and its contents as a result of feeding chopped hay.

4.3.4 Apparent digestibility of energy and nitrogen balance

Expt 1(a) and 1(b): The mean apparent digestibility of the energy of dried grass was 73.2 $\pm$ 2.3% and 58.5 $\pm$ 0.9% for the chopped hay. The limited evidence available showed no change in apparent digestibility with either food following shearing, in both experiments.

Expt 2: The apparent digestibility of the foods and the nitrogen retained by the sheep are summarised in Table 4.7. The apparent digestibility of the chopped hay was depressed following shearing ($P < 0.05$). There was no significant relationship between the DM intake of the dried grass (g x) and the apparent digestibility of the energy of the dried grass (% y). The corresponding relationship for the chopped hay was significant ($P < .10$, $r = 0.67$, 6 df, $b = 0.01 \pm .003$, $s_{y.x}$ 4.8%) and was significant ($P < 0.05$) for the ground hay ($r = 0.76$, 6 df, $b = .01 \pm .002$, $s_{y.x}$ 1.5%). The apparent digestibility of the energy of the ground hay was less than that for the chopped hay ($P < 0.01$), but there was no significant differences between the two foods in the apparent digestibility of nitrogen. All sheep appeared to be in positive nitrogen balance, with nitrogen retained per day being less ($P < 0.01$) for sheep receiving chopped hay and ground hay than those receiving dried grass. There were no significant differences in nitrogen retained between the sheep fed the chopped hay or ground hay, nor were there any significant differences between shorn and unshorn sheep in the amounts of nitrogen retained.

TABLE 4.7 Expt 2. Apparent digestibility of energy and nitrogen, nitrogen retained, and mean retention time of food residues obtained with sheep receiving dried grass, chopped hay or ground hay, before and after shearing

Diet	Treatment	Period 1	Period 2	SE	Period 1	Period 2	SE
		Apparent digestibility of energy (%)			Mean retention time(h.)		
Dried grass	shorn	73.8	73.3	0.6	33.9	33.6	1.8
	unshorn	72.4	74.6		31.3	34.4	
Chopped hay	shorn	55.3	51.3	0.8	32.4	27.2	1.8
	unshorn	56.4	54.1		34.3	30.7	
Ground hay	shorn	48.7	46.2	0.8	27.3	23.8	1.2
	unshorn	51.5	50.5		30.1	31.0	
		Apparent digestibility of nitrogen (%)			Nitrogen retained (g/24 h.)		
Dried grass	shorn	N.D.	72.5	1.4	N.D.	5.77	0.23
	unshorn		72.6			5.70	
Chopped hay	shorn	N.D.	48.7		N.D.	2.05	
	unshorn		52.9			1.93	
Ground hay	shorn	N.D.	45.3		N.D.	1.88	
	unshorn		46.3			1.51	

N.D. = not determined

<u>Expt 3</u>: Mean apparent digestibilities of the energy of the ground hay are given in Table 4.8. There was no change in the apparent digestibility of the energy of the ground hay following shearing.

TABLE 4.8 Expt 3. Apparent digestibility of energy and mean retention time of food residues using ^{144}Ce, and obtained with sheep offered ground hay before and after shearing

Measurements		Period 1	Period 2	SE	Significance of differences
Apparent digestibility of energy (%)	shorn	51.6	51.1	0.7	NS
	unshorn	51.9	53.0		
Mean retention time (h.)	shorn	34.9	29.7	1.6	+
	unshorn	32.5	35.0		

Expt 4: The mean apparent digestibility of the energy of the chopped hay was 54.9 ± 1.2%

4.3.5 Mean retention times of food residues in the alimentary tract

Expt 1(a): Mean retention times of food residues were 31.3 ± 2.6 h. for the dried grass, and 36.5 ± 0.9 h. for the chopped hay. Mean retention times were lower by 3.2 h. for the chopped hay after the sheep were shorn, and were higher by 2.0 h. for the unshorn sheep fed chopped hay, in Period 2. There was a highly significant negative relationship ($P < 0.01$) between the DM intake of the chopped hay (kg,x) and mean retention time (h.,y) of the hay ($r = -0.77$, 8 df, $b = -.04 \pm .001$, sy.x, 2.2 h.). There was no change in the mean retention times of dried grass when sheep were shorn, although mean retention times with the unshorn sheep increased by 3.7 h. in Period 2. However the changes were not statistically significant nor was there a significant relationship between the voluntary intake of dried grass and mean retention time of food residues.

Expt 1(b): Mean retention times of the hay residues were 36.3 and 31.8 ± 1.5 h. for Period 1 and Period 2 (shorn) respectively. Corresponding values for the dried grass were 34.7 and 28.3 ± 3.8 h.

Expt 2: Although it appeared that mean retention times for the chopped hay were lower following shearing, (Table 4.7) these differences were insufficient to reach significance, but a highly significant negative relationship ($P<0.01$), ($r = -0.93$, 6 df, $b = -0.02 \pm .003$, sy.x 1.7) was obtained between DM intake (kg, x) and retention time (h., y). The corresponding relationship was significant ($P<0.10$) for the ground hay ($r = -0.64$, 6 df, $b = -.007 \pm .003$, sy.x 2.7) but there was no significant relationship between these parameters for the dried grass.

Expt 3: The mean retention time of ground hay residues determined with the shorn sheep in Period 2 were significantly less ($P<0.10$) than corresponding values obtained with the unshorn sheep (Table 4.8). A significant negative relationship ($P<0.05$) was obtained between the DM intake of the ground hay (kg, x) and retention time (h., y, $r = -0.57$, 14 df, $b = -.009 \pm .004$, sy.x 4.4 h.).

4.3.6 Digestion of cellulose in the rumen

Expt 1(a) and 1(b): The times taken for the cotton threads, placed in the ventral sac of the rumen, to lose 30% of their weight were less for the hay than the dried grass (Table 4.9). No effect of shearing was evident in the results obtained.

TABLE 4.9 Expt 3. Time for 30% loss of weight of cotton threads placed in the ventral rumen of sheep receiving chopped hay or dried grass, before (P_1) and after (P_2) shearing

Expt	Period	Time (h.) for 30% loss of weight		Remarks
		Chopped hay	Dried grass	
1(a)	1	25	30	all sheep unshorn
1(a)	2	22	33	shorn
		23	34	unshorn
1(b)	1	23	34	all sheep unshorn
	2	21	29	all sheep shorn

4.3.7 Live weights and live weight changes

Mean live weights of the sheep at the beginning of all experiments are given in Table 4.1.

Expt 1(a): There were insufficient data to obtain meaningful comparisons between shorn and unshorn animals. Mean live weight changes taken over the whole of the experiment were 80 g/24 h. for the sheep receiving dried grass, and -49 g/24 h. for those fed chopped hay.

Expt 2: Mean daily live weight changes over the post-shearing period are summarised in Table 4.10. With the exception of the unshorn sheep in Period 2, liveweight gains were greater with the sheep fed dried grass. It is probable that much of the increased live weight gain of the shorn sheep receiving chopped hay and ground hay in Period 2 arose through a greater alimentary tract fill, as a consequence of the increase in food intake.

TABLE 4.10 Expt 2. Mean daily live weight changes (g/24 h.) of sheep receiving dried grass, chopped hay or ground hay, before (P_1) and after (P_2) shearing

Diet	Treatment	Period 1 (g/24 h.)	Period 2 (g/24 h.)	SE	Significance of difference
Unadjusted					
Dried grass	shorn	148	135	27	*
	unshorn	110	10		
Chopped hay	shorn	50	112	29	*
	unshorn	-63	72		
Ground hay	shorn	69	112	43	NS
	unshorn	15	-5		
Adjusted on the basis of empty live weights					
Dried grass	shorn	153	133	25	+
	unshorn	108	42		
Chopped hay	shorn	23	27	41	NS
	unshorn	-93	43		
Ground hay	shorn	52	-9	37	NS
	unshorn	1	11		

SE = Standard error of period means

Live weight gains were therefore adjusted on the basis of equations relating DM intake (x, kg/24 h.) to the weight of the contents of the alimentary tract (y, kg), determined at slaughter. The data for the ground hay and chopped hay were obtained in Expts 3 and 4 respectively, with that for the dried grass being obtained in the experiment dealing with the effect of body condition on voluntary intake (Chapter 5). The equations were as follows:-

(1) Chopped hay:

$y = 0.68 + (5.51 \pm 1.35)\ x$, sy.x, 0.33 kg ($P < 0.01$)

(2) Ground hay:

$y = 4.49 + (3.40 \pm 1.32)\ x$, sy.x, 0.61 kg ($P < 0.05$)

(3) Dried grass:

$y = 3.87 + (2.56 \pm 0.23)\ x$, sy.x, 0.72 kg ($P < 0.01$)

The adjusted live weight gains are summarised in Table 4.10 and show that most of the increase in live weight gain in Period 2 compared with Period 1, with the shorn sheep receiving the chopped hay or ground hay, had disappeared. The adjusted live weight gains of the unshorn sheep receiving dried grass were still lower in Period 2 compared with the shorn sheep.

Expt 3: Changes in live weight based on actual measurements, as well as those based on empty live weights, are summarised in Table 4.11. The empty live weights were calculated using equation (2). The results show that the increase in alimentary tract contents, resulting from higher food intakes of the shorn sheep, partly contributed to the greater actual live weight gains in Period 2. Even so the adjusted live weight gains of the shorn sheep were significantly greater ($P < 0.01$) in Period 2 than in Period 1.

TABLE 4.11 Expt 3. Mean daily live weight changes of sheep receiving ground hay, before (P_1) and after (P_2) shearing

Live weight change	Treat-ment	Period 1	Period 2	SE	Significance of differences
Live weight change (g/24 h.)	shorn	97	230	31	**
	unshorn	93	-29		
Live weight change (g/24 h.) based on empty live weights	shorn	92	176	29	**
	unshorn	162	-26		

4.3.8 Measurements relating to the alimentary tract and alimentary tract fill

(i) Indirect measurement of DM in the reticulorumen in Expt 1(a):

The amounts of DM in the reticulorumen (estimated by using PEG) of the sheep in Expt 1(a), together with mean daily DM intakes at the time of estimation are given in Table 4.12. There were no differences in the amount of DM in the reticulorumen of the sheep receiving chopped hay, before and after they were shorn, despite the considerably higher intake of the sheep following shearing.

TABLE 4.12 Expt 1(a). Amount of dry matter (g), (estimated by using polyethylene glycol), in the reticulorumen of sheep receiving chopped hay or dried grass, before (P_1) and after (P_2) shearing, and dry matter intakes over the period of estimation

Measurement	Chopped hay Shorn	Chopped hay Unshorn	Dried grass Shorn	Dried grass Unshorn
DM in reticulorumen(g)				
Period 1	459	597 ± 27 **	533	436 ± 31 *
Period 2	481	447	519	397
DM intake (g/24 h.)				
Period 1	715	1140	1561	1124
Period 2	1050	1092	1955	1328

This result is consistent with the shorter retention time of the chopped hay residues of the shorn sheep in Period 2 compared with Period 1. There were greater amounts of DM in the reticulorumen of the unshorn sheep receiving chopped hay in Period 1 ($P < 0.01$) than in Period 2. The values for the unshorn sheep in Period 1 were also greater ($P < 0.05$) than those for the shorn group of sheep in both periods.

(ii) Slaughter data:

Table 4.13 summarises the data obtained at slaughter in Expt 3 and 4. The only measurements showing no significant differences between the shorn and unshorn animals, for both foods, were, those for

TABLE 4.13 Voluntary intakes and live weights prior to slaughter, and digestive tract parameters by sheep receiving chopped hay or ground hay

Measurements	Expt 3. Ground hay			Expt 4. Chopped hay		
	Unshorn	shorn	SE	Unshorn	shorn	SE
DM intake mean 7 days prior to slaughter (g/24 h.)	1195	1773	183 *	1129	1428	110 NS
Live weight at slaughter (kg)	40.7	43.8	2.0 NS	53.4	52.0	1.7 NS
Empty liveweight at slaughter (kg)	32.4	32.2	1.6 NS	44.0	40.6	1.7 NS
Volume of reticulo-rumen (l)	7.9	11.1	1.4 NS	11.6	11.8	1.3 NS
Contents of rumen (g)	5675	7664	709 +	7234	8147	860 NS
DM in the reticulo-rumen (g)	613	802	132 NS	496	989	80 **
‡Adjusted DM in the reticulorumen (g)	277	469	69 +	241	461	66 +
Contents of abomasum and omasum (g)	697	1131	100 *	401	639	140 NS
Contents of intestines (g)	1944	2830	273 *	1772	2566	358 NS
Contents of whole tract (g)	8318	11626	820 *	9406	11350	121 NS
DM in whole tract (g)	934	1171	139 NS	683	1313	104 **
DM content of reticulo-rumen ingesta (g)	10.6	10.2	0.9 NS	6.7	12.2	0.6 **
Weight of the reticulorumen (g)	852	1050	107 NS	921	1077	43 *
Weight of the abomasum and omasum (g)	362	462	17 **	426	456	24 NS
Weight of intestines (g)	985	1454	73 **	1100	1436	81 *
Weight of whole tract (g)	2200	3217	247 *	2447	2970	138 *
Weight of abdominal fat (g)	1462	1218	223 NS	3469	1948	597 NS

‡Adjusted DM in reticulorumen = DM in reticulorumen - DM eaten on morning of slaughter

NS, Non significant +, $P < 0.10$ *, $P < 0.05$
**, $P < 0.01$

the volume of the rumen, and weight of abdominal fat. All of the measurements, except the weight of abdominal fat, whether significant or not, were greater for the shorn sheep compared with the unshorn sheep, with both the chopped and the ground hay. The amount of DM in the reticulorumen of the shorn sheep receiving the chopped hay appeared to be higher than might be expected from the difference in mean DM intake between the shorn and unshorn sheep. This could be partly attributed to the greater DM intake ($P < 0.01$) of the shorn sheep, of 528 g, compared with the unshorn sheep of 255 g, on the morning of slaughter. An arbitrary allowance for this was made by subtracting the food eaten on the morning of slaughter from the amount of digesta DM in the reticulorumen. This considerably reduced, although it did not eliminate differences in the amount of DM in the reticulorumen between the two groups of sheep. There were no significant differences in DM intake on the morning of slaughter, between the shorn and unshorn sheep receiving ground hay. A noteworthy feature of the results was the greater weights of various alimentary organs with the shorn sheep compared with the unshorn sheep in both experiments.

Relationships between DM intake (g/24 h., x) and various alimentary tract measurements (y) are summarised in Table 4.14. The relationship between DM intake and the amount of DM in the reticulorumen for both diets is illustrated in Fig.4.4. Relationships were almost all stronger for the unshorn compared with the shorn sheep (Table 4.14). Most of the relationships for the pooled data were significant for the chopped hay, but not the ground hay. Fig.4.4 provides an example of the nature of the relationships.

4.3.9 Feeding behaviour:

A summary of feeding behaviour obtained in Expt 1(a), 1(b) and 2 is given in Table 4.15. The time spent eating dried grass was less than that spent eating hay, and almost twice the time was spent eating a unit amount of hay compared with grass. Ruminating times were also less for dried grass compared with the hay, particularly when expressed per unit of intake. There were no differences in the time spent ruminating between the chopped hay and ground hay, but the sheep spent less time eating the ground hay than the chopped hay. The shorn sheep receiving chopped hay spent more time ruminating than the unshorn sheep in Expt 1(b). Comparisons in feeding behaviour between shorn and unshorn sheep in Expt 1(a) and 2 were not available.

TABLE 4.14 Expt 3 and 4. Significance of relationships, and correlation coefficients between dry matter intake and various alimentary tract measurements, for sheep receiving ground hay or chopped hay

Relationships	Ground hay Unshorn	Ground hay shorn	Chopped hay unshorn	Chopped hay shorn
DM intake(g/24 h.x) versus y(g):				
DM in the reticulorumen	.96 *	.51 NS	.77 NS	.87 NS
Wet contents of intestine	.66 NS	.10 NS	.99 **	.56 NS
DM caudal to rumen	.85 NS	.38 NS	.96 *	.21 NS
Wet contents of tract	.85 NS	.53 NS	.96 *	.67 NS
DM in tract	.98 *	.47 NS	.87 NS	.97 NS
Weight of abomasum and omasum	.97 *	.10 NS	.34 NS	.75 NS
Weight of tract	.85 NS	.95 *	.77 NS	.65 NS

TABLE 4.15 Expt 1(a), 1(b) and 2. Mean time spent eating and ruminating dried grass, chopped hay or ground hay

Experiment and Diet	Eating Min/24 h.	Eating Min/g DM intake	Ruminating Min/24 h.	Ruminating Min/g DM intake
Expt 1(a)				
Dried grass Chopped hay	222 282 ± 23 *	.15 .28 ± .02 **	510 550 ± 23 NS	.35 .55 ± .05**
Expt 1(b)				
Dried grass Chopped hay	183 324 ± 26**	.14 .28 ± .03 **	492 565 ± 30 *	.37 .48 ± .03**
Dried grass shorn Dried grass unshorn	201 167 ± 24NS	.13 .15 ± .02 NS	536 455 ± 38 NS	.34 .39 ± .03NS
Chopped hay shorn Chopped hay unshorn	334 316 ± 47NS	.32 .24 ± .05 NS	620 520 ± 26 **	.52 .44 ± .04 *
Expt 2				
Chopped hay Ground hay	312 222 ± 30**	.31 .25 ± .04 NS	572 572 ± 39 NS	.59 .61 ± .06NS

NS, non significant

*, $P < 0.05$

**, $P < 0.01$

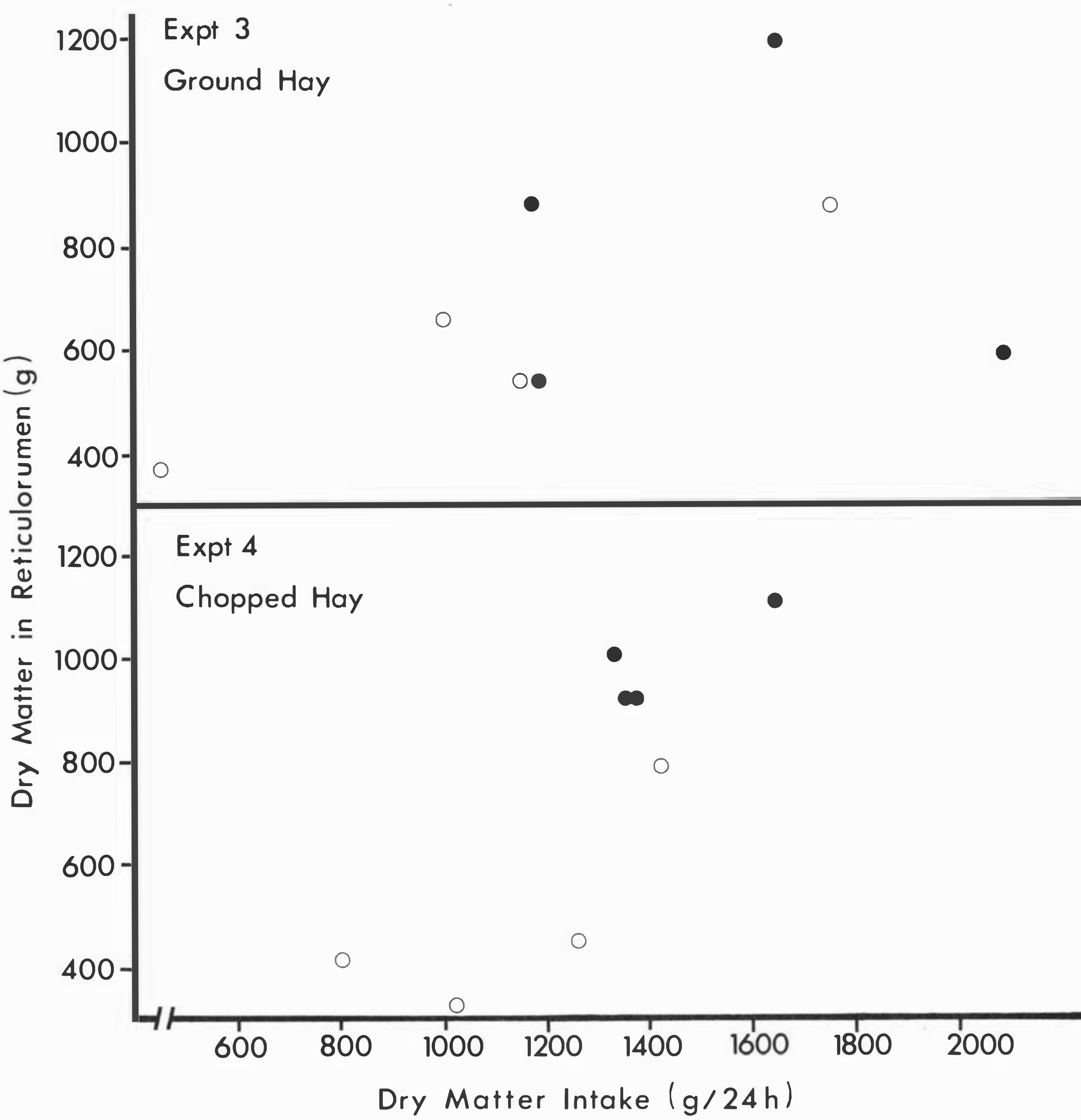

FIGURE 4.4 Relationships between dry matter intake and the amount of dry matter in the reticulorumen of sheep, determined at slaughter.

○, unshorn; ●, shorn.

4.4 DISCUSSION

4.4.1 Voluntary food intake

The results obtained in these experiments showed that changes in voluntary food intake of sheep following shearing varied with the type of diet, and its physical form.

The increases in voluntary food intake of sheep receiving both chopped hay or ground hay following shearing, in the present experiments, were more consistent than the changes observed, in the intake of dried grass. The extent of the increases in intake for chopped hay agreed with those obtained by other workers, using similar diets. It was calculated from the data of Minson & Ternouth (1971), and Weston (1970) that the estimated ME intake (DE x 0.82) increased by 150 to 290 kcal/24 h. when sheep were shorn. Similar responses with chopped hay were noted in the present series of experiments, with mean increases of 175 and 149 kcal estimated ME/24 h. for intact and fistulated sheep respectively (Chapter 3), and 235 kcal in Expt 2, in the present chapter. The main exception to this was the large increase in intake of the sheep receiving chopped hay in Expt 1(b). The chopped hay in this experiment had a higher digestibility than in any other experiment, which may have contributed to this difference. However this result is based on limited evidence, obtained with two sheep, with no unshorn controls. The mean increases in estimated ME intake of the sheep receiving ground hay, when they were shorn, of 385 kcal/24 h. in Expt 2 and 393 kcal/24 h. in Expt 3, indicates that grinding had the effect of enhancing the response to shearing. The net increase in the estimated ME intake of ground hay at the time of maximum response of 572 and 667 kcal/24 h. for Expt 2 and 3 respectively is considerable. That the increase in the food intake of the sheep receiving the ground hay was sufficient to meet the increase in energy demand following shearing is indicated by live weight changes which were at least maintained in Expt 2 and increased in Expt 3, and are in contrast to the results obtained with the sheep fed chopped hay in the earlier experiment (Chapter 3).

Evidence gained by Blaxter & Wilson (1963) suggested that a minimum of 8.5% crude protein was needed to ensure maximum intake of hay by sheep. Crude protein levels of the hay used in the present experiments were above this value and were higher than the crude protein level of the chopped hay used in the earlier experiment (Chapter 3). Therefore it is probable that intake was not limited by low levels of protein in the present experiment. The positive nitrogen balance of the sheep receiving hay in Expt 2, supports this contention.

In only one case was there an appreciable increase in the intake of dried grass following shearing (Expt 1(a)), but the results of this experiment were probably affected by the emptying of the reticulorumens at the end of Period 1. It was also noted that the voluntary intakes of the unshorn animals receiving dried grass in some cases decreased, as the experiment progressed. While there may have been only small increases in the voluntary intake of dried grass following shearing, it did appear, to some extent, to prevent the fall in intake noted with the unshorn sheep (Expt 2). The reasons for this lack of response to shearing are difficult to explain,as it was assumed from the work of Armstrong, Blaxter, Graham & Wainman (1959) that the ambient temperature of 13^{o}C chosen for the present series of experiments would have been sufficiently below the critical temperature of shorn sheep to have resulted in a considerable increase in energy expenditure. Hence an increase in the voluntary intake of dried grass might have been expected, particularly as physical factors limiting intake may not have been important.

Decreased voluntary intakes by ruminants when fat have been observed by a number of workers, (Schinckel, 1960; Graham, 1969; Foot, 1972 with sheep, and Bines, Suzuki & Balch, 1969 with cattle). Voluntary food intake may be restricted in fat animals by the presence of abdominal fat, as has been shown by Tayler (1959), or it is possible that a mechanism postulated by Kennedy (1953) was operating, where some compound released from fat depots in proportion to their size, inhibited intake. Minson & Ternouth (1971) observed that shorn sheep consumed no more lucerne hay of a high quality, with a digestibility of 70.6%, than did unshorn sheep, whereas the intakes of their shorn sheep, receiving poor hay were higher than the unshorn sheep. The digestible DM intakes of the sheep receiving the lucerne hay were double those receiving the poor hays. The sheep receiving lucerne hay also gained weight throughout the experiment, whereas the sheep receiving the poor hays lost weight, or at best barely maintained it. The authors were unable to offer an explanation of these results beyond suggesting that

"when the food intake is greatly in excess of the

> maintenance requirements of sheep, a mechanism other than one maintaining an energy balance limits food intake".

It is possible that with sheep receiving a food of low DE concentration, a depletion of abdominal fat occurs and permits a greater increase in rumen volume and hence a greater increase in intake, than with a food of high DE concentration, but evidence is lacking.

4.4.2 Retention times of food residues and apparent digestibility

With chopped hay in Expt 1(a) and 1(b) and ground hay in Expt 3, retention times were reduced following shearing. There was also a highly significant negative relationship ($P < 0.01$) between DM intake and retention time with the chopped hay, but not with the dried grass. In Expt 2, this relationship was highly significant for chopped hay ($P < 0.01$), significant ($P < 0.10$) for the ground hay, not significant for the dried grass, and in Expt 3, highly significant ($P < 0.01$) for the ground hay. This suggests that physical capacity of the tract played a part in limiting the intake of both the chopped and ground hay. It is also apparent that these physical effects are modified by the particle size of the feed even though the particle size of the ground hay was not small enough to have affected the time spent ruminating.

Unlike the earlier experiment described in Chapter 3, no clear-cut depressions occurred in the apparent digestibility of the hay following shearing, as only with the chopped hay in Expt 2 was apparent digestibility depressed. This may be a reflection of the limited amount of data available on apparent digestibility.

4.4.3 Measurements relating to the alimentary tract and alimentary tract fill

The amount of DM in the reticulorumen, estimated by using PEG, of the sheep receiving chopped hay in Expt 1(a) did not increase following shearing, in contrast to the results obtained in an earlier experiment (Chapter 3) and in Expt 4 (see Table 4.13). Inconsistencies in the amount of DM in the reticulorumen of the unshorn sheep receiving dried grass were also noted, so that the accuracy of the indirect estimations of DM in the reticulorumen could be questioned. That voluntary intake may have had an effect on the amount of DM in the reticulorumen in Expt 1(a) is indicated by the significant positive relationships obtained between these two variables with both diets.

The amounts of both wet or dry contents of the alimentary tract, or parts of the tract determined at slaughter, were generally greater with the shorn sheep than the unshorn controls with both chopped hay and ground hay. This increase substantiates earlier work in Chapter 3 when it was postulated that a new threshold to reticulorumen capacity is set in response to an increased energy demand following shearing. The amounts of abomasal, omasal and intestinal contents were greater with the shorn sheep receiving ground hay compared with the unshorn animals, whereas with the shorn sheep receiving chopped hay there was no such clearcut increase in this part of the tract. This suggests that the particles of ground hay may have left the reticulorumen at a faster rate than the particles from chopped hay.

Stronger relationships were obtained between DM intake and various alimentary tract measurements for the unshorn sheep compared with those for the shorn sheep. This was observed with both diets, and suggests that the physical capacity of the tract may have been of lesser importance in limiting intake with the unshorn, than the shorn sheep.

The weights of the alimentary organs of the shorn sheep were heavier than those of the unshorn sheep receiving both the chopped hay and ground hay. The data for the sheep receiving the chopped hay needs to be treated with caution, as the sheep in the shorn group in Period 1 had significantly higher intakes ($P < 0.10$) than those in the control group. It is possible that the shorn group of sheep receiving chopped hay may have had heavier alimentary organs than the unshorn group of sheep at the start of the experiment with chopped hay. No such objections apply to the experiment with ground hay, as the voluntary intakes were similar between the two groups of sheep at the start of the experiment. No measurements of the alimentary tract other than weight were taken, so that no conclusions can be made as to whether the increased weights of the organs was because of an increase in volume or thickness of the wall, or a combination of both. Fell, Campbell & Boyne (1964) observed a rapid increase in the weight of the wall of the alimentary tract as lactation progressed, with grazing ewes, and the intestines reached their greatest weight at about 80 days after lambing. Later Fell, Campbell, Mackie & Weekes (1972), working with ewes fed indoors, again observed this hypertrophy of the alimentary organs during lactation. Maximum values for the hypertrophy of the rumen mucosa occurred in the 6th week of lactation,and the small intestine reached its maximum weight after the 4th week of lactation, considerably earlier than noted with the grazing ewes. Campbell & Fell (1964) observed that the hypertrophy of the alimentary canal of rats when lactating, is a consequence of increased food consumption associated with lactation. If the increased weight of the alimentary organs means that they have an increased capacity, then much of the increase in food intake following shearing could be accommodated without a concomitant increase in the distension of the alimentary tract. Although the increase in energy expenditure must have occurred immediately following shearing, increases in intake were delayed. This illustrates the imprecise nature of short-term control of voluntary intake, probably partly because it has to await hypertrophy of the alimentary tract.

4.4.4 Digestion of cellulose in the rumen

The measurement of the rate of breakdown of cellulose in Expt 1(a) and 1(b) was carried out with the hope that it would provide information on one of the factors influencing intake (see Section 1.2.2.3). No difference in the rate of digestion was observed when sheep were shorn, but the evidence was too limited to suggest that this was unimportant in influencing intake. For the reasons mentioned earlier, (Section 4.1) the determination of cellulose breakdown was not carried out in the other experiments.

4.4.5 Feeding behaviour

Eating and ruminating times were similar with the chopped and ground hays, but were considerably greater than the times spent on these activities by sheep receiving the dried grass. There is no evidence in this experiment that the time spent eating and ruminating influenced intake.

4.4.6 Conclusion

The evidence obtained supported the results obtained in Chapter 3, in that the voluntary intake of sheep receiving hay increased following shearing. In addition the results showed that the response, in terms of an increase in voluntary intake, was greater for ground hay than chopped hay. This suggested that one of the factors involved in the control of intake, and the response to shearing, was the rate at which food particles could be reduced in size to pass from the reticulorumen.

It appeared that the increase in the intake of either chopped hay or ground hay following shearing could be accommodated partly by a decrease in the retention time of food residues, and partly by the ability of the alimentary tract to increase its capacity. The decrease in the intake of dried grass by unshorn sheep as the experiment progressed suggested that body condition may have influenced the food intake of these animals. The irregular responses to shearing in terms of changes in voluntary intake by the sheep receiving dried grass were difficult to explain, although in Expt 1(a) and 1(b) it could be claimed that insufficient numbers of sheep were used to produce meaningful results. Nevertheless the responses with dried grass were different from those obtained, using chopped or ground hay. The nature of the results obtained with dried grass in the present chapter indicated the need for more information on the voluntary intake characteristics of sheep receiving this food. This forms the basis of the next chapter.

CHAPTER 5

THE EFFECT OF BODY CONDITION AND OF SHEARING ON VOLUNTARY INTAKE OF SHEEP RECEIVING DRIED GRASS

SUMMARY

Twenty 15-month old Romney wethers were used to compare the effects of body condition and of shearing on the voluntary intake of dried grass. Ten of the sheep were fed restricted amounts of food for 60 days, the "thin" group, and 10 were fed *ad libitum* for the same period, the "fat" group. Live weights at the end of the period of differential feeding were 29.5 and 40.0 kg for the thin and fat sheep respectively. Following a period of 14 days when all sheep were fed *ad libitum*, five sheep in each group were shorn and five were left unshorn as controls, and received dried grass *ad libitum* for a further four weeks. At the end of the experiment all sheep were slaughtered, and various measurements relating to the alimentary tract were made.

There was an increase in the voluntary food intake of the fat sheep following shearing, whereas intakes of the fat unshorn sheep declined over the experimental period. Digestible energy intake, per unit of metabolic size, of the thin shorn sheep was higher than all other groups, and it appeared that this resulted from a combination of the stimulus of shearing, and an increase in voluntary intake following a period of food restriction.

The lack of significant negative relationships between the amount of abdominal fat and digestive tract contents, or between the amount of abdominal fat and voluntary food intake, suggested that physical constriction of the alimentary tract by abdominal fat was not a factor limiting the intakes of the fat unshorn sheep. The lack of relationships between voluntary intake and the wet and dry contents of the reticulorumen, and the strong relationship between intake and weight of the empty reticulorumen suggested that the physical capacity of this organ was playing a part in limiting intake, whereas the strong relationship between

intake and the wet and dry contents of the hind gut suggested that the capacity of this portion of the tract was not limiting intake.

The evidence obtained indicated that physical factors placed a ceiling on voluntary intake, but that the ceiling varied depending upon the energy requirements and body condition of the animals.

5.1 INTRODUCTION

In previous work (Chapter 4) investigating the effect of shearing on voluntary food intake of sheep, responses varied, depending upon the diet fed. Generally with hay, there was a consistent increase in voluntary intake following shearing, but with dried grass the response was irregular. It is difficult to reconcile these results with the conclusion of Conrad, Pratt & Hibbs (1964) that the primary determinant of food intake, when the apparent digestibility of a food is greater than about 67%, is the physiological state of the animal, whereas at lower apparent digestibilities physical factors, mainly the capacity of the digestive tract, limit voluntary food intake. Under this hypothesis it might have been expected that the intake of dried grass would have increased in a more predictable manner to meet an increase in energy expenditure consequent on shearing, in these earlier experiments. It was also noted in some of this earlier work (Chapter 4), that the intake of unshorn sheep declined after a period of ad libitum feeding with dried grass. It appeared that shearing, whilst it did not always result in large increases in intake, did prevent the fall in intake noted with the unshorn sheep. A number of workers, e.g. Schinckel (1960) and Graham (1969) have observed a progressive decline in the food intake of sheep, associated with increasing bodily fatness, and Forbes (1969) demonstrated an additive effect of an increase in the size of the uterus in pregnancy and an increase in abdominal fat, in depressing reticulorumen volume. Tayler (1959) working with cattle, observed a negative relationship between internal fat and voluntary intake, and it is possible that the decline in intakes of sheep receiving dried grass, noted in the earlier work reported in Chapter 4, may have been brought about in a similar manner. There are also indications that the opposite effect may occur, that is, an enhanced intake following food restriction (Bines, Suzuki & Balch, 1969 with cows; Foot & Greenhalgh, 1969 with pregnant ewes; Allden & Young, 1964 with sheep grazing pasture) although the extent of this effect is difficult to determine.

The effect of shearing on the voluntary intake of sheep has been investigated in a number of experiments (Weston, 1970; Minson & Ternouth, 1971; Wodzicka-Tomaszewska, 1963 & 1964), but the effects of shearing on the voluntary intakes of sheep differing in body condition does not appear to have been studied.

The objective of this experiment was to provide evidence on the effects of shearing on voluntary intake of sheep receiving dried grass, and differing in body condition, in an attempt to explain results obtained in earlier work. It was also hoped that data obtained at slaughter, such as alimentary tract fill and amount of abdominal fat, might help explain some of the mechanisms involved in the control of food intake.

5.2 MATERIALS AND METHODS

5.2.1 Plan of the experiment

Twenty Romney wethers, approximately 15 months old at the start of the experiment, were paired for live weight and were allocated to a fat or thin group. The mean live weights of the groups at the beginning of the experiment were 33.5 ± 1.4 and 34.3 ± 1.4 kg for the "fat" and "thin" groups respectively.

An outline of the experiment showing the sequence of feeding in the various periods is given in Table 5.1. The objectives were to obtain two groups of sheep differing in live weight by approximately 10 kg over a period of 60 days. The aim with the thin group was not to restrict intake too severely to achieve this difference, particularly in the second stage of the preliminary period, as too great a food restriction, from the evidence of Keenan, McManus & Freer (1970), can affect the extent to which sheep increase intake following realimentation. At the end of the second preliminary period, the sheep within their body condition group were paired on the basis of their intakes, and sheep within pairs were allocated at random to shorn and unshorn groups, with the restriction that two of the sheep, one fat and one thin with very high intakes, were placed in the shorn groups. The four groups of sheep were as follows:-

Fat shorn, Fat unshorn

Thin shorn, and Thin unshorn

TABLE 5.1 Outline of the experiment showing the duration of the periods, and feeding within each period

Periods	Duration (days)	Times of feeding	Fat group	Thin group
Training period	14	0900 h.	Chopped hay *ad libitum*	
Preliminary Period 1(PP1)	28	0900 h.	Chopped hay 750g) concentrate-) oat husk 750g) mixture)	Chopped hay 500g)) barley straw 100g))
Preliminary Period 2(PP2)	32	0900 h. & 1600 h.	Dried grass *ad libitum*	dried grass 200g chopped hay 500g
Standardisation period (S.P.)	14	0900 h. & 1600 h.	dried grass *ad libitum*	
Experimental period (E.P.)	28	0900 h. & 1600 h.	dried grass *ad libitum*	

5.2.2 Foods and feeding

Because of the limited supply of dried grass, various diets which were available were used to achieve differences in body condition over the experimental period. The hay and pelleted concentrate-oat husk mixture were the same as those used in a previous experiment (Chapter 3), and apparent digestibility figures obtained earlier were used to estimate intakes of DE. Apparent digestibility values for the barley straw were provided by G.F. Wilson, Massey University (unpublished data). The dried grass was the same as that used in a previous experiment (Chapter 4) and was supplied in a chopped form by New Zealand Grassmeal Ltd., Tahuna.

The sheep were held in feeding crates in two temperature controlled rooms at an ambient temperature of 13°C ± 1°C and were fed as shown in Table 5.1.

5.2.3 General management and measurements

Voluntary intake and apparent digestibility of the dried grass were determined as described in Section 4.2.3. The apparent digestibility of the dried grass was determined using two sheep in each treatment group, by total collection of faeces over 14 days. Digestible energy intakes for all sheep were calculated using the apparent digestibility values obtained with these sheep. The mean retention time of food residues using ^{144}Ce were obtained at the same time, with the same sheep, and results were expressed as mean retention times, using the method of Castle (1956) as described in detail in Section 2.2.4.

Respiration rates were obtained at 1400 h. for all sheep on two days in the standardisation period, and on two days in the first week of the experimental period. The length of wool remaining after shearing was measured on each sheep at nine points, three on the dorsal mid-line and three on each side. The body condition of the sheep was defined by the method of scoring of Russel, Doney & Gunn (1969) at the beginning of the experimental period. The sheep were weighed before feeding at weekly intervals, with results expressed as fleece-free live weights. The chemical composition of the dried grass was determined as described in Section 3.1.5.

All animals were slaughtered at the end of the experiment. The sheep received food and water to within 2 h. of slaughter, which took place from 1300 h. on each of four days. Immediately after slaughter the alimentary tracts were removed and the various organs were tied off. The volume of the reticulorumen was obtained by water displacement and the empty weights of the reticulorumen, omasum, abomasum, intestines and weights of the omental, mesenteric and kidney fat were obtained. The wet contents of the organs were measured and the dry weights of the contents of the reticulorumen and whole tract were determined by drying samples at 90°C for 48 h.

5.2.4 Statistical analysis

The effect of shearing on voluntary intake was analysed by analyses of covariance and analyses of variance. Regression analyses were used to compare relationships between voluntary intake or live weight and various alimentary tract measurements.

5.3 RESULTS

5.3.1 Chemical composition of the dried grass

The chemical composition of the dried grass was as follows:-

crude protein	18.8	)
ether extract	5.4	) % of DM
acid detergent fibre	24.3	)
ash	10.7	)
gross energy	4.40	kcal/g DM
digestible energy	3.04	± 0.07 kcal/g DM

5.3.2 Fleece weights

Air-dried fleece weights were significantly greater for the fat sheep than the thin sheep ($P < 0.01$) and were as follows:-

Fat shorn	4.1	
Fat unshorn	4.8	± 0.26 kg
Thin shorn	3.5	
Thin unshorn	3.6	

The mean length of wool remaining after shearing was 1.6 ± 0.04 mm.

5.3.3 Voluntary food intake

Mean daily voluntary food intakes are summarised in Table 5.2 and changes in mean daily voluntary food intakes are illustrated in Fig.5.1. These show, in general, that the voluntary food intake of the thin sheep was greater than that of the fat sheep and was greater for the shorn sheep than the unshorn sheep. A significant relationship ($P < 0.05$) was obtained between empty body weight (live-weight - weight of alimentary tract contents determined at slaughter) and DM intake over the week prior to slaughter. Transformation of the data to logarithms gave a value for b in the equation, DM intake g/24 h. = aW^b of 0.79 ± 0.37 for the pooled data. The standard error was large and the exponent was not significantly different from 1.0. However the accepted exponent of 0.75 (Kleiber, 1965) was used to express DE intake as a proportion of metabolic size, to enable comparisons to be made with the results of other workers, independent of the size of the animal. When expressed per unit of metabolic size, DE intakes were similar between all treatments over the standardisation period, but varied widely over the experimental period. There were no significant differences in DM and

TABLE 5.2 Mean voluntary intakes of dried grass, retention times of food residues, respiration rates and apparent digestibility of the dried grass, with fat and thin sheep, shorn and unshorn

Measurements		Fat shorn (FS)	Fat unshorn (FC)	Thin shorn (TS)	Thin unshorn (TC)
DE intake (kcal/kg 0.75/24 h.)	PP1	209	220	90	97
DE intake (kcal/kg 0.75/24 h.)	PP2	260	245 ± 8	112	114 ± 4
DM intake(g/24 h.)	S.P.	1485	1326	1292	1169 ± 84 NS
	E.P.	1564	1134	1710	1406 ± 105**
DE intake(kcal/24 h.)	S.P.	4450	4024	3896	3560 ± 238NS
	E.P.	4754	3441	5164	4278 ± 299**
DE intake(kcal/kg$^{0.75}$/24 h.)	S.P.	261	250	265	264 ± 12NS
	E.P.	267	209	317	285 ± 9**
Change in DE intake (kcal/24 h.) between S.P. & E.P.		304	-583	1268	718
Mean retention time (h.)		27.4	29.1	24.1	25.8 ± 2.7NS
Apparent digestibility of energy (%)		69.4	69.0	68.1	69.7 ± 0.5NS
Respiration rate/min	S.P.	121	114	36	41 ± 9.5**
	E.P.	27	114	24	104 ± 7.3**

Significance of differences
Voluntary intake during the
Experimental Period

	DM intake (g/24 h.)	DE intake (kcal/24 h.)	DE intake (kcal/kg $^{0.75}$/24 h.)
TS v FC	**	**	**
TS v FS	NS	NS	**
TS v TC	+	+	+
TC v FS	NS	NS	NS
TC v FC	NS	+	**
FC v FS	*	**	**

**, $P < 0.01$ PP1 = Preliminary Period 1
*, $P < 0.05$ PP2 = Preliminary Period 2
+, $P < 0.10$ S.P. = Standardisation period
NS, Non significant E.P. = Experimental period

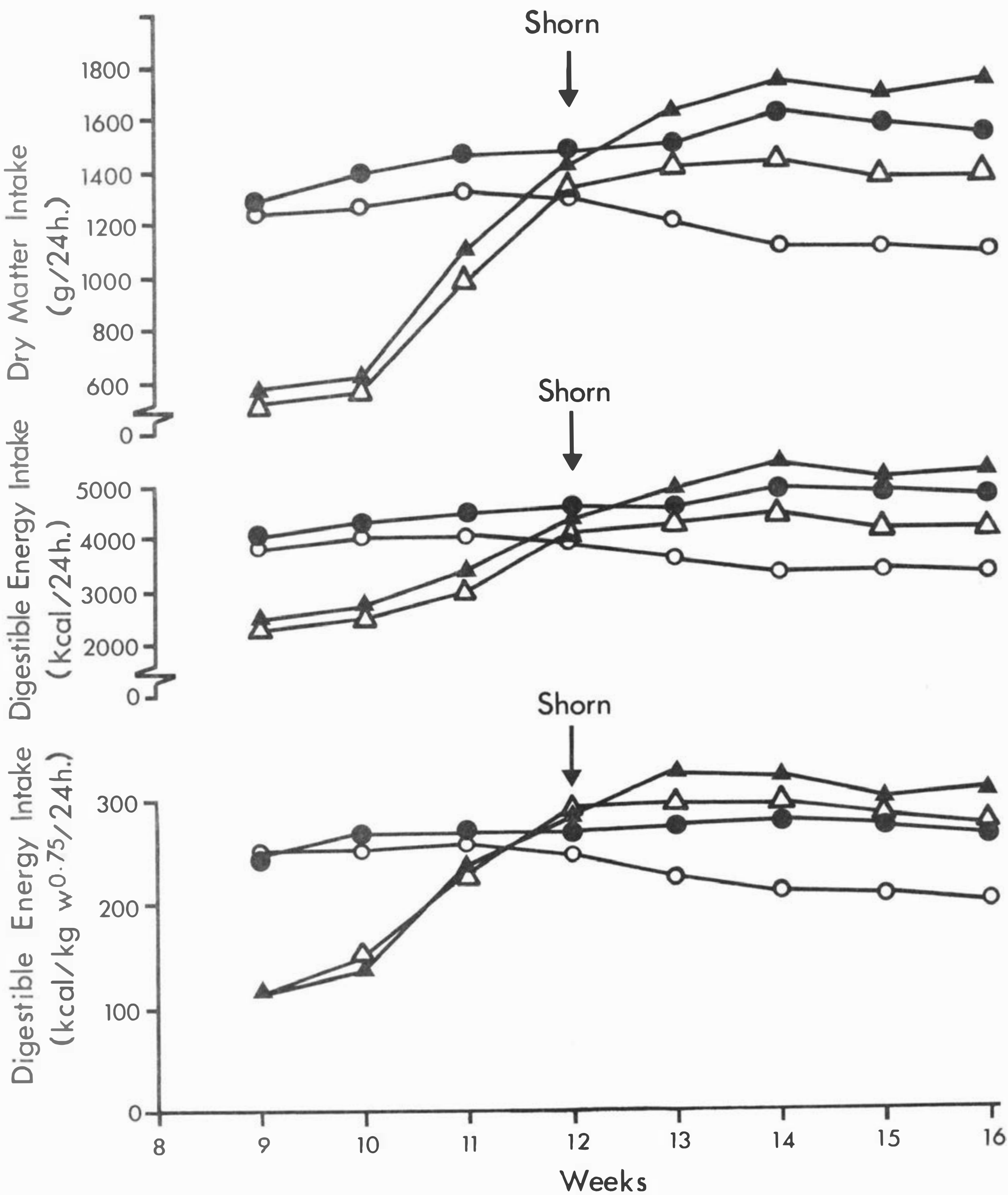

FIGURE 5.1 Mean daily voluntary intake by fat and thin sheep receiving dried grass, before and after shearing:
● fat shorn; ○ fat unshorn;
▲ thin shorn; △ thin unshorn.

DE intake between the thin shorn and fat shorn animals over the experimental period, but the voluntary intake of DE per unit of metabolic size was significantly higher for the thin shorn sheep ($P<0.01$) than the fat shorn sheep.

5.3.4 Apparent digestibility, retention time of food residues and respiration rates

These are summarised in Table 5.2. Because of the variation between animals, and as there were only two animals per treatment, the large differences in retention times were not statistically significant between treatments. A large decrease in respiration rate occurred following shearing. The low respiration rate of the thin sheep, compared with the fat sheep, in the standardisation period is also apparent. The increase in respiration rate of the thin unshorn sheep over the Experimental Period was associated with an increase in voluntary intake.

5.3.5 Live weights and live weight changes

Live weight gains over the standardisation and experimental periods were adjusted on the basis of a significant relationship ($P<0.01$) between DM intake and the total weight of the gut contents observed at slaughter. The regression equation, $y = 3.87 + (2.56 \pm 0.23)\ x$, sy.x $\pm$ 0.72 kg was used to estimate empty live weights and from this to estimate adjusted live weight changes.

Actual and adjusted live weights and live weight changes are summarised in Table 5.3. One of the objectives of the experiment was to obtain two groups of sheep differing in live weight by approximately 10 kg. A further objective was to obtain this difference at a slower rate over the month preceding the experimental period. The evidence given in Table 5.3 for live weight changes over preliminary Period 1, and preliminary Period 2 show that these objectives were largely achieved. Using live weight gains adjusted for differences in alimentary tract contents, instead of actual live weight gains over the experimental period, altered the interpretation of the results to the extent that differences in live weight gains between the thin shorn and thin unshorn sheep were not significant, following the adjustment.

TABLE 5.3 Mean live weights and live weight changes of fat and thin sheep receiving dried grass, before and after shearing

Measurements		Fat shorn (FS)	Fat unshorn (FC)	Thin shorn (TS)	Thin unshorn (TC)
Live weight change (g/24 h.)	PP1	89	120 ± 12	-144	-169 ± 14
Live weight change (g/24 h.)	PP2	177	164 ± 17	- 3	- 25 ± 9
Live weight (kg) at end of PP2	actual	41.0	39.0	31.1	28.0 ± 1.9
	empty	33.8	32.0	25.7	22.8 ± 1.8
Actual live weight gain (g/24 h.)	E.P.	119	20	229	164 ± 20
Adjusted live weight gain (g/24 h.)	E.P.	108	39	189	143 ± 17

Significance of differences

	Live weight at end of PP2 (kg)		Live weight gain over E.P. (g/24 h.)	
	actual	adjusted	actual	adjusted
TS v FC	*	*	**	**
TS v FS	**	**	**	**
TS v TC	NS	NS	*	NS
TC v FS	**	**	NS	NS
TC v FC	**	**	**	**
FC v FS	NS	NS	**	*

PP1 = Preliminary period 1

PP2 = Preliminary period 2

E.P. = Experimental period

NS , Non significant

* , $P < 0.05$

** , $P < 0.01$

TABLE 5.4 Voluntary intakes and live weight at the end of the experimental period as well as digestive tract parameters showing significant differences between treatment groups

Measurements	Fat shorn (FS)	Fat unshorn (FC)	Thin shorn (TS)	Thin unshorn (TC)
DM intake 7 days prior to slaughter (g/24 h.)	1546	1087	1765	1382 ± 113
Live weight at slaughter (kg)	47.4	42.1	43.8	38.9 ± 2.1
Empty live weight(kg) at slaughter	39.7	35.5	35.4	31.5 ± 1.8
DM in reticulorumen(g)	706	573	741	597 ± 45
Weight of reticulo-rumen (g)	1004	809	1003	913 ± 48
Weight of abdominal fat (g)	1830	1593	1279	901 ± 134
Wet contents of tract/kg L.W. (g)	164	157	192	193 ± 4.7

Significance of differences

	DM intake	Empty liveweight	DM in rumen	Wt.of rumen	Wt.abdominal fat	Wet contents tract/kg L.W.
TS v FC	**	NS	*	*	NS	**
TS v FS	NS	NS	NS	NS	**	**
TS v TC	*	NS	*	NS	+	NS
TC v FS	NS	*	NS	NS	**	**
TC v FC	+	NS	NS	NS	**	**
FC v FS	*	NS	+	*	NS	NS

NS = Non significant

+ , $P < 0.10$

* , $P < 0.05$

** , $P < 0.01$

TABLE 5.5 Significance of relationships and correlation coefficients between intake or live weight and various alimentary tract measurements for fat and thin sheep, shorn and unshorn

Relationships	Pooled 18df	Fat 7df	Thin 7df	Fat shorn 3df	Fat unshorn 3df	Thin shorn 3df	Thin unshorn 3df
DM intake (g/24 h.)(x):							
Weight of rumen (g)	.73**	.68**	.88**	.78NS	.71NS	.90*	.85+
Weight of tract (g)	.66**	.65*	.80**	-.01NS	.92*	.96**	.40NS
Wet contents of intestine(kg)	.74**	.82**	.69*	.95*	.89*	.78NS	.26NS
Wet contents of tract (kg)	.78**	.84**	.67*	.97**	.55NS	.75NS	.13NS
DM post rumen (g)	.61**	.45NS	.68*	.85+	.51NS	.86+	.03NS
DM in tract (g)	.63**	.76*	.74*	.91*	.56NS	.77NS	.05NS
Weight of abdominal fat (g)	.29NS	.59NS	.44NS	.34NS	.93*	-.19NS	.70NS
Live weight(kg)(x):							
Weight of abdominal fat (g)	.64**	.70*	.57+	.55NS	.93*	.30NS	.53NS
Weight of tract (g)	.73**	.66*	.87**	.31NS	.85+	.94*	.97**
Wet contents of tract (kg)	.63**	.84**	.67*	.97**	.55NS	.75NS	.13NS
DM intake(g/24 h.)	.76**	.92**	.76*	.89*	.97**	.87+	.46NS
Adjusted liveweight (kg)(x):							
Wet contents of tract	.38NS	.67*	.59NS	.96**	.08NS	.36NS	.75NS
DM intake (g 24/h.)	.48*	.87**	.71*	.87+	.87+	.76NS	.50NS

5.3.6 Slaughter data

Dry matter intake and live weight before slaughter, together with data obtained at slaughter showing significant differences between treatments are summarised in Table 5.4. There were no significant differences between treatments for reticulorumen volume, wet contents of the reticulorumen, DM in the whole tract, wet weight and dry weight of the contents of the intestines, weight of the omasum and abomasum and weight of the intestines. Reticulorumen weights were lower for the fat unshorn sheep than the thin shorn or fat shorn sheep. The two heaviest sheep, (see Section 5.2.1), one each in the shorn groups, also had the heaviest reticulorumens. Omitting the data for these sheep from the statistical analysis decreased the standard error, but the differences noted above were still significant ($P < 0.05$). In addition the difference in the weights of the reticulorumens, in favour of the thin unshorn sheep compared with the fat unshorn sheep, now reached significance ($P < 0.10$).

Some of the significant relationships between intake or live weight and various parameters are summarised in Table 5.5. No significant relationships were noted between DM intake (x) and weight of wet or dry reticulorumen contents or weight of abdominal fat (y), nor between the weight of abdominal fat (x) and the wet or dry contents of the reticulorumen or alimentary tract as a whole (y). No obvious patterns emerge from these relationships, although the relationships for individual treatment groups (DM intake as the independent variable) were weaker for the thin unshorn sheep, compared with the other treatment groups.

The relationship between live weight and weight of the alimentary tract, or its contents, contains a common element between the variables, and the use of the adjusted or empty live weight as the independent variable resulted in most of the relationships being non significant.

5.4 DISCUSSION

The results showed that the voluntary intake of sheep receiving dried grass was affected by both body condition and shearing. Voluntary food intake of the fat sheep increased when they were shorn, the mean increase over the four weeks of the experimental period being 304 kcal ME/24 h. This is in contrast to results obtained in earlier experiments (Expt 1(a), 1(b) and 2 in Chapter 3) on the effects of shearing on the voluntary intakes of sheep receiving dried grass. In the earlier experiments, responses varied greatly, and the results in terms of changes in intake with shearing were inconclusive. Because more animals were used per treatment, the information gained in the present experiment is considered to be more reliable than that obtained in the earlier work, so that it does appear that the intake of a food of high DE concentration can increase substantially, to meet an increase in energy expenditure.

The decrease in voluntary intake after sheep had received dried grass ad libitum for some time, confirms earlier observations (Chapter 4). Decreased voluntary intakes by fat ruminants have been observed by a number of workers e.g. Schinckel (1960), Graham (1969) and Foot (1972) with sheep, and by Hutton (1963), and Bines, Suzuki & Balch (1969) with cattle. The decreased intakes in the present experiment occurred with sheep which were presumably still at the growing stage (18 mo of age) when the continuing demands of growth might have been expected to have maintained intake. Besides, the animals were not obese, but could be classified as moderately fat, with a condition score of 4, using the methods and rating developed by Russel, Doney & Gunn (1969). Graham (1969) observed decreased intakes with fat mature sheep, but Graham & Searle (1972) observed no such change with young sheep. However Hutton's (1963) cattle included a proportion of immature animals. Unlike the results obtained by Forbes (1969), no significant negative relationships were noted between the amount of abdominal fat and digestive tract contents, and unlike those of Tayler (1959), no significant negative relationships were noted between the amount of abdominal fat and voluntary intake. In the present experiment the reverse was true, in that there was a significant positive relationship ($P < 0.05$) between DM intake and abdominal fat with the fat unshorn sheep. The high respiration rates of the fat unshorn sheep suggest that intake may have been inhibited by heat stress, although this would probably not account for the progressive decline in food intake which was observed.

Voluntary intakes of the thin unshorn sheep in the experimental period were such that some compensatory eating probably occurred, although its extent was difficult to judge. The level of intake of the thin sheep following shearing was considerably higher than the other groups of sheep. As DE intakes per unit of metabolic size were similar for the two groups of thin sheep over the standardisation period, the difference in intake between these two groups in the experimental period of 32 kcal DE/kg $^{0.75}$/24 h. or approximately 500 kcal DE/24 h. (410 kcal ME for a 40 kg sheep) could represent the increased intake due to shearing.

The voluntary intakes of the thin shorn sheep over the experimental period of 317 kcal DE/ kg $^{0.75}$/24 h. were considerably higher than voluntary intakes observed by other workers for sheep receiving diets of a similar DE concentration. Digestible energy intakes of 265 kcal/ kg $^{0.75}$/24 h. were observed by Donefer, Lloyd & Crampton (1963), 226 kcal by Dinius & Baumgardt (1970) and 253 kcal by Dinius, Peterson, Long & Baumgardt (1970). The evidence indicates that the voluntary food intakes of the thin unshorn sheep were enhanced by realimentation, following a period of restricted feeding, and that the increase in voluntary food intake by the thin shorn sheep was influenced by the combined effects of shearing and realimentation.

There is evidence that the food intake of sheep and cattle increases, following a period of undernutrition, (Bines, Suzuki & Balch, 1969; Foot & Greenhalgh, 1969; Allden & Young, 1964), but Allden (1968a), Meyer & Clawson (1964) and Keenan, McManus & Freer (1970) observed little or no increase. According to Allden (1970) there is evidence that undernutrition imposed at different stages of life may affect food intake in different ways during the recovery period. Thus Allden (1968(a) and (b) observed little or no recovery in intake with sheep undernourished in the first six months of life, whereas sheep undernourished over the second six months of life increased their intakes and rapidly overcame their growth handicap following realimentation. The observation was also made by Allden (1970) that pasture consumption, following the restoration of a "normal" diet after a period of restriction, was greatest in animals which have shown considerable weight losses. This was not supported by the observations of Keenan, McManus & Freer (1970) who observed no relative increase in voluntary food intake between sheep that had previously been fed to maintain weight and those that had been fed at submaintenance levels. The sheep which had been severely restricted ate less food during the first fortnight following realimentation, compared with the sheep that had been previously fed at a maintenance level. It was this observation that determined the experimental plan in the present experiment.

Live weight gains for the thin sheep were greater than those for the fat sheep in the experimental period, but live weight gains for all sheep were lower than might have been expected from estimates based on Agricultural Research Council (1965) standards. They were approximately 850, 470, 540 and 300 kcal DE/24 h. lower than the published values for the fat shorn, fat unshorn, thin shorn and thin unshorn groups respectively. The largest discrepancies were noted with the shorn sheep and probably partly reflect the greater heat production of these sheep.

Interpretation of the slaughter data was confounded by the fact that the thin sheep had regained a large proportion of their live weight over the experimental period. However, differences in voluntary intakes between the groups of sheep were still large at slaughter. In contrast to the results obtained in Expt 3 and 4, Chapter 4, there were no significant differences between treatment groups for rumen volume, wet matter, and DM in the whole tract and in the intestines. There were significant differences between treatment groups in the amount of DM in the reticulorumen, with highest values being observed with the thin shorn sheep and fat shorn sheep. This confirms results obtained earlier (Chapter 3 and Expt 4, Chapter 4).

The significance of the various relationships between DM intake and the various alimentary tract parameters is difficult to assess. There were no significant relationships between DM intake and dry or wet contents of the reticulorumen with any of treatment groups or when the data were pooled. The amount of wet matter in the reticulorumen was similar for all sheep regardless of treatment, with the exception of one animal in the thin shorn group with a high value, and one in the fat control group with a low value. There was a significant relationship between DM intake and wet and dry contents of the hind gut ($P < 0.01$). Mäkelä (1956) working with cattle fed hay, observed that the amount of wet contents of the reticulorumen were similar between animals, despite differences in intake. He obtained good relationships between DM intake and DM in the reticulorumen and the hind gut. Ingalls, Thomas, Tesar & Carpenter (1966) observed "no clear-cut" relationship between DM intake and the amount of DM in the reticulorumen of sheep receiving various hays. This led them to state "that there were probably other factors playing a role in controlling <u>ad libitum</u>

intake of high quality hays". Presumably they meant factors other than fill in the reticulorumen, but their statement is hard to substantiate. A number of workers (Ingalls, Thomas, Tessar & Carpenter, 1966; Hutton, Hughes, Newth & Watanabe, 1964; Forbes, 1969) have interpreted significant relationships between intake and fill in various alimentary organs of sheep and cattle as suggesting that fill of these organs was not important in limiting intake. If this is a valid conclusion, the results obtained in the present experiment suggest that fill of wet or DM in the reticulorumen, but not in the hind gut, may have limited intake. As already noted in Chapter 4, the interpretation of these relationships needs to be treated with caution. That the capacity of the reticulorumen played a part in limiting intake is also indicated by the significant ($P < 0.01$) positive relationship between DM intake and weight of the reticulorumen, a result also obtained with lambs by Wardrop & Coombe (1960 and 1961) and in cattle by Mäkelä (1956).

Mean retention times of food residues were considerably lower than values for sheep receiving dried grass reported by Blaxter, Graham & Wainman (1956), and there is a possibility that the use of ^{144}Ce underestimated retention times in the present experiment (see Chapter 2). The data on retention times with their high standard errors were insufficiently replicated to show statistically significant differences between groups. However there was a negative relationship ($P < 0.05$) ($r = -0.92$ df 3) between DM intake and retention time for the fat sheep, but no significant relationship between these variables for the thin sheep. If retention time is one of the factors which determines fill in the tract, then this further indicates that physical factors may have been of some importance, at least with the fat sheep.

5.5 CONCLUSION

The evidence obtained in this experiment indicated that metabolic as well as physical factors played an important part in controlling the level of voluntary intake by sheep receiving dried grass. Thus the voluntary intakes of the fat sheep increased when they were shorn, presumably to meet an increase in energy expenditure. Evidence was also provided, that thin sheep increased their voluntary intake to such an extent that live weights recovered rapidly as the experiment progressed, and there was evidently a strong drive to overcome the energy deficit imposed by a period of underfeeding. There was also evidence of an additive effect of shearing and body condition, resulting in a considerable increase in voluntary intake of the thin sheep following shearing. Data obtained at slaughter indicated that physical factors may still have been operating, but probably at various levels with the different groups of sheep. The results illustrated a drive to overcome energy deficits overriding physical factors limiting voluntary intake. The increase in voluntary intake appeared to be achieved largely through an increase in the amount of the contents of the reticulorumen. Results obtained on the retention time of food residues were inconclusive. Evidence, substantiated by earlier work, showed that the voluntary intake of unshorn sheep receiving dried grass declined after a period of ad libitum feeding. Restriction of the body cavity by abdominal fat did not appear to be a cause of the decline.

The extent to which the increase in voluntary intake met an increase in energy expenditure when sheep were shorn was in doubt in many of the experiments reported in this and preceding Chapters. Evidence from live weight changes was often limited, because of the small numbers of animals used. For this reason the extent of the increase in heat production, when sheep receiving dried grass or ground hay are shorn, forms the objective of the experiments reported in the following Chapter.

CHAPTER 6

THE EFFECTS OF SHEARING ON THE HEAT PRODUCTION AND ACTIVITY OF SHEEP RECEIVING DRIED GRASS OR GROUND HAY

S U M M A R Y

1. Measurements of oxygen consumption (values converted to heat production) were obtained in two experiments with Romney wethers, before and after they were shorn. The sheep were fed either ground hay or dried grass, just below the *ad libitum* level, so that as far as possible intakes were constant. The ambient temperature at all times throughout both experiments was maintained at $13^{\circ}C \pm 1^{\circ}C$.

In Expt 1, oxygen consumption was measured with eight sheep in rotation using a single calorimeter and in Expt 2, oxygen consumption was measured with four sheep in rotation, using a ventilated hood. At the same time in Expt 2, the times the sheep spent standing, lying, eating and ruminating were measured.

2. Oxygen consumption, and hence heat production, increased following shearing in both experiments. In Expt 1, heat production was significantly greater ($P < 0.05$) on days 1, 8 and 16 following shearing, compared with pre-shearing values, for the sheep receiving dried grass. For sheep receiving ground hay, heat production was greater on day 1 ($P < 0.05$) and day 8 ($P < 0.01$) following shearing, compared with pre-shearing values. The mean maximum increase in heat production following shearing was 553 kcal/24 h. (25%) for the sheep receiving dried grass and 283 kcal (17%) for those receiving ground hay.

3. The increases in heat production following shearing in Expt 2 supported the results in Expt 1, although the maximum increases were rather less; 21% for the sheep receiving dried grass and 13% for those receiving ground hay.

4. The time spent standing increased considerably when the sheep were shorn and although eating times decreased, it appeared, from the evidence on the energy cost of standing,

that this change in behaviour made a considerable contribution to the increase in energy expenditure following shearing.

5. The results of the experiments were discussed briefly in relation to published results dealing with the effect of shearing on the heat production of sheep.

6.1 INTRODUCTION

The effects of shearing on voluntary intake of sheep receiving a number of different foods have been reported in the preceding chapters. In general, voluntary food intakes increased following shearing with greatest increases occurring with ground hay (Chapter 4). The increases in voluntary intake of sheep receiving chopped hay were generally smaller than those observed when ground hay was fed, and with dried grass increases were irregular in some experiments. With dried grass, the condition of the animal was shown to affect the response in terms of a change in voluntary intake following shearing (Chapter 5), with thin sheep showing a considerable increase in voluntary intake.

The observations of Armstrong, Blaxter, Graham & Wainman (1959) that the heat production of closely clipped sheep increased by 900 - 1200 kcal at ambient temperatures similar to those used in the present series of experiment, do not agree well with the extent of the increase in voluntary intake following shearing observed in many of the shearing experiments. The factors affecting voluntary food intake are so varied and complex that the lack of consistent close relationships between voluntary food intake and energy expenditure is not surprising. Thus inhibitory factors such as the rate at which food particles are broken down and removed from the reticulcrumen, time take for the alimentary tract to hypertrophy and body condition of the animals, could affect this relationship.

The objective of the present experiments was to determine the extent to which the heat production of sheep receiving dried grass or ground hay was increased following shearing. In addition, in a second experiment, the effects of shearing on the activity of the sheep was measured.

6.2 MATERIALS AND METHODS

6.2.1 Plan of experiments

The Romney wethers used in the experiments were fed dried grass or ground hay *ad libitum* in crates, at an ambient temperature of $13^{\circ}C \pm 1^{\circ}C$ for a period of one month prior to the start of Expt 1. The sheep used as controls in Expt 1 were used in Expt 2, and had therefore spent a considerably longer period adapting to the conditions of the experiment. The sheep were introduced to the calorimeter, used in Expt 1, on a number of occasions during the training month. Intakes were adjusted to below *ad libitum* two weeks prior to the beginning of Period 1 in Expt 1, in an endeavour to maintain intakes constant within sheep, throughout the experiment. Both experiments were divided into 2 periods, Period 1 when all sheep were unshorn, and Period 2 when half the sheep were shorn. The plan of both experiments is given in Table 6.1.

TABLE 6.1 Plan of experiments concerned with the effect of shearing in changing the heat production of sheep receiving dried grass or ground hay

	Duration (days)	Dried grass Number of sheep	Ground hay Number of sheep	Periods in calorimeter/sheep (24 h.)
Expt 1				
Period 1	35	4 unshorn	4 unshorn	3
Period 2	45	2 shorn 2 unshorn	2 shorn 2 unshorn	5 (Days 1, 8, 16, 24, 45)
Expt 2				
Period 1	10	2 unshorn	2 unshorn	2
Period 2	32	1 shorn 1 unshorn	1 shorn 1 unshorn	5 (Days 1, 8, 12, 18, 32)

Expt 1: Eight Romney wethers were used, four receiving dried grass and four receiving ground hay. Feeding took place twice daily at 0830 h. and 1630 h. and water was available at all times. The oxygen consumption of each sheep was measured in a calorimeter at an ambient temperature of $13^{\circ}C$ for periods of 24 h. Three such measurements were made during the 35 days of Period 1. Two sheep on each food were shorn

and two were left unshorn as controls at the end of Period 1. Oxygen consumption was again measured with all sheep on days 1, 8, 16, 24 and 45 following shearing (Period 2). The changeover of sheep in the calorimeter took place at 1300 h. When not in the calorimeter, the sheep were held in their feeding crates at an ambient temperature of 13 $\pm$ 1^{o}C. As there was only one calorimeter, shearing was carried out on different days, so that each sheep was able to spend its 24 h. period in the calorimeter at the specified times, following shearing, in both Expt 1 and Expt 2.

Expt 2: The four sheep which were not shorn in Expt 1 were used in this experiment, two receiving dried grass and two receiving ground hay. The dried grass and ground hay were from the same batch of food used in Expt 1. Feeding and management were the same as for Expt 1, except that feeding levels were restricted still further to ensure a minimum of refusals, and oxygen consumption was measured using a ventilated hood over periods of 24 h. The small volume of the ventilation hood, compared with the calorimeter, made it possible to measure changes in oxygen consumption associated with changes in activity of the sheep more rapidly and accurately.

The oxygen consumption was determined with each sheep for 24 h. on two occasions, separated by one week in Period 1. One sheep on each food was then shorn and one left unshorn as a control and oxygen consumption measured on days 1, 8, 12, 18 and 32 following shearing (Period 2). More frequent measurements were taken in the early part of the post-shearing period, as results obtained in Expt 1 showed that most of the changes in oxygen consumption occurred at this time. As in Expt 1, the changeover between sheep took place at 1300 h. When not in the ventilated hood, the sheep were held in their feeding crates at an ambient temperature of 13^{o}C.

6.2.2 Measurements

Oxygen consumption was measured in a calorimeter in Expt 1 described by Holmes (1973) and in a ventilated hood in Expt 2 (Holmes 1971) of open-circuit design, similar to that described by Webster & Hicks (1967).

Air was drawn through the calorimeter or hood at a controlled rate by a rotary pump and was cooled to between 2 - 5^{o}C, then re-warmed to 28^{o}C in a thermostatically controlled room before passing through a dry gas meter. The measured volume of air was corrected to conditions of standard temperature and pressure. The oxygen content of small samples of ingoing and exhaust air, drawn through silica gel, was measured by a paramagnetic analyser, (Model O.A.137, Servomex & Co., range 19 - 21% O_2), which was calibrated daily against gases of known oxygen content. The output of the analyser was connected to a potentiometric recorder and charts from the recorder were integrated with a planimeter. Oxygen consumption was determined by multiplying the corrected ventilation rate by the difference in oxygen content between the ingoing and exhaust air. The measurement system had been tested by burning a weighed amount of ethanol in a ventilated chamber. Measured oxygen consumption varied between 93.5 and 100% of calculated consumption in nine tests carried out by Dr C.W. Holmes of Massey University. The ventilation rate was controlled to ensure that the exhaust air contained between 19.8 - 20.2% oxygen.

Heat production was calculated using the equation derived by McLean (1972) :

$$H = 4.89 \; VoX$$

where H = heat produced (kcal/24 h.)
and VoX = oxygen consumed (l/24 h.).

McLean stated that the above equation estimates heat production with an accuracy to within $\pm$ 2%.

In Expt 2, the time spent eating and ruminating was measured by pressure changes from a balloon attached to the lower jaw of the sheep. The time spent standing and lying was monitored through a thermocouple attached to the floor grating so that it came into contact with the animal's belly as it lay down. The resultant temperature change was recorded on a Philips recorder.

The apparent digestibility of the foods were determined with all sheep in Expt 1 by total collection of faeces over 14 days. Urine was collected daily over the same period at a pH of 2-2.5, maintained with 0.1N H_2SO_4. Fresh faeces and urine were analysed for nitrogen by the Kjeldahl method (AOAC,1965) and the nitrogen retained was determined. Gross energy of oven dried feed and faeces were determined using an adiabatic bomb calorimeter. Liveweights of the sheep in both experiments were determined before the morning feed, immediately before they entered the calorimeter or ventilated hood.

6.2.3 Diets

The dried grass was the same as that used in the experiment described in Chapter 5. The ground hay was similar to that used in a previous experiment (Expt 2, Chapter 4), and had been ground with a hammer mill to pass through a 2.5 mm screen. The foods were analysed for ash, ether extract, crude protein (AOAC, 1965) and acid detergent fibre (Van Soest, 1963). The chemical composition of the foods are presented in Table 6.2.

TABLE 6.2 Chemical composition of dried grass and ground hay used in Expt 1 and Expt 2 (g/100 g DM)

Measurement	Dried grass	Ground hay
Crude protein	17.6	10.3
Ether extract	5.4	3.8
Acid detergent fibre	24.3	31.4
Ash	10.7	8.6
Gross energy (kcal/g DM)	4.40	4.35

6.2.4 Analysis of results

The heat production (kcal/24 h.) of each sheep was analysed separately in both Expt 1 and 2 by analysis of variance for differences between days. The heat production and times spent eating, ruminating and standing by the sheep (Expt 2) were separated into seven 3 h. periods, for each 24 h. spent in the respiration hood. The first three hours of each 24 h. (1300 - 1600 h.) were excluded to allow the animals to settle down and the equipment to reach equilibrium.

Multiple regression relationships between heat production (kcal/ 24 h.) or heat production (kcal/24 h./$kg^{0.75}$)(y) and eating (x_1), ruminating (x_2) and standing (x_3) were computed separately for each sheep, and for Period 1 and for the mean of days 1 and 8 following shearing. However no reliable estimate could be made of the energy cost of each activity because of the close relationship among the independent variables.

A closer examination of the original recorder charts was therefore carried out with comparisons being made as shown in Table 6.3, with the cost of each activity being calculated by a difference method. Comparisons were made between measurements of heat production, over the last 10 min of a minimum of 20 min steady state for a particular activity, compared with an adjacent period, either preceding or following, in another activity.

TABLE 6.3 Expt 2. Method of analysing the energy cost of various activities

Comparisons	No. of observations
L v RL	48
RL v L	51
S v SE	7
SE v S	9
SR v S	2
S v L	9
SR v LR	1

L = Lying
S = Standing
R = Ruminating
E = Eating

Thus there were a total of 101 observations for ruminating, 16 for eating, and 10 for standing. The data for standing and eating were unfortunately such that no comparisons were available to assess the effects of shearing on the energy cost of these activities.

6.3 RESULTS

6.3.1 Expt 1: The aim of maintaining food intake constant within sheep was not always successful and some variation occurred. In particular, low intakes were observed with sheep D on the third day of Period 1, with an intake of 1630 kcal compared with the mean for the period of 2295 kcal DE/24 h., and with sheep B on the first day of Period 1 of 1783 kcal, compared with a mean of 2941 kcal DE/24 h. for the period. The low intakes were associated with low heat productions and the values for these days were omitted for sheep D and B, in arriving at the difference in heat production between Periods 1 and 2 shown in Table 6.4. Digestible energy intakes, per unit of metabolic weight, of the sheep receiving dried grass decreased as the experiment

TABLE 6.4 Expt 1. Mean digestible energy intake, heat production, live weight change and nitrogen balance of shorn and unshorn sheep fed dried grass or ground hay

Measurement		Ground hay				Dried grass			
		Shorn		Unshorn		Shorn		Unshorn	
Sheep No.		D	9	C	3	A	2	B	10
Apparent digestibility of energy (%)	P1	53.3	52.5	51.1	53.8	73.5	72.3	74.3	74.8
	P2	54.5	49.8	50.8	54.6	74.8	71.2	74.0	73.5
DE intake (kcal/24 h.)		2350±111	2381±53	2241±44	2711±35	3841±135	3487±37	2884±164	3875±58
DE intake (kcal/kg $^{0.75}$/24 h.)		167±8	177±4	137±3	156±5	219±6	231±5	177±9	239±5
Heat production									
Mean Period 1		1660	1667	1640	1956	2178	2224	1791	2321
Maximum Period 2		1970	1924	1745	1696	2740	2769	1906	2399
Difference		310	257	105	-260	562	545	115	78
Mean fleece-free live weight Period 1 (kg)		34.6	32.4	36.8	39.9	42.3	34.6	38.7	37.9
Live weight change (g/day)									
Whole experiment		-46±56	-24±62	-8 ±40	13±13	86±23	111±28	98±50	151±49
Period 1		-93	-9	+43	-3	108	151	94	105
Period 2		-28	-30	-29	+20	77	95	100	170
Fleece weight (kg)		3.9	4.1			5.0	5.6		
Nitrogen balance									
N intake (g/24 h.)	P1	15.2	17.6	15.9	17.6	34.0	31.6	26.1	34.9
	P2	18.3	18.6	14.3	19.1	34.8	32.3	26.4	34.8
N retained (g/24 h.)	P1	0	1.1	0.1	1.3	6.1	6.1	4.3	6.6
	P2	1.8	1.0	-.9	1.8	6.4	3.5	5.6	5.9

P1 = Period 1 P2 = Period 2

progressed and the animals gained weight. This did not occur with the sheep fed ground hay.

The maximum heat production of the shorn sheep occurred on the first day following shearing, with the exception of sheep 2, where the maximum occurred on the eighth day. Changes in heat production as the experiment progressed are shown in Fig. 6.1. For sheep receiving dried grass, heat production was significantly higher ($P < 0.05$) than pre-shearing values for days 1, 8 and 16 following shearing and had returned to pre-shearing values by day 24. With the sheep receiving hay, heat production was significantly higher on days 1 and 8 following shearing ($P < 0.05$ and $P < 0.01$ respectively), and there was no significant difference between pre-shearing heat production and heat production on day 16. Maximum increases in heat production above the pre-shearing values were 18.7 and 15.4% for the two sheep receiving ground hay, and 25.8 and 24.3% for the sheep receiving dried grass. There were no significant differences in heat production between days for the unshorn sheep receiving either dried grass or ground hay, although the heat production of sheep C and B was somewhat higher on day 1 in Period 2, compared with other days. With both these sheep, DE intake was 200 kcal higher at this time, which difference probably accounted for their increase in heat production.

The mean heat production of the sheep (mean for Period 1 and 2) receiving dried grass of 2098 kcal/24 h. was significantly higher ($P < 0.01$) than the value of 1731 ± 68 kcal/24 h. of the sheep receiving ground hay. Differences in heat production between sheep within foods were also apparent, and reflected differences in DE intakes between the sheep. There was a highly significant relationship ($P < 0.01$) between DE intake (x, mcal/24 h.) and heat production (y, mcal/24 h.) for the preliminary period ($y = 0.84 + (0.38 \pm 0.03)\,x$, $s_{y.x} \pm 0.01$ mcal, $r = 0.94$, 22 df). The regression equation was used to compare results of the present experiment with those for minimum heat production of sheep receiving dried grass, as determined by Graham, Wainman, Blaxter & Armstrong (1959) and are presented in Table 6.5. The estimated DE intakes appearing in Table 6.5 were derived from the ME intakes they obtained, using a conversion factor of 0.82 (Blaxter, Clapperton & Martin, 1966). The two sets of data show close agreement and provide evidence that the sheep over the pre-shearing period, in the present experiment, were probably at minimum heat production for their particular feeding level.

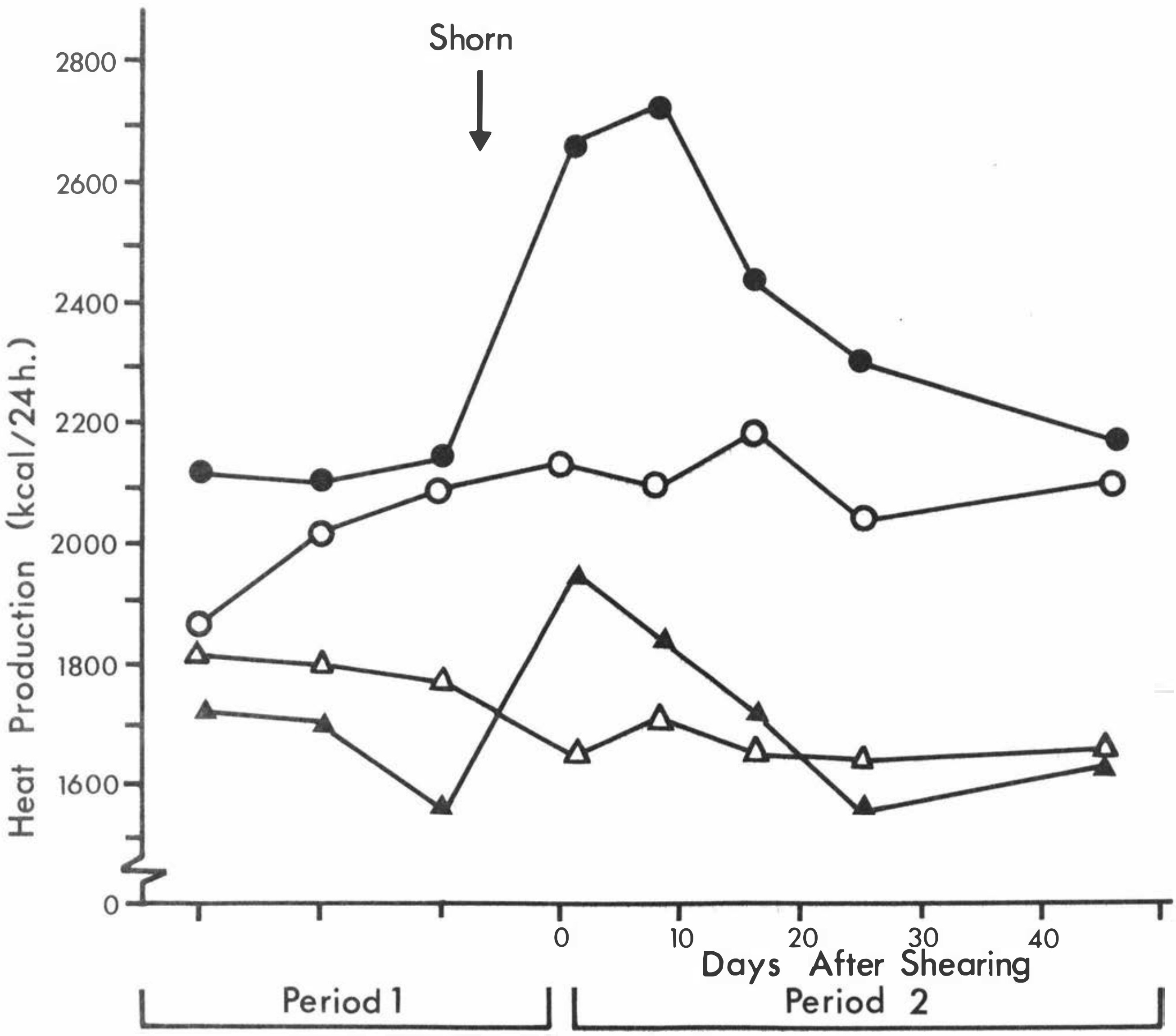

FIGURE 6.1 Experiment 1. Mean daily heat production of sheep, before and after shearing:
● dried grass, shorn; ○ dried grass, unshorn;
▲ ground hay, shorn; △ ground hay, unshorn.

TABLE 6.5 A comparison of heat production obtained in Expt 1 with the heat production of sheep determined by Graham et al (1959)

Estimated DE intake (kcal/24 h.)	Graham et al (1959)	Heat production(kcal/24 h.) Expt 1: Derived from regression equation
1524	1339	1417
2810	2005	1908
4134	2406	2411
1495	1464	1408
2895	2018	1926
3764	2560	2270

All sheep receiving dried grass were in positive nitrogen balance (Table 6.4), but some of the sheep receiving ground hay were in negative balance. There was no apparent effect of shearing on nitrogen retention.

The sheep receiving dried grass increased in weight throughout the experiment, whereas liveweights of the sheep receiving ground hay decreased. There was no evidence, with the sheep fed ground hay, of an increase in live weight loss when the sheep were shorn. With the sheep receiving dried grass, there was evidence of a reduced liveweight gain after shearing as shown by the result for Period 1 and 2 given in Table 6.4. These rather inconclusive results reflect inaccuracies in the measurement of live weight, plus insufficient replication over too short a period.

6.3.2 Expt 2: With the exception of sheep C, variation in DE intake between days was lower than in Expt 1. With sheep C much of the variation arose through a low intake of 1365 kcal DE on the 12th day of Period 2, compared with the mean of 1778 kcal over Periods 1 and 2. Increases in heat production following shearing were observed (see Table 6.6), although they appeared to be less than those obtained in Expt 1. Maximum increases were 13% for the sheep receiving ground hay and 21% for those receiving dried grass, and confirmed the greater increase noted with sheep receiving dried grass in Expt 1. The regression equation relating DE intake and heat production derived from the data from Period 1 in Expt 1 was used to compare predicted and actual heat

TABLE 6.6 Expt 2. Mean digestible energy intake, heat production, times spent standing, eating and ruminating and live weight, live weight changes and fleece weights of shorn and unshorn sheep fed dried grass or ground hay

Measurements	Ground hay Shorn	Ground hay Unshorn	Dried grass Shorn	Dried grass Unshorn
Sheep No.	3	C	B	10
DE intake				
(kcal/24 h.)	2609 ± 5	1778 ± 110	3086 ± 21	3920 ± 25
(kcal/kg $^{0.75}$/24 h.)	160 ± 1	121 ± 7	174 ± 2	211 ± 2
Heat production (kcal/24 h.)				
Mean Period 1	1889	1757	1850	2313 ± 48
Maximum Period 2	2136	1722	2239	2262
Difference	247	- 35	389	- 51
Mean fleece-free live weight Period 1 (kg)	41.4	36.9	46.5	48.2
Time spent standing (h.)				
Mean Period 1	4.9	4.9	4.5	9.1
At time of maximum heat production	16.2	4.2	21.0	7.8
Change in energy cost of standing (kcal)	150	- 8	246	- 20
Time spent eating(h.)				
Mean Period 1	3.0	2.8	4.0	2.6
At time of maximum heat production	1.8	2.8	2.5	2.1
Change in energy cost of eating (kcal)	- 46	0	- 65	- 22
Time spent ruminating(h.)				
Mean Period 1	7.7	5.9	5.4	8.3
At time of maximum heat production	6.2	6.8	3.9	6.4
Change in energy cost of ruminating (kcal)	- 16	9	- 18	- 24
Total change in cost of activities (kcal)	88	1	163	- 66
Live weight change				
End Period 1 to end Period 2(g/24 h.)	-102	- 51	43	105
Fleece weights(kg)	5.40	5.35	6.17	5.94

productions obtained in Period 1 of Expt 2. Results are presented in Table 6.7 indicating that the heat productions in the two experiments were similar for the particular levels of DE intake.

The heat production of the sheep and their activity, divided into 3 h. periods, are illustrated in Figs. 6.2, 6.3, 6.4 and 6.5. Period 1 is the mean of two days, Period 2(a) is the mean of days 1 and 8 post-shearing and Period 2(b) is the mean of days 12, 18 and 32 post-shearing.

TABLE 6.7 A comparison of heat production of sheep between Expt 1 and Expt 2, determined during Period 1 in each case

DE intake (kcal/24 h.)	Heat production (kcal/24 h.)	
	Results Expt 2	Results calculated from regression equation, Expt 1
3932	2313	2333
3027	1850	1990
2607	1888	1831
2007	1757	1603

The most outstanding change in behaviour was the large increase in the time spent standing when the sheep were shorn. The time spent standing was at a maximum on days 1 and 10 following shearing, but was still elevated 32 days after shearing. There were no differences between the unshorn sheep receiving dried grass and those receiving ground hay in the time spent eating and ruminating. With both foods, the sheep reduced the time spent eating following shearing. Limited evidence indicated that ruminating time was reduced following shearing, although the unshorn sheep 10 also reduced its ruminating time in Period 2. (Table 6.6). Examination of Figs. 6.2, 6.3, 6.4 and 6.5 shows that diurnal changes in heat production were evident with lowest values occurring between approximately 2100 and 0700 h. Highest values for heat production coincided with the combined activities of standing and eating.

The energy costs of various activities have been summarised in Table 6.8 along with results obtained by other workers. A large number of observations on the energy cost of rumination were obtained in the

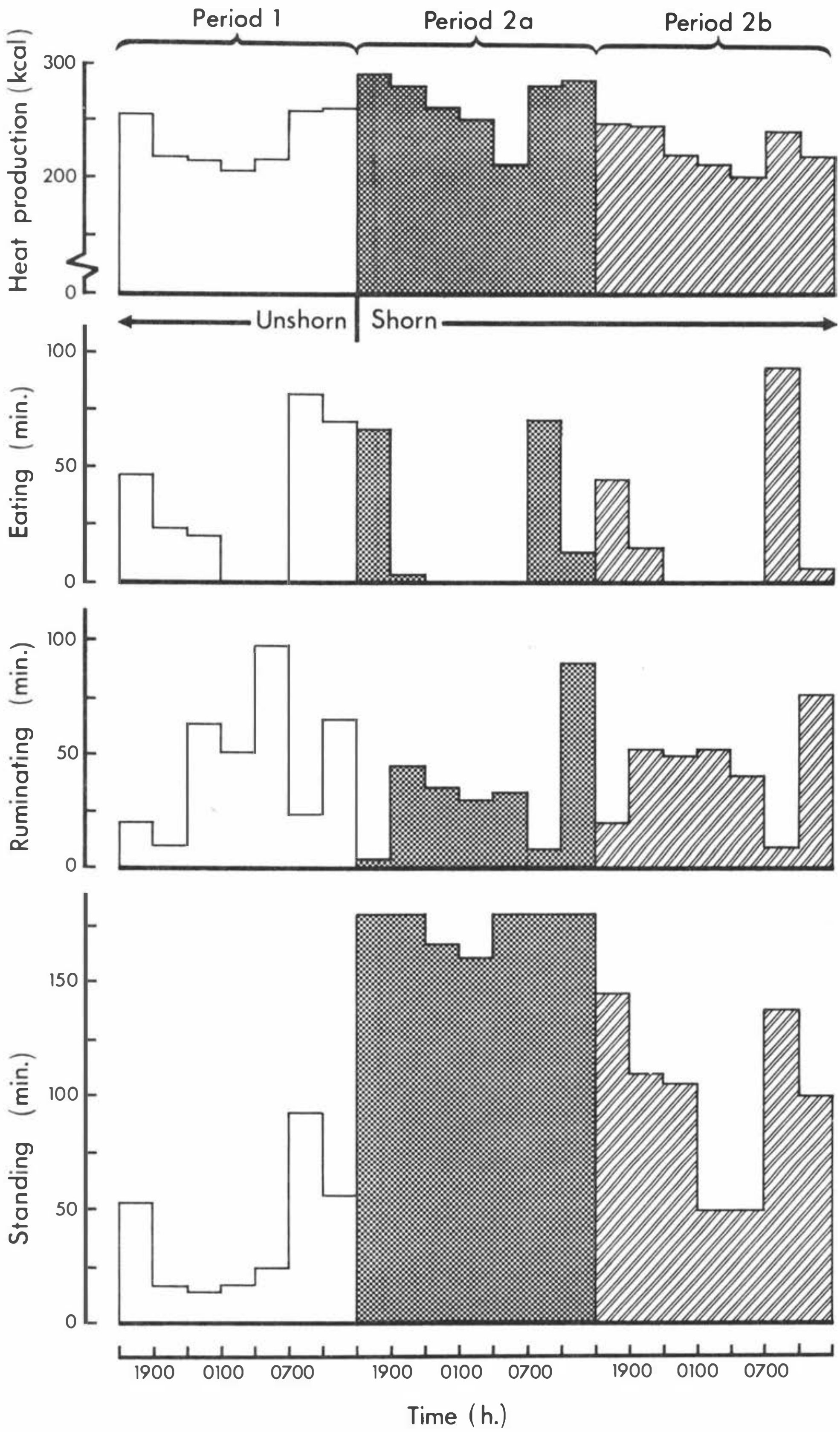

FIGURE 6.2 Experiment 2. Heat production and time spent eating, ruminating and standing by Sheep B, receiving dried grass. Period 1, mean of 2 days; Period 2(a), mean of days 1 and 8; Period 1(b), mean of days 12, 18, 32.

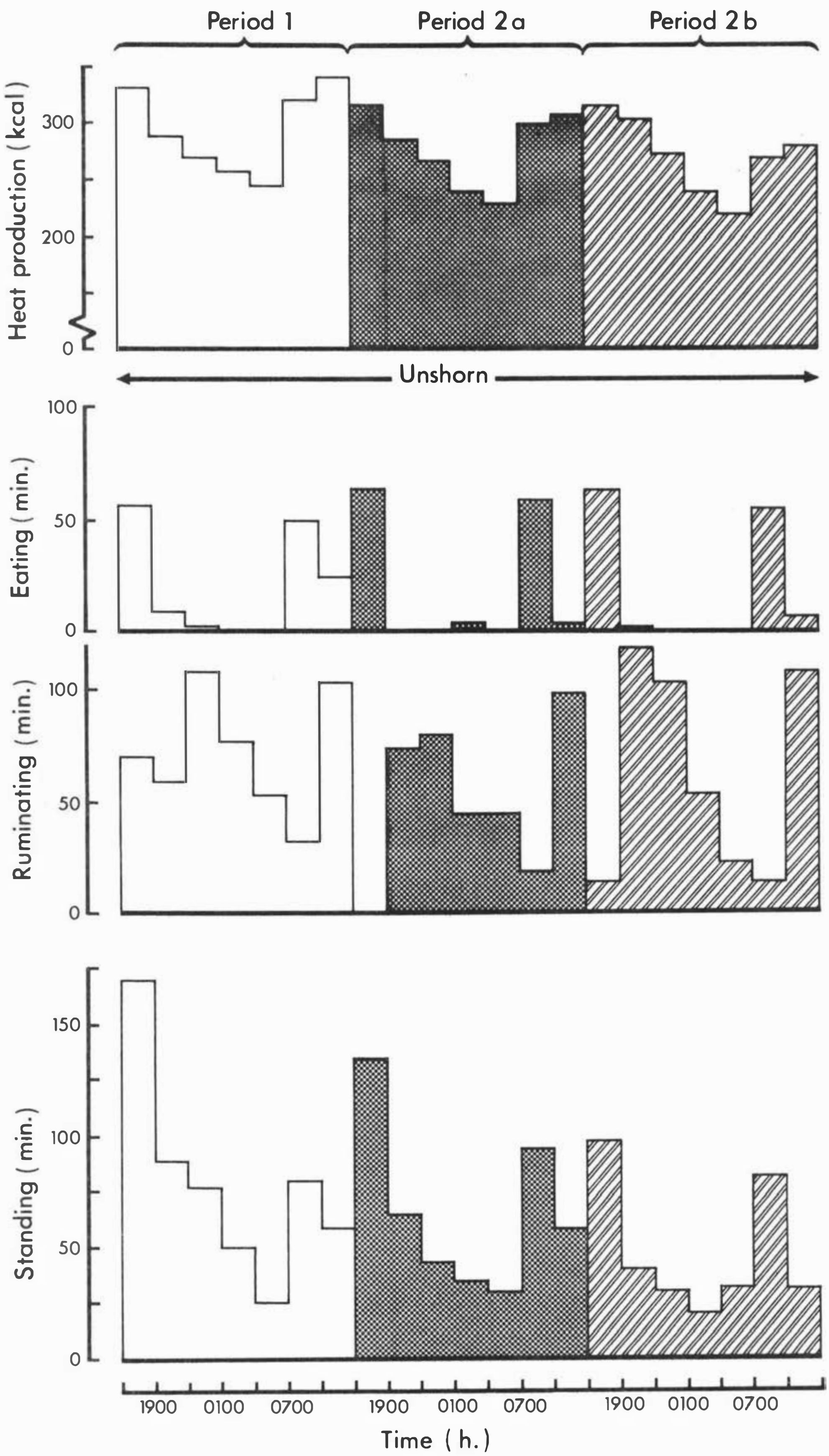

FIGURE 6.3 Experiment 2. Heat production and time spent eating, ruminating and standing by Sheep 10, receiving dried grass. Period 1, mean of 2 days; Period 2(a), mean of days 1 and 8; Period 2(b), mean of days 12, 18, 32.

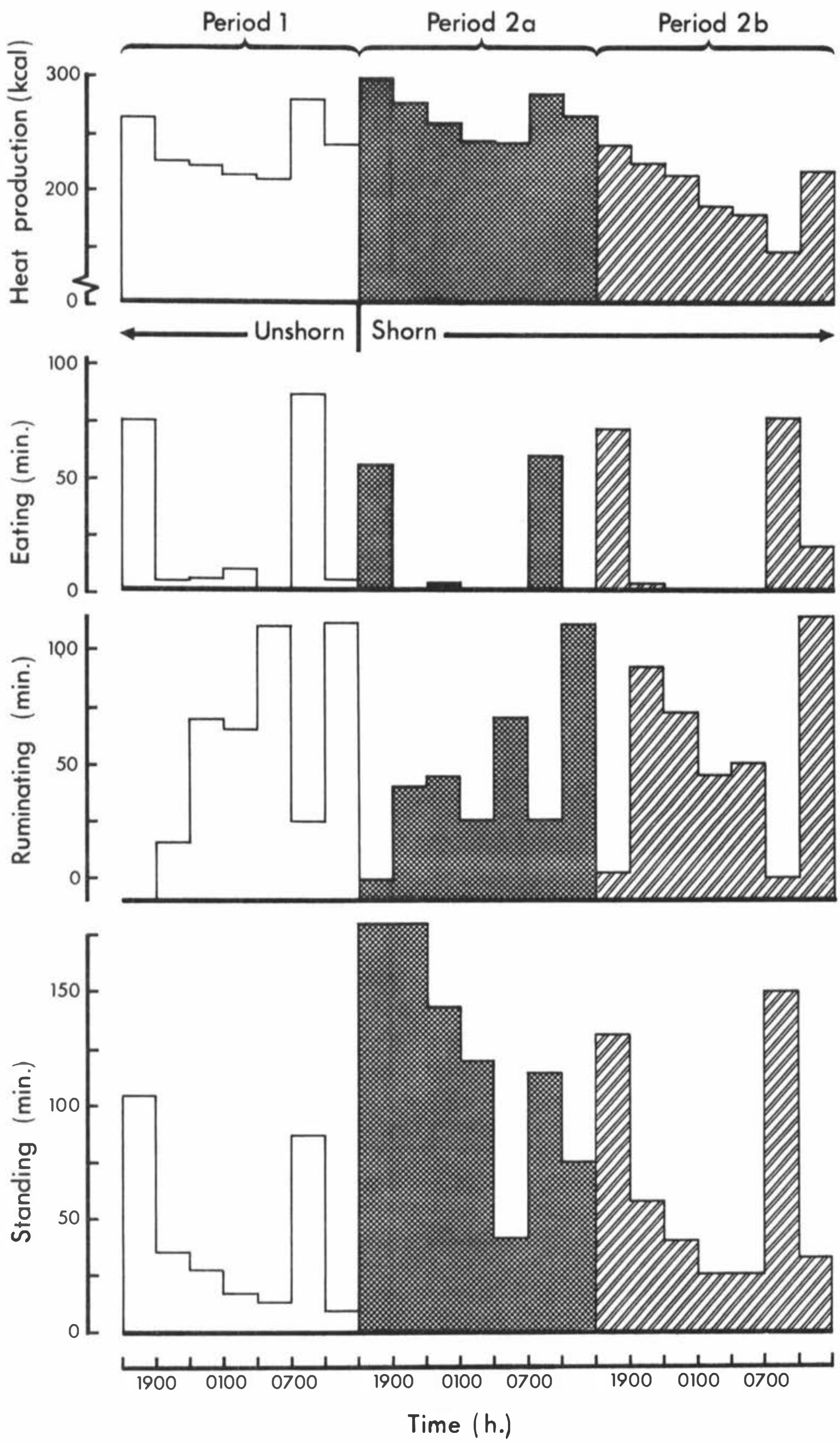

FIGURE 6.4 Experiment 2. Heat production and time spent eating, ruminating and standing by Sheep 3, receiving ground hay. Period 1, mean of 2 days; Period 2(a), mean of days 1 and 8; Period 2(b), mean of days 12, 18, 32.

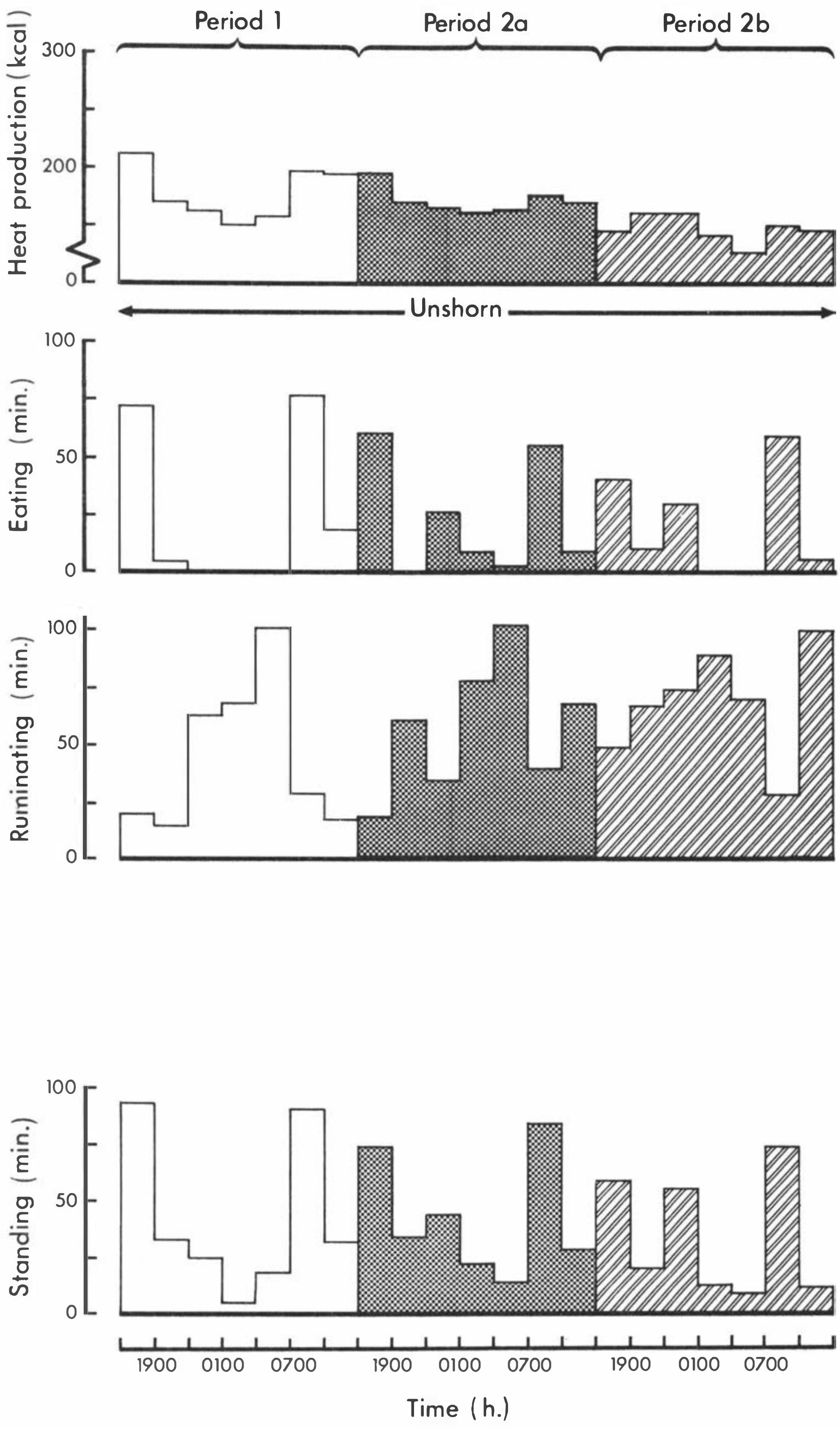

FIGURE 6.5 Experiment 2. Heat production and time spent eating, ruminating and standing by Sheep C, receiving ground hay. Period 1, mean of 2 days; Period 2(a), mean of days 1 and 8; Period 2(b), mean of days 12, 18, 32.

present experiment and comparisons were available between unshorn and shorn sheep. However, no differences were observed in the energy cost of rumination between shorn and unshorn sheep. The number of comparisons available by which the energy costs of eating and standing were estimated were limited to both the shorn sheep in the post-shearing period, thus eliminating any comparisons with the cost of these activities with the unshorn sheep.

TABLE 6.8 The energy costs of various activities of sheep from the data obtained in Expt 2 and in comparison with other results

Activity (kcal/h./kg L.W.)	Graham(1964)	Ustjanzew(1911)	Present experiment
eating	0.54 ± 0.05	0.77 ± 0.02	0.93 ± 0.05
ruminating	0.24 ± 0.03	0.24	0.26 ± 0.01
standing	0.34 ± 0.02		0.32 ± 0.03

There was a suggestion that the energy expenditure of eating varied, depending on whether the comparison of eating was made with standing, preceding or following the period of eating, i.e. S v SE or SE v S. Thus with sheep B, S v SE was 0.96 kcal/kg LW/h. (4 observations), compared with SE v S of 0.77 kcal (3 observations). With sheep 3 the differences between the two methods of measurement were much less, i.e. 1.01 kcal/kg LW/h. (3 obser ations) and 0.96 kcal (6 observations) for S v SE and SE v S respectively.

The mean energy costs of the various activities, obtained in the present experiment, were used to calculate changes in energy expenditure associated with changes in activity of the sheep between Periods 1 and 2. These changes, together with the net change in energy expenditure are summarised in Table 6.6, which shows that whilst the time spent eating and ruminating decreased following shearing, the increase in the time spent standing was such to have contributed substantially to an increase in energy expenditure.

The rate of live weight loss was greater with the shorn sheep receiving ground hay, despite the higher intake of this animal compared with the unshorn sheep. The live weight gain of the shorn sheep receiving the dried grass was less than the unshorn sheep but its intake was also less. Live weight gain per unit of DE intake (kcal/kg$^{0.75}$) was 0.25 and 0.49 g/24 h. for the shorn and unshorn sheep receiving dried grass respectively.

6.4 DISCUSSION

The increases in heat production when sheep were shorn in Expt 1 amounted to a maximum of 553 kcal (25%) for the sheep receiving dried grass, and a maximum of 283 kcal (17%) for those receiving ground hay. These increases are considerably below the maximum increase in fasting heat production of 44% obtained by Farrell & Corbett (1970) when merino sheep were shorn. However conditions in the present experiment were not comparable with those of Farrell & Corbett who measured fasting heat production soon after sheep were taken from pasture.

The increases in heat production were also less than those observed by Armstrong, Blaxter, Graham & Wainman (1959) when sheep were closely clipped to give a fleece length of 0.1 cm. They fed their sheep dried grass at three levels, 600, 1200 and 1800 g DM/day, and taking into account the lower digestibility of their dried grass, the levels used in the present experiment corresponded to their high level for the sheep fed dried grass, and to their medium level for those receiving ground hay. At their high level of feeding, heat production increased by 8 - 900 kcal/24 h., and at the medium level the increase was over 1100 kcal/24 h. at an environmental temperature of 13°C. They also found that the environmental temperature corresponding to minimum heat production was 33°C for the medium level and 24 - 27°C for the high level of feeding. The present results therefore differ on two counts: (1) the increase in heat production following shearing was less and (2) the increase in heat production was greater with the sheep receiving dried grass than with those receiving ground hay, a reverse of the result obtained by Armstrong, Blaxter, Graham & Wainman (1959), where the lowest levels of feeding resulted in the greatest increase in heat production, at a given environmental temperature. However their results are not strictly comparable, as the variation in level of intake was obtained by varying the amount of the same food, whereas in the present experiment two foods differing widely in apparent digestibility were used. The sheep in the present experiment were not clipped as closely as those of Armstrong, Blaxter, Graham & Wainman (1959) (0.2 cm as against 0.1 cm), but it is unlikely that this would have caused all the difference between the present work and those of the above workers. The total insulation of the sheep consists of the insulation of the body tissues, insulation of the air-fleece interface and insulation of the fleece (Joyce, 1968). With newly shorn sheep, the contribution of fleece insulation to total insulation is small and an increase in fleece length from 0.1 to 0.2 cm would increase total insulation by approximately 4 - 5%.

The observations of Farrell, Leng & Corbett (1972) that the increase in heat production when sheep were shorn varied with the body condition of the animals, points to a possible source of variation between the results of Armstrong, Blaxter, Graham & Wainman (1959) and those of the present experiment. Farrell, Leng & Corbett (1972) observed that the critical temperature for a well-nourished sheep (live weight 36 kg) after shearing was about 27°C, whereas for an under-nourished sheep (live weight 25 kg), the critical temperature was about 38°C. They calculated that heat production increased by 30 kcal/m^2 for each 1°C decrease in ambient temperature below the critical for the well-nourished sheep, and by 43 kcal/m^2 for an under-nourished sheep. On this basis, the increase in heat production following shearing, at an ambient temperature of 13°C, would have been approximately 420 kcal and 900 kcal/24 h. for the well-nourished and under-nourished sheep respectively. Whilst the above results obtained with the well-nourished sheep are much closer to the results reported in the present experiment for the sheep receiving dried grass, they do little to support the results obtained with the sheep receiving ground hay, which barely maintained their live weights and could have been considered to be under-nourished compared with the sheep receiving dried grass. From the work of Farrell, Leng & Corbett (1972), a greater increase in heat production than that observed, might therefore have been expected, when the sheep receiving ground hay were shorn. The sheep of Armstrong, Blaxter, Graham & Wainman (1959) were exposed to a particular temperature for only 7 days, whereas the sheep in the present experiment were kept at an ambient temperature of 13°C for over 60 days prior to shearing, although it is difficult to see how this would have affected the results obtained.

A feature of the present experiment was the rapid return of heat production to pre-shearing values, which does not agree with the observations of Farrell & Corbett (1970), who noted that fasting heat production remained elevated for a long period, and did not return to pre-shearing levels until up to 133 days after shearing. However the present results are supported to some extent by those of Wodzicka-Tomaszewska (1963), who observed a rapid increase and decline in heart rate when sheep were shorn; with values returning to pre-shearing levels within 15 to 16 days after shearing.

A possible source of variation between experiments could arise through the use of animals of different ages and breeds. Farrell & Corbett (1970) and Farrell, Leng & Corbett (1972) used adult merino ewes and wethers, and Armstrong, Blaxter, Graham & Wainman (1959) used adult Halfbred x Down wethers, whereas immature Romney wethers were used in the present experiment. Large differences in tissue insulation between breeds were observed by Joyce (1968), with Cheviot sheep having approximately twice the tissue insulation values of Down type breeds. No data were available for Romneys however, but the observations do establish that breed differences exist.

The energy cost of ruminating agrees very closely with values obtained by Graham (1964), and Ustjanzew (1911), cited by Graham (1964). There was also good agreement for the energy expenditure of standing, between the results obtained in the present experiment and those of Graham (1964). Graham (1966) stated that there was evidence (unpublished) to show that the energy cost of standing may be less for thin shorn sheep. No evidence was obtained in the present experiment to support this statement, as the energy expenditure of standing was obtained only with sheep after they had been shorn. Blaxter & Joyce (1963) obtained no statistically significant increase in energy expenditure with sheep standing, compared with lying. Their results were obtained with tracheotomized sheep. The energy expenditure of standing of sheep, determined by Webster & Valks (1966) was also considerably lower (0.12 kcal/kg LW/h.) than the values obtained in the present experiment. No explanation can be offered for these very low values, compared with the values obtained in the present experiment, and those of Graham (1964).

The energy expenditure of eating was considerably above the value determined by Graham (1964), but not greatly above that of Ustjanzew (1911) or of the value of 0.83 kcal/kg LW/h. determined by

Webster & Hays (1968). It is possible that the values for the energy expenditure of eating in the present experiment were somewhat inflated in that 9 out of the 16 observations were made with the period of standing only, following the period of standing and eating. Nevertheless the evidence shows that there is considerable energy expenditure involved in the act of eating and it does not support the statement by the Agricultural Research Council (1965) that the cost of grazing which also includes walking, is small.

Hutchinson & McRae (1969) noted that shorn sheep at pasture spent more time standing, and also that the rate of eating increased after shearing, both observations also noted in the present experiment. Despite the decrease in time spent eating following shearing, the increase in standing time was so substantial that it meant that an appreciable proportion of the increase in heat production following shearing could be attributed to a change in behaviour.

6.5 CONCLUSION

In most of the experiments studying the effects of shearing on voluntary food intake reported in the previous chapters, the increases in intake did not reach the levels that might have been expected from the large increases in fasting heat production noted by Farrell & Corbett (1970) or the considerable increase in heat production obtained by Armstrong, Blaxter, Graham & Wainman (1959), and Farrell, Leng & Corbett (1972), when sheep were shorn. There are a number of reasons why changes in intake do not fully compensate for an increased energy expenditure following shearing. Some have been demonstrated in the shearing experiments reported in the preceding Chapters, e.g. the limitations imposed by the rate at which food particles are removed from the reticulorumen, and the effect of body condition with a food of high digestibility, such as dried grass.

In one experiment (Chapter 5) it appeared that the maximum response of 1040 kcal ME obtained with thin shorn sheep approached the increases in heat production observed by Armstrong, Blaxter, Graham & Wainman (1959). However the increase in intake was apparently reinforced by the thin condition of the animals, and it appeared that the increase due to the effects of shearing may have been closer to 450 kcal ME/24 h.

If the results in the present experiment represent a truer picture of the extent of the increase in heat production following shearing, under the conditions obtaining in the series of shearing experiments reported, then the increases in intake observed in these experiments more nearly matched the increase in energy expenditure following shearing.

The relationships between the increase in food intake of sheep when they are shorn, and the increase in energy expenditure are discussed in more detail in the following chapter.

CHAPTER 7

GENERAL DISCUSSION

7.1 Introduction

The main theme of the work reported in this thesis was concerned with factors controlling food intake. A series of experiments were also conducted with the objective of studying various methods of measuring the retention time of food residues, because of the projected intensive use of this measure in the main experiments. The results of this investigation have been reported in Chapter 2, and as they fall outside the main theme of the work, details will not be discussed further.

A study was also made of the change in heat production when sheep receiving dried grass or ground hay were shorn. This was carried out in an attempt to equate changes in heat production with the changes in voluntary food intake observed when sheep were shorn in the earlier experiments. In no case did the increase in the heat production of sheep following shearing approach the increase in heat production of shorn sheep observed by Armstrong, Blaxter, Graham & Wainman (1959). However evidence provided by Farrell, Leng & Corbett (1972) showed that the heat production of well nourished sheep increased to a lesser extent following shearing, than that of under-nourished sheep.

In the following discussion, the changes in intake observed in the experiments described in the preceding chapter will be related to changes in heat production of sheep following shearing. An attempt will be made to synthesise the results of the experiments to show whether or not the hypotheses in Section 1.5 were supported.

7.2 Establishment of hypotheses on the control of food intake

This has been dealt with in detail in Chapter 1, (Section 1.5) where physical and metabolic factors controlling food intake in ruminants were discussed, but a brief recapitulation is relevant at this stage.

With roughages in the long form, and of low apparent digestibility, voluntary food intake appears to be limited by the capacity of the alimentary tract, and the rate at which food residues are removed from the tract, or more particularly the reticulorumen (see Section 1.3.4). Conrad, Pratt & Hibbs (1964) showed that physical factors were of major importance in controlling food intake when the DM digestibility of the ration was lower than 67%. Above this, metabolic factors assumed greater importance and food intake was related to energy demand, so that as the intake of energy increases, the productive output of the animal increases. On the basis of the above and the evidence reviewed in Chapter 1, experiments were carried out to examine the following hypotheses:-

1. that an increase in energy expenditure, induced by shearing, would result in a minimal increase in the voluntary intake of sheep receiving diets of low apparent digestibility, and that the intake of sheep receiving food of high apparent digestibility would increase to meet the increase in energy demand

2. that a change in the physiological state of sheep, induced by shearing would affect measurements (such as retention time of food residues and amounts of digesta in the alimentary tract), concerned with the physical control of voluntary food intake.

7.3 The voluntary intake of chopped hay and ground hay

The hays used were all of low apparent digestibility, (approximately 48 to 53%) although the hay used in Expt 1, Chapter 4 was rather higher at 58%. There were consistent increases in the voluntary intakes of the sheep receiving the hays, following shearing. Thus apparent digestibility, retention time of food residues, and physical factors in general are not the only factors controlling the intake of sheep receiving these diets. The considerable increases in voluntary intake occurred, despite the low apparent digestibility, where physical factors might have been expected to be dominant. The results therefore do not support the first hypothesis that an increase in energy expenditure would be associated with a minimal increase in the voluntary intake of foods of low apparent digestibility.

The extent to which the increase in the intake of the hays met the increase in energy expenditure of sheep, following shearing, will now be considered. A summary of the experiments using chopped hay and ground hay, with the increases in ME following shearing, are given in Table 7.1, and are also compared with increases calculated from the results provided by Minson & Ternouth (1971) and Weston (1970). The results of Minson &

Ternouth's second experiment are included, as the mean ambient temperature of 13°C was comparable to that used in the present experiment, whereas their other experiment was conducted at a mean ambient temperature of 25°C. Weston (1970) carried out three experiments with the ambient temperatures varying between 6 and 16°C.

TABLE 7.1 Increases in estimated ME intake following the shearing of sheep receiving hay, in various experiments

Experiments	Crude Protein (%)	Apparent digestibility of energy(%)	Increase in ME intake over 4 weeks following shearing (kcal/24 h.)	Ambient Temperature
Long hay				
Chapter 3				
intact			175	13°C
fistulated	7.8	50	149	13°C
Chapter 4 Expt 1(b)	10.4	59	679	13°C
Chapter 4 Expt 2	10.2	53	235	13°C
Ground hay				
Chapter 4 Expt 2	9.2	49	385	13°C
Expt 3	10.0	52	393	13°C
Long hay				
Minson & Ternouth (1971) Expt 2				
Pangola	4.0	47	286	13°C
Setaria	9.0	51	238	13°C
Weston (1970)				
Wheaten hay	4.7	57	215	6 - 16°C

The increases in ME intake, summarised in Table 7.1, can then be compared with the mean increases in heat production following shearing, observed in the experiments reported in Chapter 6. Table 7.2 summarises the results in terms of the net mean increase in heat production over 24 days following shearing in Experiment 1 and over 18 days in Experiment 2, compared with the mean for the pre-shearing period.

TABLE 7.2 Difference in heat production between Period 1 and 2 (Period 2 over 24 days in Expt 1, and 18 days in Expt 2 following shearing) for shorn and unshorn sheep, receiving dried grass or ground hay

Experi-ments	Ground hay (kcal/24 h.)	Dried grass (kcal/24 h.)
Expt 1		
Shorn	98	332
Unshorn	-96	67
Net	194	265
Expt 2		
Shorn	91	191
Unshorn	-58	-92
Net	149	283

Thus in Expt 1 the mean net increase in heat production when the sheep receiving chopped hay were shorn, was 194 kcal/24 h. The increase in ME intake of the two groups of sheep receiving the low protein chopped hay (Chapter 3) scarcely met the expected increase in heat production, particularly as the net availability of ME would at the most be 90% (Graham, Wainman, Blaxter & Armstrong, 1959) and could well be lower. The inability of the sheep receiving the low protein hay to increase voluntary intake sufficiently to meet the increased energy expenditure resulted in an increase in the rate of live weight loss after shearing. In contrast to this result, the increment of ME following shearing of the chopped hay of higher crude protein content (Expt 2, Chapter 4), more nearly met the increase in energy expenditure. The large increase in ME intake observed when the sheep receiving chopped hay in Expt 1(b) were shorn may have been associated with the higher apparent digestibility of this hay compared with the other hays, but limited reliance can be placed on this result as only two sheep were used, and there were no unshorn control animals.

With the ground hay used in Expt 2, Chapter 4, the protein content and apparent digestibility were not greatly different from the chopped hay used in the experiment described in Chapter 3, yet the increase in ME intake following shearing was considerably greater, and on the basis of the results obtained in Chapter 6, would more than compensate for the increase in energy expenditure. An increased live weight gain might have been expected as a result, but there were no significant changes in live weight gains after the sheep were shorn. This lack of a positive result may have been a reflection of the inaccuracies inherent in live weight gain as a measurement, and the small number of animals used. The increase in the ME intake of sheep receiving the ground hay used in Expt 3, Chapter 4 was also similar to that observed in Expt 2. In Expt 3 the live weight gains of the sheep were higher following shearing, indicating that the increase in intake had more than compensated for the increase in energy expenditure.

The extent of the increase in voluntary intake of the sheep receiving chopped hay in the present experiments agrees well with the increases observed by Minson & Ternouth (1971) and Weston (1970). The latter worker noted an increase in the rate of live weight loss of sheep following shearing in experiments carried out at the lowest ambient temperature (6 to 7°C), but live weight gains were maintained following shearing in a second experiment, where ambient temperatures were higher (minimum 8 to 9°C and maximum 17 to 19°C). Minson & Ternouth (1971) observed that live weight changes were similar for shorn and unshorn sheep receiving hay. Their data suggested that the increased energy expenditure of the shorn sheep were being met by increases in energy intake similar to those obtained in the present series of experiments. The above evidence, together with that obtained in the present intake experiments, suggests that the heat production of the sheep following shearing did not increase to the extent observed by Armstrong, Blaxter, Graham & Wainman (1959) and Farrell, Leng & Corbett (1972) but may have been closer to that observed in the experiments reported in Chapter 6.

Thus an important assumption in this discussion, is that the increase in heat production observed in the two experiments reported in Chapter 6 was a true representation of the increase in energy expenditure occurring, when sheep were shorn, in the series of intake experiments. Evidence obtained in the preceding Chapters supported the second hypothesis (see Section 1.5), in that changes occurred in measurements associated with the physical control of food intake, following shearing. An increase in the amount of DM in the reticulorumen, and the tract caudal to the reticulorumen, was observed with the sheep receiving chopped hay and ground hay respectively, following shearing (Chapter 3 and 4).

Depletion of abdominal fat would permit a greater fill of the alimentary organs, but is an unlikely explanation for the results obtained. It is considered more likely that the evidence supported the hypothesis proposed by Egan (1970), that mechanisms exist which override fill or permit the resetting of the fill mechanism at a new higher level. It is evident that the increased energy demand following shearing must have invoked a strong positive change in the set point affecting the reference input (see Section 1.3.6) to allow an increase in the intake of a food of low DE concentration, where physical factors controlling intake appear to be dominant.

Other changes in measurements, associated with the control of intake by physical means, occurred following shearing, although no evidence was provided concerning cause and effect relationships. The mean retention time of food residues decreased in many of the experiments. This would probably result in a less than proportionate increase in alimentary tract fill, with an increase in intake. Evidence was also provided (Expt 3 and 4, Chapter 4) that hypertrophy of the gut, measured as an increase in the weight of the alimentary tract or its various organs, occurred when sheep were shorn. This would mean that extra ingesta could be accommodated without resulting in a commensurate increase in gut distension. Hypertrophy of the alimentary organs would not occur immediately, and this delay would help to explain the relatively slow increase in voluntary food intake following shearing, despite the rapid increase in heat production (see Chapter 6). The various changes that occurred do not necessarily mean that physical factors limiting intake were removed. The presence of physical factors was indicated by the significant negative relationship between the voluntary intake of sheep receiving the hays and retention time, as well as the positive relationship between voluntary intake and weight of the alimentary organs.

Following shearing, the increase in voluntary intake of sheep receiving ground hay was greater than that of sheep receiving chopped hay : this is consistent with the postulation that the rate of removal of DM from the reticulorumen imposes a limitation on intake. The sheep receiving ground hay were apparently able to increase their voluntary intake sufficiently to meet the increase in energy demand following shearing, because of the removal of an important physical limitation.

7.4 Intake of foods of high apparent digestibility

In all experiments, mean voluntary food intakes of the sheep were higher when receiving the concentrate-oat husk mixture or the dried grass compared with the hays. The results are in agreement with the general positive relationship between intake and digestibility noted by many workers (Blaxter, Wainman & Wilson, 1961; Minson, Harris, Raymond & Milford, 1964). Considerable live weight gains were made by the sheep receiving the concentrate-oat husk mixture and the dried grass, although live weight gains were reduced in some of the experiments where decreases in intake occurred with unshorn control sheep receiving dried grass.

The coefficient of variation for voluntary intake of sheep receiving the concentrate-oat husk mixture was high and the number of animals used was insufficient to produce significant differences. Thus the effects of shearing on the voluntary intake of this food were inconclusive. However a number of the measurements other than intake, which were obtained with the concentrate-oat husk mixture, deserve comment. These will be discussed in relation to the measurements obtained with the chopped hay. Most of difference in apparent digestibility between the concentrate-oat husk mixture and chopped hay occurred in the rumen, with a mean apparent digestibility of the DM of 50% and 30% respectively. The low nitrogen content of the chopped hay probably resulted in a slower rate of microbial digestion of this diet (Blaxter, 1962) thus contributing to a slower rate of removal from the reticulorumen. It is probable that a considerable proportion of the differences in intake between the two foods arose through differences in the rate at which food particles were broken down by mastication and microbial digestion, and the rate at which DM passed to the omasum. The considerably greater amount of digesta DM in the reticulorumen of the sheep receiving the concentrate-oat husk mixture, compared with that of those receiving the chopped hay, indicated that reticulorumen DM fill itself may not be a controlling factor limiting voluntary intake. A critical fill may be set at levels determined by other factors, such as the wet weight of the contents, or the rate at which food particles are broken down and removed from the reticulorumen. Further support for this contention was provided by the evidence produced in Chapter 3. Despite large differences in voluntary intake between the sheep receiving the concentrate-oat husk mixture and that of those receiving the chopped hay, the amount of DM leaving the reticulorumen was similar in both diets, before and after shearing. Unlike the consistent increases in intake of sheep receiving hay when they were shorn, changes in intake of sheep receiving dried grass were often irregular. Thus in Expt 1(a), Chapter 3, the intake of the sheep increased following shearing, whereas they decreased as the experiment progressed in Expt 1(b). However no great reliance can be placed on these results for the reasons explained in Chapter 3.

In Expt 2, Chapter 3, a decline in intake of both the shorn and unshorn sheep receiving dried grass was observed. With the shorn sheep, the mean rate of decline in ME intake was 185 kcal/24 h. and with the unshorn sheep it was 455 kcal/24 h. It could therefore be considered that shearing slowed the rate of decline to the extent of 270 kcal/24 h. On the basis of these observations, obtained with unshorn sheep, it was postulated that the body condition of the sheep could affect the voluntary intake of dried grass, and affect the response to shearing, so that a further experiment was conducted (Chapter 5) to examine the effects of shearing fat and thin sheep on the voluntary intake of dried grass. There was good evidence that fat sheep increased their intake when they were shorn. The mean increase was 304 kcal ME over the whole four weeks of the post-shearing period, and according to the increase in heat production summarised in Table 7.2 would probably have met the increase in energy expenditure when the sheep were shorn.

The decline in intake of the fat unshorn sheep receiving the dried grass supported the results obtained with the unshorn sheep receiving dried grass in Expt 1(b) and Expt 2 in Chapter 4. The evidence obtained at slaughter indicated that physical restriction of the abdominal cavity by fat was probably not involved in this decrease in voluntary intake. The amount of DM in the reticulorumen and the total contents of the tract were also lowest for the fat unshorn sheep compared with the fat shorn and thin shorn groups. It was therefore considered that physical factors were probably unimportant in restricting the intake of dried grass by the fat unshorn sheep, but that some mechanism such as that postulated by Kennedy (1953), where some compound was released from fat depots in proportion to their size, may have been involved.

Measurements associated with the physical control of food intake varied between shorn and unshorn sheep receiving dried grass, although the evidence was not as clear-cut as that obtained with the sheep receiving hay. The reticulorumens were heavier and there was a greater amount of DM in the reticulorumen of the shorn sheep, than the unshorn sheep. Unlike the chopped hay or ground hay, no evidence was obtained that retention times of food residues were reduced in the shorn, compared with the unshorn sheep receiving dried grass and unlike the hay, there were no significant negative relationships between voluntary intake and retention time.

The very large increase in the intake of dried grass of the thin shorn group appeared to result from the combined effects of shearing and realimentation and illustrated the considerable flexibility of the system controlling voluntary intake, by its ability to cope with a considerable increase in intake. It further indicated that energy demand was important in determining the level of intake, and generally demonstrated the effect of metabolic control overriding physical control.

7.5 CONCLUSION

The hypothesis that the intake of foods of high apparent digestibility would increase to meet the increase in energy expenditure, when sheep were shorn, received little support from the results of experiments reported in Chapter 4 (Expt 1(b) and Expt 2) or from the results of Minson & Ternouth (1971) with their lucerne hay, but received support from the results obtained with the fat shorn group of sheep receiving dried grass (Chapter 5).

The consistent increase in the intake of foods of low digestibility when sheep were shorn, observed in all experiments, did not support the hypothesis than an increase in energy expenditure would result in a minimal increase in the intake of such foods. It was apparent that the increase in intake when sheep were shorn was accommodated partly through a range of changes in measurements associated with the physical control of intake. The evidence obtained supported the contention of Egan (1970)

> "that a complex of interacting physical and metabolic factors exist in the control of food intake and that there is no simple switch-over from physical to metabolic control".

The main theme of this thesis was to study factors affecting voluntary food intake of sheep. The approach adopted was to alter the energy demand of the sheep by shearing, and to use the change as a model to investigate relationships between the DE concentration of diets, and voluntary intake.

Whilst limited conclusions can be drawn from the present work, it is the writer's belief that worthwhile advances towards understanding factors controlling voluntary intake could be made under conditions where the energy demand of animals varied widely. The subjects for such a study could be dry and lactating animals, at different stages of lactation, fat and thin animals, and animals subjected to varying environmental temperatures. As well as using diets with a wider range of DE concentration and physical form than used in the present study, changes in the levels of metabolites in the blood with changes in energy demand would need to be determined. The studies could also involve the use of techniques such as the intravenous and intraruminal infusion of metabolites. Such an approach would require considerably more resources than were used to complete the work reported in this thesis.

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