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THE UNIVERSITY OF ALBERTA

BODY COMPOSITION AND ENERGY METABOLISM IN MATURE SHEEP

BY

ALLEN EVERETT DIXON

(C)

A THESIS

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

IN

ANIMAL PHYSIOLOGY

DEPARTMENT OF ANIMAL SCIENCE

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled BODY COMPOSTION AND ENERGY METABOLISM IN MATURE SHEEP.

submitted by ALLEN EVERETT DIXON

in partial fulfiiment of the requirements for the degree of

MASTER OF SCIENCE

in ANIMAL PHYSIOLOGY.

(Supervisor)

John Fedders

Date: 30 October 1989

ABSTRACT

The effect of liveweight change on body composition and energy metabolism was examined in mature sheep. Twelve Suffolk ewes of similar body composition and weight were fed to either maintain body weight (medium), lose 10 kg (low) or gain 20 kg (high). After reaching these weights, feed intakes were adjusted to maintain animal weight. Whole animal heat production was measured biweekly using indirect calorimetry. Body composition was determined before and after weight change using tritiated water dilution. At the end of the trial, weights of the internal organs were measured and the chemical body composition of the body was determined by proximate analysis. Tissue oxygen consumption was measured *in vitro* for samples of intercostal muscle, liver and duodenum.

The influence of body condition on thermogenic capacity and resistance to cooling was also measured after weight change. Measurements taken were cold-induced summit metabolism, the time required to reach summit metabolism and the amount of time before the animals experienced mild hypothermia (a 3°C drop in rectal temperature).

The nature of the metabolic response to the change in feed intake was also examined. The metabolic heat production of the high and low animals was measured frequently after the change in feed intake.

Differences in liveweight between groups were due to the weights of body fat, protein and water. Animals in the high group had heavier liver, kidneys, reticulorumen, omasum, abomasum, skin with fleece, head and abdominal fat and carcasses than the other groups ($P<0.05$).

Heat production increased in the high animals, but was not

significantly different between groups when expressed per unit of body weight ($P=0.10$). Heat production was correlated to liver, gastro-intestinal tract and fat weights. No significant differences in tissue metabolic intensity between groups were found for muscle ($P=0.20$), liver ($P=0.87$) or duodenum ($P=0.73$).

Summit metabolic rates did not differ between groups ($P=0.33$). The time required to reach mild hypothermia was longer for the heavy animals ($P<0.05$). This indicates that body fat increases the animals resistance to cold by providing more insulation, not increasing the thermogenic capacity.

The change in metabolic heat production due to feed intake was best described linearly in the short term (20d) and exponentially in the long term (150). The rate of change was greater for animals increasing feed intake than those with decreased intake.

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Seasonal variation in forage quality or quantity creates periodic nutritional deficiencies in animals. A deficit in energy intake is critical in terms of the production of meat, milk, fibre and work and is also the most costly to correct (Allden, 1981). Often, the decision to correct an energy deficiency is based on the cost of supplemental feed. Another aspect of supplementary feeding not usually taken into consideration is the energetic cost. The choice between feeding to maintain body condition or allowing body weight to change will depend on the energetic cost of maintaining body weight.

A decrease in dietary energy causes loss of liveweight, as stored body fat is used to meet maintenance energy requirements. The contribution of stored fat tissue to maintenance energy requirements has been estimated at 8-10% of the total (Baldwin and Smith, 1974). A decrease in body fat would be expected to cause only a small drop in the energy required for maintenance. Thus, one would expect the animal to require about the same amount of energy for maintenance regardless of body weight. No advantage would be gained by allowing a large liveweight loss when it was economical to feed the animal to maintain body weight.

Graham (1967) found that as liveweight decreases, total animal heat production decreases. This suggests that either fat is metabolically active or body protein is lost with liveweight loss. In this case, total energy requirements would be less if animals were allowed to lose weight during a period of low dietary energy intake.

There would be an advantage to allow the animal to lose weight as less dietary energy would be required for maintenance.

In cold climates a change in liveweight not only changes the amount of energy retained, but may affect the animals ability to withstand cold temperatures, as body weight is related to body heat loss and thermal insulation (Mount, 1979).

The research described in this thesis was undertaken to:

a) establish the effect of liveweight change in mature animals on body composition and energy metabolism (Chapter II)

b) examine the role of body fat in cold-induced thermogenesis and resistance to cold (Chapter III)

c) gain experimental evidence for a possible time lag in metabolic rate following a sudden change in feed intake and to describe the metabolic change mathematically (Chapter IV). This paper is a cooperative effort with a summer student, Terry Andersen.

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Chapter II. Body Composition and Energy Metabolism of Mature Sheep at Different Liveweights.

INTRODUCTION

Expression of maintenance energy requirements per unit of body lean mass has been proposed as an alternative to body weight. This is because of the higher metabolic activity of lean tissue (Pullar and Webster, 1977; Webster, 1981) and the apparent close relationship between lean body mass and heat production (Graham, 1967; Toutain et al., 1977).

Weight changes in mature animal are often assumed to be a change in the amount of body fat. If lean body mass is the main determinant of rate of metabolism and metabolic energy requirements, then mature animals established at different body weights should have the same metabolic rate. McNiven's (1984) work with mature sheep established in different body condition indicated that heat production is a function of body weight, regardless of the amount of body fat. This suggests that fat may significantly contribute to whole body metabolism.

Liveweight change in the body of mature sheep resulting from a higher or lower feed intake has been found to include changes in the amount of body protein (Panaretto, 1964; Keenan et al., 1969; Farrell et al., 1972). Liver weight in particular has been associated with the change in feed intake (Keenan et al., 1969; Johnson et al., 1987).

Body composition also affects heat production in growing animals (Tess et al., 1984). A primary source of metabolic heat production has been identified as the visceral organs (Koong et al., 1985). The

association of visceral organ weight with maintenance energy metabolism in mature animals has not been clearly established.

The objective of this study was to determine the body composition and energy metabolism of mature sheep fed to reach different body weights and then maintained at these weights.

MATERIALS AND METHODS

ANIMALS: Twelve mature Suffolk ewes (39 months, 63.4 ± 4.9 kg) of similar body frame size were selected from the University of Alberta flock. They were brought indoors, dewormed (Thiabendazole, 30 ml) and injected with 500,000 IU of vitamin A and 75,000 IU vitamin D. The ewes were housed in individual metabolic crates to facilitate collection of urine and feces. Ambient temperature was maintained between 18 and 23°C, and light patterns followed natural changes. The animals were weighed weekly throughout the trial and shorn every six weeks. They had free access to water and cobalt-iodized salt.

DIET: The ewes were fed, once a day, a diet of three parts pelleted barley concentrate (CP= 178g/kg, DM= 891g/kg) and five parts chopped timothy hay (CP= 88.6g/kg, DM= 932g/kg). The apparent digestible energy of the diet was calculated as 13.2 MJ/kg DM. All animals were fed at maintenance levels (NRC, 1986), calculated to be 800 g of the diet per day. After twelve weeks, the ewes were randomly allocated to one of three treatment groups designed to maintain (medium), increase by 20 kg (high) or decrease by 10 kg (low) body weight. Low animals received 400g/d and high animals received up to 1750g/d of the diet. Upon reaching target weights, feed amounts were changed to levels estimated

to maintain body weight, 720g/d for the low animals and 1280g/d for the high animals.

BODY COMPOSITION: Body composition was estimated on day 45 or 79 and again on day 275 of the trial from tritiated water (TOH) dilution (Robelin 1975). The equivalent of 0.3 uCi TOH in 2-3 ml of physiological saline was injected intramuscularly. Blood samples were taken by venipuncture prior to injection of TOH and at daily intervals for 4 days after the injection. Plasma samples of approximately 0.5 ml were placed in 20 ml of commercial scintillation cocktail (Beckman Ready Gel) and counted in a liquid scintillation counter (Beckman LS5801). Total counts were corrected for plasma dry matter (7%) and expressed per gram of water. Tritiated water space (TWS) was determined from the extrapolation to time zero (injection time) of the relationship between the log of specific activity in the body water and time. Body fat, water and protein were estimated by separate regressions of TWS on the measured fraction and animal liveweight.

CARCASS ANALYSIS/DISSECTION: At the end of the trial the ewes were slaughtered and the free-flowing blood was caught. Blood, lungs and trachea, liver, kidneys, spleen, heart, mesenteric and intestinal fat, reproductive and digestive tracts, head, skin with fleece and feet were weighed separately, placed in plastic bags and frozen. The reticulorumen, abomasum, omasum, small intestine and large intestine were also weighed, emptied, and then reweighed before being frozen. Digesta samples from each section of the intestinal tract were taken for later dry matter determination. The carcasses were weighed, split and chilled for 24 hours and then stored at -20°C.

CHEMICAL BODY COMPOSITION: The body was divided into blood, carcass and noncarcass fractions for determination of chemical composition. The carcass and noncarcass fractions were further divided into boneless and bone.

Half of each carcass was cut into four pieces, placed into containers and autoclaved (Century 21) at 25 atmospheres and 120°C for approximately 2h. The samples were weighed before and after cooking and any weight change was assumed to be water. The lean, fat and juice was then ground in a Waring blender for approximately two minutes to form a homogenous slurry. Two samples of the slurry were taken, dried in a freeze drier and ground to a powder for analysis.

The non-carcass parts, including the fleece, head and feet, were processed together in a similar manner to the carcass. The caught blood was freeze dried in preparation for separate analysis.

Bones were removed from the tissue, scraped, weighed and dried in a 110°C oven overnight. The dried bones were frozen in liquid nitrogen immediately prior to crushing in a jaw type rock crusher (Sturtevant, London). Subsamples were taken from each bone sample by quartering the total sample twice. These subsamples were further ground prior to analysis in a small laboratory mill (Model A10, Jarke and Kunkel, Breisgau).

Ash, ether extract and Kjeldahl-N were determined in duplicate on each fraction by proximate analysis (A.O.A.C. 1980). Gross energy of the samples was determined in duplicate by bomb calorimetry (Parr Diabatic). Samples were dried overnight in a 110°C oven to correct for water absorption after freeze drying.

RESTING METABOLISM: Resting metabolism (RM) was estimated biweekly by open circuit, indirect calorimetry from whole animal respiratory gas exchange (Young et al., 1988). The ewes were suspended in warm (38°C) water during measurements to minimize muscular and thermoregulatory energy expenditures. Measurements were made 16-22 h after feeding to minimize metabolic stimulation associated with the daily feeding period. RM was calculated in watts (W) over a 15 minute period using the equation developed by McLean (1972).

DIURNAL METABOLISM: Metabolic heat production of the ewes over 24 hours was measured by means of a head hood attached to the front of the metabolic crates (Young et al., 1975). The hood was sealed except for a small space around the neck of the animal and air was drawn through the hood into the gas analysis equipment. Metabolic heat production was estimated every 30 minutes throughout the day. Relative increases in metabolic heat production with feeding allowed estimation of the heat production associated with the ingestion of food by each animal.

TISSUE OXYGEN CONSUMPTION: Immediately after slaughter, samples of intercostal muscle, liver and duodenum were taken for measurement of oxygen consumption following the procedure outlined by McBride and Milligan (1985). Duplicate tissue samples were weighed and incubated in 4 mls of Krebs Ringer buffer solution (pH 7.4 at 38°C) to which glucose (10mM) and acetate (10mM) had been added. Oxygen consumption was measured polarographically over 15 minutes using a Clark electrode and a Yellow Springs International Model 53 oxygen analyzer. The tissue samples were dried for 48h at 60°C and then weighed to determine dry matter contents.

STATISTICAL ANALYSIS: Treatment effects were tested by one-way analysis of variance (Steel and Torrie, 1980). Differences between treatment means were tested using Student-Newman-Keuls' multiple range test.

The correlation between chemical body components and RM were determined and the contribution of fat, protein, water, ash and lean (protein plus water) to RM was estimated by linear multiple regression using forward selection (SAS, 1987). Because of the close relationship between water and protein in the body, only one component was used in the regression at a time. A simple correlation between organ weights and RM was also performed and the contribution of highly correlated organs to RM was estimated by stepwise multiple regression.

RESULTS

The feeding regimes produced an average increase of 21.3 ± 1.26 kg (mean ± SD) for the high group, and a loss of 10.3 ± 2.22 kg for the low group. Over the nine months of the experiment, the animals in the medium group lost an average of 3.0 ± 2.7 kg. During the period of maintenance of treatment body weights, the high animals lost an average of 3.0 kg during the first 4 weeks, then gained 2.5 kg during the next 8 weeks. The low animals lost an average of 2.2 kg over the 12 week period.

Fat, water, protein and ash content of the ewes estimated from TOH dilution during the pre-treatment period, shows that all animals had similar body composition at the start of the trial (Table II-1). At the end of the trial, chemical composition of the digesta-free bodies showed that total fat, carcass protein and carcass ash all increased

significantly ($P<0.05$) with body weight in the high animals (Figure II-1).

Gross dissection of the animals indicated that the changes found in the chemical composition took place mainly in the carcass, intestinal fat and gastro-intestinal tract. The organs were pooled into six fractions for comparison between groups (Table II-2); 'VITAL ORGANS' (blood, kidneys, liver, lungs and trachea, heart and spleen), 'GIT' (reticulorumen, omasum, abomasum, large and small intestines), 'OFFAL' (reproductive tract, skin, feet, head), 'FAT' (mesenteric and abdominal fat), 'CARCASS' and 'GIT CONTENTS'. The high animals had significantly ($P<0.05$) higher weights than the medium or low animals in all fractions. Higher VITAL ORGAN weights were a result of heavier livers and kidneys, while larger reticulorumens, abomasums and omasums increased the GIT weight. Differences were largest in CARCASS and OFFAL fraction weights, the difference in the OFFAL fraction was due to the heavier skins and heads.

Assuming no change in body ash content, each kilogram of body weight lost in the low group contained 140g protein, 460g of fat and 400g of water, and each kilogram of weight gained in the high group was 50g protein, 500g fat and 450g water. Reid et al. (1963) reported the caloric content of fat as 39.4 kJ/g and protein as 22.5 kJ/g in the composite sheep body. Using these values, the energy content of weight loss in the ewes was 21.3 MJ/kg and of weight gain was 20.8 MJ/kg.

RM measured before the weight changes was not different for the three groups ($P=0.52$). RM after weight change increased in proportion to increases in liveweight (Table II-3). When expressed on a per unit

of body weight, RM was not significantly different (P=0.10) between groups; 1.45 W/kg for the high animals, 1.32 W/kg for the medium and 1.45 W/kg for the low animals.

The heat increment of feeding (HIF) was calculated for each ewe from its daily heat production. This was done by subtracting the average heat production (W) over a period of minimal activity (02:00h to 08:00h) from the daily heat production. The resulting heat production (W) was multiplied by time to give HIF in megajoules (MJ). High feed animals had the highest HIF (Table II-4). The relationship between feed intake (kgDM/d) and HIF (MJ/d) for the ewes in all treatments was:

$$HIF\ (MJ/d) = -2.720 + 5.913 * (kgDM/d) \quad R^2 = 0.94$$

$$SEa = 0.369 \quad SEb = 0.469$$

RM obtained by the water immersion proceedure was compared with that obtained in the hoods calculated over the same period of time that RM was measured (08:00 to 13:00). Heat production measured in the hood was higher than RM in the low and high groups. Two values for the medium animals were discarded because the animals had jarred the front of the hood open. The average heat production of the three groups measured at the same time of day was 12% higher for the hood than RM.

The metabolic activity of the tissues did not change with feeding regime, as tissue oxygen consumption did not differ significantly ($P<0.05$) between groups (Table II-5).

The correlation of empty body chemical components (protein, fat, ash, water) with RM showed a close and significant association between all components. Regression of the chemical components on RM showed that mesenteric and abdominal fat weight was the best predictor of RM:

$$RM = 38.42 + 0.849\ (Fat) + 1.089\ (Water) \qquad R^2 = 0.85$$

$$RM = 37.98 + 0.862\ (Fat) + 0.865\ (Lean) \qquad R^2 = 0.84$$

$$RM = 57.26 + 1.25\ (Fat) + 1.37\ (Protein) \qquad R^2 = 0.78$$

The simple correlation between RM, organ weights and carcass weight indicated that liver, heart, kidneys, reticulorumen, omasum, abomasum, small intestine, abdominal fat, skin and head weights were significantly ($P<0.05$) correlated with RM. When these organs were placed in a multiple regression, the prediction equation showed that reticulorumen weight predicted RM quite accurately:

$$RM\ (W) = 9.74 + 51.61\ (Reticulorumen) + 1.92\ (Fat)$$

Error mean square = 11.37 $\qquad R^2 = 0.93$

The only other organ to enter the equation was mesenteric and abdominal fat.

The addition of HIF values to the regressions of either the chemical components or organ weights and RM did not change the outcome of the prediction equations.

DISCUSSION

Establishment of maintenance feeding levels for the three groups during the post-treatment period was important to ensure that the animals were in energy equilibrium. The slight energy deficit in the medium group, as indicated by an average weight loss of 3 kg per animal over the 36 weeks of the trial, may have been due to individual animal weight differences at the start of the trial, or discrepancies between predicted and actual feed energy values. The level of feed intake for the high group in the last 12 weeks was quite accurate, as their weight

changed 0.3 kg. The low group remained in an energy deficit, as shown by the continued loss of 2.2 kg.

Although most of the liveweight change experienced by the ewes could be accounted for by fat and water, the body protein content of the high animals was significantly higher. Gross dissection showed that the protein increases took place in liver, kidneys and the organs of the gastro-intestinal tract. This increase in visceral organ mass as a result of feeding level agrees with observations of growing pigs (Koong et al., 1982; Tess et al., 1984), lambs (Winter et al., 1976; Ledin, 1983; Ferrell et al., 1986) and cattle (Murray et al., 1977; Foot and Tulloh, 1977; Richmond et al., 1988).

Higher metabolic heat production for the animals in the hood is a result of the energy expended in standing and activity, as found by Young et al., (1988). When immersed in water, the animals do not need to expend this additional energy.

The heat increment of feeding accounted for a quarter of the total diurnal heat production of the low and medium animals. In the high animals the value was almost 40% of the total. This increase in heat production with higher feed intake may be due to the phenomina of diet-induced thermogenesis observed in cafeteria-fed rats (Rothwell and Stock, 1979). Part of the excess energy given the animal in the diet is excreted from the body through increased heat production.

Higher heat production in the heavier animals was not due entirely to HIF, as calculated HIF values were not as great as the increase in RM.

The increase in visceral organ mass as a result of feed intake is

a possible source for treatment differences in RM. Burrin et al. (1989) reported a positive relationship between feed intake and the oxygen consumption of the portal-drained viscera and liver. Although the visceral organs represent a relative small portion of empty body weight, 7% to 9% in the ewes in the present study, their contribution to whole animal metabolism is high. Oxygen consumption measurements have estimated that the portal-drained viscera and liver account for 40% (Thompson et al., 1978) and 46.5% (Reynolds et al., 1986) of whole body oxygen consumption. Of the organs included in the viscera, the liver alone has been estimated to consume up to 21.5% of whole body oxygen requirements (Thompson et al., 1978). Any increase in the mass of these organs would likely result in higher metabolic rates.

That the increase in visceral organ mass and not tissue activity was the cause of increased metabolic rate is supported by the lack of a significant difference in *in vitro* tissue oxygen consumption between groups.

Close association of heat production with visceral organ mass has been found in growing pigs (Koong et al., 1982) and sheep (Ferrell et al., 1986). In mature animals, however, work by Olthoff (1985) failed to find significant change in visceral organ mass in animals of different liveweights, although heat production was higher in the heavier animals.

Simple correlations indicate the existance of an association between the factors of interest, but this association cannot be interpreted as one of cause and effect. The correlations of the chemical components and the organ weights with metabolic rate indicates

that as these organs or tissues were increasing or decreasing in weight, metabolic rate was increasing or decreasing.

Regression indicates a closer relationship between the variables, but the outcome of the equation must make biological sense. The regressions showing fat as the best predictor of RM cannot be interpreted as saying that fat is the source of increased RM. The gross dissection showed that protein increases took place in tissues, such as the liver, which have a high metabolic activity.

In summary, liveweight differences in mature sheep were not due to body fat alone, but body protein and water as well. No apparent difference was found for the *in vitro* metabolic intensity of liver, duodenum and muscle. The resting energy metabolism of mature sheep fed to maintain a 50% difference in liveweight was proportional to 1.42 W/kg and was correlated with liver, gastro-intestinal tract and fat weights.

Table II-1. Animal body composition prior to and after weight change (kg).

Treatment	Fat		Protein		Water		Ash	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Low	10.2	5.0[b]	8.6	7.8[b]	40.0	35.5[b]	2.3	2.1[b]
Medium	8.9	6.8[b]	8.4	8.3[b]	38.9	38.2[b]	2.3	2.3[ab]
High	9.7	19.4[a]	8.5	9.9[a]	39.2	48.0[a]	2.3	2.5[a]
SEm	0.97	1.53	0.13	0.37	0.69	0.91	0.03	0.08

Within columns, means with different superscripts indicate significance ($P<0.05$).

Table II-2. Body component weights of animals at slaughter (kg).

Treatment	Carcass	Vital Organs	GIT	GIT Contents	Fat	Offals
Low	24.0[b]	4.3[b]	2.7[b]	8.1[b]	1.4[b]	8.8[b]
Medium	26.8[b]	4.4[b]	2.8[b]	9.3[b]	1.6[b]	9.8[b]
High	41.0[a]	5.3[a]	3.3[a]	11.6[a]	6.8[a]	11.4[a]
SEm	0.90	0.25	0.65	0.13	0.54	0.45

Within columns, means with different superscripts indicate significance ($P<0.05$).

Table II-3. Water immersion metabolic heat production (RM) and live weight (kg) before and after weight change and diurnal heat production (hood) 16-22h post feeding, after weight change.

Treatment	Pre-treatment		Post-treatment		
	Wt(kg)	RM (W)	Wt(kg)	RM (W)	Hood (W)
Low	59.3	91.5	51.8[b]	74.8[b]	95.1
Medium	56.5	86.6	56.1[b]	79.1[b]	83.4
High	57.8	90.1	77.9[a]	96.1[a]	102.6
SEm	1.83	2.99	1.99	2.88	7.68

Within columns, means with different superscripts indicate significance ($P<0.05$).

Table II-4. Diurnal heat production and calculated heat increment of feeding (HIF).

Treatment	Daily HP (MJ/d)	FI (kgDM/d)	HIF (MJ/d)	HIF (kJ/kgDM)
Low	8.13	0.657	1.25[b]	1.90[b]
Medium	7.87	0.733	1.51[b]	2.06[b]
High	9.75	1.173	4.23[a]	3.61[a]
SEm			0.189	0.204

Within columns, means with different superscripts indicate significance ($P<0.05$).

Table II-5. Average dry weights and tissue oxygen consumption (ml O_2/min/g DM).

Treatment	Muscle*		Liver		Duodenum	
	gDM	O_2	gDM	O_2	gDM	O_2
Low	6830	0.077	215	0.050	67	0.060
Medium	8500	0.064	198	0.054	81	0.054
High	17270	0.045	300	0.052	84	0.055
SEm	37.1	0.011	16.2	0.008	8.2	0.005

Within columns, means with different superscripts indicate significance ($P<0.05$).
*Muscle dry weight is boneless carcass dry weight.

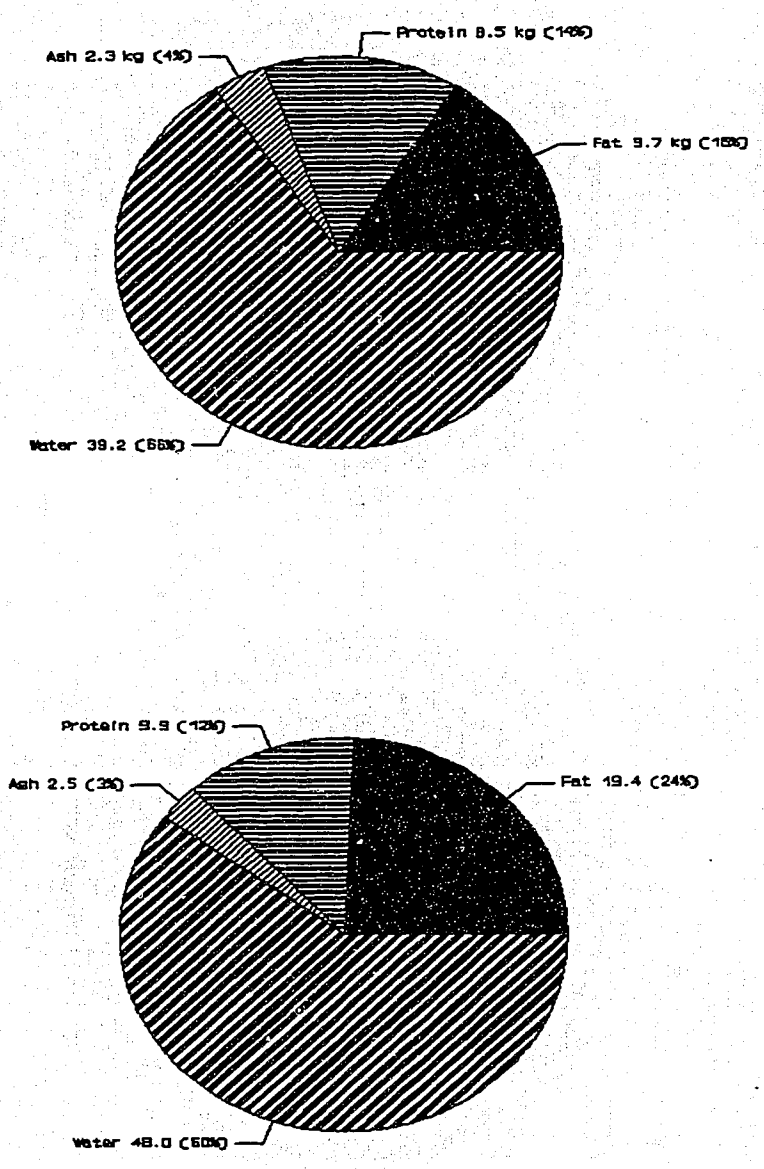

Figure II-1. Body composition of high animals at start (top) and end (bottom) of trial. Average weight at start 58 kg at end 78 kg.

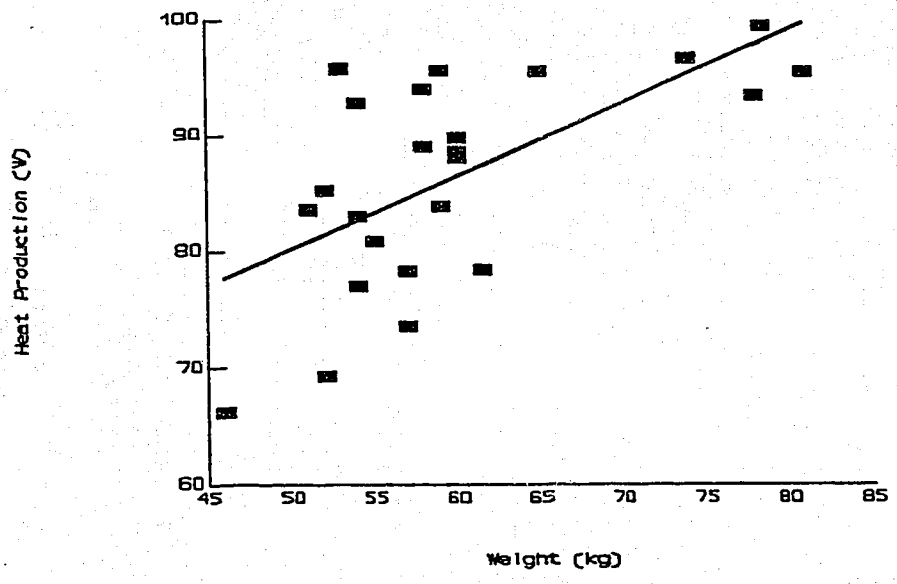

Figure II-2. Relationship between metabolic heat production and body weight for all sheep both before and after weight change. (Heat Production = 49.0 + 0.62 Weight; SEa = 7.23, SEb = 0.16, R^2 = 0.40).

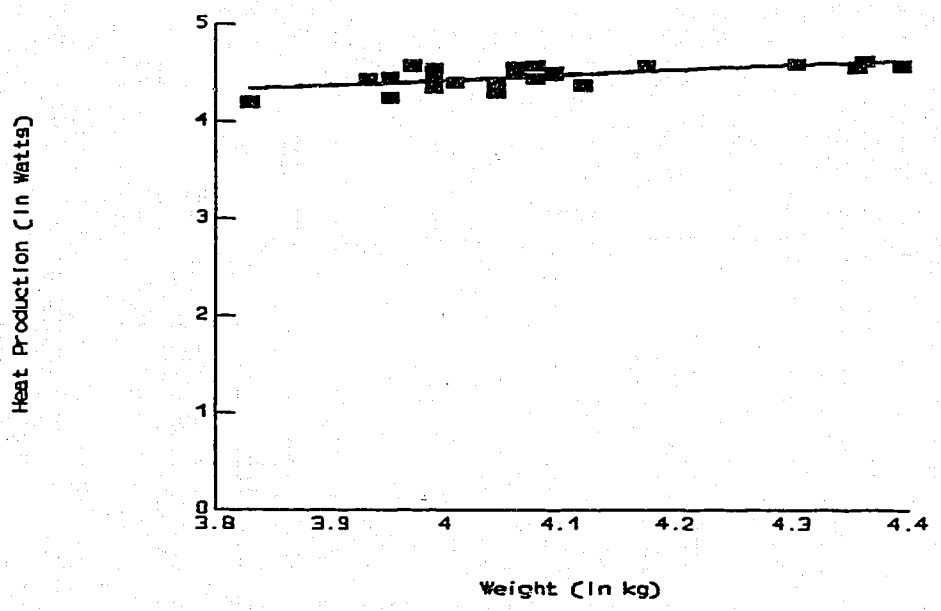

Figure II-3. Relationship between the natural log of liveweight (ln kg) and the natural log of metabolic heat production (ln W), (ln Heat Production = 2.47 + 0.49 ln Weight; SEa = 0.09, SEb = 0.12, R^2 = 0.41).

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Chapter III. THE CONTRIBUTION OF BODY FAT TO PROTECTION FROM COLD.

INTRODUCTION

The survival of a homeotherm in a cold environment depends on its ability to balance the rate of metabolic heat production against an increased rate of heat loss. As ambient temperatures decrease, body heat is conserved by increasing peripheral insulation through piloerection, reducing blood flow through the superficial tissues, increasing metabolic thermogenesis or a combination of these processes (Webster, 1974). With increasing cold stress, metabolic thermogenesis usually intensifies until a maximum rate, (summit metabolism; SM) is reached. After this, body heat loss becomes greater than the metabolic capacity of the animal and it becomes hypothermic (Alexander, 1979).

Body fat has the potential to provide energy substrates for thermogenesis in skeletal muscles (Saski and Weekes, 1986) and subcutaneous fat depots act as insulation against body heat loss (Yousef, 1987). A direct contribution, however, of body fat to cold-induced thermogenesis by increasing metabolic capacity has not been established. The objective of the present study was to determine the contribution of body fat to the cold hardiness and thermogenic capacity of animals exposed to an acute cold stress.

MATERIALS AND METHODS

ANIMALS: Twelve Suffolk ewes of similar body frame size and ranging in weight from 61 to 74 kg, were selected from the University of Alberta

flock. All ewes were older than three years at the start of the trial. The ewes were housed indoors in individual metabolic crates with ambient temperatures between 18 to 23°C. A diet consisting of five parts barley pellets (155 g protein/kgDM) and three parts chopped timothy hay (92 g protein/kgDM) was fed daily at 15:00 h. The animals had free access to water and cobalt-iodized salt.

TREATMENTS: During the first 12 weeks of the trial the ewes received 800g of feed (DE 10.1 MJ/d), which was estimated to be sufficient for maintenance of body weight (NRC, 1985). After this initial period, the animals were randomly allocated to one of three treatments; high feed level (high), low feed level (low) or unchanged feed level (medium). Feeding levels were adjusted to increase body weight of the high group by 20 kg and decrease body weight in the low group by 10 kg. After approximately 12 weeks, when the high and low animals had reached their prescribed weights, feed levels were adjusted to maintain body weights for a minimum of 6 weeks before metabolism was remeasured.

BODY COMPOSITION: Body fat was estimated prior to allocating the ewes to treatment groups and near the end of the trial. Fat was estimated from total body water using tritiated water dilution (Robelin, 1975). Each ewe was injected intramuscularly with approximately 3 uCi of tritiated water (TOH) in 2-3 ml of physiological saline. Blood samples were taken by venipuncture at 24h intervals over 4 days for determination of marker dilution in the body. Tritiated water space was calculated by extrapolation to time zero of the relationship between log

plasma specific activity and time during the four days after injection.

The ewes were slaughtered at the end of the trial and the chemical composition of the carcass and noncarcass components was determined. Water content was determined on the boneless components by freeze drying and on the bones by oven drying at 110°C. Fat was measured by petroleum ether extraction and protein was estimated from nitrogen using the Kjeldahl method (A.O.A.C., 1980). Gross energy was determined by adiabatic bomb calorimetry. The relationship between measured body fat, live body weight and tritiated water space was used to estimate animal body fat in the pretreatment period. Backfat depth at the 13th rib was also measured on the carcasses.

METABOLIC RATE: Rate of metabolic heat production was measured using an open-circuit respiratory system while the ewes were immersed to the neck in water (Young et al., 1988). Water temperature was 38°C for measurement of resting metabolism and was dropped within 5 minutes to 18°C to induce SM. The ewes remained in the cool water until their rectal temperatures fell 3°C, water temperature was then increased to 38°C to allow the animal to recover normal body temperature and metabolism. Resting and summit metabolism were calculated in watts (W) using the equation developed by McLean (1972). The measurements were made in the 10th or 11th week of the pretreatment period and 6 weeks after treatment body weights were reached.

RESISTANCE TO HYPOTHERMIA: The number of minutes to reach SM and mild hypothermia (a 3°C drop in rectal temperature) after water temperature

was reduced to 18°C, were measured for each animal. Animal resistance to hypothermia was taken as the time between reaching SM and mild hypothermia.

STATISTICAL ANALYSIS: Treatment effects were determined by analysis of variance using the SPSSx statistical package (SPSS, 1988). Differences between means were evaluated using the Student-Newman-Keuls range test.

RESULTS

Body fat accounted for approximately half the changes in weight gain in the high and low treatment groups (Table III-1). The chemical analysis of the bodies at the end of the study showed that carcass fat was 8.81 kg greater and carcass protein was 1.66 kg higher in the high animals. The difference in carcass fat was reflected in the depth of backfat at the thirteenth rib, where the high animals had almost five times the fat as the low animals (Table III-1). Noncarcass fat was 5.6 kg heavier in the high animals compared to the low animals.

The high animals had significantly higher resting metabolism on a per animal basis when compared to the medium or low animals (Table III-2). When expressed per unit of body mass, heat production was 1.24 W/kg for the high animals, 1.42 W/kg for the medium animals and 1.45 W/kg for the low animals. These differences were not significant between groups ($P<0.10$).

SM per animal did not differ significantly ($P=0.33$) as body weight increased (Figure III-1). The relationship between the natural log of body weight (ln kg) and the natural log of maximum heat production (ln

W) had a slope of -0.16, which was not significantly different from zero. When SM was expressed per unit of body mass, the high animals had significantly ($P<0.05$) lower values (6.1 W/kg) than the medium (8.6 W/kg) or low animals (10.3 W/kg).

The ratio of SM to resting metabolism was significantly lower in the medium and high animals than the low animals, reflecting the differences in resting metabolism.

The times to reach SM and to induce mild hypothermia are shown in Figure III-2. All groups took approximately 30 minutes to reach SM. After reaching SM, animals in the high group were able to maintain body core temperature significantly longer ($P<0.05$) than those in the other groups. The time to reach mild hypothermia was related to carcass fat (Figure III-3). The high animals had more carcass fat and took longer to reach mild hypothermia than the low or medium animals with less fat.

DISCUSSION

Liveweight changes in mature animals are often considered to be a change in the amount of fat tissue (McNiven, 1984). The composition of the animals in this study show considerable differences between treatments in both the fat and nonfat portions, including carcass and noncarcass protein.

The differences in the noncarcass or visceral protein in the high animals may explain the increase observed in resting metabolism. Hypertrophy of the visceral organs with increased feed intake has been found in growing animals (Rompala and Hoagland, 1987), and a positive relationship between energy intake and liver mass was demonstrated in

mature steers (Johnson et al., 1987). Burrin et al. (1989) found that blood flow and oxygen consumption in the portal drained viscera and the liver increased with a higher level of nutrition. Therefore, it is likely that the increase in RM found in the high animals was due to their larger livers and intestinal tracts (Chapter II).

That SM did not increase in the high animals does not agree with the results of Bennett (1972), who showed a positive relationship between the magnitude of SM and body weight in mature sheep. This conclusion was based on SM measurements in sheep of both sexes and a range in body conditions at mature weight. No measurement of body fat or correction for frame size was made on the animals, and differences in lean mass may explain the results. Skeletal muscle represents a major contributor to cold thermogenesis (Ivanov, 1989) so, if skeletal muscle mass increased in fatter animals, one could expect an increase in SM. While the high animals had significantly more ($P<0.05$) carcass protein, the difference may not have been great enough to cause a change in SM.

The ratio of SM to resting metabolism was less for the high animals, due to their higher resting metabolism. This demonstrates the difference between the two metabolic measurements, resting metabolism is a function of body weight and SM is a function of the thermal load imposed on the animal.

Time to reach SM was not affected by animal weight or amount of fat. This could be expected, as the time to reach SM represents amount of time required for an animal to react to an acute thermal challenge. The time to reach mild hypothermia after SM was significantly longer ($P<0.05$) in the fatter animals. This demonstrates the insulative

quality of body fat.

Bennett (1972) proposed that heavier sheep should have greater survival because he found SM related to the 0.9 exponent of body weight, while heat loss is a function of surface area. The results of this study indicate that when animals are forced to change body weight, there is no change in SM. The heavier sheep were found to have a greater survival rate not because of greater thermogenic capacity, but because of increased thermal resistance. SM therefore, is not a function of body mass but a function of the thermal load imposed on the animal.

In summary, body fat increases the cold hardiness of animals exposed to an acute cold stress by decreasing the rate of body heat loss. No evidence was found that body fat or an increase in liveweight contributes to thermogenic capacity.

Table III-1. Change in body weight and estimated body fat before and after weight change and backfat depth at the 13th rib after animal weight change.

Treatment	Body Weight (kg)		Body Fat (kg)		Backfat (mm)
	Before	Change	Before	Change	
Low	59.3	-7.5b	10.2	-5.2b	1.8[b]
Medium	56.5	-0.4b	8.9	-2.1b	2.8[b]
High	57.8	+20.1a	9.7	+9.7a	8.5[a]
SEm	2.62	1.43	0.97	0.63	1.4

Column means with different superscripts are significantly different ($P<0.05$).

Table III-2. Average resting (RM) and summit metabolism (SM) after weight change.

Treatment	Wt	RM (kg)	SM (W)	SM/RM (W)
Low	51.8[b]	74.8[b]	528	7.06[a]
Medium	56.1[b]	79.1[b]	479	6.05[ab]
High	77.9[a]	96.1[a]	478	4.97[b]
SEm	1.99	2.88	25.5	0.53

Column means with different superscripts are significantly different ($P<0.05$).

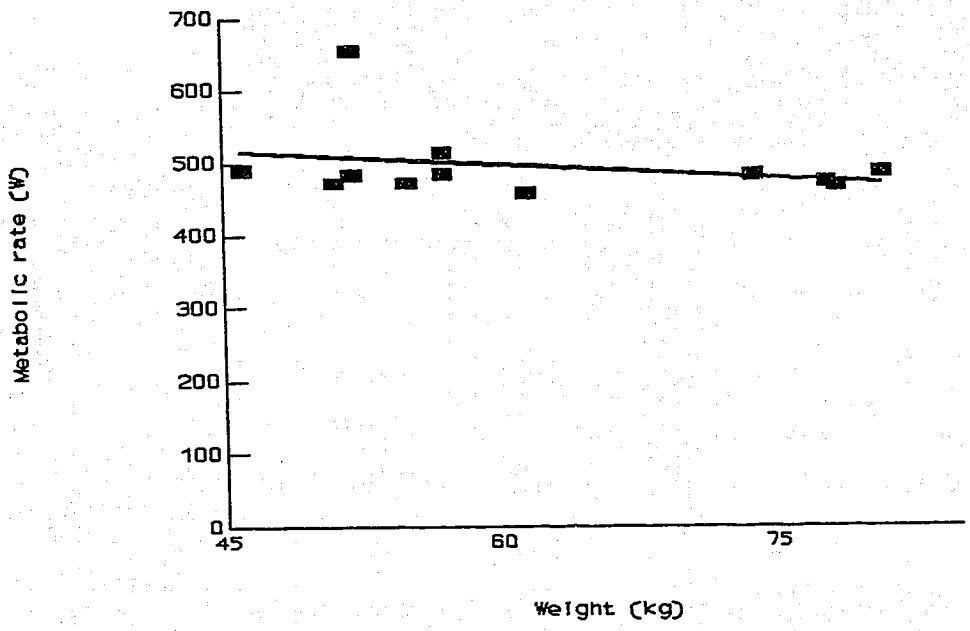

Figure III-1. Relationship between maximum heat production (SM) and live weight after weight change.

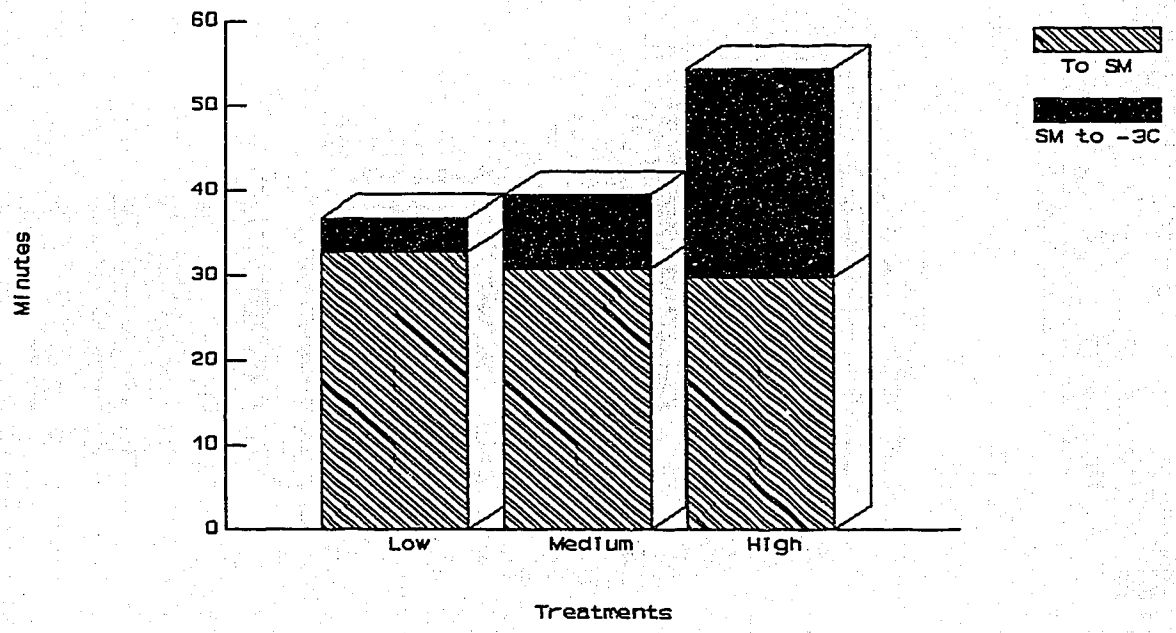

Figure III-2. Average times taken to reach summit metabolism (SM) and mild hypothermia (-3C) after summit metabolism.

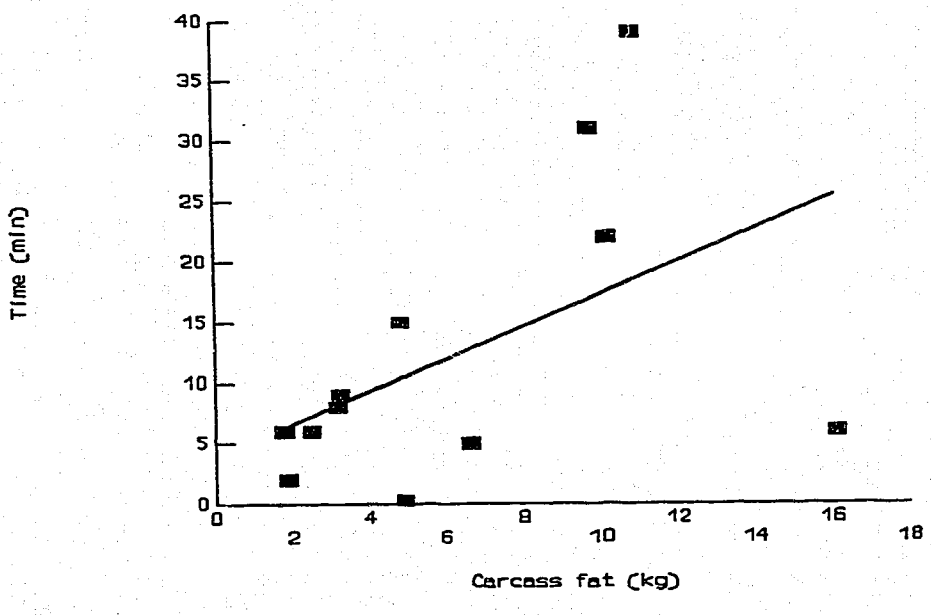

Figure III-3. Relationship between weight of carcass fat and time taken to reach mild hypothermia after summit metabolism.

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Chapter IV. The Effects of an Abrupt Change in Feed Intake on the Metabolic Rate of Mature Sheep, a Preliminary Study.

INTRODUCTION

Many models of animal energy utilization (NRC, 1985; ARC, 1980) describe the relationship between feed intake and metabolic response linearly, thereby implying an instantaneous metabolic response. Several studies have shown the existance of a lag between a change in intake and metabolic response. Monteiro (1972), in modelling the automatic control of appetite during lactation, found that a model based on milk yield which included a delay response for feed intake gave a better account of the variation in food intake than a linear model.

Black et al. (1976), in developing a model of protein and energy utilization in sheep, found that the model could not predict the response of lambs to abrupt weaning. They found, by trial and error, that when metabolic rate was moved exponentially over 20 d to a new equilibrium after a change in nutrition, simulated balances were close to the actual observations.

Nagorcka (1977) analyzed data on the effect of feed intake on wool growth and observed a delay of about 25 days in wool growth after a diet change. Turner and Taylor (1983) proposed that the results of Nagorcka could be used to describe adaptive change in the energy metabolism of cattle.

These models are deductive and lack experimental evidence to describe the nature of metabolic response to changed feed intake. An adaptive change in metabolism could be determined from a series of

measurements made prior to and after an abrupt change in feed intake. The objectives of this study were to determine the lag time in metabolic response after an abrupt change in feed intake, to describe the change mathematically and to compare the rate of change between animals subjected to increased and decreased intakes.

MATERIALS AND METHODS

ANIMALS: Twelve non-lactating Suffolk ewes of similar body frame size, weighing between 51 and 73 kg were selected from the University of Alberta flock. Average age at the start of the trial was 39 months. The ewes were kept indoors in individual metabolic crates with ambient temperatures between 18 and 23°C. A diet of 3 parts barley pellets (CP 155 g/kg) and 5 parts chopped timothy hay (CP 92 g/kg) was fed daily at 15:00 h. The digestible energy content of the complete diet was 13.2 MJ/kg. The animals had free access to water and cobalt-iodized salt. The ewes were weighed weekly and shorn every 6-8 weeks.

TREATMENTS: During a 84 week pre-treatment period the ewes received 800g daily of the diet. This was estimated to be sufficient for maintenance of body weight (NRC, 1985). After the initial period, the ewes were randomly allocated to one of three treatments; high feed intake (high), low feed intake (low) or unchanged feed intake (medium). On day 1 daily feeding level was increased in small increments over 12 days to 1500g for the high group, while the low group had their feeding level cut to 400g. The animals remained at these levels until target weight changes of +20 kg for the high group and -10 kg for the low group

were met. Feed intake for the high animals was decreased on day 105. The low animals reached their target weight at day 42 at which time their feed level was increased.

METABOLIC RATE: Respiratory gas exchange was measured using an open-circuit respiratory system while the ewes were immersed to the neck in warm (38°C) water (Young et al., 1988). Resting metabolism (RM) was calculated in watts (W) using the equation developed by McLean (1972). RM was measured five times during the pre-treatment period, every second day on the low and high animals for ten days and on days 13 and 19 and thereafter at 14 d intervals until day 150.

DATA ANALYSIS: The length of the lag period was calculated as the number of days before RM reached a new stable level. To describe the lag mathematically, RM values obtained between days 1 and 150 were regressed over time using the following models:

Model 1a: (Linear)	$M = a + bt$;	days 1-20
Model 1b: (Linear)	$M = a + bt$;	days 1-150
Model 2a: (Natural log)	$M = ae^{bt}$;	days 1-20
Model 2b: (Natural log)	$M = ae^{bt}$;	days 1-150
Model 3: (Exponential)	$M = xe^{a(1/t)}$;	days 1-150

Where M = metabolic rate (RM), a = the metabolic rate at day 1, b = change in metabolic rate, t = the number of days after day 1 and x = a constant. Models designated as having the best fit were those with the lowest residual mean squares and the highest coefficients of determination (R^2).

The rates of change (b) in metabolism for increasing and decreasing animals was compared using a one-way analysis of variance (Steel and Torrie, 1980).

The rates of change were used to calculate the 68% response time, using the equation $t = \ln 0.68/b$. This response time gives the number of days when 68% of the total expected metabolic response is reached.

RESULTS

Average changes in metabolism in response to increasing or decreasing feed intake are shown in Table IV-1. RM measurements on day 1 and day 3 were lower than the pretreatment averages for all animals. After this, RM increased from days 1 to 20 for all high sheep, and continued to decrease for the low sheep. One exception in the low group, sheep #527, had a slight increase in RM from day 1 to day 20. The sheep on the low intake had a gradual increase in RM following day 20.

The regression constants of models which met the criterion are summarized for the two groups in Table IV-2. The y-intercept (a) of the linear model (1) predicts RM in the pre-treatment period. The y-intercept (a) for the exponential model (3) predicts RM after the sheep have become adapted to the treatment feeding level.

Low Intake: The linear model best described RM between days 1 and 20 for the sheep on low intake, followed closely by the natural log model. The change in RM between days 1 and 150 was best predicted by the exponential model. Although this model underpredicted RM in the last three measures of the test for two sheep, it gave reasonable predictions

for the rest of the period and for the entire period of the two other sheep. The linear model of days 1-150 tended to underpredict RM initially and near the end and overpredict in the mid portion (days 9-49).

Medium Intake: Both the linear and natural log models fit the RM data for these sheep poorly. The R^2 values were very low for both predictions and no pattern of fit with either model was evident, as the data points were well distributed around the predicted line. The slopes (b) for both equations were very close to zero.

High Intake: The change in RM over days 1 to 20 was best described by the linear model. In the 1 to 150 day period the exponential model described changes in RM most accurately. It tended to underpredict RM on day one and overpredict on days 3 and 5. The linear model generally underpredicted RM over days 1 to 150 between days 7 and 64 and overpredicted RM on days 1 and 3. The natural log model followed a similar pattern to the linear model, with smaller deviations.

The average rate of change in metabolism (b) for the linear model over days 1 to 20 had a greater absolute slope for the high group. This indicates that metabolism was changing at a greater rate in the high group than in the low group.

Metabolic rates stopped increasing for high sheep and stopped decreasing for low sheep between days 19 and 34 (Table IV-1). An exact day could not be established because at this point, measurements were only taken weekly.

The calculated 68% response times (Table IV-3), show large variations. An estimate of the 68% response time of 14 to 21 days was

indicated from the natural log model for days 1-20. The natural log model from days 1-150 and the exponential model did not provide reasonable answers.

DISCUSSION

The results of this study confirm the existance of a time lag in metabolic equilibrium after abrupt changes in feed intake. However, the accuracy of the models in describing the change in metabolism is restricted by the low number of animals, as shown in the large standard errors.

The initial drop in RM found in all animals at the start of the intensive measurements was not expected. This phenomena may have been a result of the animals becoming accustomed to the procedures involved. This is supported by the wide variation in RM during the pretreatment period. Graham also found that metabolic rates decrease as animals became accustomed to their surroundings and the measurement techniques (Blaxter, 1967).

The low sheep could be considered as the preferred group for observation of metabolic adaptation, as their intake was dropped sharply. The response to the treatment, however, was variable; two animals had rapid declines in metabolic rate, one had roughly half the response of the first two, and one had an slight increase in metabolic rate. However, the sheep that had an increase in metabolism had a metabolic rate of 57.5 W on day 1 compared to its pre-experiment average of 85.6 W. This was the largest difference of the sheep on reduced intake and may suggest the value obtained on day 1 was exceptionally low

due to biological variability.

The gradual increase in RM which occurred in the low group after the intensive period of measurement may be a result of the adaptation of the animal to the low feed intake, such as found by Leger and Sayers (1977). The more likely explanation is the increase in feed intake on day 42.

The high sheep had their feeding level gradually increased over 12 days, which could confound the adjustment in metabolism with heat production associated with feeding. The results showed that while the rate of increase in metabolism was greater than rate of decrease, it took the animals at least 5 days to reach the pretreatment RM levels after the initial drop.

The linearity of metabolic change in the short term may have been affected by the change in heat production associated with feeding. It has been estimated that a fast of 3-4 days is needed to reduce the heat production from food in the gut of ruminants (Marston, 1948). This would mean that for the first 4 days RM of the low animals would be affected by the previous level of feed intake. In the high group, the feed intake increase would give more heat from digestion as well as the metabolic response. For this reason, the long-term exponential relationship between metabolism and the change in feed intake may give a more accurate description of the metabolic response.

A subjective estimate was made of the lag in metabolic response from the feed intake change to where RM became constant. The wide range of 19-34 days reflects the constraints of the measurement times, but agrees with the first order lag constants of 24, 20, 32.5 and 24-31 days

estimated by Turner and Taylor (1983) from the data of Nagorcka (1977), Black et al. (1976), Monteiro (1972) and Ledger and Sayers (1977), respectively.

The large differences in the 68% lag time values was probably a result of the poor fit of the equations. The estimations from the natural log equation days 1-20 of 14 to 21 days agree with the literature values cited above.

In conclusion, the lag time in metabolic rate following an abrupt change in feed intake and expressed as 68% of the full response was observed to be between 19 and 34 days. In the short term (20d), the change in metabolic rate was best described linearly, while in the long term (150d), it was best described exponentially. The rate of change in metabolism was greater for the animals with increased feed intake than those on decreased intake. These results emphasize the importance of taking a lag in metabolic response into consideration when designing feeding trials and when developing computer simulations models involving changes in food intake and energy metabolism.

Table IV-1. Summary of metabolic heat production (RM) during measurement period.

Reduced intake:

Sheep #404			Sheep #478		
Day	Wt (kg)	RM (W)	Day	Wt (kg)	RM (W)
-70	60	95.0	-68	72	95.5
-62	64	78.5	-64	72	90.0
-56	62	160.5	-54	70	147.5
-35	62	88.5	-40	71	95.7
-16	58	94.1	-6	67	96.5
1	60	71.0	1	65	82.9
3	59	71.1	3	63	72.1
5	57	70.2	5	63	68.3
7	57	71.5	7	62	73.3
9	57	62.7	9	63	70.5
13	56	65.2	13	61	61.8
19	56	73.1	19	61	56.6
34	54	66.6	34	57	66.9
49	55	72.2	49	56	61.8
63	53	96.2	63	57	75.7
72	54	74.8	72	57	74.6
92	54	66.2	92	58	66.1
105	54	69.4	105	57	67.2
119	53	99.9	119	55	73.5
134	51	90.2	134	55	77.9
146	52	81.5	147	57	80.4

Table IV-1 (continued). Summary of metabolic heat production (RM) during measurement period.

Reduced intake:

Sheep #487 Day	Wt (kg)	RM (W)	Sheep #527 Day	Wt (kg)	RM (W)
-69	53	89.0			
-64	58	97.0	-71	63	93.9
-54	55	125.5	-66	66	84.5
-41	57	85.3	-56	64	157.0
-40	57	94.5	-34	62	86.8
-5	56	95.0	-7	62	77.0
1	55	70.7	1	60	57.5
3	54	68.6	3	59	60.4
5	53	62.1	5	58	58.0
7	53	63.1	7	58	62.6
9	53	55.6	9	57	59.7
13	51	57.5	13	58	60.6
19	50	50.3	19	57	61.0
34	50	57.0	34	55	65.5
49	48	57.0	49	53	61.7
64	45	69.7	63	52	71.8
72	46	59.1	72	53	68.6
91	46	53.0	92	53	63.1
105	47	55.2	105	54	64.0
119	45	79.0	119	50	73.2
133	46	62.9	134	51	69.9

Table IV-1 (continued). Summary of metabolic heat production (RM) during measurement period.

Intake unchanged:

Sheep #348			Sheep #425		
Day	Wt (kg)	RM (W)	Day	Wt (kg)	RM (W)
-70	66	95.5	-70	64	99.3
-64	59	106.0	-65	63	76.5
-55	54	208.5	-54	64	128.0
-34	53	85.0	-41	68	88.5
-14	53	83.1	-5	59	86.2
			0	59	71.0
6	55	75.0	7	60	72.8
20	55	72.1	21	60	72.0
36	54	77.4	36	60	68.4
51	52	76.3	49	58	73.1
65	51	75.1	63	58	77.9
72	52	79.9	73	58	73.1
91	53	68.3	92	59	60.8
106	53	83.9	107	60	66.1
119	50	93.6	121	56	70.0
133	52	87.1	135	56	73.5
149	51	75.6	149	56	72.1

Sheep #459			Sheep #520		
Day	Wt (kg)	RM (W)	Day	Wt (kg)	RM (W)
-71	63	79.1	-70	69	92.6
-65	61	81.0	-65	68	85.5
-54	61	90.5	-55	64	92.0
-41	62	73.5	-34	62	85.0
-6	57	72.0	-14	60	85.1
7	55	64.5	6	62	66.6
21	55	77.7	20	62	63.3
36	55	80.4	36	60	60.5
51	56	69.3	51	61	69.4
65	57	74.0	65	58	70.8
73	58	68.4	72	60	77.8
91	58	63.8	93	61	76.6
107	58	61.2	107	61	65.6
121	55	83.0	121	58	68.0
135	57	70.3	133	58	70.1
147	57	71.7	149	62	66.7

Table IV-1 (continued). Summary of metabolic heat production (RM) during measurement period.

Intake increased:

Sheep #116			Sheep #410		
Day	Wt (kg)	RM (W)	Day	Wt (kg)	RM (W)
-71	62	94.4	-70	59	89.0
-65	60	90.0	-63	67	97.5
-55	57	91.0	-56	64	92.5
-33	56	73.0	-35	61	82.0
-7	54	74.0	-16	60	83.3
1	55	55.5	1	61	71.6
3	54	69.3	3	62	79.7
5	55	73.8	5	64	82.8
7	55	87.9	7	65	84.2
9	56	88.4	9	66	92.2
13	58	84.6	13	69	83.7
19	61	93.2	19	70	83.3
34	64	91.6	34	72	91.2
49	69	100.7	49	76	89.2
64	72	99.7	63	76	95.4
72	72	90.5	72	79	101.6
92	75	87.1	92	80	91.8
105	77	96.7	105	80	89.7
119	72	99.2	120	78	97.4
134	74	99.9	132	78	98.6
147	74	101.1	147	81	97.7

Table IV-1 (continued). Summary of metabolic heat production (RM) during measurement period.

Intake increased:

Sheep #479			Sheep #517		
Day	Wt (kg)	RM (W)	Day	Wt (kg)	RM (W)
-72	63	96.5	-69	67	90.5
-66	62	109.5	-64	67	90.5
-55	62	177.5	-54	65	121.5
-42	63	89.0	-40	67	96.0
-7	62	113.5	-5	60	95.5
-1	60	89.0	1	61	71.8
1	60	56.1			
3	62	72.7	3	61	65.7
5	63	83.9	5	62	70.1
7	63	89.7	7	63	74.2
9	65	88.2	9	64	84.3
13	66	89.7	13	68	90.7
19	70	104.8	19	69	93.9
34	70	98.0	34	73	101.1
49	72	99.8	49	74	101.8
63	77	91.6	63	76	99.5
72	78	102.6	72	77	93.5
92	80	95.5	92	77	84.0
105	80	93.1	105	78	94.3
119	78	115.3	119	76	87.0
132	78	97.2	134	77	96.3
147	79	95.5	147	78	101.7

Table IV-2. Summary of constants for significant regression equations with residual mean square (MSE) and coefficient of determination (R^2) for animals on decreased (low) or increased (high) feed intake.

Equation: Linear (M = a + bt), for days 1-20.

Treatment	n	a	b	R^2	MSE
Low	7	69.5	-0.56[b]	0.64	10.6
High	7	68.5	1.53[a]	0.68	34.9
SEm		4.23	0.356		

Equation: Exponential [$M = xe^{a(1/t)}$], for days 1-150.

Treatment	n	x	c	MSE
Low	16	65.3	0.061	49.01
High	16	95.8	-0.479	39.61
SEm		2.20	0.285	

Table IV-3. Calculated 68% response time in metabolism (days) after an abrupt change in feed intake, as estimated from the slopes of the regression lines (b).

Natural log model (model 2) Days 1-20 Animal	b	$T_{0.68}$ (d)
Low Intake		
404	-0.0008	485
478	-0.0184	21
487	-0.0183	21
527	0.0024	160
High Intake		
116	0.0238	16
410	0.0062	62
479	0.0279	14
517	0.0197	20

Days 1-150 Animal	b	$T_{0.68}$ (d)
Low Intake		
404	0.0016	241
478	0.0006	643
487	-0.0030	129
527	0.0010	386
Medium Intake		
348	0.0009	426
425	-0.0002	1928
459	-0.0001	3857
520	0.0004	964
High Intake		
116	0.0021	184
410	0.0014	275
479	0.0020	193
517	0.0014	275

Exponential Model (Model 3) Days 1-20 Animal	b	$T_{0.68}$ (d)
Low Intake		
404	0.0239	16
478	0.1638	2
487	0.2308	2
527	-0.1753	2
High Intake		
116	-0.6817	1
410	-0.3306	1
479	-0.4256	1
517	-	-

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Chapter V. General Discussion

The seasonal variations in quality or quantity of feed for grazing ruminants is usually met by one of two strategies; supplementary feeding or allowing weight to fluctuate. The strategy followed will depend, in part, on the type of livestock enterprise. In an extensive grazing enterprise, where the animals depend on grazing for most of their feed, will most likely only receive feed supplements to prevent starvation (Burns, 1981). In an intensive enterprise which depends on the economic return of animal products, the animals will be more likely receive enough supplementary feed to maintain body weight in order to prevent decreaed production (Ibid).

The economic cost of supplemental feed will be more important in the extensive enterprise because of its low inputs. In this situation, there may be an economic advantage in allowing the animals to gain weight when feed is plentiful and then let the animals use the stored body energy during the period of poor feed.

The cost to the animal of weight fluctuations in terms of energetics will depend on the effect body weight change has on energy requirements for maintenance. If live weight change is comprised of fat tissue alone and if fat tissue has low metabolic activity, then a change in weight would not be expected to affect energy requirements. In this case it would be more economical to allow the animal to lose weight when feed was poor and regain weight when feed was of good quality and plentiful.

Mature animal liveweight change in the present experiment affected

not only the weight of body fat, but also liver, kidneys and gastro-intestinal organs weights (Chapter II). This agrees with similar work in growing animals (Koong et al., 1982; Tess et al., 1984).

The increase in liveweight was also related to higher levels of metabolic heat production. Although the weight of fat was highly correlated with heat production, a cause and effect relationship could not be established due to the high correlations of liver and kidney weights with heat production as well. Liver mass has been shown to be related to animal heat production (Burrin et al, 1989) and may have been responsible for the increased heat production. In order to determine the contribution of fat alone, one would have to measure liver and kidney heat production separately and substract them from the whole animal heat production.

The ability of animals to withstand acute cold temperatures is a function of their capacity to produce body heat and their ability to minimize heat loss from the body (Webster, 1974). If body fat was metabolically active then one would expect an increase in the maximum rate of heat production upon exposure to acute cold. Bennett (1972), found a relationship between the genetically determined mature body mass and maximum heat production. This was not evident in the present trial where animals were fed to reach different weights, as increases in body fat in the carcass and the intestines of the heavier animals did not increase their maximum thermogenic capacity (Chapter III). The resistance of the heavy animals to body cooling increased, most likely a result of their thicker layer of subcutaneous fat.

The metabolic rate of mature animals is also dependent on their

level of feed intake. A sudden change in feed intake does not have an immediate effect on metabolic heat production (Chapter IV). The preliminary results indicate that a lag of between 18 and 34 days exists, which agrees with predictions of Turner and Taylor, (1983). In the short term the change was best described linearly, whereas in the long term an exponential equation described the change best.

In conclusion, thin animals require less feed energy for maintenance than heavy animals, most likely because of heavier livers and kidneys. In a situation where the animals are subject to acute cold temperatures, heavier animals are able to cope better because of increased resistance to body cooling.

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Appendix 1. Summary of coefficient values of the five different models tested for individual sheep.

Model 1a: Linear M = a + bt for days 1-20.

Sheep	n	a	b	R^2	std err of b coeff.
Low intake					
404	7	69.65	-0.0480	0.6100	0.2730
478	7	79.45	-1.2400	0.8279	0.2529
487	7	70.02	-1.0920	0.8783	0.1820
527	7	58.82	0.1410	0.2477	0.1101
High intake					
116	7	64.40	1.7888	0.6887	0.5378
410	7	78.54	0.4860	0.2431	0.3825
479	7	59.19	2.1171	0.9047	0.3073
517	7	71.84	1.7175	0.8847	0.2772

Model 1b: Linear M = a + bt for days 1-150.

Sheep	n	a	b	R^2	std err of b coeff.
Low intake					
404	16	66.92	0.1240	0.4338	0.0378
478	16	68.25	-0.0438	0.0956	0.0355
487	16	60.52	-0.0210	0.0405	0.0270
527	16	60.31	0.0661	0.4959	0.1780
Medium intake					
348	11	72.70	0.0761	0.2461	0.0444
425	11	72.16	-0.0163	0.0290	0.0314
459	11	71.83	-0.0068	0.0021	0.0496
520	11	66.44	0.0288	0.0692	0.0352
High intake					
116	16	79.44	0.1698	0.4567	0.0495
410	16	82.82	0.1206	0.5832	0.0272
479	16	78.60	0.1567	0.3300	0.0597
517	16	86.31	0.1247	0.3306	0.0474

Model 2a: Natural log $M = ae^{bt}$ for days 1-20.

Sheep	n	a	b	R^2	std err of t coeff.
Low intake					
404	7	69.41	-0.0008	0.0077	0.0040
478	7	79.83	-0.0184	0.8544	0.0034
487	7	70.11	-0.0183	0.8920	0.0028
527	7	58.56	0.0024	0.2534	0.0018
High intake					
116	7	64.07	0.0238	0.6541	0.0078
410	7	78.26	0.0062	0.2580	0.0047
479	7	59.74	0.0279	0.8709	0.0048
517	7	72.24	0.0197	0.8639	0.0035

Model 2b: Natural log $M = ae^{bt}$ for days 1-150.

Sheep	n	a	b	R^2	std err of t coeff.
Low intake					
404	16	67.35	0.0016	0.4374	0.0005
478	16	68.03	0.0006	0.0968	0.0005
487	16	60.34	-0.0030	0.0324	0.0005
527	16	60.34	0.0010	0.5072	0.0003
Medium intake					
348	11	72.97	0.0009	0.2369	0.0006
425	11	72.24	-0.0002	0.2872	0.0005
459	11	71.52	-0.0001	0.0022	0.0007
520	11	66.02	0.0004	0.0770	0.0005
High intake					
116	16	78.26	0.0021	0.4118	0.0007
410	16	82.26	0.0014	0.5679	0.0003
479	16	77.48	0.0020	0.3273	0.0008
517	16	85.63	0.0014	0.3337	0.0005

Model 3a: Exponential $M = xe^{a(1/t)}$ for days 1-150.

Sheep	n	x	a
Low intake			
404	16	69.22	0.0239
478	16	69.08	0.1637
487	16	57.57	0.2308
527	16	65.29	-0.1753
High intake			
116	16	95.57	-0.6817
410	16	94.05	-0.3306
479	16	97.77	-0.4256
517	16	N/A	N/A

Appendix 2. Comparison of average of pretreatment RM and predicted values.

Sheep	Actual*	Model 1a	Model 1b	Model 2a	Model 2b
Low intake					
404	89.0	69.7	66.9	69.4	67.4
478	95.4	79.5	68.3	79.8	68.0
487	92.8	70.0	60.5	70.1	60.3
527	85.6	58.8	60.3	58.6	60.3
Medium intake					
348	92.4		72.7		73.0
425	84.3		72.2		72.2
459	76.4		71.8		71.5
520	87.1		66.4		66.0
High intake					
116	82.9	64.4	79.4	64.1	78.3
410	88.0	78.5	82.8	78.3	82.3
479	96.0	59.2	78.6	59.7	77.5
517	93.1	71.4	86.3	72.2	85.6

*Values are an average of four RM measurements taken during the pretreatment period.

Appendix 3. Summary feed intake of sheep during the experimental period on an as-is basis, (H = hay, P = pellets).

Day	Low			Medium			High		
	H	P	Total	H	P	Total	H	P	Total
-50	300	500	800	300	500	800	300	500	800
-25	300	500	800	300	500	800	300	500	800
- 1	300	500	800	300	500	800	300	500	800
0	150	250	400	300	500	800	400	600	1000
3	150	250	400	300	500	800	450	700	1150
5	150	250	400	300	500	800	500	800	1300
7	150	250	400	300	500	800	550	900	1450
12	150	250	400	300	500	800	600	900	1500
26	150	250	400	300	500	800	600	1000	1600
42	200	330	530	300	500	800	600	1100	1700
105	270	450	720	300	500	800	480	800	1280

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