

The effect of compensatory growth on body composition in sheep

J.C. Greeff, H.H. Meissner, C.Z. Roux and R.J. Janse van Rensburg

Animal and Dairy Science Research Institute, Irene

Sixty Merino lambs were randomly allotted to one of six feeding levels. The feeding levels were *ad libitum* (control) and 0,82; 0,72; 0,65; 0,55 and 0,45 of *ad libitum*. The feeding levels were calculated from the average weekly feed intake of the *ad libitum* group. From 25 to 33 kg live mass, the lambs received restricted feeding except for the control group. At 33 kg live mass, half of each group were slaughtered, whilst the remainder were fed *ad libitum* up to 45 kg live mass when they were slaughtered. The 0,55 and 0,45 groups were prematurely put on *ad libitum* at 31 and 28 kg live mass respectively as the *ad libitum* group reached 45 kg live mass before the 0,55 and 0,45 groups reached 33 kg live mass. Individual feed intakes and live masses were determined weekly. With the aid of the allometric-autoregression model, moisture retention, protein and fat deposition rates were calculated. Moisture retention relative to fat deposition of the 0,65; 0,55 and 0,45 *ad libitum* groups were lower than the *ad libitum*, 0,82 and 0,72 *ad libitum* groups during the restriction phase. Fat relative to protein deposition of the first mentioned three groups were higher than the last mentioned three groups. During the realimentation phase the reverse pattern was found.

S. Afr. J. Anim. Sci. 1986, 16: 162 – 168

Sestig Merino lammers is ewekansig aan een van ses voedingspeile toegeken. Die voedingspeile was *ad libitum* (kontrole) en 0,82; 0,72; 0,65; 0,55 en 0,45 van *ad libitum*. Die voedingspeile is vanaf die gemiddelde weeklikse voerinnname van die *ad libitum*-groep bereken. Vanaf 25 tot 33 kg lewende massa het al die lammers behalwe die kontrolegroep, beperkte voeding ontvang. Op 33 kg lewende massa is die helfte van elke groep geslag en is die res op *ad libitum*-voeding geplaas tot op 45 kg lewende massa, waarna hulle geslag is. Die 0,55 en 0,45 groepe is voor 33 kg lewende massa op onderskeidelik 31 en 28 kg lewende massa op *ad libitum*-voeding geplaas aangesien die *ad libitum*-groep 45 kg lewende massa bereik het voordat eersgenoemde groepe 33 kg lewende massa bereik het, en toe geslag is. Individuele voerinnames en massas is weekliks bepaal. Met behulp van die allometrie-outoregressiemodel is vogretensie, proteïene en vetneerleggingstempo's beraam. Vogretensie relatief tot vetneerlegging van die 0,65; 0,55 en 0,45 van *ad libitum* groepe was heelwat minder as die *ad libitum*-, 0,82 en 0,72 van *ad libitum* groepe gedurende die beperkingsfase. Proteïene relatief tot vetneerlegging van eersgenoemde drie groepe was hoër as laasgenoemde drie groepe. Gedurende die realimentasiefase is die omgekeerde patroon gevind.

S.-Afr. Tydskr. Veek. 1986, 16: 162 – 168

Keywords: Growth, sheep, restriction, realimentation, body composition

Extract from a M.Sc. Agric treatise submitted by the senior author to the University of Pretoria

J.C. Greeff,* C.Z. Roux en R.J. Janse van Rensburg

Animal and Dairy Science Research Institute, Private Bag X2, Irene, 1675 Republic of South Africa

H.H. Meissner

Department of Animal Science, Faculty of Agriculture, University of Pretoria, Pretoria, 0001 Republic of South Africa

*To whom correspondence should be addressed

Received 11 May 1985

Introduction

The effect of compensatory growth on body composition in sheep has been studied by various researchers and conflicting results have been obtained. Some experiments have shown that there are no differences in body composition between continuously grown and realimented animals (Kellaway, 1973; Searle & Graham, 1975; Thornton, Hood, Jones & Re, 1979). Other researchers have shown that realimented sheep are leaner than continuously grown animals (McManus, Reid & Donaldson, 1972; Burton, Anderson & Reid, 1974 and Drew & Reid, 1975) whilst others have shown that realimented animals contain more fat (Wilson & Osbourn, 1960; Meyer & Clawson, 1964; Ledin, 1983; Notter, Ferrell & Field, 1983). Some contradictions could be due to different restriction levels, different periods of restriction and realimentation, different protein levels, and different breeds of animals which differ in mature size. However, according to Butler-Hogg (1984) there are still disagreements as to the effect that compensatory growth has on the body composition of animals. According to the ARC (1980) this problem needs more attention to elucidate this phenomenon. This paper reports on the effect of various degrees of feed restriction and subsequent realimentation on body composition and is closely related to the paper by Greeff, Meissner, Roux & Janse van Rensburg (1986).

Material and Methods

Design

Sixty Merino lambs were selected and randomly allotted to one of six feeding levels. The feeding levels were *ad libitum* and 0,85; 0,75; 0,65; 0,55 and 0,45 *ad libitum*. Feeding levels of restricted groups were based on the average weekly feed intake of the *ad libitum* group. Feeding levels ascertained from 25 to 33 kg live mass. On attaining 33 kg live mass half of the animals of each group were slaughtered, while the remainder were then fed *ad libitum* up to slaughter at 45 kg live mass. A further 14 lambs were slaughtered at 25 kg live mass for an indication of body composition at the beginning of the experiment.

Some of the lambs on the 0,85 and 0,75 *ad libitum* diets did not always consume their allocated amounts of feed during the restriction phase, with the result that these two groups were effectively restricted to 0,82 and 0,72 *ad libitum* respectively. Greeff (1984) indicated that season possibly exerted the same influence on appetite and efficiency of feed utilization as in the case of the *ad libitum* group, thus causing this phenomenon.

Table 1 Composition of the diet (air-dry basis)

Lucerne hay	50%
Maize meal	38%
Fish meal	10%
Monosodium phosphate	1,0%
Calcium carbonate	0,5%
Salt	0,5%
Vitamins and minerals ^a	0,1%
Moisture (%)	10,5%
Crude protein	16,2% in DM
Metabolizable energy	9,4 MJ/kg DM

^aCommercial mixture

Diet

A standard pelleted diet was used for all groups. The composition of the diet is shown in Table 1.

Management during the experiment

Animals and Housing

Lambs were housed in individual pens from 2 weeks prior to the beginning of the experiment until slaughter. Animals were fed individually, and each lamb's allocated amount of feed weighed out at the beginning of each week. Feed was given in equal portions twice daily, in the morning and afternoon. Drinking water was freely available. Feed intake and body masses were determined weekly.

Slaughter procedure

Lambs were shorn before slaughter with an electrical shearing handpiece. About 5 mm wool remained on the skin. Lambs were slaughtered by cutting the jugular vein and skinned in the usual way. The blood was collected and stored with the empty gut, head, skin and feet in air-tight plastic bags in a deep-freeze for chemical analysis. Carcasses were split medially down the back, and the right side of each carcass was stored in air-tight plastic bags in a deep-freeze for carcass evaluation. The frozen pooled offal and right half of each carcass were ground separately. Samples were taken and analysed for protein, moisture, fat and ash according to the methods of the AOAC (1970). Results of the chemical analyses of the offal and carcass were pooled to give the composition of the fleeces-free empty body.

Statistical analyses

The statistical analyses are based on the allometric relationships between cumulative digestible energy (DE) intake until slaughter, as an animal at any given time is the product of all feed previously consumed.

As the cumulative feed intake from conception until the beginning of the experiment was unknown, it had to be estimated. The slope and intercept of $\ln(\text{body mass})$ against $\ln(\text{cumulative feed intake})$ of lamb W15 of Meissner (1977) were used to determine a cumulative DE intake at the start of the experiment. According to Roux (personal communication) a precise value is not essential as the relative error decreases quite rapidly as cumulative DE intake increases.

Roux (1976, 1981) and Roux, Meissner & Hofmeyr (1982) showed that $\ln(\text{body mass})$ or $\ln(\text{component of body mass})$ against $\ln(\text{cumulative feed intake})$, describes a straight line when measured in temporal sequence on the same animal or group of animals. All the statistical information is then incorporated in the intercept and slope of the regression line.

In this experiment DE intake was used as the measure of feed intake.

Roux (1981) and Roux & Meissner (1983) also indicated that the relationship over time between cumulative feed intake, body protein and fat can be described by

$$x(t) = x + (x(0) - \alpha) \rho^t \quad (1)$$

where $x(t) = \ln(\text{DE intake})$ at time t ; $x(0)$ = starting point of the observations; α = limit mass (= $a/1 - \rho$); and ρ = slope of the autoregression of $\ln(\text{cumulative DE intake})$

From Roux, Meissner & Hofmeyr (1982) it can be expected that ρ is the same for all carcass components described by equation (1).

Ordinary statistical tests were applied to these parameters and differences between groups were established by means of an analysis of variance procedure (Snedecor & Cochran, 1967).

Results and Discussion

A peculiar phenomenon in growth and feed intake occurred in the *ad libitum* group which exhibited a clear break in growth and feed intake between 5 and 19 January 1981. Intercept (a) and slope (b) of the regression lines of $\ln(\text{body mass})$ against $\ln(\text{cumulative DE intake})$, before and after the break for individual lambs of the *ad libitum* group that completed the experiment, are indicated in Table 2.

Table 2 Intercept (a) and slope (b) of $\ln(\text{body mass})$ against $\ln(\text{cumulative DE intake})$ before and after the break for individual lambs of the *ad libitum* group that completed the experiment

Lamb no	Before			After		
	a	b	r^2	a	b	r^2
A2	0,8399	0,3581	0,9856	-0,7259	0,5688	0,9876
A3	1,1055	0,3281	0,9522	0,0670	0,4704	0,9658
A4	1,0296	0,3402	0,9279	-0,1244	0,4903	0,9909
A5	0,5413	0,4040	0,9848	-0,0819	0,4914	0,9418
A10	1,1228	0,3293	0,9505	-0,6337	0,5574	0,9859
A11	0,3117	0,4375	0,9845	0,2523	0,4460	0,9927

Except for lamb A11, significant differences between regression lines before and after the break were found in all cases and the change in slope was in all cases in the same direction. The probability that this may happen by chance is $(1/2)^6$ assuming that chance in either direction is equally possible. Blaxter & Boyne (1982) indicated that season can affect metabolic rate of sheep kept at maintenance and found that the turning point occurred at the change-over of the seasons. However, Webster, Smith & Brockway (1972), found no change in the metabolism of lambs during winter and spring but Webster, Smith & Mollison (1982) indicated that season had a significant effect on the predicted basal metabolism of bulls and that the turning point also occurred at the change of the seasons. According to the references cited by Blaxter & Boyne (1982) voluntary intake may in part be determined by the rate of metabolism. Thus it was concluded that season could have been the causal agent. If no seasonal effect existed, the change in slope upwards or downwards would have been equally likely. Thus it was necessary to fit separate regression equations for the *ad libitum* group during the restriction and reimplementation phases.

Certain lambs of the 0,55 and 0,45 *ad libitum* groups showed no mass increases at the beginning of the experiment.

Some lambs only showed mass increases about 4–6 weeks after commencement of the experiment. As body composition at this time was unknown, it was not known whether body composition changed during the period of mass stasis and it was necessary to use body composition at the beginning of the experiment in the statistical analyses. The allometric parameters, slope and intercept of $\ln(\text{body mass})$ against $\ln(\text{cumulative DE intake})$ and the autoregression parameters, ρ and α of $\ln(\text{cumulative DE intake})$ of Table 1, of Greeff, Meissner, Roux & van Rensburg (1986) were used in the calculations of this paper. Table 3 indicates the means and standard errors of wool-free empty body mass and lean body mass, protein, moisture and fat as a percentage of wool-free body mass obtained directly. The values for the 25 kg live mass slaughter group were $19,8 \pm 0,04$ kg wool-free empty

Table 3 Wool-free empty body mass and lean body mass, protein, moisture and fat as a percentage of wool-free empty body mass of the different groups slaughtered at 33 and 45 kg live mass ($\bar{x} \pm SE$).

Group	Live mass	
	33 kg	45 kg
Wool-free empty body mass (kg)		
<i>Ad libitum</i>	27,5 ^a ± 0,07	36,3 ^a ± 0,31
0,82 <i>ad libitum</i>	27,4 ^a ± 0,16	36,6 ^a ± 0,17
0,72 <i>ad libitum</i>	27,4 ^a ± 0,34	34,8 ^a ± 0,19
0,65 <i>ad libitum</i>	26,4 ^a ± 0,16	36,2 ^a ± 0,25
0,55 <i>ad libitum</i> ¹	24,9 ^b ± 0,39	36,6 ^a ± 0,15
0,45 <i>ad libitum</i> ²	23,8 ^b ± 0,04	34,8 ^a ± 0,18
Lean body mass (%)		
<i>Ad libitum</i>	78,9 ^a ± 0,35	69,9 ^a ± 0,84
0,82 <i>ad libitum</i>	78,3 ^a ± 1,14	66,5 ^a ± 1,33
0,72 <i>ad libitum</i>	78,5 ^a ± 0,67	70,5 ^a ± 0,85
0,65 <i>ad libitum</i>	73,7 ^a ± 0,40	69,1 ^a ± 0,90
0,55 <i>ad libitum</i> ¹	75,0 ^a ± 0,54	70,1 ^a ± 0,78
0,45 <i>ad libitum</i> ²	76,0 ^a ± 0,68	64,6 ^a ± 0,61
Protein (%)		
<i>Ad libitum</i>	17,9 ^a ± 0,001	14,9 ^a ± 0,002
0,82 <i>ad libitum</i>	16,1 ^b ± 0,001	14,2 ^a ± 0,002
0,72 <i>ad libitum</i>	16,4 ^b ± 0,001	15,1 ^a ± 0,001
0,65 <i>ad libitum</i>	15,8 ^{bc} ± 0,001	15,2 ^a ± 0,001
0,55 <i>ad libitum</i> ¹	15,5 ^{bc} ± 0,001	15,1 ^a ± 0,001
0,45 <i>ad libitum</i> ²	15,5 ^{bc} ± 0,001	14,3 ^a ± 0,001
Moisture (%)		
<i>Ad libitum</i>	56,5 ^a ± 0,40	50,8 ^a ± 0,61
0,82 <i>ad libitum</i>	57,9 ^a ± 0,97	47,9 ^a ± 1,22
0,72 <i>ad libitum</i>	57,6 ^a ± 0,68	51,3 ^a ± 0,79
0,65 <i>ad libitum</i>	53,1 ^a ± 0,36	49,4 ^a ± 1,02
0,55 <i>ad libitum</i> ¹	55,0 ^a ± 0,36	49,9 ^a ± 0,59
0,45 <i>ad libitum</i> ²	55,0 ^a ± 0,78	45,5 ^a ± 0,48
Fat (%)		
<i>Ad libitum</i>	20,9 ^a ± 0,32 ^a	29,8 ± 0,84 ^a
0,82 <i>ad libitum</i>	21,6 ^a ± 1,17 ^a	33,6 ± 1,37 ^a
0,72 <i>ad libitum</i>	21,2 ^a ± 0,63 ^a	29,4 ± 0,98 ^a
0,65 <i>ad libitum</i>	25,9 ^a ± 0,42 ^a	30,9 ± 0,92 ^a
0,55 <i>ad libitum</i> ¹	24,7 ^a ± 0,53 ^a	29,6 ± 0,80 ^a
0,45 <i>ad libitum</i> ²	23,6 ^a ± 0,65 ^a	35,2 ± 0,58 ^a

^{abc}Means with the same superscript within columns and body component do not differ significantly ($P < 0,05$)

¹Slaughter mass of the 0,55 *ad libitum* group at the end of restriction phase was 31 kg.

²Slaughter mass of the 0,45 *ad libitum* group at the end of the restriction phase was 28 kg.

body mass; $87,2 \pm 0,09\%$ lean body mass; $18,1 \pm 0,001\%$ protein; $64,4 \pm 0,001\%$ moisture and $12,6 \pm 0,001\%$ fat. These means are presented for those readers who are not acquainted with the model, but discussion of the results follows from the values calculated from the allometric-autoregression model.

The parameters of the regression equations of $\ln(\text{body component})$ against $\ln(\text{cumulative DE intake})$ are indicated in Table 4 and $\ln(\text{body component})$ against $\ln(\text{wool-free empty body mass})$ are indicated in Table 5 for the restriction and realimentation phases. Where no significant differences exist between groups, the raw data for those groups were pooled and a new regression line was calculated.

No significant differences were found between regression lines for the different treatments for $\ln(\text{fat})$ against $\ln(\text{cumulative DE intake})$ but significant differences were found for $\ln(\text{fat})$ against $\ln(\text{empty body mass})$. Hence, it was decided to calculate fat deposition from the difference of $\ln(\text{empty body mass})$ against $\ln(\text{cumulative DE intake})$ and $\ln(\text{lean body mass})$ against $\ln(\text{cumulative DE intake})$ where lean is the sum of protein, moisture and ash, as differences in $\ln(\text{fat-free empty body mass})$ imply that differences in fat exist between groups. These parameters were used to calculate protein and fat deposition rates at different live masses.

The time taken for each group to complete the restriction and realimentation phases took progressively longer as the restriction increased (Greeff, *et al.*, 1986). It should therefore be kept in mind that the 0,55 and 0,45 *ad libitum* groups did not complete the total restriction phase and were put on *ad libitum* feed intake at an average live body mass of 31 and 28 kg respectively. This had the effect that these two groups had to gain an additional 2 and 5 kg respectively above the 12 kg that all the other groups had to gain to reach the target mass of 45 kg. The general tendency during the realimentation phase was that as the previously imposed period of restriction increased, the time to complete the realimentation phase became shorter up to the 0,55 *ad libitum* group whereafter it increased again.

Protein

Deposition rates of protein at different live masses, are illustrated in Figure 1 for the restriction and realimentation phases.

It is clear from Tables 4 and 5 that the slopes of the regression lines of protein against $\ln(\text{cumulative DE intake})$ and $\ln(\text{cumulative body mass})$ decreased progressively as restriction during the restriction phase increased. Figure 1 illustrates the same pattern and this reduction in protein deposition, relative to the *ad libitum* group, caused less protein to be deposited

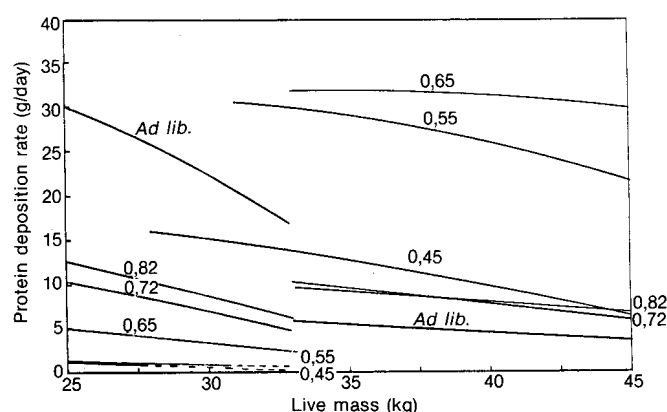


Figure 1 Protein deposition during the restriction and realimentation phases

Table 4 Regression parameters intercept (a) and slope (b) of body component against ln(cumulative DE intake)

Treatment	ln(wool-free empty body mass)		ln(lean)		ln(protein)		ln(moisture)	
	a	b	a	b	a	b	a	b
Restriction phase								
<i>Ad libitum</i>	0,0385	0,4456	1,1049	0,2639	-1,5349	0,4249	0,8842	0,2513
0,82 <i>ad libitum</i>	0,4925	0,3770	1,1049	0,2639	-0,3597	0,2472	0,8842	0,2513
0,72 <i>ad libitum</i>	0,4925	0,3770	1,1049	0,2639	-0,3597	0,2472	0,8842	0,2513
0,65 <i>ad libitum</i>	1,0769	0,2886	2,0659	0,1185	0,2570	0,1539	2,0652	0,0725
0,55 <i>ad libitum</i>	1,4757	0,2282	2,3789	0,0710	0,8860	0,0587	2,0652	0,0725
0,45 <i>ad libitum</i>	1,4757	0,2282	2,3789	0,0710	0,8860	0,0587	2,0652	0,0725
Realimentation phase								
<i>Ad libitum</i>	-0,1093	0,4627	1,5926	0,2013	0,5726	0,1394	1,3884	0,1863
0,82 <i>ad libitum</i>	-0,1093	0,4627	1,5926	0,2013	-0,4675	0,2647	1,3884	0,1863
0,72 <i>ad libitum</i>	-0,1093	0,4627	1,5926	0,2013	-0,4675	0,2647	1,3884	0,1863
0,65 <i>ad libitum</i>	-3,4130	0,8779	-2,4131	0,7070	-0,8612	0,8247	-2,3751	0,6598
0,55 <i>ad libitum</i>	-3,4130	0,8779	-2,4131	0,7070	-4,8612	0,8247	-2,3751	0,6598
0,45 <i>ad libitum</i>	-1,5288	0,6288	0,1792	0,3633	-2,3758	0,4926	0,1395	0,3252

Table 5 Regression parameters intercept (a) and slope (b) of body component against ln(wool-free empty body mass)

Treatment	ln(body mass)		ln(fat)		ln(protein)		ln(moisture)	
	a	b	a	b	a	b	a	b
Restriction phase								
<i>Ad libitum</i>	0,3676	0,9571	-6,6808	2,5448	-1,5814	0,9568	0,4669	0,6946
0,82 <i>ad libitum</i>	0,3676	0,9571	-6,6808	2,5448	-0,7039	0,6625	0,4669	0,6946
0,72 <i>ad libitum</i>	0,3676	0,9571	-6,6808	2,5448	-0,7039	0,6625	0,4669	0,6946
0,65 <i>ad libitum</i>	-0,0009	1,0810	-9,1395	3,3720	-0,2280	0,5041	1,2783	0,4222
0,55 <i>ad libitum</i>	0,1458	1,1311	-9,1395	3,3720	-0,2480	0,5041	1,2783	0,4222
0,45 <i>ad libitum</i>	0,3423	1,1953	-11,5562	4,1767	0,7166	0,1864	1,8784	0,2224
Realimentation phase								
<i>Ad libitum</i>	0,6601	0,8774	-5,6349	2,2272	-0,6211	0,2950	0,9775	0,5343
0,82 <i>ad libitum</i>	0,6601	0,8774	-5,5771	2,2272	-0,2633	0,5286	0,9775	0,5343
0,72 <i>ad libitum</i>	0,6601	0,8774	-5,6049	2,2272	-0,8173	0,6980	0,9775	0,5343
0,65 <i>ad libitum</i>	0,6601	0,8774	2,5943	1,3865	-1,3633	0,8539	0,0113	0,8073
0,55 <i>ad libitum</i>	0,6601	0,8774	-2,6299	1,3865	-1,9765	1,0336	0,0081	0,8073
0,45 <i>ad libitum</i>	0,6601	0,8774	-5,3749	2,2272	-1,2121	0,7935	0,8722	0,5343

in all restricted groups.

During the realimentation phase, protein deposition of all previously restricted groups increased, whilst protein deposition of the *ad libitum* group declined quite drastically. This may be connected with the effect of season and agrees completely with the findings of Webster, Smith & Mollison (1982) who found that bulls had a higher predicted basal metabolic rate from January until July than from August to December. They speculated that the most likely reason is that the pattern of metabolism shifts from season to season to enhance fat deposition before the winter period of undernutrition, by reducing both protein deposition and consequently heat production. Figure 2, illustrating fat deposition, confirms that for the *ad libitum* group fat deposition was higher after 33 kg live mass than previously. This break occurred between 5 and 19 January 1981.

Relative to protein deposition in the *ad libitum* group, all the other restricted groups showed compensatory growth in protein during the realimentation phase. This agrees with the findings of Reid, Bensadoun, Bull, Burton, Gleeson, Han, Joo, Johnson, McManus, Paladines, Stroud, Tyrrell, van Niekerk & Wellington (1968); Keenan, McManus & Freer

(1969) and Thompson, Bickel & Schürch (1982) that protein deposition increased after a period of undernutrition. The general pattern was an increase in protein deposition until a previously imposed restriction of 0,65 *ad libitum*, whereafter it declined, although no significant differences were found between the 0,82 and 0,72 *ad libitum* groups.

Fat

Fat deposition was calculated by subtracting growth in lean mass from growth in empty body mass. Figure 2 illustrates fat deposition of the restricted groups during the restriction and realimentation phases at different live masses.

There was a progressive decline in fat deposition as restriction during the restriction phase increased. With a restriction of 0,82 *ad libitum* there was a drastic decrease of about 50% in fat deposition rate during the restriction phase, whereas the decline in fat deposition of the other restricted groups was rather small and not in accordance with the level of restriction.

During the realimentation phase a drastic increase in fat deposition occurred in all experimental groups. Relative to the *ad libitum* groups, the 0,45 and 0,82 *ad libitum* groups did not show an increase in fat deposition during the realimentation

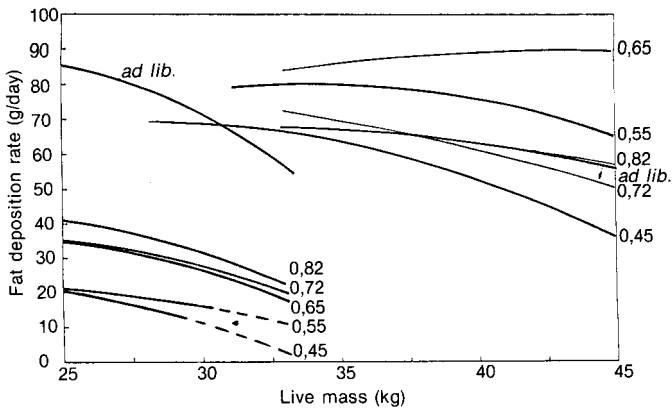


Figure 2 Fat deposition during the restriction and realimentation phases

phase. Only the 0,72 *ad libitum* group showed a higher fat deposition than the *ad libitum* group up to a live body mass of about 37 kg whereafter it declined. The 0,65 *ad libitum* group showed the biggest response in fat deposition until the end of the experiment with the 0,55 *ad libitum* group showing a slightly smaller response, which declined as the mass of this group increased.

Fat/protein ratio

The proportions of fat deposition for every gram of protein deposited at different live masses for the various restriction levels are indicated in Figures 3a and 3b for the restriction and realimentation phases respectively. There was a slight increase in the fat:protein ratio as live mass increased. In terms of feeding level this ratio stayed constant up to the 0,72 *ad libitum* group. More severe restrictions caused a drastic increase in the fat:protein ratio, up to the 0,55 *ad libitum* group, whereafter it declined slightly. This indicates that from a restriction level of about 0,72 *ad libitum* more energy was

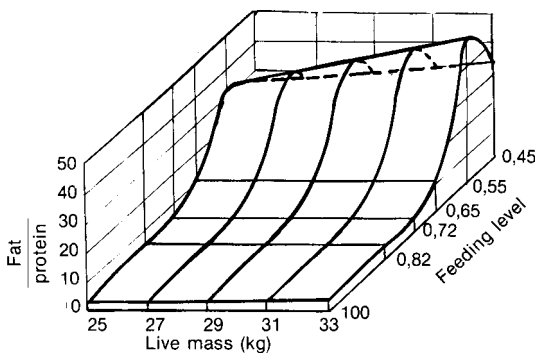


Figure 3a Fat:protein ratio at different live masses during the restriction phase

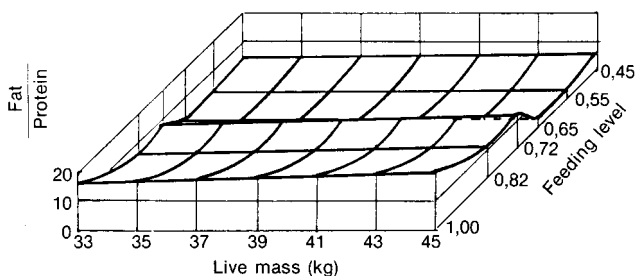


Figure 3b Fat:protein ratio at different live masses during the realimentation phase

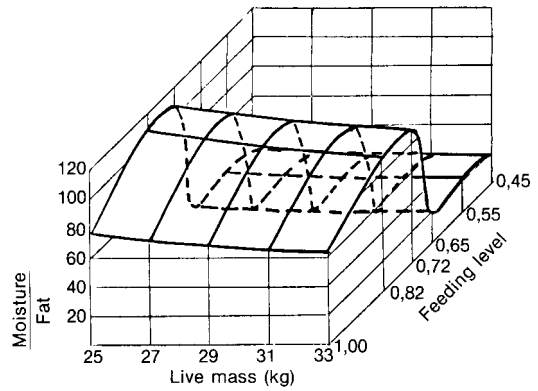


Figure 4a Moisture:fat ratio at different live masses during the restriction phase

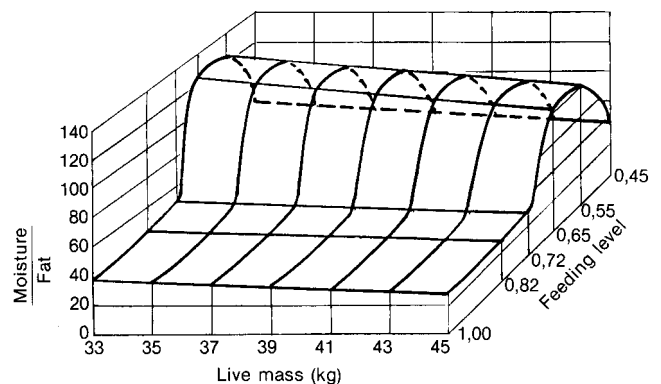


Figure 4b Moisture:fat ratio at different live masses during the realimentation phase

converted to fat than protein. This may indicate that a slow shift to other metabolic pathways takes place as restriction increases. It is also clear that the shift is in the direction of a higher energy content in body mass gain as fat has a higher energy level.

During the realimentation phase the *ad libitum*, 0,82 and 0,72 of *ad libitum* groups deposited more fat than protein whereas the 0,65, 0,55 and 0,45 *ad libitum* groups deposited much less fat than protein than during the restriction phase. A decrease in fat:protein ratio occurred from the 0,72 to the 0,65 *ad libitum* group, whereafter only a small increase in the fat:protein ratio was noticed. The drastic increase in fat deposition relative to protein deposition from the 0,65 to the 0,45 *ad libitum* group suggests that the moisture content of the body must have changed. Figures 4a and 4b indicate the moisture:fat ratio for the restriction and realimentation phases. As the restriction increased an increase in fat:moisture ratio occurred up to the 0,72 *ad libitum* group, whereafter a very sharp decrease was noticed that stayed constant up to the 0,45 *ad libitum* group.

During the realimentation phase a small increase in the moisture:fat ratio occurred up to the 0,72 *ad libitum* group but as restriction increased during the restriction phase, a sharp increase in the moisture:fat ratio took place up to the 0,55 *ad libitum* group, whereafter a relatively sharp decline was noticed. It is clear that the 0,65 and 0,55 of *ad libitum* groups have drastically compensated for the reduction in moisture retention during the restriction phase as against the partial compensation of the 0,45 *ad libitum* group. This can also be seen in Table 6 which indicates the amount of moisture in the body at different live masses for the different restriction

Table 6 Moisture (kg) at different live masses and restriction levels

Body mass (kg)	Restriction level					
	<i>Ad lib.</i>	0,82	0,72	0,65	0,55	0,45
Restriction phase						
25	12,6	12,6	12,6	12,6	11,3	11,2
27	13,4	13,4	13,4	13,0	11,6	11,3
29	14,1	14,1	14,1	13,4	12,0	–
31	14,8	14,8	14,8	13,7	12,3	–
33	15,5	15,5	15,5	14,1	–	–
Realimentation phase						
29	–	–	–	–	–	12,4
31	–	–	–	–	12,9	13,0
33	15,0	15,0	15,0	13,8	13,7	13,5
35	15,5	15,5	15,5	14,5	14,5	14,0
37	16,0	16,0	16,0	15,3	15,2	14,4
39	16,6	16,6	16,6	16,0	16,0	14,9
41	17,1	17,1	17,1	16,8	16,7	15,4
43	17,6	17,6	17,6	17,5	17,5	15,8
45	18,1	18,1	18,1	18,3	18,3	16,3

levels during the restriction and realimentation phases. These were calculated from the regression equations in Table 5.

From Table 6 it is clear that no differences in moisture content exists between the *ad libitum*, 0,82 and 0,72 *ad libitum* groups during the restriction and realimentation phases, but significant differences exist between the 0,65; 0,55 and 0,45 *ad libitum* groups for the restriction phase. During the realimentation phase, the first three groups differ significantly from the last three groups, whilst the 0,45 *ad libitum* group differs significantly from the 0,65 and 0,55 *ad libitum* groups. At the end of the restriction phase the *ad libitum* and 0,82 and 0,72 *ad libitum* groups had more moisture than the other restriction groups, but the 0,65 and 0,55 *ad libitum* groups compensated to such an extent during the realimentation phase that they contained more moisture than the first three groups at 45 kg live mass. In both phases the 0,45 *ad libitum* group had less moisture than any of the other groups and the reason for this can be seen in Figure 4a and 4b. During the restriction phase the moisture:fat ratio was very low and during the realimentation phase compensation in moisture content did not take place to the same extent as in the 0,65 and 0,55 *ad libitum* groups, with the result that high fat deposition and low moisture retention occurred in this group.

Conclusion

The results indicate that during and after a period of undernutrition between *ad libitum* and maintenance, sheep exhibit compensatory growth to varying degrees depending on the previously imposed restriction. It is clear that the effect of a feed restriction less than 0,72 *ad libitum* does not change body composition. This confirms the findings of Notter, Ferrell & Field (1983) for the restriction phase. Only as the restriction increases during the restriction phase will body composition change with a tendency to increase fat deposition. This agrees with the results of Ledin (1983) and Notter, Ferrell & Field (1983) who found that rams fed at maintenance for 105 days were fatter than rams fed *ad libitum* to the same mass. This indicates that a possible shift in metabolic pathways took place. According to Webster (1980) an inverse relationship exists between fatness and heat production. As protein turnover rate is the major source of metabolic heat production (Webster, 1980), protein turnover rate could have been

reduced and thus also heat production, thus lowering fasting metabolism. This effect could have been triggered off by an insufficient supply of essential amino acids at cellular level.

After a period of feed restriction, when feed is available in abundance, composition of growth of the *ad libitum*, 0,82 and 0,72 *ad libitum* groups were about the same. From the 0,65 *ad libitum* group a dramatic increase in moisture retention occurred up to the 0,55 *ad libitum* group, confirming the results of the 60% restriction group of Ledin (1983). This resulted in higher moisture contents than in the first three groups. From the 0,55 to the 0,45 *ad libitum* group, a decrease in moisture retention relative to fat deposition took place. This resulted in fatter animals, probably caused by an improved efficiency of utilization of metabolizable energy for fat deposition.

References

- AOAC, 1970. Official methods of analysis of the Association of Official Analytical Chemists, 11th Ed. (Ed.) Hortwitz, W. Washington: Ass. Off. Anal. Chem.
- ARC, 1980. The nutrient requirements of ruminant livestock. Technical review by an agricultural research council working party. Printed by Unwin Brothers. The Gresham Press, Old Working, Surrey.
- BLAXTER, K.L. & BOYNE, A.W., 1982. Fasting and maintenance metabolism of sheep. *J. Agric. Sci. Camb.* 99, 611.
- BURTON, J.H., ANDERSON, M.S. & REID, J.T., 1974. Some biological aspects of partial starvation. The effect of weight loss and regrowth on body composition in sheep. *Brit. J. Nutr.* 32, 515.
- BUTLER-HOGG, B.W., 1984. Growth patterns in sheep: changes in the chemical composition of the empty body and its constituent parts during weight loss and compensatory growth. *J. Agric. Sci. Camb.* 103, 17.
- DREW, K.R. & REID, J.T., 1975. Compensatory growth in immature sheep. I. The effects of weight loss and realimentation on the whole body composition. *J. Agric. Sci. Camb.* 85, 193.
- GREEFF, J.C., 1984. Die effek van kompensatoriese groei op liggaamsamestelling en doeltreffendheid van voerverbruik by skape. M.Sc. Agric. tesis, Universiteit van Pretoria.
- GREEFF, J.C., MEISSNER, H.H., ROUX, C.Z., & JANSE VAN RENSBURG, R., 1986. The effect of compensatory growth on feed intake, growth rate and efficiency of feed utilization in sheep. *S.Afr. J. Anim. Sci.* 16, 162.
- KEENAN, D.M., McMANUS, W.R. & FREER, M., 1969. Changes in the body composition and efficiency of mature sheep during loss and regain of live weight. *J. Agric. Sci. Camb.* 72, 139.
- KELLAWAY, R.C., 1973. The effects of plane of nutrition, genotype and sex on growth, body composition and wool production in grazing sheep. *J. Agric. Sci. Camb.* 80, 17.
- LEDIN, I., 1983. Effect of restricted feeding and realimentation on compensatory growth, carcass composition and organ growth in lambs. *Swedish J. Agric. Res.* 13, 175.
- McMANUS, W.R., REID, J.T. & DONALDSON, L.E., 1972. Studies on compensatory growth in sheep. *J. Agric. Sci. Camb.* 79, 1.
- MEISSNER, H.H. 1977. An evaluation of the Roux mathematical model for the functional description of growth. Ph.D. thesis, UPE.
- MEYER, J.H. & CLAWSON, W.J., 1964. Undernutrition and subsequent realimentation in rats and sheep. *J. Anim. Sci.* 23, 214.
- NOTTER, D.R., FERRELL, C.L. & FIELD, R.A. 1983. Effects of breed and intake level on allometric growth patterns in ram lambs. *J. Anim. Sci.* 56, 380.
- REID, J.T., BENSADOUN, A., BULL, L.S., BURTON, J.H., GLEESON, P.A., HAN, I.K., JOO, Y.D., JOHNSON, D.E., McMANUS, W.R., PALADINES, O.L., STROUD, J.W., TYRRELL, H.F., VAN NIEKERK, B.D.H. & WELLINGTON, G.W., 1968. Some peculiarities in the body composition of animals. Proc. Symp. Body composition in

- animals and man. Missouri, 1967, Washington D C, National Academy of Sciences.
- ROUX, C.Z., 1976. A model for the description and regulation of growth and production. *Agroanimalia*. 8, 83.
- ROUX, C.Z., 1981. Animal growth in the context of time series and linear optimal control systems. *S. Afr. J. Anim. Sci.* 11, 57.
- ROUX, C.Z. & MEISSNER, H.H., 1983. Growth and feed intake patterns. 1. The derived theory. In *Herbivore Nutrition in the Subtropics and Tropics*. pp. 672–690. Eds F.M.C. Gilchrist & R.I. Mackie. The Science Press, Craighall, South Africa.
- ROUX, C.Z., MEISSNER, H.H. & HOFMEYR, H.S., 1982. The division of energy during growth. *S. Afr. J. Anim. Sci.* 12, 1.
- SEARLE, T.W. & GRAHAM, N. Mc C., 1975. Studies of weaner sheep during and after a period of weight stasis. II. Body composition. *Aust. J. Agric. Res.* 26, 355.
- SNEDECOR, G.W. & COCHRAN, W.G., 1967. *Statistical methods*. 6th Ed., The Iowa State University Press, Ames, Iowa, U S A.
- THOMSON, E.F., BICKEL, H. & SCHÜRCH, A., 1982. Growth performance and metabolic changes in lambs and steers after mild nutritional restriction. *J. Agric. Sci.* 98, 183.
- THORNTON, R.F., HOOD, R.L., JONES, P.N. & RE, V.M., 1979. Compensatory growth in sheep. *Aust. J. Agric. Res.* 30, 135.
- WEBSTER, A.J.F., 1980. The energetic efficiency of growth. *Livest. Prod. Sci.* 7, 243.
- WEBSTER, A.J.F., SMITH, J.S. & BROCKWAY, J.M. 1972. Effects of isolation confinement and competition for feed on the energy exchanges of growing lambs. *Anim. Prod.* 15, 189.
- WEBSTER, A.J.F., SMITH, J.S. & MOLLISON, G.S., 1982. Energy requirements of growing cattle. Effects of sire breed, plane of nutrition, sex and season on predicted basal metabolism. In *Energy Metabolism of Farm Animals*. Proc. 9th Symp. held at Lillehammer, Norway. September 1982.
- WILSON, P.N. & OSBOURN, D.F., 1960. Compensatory growth after undernutrition in mammals and birds. *Biol. Rev.* 35, 324.